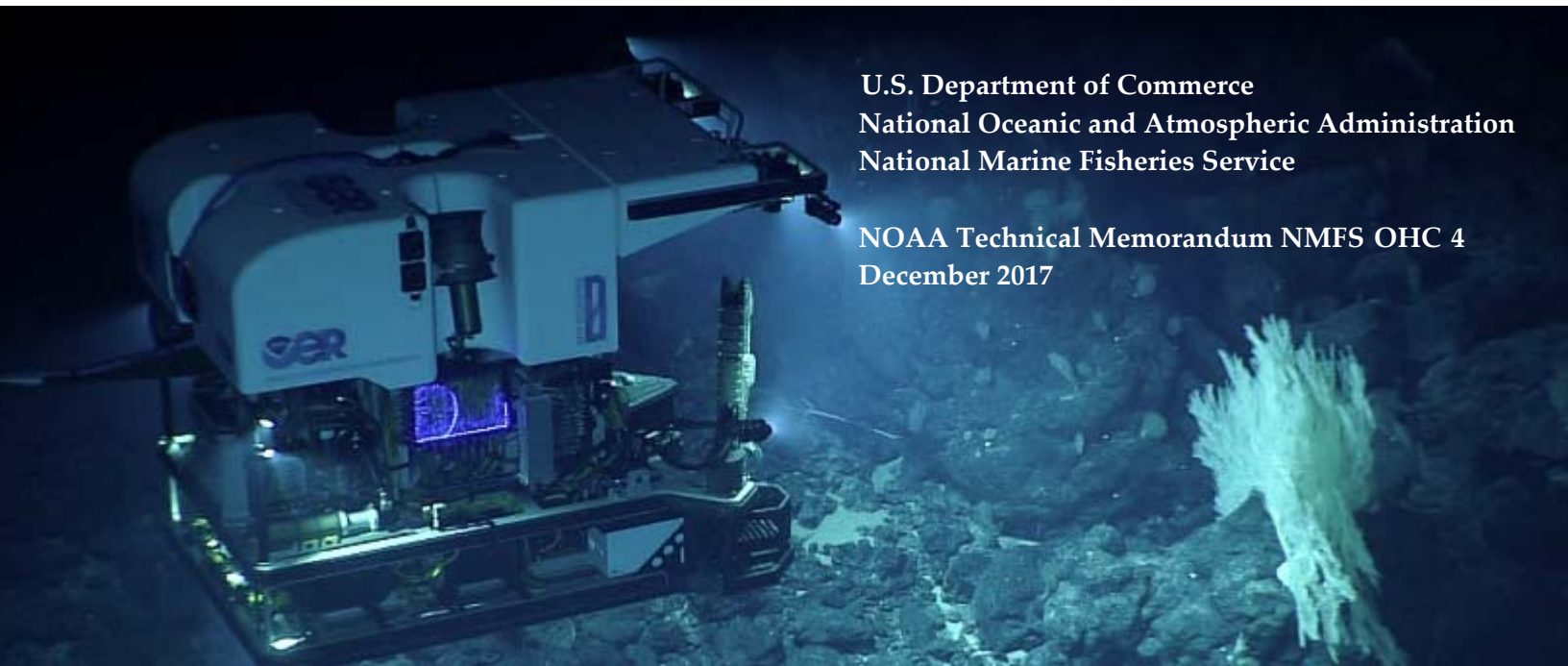




The State of Deep-Sea Coral and Sponge Ecosystems of the United States

Thomas F. Hourigan, Peter J. Etnoyer, and Stephen D. Cairns



U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

NOAA Technical Memorandum NMFS OHC 4
December 2017

The State of Deep-Sea Coral and Sponge Ecosystems of the United States

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**NOAA Technical Memorandum NMFS-OHC-4
December 2017**



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Recommended citation for full report:

Hourigan TF, Etnoyer PJ, Cairns SD (2017). The State of Deep-Sea Coral and Sponge Ecosystems of the United States. NOAA Technical Memorandum NMFS-OHC-4. Silver Spring, MD. 467 p.

Recommended citation for individual chapters (e.g., Alaska Chapter):

Stone RP and Rooper CN (2017) State of Deep-Sea Coral and Sponge Ecosystems in the Alaska Region. In: Hourigan TF, Etnoyer PJ, Cairns SD (eds.). The State of Deep-Sea Coral and Sponge Ecosystems of the United States. NOAA Technical Memorandum NMFS-OHC-4. Silver Spring, MD. 35 p.

Copies of this report may be obtained from:

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Or online at:

<http://deepseacoraldata.noaa.gov/library> or <http://spo.nmfs.noaa.gov/tm/>

Cover photos: Top – A sculpin rests on a large red tree coral off Alaska's Glacier Bay National Park. Image courtesy of the Deepwater Exploration of Glacier Bay National Park expedition and University of Connecticut Northeast Underwater Research, Technology & Education Center. Bottom – View of remotely operated vehicle *Deep Discoverer* investigating a large primnoid coral colony. Image courtesy of the NOAA Office of Ocean Exploration and Research.

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Zoanthids overgrowing coral off
the Northwest Hawaiian Islands.
Courtesy of the NOAA Office of
Ocean Exploration and Research.



Executive Summary

Corals and sponges create the most important biogenic habitats in the deep sea, and support ecosystems of incredible variety and biodiversity. In 2007, the United States National Oceanic and Atmospheric Administration (NOAA) published the first peer-reviewed report on the *State of Deep Coral Ecosystems of the United States* (Lumsden et al. 2007). The 2017 report on the *State of Deep-Sea Coral and Sponge Ecosystems of the United States* updates information on deep-sea coral ecosystems and management efforts to protect them over the last decade, and presents a first summary of information on U.S. deep-sea sponge ecosystems. It consists of an introduction, six regional chapters with accompanying on-line resources, and six spotlight chapters that highlight advances on crosscutting themes.

The introductory chapter (Hourigan et al., **Chapter 1**) outlines the purpose of the report and introduces deep-sea coral and sponge ecosystems. It presents national-level efforts since 2007 that have influenced regional-level research and conservation. NOAA's 2010 *Strategic Plan for Deep-Sea Coral and Sponge Ecosystems: Research, Management, and International Cooperation* guides the agency's approach. New research on these ecosystems has been led by NOAA's Deep Sea Coral Research and Technology Program, which began operations in 2009, and by NOAA's Office of Ocean Exploration and Research in partnership with the Department of the

Interior's Bureau of Ocean Energy Management (BOEM) and U.S. Geological Survey (USGS). Chapter 1 concludes with a synthesis of the conservation status of U.S. deep-sea coral and sponge ecosystems as revealed by the regional chapters that follow.

Cairns et al. (**Chapter 2**) present a brief introduction to discovery of deep-sea coral and sponge species. As of 2016, 662 species of corals are known to occur in U.S. waters below 50 m. This list includes 62 new species and three new genera described since 2007. Octocorals (soft corals, gorgonians and sea pens) account for over half of deep-sea coral species richness, followed by the azooxanthellate Scleractinia (stony corals), Antipatharia (black corals), and the stylasterids (lace corals). The Gulf of Mexico has been the most extensively sampled region for deepwater corals and has the highest recorded species richness (227 species), but it is clear that a large number of undescribed species still occur in each U.S. region. In contrast to corals, the deep-water sponge fauna of the U.S. has not been systematically inventoried. It is likely that the species richness of deepwater sponges exceeds that of corals, and research over the last decade has resulted in many new collections in Alaska, the West Coast and Hawai'i. However most specimens remain to be described. New genetic techniques are complementing existing morphological analyses, and hold promise of expanding our knowledge of both the taxonomy and population genetics of deep-

sea corals and sponges. The first ever [Comprehensive List of the Deep-Water Corals occurring in the EEZ of the United States and its Possessions](https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report) is an online supplement that documents all deepwater coral species reported to occur within U.S. waters as of 2016. The comprehensive list is derived from seven regional species lists, all of which are available on NOAA's Deep-Sea Coral Data Portal: <https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>.

Stone & Rooper (**Chapter 3**) report on research conducted in Alaska since 2007, including extensive new surveys under NOAA's Deep Sea Coral Research & Technology Program. This research continues to show that the region is home to diverse ecosystems supported by extraordinary coral and sponge resources. Of particular importance are the rich deep-sea coral and sponge gardens in the Aleutian Islands and the red-tree coral groves in the Gulf of Alaska, both of which are more extensive than previously known. These aggregations appear to provide important habitat to several fisheries of national and international importance. Bottom-contact fisheries continue to be the primary threat to these habitats, and bycatch of corals and sponges is high compared to other U.S. regions, especially in certain Aleutian Islands bottom trawl fisheries.

Bottom-contact fishing, particularly bottom trawling, is the most immediate threat to

deep-sea coral and sponge habitats in most areas where such fisheries are active. Rooper et al. (**Chapter 4**) summarize the known interactions between fishing gear and deep-sea corals and sponges in U.S. waters. They highlight studies on the effects of mobile and fixed-location fishing gears on deep-sea corals and sponges. Damage from mobile gear (e.g., bottom trawls) is well documented. Fewer studies have explored impacts of fixed gears, such as bottom-set longlines, gillnets and traps. These deserve additional attention, as they may be used in rougher habitats that are preferred by deep-sea corals and sponges, but are inaccessible to trawls. Many vulnerable deepwater areas in the U.S. exclusive economic zone (EEZ) have been closed to gears that impact deep-sea corals and sponges – considered the most effective management measure to address fisheries interactions. There has also been some success in modifying fishing gears and practices (e.g., reducing roller size or raising the sweeps on trawls) that may reduce impacts of these gears on deep-sea corals and sponges.

Clark et al. (**Chapter 5**) review information since 2007 that has advanced our understanding of deep-sea coral and sponge abundance and distribution off the U.S. west coast. This understanding has been catalyzed by new research under NOAA's Deep Sea Coral Research & Technology Program and data syntheses associated with the Pacific Fishery Management Council's 5-year review of Pacific coast groundfish

essential fish habitat (EFH). Deep-sea corals on hard substrata are widely distributed and the composition of assemblages changes with depth. The dominant species in many areas are small and occur at relatively low densities, but in certain areas (e.g., ridges of seamount and certain banks, particularly in the Southern California Bight), large gorgonians may occur in patches of high density. As in other regions, information on deep-sea sponges is much more rudimentary, however, it appears that in many hard-bottom habitats in deeper waters, sponges are more abundant than corals.

Fishing with bottom-contact gear, especially bottom trawls, remains the most immediate threat to both deep-sea coral and sponge ecosystems. While many areas expected to be prime habitat for corals and sponges were protected from trawling either indirectly in 2001 or directly in 2006, continued bycatch in commercial trawl fisheries indicates that significant interactions remain, and in many cases are restricted to relatively discrete areas. Among other stressors, ocean acidification will be a major long-term concern for some corals. Since 2007, new protected areas have been established in state waters, and National Marine Sanctuaries (Monterey Bay and the Greater Farallones) have been expanded to include deeper habitats containing important deep-sea coral and sponge ecosystems.

Hawai'i is the only U.S. state with major black and precious coral harvest industries. Wagner et al. (**Chapter 6**) provide a brief history of the black coral fishery and its current management. They show how recent research on the taxonomy, distribution, reproduction and life history of black corals has increased our knowledge of these taxa and may inform future management.

The U.S. Pacific Island Region consists of more than 50 oceanic islands stretching over a vast area of the central and western Pacific. Parrish et al. (**Chapter 7**) summarize new information on the deep-sea coral and sponge ecosystems found on island slopes, oceanic ridges and seamounts of the region. As in the 2007 report, most of the information from the region is limited to the Hawaiian Archipelago, however, a major three-year NOAA campaign of exploration and research is underway, which will provide the first surveys of many deep-sea areas in the U.S. territories. The last ten years of research have used available data to study the taxonomy, biology, reproduction and growth of certain coral taxa – especially black corals. Habitat suitability models have been developed for deepwater corals, and the first steps to characterize the sponge community has begun. Hawai'i's deep-sea sponges represent a rich and diverse fauna that form important, and sometimes extensive, biogenic habitats.

In 2009, major areas of the U.S. Pacific Islands were included in three new Marine National Monuments (Marianas Trench, Rose Atoll, and Pacific Remote Islands Marine National Monuments [PRIMNM]). Portions of the PRIMNM were expanded in 2014, and the Papahānaumokuākea Marine National Monument was extended to encompass the entire EEZ around the Northwestern Hawaiian Islands in 2016, forming the largest contiguous fully protected conservation area in the U.S., and currently the largest marine conservation area in the world.

Predictive habitat modeling is increasingly used to help identify areas that are most likely to harbor deep-sea coral and sponge taxa. Guinotte et al. (**Chapter 8**) review modeling methodologies and their application in each U.S. region. The growth and adoption of these techniques are fueled by recent improvements in input data quality/quantity, the low cost of producing and updating the models, and the need to identify habitat across large spatial extents for management. The spatial resolution of model results has improved in the last decade to the point where model outputs are now used to target areas for field sampling efforts and to help inform regional Fishery Management Council management actions designed to protect deep-sea coral habitats. Both the North Pacific and Mid-Atlantic Fishery Management Councils have recently used predictive deep-sea coral habitat models to inform management decisions.

Packer et al. (**Chapter 9**) review research and management of deep-sea corals and sponges in the U.S. Northeast region since 2007. Multibeam mapping and initial visual surveys since 2010 have been conducted in almost all the submarine canyons off the Northeast coast, as well as the New England seamounts within the EEZ, and significant areas in the Gulf of Maine. Rich octocoral gardens were discovered at several sites within the Gulf of Maine that serve as habitat for large numbers of redfish. Studies in Baltimore and Norfolk Canyons off Virginia allowed more detailed descriptions of the distribution and life history of deep-sea corals. Knowledge gaps still exist for many of these organisms, especially for sponges, but these studies have contributed greatly to our regional knowledge of deep-sea coral diversity, distribution, and habitat characteristics.

Based on this new information, and recognizing that bottom-contact fisheries represent the most urgent threat to these habitats, the New England and Mid-Atlantic Fishery Management Councils have moved forward on plans for deep-sea coral habitat protection, especially those for the submarine canyons and the Gulf of Maine. This action led to the creation of the 99,000 km² Frank R. Lautenberg Deep-Sea Coral Protection Area in the Mid-Atlantic, and was a major factor behind creation of the Northeast Canyons and Seamounts Marine National Monument. The New England Fishery Management Council has proposed new deep-sea coral protections

for the Gulf of Maine, and is working on additional protections for offshore canyon areas in 2017.

Deep-sea corals are among the slowest growing, longest-lived skeletal accreting marine organisms. Prouty et al. (**Chapter 10**) explore the new techniques that are yielding information about the age and growth of deep-sea corals. Studies over the last decade have revealed black and gold corals that can live for thousands of years. Understanding age, growth rate, and lifespan characteristics allows assessment of vulnerability and recovery from perturbations for coral habitats, and can thereby inform effective management and conservation strategies. The ability to accurately age deep-sea corals has allowed their use as biogeochemical proxies that provide a unique view of marine climate and environmental change over time. This progress has allowed scientists to look back into the coral's climate history using stable and radioisotope techniques, and incorporate this information into models of future climate change.

As described by Boland et al. (**Chapter 11**), the deep-sea coral habitats of the Northern Gulf of Mexico have received the most extensive research of any U.S. region over the last decade. This coverage includes major collaborative research programs led by BOEM, ongoing research by NOAA's Flower Garden Banks National Marine Sanctuary, as well as natural resource damage assessments following the

Deepwater Horizon oil spill. The availability and interpretation of industry-provided seismic reflectivity data have enhanced our understanding of the relatively rare areas of hard substrata that define the distribution of most of the region's deep-sea corals. Studies have led to increased understanding of genetic diversity, age, growth, and reproduction of deep-sea corals. Sponge communities (at least high-density communities) appear to be relatively rare in the Gulf of Mexico compared to corals.

The Deepwater Horizon incident was a landmark event with major revelations related to deep spill impacts including the dynamics of deep plumes, and potential for impacts to deepwater habitats from horizontal transport of hydrocarbon plumes and from oiled marine snow. Octocoral habitats at both deep-sea and mesophotic depths were among the habitats damaged in the spill. The results of research and damage assessments have led to increased awareness among managers and the public.

BOEM has instituted new regulatory policies for the oil and gas industry dealing with biological communities in the Gulf, in addition to numerous changes in regulatory policies related to drilling safety. The Flower Garden Banks National Marine Sanctuary is currently exploring alternatives for boundary expansion to protect known high value benthic habitats and cultural resources in the north-central Gulf of Mexico.

Morrison et al. (**Chapter 12**) review research on population connectivity of deep-sea corals. Understanding connectivity through exchange of larvae among populations and the processes that influence connectivity can help inform conservation efforts. The authors provide an overview of concepts and discuss how new molecular genetic techniques are being used to understand the population structure of deep-sea corals. They review a number of studies in U.S. waters, including the first ocean basin-scale description of the population structure of the most important reef-forming deep-sea coral, *Lophelia pertusa*. They conclude by identifying specific research questions that may guide future studies of connectivity among deep-sea corals.

Hourigan et al. (**Chapter 13**) review how new research has improved our understanding of deep-sea coral and sponge ecosystems of the Southeast U.S., and how this new understanding has informed major new management efforts. New mapping and surveys have confirmed that the Southeast U.S. harbors the nation's highest

concentration of deep-sea coral reefs, and probably ranks among the top such provinces globally. In addition to branching stony corals, gorgonians, black corals and sponges are important contributors to habitat structure in areas of hard bottoms, enhancing local biodiversity by providing habitat for a large number of associated species. Despite research progress, much of this region remains unexplored. The last decade has also seen regional-scale actions to protect deep-sea coral reef provinces from fishing impacts through a series of deepwater Coral Habitat Areas of Particular Concern. A new network of shallower marine protected areas is providing similar benefits to shelf-edge coral and sponge habitats. These new fishing measures, developed by the South Atlantic Fishery Management Council and implemented by NOAA, have significantly reduced the scope for fishing damage to deep-sea coral and sponge habitats.

Thank you for reading. We look forward to the next ten years of deep-sea exploration and discovery.

Acknowledgments

This report would not have been possible without the assistance of Heather Coleman, Catherine Polk, and Fan Tsao, who contributed many hours to layout and organization of the report. Robert McGuinn was responsible for all of the annex coral maps and many of the individual chapter maps. The editors are indebted to the large number of regional and subject matter experts who served as peer reviewers for each chapter and online species list. Special thanks to Andrea Quattrini, Sandra Brooke, Joshua DeMello, and Les Watling, who reviewed several chapters; and Marcelo Kitahara, Alberto Lindner, Dennis Opresko, Andrea Quattrini, Daniel Wagner, and Gary Williams, who reviewed multiple regional coral species lists. Finally, we wish to thank all of the authors for their patience during the extended development time for this report.

Unless otherwise noted, photographs are credited to NOAA. Most images were taken during expeditions sponsored by NOAA's Office of Ocean Exploration and Research and NOAA's Deep Sea Coral Research and Technology Program.



Iridogorgia soft coral with squat lobsters in the northwestern Gulf of Mexico. Courtesy of the NOAA Office of Ocean Exploration and Research.



INTRODUCTION TO THE STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE UNITED STATES

1. Introduction

Large, long-lived, sessile organisms contribute structural complexity to seafloor habitats and play an important role in marine ecosystems. In deep or cold oceanic waters, corals and sponges are the most important organisms forming such biogenic habitats (Roberts et al. 2009, Buhl-Mortensen et al. 2010, Hogg et al. 2010, Rossi et al. 2017). They increase the physical heterogeneity of habitat, provide refuge and substrate, increase the number and availability of micro-habitats for other organisms, and thereby create hotspots of biological diversity in the deep sea.

Deep-sea corals, also known as cold-water corals, have become a major focus of new deep-sea research and conservation, both in the United States and worldwide. Recent reviews (Hovland 2008, Roberts et al. 2009, Cordes et al. 2016a) have highlighted the value of the habitats they create and their vulnerability to anthropogenic impacts.

In comparison to deep-sea coral habitats, deep-sea sponge grounds have, until recently, been relatively overlooked and poorly understood (Hogg et al. 2010). This too is beginning to change as new research has highlighted the extent and importance of these habitats (Maldonado et al. 2016).

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Squat lobster on an Iridogorgia octocoral in the Johnston Atoll component of the Pacific Remote Islands Marine National Monument.



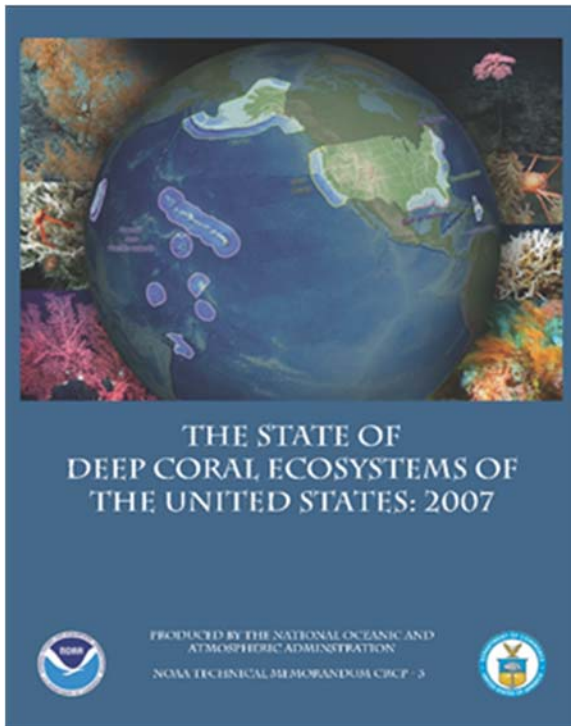
Deep-sea coral and sponge ecosystems have become a major focus of international conservation efforts. United Nations General Assembly resolutions (UNGA Resolutions 61/105, 64/72, and 66/68) have identified cold-water coral habitats as vulnerable marine ecosystems in need of protection from significant adverse impacts of deep-sea bottom fishing on the high seas. In response, international guidelines on deep-sea fishing (FAO 2009) and conservation actions by Regional Fishery Management Organizations worldwide have focused on protecting coral and sponge habitats as vulnerable marine ecosystems. The Conference of the Parties to the Convention on Biological Diversity (Decision IX/20: CBD 2008) adopted scientific criteria (Annex I to the decision) for identifying ecologically or biologically significant marine areas in need of protection in the open ocean and deep sea. Deep-sea coral and sponge habitats meet the criteria for such designation.

The State of Deep-Sea Coral and Sponge Ecosystems of the United States presents new information gathered over the last decade in the U.S., and summarizes how this information is increasingly being used to inform our nation's ocean resource management. This introduction describes the purpose and purview of the report, and provides a brief summary of national-level activities over the last decade that have supported progress in research, conservation and management.

II. About This Report

In 2007, the United States National Oceanic and Atmospheric Administration (NOAA) published the first peer-reviewed report on the *State of Deep Coral Ecosystems of the United States* (Lumsden et al. 2007; hereinafter referred to as the "2007 Report"). The 2007 Report summarized research on these communities in U.S. waters up to 2006, focusing on the biology and importance of structure-forming deep-sea corals and the communities they support, the threats they face, and their distribution and conservation status in U.S. waters. In the decade since 2007, there has been a tremendous expansion of interest in the science and management of these ecosystems in the U.S. and internationally.

The State of Deep-Sea Coral and Sponge Ecosystems of the United States serves as an update to the 2007 Report. It consists of six regional chapters that cover new information on research and efforts to conserve deep-sea coral ecosystems since 2007. The regional chapters also provide the first summary of research on deepwater sponge ecosystems – though for most regions this information is relatively limited. This volume does not include a U.S. Caribbean chapter, as there has been relatively little new information from waters surrounding Puerto Rico, the U.S. Virgin Islands, and Navassa Island since information from that region was last reviewed (Lutz and Ginsburg 2007). Each chapter is accompanied



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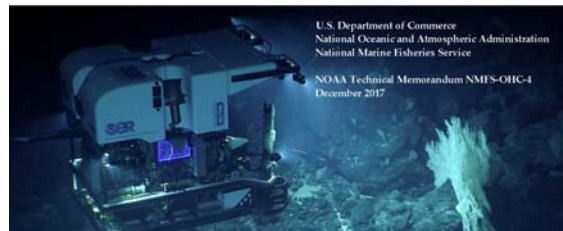


Figure 1. The 2017 State of Deep-Sea Coral and Sponge Ecosystems of the United States provides an update to the first NOAA report, State of Deep-Sea Coral Ecosystems of the United States: 2007.

by an online list of deep-sea coral species known from that region. These independently citable and peer-reviewed lists (including a U.S. Caribbean list) update species inventories contained in the 2007 Report, and substantially increase the number of taxa recorded in U.S. waters. NOAA will work with the taxonomists to update these online deep-sea coral species lists regularly and supplement them with similar species lists for deep-sea sponges.

The 2007 Report contains a large amount of background information on regional ecosystems and management efforts prior to 2007, and the current report is not meant to replace this. Rather, it builds on the 2007 Report, and provides an update on new

research and management efforts that have occurred through 2016.

In addition to the regional update chapters, this report includes six spotlight chapters that highlight cross-cutting themes. Each chapter is written by leading experts with an emphasis on how research conducted in the U.S. has contributed globally to our understanding of deep-sea coral species discovery (Cairns et al., Chapter 2), population connectivity (Morrison et al., Chapter 12), predictive modeling (Guinotte et al., Chapter 8), age and growth of deep-sea corals (Prouty et al., Chapter 10), fishing impacts (Rooper et al., Chapter 4), and a case study on managing black coral harvests (Wagner et al., Chapter 6).



III. Corals and Sponges: Key Components of Deep-Sea Biogenic Habitats

Deep-sea corals and sponges occur throughout the world's oceans. Many species attain large sizes and occur in sufficient densities to create habitat for numerous associated organisms, thereby forming the basis for remarkably complex and fragile benthic communities. These habitat-forming or structure-forming species (NOAA 2010) act as "ecosystem engineers" (Jones et al. 2007). Rossi et al. (2017) have dubbed deep-sea coral and sponge habitats "marine animal forests," due to the structural and functional similarities of these communities with terrestrial forests. The three-dimensional features formed by many deep-sea corals and sponges provide habitat for numerous fish and invertebrate species and thereby enhance the biological diversity of many deepwater ecosystems. There is increasing evidence that these habitats may play important ecosystem functions, acting as hotspots of carbon and nutrient recycling in the food-limited deep ocean (Cathalot et al. 2015, Maldonado et al. 2016).

In addition to habitat and ecosystem functions, deep-sea corals and sponges are also valuable to humans in their own right. Cnidarians (predominantly octocorals) and especially sponges are the most important sources of marine natural products (Leal et al. 2012).

Mehbub et al. (2014) reviewed new sponge-derived natural products from 2001 to 2010, which represented about 29% of all marine

Box 1. Defining Deep-Sea Corals and Sponges

In this report, "deep-sea corals" and "deep-sea sponges" are defined as corals or sponges that do not depend upon symbiotic algae and light for their metabolic requirements, and generally occur at depths below 50 m (NOAA 2010). Deep-sea corals are also referred to as cold-water corals (e.g., Roberts et al. 2009) and were called deep corals in the 2007 Report (Lumsden et al. 2007).

Structure-forming deep-sea corals and sponges are those larger species that provide three-dimensional structure above the seafloor that can be used as habitat by other species. In the case of corals, these include both deep reef-building stony corals (e.g., *Lophelia pertusa*), as well as gorgonians, gold corals, and black corals, which often have branching tree-like forms and either occur singly or occur in aggregations that increase their habitat value. The most important deep-sea structure-forming sponge species are those in the classes Demospongiae and Hexactinellida.

natural products discovered during this decade. Bath sponges have been harvested for centuries, but now other sponges are being studied for insights into new industrial products ranging from fiber optics (Aizenberg et al. 2005) to nanocrystals (Morse 2007). Black,



pink, and red corals are the basis for a large jewelry industry (Wagner et al., this volume).

III.1. Deep-Sea Corals

Deep-sea corals, also referred to as cold-water corals, are a taxonomically and morphologically diverse group of cnidarians distinguished by their predominant occurrence in deep or cold oceanic waters. Cairns (2007) defined corals as “animals in the cnidarian classes Anthozoa and Hydrozoa that produce either calcium carbonate (aragonitic or calcitic) secretions resulting in a continuous skeleton or as numerous, usually microscopic, individual sclerites, or that have a black, horn-like, proteinaceous axis.” Table 1 shows the major taxa of deep-sea corals. The anthozoan hexacorals include stony corals (Order Scleractinia), black corals (Order Antipatharia), and several species parazoanthid gold corals (Order Zoantharia – in the genera *Kulamanamana* [formerly *Gerardia*] and *Savalia*; Sinniger et al. 2013).

The anthozoan octocorals include the true soft corals, stoloniferan corals, gorgonians (Order Alcyonacea), sea pens (Order Pennatulacea), and helioporids (the shallow-water blue coral and the deepwater lithotelestids in the order Helioporacea). Recent molecular phylogenetic studies indicate that the anthozoan subclass Octocorallia is likely monophyletic, but the orders (Alcyonacea, Pennatulacea, and Helioporacea) within the octocorals are likely

not (McFadden et al. 2010). Most modern taxonomists treat the large and morphologically diverse soft and gorgonian corals as the single order, Alcyonacea (Daly et al. 2007). Here, as in the 2007 Report, we continue to treat the gorgonians (alcyonaceans with a proteinous and/or calcitic supporting skeletal axis; i.e., species currently included in the suborders: Scleraxonia, Holaxonia, and Calcaxonia) separately from the other alcyonaceans (true soft corals and stoloniferans). We do this for practical reasons (discussed in Hourigan et al. 2007), since many gorgonians are major structure-forming species (in contrast to soft-bodied alcyonaceans, which typically are not), and many surveys report corals as “gorgonians” based on gross morphology when species or family-level identifications are lacking. This practice also allows comparison to the 2007 Report. In the online species lists, however, we have included the gorgonians in the order Alcyonacea in keeping with generally accepted taxonomic reviews (Fabricius and Alderslade 2001, Daly et al. 2007, Watling et al. 2011).

Corals in the class Hydrozoa (sometimes called hydrocorals) are only distantly related to other corals (in class Anthozoa). Most deep-sea species are limited to a single family, Stylasteridae (the stylasterid or lace corals, in the order Anthoathecata). The order Hydrozoa also includes the calcified shallow-water fire corals (Family Milleporidae), and three species



of long horn corals, only one of which lives in deep water (Cairns 2007).¹

Although more than 600 species of scleractinian corals occur deeper than 50m (Cairns 2007), most are solitary corals and only about 20 are considered framework-forming (constructional) species that contribute to deepwater coral reefs or bioherms (Roberts et al. 2009). The six most significant species are *Lophelia pertusa*, *Solenosmilia variabilis*, *Goniocorella dumosa*, *Oculina varicosa*, *Madrepora oculata*, and *Enallopsammia profunda* (Roberts et al. 2009). In U.S. waters, deep-sea coral bioherms constructed primarily by *O. varicosa*, *L. pertusa*, and *E. profunda* occur in the Southeast U.S. and by *L. pertusa* in the Gulf of Mexico. Deep-sea coral reefs support faunal communities that are much higher in biomass and diversity than surrounding unstructured deep-sea habitats (Cordes et al. 2008, Roberts et al. 2009, Rossi et al. 2017). Deepwater reefs may also provide an important link between the benthos and diel vertical migrating mesopelagic fishes and macronekton invertebrates (Gartner et al. 2008, Davies et al. 2010).

Since 2007, there has been an increased focus on other types of deep-sea coral habitats, both in the U.S. and internationally. This includes high density aggregations of gorgonians or black corals, often referred to as coral “gardens,” and groves of sea pens (Buhl-Mortensen et al. 2010, 2017; Auster et al. 2013; Stone et al. 2005; Stone 2014; De Clippele et al. 2015; Pérez et al. 2016).

These have much broader depth and geographic distributions than deep-sea stony coral reefs, and have also been recognized as important biodiversity hotspots in the deep sea (Buhl-Mortensen et al. 2017).

III.2. Deep-Sea Sponges

Sponges are sessile animals in the phylum Porifera, and are among the oldest lineages of animals (Hooper and van Soest 2002). Most species are marine, found from tropical to polar environments and from very shallow to abyssal depths (van Soest et al. 2012). There are four extant classes: Demospongiae (the largest class – sometimes referred to as siliceous and horny sponges), Homoscleromorpha (recently separated from the demosponges), Calcarea (calcareous sponges) and Hexactinellida (glass sponges) (Table 2). The World Porifera Database (Van Soest et al. 2017) lists over 9575 extant species of marine sponges (7,742 Demospongiae, 878 Hexactinellida, 834 Calcarea, and 121 Homoscleromorpha). The phylogeny, systematics, and taxonomy of sponges have recently undergone extensive revisions, and many aspects remain unresolved. The *Systema Porifera* (Hooper and van Soest 2002) represented a major systematic revision of the phylum. This revision was supplemented by recent major revisions to the orders, Homoscleromorpha (Gazave et al. 2010), Demospongiae (Morrow and Cárdenas 2015), and Hexactinellida (Dohrmann et al. 2017).

¹ A few species of other branching deepwater hydrozoans produce chitinous skeletons (e.g., *Hydrodendron gorgonoide*, Order Leptothecata), reach large sizes, and

may provide habitat functions similar to many deep-sea corals. While morphologically-similar to gorgonians, these are currently not considered to be corals.



Table 1. Corals in the phylum Cnidaria that occur in deepwater (> 50 m).

Class	Subclass	Order	Common Names	Habitat Contribution
Anthozoa	Hexacorallia	Scleractinia	Stony corals	A few branching species form deep-water biogenic reef frameworks known as bioherms, coral banks, or lithoherms. Most deep-sea species are small solitary cup corals.
		Antipatharia	Black corals	Many branching forms, some of which can reach large sizes. Often co-occur with gorgonians.
		Zoantharia	Gold corals	Only a few species in the family Parazoanthidae form rigid skeletons. They parasitize other corals and need other coral hosts to settle on. Gold corals can live for over 2000 years.
	Octocorallia	Alcyonacea	True soft corals and stoloniferan corals	Soft-bodied species. Most are small and although they can occur in significant densities do not appear to be major structure-forming species.
		Gorgonacea (= Alcyonacea, in part)	Gorgonians	Many branching forms that can reach large sizes. A number of species can occur in dense aggregations.
		Pennatulacea	Sea pens	Unlike most other coral orders, sea pens are mostly found on soft sediments, where they can form dense beds that provide important habitat.
		Helioporacea	Lithotelestids	Only three species in one genus are known from deep water. Contribution to habitat is unknown.
	Hydrozoa	Hydroidolina	Anthoathecata	Stylasterids or lace corals (Family Stylasteridae)
Longhorn hydrozoans				Only one species (in the Family Hydractiniidae) of this group is known from deep water. Not an important structure-forming species.



Deep-sea sponges can play ecological roles similar to those of deep-sea corals, creating significant three-dimensional structure on the sea floor that is used by numerous species (Freese and Wing 2003, Bell 2008, NOAA 2010, Buhl-Mortensen 2010, Stone 2014, Hogg et al. 2010, Maldonado et al. 2016). Although they can be found on many different bottom types, most occur on hard substrata (van Soest et al. 2012), also favored by most deep-sea corals. Individual sponges can host a rich complement of microorganisms (Taylor et al. 2007, Webster et al. 2012) and serve as habitat for a variety of larger taxa, including both commensal and obligate symbionts (Klitgaard 1995, Buhl-Mortensen 2010). For example, Sedberry et al. (2004) reported 947 invertebrates representing ten taxonomic groups living in just five individual deepwater sponges of different genera collected in the Southeast U.S. region. Sponge aggregations can range from small patches to dense “sponge grounds” in many deep-sea areas. These deep-sea sponge grounds remain poorly mapped and understood, prompting Hogg et al. (2010) to christen them “Cinderellas of the deep seas.”

Demosponge Aggregations: A variety of demosponges can create monospecific or multispecies aggregations. In the Aleutian Islands of Alaska, demosponges greatly outnumber corals and are a primary component of highly diverse coral and sponge gardens (Stone et al. 2011).

Demosponges in the order Tetractinellida (formerly order Astrophorida) can form dense and extensive aggregations (commonly known as astrophorid sponge grounds) on gravel and coarse sand bottoms from 150 – 1,700 m deep in cold temperate and arctic regions (Maldonado et al. 2016). Off Norway, the most abundant sponges on these grounds (e.g., *Geodia barretti*) can reach sizes of 1 m and biomasses as high as 45 kg/m² (Kutti et al. 2013). Similar sponge grounds are found along the continental shelf and slopes off Labrador and Newfoundland (Murillo et al. 2012; Knudby et al. 2013; Beazley et al. 2015). Smaller aggregations of tetractinellid sponges are common in the deep sea at lower latitudes. Other unique types of deep-sea demosponge aggregations include “lithistid” sponge grounds and carnivorous sponge grounds (Maldonado et al. 2016). *Glass Sponge Reefs and Aggregations:* In the northeast Pacific off British Columbia, glass sponges (class Hexactinellida) in the order Sceptrulophora form unique sponge reefs up to 19 m high and many km long at depths of 90-240 m (Conway et al. 2001, 2005). Smaller glass sponge reefs have recently been documented in Southeast Alaska (Stone et al. 2014, Stone and Rooper, this volume). Elsewhere, glass sponges can form dense, sometimes monospecific, aggregations principally at depths below 300 m (Maldonado et al. 2016). In abyssal depths, small glass sponges are among the few organisms providing refuge for other species (Beaulieu 2001).



Table 2. Sponges in the phylum Porifera that occur in deep water (> 50 m).

Class	Subclass	Order	Common Names	Habitat Contribution
Demospongiae	Heteroscleromorpha	18 Orders	Demosponges	Demosponges are a large, diverse group. Many species reach large sizes and along with glass sponges represent a major structure-forming taxon in deep water.
	Keratosa	Dendroceratida Dictyoceratida		
	Verongimorpha	Chondrillida Chondrosiida Verongiida		
Hexactinellida	Amphidiscophora	Amphidiscosida	Glass sponges	Glass sponges along with demosponges represent the primary structure-forming deepwater taxa. A few species form large reefs or bioherms in Southeast Alaska and British Columbia.
	Hexasterophora	Hexasterophora incertae sedis Lychniscosida Lyssacinosida Sceptrulophora		
Calcarea	Calcaronea	Baerida Leucosolenida Lithonida	Calcareous sponges	Most calcareous sponges are found in shallow water. A few species occur in deeper water.
	Calcinea	Clathrinida Murrayonida		
Homoscleromorpha	--	Homosclerophorida	--	A small group of mostly encrusting forms in deep water.



Figure 2. Dense community of glass sponges on Pioneer Seamount in the Northwestern Hawaiian Islands.

Dense aggregations of filter-feeding deep-sea sponges may also play an important ecosystem function in nutrient and biogeochemical cycles. They filter large amounts of water and can convert dissolved organic matter into particulate organic matter, which in turn is used by other organisms (Maldonado et al. 2016). In this way, sponges may play an important role in carbon, nitrogen, and silicate cycling and enhancing local productivity.

There is international recognition that deep-sea sponge grounds represent vulnerable habitats. Deep-sea sponges have been recognized as a key component of vulnerable marine ecosystems (FAO 2009) and create habitats that

meet the criteria for Ecologically and Biologically Significant Areas in the deep sea (Hogg et al. 2010). Deep-sea sponge ecosystems also face many of the same threats as deep-sea corals – particularly damage from bottom trawling (Freese et al. 1999, Freese 2003, Wassenberg et al. 2002, Hogg 2010, Stone and Rooper, this volume). Deep-sea sponge aggregations are a habitat type listed on the OSPAR list of Threatened and/or Declining Species and Habitats (OSPAR 2008). This recognition led NOAA to include deep-sea sponges in its 2010 *Strategic Plan for Deep-Sea Coral and Sponge Ecosystems* (see below and Box 2).

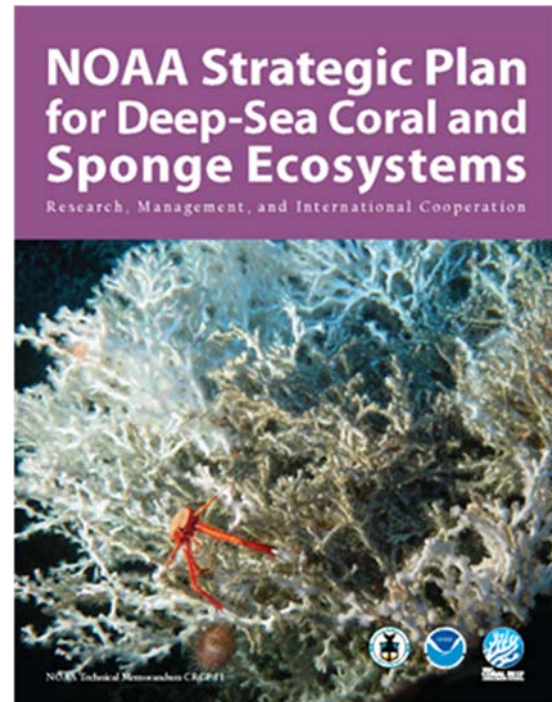


IV. U.S. National Overview

IV.1. A Strategic Approach

The National Oceanic and Atmospheric Administration (NOAA) is the lead federal agency mandated to conserve and manage the nation's marine resources, including deep-sea coral and sponge ecosystems. In 2010, NOAA published a *Strategic Plan for Deep-Sea Coral and Sponge Ecosystems: Research, Management, and International Cooperation* (NOAA 2010, Box 2). The plan identifies goals, objectives, and approaches to guide NOAA's research, management, and international cooperation activities on deep-sea coral and sponge ecosystems.

Of particular consequence was the Strategic Plan's approach to managing bottom-fishing impacts to deep-sea coral and sponge habitats. Bottom-contact fishing gears, especially bottom trawls, currently present the most important and widespread threat to deep-sea coral and sponge habitats, both worldwide (Roberts et al. 2009, Hogg et al. 2010, Ragnarsson et al. 2017) and within many U.S. regions (Hourigan et al. 2007, Rooper et al., this volume). Because NOAA's National Marine Fisheries Service (NMFS), in partnership with the regional Fishery Management Councils, is the federal agency responsible for managing fisheries in the U.S. exclusive economic zone (EEZ) where most deep-sea corals and sponges occur, managing fishing threats to these ecosystems is a primary focus of the Strategic Plan.



Box 2. Strategic Plan

NOAA's 2010 *Strategic Plan* guides the agency's objectives and approaches in three areas related to deep-sea coral and sponge ecosystems:

1. **Exploration and Research** –provides decision-makers with scientific information to enable effective ecosystem-based management.
2. **Conservation and Management** – guides NOAA efforts to enhance protection of these ecosystems, working with the Regional Fishery Management Councils, other Federal agencies and partners. NOAA's strategy is based on authorities provided through the Magnuson-Stevens Fishery Conservation and Management Act (MSA) and the National Marine Sanctuaries Act.
3. **International Cooperation** – describes NOAA's participation in international activities to study and conserve vulnerable deep-sea coral and sponge ecosystems.



The NOAA Strategic Plan supports area-based (i.e., spatially-explicit) protection of identified areas of high density structure-forming deep-sea corals or sponges, and recommends a precautionary approach to prevent expansion of the most damaging fishing activities into unsurveyed areas that might contain deepwater corals, sponges, and other vulnerable biogenic habitats (Hourigan 2014). This approach formed the basis of the historic protection measures proposed by the Mid-Atlantic Fishery Management Council and instituted by NOAA in 2016 (see Packer et al., this volume). The Strategic Plan also highlighted the importance of measuring and addressing fisheries bycatch of deep-sea corals and sponges. The NMFS [National Bycatch Reduction Strategy](#) (NMFS 2016a) calls upon the agency to: (1) identify areas of high bycatch of deep-sea corals and sponges; (2) to work with regional Fishery Management Councils and the fishing industry to close these areas to high-bycatch gears as called for in the *Strategic Plan for Deep-Sea Coral and Sponge Ecosystems*; and (3) to collect better data on coral bycatch and post-interaction mortality. The agency's most recent U.S. National Bycatch Report (NMFS 2016b) contains quantitative information on the bycatch of deep-sea corals and sponges off the West Coast and Alaska.

Within the U.S. government, interest in these deepwater ecosystems is not limited to NOAA. The U.S. Geological Survey (USGS) released *Strategic Science for Coral Ecosystems 2007-2011* (USGS 2007), which described the information needs of resource managers for both shallow and deep coral ecosystems and summarized

research conducted by USGS scientists and partners. The agency-shared long-term vision is to develop a more complete understanding of the physical, chemical, and biological processes – both natural and anthropogenic – that control or influence the structure, function, and ecological relationships within coral communities.

IV.2. Research Advances Understanding

IV.2.i – Deep-sea science spurred by advances in technology

Research on U.S. deep-sea coral and sponge ecosystems has benefited from the availability of new tools and techniques (Fig. 3). In 2008, NOAA commissioned the *Okeanos Explorer* to systematically explore our largely unknown ocean for the purpose of discovery and the advancement of knowledge. [Telepresence](#) uses satellite communications to allow scientists from around the world to participate in expeditions remotely by connecting the ship and its discoveries live with audiences ashore. The NOAA Ship *Okeanos Explorer* is joined by the Ocean Exploration Trust's E/V *Nautilus*, also equipped with telepresence capabilities, and a new generation of NOAA fisheries research vessels conducting deep-sea coral and sponge research in U.S. waters. These and other vessels have begun to map the seafloor more systematically, and at higher resolution, using multibeam sonar. Meanwhile, improvements to remotely-operated vehicles (ROVs), autonomous underwater vehicles (AUVs) and other equipment (Fig. 3) have provided for more detailed surveys, revealing previously

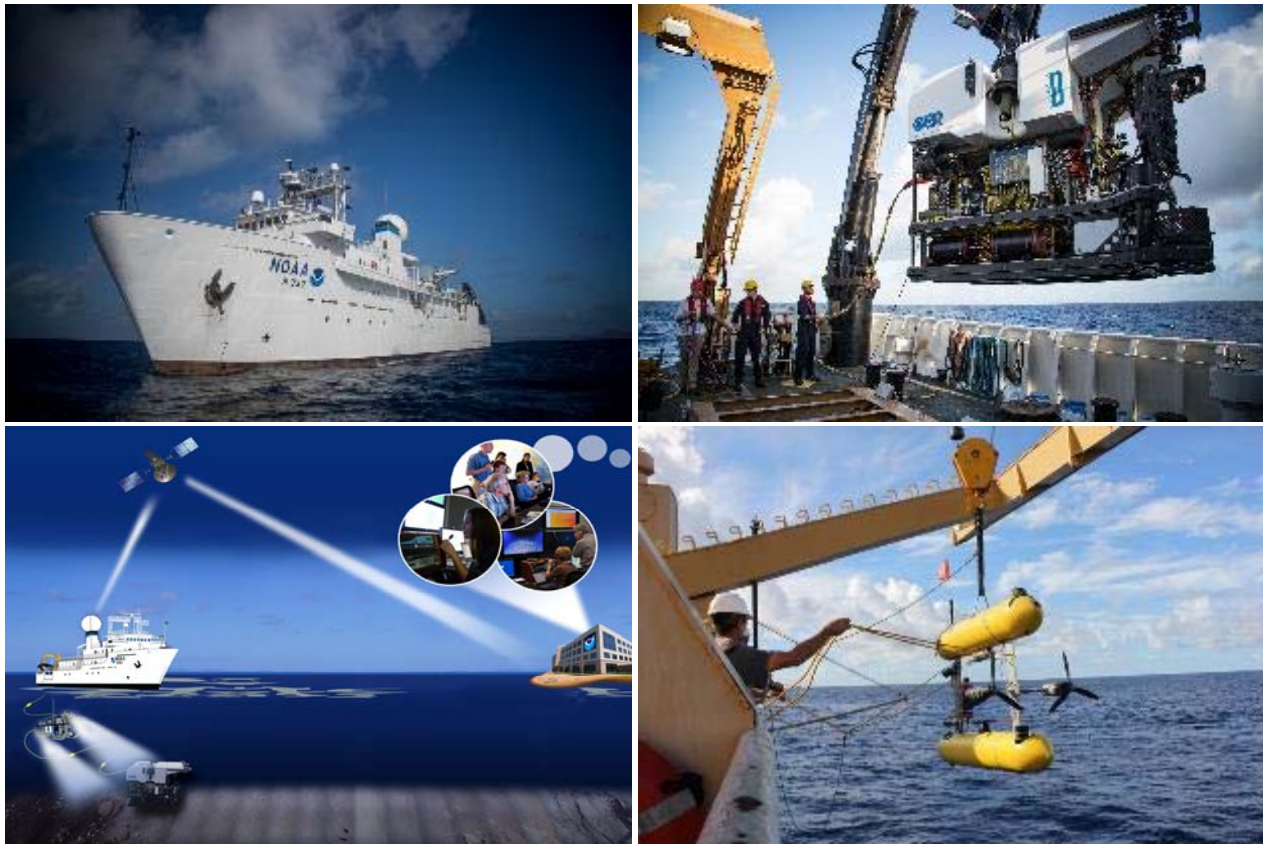


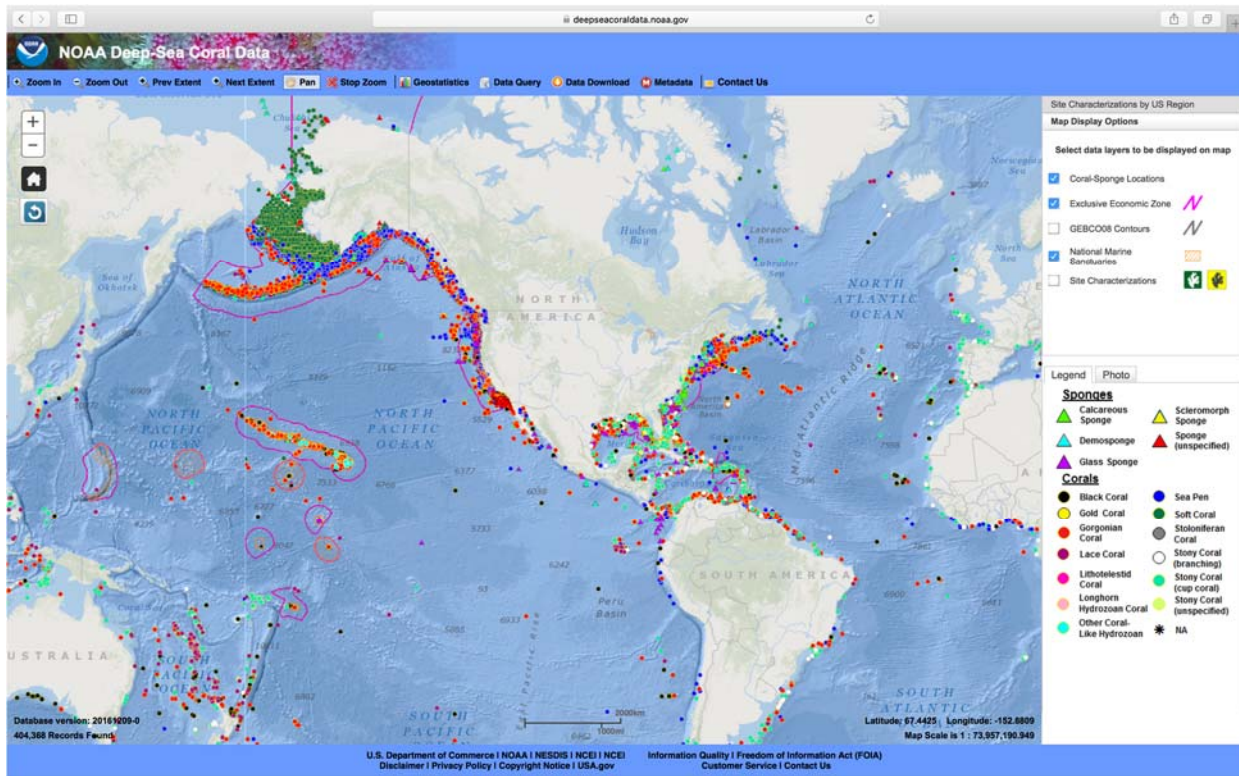
Figure 3. Advanced Technology used to explore and understand deep-sea coral and sponge ecosystems: a) NOAA Ship Okeanos Explorer; b) Deep Discoverer ROV; c) Telepresence-enabled exploration; d) SeaBed AUV.

unknown habitats to depths of 6000 m. In addition to new survey technologies, understanding of these ecosystems has benefitted from a host of other new approaches. As reviewed by Cairns et al. (this volume), new genetic techniques have revolutionized our understanding of taxonomy and systematics, and are being applied for the first time to understanding the connectivity of deep-sea coral and sponge populations (e.g., Morrison et al., this volume). Predictive modeling of deep-sea coral habitats has advanced considerably, and is helping target both new research and conservation efforts (Guinotte et al., this volume). Other new techniques allow corals to

tell the history of past oceanographic conditions they have experienced (Prouty et al., this volume), and reveal the remarkable microbial associates of deep-sea corals (e.g., Kellogg et al. 2016) and sponges. Sponges, in particular, host exceptionally dense and diverse microbial communities (reviewed by Taylor et al. 2007, Webster et al. 2012, Thomas et al. 2016).

IV.2.ii – NOAA’s Deep Sea Coral Research and Technology Program

NOAA’s Deep Sea Coral Research and Technology Program is the only U.S. national program dedicated to research on deep-sea coral ecosystems. It was established in the 2007



Box 3. National Database for Deep-Sea Corals and Sponges
 (<https://deepseacoraldata.noaa.gov>)

NOAA’s Deep Sea Coral Research and Technology Program has compiled a database of the known locations of deep-sea corals and sponges, beginning in U.S. waters (Hourigan et al. 2015). Representing the most comprehensive collection of deep-sea coral and sponge records and information for U.S. waters, the database is available publicly in NOAA’s Deep-Sea Coral Data Portal. The portal includes a digital map displaying more than 500,000 records. The National Database includes records from samples archived in museums and research institutions, reported in the scientific literature, as well as observations collected during deep-water surveys conducted by NOAA and other research institutions.

In addition to showing locations of corals and sponges, the fully searchable map also provides access to the following:

- In situ photos of the organisms.
- Extensive associated data available for download about coral and sponge observations, including record provenance, details about where and how they were observed or collected, and, where available, ecologically important information, such as their density, size, and habitat.
- Reports that characterize the deep-sea coral and sponge habitats surveyed over the past decade by scientists from NOAA, other agencies, and universities.
- Deep-sea coral habitat suitability model layers.

The National Database for Deep-Sea Corals and Sponges is continually expanding, incorporating new records from recent fieldwork observations and historic archives quarterly. Additional software tools for data exploration and analysis are under development. The Portal also offers information about studies funded by the Deep Sea Coral Research and Technology Program since 2009 and a growing library of NOAA publications on deep-sea corals and sponges.



reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act (MSA, Section 408), the nation's primary fisheries management legislation. The mission of the program is to provide the science needed to conserve and manage vulnerable deepwater ecosystems. While focused on deep-sea corals, NOAA has informed congress and the public that the program will also collect complementary information, if available, on high biodiversity deep-sea sponge habitats (NMFS 2008).

The Deep Sea Coral Research and Technology Program began operations in 2009. It has conducted 3-4 year field research initiatives in nearly all U.S. regions, as outlined in the regional chapters that follow. Surveys conducted by the program and its partners have supported management efforts across the country, including identification of vulnerable coral and sponge habitats to be protected from damaging bottom-fishing gears, expansion of National Marine Sanctuaries and Monuments, and the establishment of the [Northeast Canyons and Seamounts Marine National Monument](#).

These field initiatives have been supplemented by targeted projects to map deep-sea coral distributions, model predicted deep-sea coral habitat (Guinotte et al., this volume), study coral genetics and connectivity (e.g., Everett et al. 2016), and support coral bycatch reduction. Data collected by the Deep Sea Coral Research

and Technology Program and its partners contribute to NOAA's National Database for Deep-Sea Corals and Sponges (Box 3, Hourigan et al. 2015) and are available through the program's map portal (www.deepseacoraldata.noaa.gov).

IV.2.iii – Other major research programs

The last decade also saw the results from major U.S. interagency collaborations focused on deep-sea coral ecosystems led by the Department of Interior's Bureau of Ocean Energy Management (BOEM, formerly Minerals Management Service), in collaboration with the U.S. Geological Survey (USGS) and NOAA, and sponsored by the National Oceanographic Partnership Program (NOPP). As described by Boland et al. (this volume), major multidisciplinary studies were conducted in the Gulf of Mexico during the 2004-2006 (*Lophelia I*; Sulak et al. 2008), 2005-2009 (*Chemo III*; Brooks et al. 2014) and 2008-2012 (*Lophelia II*; Brooks et al. 2016). These studies, particularly *Lophelia II*, produced unprecedented new information on the biology and life history of major structure-forming corals (*Lophelia pertusa*, the black coral *Leiopathes* sp., and the gorgonian *Callogorgia* spp.), community structure, trophic relationships, and other aspects of these deep-sea coral communities (Brooks et al. 2016). A similar collaboration was conducted in the Mid-Atlantic's Baltimore and Norfolk Canyons (Packer et al., this volume).



IV.3. Conservation Status of U.S. Deep-Sea Coral and Sponge Ecosystems

Understanding the conservation status of deep-sea coral and sponge ecosystems requires information on the following topics: (1) the spatial distribution of these biogenic habitats; (2) the spatial extent and intensity of anthropogenic activities that pose potential threats and their overlap with biogenic habitats; (3) the sensitivity of these ecosystems to different impacts and their recovery potential; and (4) the effectiveness of management measures to address these threats (Ragnarsson et al. 2016). There has been substantial progress over the last ten years on each of these fronts in regard to deep-sea coral and sponge ecosystems.

IV.3.i – Spatial distribution of U.S. deep-sea corals and sponges

Deep-sea habitats are difficult and expensive to survey. The United States has the world's second largest exclusive economic zone (EEZ), most of it below the edge of the continental shelf (i.e., greater than ~200 m deep). This area remains largely unmapped, and the areas visually surveyed for deep-sea corals or sponges are miniscule. Nevertheless, the last decade has seen a more systematic approach to both mapping the seafloor and understanding the distribution of deep-sea habitats. This information has been identified as the first priority nationally for management (Hourigan 2014, regional chapters in this Report).

Deep-Sea Coral Distributions: Structure-forming corals are widespread in deeper waters of all regions except the U.S. Arctic. Although largely unexplored, only sea pens and one soft coral (*Gersemia* sp.) have been reported from the Chukchi Sea and Beaufort Seas (Stone and Rooper, this volume). This result contrasts to the Arctic north of the Atlantic, where extensive and relatively diverse coral habitats have been discovered off Canada, Greenland, and Norway (Roberts et al. 2009). NOAA's National Database for Deep-Sea Corals and Sponges (Box 3) has resulted in the first comprehensive maps of coral presence in areas of U.S. waters that have been sampled (map annexes in each regional chapter). Predictive habitat models allow some extrapolation of these data to unsurveyed areas (Guinotte et al., this volume). Such maps and models of coral presence, however, do not yet capture the local extent of habitats nor the density and diversity of corals within the habitats – features that are most important for determining their conservation value.

Although deep-sea corals occur widely, areas of high-density aggregations (e.g., coral “gardens”) are highly localized, and may be small (many on the scale of tens to hundreds of meters across). They therefore represent a comparatively rare habitat type. Yet these coral garden areas support diverse communities of other organisms and represent hotspots of biological diversity in the deep sea (e.g., Auster et al. 2013, Stone 2014). Their diversity and rarity makes them both extremely valuable and extremely vulnerable.



The only true deepwater stony coral reefs (bioherms) have been observed in the U.S. Southeast (Hourigan et al., this volume) and Gulf of Mexico (Boland et al., this volume), and most recently on seamounts of the Northwestern Hawaiian Islands and Emperor Seamount Chain (Baco et al. 2017). Some deep-sea reef formations may also occur in unsurveyed areas of the U.S. Caribbean. U.S. deepwater coral reefs are most diverse and numerous in the Southeast, where they probably rank among the most extensive deep-sea coral reef provinces in the world. These reefs, along with coral and sponge gardens in the Aleutian Islands, represent the largest extents of highly diverse U.S. deep-sea coral communities. However, every U.S. region contains truly remarkable habitats, often in areas of clear water – on ridges, seamounts, canyon walls and shelf-edge breaks – where there is hard substratum, sufficient food, and moderate to strong currents.

New explorations continue to reveal amazing new habitats. Deep-sea surveys in the U.S. Pacific Island Territories began in 2016 (too recent to be reflected in the U.S. Pacific Islands summary; Parrish et al., this volume), revealing extensive and dense coral and sponge gardens on ridges and seamounts. New research has also uncovered unexpectedly rich habitat areas within the current bottom-fishing footprint that appear to have escaped damage (e.g., coral gardens in the Gulf of Maine, Northern California, and Aleutian Islands). These areas represent conservation priorities, as they face the most immediate threats from bottom-fishing.

Deep-Sea Sponge Distributions: The Gulf of Mexico (Rützler et al. 2009) and the Aleutian Islands in Alaska (Stone et al. 2011) are the only regions with moderately systematic lists of deep-sea sponge species, although species lists exist for certain sub-areas (e.g., California, Lee et al. 2007). Mapping of sponge distributions has barely begun, and with the exception of some Alaskan areas (Rooper et al. 2014, Rooper et al. 2016), no predictive habitat models have been developed to date. The most comprehensive picture of sponge presence comes from scientific trawl surveys conducted off Alaska and the U.S. West Coast (Clarke et al., this volume) – though most records are only recorded as “Porifera,” and the surveys cannot access areas of rough topography that may be especially important habitats for many species. These surveys indicate that certain areas have high bycatch of sponges and likely represent high-density sponge grounds. These include monospecific sponge grounds in Alaska’s Bristol Bay (B. Stone pers. comm.), and highly diverse sponge gardens in the Aleutian Islands that have also been visually surveyed (Stone 2014, Goddard et al. 2017). Bycatch of sponges from commercial fisheries off the U.S. West Coast and Alaska is an order of magnitude larger by weight than the bycatch of corals, and the Alaska sponge bycatch is 50 to 100 times higher than off the West Coast. This trend supports the generalization that high-density deep-sea sponge grounds are more common in cold temperate waters (Maldonado et al. 2016).

Pile and Young (2006) reported that the deep-sea glass sponge, *Sericolophus hawaiiicus*, forms dense beds (mean density: 4.7/m²) over



Figure 4. Massive glass sponge discovered at a depth of 2117 m in the Northwestern Hawaiian Islands. The picture shows the sponge and the ROV Deep Discoverer. The sponge was estimated to be over 3.5 m in length, 2.0 m in width and 1.5 m in height, making it the largest sponge recorded to date.

extensive areas at depths between 360 – 460 m off the Big Island of Hawaii. Unlike many deep-sea sponges that occur only on hard substrata, *S. hawaiiicus* is adapted to anchor in the sand. Recent explorations in both the Hawaiian Archipelago and other U.S. Pacific Islands and seamounts have revealed dense aggregations of glass sponges on rocky ridges. These explorations included the discovery of what may be the largest sponge ever reported (Wagner and Kelley 2016; Fig. 4).

There have been no systematic surveys of deep-sea sponge habitats in other U.S. regions. Our understanding of these ecosystems has been hampered by lack of appreciation of their importance, and by limited U.S. expertise in taxonomy and ecology of deepwater sponges.

IV.3.ii – Anthropogenic threats

The 2007 Report summarized information on anthropogenic threats to deep-sea coral ecosystems in U.S. regions (Hourigan et al. 2007). Bottom trawl fisheries were the most serious threat in Alaska, the U.S. West Coast, Northeast, and Southeast regions. Other bottom-tending gear, including traps, bottom-set longlines, and gillnets can also damage deep-sea corals (Baer et al. 2010, Sampaio et al. 2012, Rooper et al., this volume). These gears may be used preferentially in steep and rocky habitats (i.e., areas of high rugosity) that are inaccessible for trawling, thereby representing the primary fishing gear damaging corals and sponges in such areas. Oil and gas development was considered a moderate threat in the Gulf of Mexico, and invasive species and precious coral harvests were of particular concern in Hawaii. Other threats, while possibly significant at a local level, had relatively small footprints compared to bottom fishing. At the time, there was insufficient information on potential impacts of climate change to these ecosystems to assign a threat level.

The last decade has seen an increase in awareness of potential threats to deep-sea ecosystems (Ramirez-Llodra et al. 2011, Mengerink et al. 2014, Koslow et al. 2016). Ramirez-Llodra et al. (2011) concluded that impacts to the deep sea were increasing globally, with deep-sea coral habitats among the most vulnerable, and fishing, especially bottom trawling, being their most serious current threat. Climate-related changes, including ocean acidification, ocean warming, and changes in deep-sea current regimes and



productivity were expected to become major threats in the future. This general conclusion based on scientific expert opinion is supported by recent reviews of threats to deep-sea coral ecosystems by other authors (Roberts et al. 2009, Cordes et al. 2016a, Koslow et al. 2016, Ragnarsson et al. 2017), each of which highlighted vulnerability to threats from fishing, fossil fuel exploitation, climate change, and ocean acidification. Reviews of impacts to deep-sea sponge ecosystems have also identified bottom-trawling as the most serious current impact (Hogg et al. 2010, Maldonado et al. 2016).

Table 3 provides an updated summary of anthropogenic threats to deep-sea corals and sponges in U.S. regions based on published literature and expert judgement (reviewed in the regional Chapters), and compares these to threats described in the 2007 Report. We assume that impacts to sponges from physical disturbances are qualitatively similar to impacts to corals from the same activities (e.g., Stone 2014). The following represent the major changes to the 2007 threat assessment:

Bottom Fishing: Damage from bottom trawling is still considered the biggest threat to deep-sea coral and sponge ecosystems where it occurs in U.S. regions where these gears are used (Alaska, U.S. West Coast, Northeast U.S.). Bottom trawling in the Southeast U.S. and Gulf of Mexico is restricted to a small number of vessels engaged in deepwater shrimp fisheries. There is still incomplete information on the footprint of bottom-fisheries in the U.S., but information has improved in certain areas (e.g.,

the West Coast; see Clarke et al., this volume). In a series of National Bycatch Reports (NMFS 2011, 2013, 2016b), NOAA quantified the bycatch of corals and sponges by fishery in Alaska (2003-2005; 2010-2013) and the U.S. West Coast (2011-2013). There continues to be significant bycatch of corals and sponges – primarily from a limited number of trawl fisheries and from relatively discrete locations within these large regions. The highest rates by far are from the rockfish trawl fishery in the Aleutian Islands. As noted by Rooper et al. (this volume), fixed gears (e.g., bottom-set longlines, gillnets, and traps) can also damage deep-sea corals and sponges, but less is known about the extent of their impacts. Their footprint is certainly orders of magnitude smaller than that of trawling, but may allow targeting of prime coral or sponge habitats that are unsuitable for trawling. Steps taken by the South Atlantic and Mid-Atlantic Fishery Management Councils have significantly increased the area of protected deep-sea coral and sponge habitats, reducing the threat from bottom-fishing impacts to the most important areas.

Oil and Gas Development: The potential impacts of oil and gas development came into stark focus with the Deepwater Horizon oil spill (Boland et al., this volume). Deep-sea coral habitats at three sites from 6-22 km away from the wellhead (White et al. 2012, Fisher et al. 2014a, Fisher et al. 2014b) were damaged by the oil spill – evidently as a result of a deepwater plume. Gorgonians at mesophotic depths (60–88 m) in areas below the surface oil slick also exhibited significant declines in condition

INTRODUCTION TO THE STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE UNITED STATES



Table 3. Summary of perceived levels of threats (based on Lumsden et al. 2007 and chapters within this report) to deep-sea coral communities (2007 and 2017) and sponge communities (2017) for U.S. regions. NA = Not Applicable (i.e., this threat is prohibited or does not occur anywhere within the region).

Note: Perceived threat levels reflect only the occurrence of these stressors in a region and their potential, if unmitigated, to damage deep-sea coral and sponge communities. They do not indicate the actual impacts of each stressor, which can vary widely within and among regions. Since the location of deep-sea coral and sponge habitats is incompletely known, there is uncertainty over their degree of overlap with human activities. The U.S. has taken substantial management steps to mitigate many threats, and the change in perceived threats for fishing in the Northeast and Southeast reflect recent protections. The 2007 Report did not separate ocean acidification from climate change, and deep-sea mining was not analyzed as a potential threat.

THREATS	U.S. REGIONS													
	Alaska		West Coast		Pacific Islands		Northeast		Southeast		Gulf of Mexico		Caribbean	
	2007	2017	2007	2017	2007	2017	2007	2017	2007	2017	2007	2017	2007	2017
Bottom Trawl Fishing Impacts	High	High	High	High	NA	NA	High	Medium	High	Medium	Low - Medium	Low - Medium	NA	NA
Other Bottom Fishing Impacts	Low - Medium	Medium	Low - Medium	Low - Medium	Low	Low	Low - Medium	Low - Medium	Low - Medium	Low - Medium	Low - Medium	Low - Medium	Low	Low
Deep-Sea Coral Harvest	NA	NA	NA	NA	Medium	Medium	NA	NA	NA	NA	NA	NA	NA	NA
Oil & Gas Development	Low	Low	Low	Low	NA	NA	NA	Low	NA	Low	Medium	Medium	NA	NA
Cable Deployment	Low	Low	Low	Low	Unknown	Low	Low	Low	Low	Low	Low	Low	Unknown	Low
Sand and Gravel Mining	Low	Low	NA	NA	NA	NA	Low	Low	Low	Low	Low	Low	NA	NA
Deep-Sea Mining		Low		Low		Low - Medium		Low		Low		Low		Low
Invasive Species	Unknown	Unknown	Unknown	Unknown	Medium	Medium	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Climate Change	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Ocean Acidification		Medium		Medium		Medium		Low		Low - Medium		Low - Medium		



(Etnoyer et al. 2016, Silva et al. 2016). Cordes et al. (2016b) recently reviewed the environmental impacts of the oil and gas industry: when potential accidental spills are taken into account, the potential threat posed by oil and gas development in the Gulf of Mexico to deep-sea coral ecosystems is greater than originally supposed by Hourigan et al. (2007). The Deepwater Horizon oil spill was a rare, worst-case scenario, and greatly improved measures have been put in place to prevent this kind of spill from happening again. During the last decade, offshore oil and gas exploration and leasing has been considered for additional regions, including Alaska (Stone and Rooper, this volume) and the Mid-Atlantic (Packer et al., this volume). While active fossil fuel development in these regions is currently on hold, the increased possibility of this moving forward in the future is reflected in Table 3.

Renewable Energy: Offshore renewable energy, especially offshore wind energy, has recently become a major driver for more comprehensive ocean planning in a number of regions. The nation's first offshore wind installation began operations off Rhode Island in 2016 (Packer et al., this volume). Most offshore wind facilities are expected to be sited on the continental shelf relatively close to shore, and thus are less likely to impact major deep-sea coral and sponge habitats. There is, however, the potential for anchored wind turbines in deepwater areas nearshore (e.g., in Hawaii), which could affect deep-sea coral and sponge habitats. Developers have also proposed potential marine current energy off southeastern Florida (Vinick et al.

2012) and ocean thermal energy conversion projects off Hawaii and southeastern Florida that could damage deepwater biogenic habitats. Any proposed activities would result in site-specific surveys conducted to avoid impacts from installations.

Deep-Sea Mining: There are currently no proposals for deep-sea mining within U.S. waters. Nevertheless, there is increasing interest and capacity for deep-sea mining worldwide. Deep-sea mineral resources contain commercially important quantities of high-grade ores increasingly valued in modern technology (Hein 2010, Hein et al. 2013). The principal deep-sea mineral resources being considered for mining include the following:

- Polymetallic manganese nodules, generally occurring at abyssal depths (3,500 – 6,000 m).
- Seafloor massive sulfides, also known as polymetallic sulfides, associated with active or extinct hydrothermal vents.
- Cobalt manganese crusts on seamounts. The prime crustal zone occurs in the North Pacific, including areas around Hawaii and U.S. Pacific territories.
- Phosphorite nodules, typically found between 200-400 m depth.

Mining, if it occurs, is likely to completely destroy deep-sea coral or sponge habitats within its footprint (Ramirez-Llodra et al. 2011, Levin et al. 2016). Additional impacts are expected from sediment plumes produced during mining operations. Currently the greatest concern in U.S. waters appears to



impacts from mining to the particularly rich deep-sea coral and sponge habitats on seamounts in the U.S. Pacific Islands (Parrish et al., this volume). Many of these occur in the Prime Crust Zone of the Central Pacific (Schlacher et al. 2014), which contains large concentrations of commercially valuable deep-sea minerals (Hein et al. 2013).

Climate Change and Ocean Acidification: There are still many unknowns concerning the potential impacts of climate change and ocean acidification on deep-sea coral ecosystems. The 2007 Report did not assign a level of threat to these ecosystems in the United States from climate change due to a lack of information (Hourigan et al. 2007). Since then, the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) concluded that ocean warming has affected deep-sea ecosystems at least down to 2000 m (Hoegh-Guldberg et al. 2014). Effects of warming on deep-sea coral and sponge communities include direct impacts on survival (e.g., Brooke et al. 2013, [coral]) and growth (Stone et al. 2017, [coral]), and an array of indirect effects linked to increasing water temperature (Sweetman et al. 2017). These include decreased dissolved oxygen concentrations (Keeling et al. 2010, Levin and Le Bris 2015), altered hydrodynamics (Birchenough et al. 2015), or decreased productivity of surface waters and export of food to the deep-sea (Jones et al. 2014).

Rising atmospheric carbon dioxide (CO₂) is also directly responsible for ocean acidification with associated changes in carbonate chemistry that

affect coral calcification (Guinotte et al. 2006). Ocean acidification results from net uptake by the ocean of CO₂ emissions, which decreases carbonate ion concentration in ocean waters (Feely et al. 2004). Worldwide, ocean waters from 200–3000 m are expected to face the largest reductions in pH by the year 2100 (Sweetman et al. 2017). This decrease has been forecast to hamper production of biogenic carbonates (aragonite and calcite) in the skeletons of corals, and is likely to be most problematic for reef-forming stony corals. The deep waters of the northeast Pacific have the shallowest aragonite and calcite saturation horizon, and may provide a unique opportunity to study the response of deep-sea corals to ocean acidification. Corals in this region could be surviving in potentially corrosive water conditions for some months of the year (Feely et al. 2008).

In Table 3 we have divided climate impacts into two categories – climate changes and ocean acidification. We identify the latter as a low to medium threat to deep-sea corals currently, but is likely to become a high threat in the future. Threats from ocean acidification are highest where the aragonite saturation horizon is shallowest (in the North Pacific) and where there are deep-sea scleractinian coral reefs, which are expected to be especially vulnerable to dissolution. These factors come together in the newly discovered deepwater reefs in the Northwestern Hawaiian Islands and Emperor Seamounts (Baco et al. 2017). There are likely synergies between ocean acidification and other impacts of climate change.



Compared to corals, there is little information on potential responses of sponges to climate change and ocean acidification. Kahn et al. (2012) observed changes in abyssal sponge populations correlated with climate-driven changes in particulate organic carbon. Bennett et al. (2017) presented initial experiments with shallow-water sponges that found that high temperatures may adversely affect sponge survival. In their experiments, elevated partial pressure of carbon dioxide ($p\text{CO}_2$) alone did not result in adverse effects, however it exacerbated temperature stress in heterotrophic sponges, but not in phototrophic species. We are not aware of similar experiments with deep-sea sponges, all of which are heterotrophic.

IV.3.iii – Vulnerability of Deep-Sea Coral and Sponge Ecosystems to Threats

Most deep-sea corals and sponges are highly vulnerable to physical impacts such as those from bottom trawling (Roberts 2009, Hogg 2010). Recovery from damage will depend on extent of the damage, and the ability of the damaged organisms to recover or for new recruits to settle and grow. This, in turn, is governed by the life-history characteristics of deep-sea corals and sponges, which tend to include slow growth, late maturity, extreme longevity, and infrequent recruitment events, all of which make these organisms particularly slow to recover from disturbances (Roberts et al. 2009, Hogg et al. 2010).

Since the 2007 Report there has been growing evidence for extreme age and slow growth of deep-sea corals (Prouty et al., this volume). Roark et al. (2009) reported that Hawaiian gold

corals and one species of black coral could reach ages of 2,500 to over 4,000 years, respectively. Even relatively shallow-water holaxonian corals in Alaska may take 60 years to reach maximum size (Stone et al. 2017). There have been few studies of recruitment of deep-sea corals in U.S. waters, but most evidence points to relatively low and episodic recruitment (Cordes et al. 2016a).

Clark et al. (2016) found that corals and sponges were highly vulnerable to fishing impacts, and their life history attributes meant that, once damaged, the recovery potential of biogenic habitats was highly limited. They concluded that recovery would take decades to centuries after fishing had ceased. There have been few studies investigating recovery of damaged deep-sea coral habitats in U.S. waters, but observations to date indicate that its potential is very limited (Stone and Rooper, this volume).

Sponges are also extremely vulnerable to damage from fishing gears (Freese et al. 1999, Freese 2001, Stone 2014, Stone et al. 2014, Maldonado et al. 2016, Malecha and Heifetz 2017). Suspended sediments associated with bottom trawling may also adversely affect deep-sea sponges (Tjensvoll et al. 2013). Less is known about the life history of sponges than of deep-sea corals, however, there is growing evidence that many species are slow-growing and long-lived. The massive shallow-water demosponge, *Xestospongia muta* from the Florida Keys, is estimated to live for more than 2300 years (McMurray et al. 2008). The deep-sea glass sponge, *Monorhaphis chuni*, may hold the



distinction of being the longest-lived animal on earth. Jochum et al. (2012) measured oxygen isotopic ratios and Mg/Ca ratios from a giant basal spicule of a specimen collected at 1110 m, and estimated that the sponge had been growing for $11,000 \pm 3,000$ years.

The glass sponge, *Aphrocallistes vastus*, is widely distributed in the northern Pacific Ocean from Panama through the Bering Sea and to Japan (Stone et al. 2011). Austin et al. (2007) concluded that juveniles of this species can reach a moderate size within 10-20 years on glass sponge reefs off British Columbia, but may require a century to reach full size. They also found that the species was very susceptible to physical damage and that recruitment appeared to be rare at their study site. Kahn et al. (2016) observed recruitment, growth, and response to damage of glass sponge reefs over a three year period. They observed recruitment, as well as growth of sponges ranging from 0-9 cm/year, but sponges did not recover from experiments simulating larger scale damage. The authors concluded that the sponge reefs are not resilient to disturbances such as bottom trawling.

In conclusion, research over the last decade has provided increased evidence for the high vulnerability and low resilience of deep-sea coral and sponge habitats and the communities they support. This conclusion emphasizes the value of management measures to protect remaining undamaged deep-sea coral and sponge communities.

IV.3.iv – Actions to conserve U.S. deep-sea coral and sponge ecosystems

The 2007 Report summarized steps taken within U.S. waters to manage impacts to deep-sea corals and other deepwater habitats. These efforts primarily focused on NOAA's National Marine Sanctuaries and area-based fishing gear closures developed by the regional Fishery Management Councils. The latter addressed the most immediate threat to vulnerable benthic habitats: a few relatively small areas were specifically established to protect deep-sea coral habitats, e.g., the Oculina Banks Habitat Area of Particular Concern (established in 1983 and expanded in 2000), Alaska Sitka Pinnacles Marine Reserve (2000), and Aleutian Islands and Gulf of Alaska Coral Habitat Conservation Areas (2006). Additional deepwater areas in U.S. waters have been established for general habitat protection (Sutter et al. 2013).

New Areas Protected from Fishing: The 2007 Magnuson-Stevens Act reauthorization recognized the importance of deep-sea coral habitats and provided new discretionary authority to protect these habitats in their own right (MSA Sec. 303(b)(2)). Since then, Fishery Management Councils in each region have actively included deep-sea coral ecosystems in discussions of conservation measures (Hourigan 2014). Large-scale, area-based conservation measures have specifically targeted deep-sea coral ecosystems for protection. In 2010, the South Atlantic Fishery Management Council established five



deepwater Coral Habitat Areas of Particular Concern that protect deepwater coral reefs in an area of 62,717 km² (Hourigan et al., this volume). The Mid-Atlantic Fishery Management Council was the first to use the new MSA discretionary authority to protect deep-sea coral habitat regardless of formal recognition as Essential Fish Habitat (Packer et al., this volume). The Council proposed the designation of the Frank R. Lautenberg Deep-Sea Coral Protection Area, encompassing more than 99,000 km² (~38,000 square miles) in 2015. NMFS approved this amendment in 2016, establishing the largest protected area in the U.S. Atlantic. This conservation approach was based on NOAA's *Strategic Plan for Deep-Sea Coral and Sponge Ecosystems*, protecting specific canyons where deep-sea corals had been found, as well as freezing the footprint of most bottom fisheries to prevent expansion into new deepwater habitats. The New England Fishery Management Council is exploring major deep-sea coral protections in 2017 using the same approach and authority.

New and Expanded National Monuments and Sanctuaries: New discoveries of rich deep-sea coral and sponge habitats have also resulted in other important advances in deep-sea conservation. In the U.S. Pacific Islands, Presidential proclamations 8335-8337 (January 2009) designated three new National Monuments: the Marianas Trench Marine National Monument, Rose Atoll Marine National Monument, and Pacific Remote Islands Marine National Monument. The Pacific Remote Islands Marine National Monument

and the existing Papahānaumokuākea National Marine Monument (established in 2006) were subsequently expanded by Presidential proclamation in 2014 and 2016, respectively. These new and expanded Monuments protect important deep-sea and seamount habitats and form the largest network of marine protected areas in the U.S. (Parrish et al., this volume). In 2016, the first marine national monument in the Atlantic Ocean, the Northeast Canyons and Seamounts Marine National Monument, was established under the authority of the Antiquities Act of 1906 (Packer et al., this volume). This new monument protects several submarine canyons and the four New England seamounts in the U.S. EEZ. The Presidential Proclamation specifically referenced deep-sea corals, along with “other structure-forming fauna such as sponges and anemones,” as resources that “create a foundation for vibrant deep-sea ecosystems” and are extremely sensitive to disturbance from extractive activities.

Several of NOAA's national marine sanctuaries have also undergone major expansions in the last decade. In 2008, NOAA incorporated Davidson Seamount — a volcanic seamount that is home to rich deep-sea coral and sponge habitats — into the Monterey Bay National Marine Sanctuary, providing comprehensive management in addition to the 2006 EFH bottom-gear closure. In 2012, the Fagatele Bay sanctuary expanded to protect five additional areas and became the National Marine Sanctuary of American Samoa. In 2015, NOAA expanded the boundaries of Cordell Bank and Gulf of the Farallones National Marine



Sanctuaries to an area north and west of their old boundaries, to include new deepwater areas surveyed by the Deep Sea Coral Research and Technology Program. These expansions were motivated, in part, by the discovery of important deep-sea coral habitats. Most of the existing sanctuaries have also been actively exploring the deeper extents of their protected areas (e.g., Clarke et al., this volume, and Boland et al., this volume) and incorporating results into their management plans.

Offshore Energy Management: The Bureau of Ocean Energy Management (BOEM) manages renewable energy development in federal waters. The Deepwater Horizon disaster has prompted review and strengthening of offshore oil and gas regulations (Boland et al., this volume). Mesophotic and deep-sea coral habitats will also be a priority for restoration activities in the Gulf of Mexico over the coming decade under the *Deepwater Horizon Oil Spill Final Programmatic Damage Assessment and Restoration Plan*. The last decade has also seen the first offshore leases for wind energy development off the U.S. East Coast (Packer et al., this volume). While these offshore wind farms do not extend into deep water, this development has become a major driver for regional ocean management planning efforts. A number of regions have begun to incorporate deep-sea coral observation and predicted habitat information into their broader plans to protect vulnerable ecosystems (e.g., the Mid-Atlantic Regional Council for the Ocean).

In summary, the last decade has seen deep-sea biogenic habitats, especially deep-sea coral

habitats, taking an increasingly central role in ocean planning and conservation in every U.S. region. Interest in these ecosystems seems likely to continue as we learn more about their value and vulnerability.

V. Conclusions

Deep-sea coral research over the decade since the 2007 Report on the *State of Deep Coral Ecosystems of the United States* has become more targeted, systematic, and collaborative. As described in the chapters that follow, this trend has resulted in tremendous advances in our understanding of the distribution of many taxa, as well as insights into the basic biology and ecology of these organisms. In contrast, knowledge of deep-sea sponges remains rudimentary at best, despite our increasing recognition of their importance to deep-sea ecosystems. Even a basic understanding of the life history of the most important structure-forming species and their distribution in U.S. waters continues to elude researchers and managers.

The new research has led to increased awareness of the beauty, ecological importance, and fragility of deep-sea ecosystems. This awareness is manifested in new conservation measures directed toward the deep sea, especially deep-sea coral habitats. Most important among these have been the new Marine National Monuments in the U.S. Insular Pacific and Northeast U.S., and large new fishery management zones that will protect over 175,000 km² of deep-sea areas off the U.S. East Coast, including many important deep-sea



coral habitats. Deep-sea sponge grounds have received no specific protections, though many are likely included in these recent large-scale conservation areas that address bottom-fishing.

As marine research and management move forward, conservation of these remarkable ecosystems will be enhanced by continued mapping of deep-sea biogenic habitats, and research focused on understanding their structural diversity, ecological function, and contribution to biodiversity and ecosystem productivity. Each of the following chapters contains recommendations for future research.

The next steps in conservation will use this improved understanding to apply a more targeted approach to identifying high priority areas for protection. Based on the success in “freezing the footprint” of the most damaging fishing gears, future progress will likely require management within existing fishing areas, using a collaborative approach with fishers and other resource users that promotes sustainable use while protecting the most valuable benthic communities. Future progress will also need to address increasing economic uses of deep-sea resources (e.g., deep-sea mining) and the potential impacts of a changing climate.

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109:20303-20308



Newly described species of stylasterid coral, *Crypthelia kelleyi*, discovered in 2015 on a CAPSTONE expedition to the Northwestern Hawaiian Islands. Courtesy of the NOAA Office of Ocean Exploration and Research.



SPECIES DISCOVERY OF DEEP-WATER CORALS AND SPONGES IN U.S. WATERS (2007-2016)

I. Discovery of Deep-Water Corals

In order to understand biodiversity and to conserve a biota, or to simply converse about it in a meaningful manner, one must know the names of the units being discussed – the species. The 2007 “State of Deep Coral Ecosystems” report (Lumsden et al. 2007) concentrated on the most ecologically important species - the structure-forming deep-water corals (highlighted in Appendices 1.1, 1.2, and elsewhere). In seven articles, each on a different region of the United States (U.S.), the authors dutifully included detailed lists of the deep-water coral species found within each region, sometimes subdividing their regions into smaller subunits. Yet, there was never a comprehensive synthesis or grand tally of how many deep-water coral species occur in U.S. waters in the 2007 report.

Admittedly, a ‘comprehensive synthesis’ requires some time and effort, but this can initially be accomplished by comparing the seven previously published regional lists (Lumsden et al. 2007) with the new online regional species lists associated with this report ([Online Annexes](#)). Taking into account revisions in taxonomy and eliminating duplicate entries, i.e., those species occurring in two of more of the seven regions, resulted in a comprehensive list ([Online Annex](#))¹. Table 1 summarizes the number of species in each of the five groups of corals known to inhabit the seven geographic regions.

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¹ Pacific Islands region is composed of the Hawaiian Islands, Guam, American Samoa, Northern Mariana Islands, and Pacific Remote Islands (Baker I., Howland I., Jarvis I., Johnston Atoll, Kingman Reef, Palmyra Atoll, and Wake I.); and the Caribbean region is composed only of Puerto Rico, the U.S. Virgin Islands, Navassa I., and Sarranilla Bank.



Number of Species of Deep Sea Corals

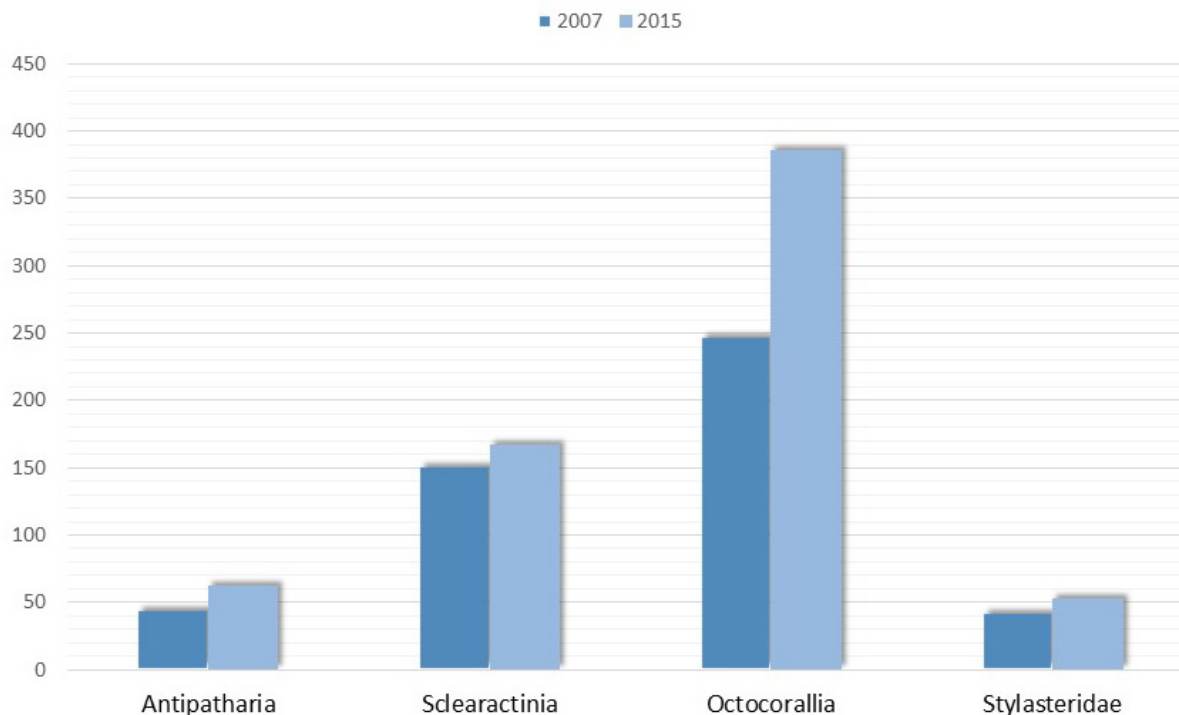


Figure 1. The number of deep coral species known from four taxonomic groups occurring in US waters as of 2007 (left bar, dark blue) and newly identified species as of 2016 (right bar, light blue).

	Antipatharia		Scleractinia		Zoanthidea		Octocorallia		Stylasteridae	
	2007	2016	2007	2016	2007	2016	2007	2016	2007	2016
Northeast U.S.	0	1	16	17	0	0	37	47	0	0
Southeast U.S.	2	14	57	77	0	0	42	92	7	15
Gulf of Mexico	17	28	47	72	0	0	44	118	8	9
U.S. Caribbean	9	13	42	45	0	0	23	43	14	14
U.S. West Coast	3	7	17	19	0	0	39	80	4	6
Alaska	10	8	8	9	0	0	45	58	12	23
Hawaii	20	21	53	54	0	1	93	104	4	4
Gross Totals	61	92	237	293	0	1	323	542	49	71
Corrected Totals	45	60	151	163	0	1	247	385	42	53
<i>New taxa since 2007</i>		15		12		1		138		11

Table 1. Comparison of numbers of deep-water coral species by region between 2007 and 2016. Gross totals include species that overlap in two or more regions. Corrected totals eliminate the overlapping species. Taxa not identified to species level not included.



Among the 662 deep-water corals presently known from U.S. waters (Table 1, and comprehensive species list herein), Octocorallia have by far the highest species richness (58.2% of the grand total), followed by the azooxanthellate Scleractinia (24.6%), Antipatharia (9.1%), and the Stylasteridae (8.0%). The rank order of these four major groups is consistent with three other comprehensive lists of deep-water corals made for other oceanic regions, specifically the Gulf of Mexico (Cairns and Fautin 2009: 354 species), New Zealand (Cairns et al. 2009: 376 species), and European waters (Costello et al. 2001: 261 species). From this table one can also calculate that the most species-rich regions are the Gulf of Mexico (227 species), southeastern US (198 species), and Hawaii (184 species); the most depauperate regions being the northeastern U.S. (65 species) and Alaska (98 species). Table 1 can then form the basis for what progress has been made between mid-

2007 to 2016 in describing deep-water coral species richness of the seven U.S. regions.

Progress is inevitably a function of research effort. In the U.S., deep-water coral research is supported by the National Oceanic and Atmospheric Administration (NOAA), the Smithsonian, the U.S. Geological Survey (USGS), the Bureau of Ocean Energy Management (BOEM), the National Science Foundation (NSF), academia, and private industry, among others. These groups are all invested in the exploration, sampling, and systematics of deep-water corals and their habitats. Examples of new species discoveries are shown in Figures 2a, 2b, and 3.

A regional increase in species richness can occur in three ways: (1) by the description of new species, (2) by the discovery of a range extension into U.S. waters of a previously described species, and (3) by the addition of species previously overlooked. It is relatively

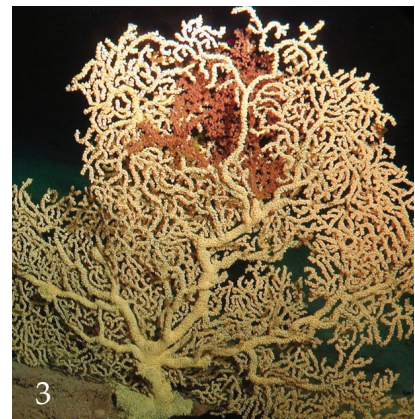
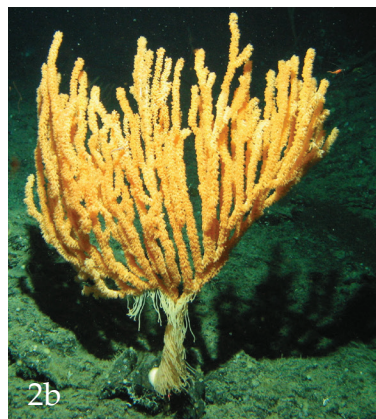
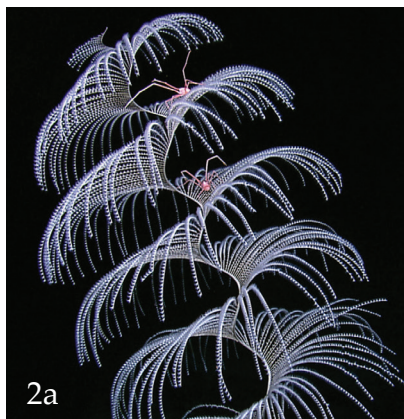


Figure 2a. *Iridogorgia magnispiralis* at 2200 m depth, a new record for the northern Gulf of Mexico, from NOAA's Okeanos Explorer expedition of 2012.

Figure 2b. *Isidella tentaculum* at 891 m depth, a new species in the Northeast Pacific described in 2008, from NOAA's Gulf of Alaska Seamount Expeditions aboard RV Atlantis in 2002 and 2004.

Figure 3. An in-situ image of a zoanthid gold coral from Hawaii called *Kulamanamana haumeaee* (Sinniger et al. 2013). The colony represents a new genus and species of gold coral, previously thought to be in a different genus, *Salvia* or *Gerardia*. Image credit: Public Library of Science One.



easy to compile a list of the new species for a region but somewhat harder to ascertain if there has been a range extension, as evidence of the latter is often buried in the literature. After a thorough review of the scientific literature, we have determined that 62 new species and three new genera of deep-water corals had been newly described from U.S. waters between 2007 and 2016. In addition, numerous species had been reported as a result of range extensions, and as having been previously overlooked. The rate of 62 new species in ten years equates to 6.2 new species per year, or an annual worldwide increase in described species of 0.19% (6.2/3336 known deep-water coral species; Cairns 2007b). This is considerably lower than the annual increase in new species descriptions for Scleractinia over a 30-year period, as calculated by Cairns (1999) as 1.23%, although his rate applied to both deep- and shallow-water species around the world, and the 0.19% rate is limited to the deep-water species from U.S. waters. Table 1 and Figure 1 show that the most actively growing group was the Octocorallia, increasing by 138 names, or 55.9%, since 2007.

The relatively high number of new octocorals is due, at least in part, to the large size of the group, their poorly known taxonomy, and to the revisionary papers on the fauna of: (1) the New England Seamounts (Watling 2007, Simpson and Watling 2011, Watling and France 2011, Pante and Watling 2011, Cairns 2007c); (2) the Hawaiian Islands (Cairns and Bayer 2007, Cairns 2009, 2010); (3) the U.S. west coast (Cairns 2007c); and (4) the Alaskan waters (Cairns 2011, Cairns and Baco 2007). Most of those specimens have been collected by NOAA research vessels. Also, many new records of all taxonomic groups were based on as yet unpublished museum records and other gray literature reports. A revisionary work by Cairns and Lindner (2011) on the Alaskan stylasterids served to increase the number

of species in this deep-water coral group by 26.2%. Relatively few species were added to the U.S. antipatharian and scleractinian fauna, their components increasing by 33.3% and 7.9%, respectively. It is of interest to note that of the 62 new species described during this period, 16 (26%), were additionally characterized by molecular sequencing, usually of mitochondrial genes (Cairns and Baco 2007, Etnoyer 2008, Watling and France 2011, Pante and Watling 2011, Cairns and Lindner 2011, Opresko et al. 2012, and Tu et al. 2016).

Three faunistic lists were also published during this period, which helped to increase the number of species in U.S. waters: (1) Felder and Camp (2009), all taxa at all depths for the Gulf of Mexico; (2) DeVicor and Morton (2010), octocorals from the South Atlantic Bight from 0-200 m; and (3) Watling et al. (2011), octocorals at all depths and regions, the latter allowing for cross-checking of taxonomic names of the Atlantic regions, a guide to some of the range extensions for these regions, and the addition of some species that had been overlooked in the 2007 report. Based on Watling et al. (2011) eight species were added to the U.S. fauna (5 octocorals and 3 stylasterids), mainly from the southeastern region. The total number of deep-water corals now known from U.S. waters is 662 species, up 177 (36.5%) from the 485 species listed in 2007 (Table 1), representing 19.8% of the total known deep-water coral fauna (Cairns, 2007b). Sixty-two of the 177 new names were newly described (see the comprehensive species list) and 115 had been previously overlooked.

In summary, we believe that a significant amount of work is being done to discover new species, document range extensions, and to uncover previously overlooked records of deep-water corals in U.S. waters leading to numerous descriptions, especially in the group



Octocorallia. We expect that future increases in species descriptions will likely fall in that group. We also acknowledge that it is not the lack of collections that hinders advancement but the lack of manpower that limits progress and causes uneven growth (Cairns 2007b). A pertinent example of this is the dissertation by K. Muzik (1979), containing the description of 18 new species of Hawaiian deep-water octocorals, which remains unpublished.

II. Species Discovery of Deep-Water Sponges

Sponges are one of the simplest, oldest-living metazoan phyla and one of the most abundant groups of benthic marine organisms (Fig. 4). They are more diverse than corals, and single- or multi-species sponge aggregations may play a similarly important role in the ecology of deep-sea ecosystems (Maldonado et al. 2016). At present, there are approximately 8500 described species with perhaps as many yet to be discovered. Worldwide, about 50 new species are described each year (Cárdenas et al. 2012). The systematics of sponges are particularly challenging given their ancient origin, simple body organization, complex microbial associations and morphological plasticity. As a result, phylogenetic relationships within the Porifera remain mostly unresolved, and this hampers progress in basic studies of sponge biology and biodiversity, including comparative evolutionary studies that use sponge species as model organisms as well as efforts to conserve or economically exploit sponges.

The deep-water sponge fauna of the U.S. has not been inventoried as systematically as the deep-water coral fauna. There are important historical collections dating back decades or more for most regions but there have

been few dedicated efforts in recent years to collect sponges beyond those provided opportunistically. The 2006 Magnuson-Stevens Reauthorization Act established the Deep Sea Coral Research and Technology Program, but made no specific provision to consider deep-water sponges, and they were not included in the 2007 NOAA Report (Lumsden et al. 2007). Still, deep-water sponges are abundant in the same depth range as deep-water corals, have complex structure that provides habitat for other fauna, and face many of the same threats as deep-water corals (e.g. Hogg et al. 2010). Additionally, sponges and their associates produce a diverse array of chemicals that are of interest for biotechnology (Pomponi et al. 2007). Accordingly, the NOAA Strategic Plan for Deep-sea Coral and Sponge Ecosystems (2010) provides nearly equal emphasis on the deep-sea sponge and coral fauna, and clear guidance to include sponges in research and management efforts.

Whereas sponges have taken a back seat to their more charismatic deep-water counterparts, there is strong evidence that poriferans provide important habitat for fish and invertebrates. With that in mind, sponges were specifically collected during submersible cruises in the Aleutian Islands of Alaska in 2003–2004. This was done, in part, to construct a field guide (Stone et al. 2011) and to help establish a useful fisheries bycatch monitoring program. Ninety-four (94) sponge species were collected during this period, and 28 (30%) were new to science! This high rate of new species discovery, and many new range extensions, clearly indicated that the sponge fauna of the region is poorly documented. In response to these findings, NOAA scientists boarded regional groundfish survey vessels during the summer of 2012 and, with the new guide in hand, collected 118 unfamiliar bycatch specimens. These new collections



Figure 4. Sponge gardens (areas of particularly diverse and abundant sponge fauna) were discovered in the central Aleutian Islands in 2004. Seven species of sponges are visible in this photograph, including two new to science and recently described.

will undoubtedly yield many new discoveries and provide insight into the true species diversity of the region. Since 2004, more casual collections in other regions of Alaska (e.g., the Bering Sea and Gulf of Alaska) have yielded additional species that have either been recently described or are awaiting formal description.

More than 55 taxa, principally hexactinellids, have been opportunistically collected along the Pacific Coast as part of NOAA's Deep Sea Coral Research and Technology Program three-year research initiative in that region (Clarke et al., this report). Approximately 28 taxa (51%) are believed to be new to science and await formal identification. Thirty hexactinellid specimens were recently collected during an expedition to the Necker Ridge in the Northwest Hawaiian Islands and 19 taxa, or 72%, are believed to be new to science. Other collections in the Pacific Islands Region (principally funded by NOAA through the Hawaii Undersea Research Laboratory) included 10 new species, all believed to be new to science (Chris Kelley, University of Hawaii at Manoa, personal communication).

Together, these regional collections represent a new species discovery rate of about 60%. This rate could be somewhat inflated since researchers may preferentially collect forms that are unfamiliar to them. Regardless, these data support those from Alaska and clearly indicate that the deep-water sponge fauna of the Pacific Ocean is poorly documented and that a large percentage of the total fauna are yet to be discovered.

One particularly noteworthy example of unexplored and undocumented deepwater sponge fauna was the exciting discovery of the carnivorous harp sponge *Chondrocladia lyra* off the coast of California (Lee et al. 2012) (Figure 6). This unusual group of sponges, to date found only in the Class Demospongiae, Family Cladorhizidae, differs drastically in body plan and cellular organization from the rest of the Phylum Porifera, and was only recently discovered (Vacelet and Boury-Esnault 1995). Since that time, at least 133 (as of 2014) new species of carnivorous sponges have been described, primarily in deep water (Cristobo et al. 2015). Using MBARI ROVs Tiburon, Ventana and Doc Ricketts, four

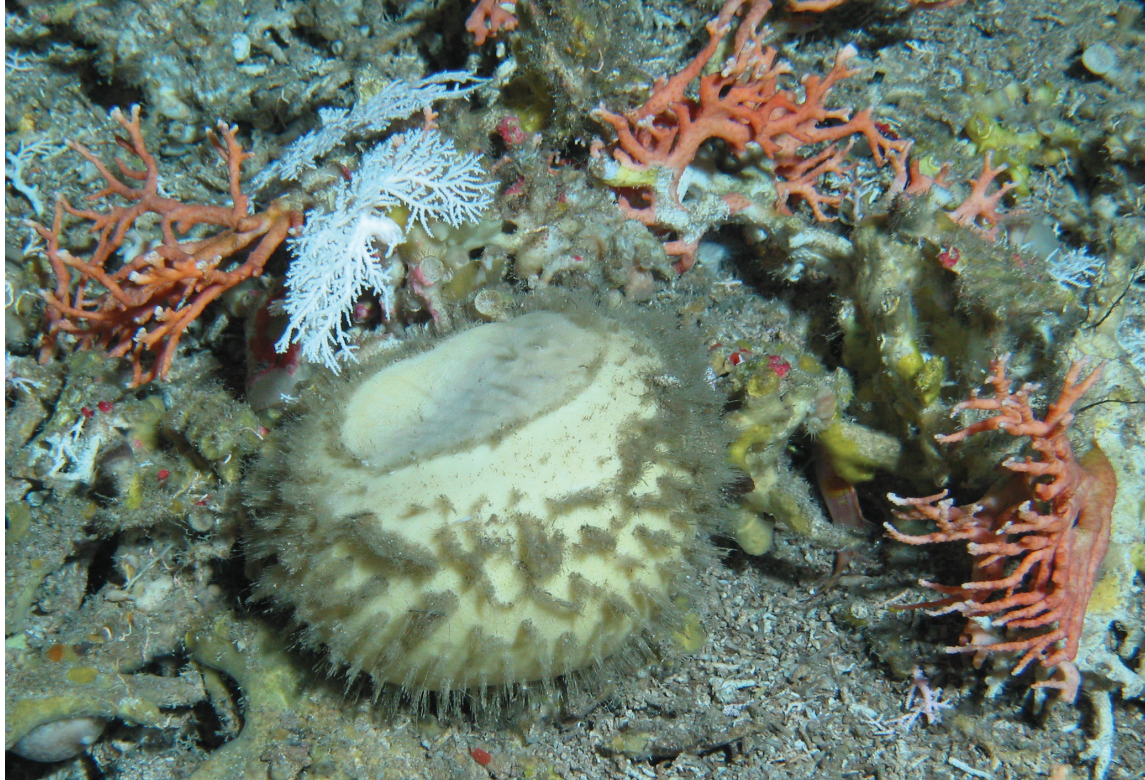


Figure 5. Undescribed species of Geodia from 118 meters depth off the coast of Florida, collected by HBOI-FAU using the Johnson-Sea-Link submersibles in 2007.

new species were collected off the west coast of the U.S. (Lundsten et al. 2014) since 2007, increasing the total of U.S. Pacific carnivorous sponge species from 7 to 11 and several more are in the process of being described (Lundsten, MBARI, pers. comm.).

Many sponge collections have been made during the past decade in the South Atlantic Bight and Gulf of Mexico with funding from NOAA. Harbor Branch Oceanographic Institute-Florida Atlantic University has collected and archived more than 1200 deep-water sponges from U.S. waters using the Johnson-Sea-Link manned submersibles (Reed et al. 2005, 2006). Rützler et al. (2009) identified 339 sponge species in a checklist of the Gulf of Mexico, of which 66 (48 demosponges and 18 hexactinellids) were identified as deep-sea sponges. Species lists have been submitted to NOAA as part of the technical (cruise

reports and several new species from these collections await formal identification (Fig.5). A new record of occurrence of the carnivorous sponge *Chondrocladia verticillata* was discovered in 2011 off the Florida Keys at a depth of 850 m by the Cooperative Institute for Ocean Exploration, Research, and Technology at HBOI-FAU, using the University of Connecticut ROV *Kraken*. Recent interest in resolving the phylogenetic relationships of the phylum Porifera has resulted in more detailed studies of these collections using molecular and morphological systematics (Dohrmann et al. 2012a, b; Hill et al. 2012). The increasing use of molecular techniques is facilitating species identification and discovery (Wörheide et al. 2007, Erpenbeck et al. 2015), and leading to significant revisions of sponge systematics (e.g., Morrow and Cardenas 2015).

There is a renewed interest in sponge taxonomy and systematics resulting from

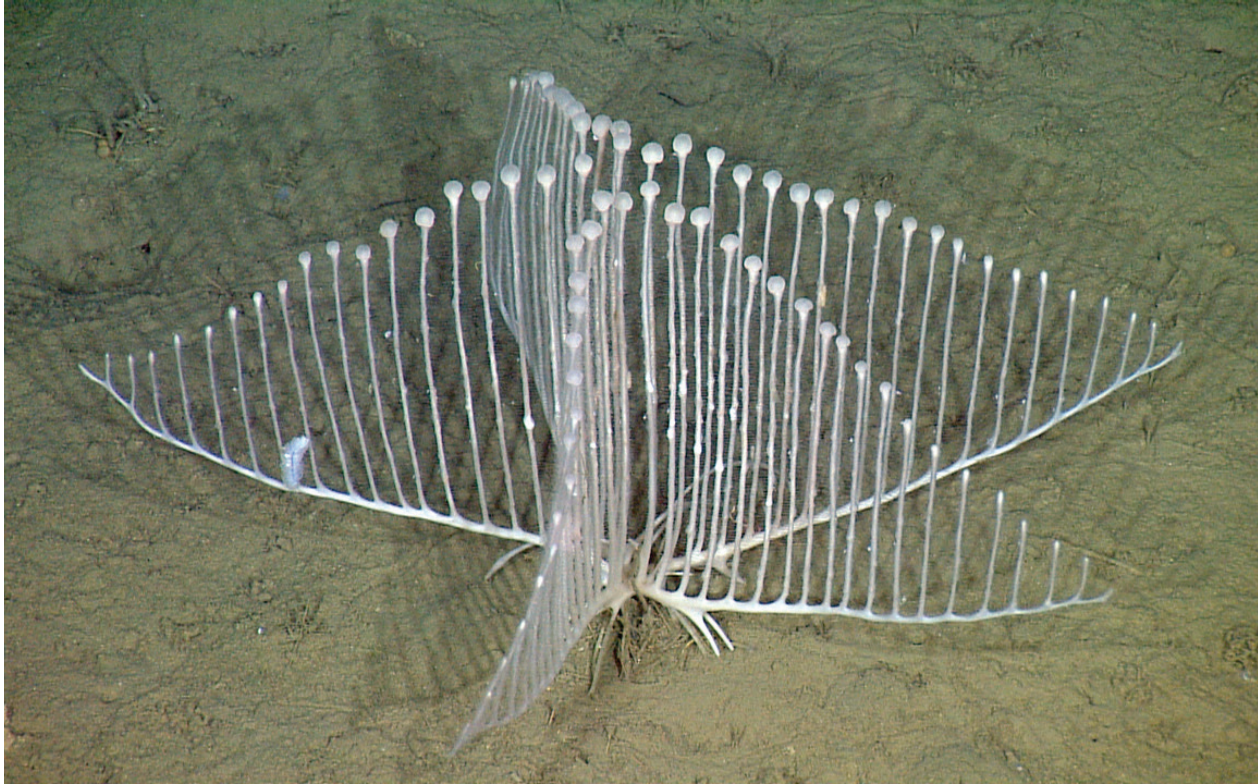


Figure 6. The carnivorous harp sponge Chondrocladia lyra with 5 vanes was collected with the ROV Doc Ricketts off California. This unusual group of sponges was discovered only a few decades ago and differs in body plan and cellular organization from all other sponges. © 2009 MBARI.

discoveries that continue to be made during exploration of poorly studied areas in U.S. waters. The discovery of sponge-associated microbial symbionts and natural products with pharmaceutical potential and the application of molecular systematics to resolve phylogenetic relationships have added to this interest. As with other deep-water fauna, there are already long queues in the laboratories of the few sponge taxonomists worldwide, suggesting that future collections should be carefully planned and coordinated with them if possible.

III. Genetic Identification of Deep-water Coral Species

An understanding of the population structure of deep-water coral species is critical to ascertaining gene flow within

and among distant populations, in order to gauge the effects of habitat loss, and meet the directives of the 2006 Magnuson-Stevens Act and the National Marine Fisheries Service (NMFS) federal mandate. A species inventory of deep-water corals off U.S. coastlines is a necessary first step toward a comprehensive understanding of the ecology and distribution of this rich and diverse faunal assemblage. Fisheries bycatch data and benthic trawl surveys can help quantify species diversity and outline their biogeographical distributions, but such estimates require accurate and defensible species-level identifications; however, the taxonomic identification of deep-water corals to the species level can be problematic for both morphological and practical reasons (see McFadden et al. 2011); in some cases, species of octocorals that appear similar

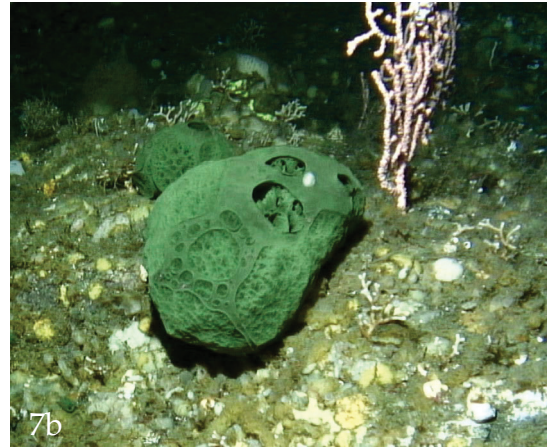
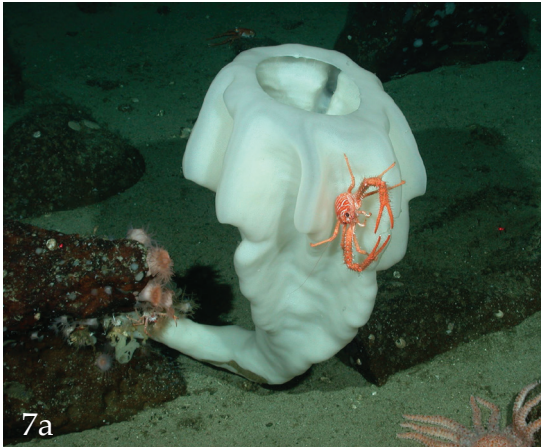


Figure 7a. An unidentified sponge in the genus *Aphrocallistes* at 255 m depth on Kidney Bank in Southern California. Many unique taxa in the Pacific Region await formal description. Image credit: NOAA Southwest Fisheries Science Center, Advanced Survey Technologies Group, La Jolla CA.

Figure 7b. The recently described sponge *Latrunculia austini* occurs at depths between 30 - 384 m in the Northeast Pacific from the Olympic Coast off Washington State to the Gulf of Alaska. These sponges have unique compounds that offer biomedical potential to curing disease. Image credit: Bob Stone, NOAA Alaska Fisheries Science Center.

may only be distinguished from one another morphologically using scanning electron microscope (SEM) images of sclerites, minute skeletal structures embedded in the fleshy tissue of these corals. Some species of deep-water corals may be defined from a single known type specimen. In other cases, the known evolutionary relationships of some coral families are so inadequate that accurate species-level designations are currently impossible. Additionally, many deep-water coral specimens are collected in trawls or dredges, which may damage the specimen or yield partial colonies at best. These difficulties, combined with a scarcity of trained morphological taxonomists, make the expanded development of genetic techniques to aid in species identification a critical necessity. It is encouraging to see, and worth noting, that students are being trained in coral taxonomy in federal (e.g., S. Cairns, P. Etnoyer) and academic laboratories (e.g., S. France, P. López-González, and L. Watling). Nevertheless, the use of genetic information,

when combined with morphology, is currently the best approach to deciphering evolutionary patterns in these species.

Voucher collections are currently being compiled at NOAA's Northwest Fisheries Science Center (Seattle, WA) and NOAA's Center for Coastal Environmental Health and Biomolecular Research (Charleston, SC) to aid in a more rapid and accurate identification of coral specimens. Such collections include one or more specimens of each potential species, with taxonomic identifications to be confirmed by relevant experts. As part of this process, SEM images may be produced for the vouchers as necessary, to either allow the direct identification of some individuals or assist morphological taxonomists with their examinations and characterizations of unknown specimens. Genomic sequences are then generated for each voucher so that DNA from additional specimens can be used to ascertain their identity in the absence of labor intensive SEM imaging or the large sample sizes required for some morphological



analyses. Choosing which area of a coral's genome to investigate is, however, not immediately straightforward.

The selection of an appropriate genetic region or regions to uniquely identify individual species is critical, requiring a fast enough mutation rate to yield sufficient differences between species, but not so many differences that sequence alignment is difficult. Animals contain two types of genetic material in their cells, which have both similar and differing characteristics: nuclear DNA and mitochondrial DNA. In diploid organisms, nuclear DNA (nDNA) is inherited from both parents—one copy of each gene being contributed by each parent—and is present as a single set of chromosomes in each somatic cell. Mitochondrial DNA (mtDNA) is inherited from an organism's mother. Each cell also contains multiple copies mtDNA because there are numerous mitochondria whereas there is only a single nucleus. Mitochondrial genomes tend to evolve more quickly than nuclear genomes because, at least in higher vertebrates, mitochondria lack the ability to "repair" accidental mutations in their DNA that arise during cell division. This higher rate of evolution is useful when attempting to identify genetic regions—termed "markers"—that exhibit sufficient diversity to distinguish individuals on a species level. As a result of these attributes, mtDNA sequencing has become the standard genetic tool for many species identifications. Recent reports, however, cite inherent problems with using mtDNA to investigate recent molecular evolution, and this must be considered when choosing an appropriate barcoding region (see Bazin et al. 2006, Galtier et al. 2009). Presently, the most concerted effort to generate a database of species-specific genetic sequences, i.e., genetic barcodes, is coordinated by the Barcode of Life (BOL) initiative

(www.barcodeoflife.org). The stated purpose for the BOL is to assist in situations where a specimen may be damaged, thereby making morphological identification difficult, or in cases where expert taxonomists are required to make a definitive identification. Barcoding would potentially solve the problem of species identification in both instances, as short DNA sequences can be generated from minimal amounts of tissue and used by non taxonomic experts to determine species designations. The genetic region targeted for most animal species is a 648 basepair region of the mitochondrial cytochrome c oxidase 1 gene (COI); however, this region is not sufficiently informative for species identification in octocorals because this subclass experiences a slower rate of evolution in their mtDNA than vertebrates (France and Hoover 2002). One reason cited for this stability is the presence of the mitochondrial MutS homolog, *msh1* (mtMSH) gene, which has high similarity and homology to mismatch-repair genes found in bacterial genomes as well as eukaryotic nuclear genes (Culligan et al. 2000). If the MutS homolog is functional in octocorals, that could explain why the mitochondrial genomes of octocorals are often not sufficiently variable to distinguish among species.

Interestingly, the mtMSH gene itself appears to be highly variable and provides an alternative to the COI gene for species identification purposes (France and Hoover 2002). The mtMSH gene has been shown to be specific for many, but not all, coral species investigated (France and Hoover 2001). The addition of other gene regions, such as the "Folmer region" of COI and an adjacent intergenic area, have demonstrated good potential as a substitute to the COI when used in combination with *msh1* at the species level (McFadden et al. 2011). Despite this increased resolution, there remain limitations in

identification of certain deep-water coral taxa. Further investigations into using alternative genes must continue.

Examples of both the utility and limitations of combined genetic and morphological identifications are now appearing in the literature (e.g., Cairns and Baco 2007; Lapien et al. 2007; Wagner et al. 2010; Baco and Cairns 2012; Pante et al. 2012). Development of the Northwest Fisheries Science Center voucher collection exemplifies their utility; a number of octocorals frequently collected in trawl surveys in the Northeast Pacific are initially identified as *Swiftia* sp. (Family Plexauridae) based on overall similarities in appearance. These samples may also be assigned a shipboard species designation within the genus *Swiftia* based on general colony formation and color. Figure 4 depicts a group of such individuals, all of which were originally identified aboard trawling vessels as *Swiftia* sp., *S. simplex*, or *S. pacifica*. Identification by a taxonomist through a detailed morphological examination including SEM images of formations and arrangements of sclerites, revealed some of these individuals actually represent two additional genera plus one additional species of *Swiftia*, despite their superficial similarities (Fig. 8). A neighbor-joining tree of pairwise differences of the mtDNA sequence data (including the Folmer region of COI plus the adjacent intergenic region, plus *msh1*) for these same specimens corroborated the taxonomic identities of these individuals (Fig. 8). On this phylogenetic tree, the horizontal branch lengths indicate the relative differences measured between individuals. Note that individuals of the same species group together in “clusters” and that the horizontal branch lengths among individuals within the same species are very short or even zero (e.g., the *Swiftia simplex* and *Swiftia spauldingi* clusters). Slightly longer branch lengths are found between

species within the same genus (e.g., the difference between *Swiftia simplex* and *Swiftia pacifica*), and the longest branch lengths are between different genera (e.g., *Leptogorgia* and *Eugorgia*). Additional specimens from this group can now be sequenced for the above genetic regions and compared to the vouchered sequences on this tree, yielding taxonomic identifications without requiring the consultation of a taxonomist for every new individual.

The use of molecular genetics in species identification alleviates pressure on the few, overworked coral taxonomists and can illuminate species distinctions when morphological distinctions are absent (as in the case of cryptic species). As previously mentioned, approximately 25% of newly described deep-water coral species included a molecular characterization of primarily mitochondrial markers. Further coordination of morphological taxonomists with genetic labs could readily contribute molecular information for the other 75% of newly described taxa. Many genetics labs across the country are now capable of generating and analyzing DNA sequence data, as is evidenced by the recent explosion in the number of institutions contributing to the BOL project.

In addition to barcode sequencing, recent advances in molecular genetic technologies are currently in use, or being developed, that may prove invaluable to the investigation of various aspects of deep-water coral species identification and genetics. Next-generation sequencing produces gigabases of data in mere days, enabling the assemblage and interrogation of entire genomes in a comparatively short amount of time. The generation of such massive amounts of molecular data also allows for the continued screening of additional genetic regions that might have utility for species-level

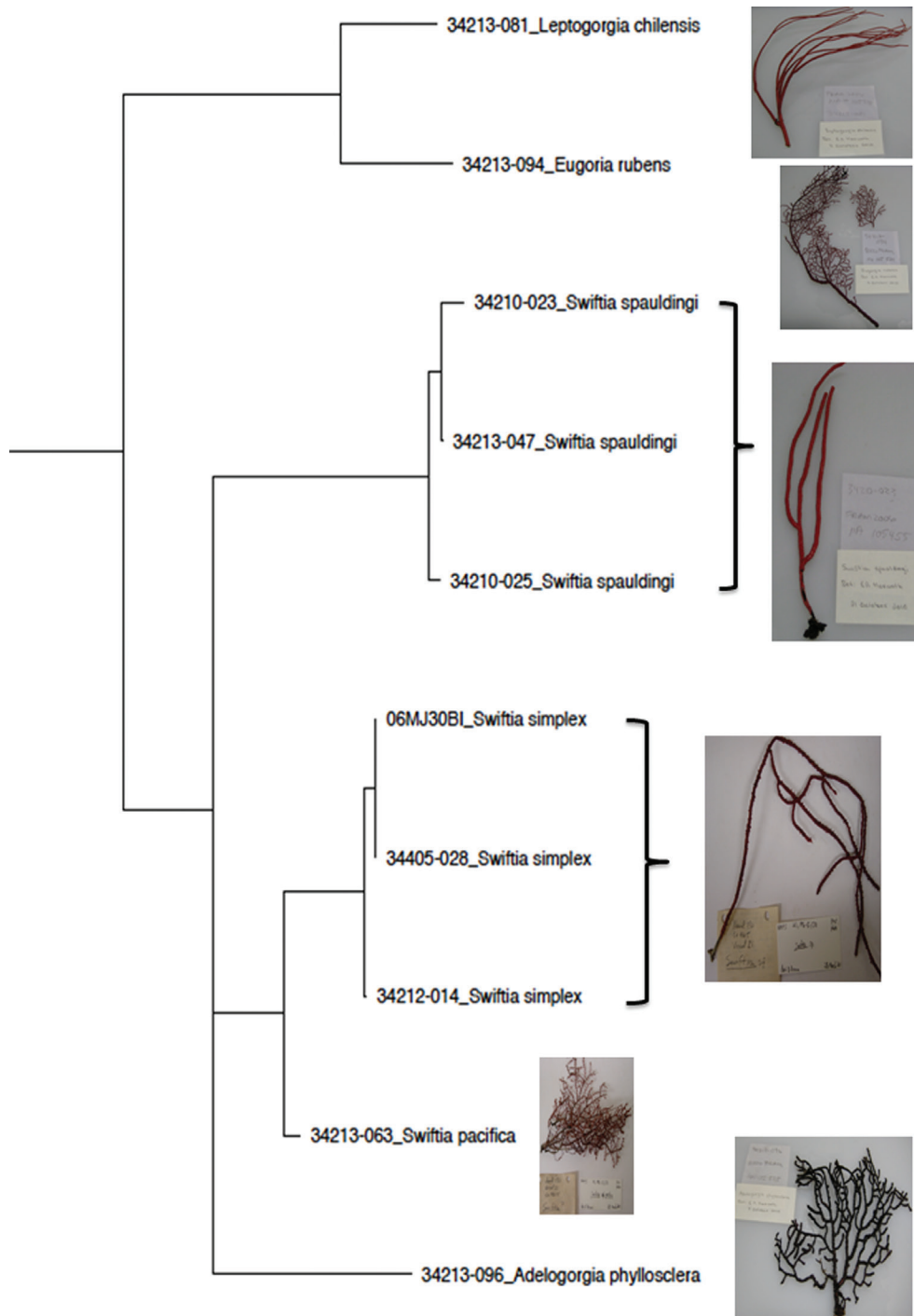


Figure 8. Phylogenetic comparison of the Fulmer region of COI plus adjacent intergenic region, plus *msh1*, of putative *Swiftia* spp. with other Plexauridae from the Northeast Pacific. The dendrogram shows three clusters of *Swiftia* specimens corresponding to three different species. *Swiftia pacifica* is more closely related to *S. simplex* than *S. spauldingi*. *Adelogorgia phyllosclera* is more closely related to *Swiftia* spp. than to two other genera - *Leptogorgia* and *Eugorgia*.



identification as well as population-level analyses. Other molecular genetic techniques that have relevant application in the genetic analysis of deep-water corals include, but are not limited to: (1) targeted amplicon sequencing (Bybee et al. 2011), which can use next-generation sequencing techniques (e.g., Roche 454, Illumina, and/or Ion Torrent platforms) and associated bioinformatics to generate large numbers of DNA barcodes simultaneously; (2) environmental DNA (eDNA), a relatively new technique that can identify the presence of species from ambient water samples, reducing the need to sample individual corals directly and increasing overall sampling opportunities; (3) microsatellites (msats), also known as simple short repeats (SSR), which are tandemly repeated stretches of 2-6 dinucleotides, and can be used to measure neutral variation among populations as well as help gauge the proportion of genetic variation among different groups within a single species; and (4) RAD sequencing (restriction site associated DNA sequencing), a genome reduction technique that is often employed to identify genetic markers—Single Nucleotide Polymorphisms (SNPs) and/or msats—that have the potential to distinguish among individuals, species, or even populations.

As we learn more about the genetic relationships among deep-water corals, we stand to gain a richer understanding of species diversity as well as ascertain the severity of pressing environmental disturbances on the health and vulnerability of habitat-forming anthozoans, a benefit that will guide the development of regulatory policies to protect these remote, productive, and fragile ecosystems.

IV. Acknowledgments

This manuscript was made more complete and more consistent in style by the reviews of Les Watling, Chris Kelley, Geoff Cook, Peter Etnoyer, Tom Hourigan, and Debe Tighe.

Online Annex - Comprehensive List of Deep-Sea Corals in the U.S. EEZ link: <https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>

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SPECIES DISCOVERY OF DEEP WATER CORALS IN U.S. WATERS (2007-2016)



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Red tree coral with a school of juvenile Pacific cod. Courtesy of the Deepwater Exploration of Glacier Bay National Park expedition and UCONN NURTEC.



STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION

1. Introduction

The marine environment of the Alaska Region can be divided into three major geographical subregions – the Gulf of Alaska, the Bering Sea including the Aleutian Island Archipelago, and the Chukchi and Beaufort Seas in the Arctic. Deep corals are widespread throughout Alaska, including the continental shelf and upper slope of the Gulf of Alaska, the Aleutian Islands, the eastern Bering Sea, and extending as far north as the Beaufort Sea. The Aleutian Islands have the highest diversity of deep corals in Alaska, and possibly in the northern North Pacific Ocean, including representatives of all major taxonomic groups and at least 50 species or subspecies that may be endemic to that region (Stone and Shotwell 2007). Additionally, the Aleutian Islands harbor high density “coral gardens” that are similar in structural complexity to shallow tropical reefs and are characterized by a rigid framework, high topographic relief and high taxonomic diversity (Stone 2006). The Aleutian Islands also support the most abundant deep-water, ahermatypic (non-reef building) coral resources in high-latitude systems reported anywhere in the world (Stone 2014).

Stone and Shotwell 2007 (hereafter referred to as the 2007 Report) highlighted diverse coral communities in Alaskan waters including 141 unique coral taxa with gorgonians and stylasterid corals being the most species rich and abundant and demonstrated that each region of Alaska has important and unique coral habitats. Detailed descriptions of each major coral group were presented along with

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*Redbanded rockfish
(Sebastes babcocki)
taking refuge in a large red
tree coral (Primnoa
pacifica) detached from
the seafloor in Dixon
Entrance, eastern Gulf of
Alaska.*



figures for each sub-region based on catch records from National Oceanic and Atmospheric Administration (NOAA) research trawl surveys (1975–2004) and the 2004 sablefish longline survey, some published records from archived specimens, and in situ observations (R. Stone, unpublished records). The process revealed that very few records existed for the Alaskan Arctic (Chukchi and Beaufort Seas) and a limited but growing body of records existed for Gulf of Alaska seamounts. Both commercial and non-commercial fish and invertebrate species had been documented in deep-sea coral habitat at varying spatial degrees, but most documented associations were suspected to be facultative rather than obligatory.

The 2007 Report also concluded that the major stressor on deep coral communities in Alaska was commercial fishing activities with bottom trawls exhibiting the highest threat based on severity of effects, extent of effects, geographic extent of use, and overlap with coral habitat. Demersal longlines and long-lined pots ranked intermediate in terms of potential threat to deep coral habitats while mid-water trawls, single pot sets, and scallop dredges were considered to pose minimal threat to those habitats. The effects of other human activities on coral habitats were discussed with only climate change and associated effects of ocean acidification noted as being sources of real concern. Recent measures to protect coral habitat via Essential Fish Habitat (EFH) by the North Pacific Fishery Management Council were detailed with special reference to Habitat Areas of Particular Concern (HAPCs) that were

implemented about the time the 2007 Report was published. Regional priorities to manage and conserve deep coral communities were outlined, with specific recommendations on future research activities that included studies on growth rates and reproductive ecology, taxonomy, the effects of ocean acidification and oil toxicity, the effects of specific fishing gear types on coral habitat, and a call for reconnaissance submersible dives in coral “hotspots” to assess their suitability as HAPCs. The 2007 Report also called for increased use of coral bycatch data from fisheries and stock assessment surveys as a source of mapping Alaska’s coral resources but noted that this would require modifications to the way data were currently being collected and the implementation of new observer training programs and publication of new field guides. This update reviews and highlights new information since the 2007 report and through 2016.

II. Update on Scientific Information

II.1. New Research – Overview

Prior to 2012, few major field research efforts funded directly by NOAA had been initiated since the publication of the 2007 Report (see Figure 1). Several small programs, focused mostly on biological processes, have been established with limited funding from various sources. A major research initiative for Alaska was established for 2012–14 as part of NOAA’s Deep Sea Coral Research and Technology Program. Here we report on new knowledge



Figure 1. Location of research projects completed or initiated since 2007.

gained about deep corals (and sponges) in the past 8 years in Alaska that includes findings for studies done prior to the 2007 but excluded from the previous Report (Stone and Shotwell 2007), as well as new resource management measures, and we provide a new list of priorities for future research.

A major research program was initiated in 2003 to investigate coral habitat in the central Aleutian Islands using the manned submersible *Delta* and the remotely operated vehicle (ROV) *Jason II*. NOAA’s National Marine Fisheries

Service (NOAA/NMFS), the North Pacific Research Board, and NOAA’s Undersea Research Program sponsored this research. A comprehensive report for this research was completed (Heifetz et al. 2007) with detailed manuscripts on damage to deep-sea coral and sponge habitats (Heifetz et al. 2009), modeling coral habitats (Woodby et al. 2009), and a comprehensive manuscript on the ecology of coral and sponge habitat (Stone 2014).

Greenpeace conducted research cruises to Pribilof and Zhemchug Canyons along the



Bering Sea continental margin in 2007 and 2012 to investigate seafloor habitats (Miller et al. 2012, Miller et al. 2015). NOAA scientists continue to collaborate with University of Maine scientists in studying the ecology of red tree coral (*Primnoa pacifica*) in shallow-water glacial fjord habitats. Additional small-scale field studies have been conducted on the biology of corals and associated species in areas closed to bottom trawling on the western Gulf of Alaska slope, rockfish habitat in the eastern Aleutian Islands and previously trawled areas in the eastern Gulf of Alaska.

II.1.i – The Alaska Coral and Sponge Initiative: a NOAA Deep Sea Coral Research and Technology Program regional fieldwork initiative in Alaska

From 2012–2015, NOAA’s Deep Sea Coral Research and Technology Program and Alaska Fisheries Science Center conducted a field research initiative in Alaska to better understand the location, distribution, ecosystem role, and status of deep-sea coral and sponge habitats (Rooper et al. 2017). The initiative was developed in consultation with the North Pacific Fishery Management Council and targeted information that could inform management.

The Alaska Coral and Sponge Initiative was comprised of a series of research projects that began in the summer of 2012:

- One mapping cruise, two ROV cruises, and one drop-camera cruise to map areas of high abundance of *Primnoa* corals in the Gulf of Alaska and study the ecological function of these habitats.
- Two cruises to determine the distribution of high abundance and diversity areas of deep-sea corals and sponges in the Aleutian Islands through modeling and field sampling using towed/drift cameras.
- New estimates of the recovery rates and sustainable impact rate for *Primnoa* corals in the Gulf of Alaska through a landscape ecology approach.
- A field study to determine the productivity of commercial fishes from coral and non-coral habitats in the Gulf of Alaska.
- A field study to develop and test the feasibility of using a towed/drift camera system to estimate the effects of commercial long-line and pot fishing on deep-sea coral and sponge communities in the Gulf of Alaska.
- Conducted a genetic study of population connectivity of red tree corals (*Primnoa pacifica*) in the eastern Gulf of Alaska.
- Initiated collection of long-term data sets of oxygen and pH from summer bottom trawl surveys.
- Established a long-term monitoring station at a shallow-water fjord coral site in Southeast Alaska.
- Examined existing and newly collected data and specimens to improve the taxonomy of deep-sea corals and sponges and conduct paleoclimatological, reproductive ecology, trophic dynamics and marine natural products studies.
- Compiled a geologically based substrate map for the Gulf of Alaska and Aleutian Islands.



In addition to these projects, the Alaska Fisheries Science Center and the Deep Sea Coral Research and Technology Program collaborated on surveys and modeling of corals and sponges on the eastern Bering Sea slope and canyons at the request of the North Pacific Fishery Management Council.

II.2. Taxonomy and Species Distributions

II.2.i – Corals

a. Coral taxonomy

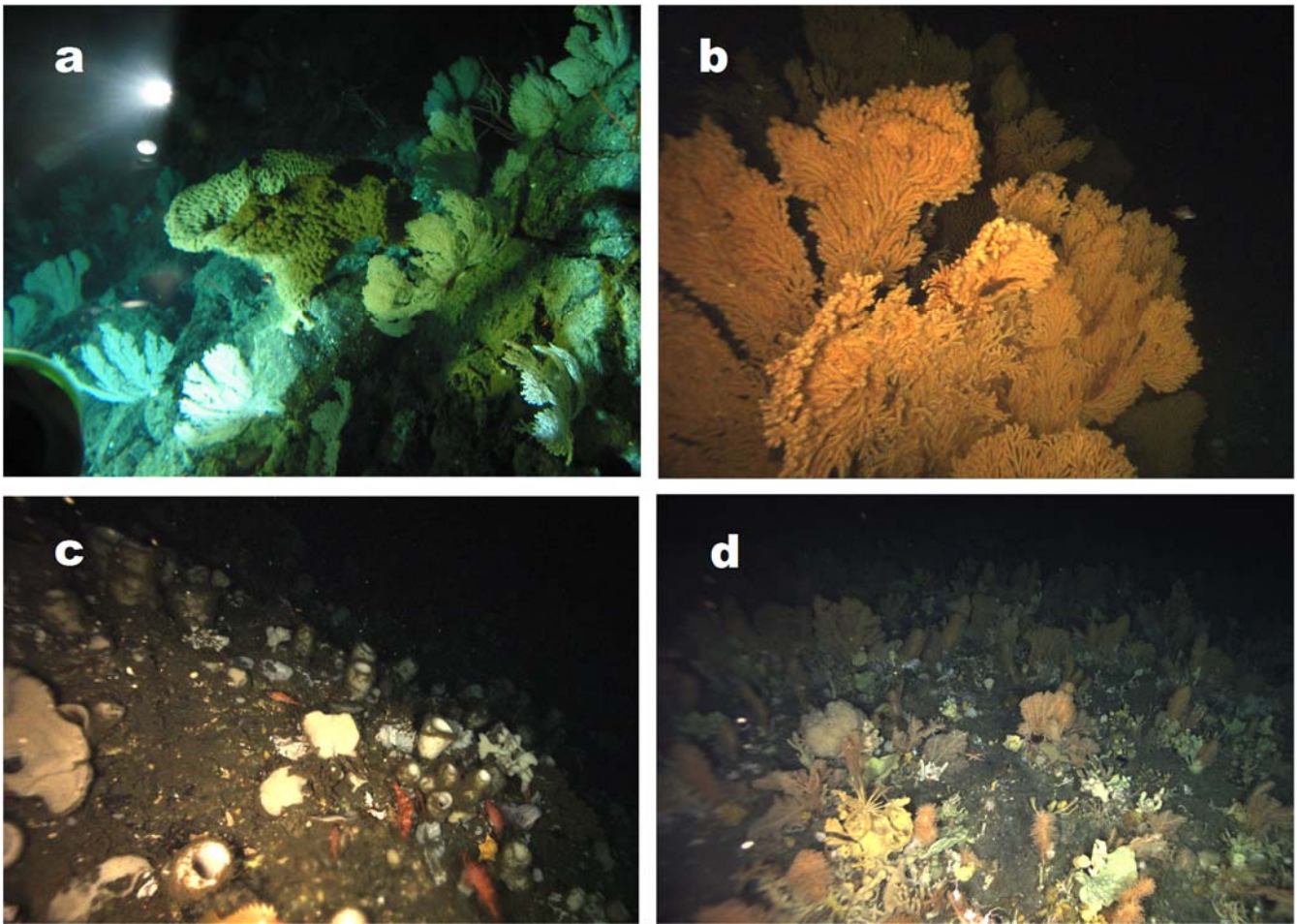
The 2007 Report listed 141 unique coral taxa including 11 scleractinians, 14 antipatharians, 15 alcyonaceans (including six stoloniferan taxa), 63 gorgonians, 10 pennatulaceans, and 28 stylasterids. The list included 52 taxa with incomplete taxonomy and several taxa that were only recently collected and awaited formal description. Since that time, Cairns and Baco (2007) described five new species of

Narella from Gulf of Alaska seamounts previously known only generically and Etnoyer (2008) described a new species of bamboo coral (*Isidella tentaculum*), a major structure forming coral, previously known only generically from deepwater areas of the Gulf of Alaska seamounts and the Aleutian Islands. Additionally two major revisions were undertaken – one on the Primnoidae from the Aleutian Islands and Bering Sea (Cairns 2011) and another on the Stylasteridae from Alaska and adjacent waters (Cairns and Lindner 2011) – both added many new species and eliminated numerous synonyms.

Advances in coral taxonomy have been made in Alaska in the past 8 years but there are still a few species to describe, both in hand and known from video footage. The updated list (Stone and Cairns 2017 – [Online Annex](#)) now includes 137 unique coral taxa (Table 1) known from Alaskan waters but still includes three dozen species with incomplete taxonomy.

Table 1. Updated summary of species richness and depth range for seven major groups of corals found in Alaskan waters. Data sources and references are found in the Online Annex 1.

TAXA	Number of Species	Depth Range (m)
Black corals (Order Antipatharia)	12	22–6328
Stony corals (Order Scleractinia)	12	401–4784
Soft corals (Order Alcyonacea, in part)		
Suborder Alcyoniina	8	10–3209
Suborder Stolonifera	6	11–591
Gorgonian corals (Order Alcyonacea, in part)	61	6–4784
Sea pens and whips (Order Pennatulacea)	14	3–2947
Lace corals (Family Stylasteridae)	24	10–2124
Total	137	3–6328



*Figure 2. Alaska seascapes: a) Rich sponge and coral habitat on Dickins Seamount in the Gulf of Alaska. b) Red tree coral (*Primnoa pacifica*) thicket on Shutter ridge in the Gulf of Alaska. c) Sponge habitat near Fairweather Ground in the Gulf of Alaska. d) Coral and sponge “garden” in the Aleutian Islands.*

Some taxa are still known only generically, possibly including some synonyms and names borrowed from other areas and used simply as placeholders. All major coral groups are in need of additional taxonomic work but the Alcyonacea and Pennatulacea are most in need of major revision. Additionally, the gorgonian families Plexauridae and Isididae are in need of taxonomic attention. Specimens are available to do the work but there is currently a shortage of taxonomists with expertise in these groups.

b. Coral distribution

The principal source of coral distribution information in Alaska continues to be catch data collected during annual research trawl surveys. Since the survey stations are located at the same approximate locations each year no new spatial information is available from that source when considered at the spatial scale of the surveys. These trawl surveys have been extended in recent years to cover new areas in the arctic and subarctic waters of the northern



Bering Sea, Chukchi Sea and Beaufort Sea. Trawl survey data are currently being used to develop models of coral and sponge distribution applicable to all Alaska regions (Rooper et al. 2014, Sigler et al. 2015). These trawl surveys have now been complemented by towed/drift camera surveys conducted in the Aleutian Islands (Goddard et al. in rev.) and eastern Bering Sea (Goddard et al. 2016).

Another tremendous source of coral distribution information is from commercial fisheries bycatch records maintained by the Alaska Fisheries Science Center and collected by observers as part of the Fisheries Monitoring and Analysis Division. Unfortunately, the taxonomic resolution presently used by observers provides little fine-scale information on coral distribution. NOAA initiated a pilot project in 2012 to improve the taxonomic identification capability of fisheries observers by providing them with training, a field guide, and a sampling protocol to test their ability (Stone et al. 2015). In general, the success of sample identification was low but highly variable. Long-term implementation of a coral identification protocol, like the one tested for this project, would require training resources beyond those currently available.

There have been few studies of population connectivity for Alaskan corals. Baco and Cairns (2012) concluded that haplotypes for corals of the genus *Narella* collected on seamounts in the Gulf of Alaska and Hawaii had relatively narrow depth and geographic ranges. Analysis of genetic connectivity for *Primnoa pacifica* in the eastern Gulf of Alaska is

ongoing and genetic markers have been developed for this very important genus of octocorals (Morrison et al. 2015).

Spatial data from major projects completed prior to the 2007 Report are now available (e.g. Stone 2014, Stone et al. 2014a,b) and additional spatial data will also soon be available as part of another NOAA project to review the submersible-collected video archives throughout Alaska. Coral specimens with precise location data archived in the Auke Bay Laboratory (n = ~400) are also currently being re-cataloged and will soon be available for spatial analyses.

Bering Sea: The canyons and slope of the eastern Bering Sea were a major focus of new surveys and analysis. Greenpeace conducted a research cruise to Pribilof and Zhemchug Canyons along the Bering Sea continental margin in 2007 (Miller et al. 2012). High densities of corals (0.43 colonies m⁻²) were reported from the canyons (combined) and principally included scattered groves of the pennatulacean *Halipteris willemoesi* and fields of the gorgonian *Plumarella aleutiana* on several transects. Miller et al. (2012) reported that Pribilof Canyon supported higher densities of corals (0.79 colonies m⁻²) and sponges (0.53 individuals m⁻²) than Zhemchug Canyon (0.07 colonies m⁻² and 0.01 individuals m⁻², respectively). Most notably, the study documented several northern range extensions and new records for the region: 1) the scleractinian *Caryophyllia alaskensis* (a northern range extension); 2) the antipatharian *Lillipathes wingi* (northernmost record in the Pacific

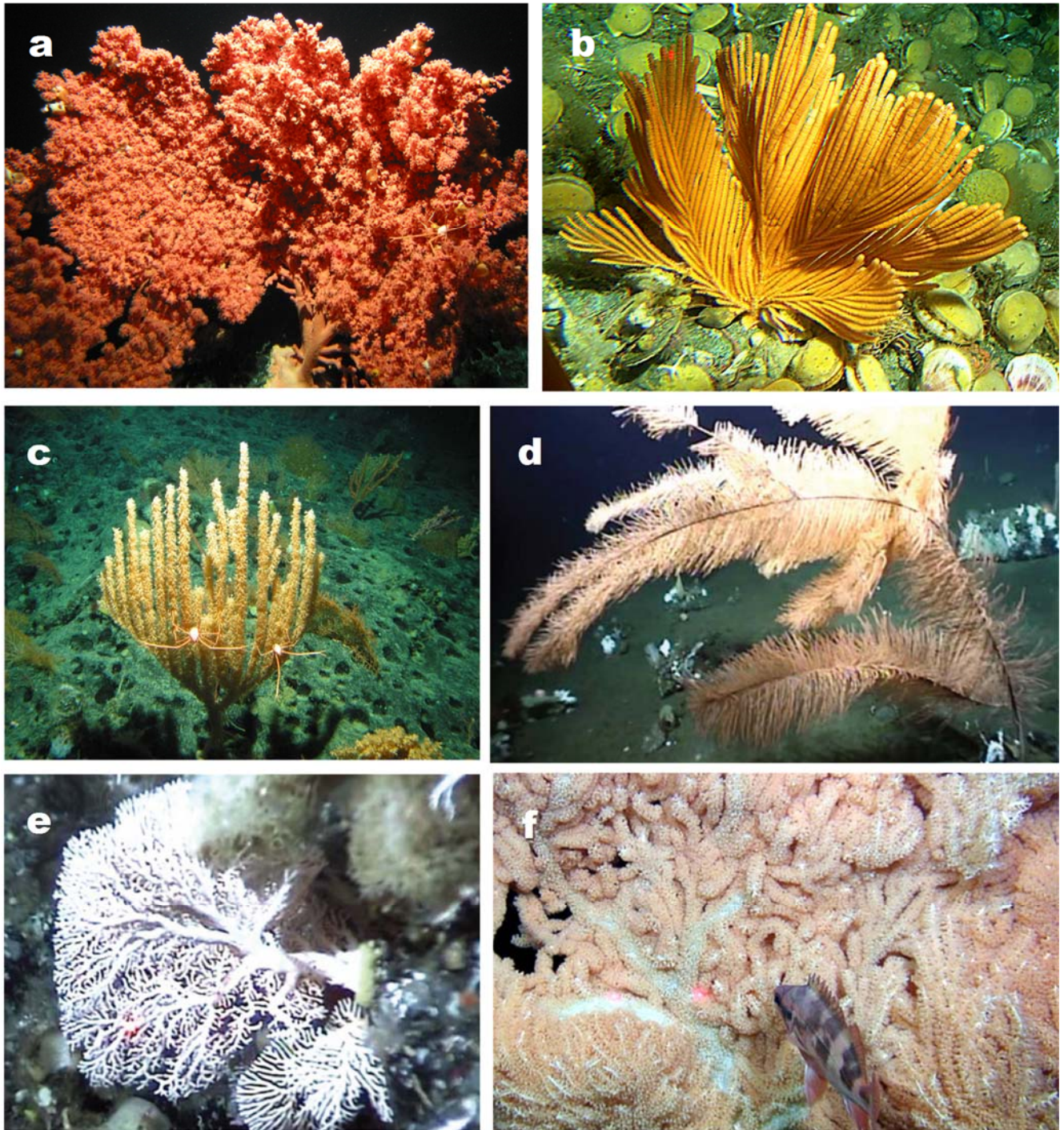


Figure 3. Deep-sea corals of Alaska: a) Large bubblegum coral (Paragorgia sp.) from Pratt Seamount in the Gulf of Alaska. b) The gorgonian Fanellia fraseri in a bed of scallops, many encrusted with the sponge Myxilla parasitica in the Aleutian Islands. c) Gorgonian coral (Isidella tentaculum) with two galatheid crabs from Welker Seamount in the Gulf of Alaska. d) Black coral (Parantipathes sp.) at a depth of 1003 m in the Aleutian Islands. e) Stylasterid coral (Stylaster campylecus) at a depth of 681 m in the Aleutian Islands. f) Sharpchin rockfish in a large Primnoa pacifica in the Gulf of Alaska.



Ocean); 3) the alcyonacean *Heteropolypus* sp. (= *Anthomastus* sp.; likely a northern range extension for the genus); 4) a stoloniferan *Clavularia* sp. (a new record for the region); 5) six gorgonians (*Plumarella aleutiana*, *Primnoa pacifica*, *P. wingi*, *Keratoisis* sp., *Swiftia pacifica*, and *Paragorgia arborea*) all representing new range extensions or new records for the region; and 6) two pennatulaceans (*Protoptilum* sp. and cf. *Pennatula* sp.), each representing a range extension.

Based on the findings of the Miller et al. (2012) study, the North Pacific Fishery Management Council requested analyses (Sigler et al. 2015, see below) and a model validation survey to determine if coral concentrations in two canyons in the eastern Bering Sea, Pribilof and Zhemchug, warranted further protection from fishing activity. The Council asked the AFSC to collect information on coral presence inside and outside the canyons, information on the height and density of corals, and the role of corals as fish habitat. They also asked scientists to document the presence and degree of fishing gear effects. The field survey was conducted in 2014 and the results were reported in Rooper et al. (2016), Goddard et al. (2016), and MacLean et al. (2017). A towed/drift stereo camera system was deployed at 250 randomly selected sites along the eastern Bering Sea shelf and outer slope. The results validated previous modeling and analysis work, confirming that coral habitat occurs both inside these two canyons and along the Bering Sea slope. In general, coral densities throughout our survey area were low where they occurred. This is not surprising as the eastern Bering Sea seafloor

contains little (~2.8% of the total observed seafloor) of the rocky habitat that most corals require for attachment. The highest concentration of coral habitat was found in Pribilof Canyon and to the northwest along the slope. Sea whip densities were highest in sandy portions of the slope through-out our survey area. Most gorgonian corals observed were < 30 cm tall, while sea whips were as tall as 1.5 m. Direct evidence of fishing (mostly trawl tracks, but also derelict gear) was observed at 32 (12.8%) of the sample sites. In total, 2.9% of the corals and 0.3% of the sponges observed were damaged. About 9% of individual sea whips observed were classified as either damaged, dead or lying horizontal on the seafloor. It was difficult to determine if the damage was human-induced (e.g., fishing or other activity) or natural (e.g., sea star predation, ocean currents). There were very few places where both clear evidence of fishing activity (e.g., trawl tracks or fishing gear) and damaged coral, sponges or sea whips occurred (3.2% of the camera transects).

Aleutian Islands: The 2007 report identified the Aleutian Islands as the region with the highest abundance and diversity of corals in Alaska. Stone (2014) presented analyses of deep-sea coral and sponge habitats from video surveys conducted from 2002–2004 in the central Aleutian Islands, greatly expanding the geographic and depth (to 2947 m) range of earlier observations. Corals were widely distributed throughout the study area, with the highest density observed at depths between 400 – 700 m. An additional 18 coral and sponge gardens were identified.



In 2012 and 2014, camera surveys were conducted at 216 randomly-selected sites throughout the Aleutian Islands and Bowers Ridge, using protocols similar to those used on the eastern Bering Sea surveys. These surveys indicated that high-density coral and sponge communities were much more extensive than previously surveyed (Goddard et al., 2017). Survey data were used to ground-truth the coral and sponge distribution models developed for the Aleutian Islands (Rooper et al. 2014; see below).

Gulf of Alaska: In August 2010, there was an 8-day cruise aboard the chartered fishing vessel *Sea Storm* to investigate three slope areas closed to bottom trawling in 2007 in the western Gulf of Alaska. These slope areas (Shumagin, Sanak, and Unalaska) were identified by fishers to potentially contain coral and sponges in virtually pristine states, as fishing has not typically occurred in these areas. The objective of the cruise was to use video cameras to determine whether corals and sponges occurred in each of the three areas and to collect data that would allow predictive modeling of their distribution there. Upright sponges (vase or arborescent morphology) occurred at all three closed areas, although they were in relatively low abundances at the Unalaska and Shumagin areas. Deepwater corals were not found at the Shumagin area and were observed only at one site in Unalaska. Corals occurred at 14 of 30 sites in the Sanak area. Sponges were distributed across all depths where video was recorded, while corals were distributed only at the shallowest locations (< 150 m) in the closed areas. The corals observed were most

commonly upright gorgonians with a fan-type morphology. Corals were present only where boulders were present and did not occur in areas with only sand and gravel substrates. Sponges occurred where both boulders and soft mud substrates were present, although they were also more likely to occur at locations with cobble or boulders present.

Areas supporting dense red tree coral (*Primnoa pacifica*) thickets in the eastern Gulf of Alaska, including the five small areas designated as HAPCs by the NPFMC in 2006, have been focal sites for studying some of Alaska's most important coral habitats. Extensive in situ work conducted there in 2005 (Stone et al. 2014a) revealed that seafloor habitats are dominated by red tree corals, hydrocorals (Stylasteridae), a few other octocorals (*Calcigorgia* spp., *Paragorgia* sp., and *Halipteris willemoesi*) in lower numbers, demosponges and in some areas dense sponge grounds of hexactinellids (mainly *Aphrocallistes vastus*, *Heterchone calyx*, and *Farrea occa*). The presence of red tree corals is highly associated with bedrock, high seabed roughness and slope (Masuda and Stone 2015) and the habitats formed by these corals and sponges provide essential habitat for some species of fish (Stone et al. 2014a).

Alaskan Arctic: New surveys conducted in the Chukchi Sea in 2009 and 2010 in association with proposed oil and gas leases (BOEM, 2012) revealed a patchy distribution of habitats structured by sedentary invertebrates. The soft coral (*Gersemia* sp.) was the primary coral species identified, with more diverse and dense coral and sea anemone communities at



nearshore sites and within Barrow Canyon. These findings were confirmed during a cruise in July 2012 led by Greenpeace.

II.2.ii – Sponges

a. Sponge taxonomy

NOAA’s Deep Sea Coral Research and Technology Program provided funding for the publication of “A Guide to the Deepwater Sponges of the Aleutian Islands Archipelago” (Stone et al. 2011). The main purpose of the guide was to promote an awareness and appreciation of the importance of the sponge fauna in the North Pacific Ocean, particularly in the Aleutian Islands where the diversity and abundance of sponges appear to be extraordinary and where bycatch in existing

fisheries continues to be a major concern for resource managers. The guide documented 196 sponge taxa from deep-water (> 80 m) in Alaskan waters (Table 2), but noted that the inventory is largely incomplete and that there are many species yet to be discovered in the region. Reiswig and Stone (2013) further described deep-water hexactinellid sponges from the central Aleutian Islands, including a new genus and eight new species in five families. A special collections project was initiated in 2012 to collect select sponge taxa in the Aleutian Islands aboard the biennial research trawl survey conducted there by NOAA. Nearly a dozen new species of sponges have already been discovered as part of this project (Lehnert et al. 2013; Lehnert and Stone 2014a, 2014b; Lehnert and Stone 2015).

Table 2. Summary of species richness and depth range for classes of sponges found in Alaskan waters, based on Stone et al. (2011) and Reiswig and Stone (2013).

CLASS	Number of Species	Depth Range (m)
Calcarea	12	5–250
Hexactinellida	52	20–2800
Demospongiae	130	0–2800
Homoscleromorpha	2	95–383
Total	196	0 – >2800

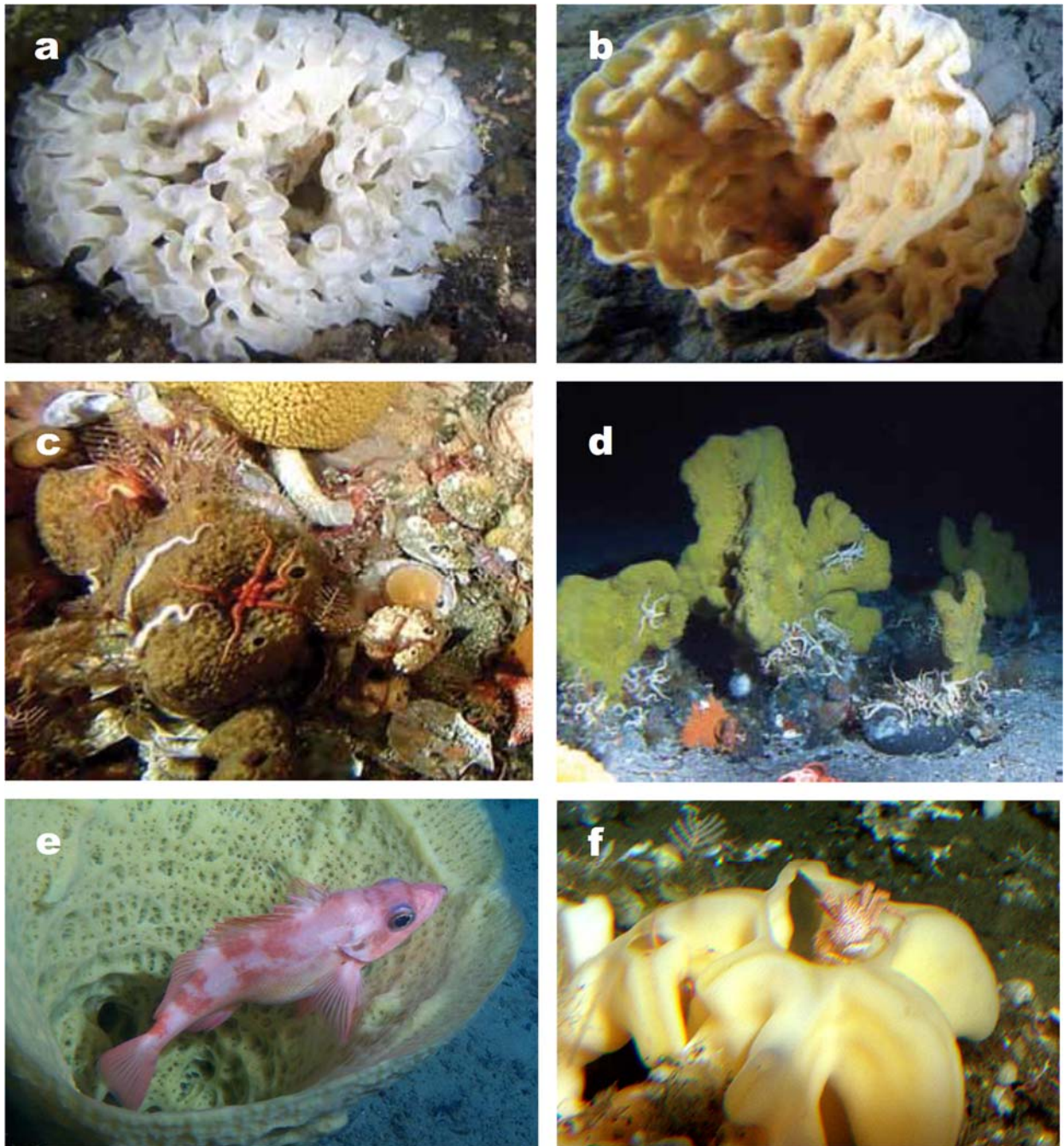


Figure 4. Deep-sea sponges of Alaska: a) Hexactinellid sponge *Farrea occa occa* at a depth of 165 m in the eastern Gulf of Alaska. b) Glass sponge *Heterochone calyx calyx* at a depth of 181 m in the eastern Gulf of Alaska. c) Demosponge *Guitarra abbotti* at a depth of 146 m in the central Aleutian Islands. d) Demosponge *Mycale (Mycale) loveni* at a depth of 96 m in the central Aleutian Islands. e) Demosponge *M. loveni* with a gravid sharpchin rockfish (*Sebastes zacentrus*) at a depth of 170 m in the eastern Gulf of Alaska. f) Glass sponge *Aphrocallistes vastus* with a juvenile golden king crab (*Lithodes aequispina*) in pre-molt condition at a depth of 190 m in the central Aleutian Islands.



b. Sponge distribution

Sponges are a major component of biogenic habitat or “living substrate” in the Gulf of Alaska, Aleutian Islands and the Bering Sea. Sponges are the most common taxon forming living substrate in the Gulf of Alaska and the Aleutian Islands (Malecha et al. 2005). Sponges reach high densities in the Aleutian Islands (Stone et al. 2011), and demosponges are a major component of the region’s coral and sponge “gardens” (Stone 2014). Sponges are also common in the Bering Sea, with some areas of very high density in Bristol Bay. Sponges have also been reported from the Alaskan Arctic (de Laubenfels 1953, BOEM 2012), but appear to have occurred in low numbers at the sites sampled.

Bycatch in fisheries and fisheries-independent surveys is a major source of information on the location of the sponge fauna, and a source of specimens for study. The guide by Stone et al. (2011) served the additional purpose of providing fisheries observers and scientists with the information necessary to adequately identify sponge fauna so that the data can be included in existing databases. These data can be used to map areas of high abundance and the locations of indicator species of vulnerable marine ecosystems. The guide was also designed for use by scientists making observations of the fauna *in situ*, with submersibles including remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs).

A research cruise (March 2010) in Portland Canal along the border between Southeast

Alaska and British Columbia, confirmed the presence of small sponge reefs detected a few years previously with sonar by the Geological Survey of Canada (Stone et al. 2014b). The reefs were similar in species composition to, but much smaller in size than, the massive bioherms reported farther south in British Columbia (Conway et al. 2005). Small patches of hexactinellid sponge reef, believed to be biohermal, were also observed in northern Southeast Alaska near Juneau, possibly indicating that these structures are more common than originally hypothesized.

II.2.iii – Modeling distribution and abundance of corals and sponges

Predictive habitat modeling for deep-sea corals and sponges provides an important tool for understanding the distribution of these organisms across Alaska’s huge geographic regions. Since the 2007 report, there has been a significant expansion in the use and utility of predictive habitat models in Alaska (Guinotte et al., this report). These include presence-only models (Maxent) of coral taxa (grouped at the Order or suborder level) for the Gulf of Alaska, Aleutian Islands and eastern Bering Sea (Guinotte and Davies 2013); models for coral gardens in the Aleutian Islands (Woodby et al. 2009; Guinotte and Davies 2013); and models for coral and sponge presence, abundance and diversity in the Aleutian Islands (Rooper et al. 2014) and eastern Bering Sea slope and canyons (Sigler et al. 2015, Rooper et al. 2016). Rooper et al. (2016) presented one of the first examples of rigorous validation of coral and sponge habitat models, using camera surveys to assess the



accuracy of predictions from a model based on trawl surveys along the eastern Bering Sea slope.

The results of these modeling studies supported observations on the relative richness of coral and sponge habitats in the Aleutian Islands compared to most other regions, and predicted that these habitats were expected to be much more widespread in the Archipelago. The North Pacific Fishery Management Council utilized model results in its deliberations on potential protections for Bering Sea canyons.

II.3. Species Associations with Deep-Sea Corals and Sponges

In Alaska, commercial fisheries species are associated with deep corals and sponges at both fine-scales (less than 10 m, e.g. Stone 2006) and at the scale of existing fisheries (e.g. Heifetz 2002). Research conducted since or not reported in the 2007 Report continue to support earlier observations that fish and crabs, particularly juveniles, are associated with coral habitat throughout Alaska and are presumably using it as refuge and as focal sites of high prey abundance (Rooper and Boldt 2005; Rooper et al. 2007; Rooper and Martin, 2012; Miller et al. 2012; Stone 2014; Stone et al. 2014a). A study in the eastern Aleutian Islands found juvenile Pacific ocean perch used these habitats as nursery areas and were closely associated with boulders and rocky areas that were extensively covered with coral and sponge (Rooper et al. 2007). All of these studies have measured association at varying scales and have utilized different methods to test association but are

noteworthy since these observations are not well quantified in many other regions and habitats where deep-sea corals occur. Not all demersal species are associated with coral habitat in Alaska. For example, Rooper and Martin (2009) found that shortspine thornyhead (*Sebastolobus alascanus*) catches were not associated with catches of corals and sponges in the Gulf of Alaska bottom trawl survey. Stone (2014) also found that some deep-water species in the Aleutian Islands are no more likely to occur with emergent epifauna than they are without emergent epifauna.

II.4. Ecological Studies (Growth, Reproductive Ecology, Microbial Ecology, and Marine Natural Products)

New studies on growth rates of Alaskan corals corroborated earlier observations from Alaska and elsewhere that they are slow-growing and consequently long-lived. Andrews et al. (2009) used ^{210}Pb techniques to determine the growth rate for two species of bamboo corals in the Gulf of Alaska ($\sim 1.4 \text{ cm y}^{-1}$ axial growth rates for *Isidella tentaculum* and $\sim 1.0 \text{ cm y}^{-1}$ for *Keratoisis* sp.). Stone et al. (2017) analyzed the growth of tagged colonies of the shallow-water holaxonian *Calcigorgia spiculifera* in Southeast Alaska over a period of five years. The growth rate of 0.6 cm y^{-1} was the slowest rate reported for any gorgonian in Alaskan waters. Andrews and Stone (unpublished data) used growth ring counts to estimate a growth rate between $1.2\text{--}1.8 \text{ cm y}^{-1}$ for the primnoid octocoral *Fanellia compressa* and Stone (unpublished data) used a



deglaciation record to estimate a growth rate for *Primnoa pacifica* that validated the rate previously established for the species (Andrews et al. 2002).

A study was undertaken on the reproductive ecology of stylasterid corals in the Aleutian Islands (Brooke and Stone 2007) that indicated that they are gonochoristic brooders with limited potential to provide sources of recruits to disjunct disturbed habitats. Studies on the reproductive ecology and ultrastructure of *P. pacifica* are being undertaken in shallow-water populations in the Tracy Arm fjords of Southeast Alaska (Waller et al. 2014) and should provide insights into the recovery dynamics of this important species.

The microbial ecology of corals was studied in both the Aleutian Islands (Gray et al. 2011) and on Gulf of Alaska seamounts (Penn et al. 2006). Both studies indicate that corals harbor unique and diverse bacterial communities that may provide the corals with a wide array of benefits including the facilitation of processes for a portion of their nutrition. The Alaska Fisheries Science Center and University of Mississippi have been routinely collecting sponges from survey trawls in the Aleutian Islands since 2004 and investigating their use as marine natural products, specifically as biomedicines. Dozens of sponge taxa have been investigated to date and a few have shown significant promise as antiviral, antimalarial, and antimicrobial agents (Na et al. 2010). Additional collections of demosponges from the Aleutian Islands are being analyzed and one species has already yielded extracts with evidence of bioactivity

against opportunistic infectious diseases, malaria, and Hepatitis C (Abbas et al. 2011).

II.5. Research Priorities and Planned or Anticipated Research Activities

In preparation for the upcoming fieldwork under NOAA's Deep Sea Coral Research and Technology Program, a workshop was held in Anchorage in September 2010 to identify research priorities for the region, including critical information needs and research activities to address these needs (NOAA 2010).

Key priorities included the following:

- Expanding our knowledge of the distribution of deep-sea corals and sponges and their habitats by analyzing existing information, new seafloor mapping and visual surveys, and by developing predictive habitat models. A geographic priority was placed on the Gulf of Alaska and Aleutian Islands.
- Determining the population characteristics of deep-sea corals and sponges, including growth rates, life history and reproductive traits, trophic dynamics, environmental tolerances, and population connectivity.
- Determining the key functions that deep-sea corals and sponges provide to managed species at different life stages.

These priorities were largely derived from ongoing research needs and objectives identified by the Program, the North Pacific Fishery Management Council, and the Essential Fish Habitat-Environmental Impact Statement process. They formed the basis of the 2012–2014 Alaska Coral and Sponge Initiative (Rooper et al. 2017).



III. Update on Management of Deep-Sea Corals and Sponges

III.1. New Information on Impacts and Stressors

III.1.i – Fishing

The 2007 Report indicated that the major stressor on deep-sea coral and sponge communities in Alaska was the impact of commercial bottom-fishing activities and new information continues to support this premise (Heifetz et al. 2009, Stone 2014, Rooper et al., this volume). Accordingly, studies on the effects of fishing on seafloor habitat continue to be a priority in Alaska with particular emphasis on the recovery rates of disturbed habitats. Studies were implemented to examine the recovery rate of sponges 13 years post- (experimental) trawling in low density sponge habitat in the eastern Gulf of Alaska (Malecha and Heifetz, unpublished data) and recovery from simulated trawl disturbance on the pennatulacean *Halipterus willemoesi* (Malecha and Stone 2009) and gorgonian *Calcigorgia spiculifera* (Malecha et al., unpublished data). In 2005, scientists used the submersible *Delta* to document ambient levels of disturbance to corals and sponges in eastern Gulf of Alaska *Primnoa* thickets set aside as HAPCs (Stone et al. 2014a). The HAPCs have been in an area closed to bottom trawling since 1998 so observations of disturbance represent those principally from longline fishing. Rooper et al. (2011) modeled the impacts of bottom trawling in the Aleutian Islands and subsequent recovery rates of corals and sponges and

predicted recovery rates were slow, especially for corals, where the coral biomass would require decades to recover.

As with corals, the primary stressor on deepwater sponge communities in Alaska is likely physical disturbance by commercial bottom-contact fishing gear. The first National Bycatch Report (NMFS 2011) identified an average annual bycatch in 2003–2005 of over 525,000 lbs. (238,000 kg) of sponges. Bottom trawl fisheries in the eastern Bering Sea and Aleutian Islands fisheries had the highest sponge bycatch. Despite extensive bottom-trawl closures in the Aleutian Islands since 2006, updates to the National Bycatch Report (NMFS 2013, 2016) showed continued high levels of sponge bycatch in certain fisheries from 2010–2013.

III.1.ii – Other stressors

The effects of other human activities on coral habitats—deployment of pipelines and cables, point-source pollution discharges, fish processing waste disposal, mineral mining, and invasive species—continue to be of minimal or nonexistent concern, although interest in offshore petroleum drilling in the arctic regions of Alaska may present concerns regarding the presence of soft corals there. The Bureau of Ocean Energy Management (BOEM) approved a Shell Oil Chukchi Sea Exploration Plan; however, Shell Oil subsequently announced in September 2015 that it would cease exploratory offshore drilling in the Arctic. Climate change and the associated effects of ocean acidification on coral and sponge habitats continue to be sources of real concern, as discussed below.



III.1.iii – Climate change and ocean acidification

Decreases in oceanic pH and resulting decreases in calcium carbonate saturation state could have profound effects on corals dependent on the extraction of calcium carbonate from seawater for skeletal building. Corals will be affected differently depending on their skeletal composition (aragonite vs. calcite vs. magnesium calcite), geographical location, and depth relative to the already particularly shallow calcium carbonate saturation horizons in the North Pacific Ocean.

The skeletal composition is unknown for most species of deep-sea corals worldwide and is known for only a handful of the 137 taxa presently documented from Alaskan waters. To that end, a study was initiated in 2010 by sorting through the extensive archives at the Auke Bay Laboratories and Smithsonian Institution; 130 specimens comprising 61 taxa from all major groups of corals (scleractinians, gorgonians, true soft corals, stoloniferans, pennatulaceans, and stylasterid corals) were selected for laboratory analyses. Multiple specimens were selected for taxa of particular ecological importance (i.e. those that form large single-species assemblages), and specimens of the same species from multiple depth and geographic zones.

Laboratory analyses were performed at the Department of Geology and Geophysics at the

Woods Hole Oceanographic Institution and the Center for Material Sciences and Engineering at the Massachusetts Institute of Technology. X-ray diffraction and full-pattern Rietveld data refinement were used to precisely determine the skeletal composition of Alaskan corals. Corals composed of high magnesium-calcite are the most soluble. Consequently, those corals, particularly those residing at depths deeper than the saturation horizon, are most at risk to decreases in oceanic pH unless they have adapted physiological processes to counter the effects.

The mineralogy data will be used in conjunction with species distribution data (depth and geographical) and the present and projected aragonite and calcite saturation horizons in Alaska to predict the effects of ocean acidification on coral resources of the North Pacific Ocean. At the completion of this project a comprehensive risk assessment will be conducted for all corals in Alaskan waters but physiological data are still needed for Alaskan coral taxa, probably in a laboratory setting, to determine if taxa respond as predicted by mineralogy and marine chemistry data. Principal Investigators of this research are Robert Stone (NOAA, AFSC), John Guinotte (Marine Conservation Institute), Angela Helbling and Anne Cohen (Woods Hole Oceanographic Institution), and Stephen Cairns (Smithsonian Institution).



III.2. New or Planned Management Actions

III.2.i – Fishing

A suite of closures were approved by the North Pacific Fishery Management Council in 2005, including the Aleutian Islands Habitat Conservation Area (AIHCA), and implemented on 28 July 2006. Since that time, five additional management activities involving spatial closures that potentially harbor deep coral and sponge habitat have been approved and implemented by the Council and NOAA.

Effective 20 March 2008, Amendment 88 to the Fishery Management Plan for Groundfish of the Bering Sea and Aleutian Islands Management Area revised the boundaries of the AIHCA to allow bottom trawling in a historically fished area (north of Agattu Island) and to prohibit bottom trawling in an area known to harbor coral and sponge habitat (west of Buldir Island). This action was intended to ensure that the intentions of the AIHCA to protect areas of coral and sponge habitat from the potential effects of bottom trawling were realized and to allow non-pelagic trawling to continue in areas

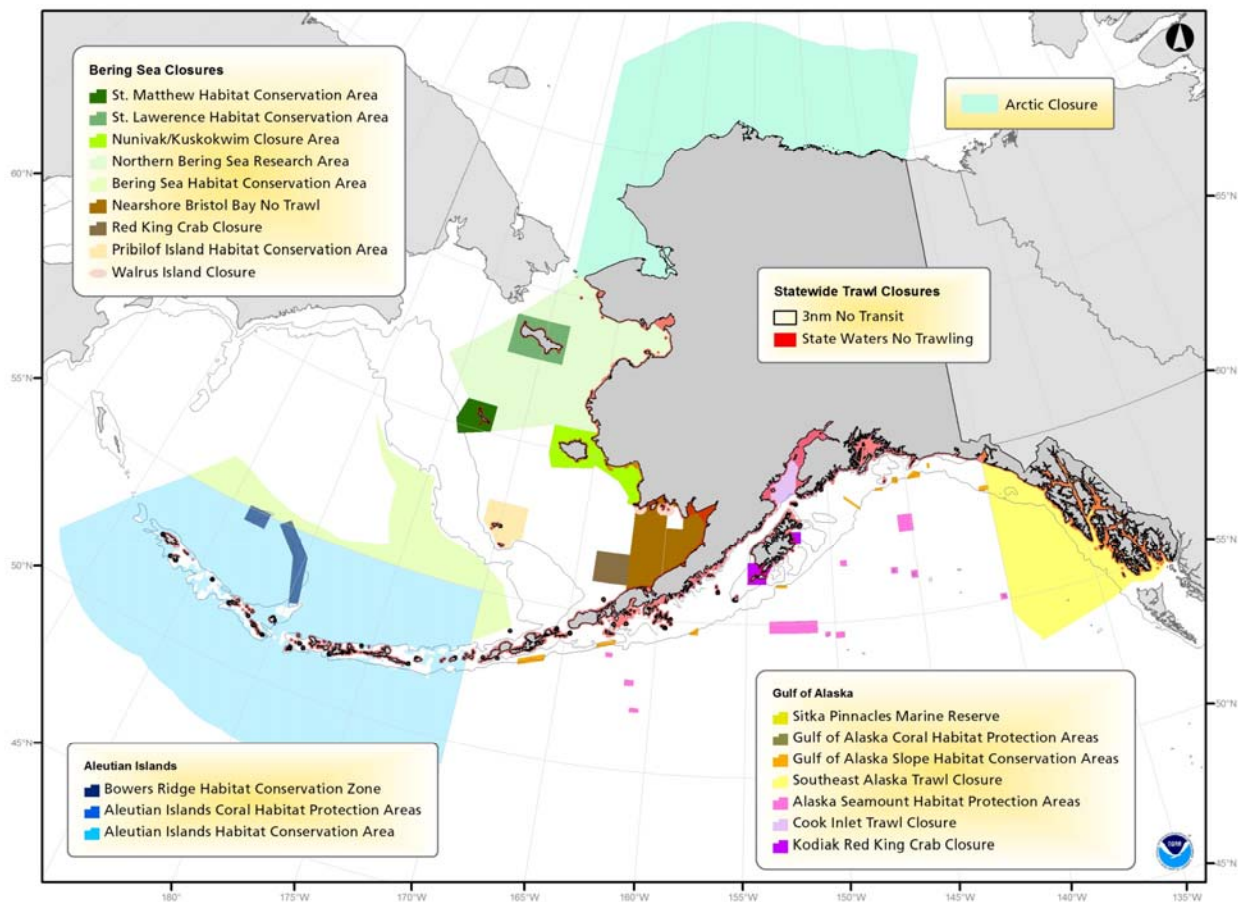


Figure 5. Commercial fishing closures in Alaska (data provided by John Olson, NMFS-Alaska Regional Office, Anchorage, Alaska).



historically fished. The opening of the area north of Agattu Island potentially puts coral and sponge habitat at risk since it has not yet been surveyed for coral and sponge habitat.

The Northern Bering Sea Research Area was implemented in 2008 and prohibited bottom trawling in a broad region there. The intention of the closure was to provide an opportunity to study the potential effects of bottom trawling on seafloor habitat before authorizing that activity there. The benthic fauna of the region is neither well studied nor known to harbor much coral or sponge habitat so the conservation relevance to these habitats is unknown.

In 2009, a new Arctic Fishery Management Plan for the Fish Resources of the Arctic Management Area (Chukchi and Beaufort Seas) was implemented, essentially closing all federal waters in the region to commercial fishing activities. The Council was concerned that changing ecological conditions could lead to the development of inadequately regulated commercial fisheries in the region that could have adverse effects including those on fish habitat. The benthic fauna of the region is not well studied and is not known to harbor much coral or sponge habitat, so the conservation relevance to these habitats is unknown.

In 2011, a trawl sweep modification requirement (Amendment 94) was implemented for vessels participating in the Bering Sea flatfish fishery that occurs exclusively on the broad and homogeneous continental shelf. The modification requires discs or bobbins providing 1–3" lift on the trawl

sweeps to limit adverse effects on low-relief seafloor biota. This gear modification has been demonstrated to reduce impacts on patches of soft corals and sponges located in those habitats (Rose et al. 2013).

Effective 1 January 2011, trawling and longlining for two major forage species (Atka mackerel and Pacific cod) of endangered Steller sea lions were prohibited in the western Aleutian Islands. Concurrently, additional restrictions in 3-nautical mile (5.56 km) buffer areas around established sea lion rookeries went into effect in the central and eastern Aleutian Islands. The closures were not directly intended to protect seafloor habitat but will clearly provide sanctuary to coral and sponge habitat from bottom trawling in those areas.

The Council also examined whether habitat protections were warranted to conserve deep-sea corals in the Eastern Bering Sea canyons and slopes. Based on analyses by NOAA (e.g., Rooper et al. 2016), the Council concluded in 2016 that deep-sea corals in these areas are not at risk from fishing, and additional habitat protections were not necessary (MacLean et al. 2017).

NOAA is examining the effectiveness of the AIHCA to protect sensitive seafloor habitat from the damaging effects of fishing activities. The approach utilizes a geographic information system (GIS) to examine patterns of coral and sponge bycatch abundance and fishing intensity before and after the closures with particular reference to areas that have remained open to fishing.



III.2.ii – Other management actions

In 2016, the Department of Interior announced final regulations to ensure that future exploratory drilling activities on the Outer Continental Shelf within U.S. waters of the Beaufort and Chukchi Seas will be conducted under the highest safety and environmental standards and subject to strong and proven operational requirements.

IV. Conclusions

Research on corals conducted in Alaska since 2007, and particularly since 2012 with extensive new surveys under NOAA's Deep Sea Coral Research and Technology Program, continue to indicate that the region is home to diverse ecosystems supported by extraordinary coral and sponge resources. The resources appear to provide important habitat to fisheries of national and international importance. There are still many important gaps in our knowledge of these ecosystems and analysis continues.

V. Acknowledgements

We thank Jon Heifetz, Wayne Palsson, and John Olson for providing helpful reviews of this manuscript. John Olson provided up-to-date background information on management activities and constructed Figure 5.

Online Annex – Comprehensive list of deep-sea corals in the U.S. Alaska region linked here: <https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>

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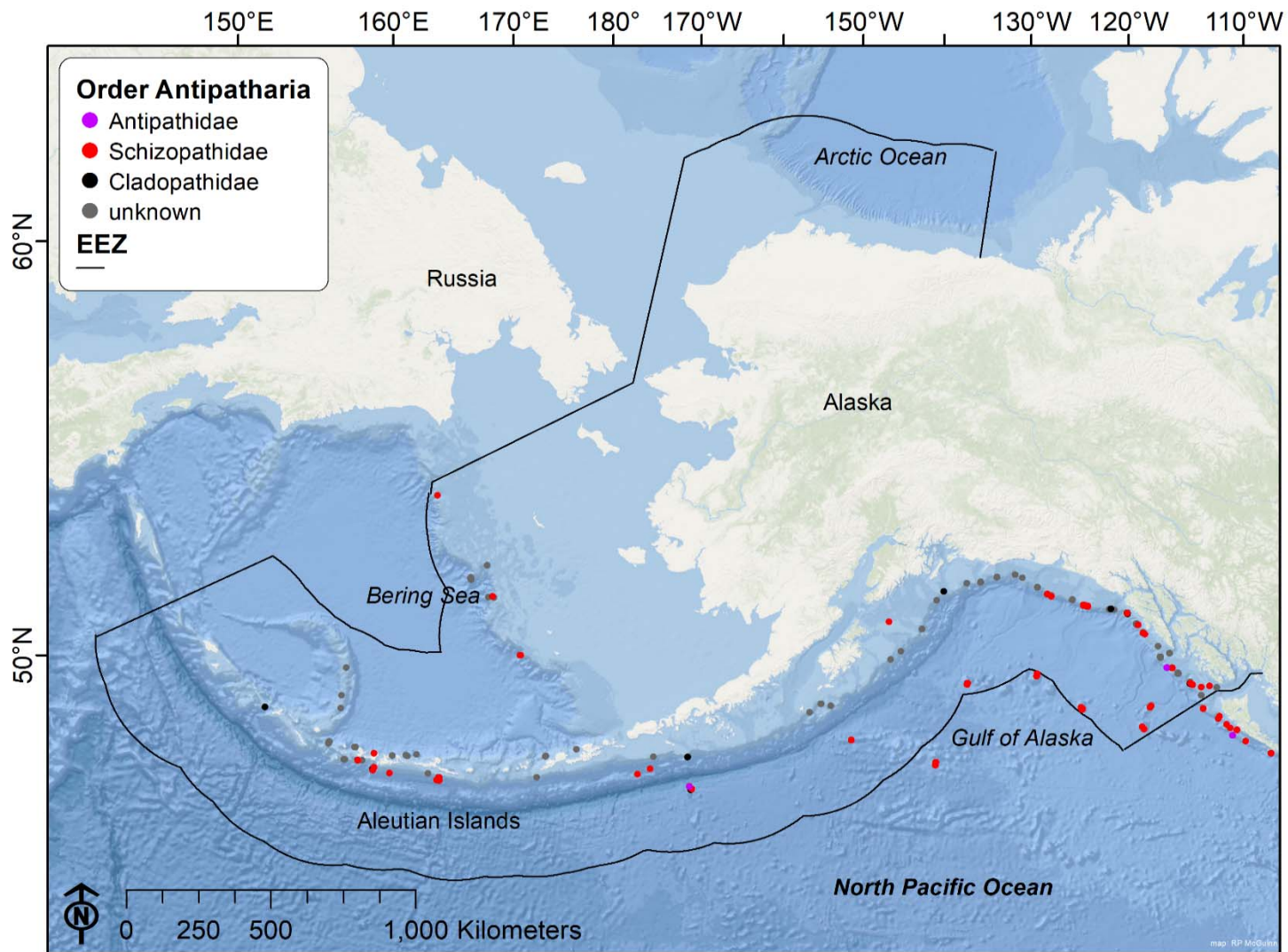
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[Online Annex 1. Deep-sea Coral Taxa in the U.S. Alaska Region: Depth and Geographic Distribution](#)

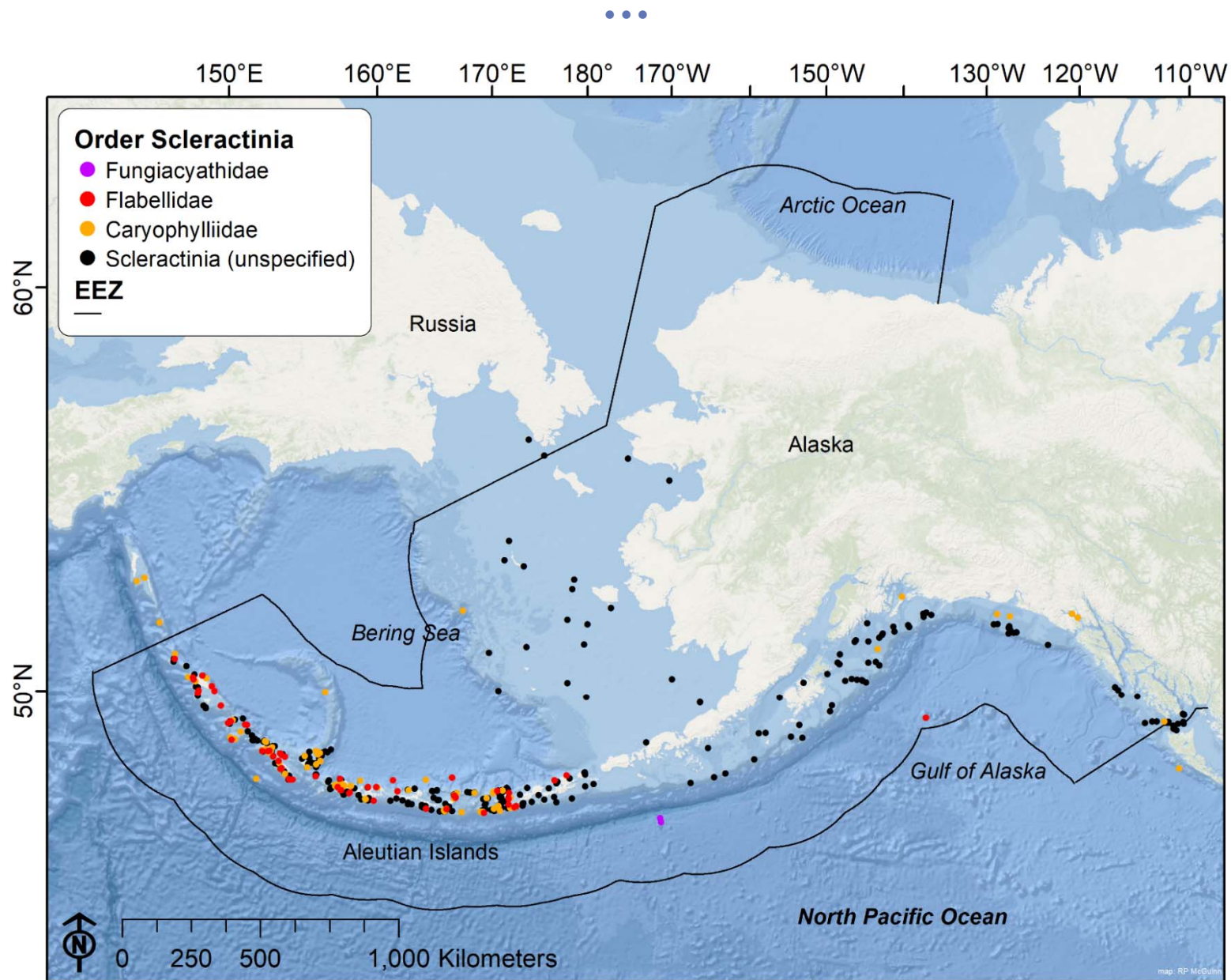


Appendix - Distribution maps for deep-sea corals and sponges in Alaska



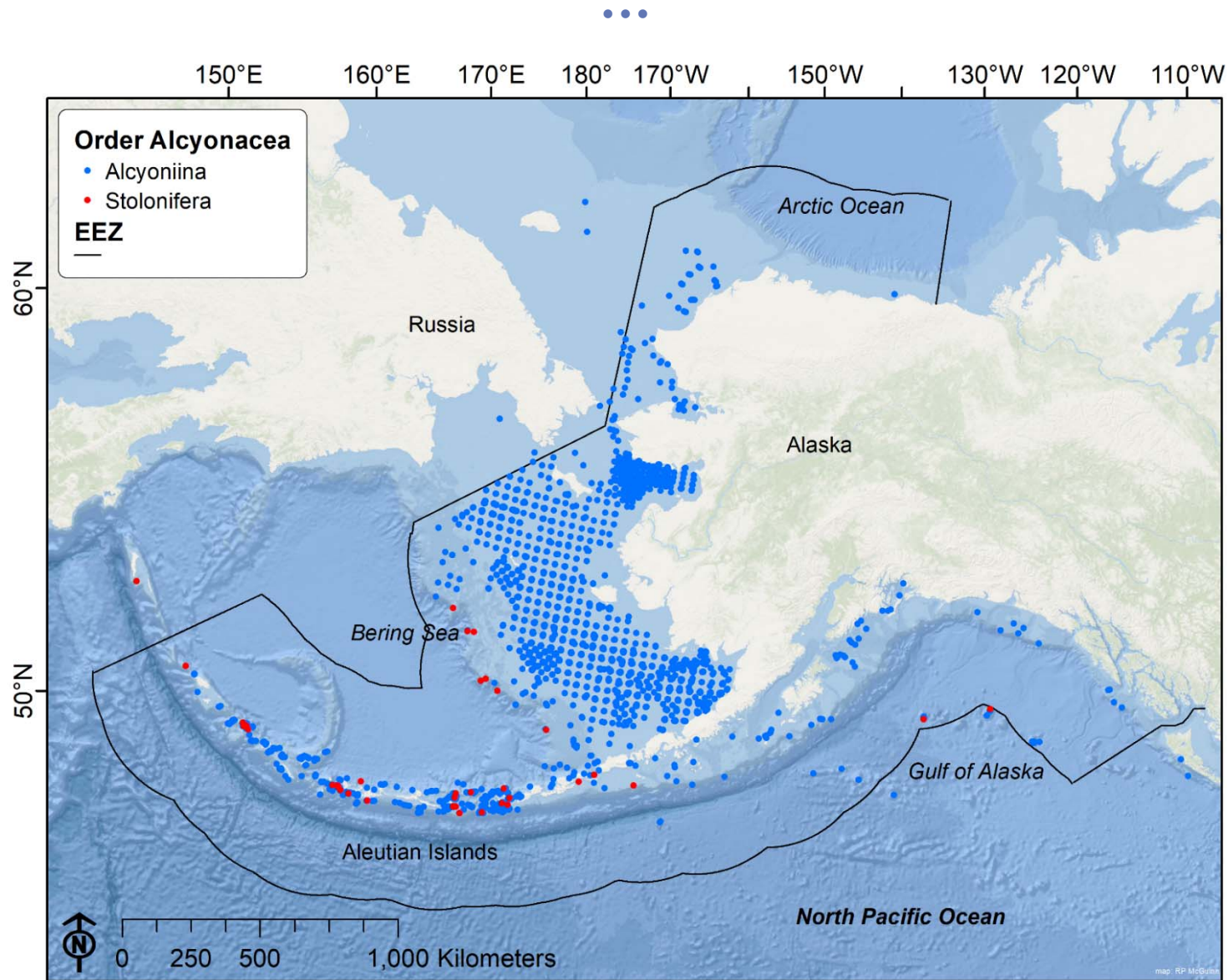
Map 1. Locations of black corals (Order Antipatharia) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



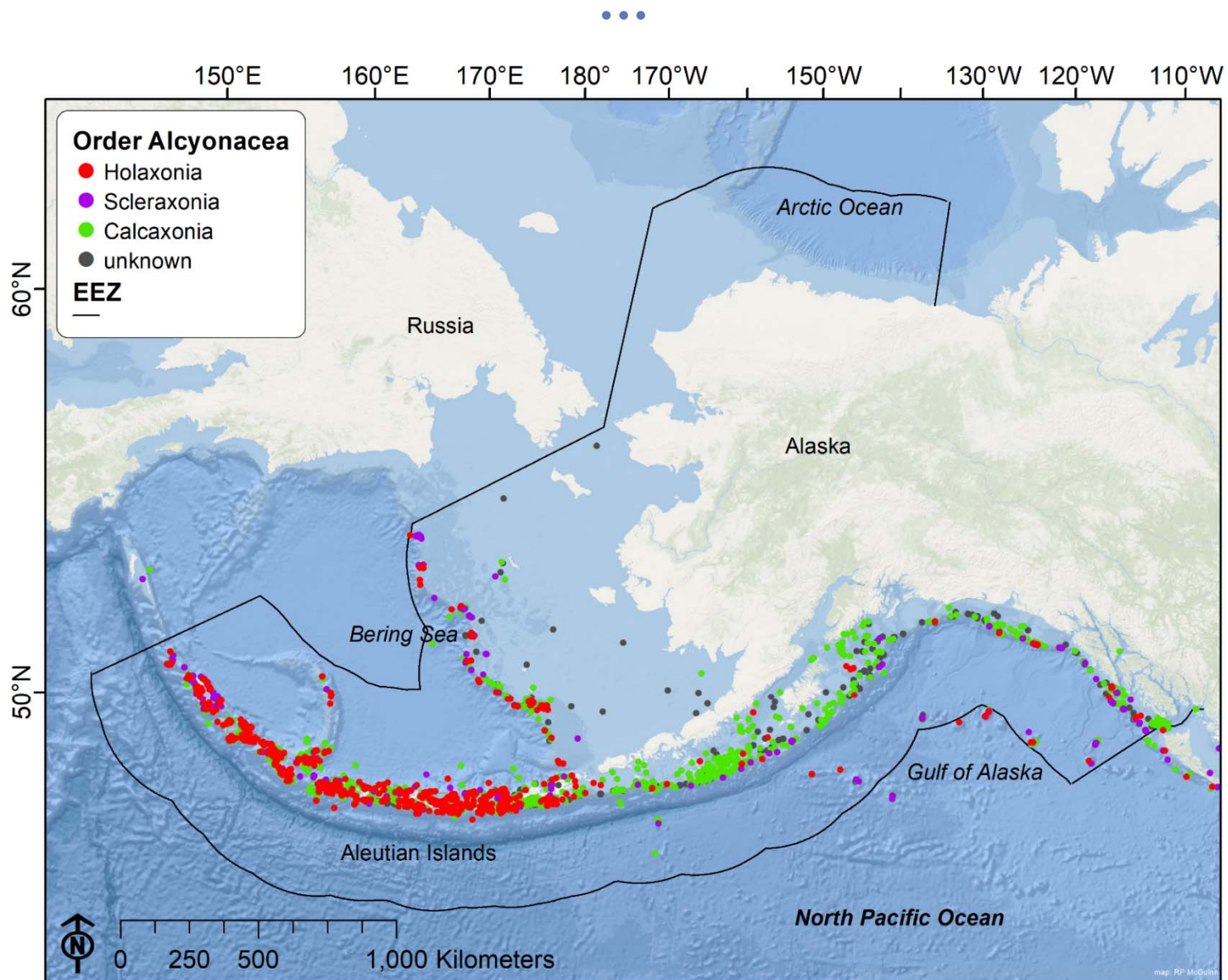
Map 2. Locations of stony corals (Order Scleractinia) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



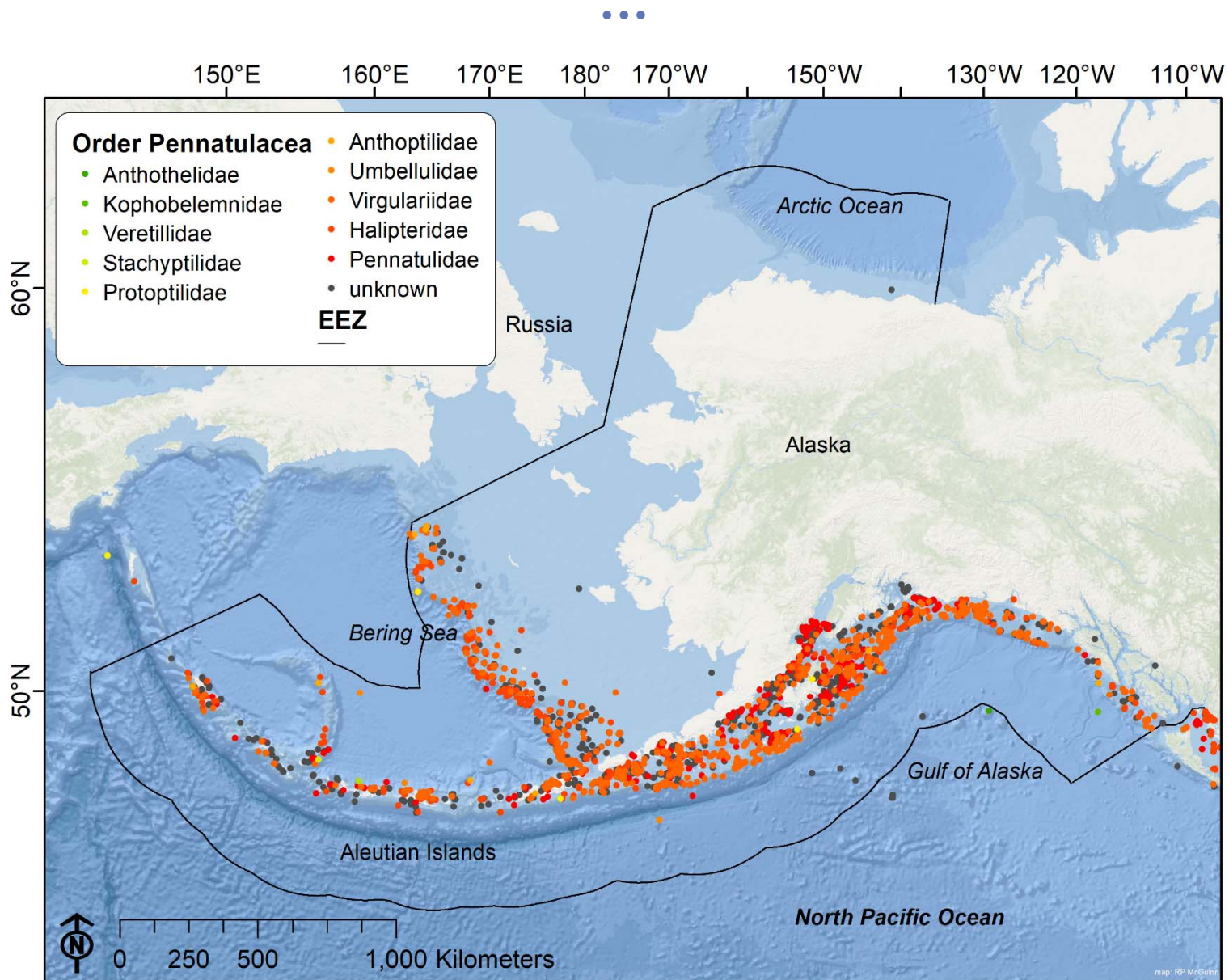
Map 3. Locations of true soft corals (Order Alcyonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



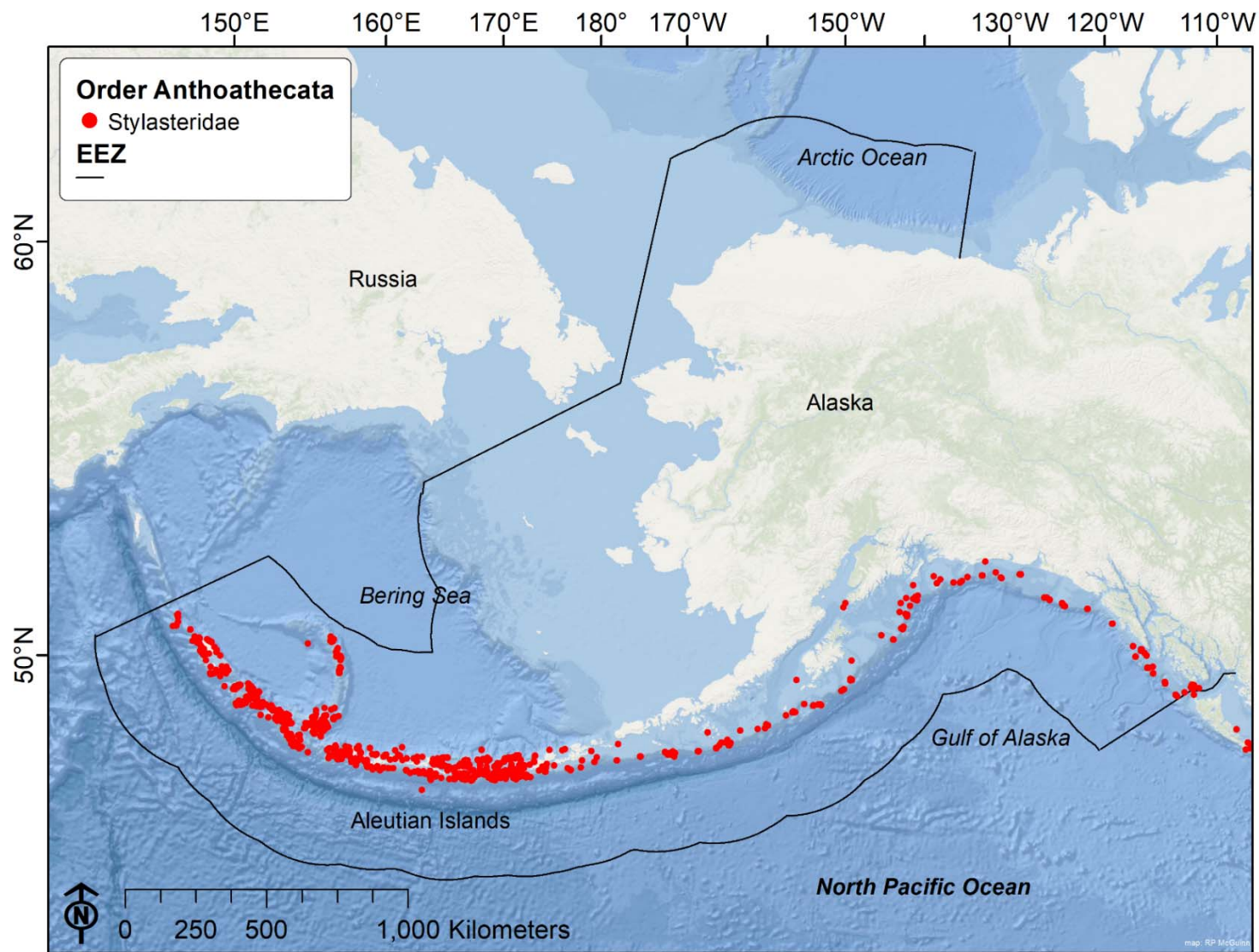
Map 4. Locations of gorgonian corals (Order Alcyonacea, in part; formerly Gorgonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



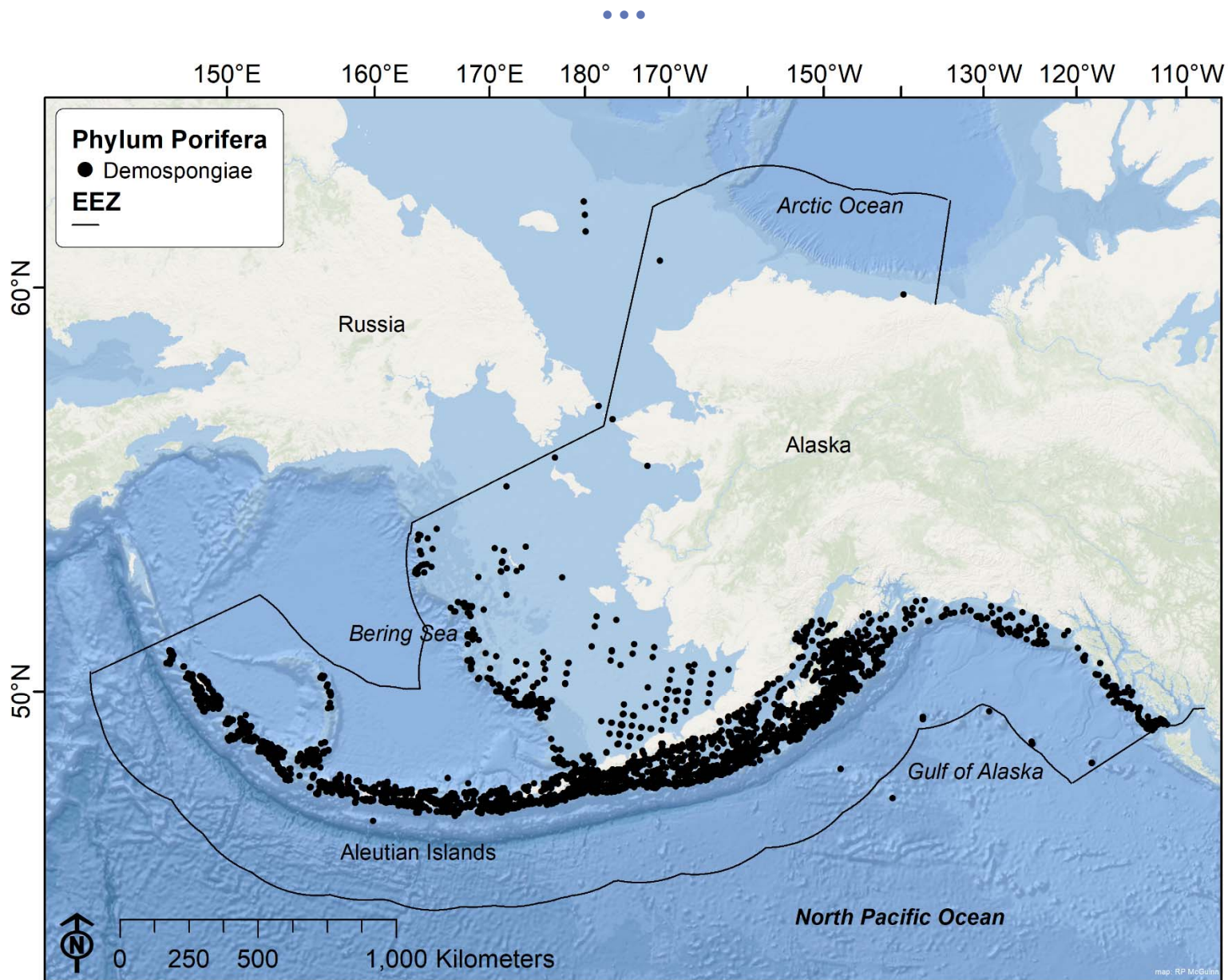
Map 5. Locations of sea pens (Order Pennatulaceae) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



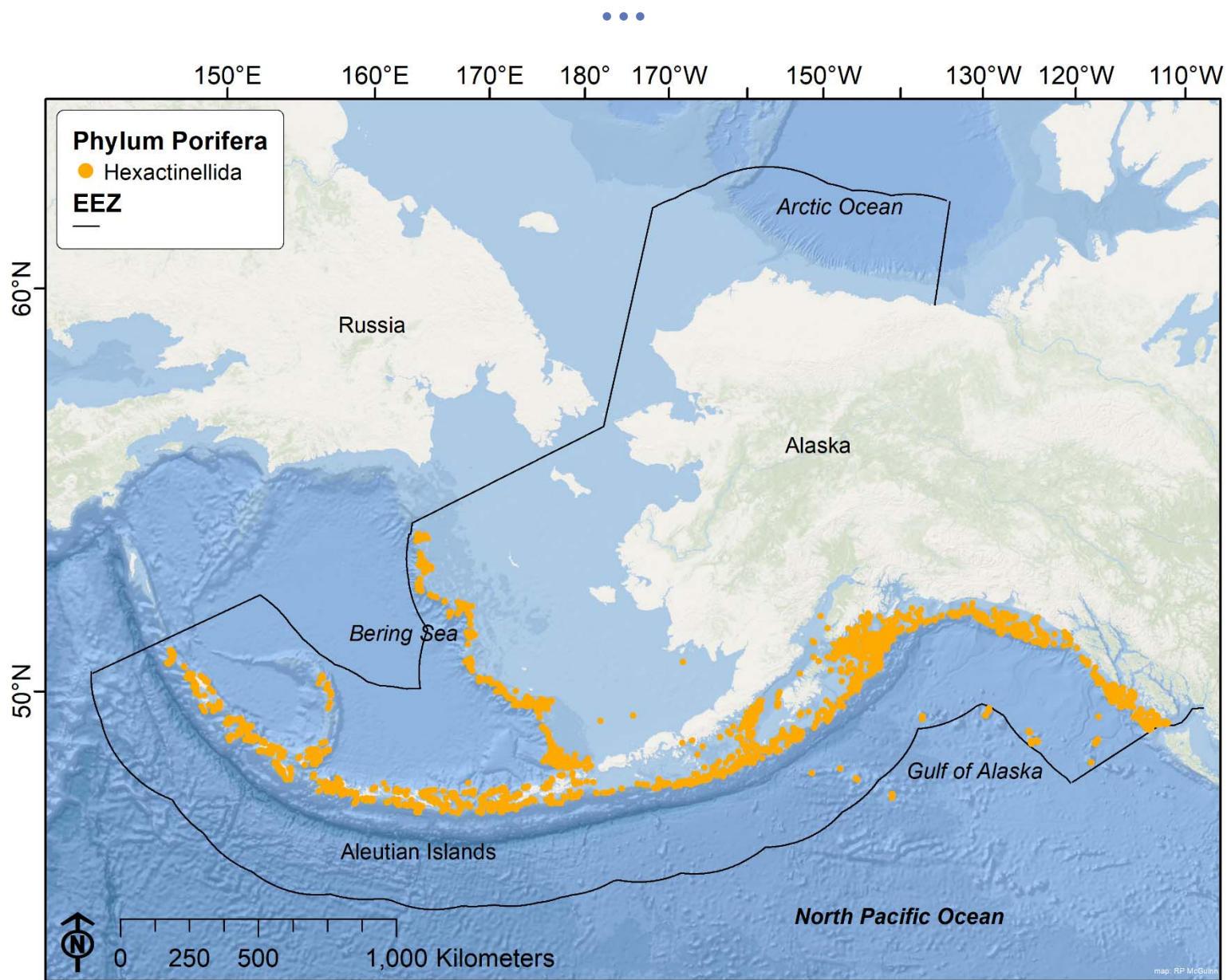
Map 6. Locations of lace corals (Class Hydrozoa, Order Anthoathecata, Family Stylasteridae) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



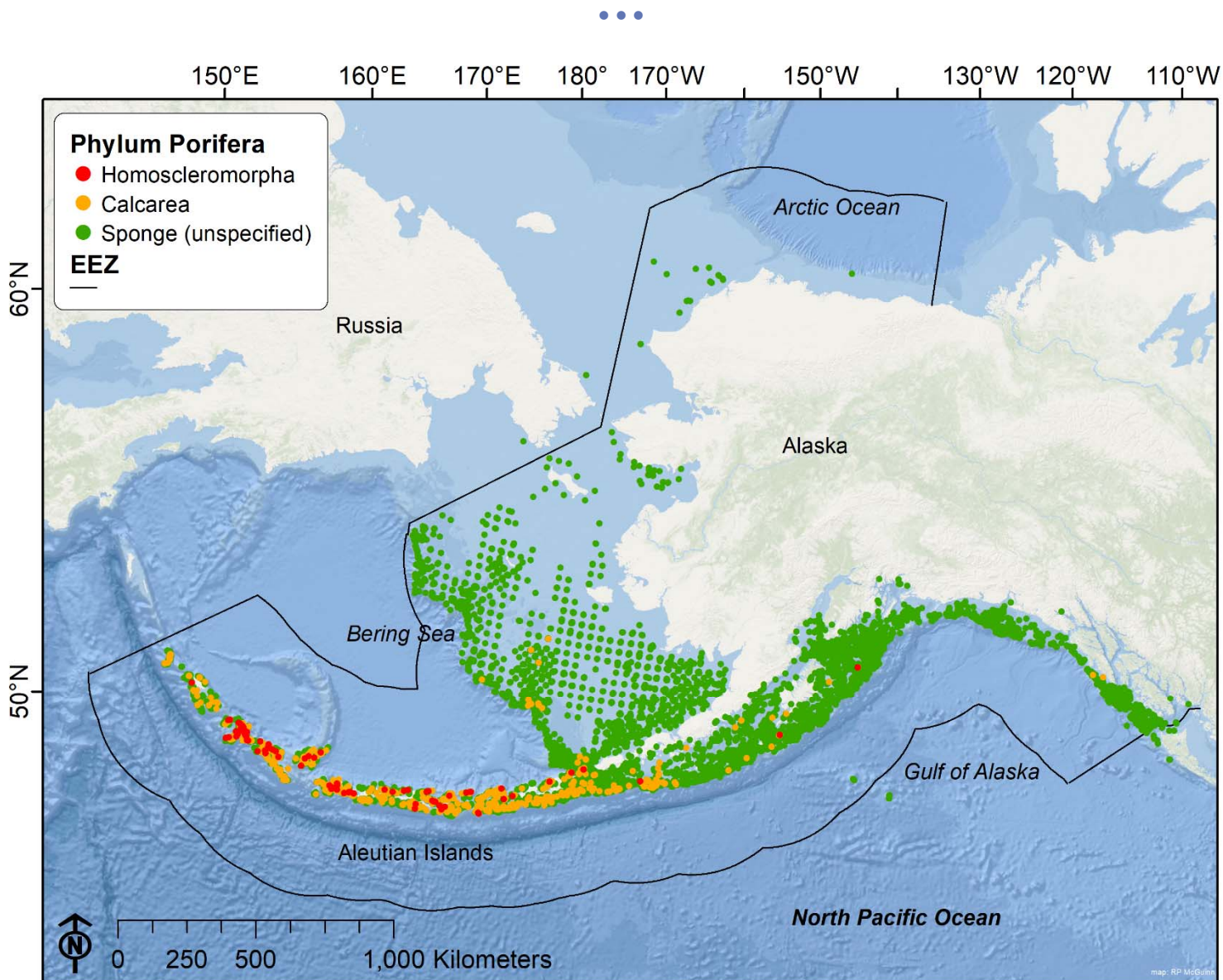
Map 7. Location of demosponges (Phylum Porifera) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



Map 8. Location of glass sponges (Class Hexactinellida) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE ALASKA REGION



Map 9. Location of calcareous (Class Calcarea) and unidentified sponges (primarily from trawl surveys) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).

Large red tree coral caught as bycatch in a bottom trawl survey off Alaska.





EFFECTS OF FISHING GEAR ON DEEP-SEA CORALS AND SPONGES IN U.S. WATERS

I. Introduction

Since the 1996 amendment of the Magnuson-Stevens Fishery Conservation and Management Act (MSA), there have been extensive efforts to identify and protect essential fish habitat (EFH). The 2007 MSA reauthorization further provided discretionary authority to protect areas containing deep-sea corals, recognizing these corals in their own right. Beginning around 2005-2007, management authorities in some regions of the U.S. acted to protect deep-sea corals and sponges. These species are slow-growing (Leys and Lauzon 1998, Stone and Wing 2001, Andrews et al. 2002, Prouty et al., this volume), comprise habitat for other species, and may take a long time to recover from damage (Gutt and Piepenburg 2003, Rooper et al. 2011). They are often damaged by mobile bottom-contact fishing gears, such as bottom-trawls (Chuenpagdee et al. 2003), and to a lesser extent by fixed-location gears, e.g. bottom longlines and bottom-set nets (Lumsden et al. 2007, Fuller et al. 2008). The 2007 report on the State of the Deep Coral Ecosystems of the United States notes that use of bottom-tending gears, especially bottom-trawls, is the largest threat to deep-sea coral communities (Hourigan et al. 2007). The report advocates further research on the effects of fishing on deep-sea corals to inform management decisions. This research priority was extended to sponges in NOAA's Strategic Plan for Deep-Sea Coral and Sponge Ecosystems (NOAA 2010). Here, we briefly summarize the known interactions between fishing gear and deep-sea corals and sponges in U.S. waters.

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II. Recent Developments in Research and Management

The effects of fishing gear on deep-sea corals and sponges are of considerable interest to fishermen, scientists, managers, environmental groups, and the general public. Since the 2007 report on the State of the Deep Coral Ecosystems of the United States, there have been efforts to:

- 1) Study the effects of mobile and fixed-location fishing gears on deep-sea corals and sponges;
- 2) Close areas where fishing may impact deep-sea corals and sponges; and
- 3) Modify fishing gears and practices to protect deep-sea corals and sponges.

Identifying areas where fishing overlaps the presence of deep-sea corals and sponges requires knowledge of fishing locations and deep-sea coral occurrences. Fishing locations are obtained from vessel monitoring systems (e.g., SAFMC 2010, 2013), logbooks or on-board observers. Coral and sponge occurrences are from observations and bycatch data for sponges and corals collected by the National Marine Fisheries Service (NMFS) observers (NMFS 2011, 2013) and bottom-trawl surveys (Clarke et al., this volume, Stone and Rooper, this volume). However, not all fisheries include observers, and not all observers collect bycatch data on corals and sponges (e.g. Packer et al., this volume). Yet bycatch data, anecdotal observations, and the spatial and depth overlap of fishing operations show that in all U.S. regions, some fishing is conducted in areas with deep-sea corals and sponges (Hourigan et al. 2007, NMFS 2011, NMFS 2013).

Based on these types of bycatch data, models have been developed that predict the

distribution of deep sea corals and sponges (Bryan and Metaxas 2007, Sigler et al. 2015, Guinotte et al., this volume, Packer et al., this volume). These models can help identify areas of overlap of sensitive invertebrates with fishing activity. However, many of these models are for small areas, have coarse spatial and taxonomic resolutions, and are insufficiently informed by observation data.

II.1. Mobile Bottom-Contact Fishing Gear

In U.S. waters, bottom-trawls are used on the continental shelf and upper slope, typically shallower than 500 m depth. In other regions of the world, bottom trawls are also used in deeper continental slope waters (Roberts 2002, Norse et al. 2012, Clark et al. 2016).

The effects of mobile bottom-contact fishing gear on deep-sea corals are well documented (reviewed by Clark and Koslow 2007, Hourigan et al. 2007, Clark et al. 2015), but less so for their effects on sponges (Van Dolah et al. 1987, Freese 2001, Wassenberg et al. 2002, Austin et al. 2007, Hogg et al. 2010). Impacts include damage and removal of the organisms (Freese 2001, Hall-Spencer et al. 2002, NRC 2002, Reed et al. 2007), changes in community composition and productivity (Hiddink et al. 2006, Hixon and Tissot 2007), and broad-scale modification of geology (Puig et al. 2012). For example, in the Aleutian Islands, damage to corals increased with fishing intensity (Heifetz et al. 2009), with the highest damage to antipatharians (15%), hydrocorals (9%) and gorgonians (6%) (Stone 2014). Additionally, coral removal by bottom-trawls accounted for over 92% of observed coral bycatch in west coast fisheries (Whitmire and Clarke 2007).

In the Gulf of Alaska, a single pass of a bottom-trawl removed 1,000 kg of *Primnoa*



coral and detached 27% of the colonies (Krieger 2001). Cumulative removals of coral by bottom-trawling in Alaska, from 1997 to 1999, were estimated at 81.5 metric tons (mt) per year, totaling about 250 mt (NMFS 2004). More recently, the bycatch of corals (including sea pens and whips), bryozoans, and hydroids were reportedly 54 mt from 2003–2005 (NMFS 2011) and 35.6 mt in 2010 (NMFS 2013). Comparable figures for Alaskan sponge bycatch were 238 mt in 2003–2005 and 271 mt in 2010 (NMFS 2011, 2013).

NOAA has determined that year-round closures to mobile bottom-tending gear are particularly effective at protecting biogenic habitats comprised of deep-sea corals and sponges (NOAA 2010, Hourigan 2014). The world's first bottom-trawl fishing closure, specifically designed to protect deep-sea corals, occurred in 1984 at Oculina Bank, a Habitat Area of Particular Concern (HAPC) off eastern Florida. In 1986, the entire Exclusive Economic Zone (EEZ) surrounding the U.S. Pacific Islands was closed to bottom-trawls and bottom-set nets and longlines. The Western Pacific Fishery Management Council had previously identified bottom-trawling by foreign fishing fleets as a threat to the region's precious coral beds (Hourigan 2014).

Most other bottom-trawl closures have been enacted since 2005, primarily to protect EFH (Hourigan 2009, Hourigan 2014, Fig. 1). This includes bottom-trawl closures between 700 and 1,750 fth (1,280–3,200 m) on the west coast of the continental U.S., as well as 34 additional areas including biogenic habitats, banks, ridges, and canyons in March 2006. This management action protected 336,698 km² (130,000 mi²) of marine habitat in Washington, Oregon, and California of EFH for groundfish.

In the Southeast U.S., five new areas

containing *Lophelia pertusa* coral were closed to bottom-contact fishing in 2010, and these were expanded in 2015 to include newly identified coral areas. In the same year, the Mid-Atlantic Fishery Management Council became the first council to use the discretionary provision of Magnuson-Stevens Act to propose establishment of a deep-sea coral protection area encompassing more than 38,000 mi². The Deep Sea Coral Amendment¹ includes measures to restrict trawls, dredges, bottom longlines, and traps within the bounds of the protection area. Areas of the Aleutian Islands in Alaska were closed to mobile bottom-contact fishing gear in 2006 (NMFS 2010). This decreased the bycatch of corals and sponges under steady or decreasing fishing effort, until 2011 (NPFMC 2012). However, data collected through 2013 indicated an increase in bycatch of coral and sponges in the Aleutian Islands, possibly due to increased fishing effort for rockfish in the region.

The cumulative effect of these management actions between 2005 and 2010 was a six-fold increase in the total area of seafloor that restricts bottom contact fishing gear within the U.S. continental EEZ (Fig. 1). The majority of the area closures in the U.S. occurred in the Pacific and North Pacific Fishery Management Council regions, and comprised more than 1.35 million km² (530,000 mi²) of the U.S. EEZ. The cumulative area of these closures represents 22% of the continental US EEZ (2,401,232 mi²). For the most part, these closures have not been monitored to determine whether protections are effective in recovering, maintaining or increasing deep-sea coral diversity and abundance.

Modifications to mobile bottom-contact fishing gear to reduce bycatch (e.g., turtle and marine

¹ <http://www.mafmc.org/actions/msb-am16>

² https://en.wikipedia.org/wiki/Exclusive_economic_zone

EFFECTS OF FISHING GEAR ON DEEP-SEA CORALS AND SPONGES IN U.S. WATERS

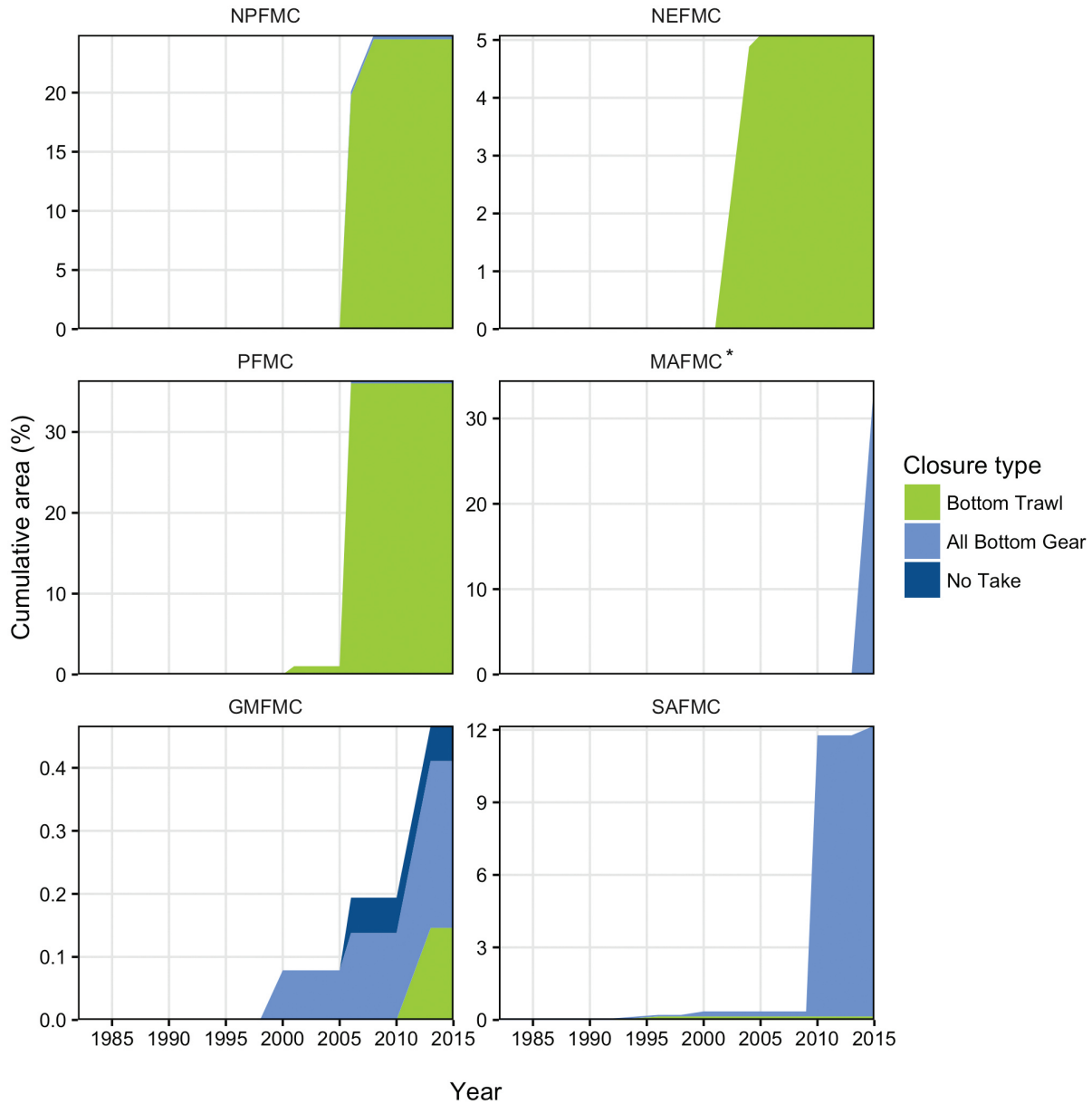


Figure 1. Cumulative areal extent of bottom closures by Fishery Management Council (FMC) region between 1982 to 2015 as a percent of EEZ in each region. Colors designate the closure type. US Regional FMCs are: GMFMC = Gulf of Mexico; SAFMC = South Atlantic; MAFMC = Mid-Atlantic; NEFMC = New England; NPFMC = North Pacific; PFMC = Pacific. The MAFMC closure (*) represents the deep-sea coral protection zones proposed in June 2015, covering 28,864 n mi². The Western Pacific Council (WPFMC) and Caribbean Council (CFMC) are not shown. The WPFMC protected the entire EEZ (1,499,972 nm²) under its jurisdiction from trawling and certain other bottom-contact fishing gears in 1983. Bottom-trawling does not occur in the CFMC region. The figure includes closures specifically designed to protect deep-sea corals and those using Essential Fish Habitat (EFH) authorities (NOAA 2011, Sutter et al. 2014). There are additional closures in place to reduce gear conflicts and other purposes, which may also protect deep-sea corals and sponges in such areas. Asterisk (*) indicates closures were proposed in 2015 and approved in 2016.

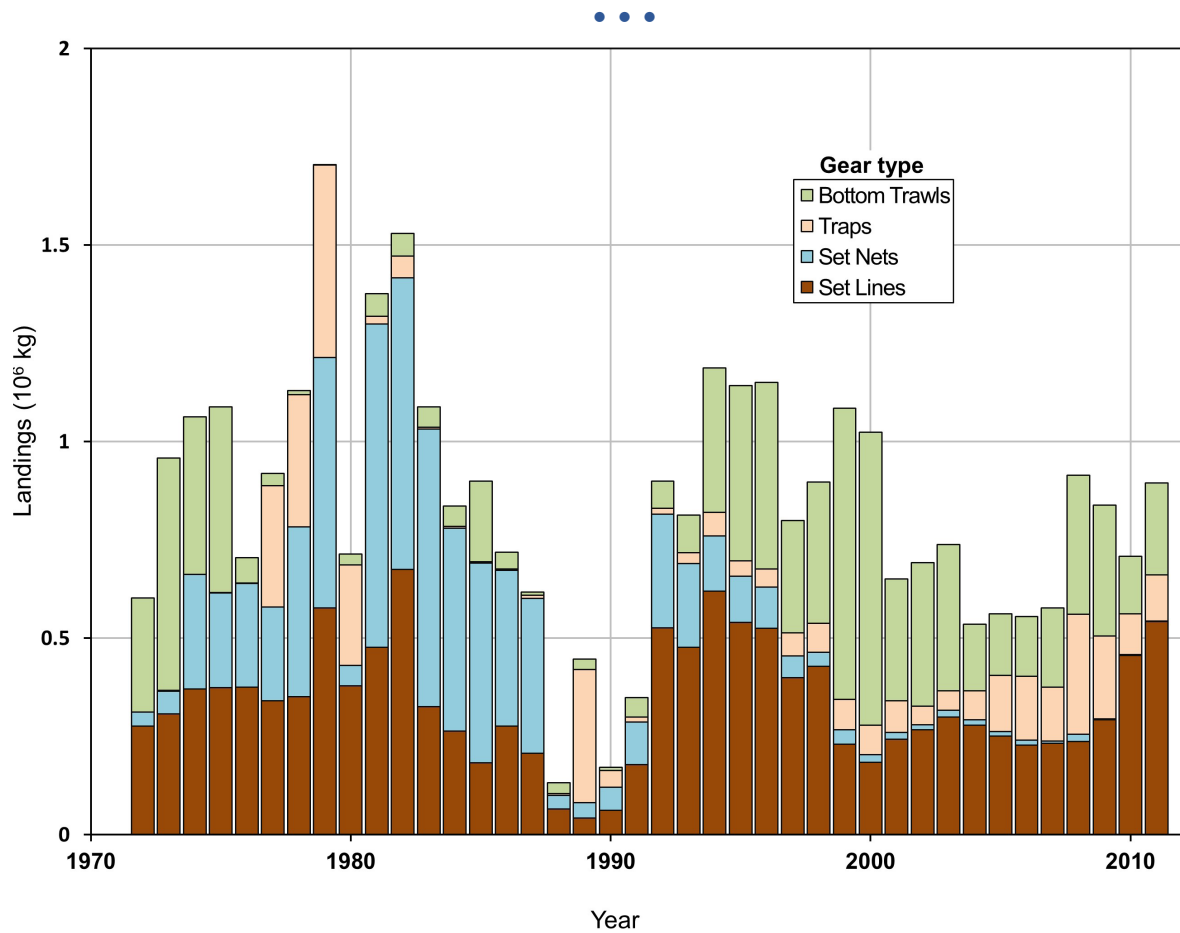


Figure 2. Commercial landings (millions of kg) of deep demersal species (> 50 m) in the Southern California Bight by gear type. Data are from California Department of Fish and Wildlife landings tickets (Perry et al. 2010; Perry et al. unpublished data) for select deep-water species codes during the time period 1972-2011.

mammal excluder devices) and negative impacts on the seabed (e.g., reducing footrope or roller size on bottom-trawls) have been an active area of research within NMFS. Some of the gear modifications and restrictions have the potential to reduce impacts on deep-sea corals and sponges. For example, in Alaska, NMFS scientists have been working with flatfish bottom-trawl fisheries since 2002 to reduce bycatch and mortality of crab and other benthic invertebrates in soft substrates without negatively affecting catches of target species (Rose et al. 2010a, Rose et al. 2010b, Rose et al. 2013). In those studies, the sweeps of bottom-trawls were raised off the seafloor using disk clusters spaced at 9-m

intervals along the trawl sweeps. This gear modification reduced crab mortality, since the modified sweeps passed over many of the crabs it encountered, but had no significant effect on flatfish catch. Additionally, these gear modifications reduced, by almost half, the damage to sea pens under the path of the trawl gear (Rose et al. 2010a). Working closely with the fishing industry and the North Pacific Fishery Management Council, new regulations were implemented in 2011 that required bottom-trawl sweep modifications in the eastern Bering Sea flatfish fishery. On the U.S. west coast, where footrope size restrictions were instituted to reduce catches of rockfish species (*Sebastes* spp.), trawl fishing effort has



shifted away from rugose habitats known to support corals and other sensitive benthic invertebrates (Bellman et al. 2005).

II.2. Fixed Bottom-Contact Fishing Gear

In addition to mobile fishing gear, there are many types of fixed gear used in commercial fishing, including traps or pots, bottom-set nets, and longlines. Fixed gears are typically deployed in a wide range of depths, including depths > 1,000 m. Most of these gears are in contact with the seafloor when fishing, and are often used in areas, such as rocky reefs. These areas may be most important for deep-sea corals and sponges that rely on rocky substrates for attachment.

In some areas, fixed-gears account for considerably more landings than mobile gears. For example, according to California Department of Fish and Wildlife (CDFW; formerly California Department of Fish and Game) annual landings reports (Perry et al. 2010), the total landings by traps, set lines, and set nets in southern California can outweigh landings by bottom-trawls, especially in recent years (Fig. 2). Nearly 64% of recent (2007-2011) deep-water demersal landings from Southern California are from fixed gears (longlines and pots) for sablefish, thornyhead, hagfish, and spot prawn. The remaining 35% from mobile gear were predominantly soft sediment fisheries for sea cucumber and sole (Perry et al. 2010, Etnoyer et al. 2013). Fishing with fixed-gear (Fig. 3A) is often conducted further offshore, over a wider portion of the continental shelf and slope than mobile gear (Fig. 3B), yet probably covers a smaller cumulative area (e.g., NMFS 2005).

Off southern California, and likely elsewhere, fixed-gear fisheries that target deep-water

demersal species operate within the depth ranges of deep-water corals and sponges with the potential for negative interactions where overlap occurs. Fixed fishing gears can interact with corals in several ways. Pots and traps can be dropped directly on top of colonies, or dragged on the bottom during deployment and recovery. Nets can snag on rocks, or be cut loose during storms. Longlines may become entangled during recovery, or when hooked fish struggle. Incidentally, museum specimens of the precious *Corallium* coral were retrieved by longline fisheries surveys off the Azores in 2005 (Sampaio et al. 2009). In the U.S. Pacific Northwest, *Paragorgia arborea* was toppled and wrapped in longlines in the Olympic Coast National Marine Sanctuary (Brancato et al. 2007) (Fig. 4A). Derelict fishing gear has also been caught on coral in other areas, such as Southern California (Fig. 4B-D), Gulf of Mexico mesophotic reefs (Etnoyer et al. 2015), Nova Scotia, Canada (Mortensen et al. 2005), and in parts of the northeast Atlantic Ocean (Sampaio et al. 2012).

There are, however, few peer-reviewed studies that rigorously examine the effects of fixed-gear fisheries on deep corals and sponges. A recent study of small-scale, shallow (< 25 m) artisanal fisheries in Mexico found that bycatch rates were negligible for traps and gillnets – less than 0.5 kg (0.12 kg of gorgonians and 0.37 kg for sponges) for each \$1,000 of revenue generated by the fishery catch – while bycatch rates of habitat-forming invertebrates (as a percentage of total catch) were ~20% for set gillnets and close to zero for traps (Shester and Micheli 2011). Damage and removal of 17% of shallow-water gorgonian corals within a meter of a set net was observed, while damage was minimal and removals were zero for traps. Although the impacted areas were relatively small for these gear types, the cumulative impact may

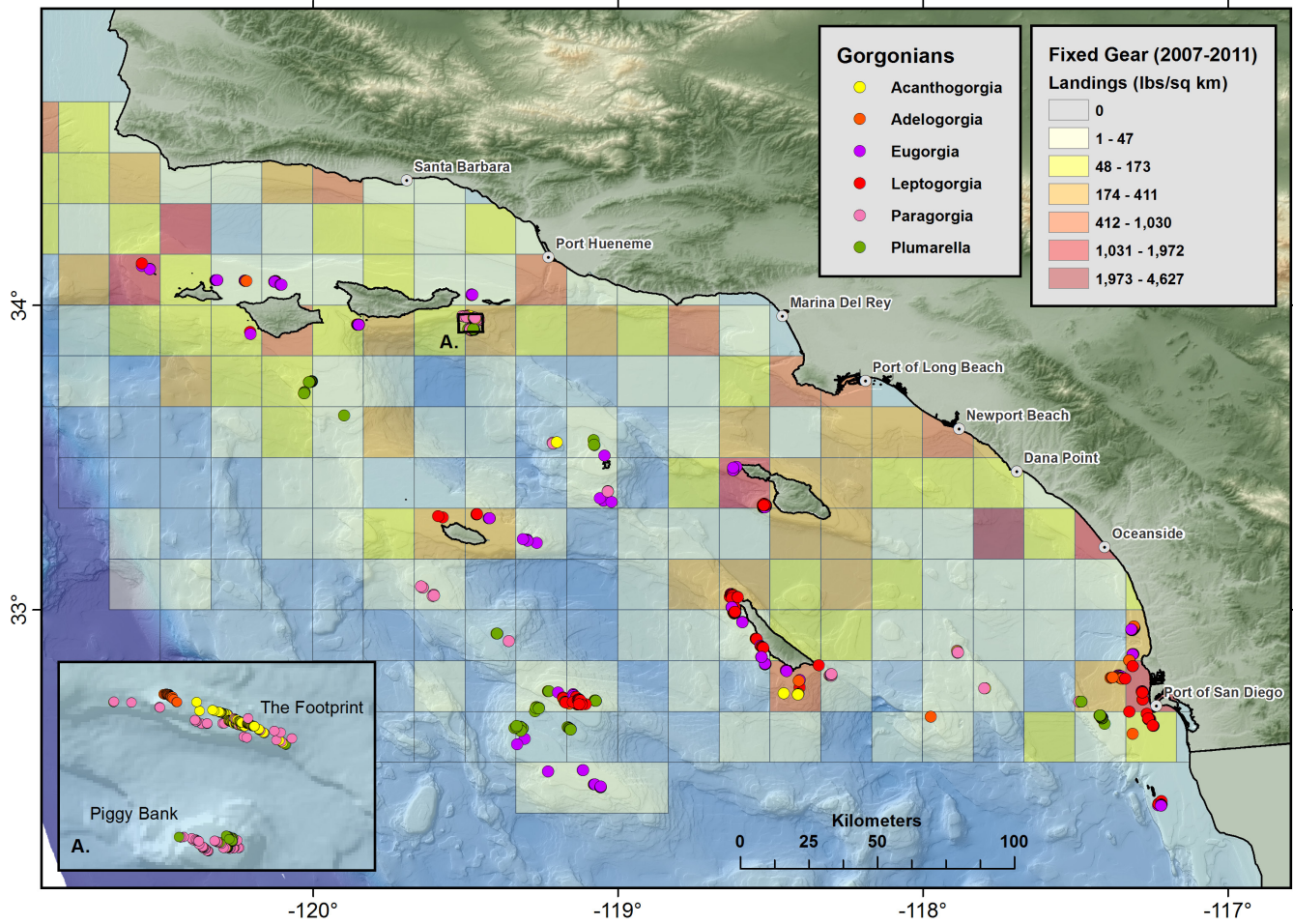


Figure 3A. Distribution of demersal landings between 2007 and 2011 for deep-water fixed gear fisheries from California Department of Fish and Wildlife catch blocks in the southern California Bight (Perry et al. 2010; Perry et al. unpublished data). Also shown are the locations of gorgonian octocorals observed during remotely operated vehicle surveys since 2006 (NOAA 2015).

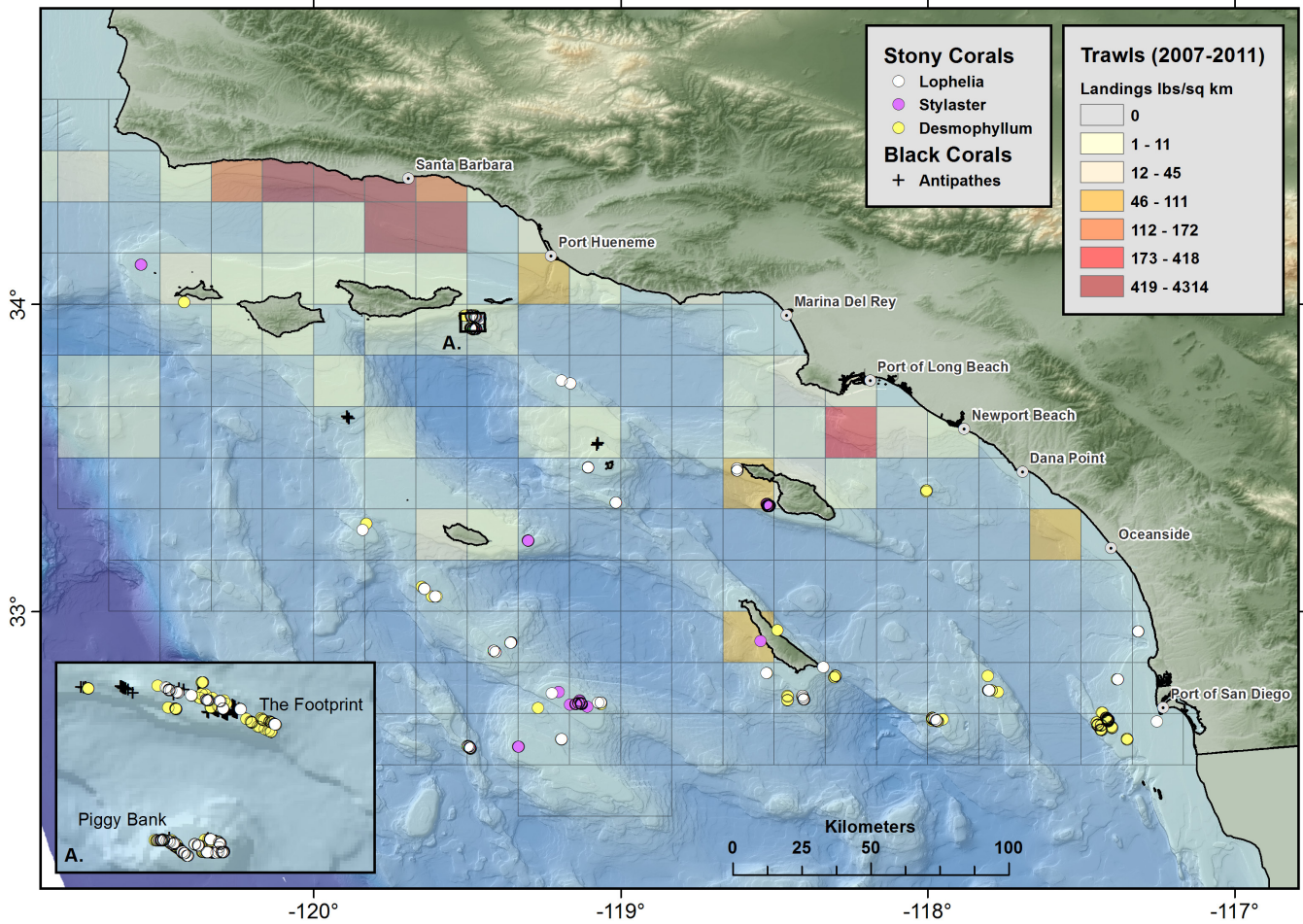


Figure 3B. Distribution of demersal landings between 2007 and 2011 for deep-water bottom-trawls from California Department of Fish and Wildlife catch blocks in the southern California Bight (Perry et al. 2010; Perry et al. unpublished data). Also shown are the locations of stony corals from surveys since 2006 (NOAA 2015).

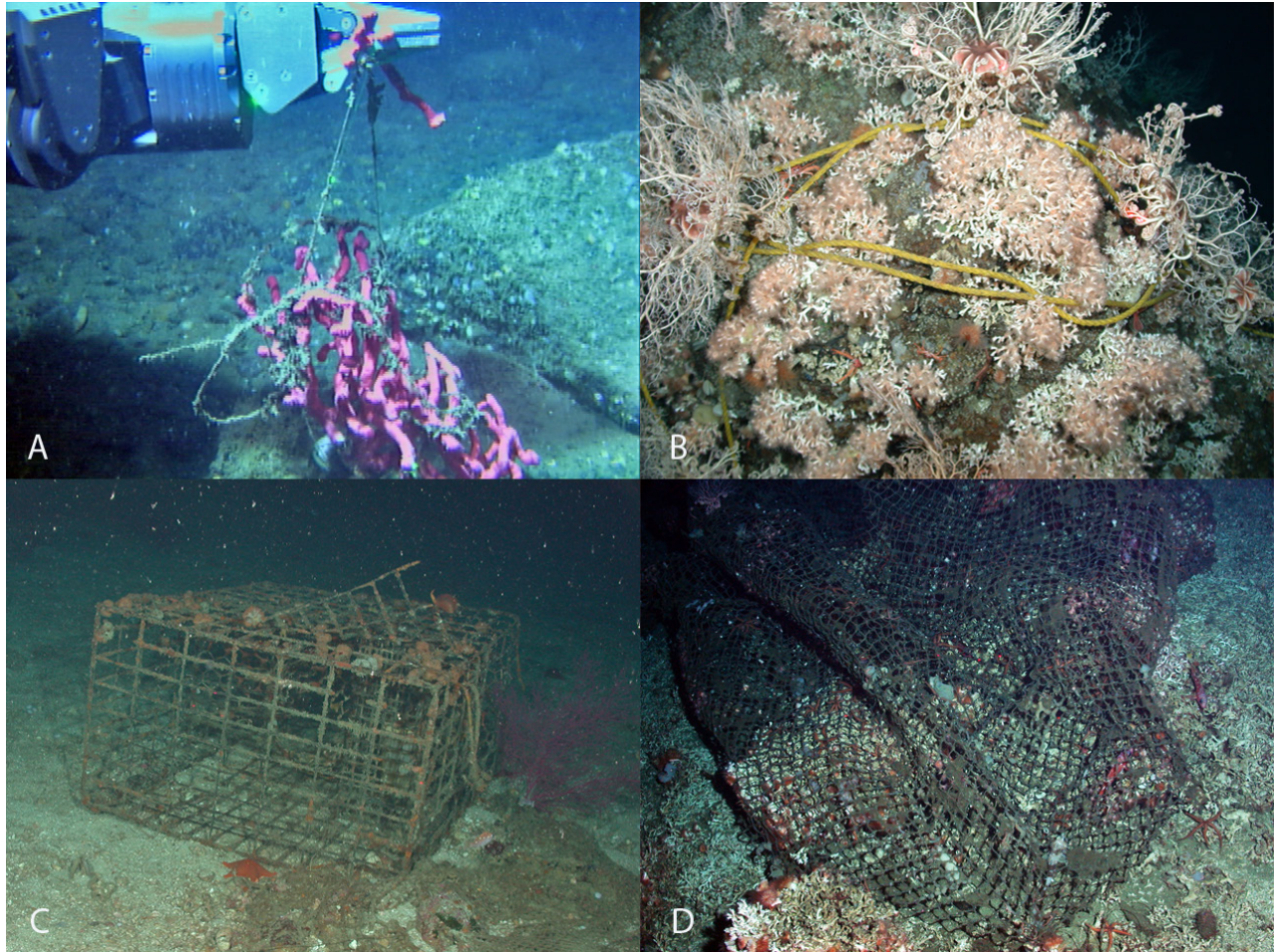


Figure 4. Images of longline and trap gear from remotely operated vehicle surveys on the US West Coast: A) Bubblegum coral (*Paragorgia arborea*) entangled in longline gear at ~200 m depth in Olympic Coast National Marine Sanctuary (OCNMS; Brancato et al. 2007); B) Scleractinian coral (*Lophelia pertusa*) colonies with yellow polypropylene line, possibly from an anchor line, or a buoy line on fixed gear; C) trap gear (center) and netting (lower right) adjacent to a purple sea fan (*Eugorgia rubens*); and D) a section of mesh from a trawl net wrapped around *Lophelia pertusa* rubble. Photo A is courtesy NOAA OCNMS. Photos B-D are courtesy of NMFS, Southwest Fisheries Science Center.

be substantial given the large number of participants in the fisheries. In the Atlantic Ocean off Canada, a review of observer data indicated that the rate of coral occurrence in longline sets (13%) was higher than that of either gillnets (7%), trawls (4%), or crab pots (0%) (Edinger et al. 2007).

In the U.S., much of the data on bycatch rates for fixed gears comes from fishery-independent surveys. For example, the catch rates for gorgonian corals in the Alaska

longline survey that operates annually at stations on the slope of the eastern Bering Sea suggest very low rates of bycatch for corals and sponges (~2-4 coral colonies or sponges per station occupied by the survey, Fig. 5).

Although some anecdotal evidence exists, there is generally less data available from U.S. fisheries to compare damage rates to coral and sponge habitat by fixed and mobile fishing gear. The most comprehensive study to date looked at damage rates in areas of

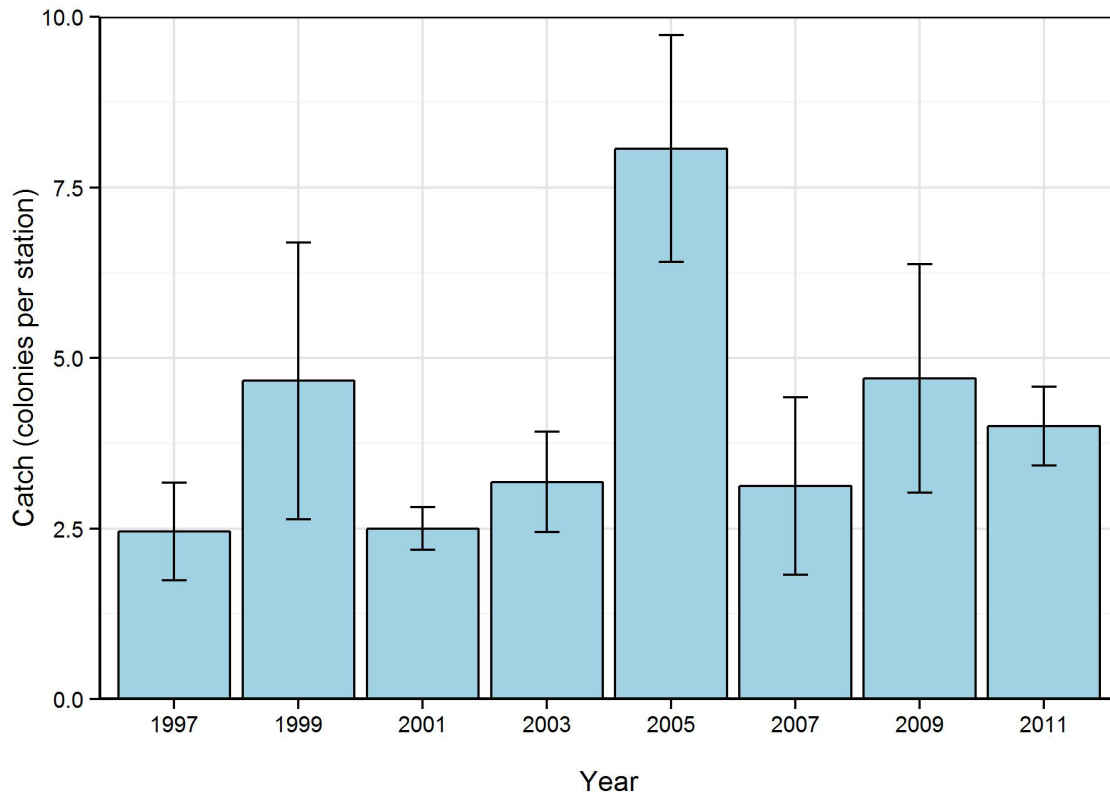


Figure 5. Catch (mean number of colonies \pm SE) of coral and sponge taxa in the Alaska Fisheries Science Center biennial longline survey of the eastern Bering Sea continental slope from 1997-2011. Data are available from the Alaska Fisheries Information Network (AKFIN, www.akfin.org).

the central Aleutian Islands that were only fished with fixed gear (pots and longlines) and found damage rates to be higher, but not significantly higher than damage rates in unfished areas (Heifetz et al. 2009). Removals of corals and sponges in Alaska by longline fisheries between 2003 and 2005 were estimated at 14 mt and 6 mt respectively, but these values constituted a minor fraction of the target species catch (NMFS 2011). Removals by pot fishing accounted for a negligible amount of coral bycatch and only 1 mt of sponge removal during the same time period.

Removals of corals and sponges by fixed gears occur in other regions as well, but some of the evidence is anecdotal. For example, bamboo corals (*Isidella* sp.) have been reported in sablefish pots off California (S. Risherman,

Marine Applied Research and Exploration, pers. comm.). *Paragorgia* bubblegum corals have been observed decorating the ceilings of salmon shacks in Neah Bay, Washington (P. Etnoyer, pers. obs.). Large black corals have been retrieved from trawl nets in Alaska, then polished and carved into decorative artifacts or jewelry (P. Etnoyer, pers. comm.).

In some places, derelict fishing gear may also damage deep-sea corals and sponges. During a rockfish study in the Aleutian Islands in 2004, a juvenile rockfish was observed residing in a tangle of derelict longline gear (Rooper et al. 2007). During that study, 4.29 ha of seafloor was observed with an underwater video camera and three separate observations of derelict longline gear were observed among corals and sponges.



Observations from remotely operated vehicles (ROVs) of derelict fixed gear in areas with deep-sea corals and sponges have also been documented in the northern Gulf of Mexico, where injuries to gorgonian octocorals were attributed to the snapper and grouper fisheries that comprise the reef-fish fishery (Etnoyer et al. 2015).

In the U.S., many areas have been closed to fishing to reduce the impacts of fixed gears on seabed habitats. For example, fifteen seamounts off the U.S. west coast and Alaska have been closed to all bottom-contact fishing gears since 2006, and a total of 7,020 m² were restricted. Other examples include “Piggy Bank” and “The Footprint” essential fish habitat area in the Channel Islands National Marine Sanctuary, which harbors abundant coral and sponge species (Yoklavich et al. 2011, 2013), that are now protected from bottom fishing of all types. Still, enforcement of these restrictions remains a challenge (C. Mobley, NOAA pers. comm.).

In a review of the impacts of gear on sensitive seabed habitats in the Southeast U.S., Barnett (2001) recommended excluding the use of bottom longlines in the vicinity of coral reefs due to their potential for entanglement. In this region, the use of bottom longlines, pots, and traps, as well as mobile gears is not allowed in the Oculina Banks HAPC, as well as in the larger deep-water Coral HAPCs, except in Golden Crab Allowable Fishing Areas or Shrimp Fishery Access Areas. We are not aware of any efforts to modify fixed bottom-contact gear to reduce their impacts.

III. Rationale for Closures

It is important to recognize that most, if not all of the management actions and research on the interactions between fisheries and

sensitive fauna have aimed to protect corals and sponges while maintaining or enhancing existing fisheries. In some cases, such as with Oculina Banks and the *Lophelia* reefs in the southeast U.S., the reef-like structure provided by a single coral species has been the impetus for protection measures. In others, such as the “coral gardens” in Alaska, management actions have focused on groups of taxa (such as groups of corals and sponges separately) rather than trying to protect an area for a particular species. Corals and sponges have also benefitted from research and management actions that were driven by management issues for other species. For example, trawl modifications to reduce bycatch of overfished species (as in the west coast footrope restrictions example above) or non-target species (as in the Alaska crab example above).

In the Gulf of Mexico, *Lophelia* reefs provide habitat for golden crab (*Chaceon fenneri*), which is fished using traps strung together and recovered from the seafloor by grappling hook. The deep-sea red crab (*Chaceon quinquedens*) can aggregate in large colonies of *Madrepora oculata* as deep as 1,000 m in the Gulf of Mexico (Boland et al., this volume). The fisheries for these species are not well developed in the Gulf of Mexico, but they do represent an emerging concern. The South Atlantic Fishery Management Council designated allowable fishing areas for golden crab pot fisheries during the establishment of Deepwater Coral HAPCs.

IV. Knowledge Gaps and Future Challenges

In most regions of the U.S., methods have been developed and employed to study the effects or anticipated effects of mobile bottom-tending fishing gear. Most of this



knowledge has been gained in response to the EFH management mandate under the 1996 amendment of the MSA, which emphasizes an ecosystem approach to management. In the last five years, the NMFS, in partnership with the fishing industry, has better characterized where fishing with bottom-tending gears is likely to occur. The extent that fishing overlaps with deep-sea coral and sponges is determined by the distribution of these organisms and fishing effort. For fisheries with observer programs, additional information on the locations and amounts of bycatch can provide some indication of the extent of interactions between fishing gear and these organisms. There is little information, however, on the relationship between bycatch observed on the vessel and the actual impact or encounter rates with corals and sponges on the seafloor. These impacts will vary among gear types, species assemblages, and seabed types. However, the effects of fixed gear on corals and sponges are poorly studied in most regions.

A better understanding of the effects of fixed fishing gear on deep corals and sponges will come as more available data on the spatial extent contacted by this gear during fishing is revealed. With this information, the footprints of the various fixed gear types, and thus the area of the impacted seafloor can be calculated. There are also estimates of the bycatch of deep-sea corals and sponges from fishing gears from mandatory observer programs in Alaska (NMFS 2011). Still unknown is the performance of the gear during setting, fishing, and retrieval, and the amount of derelict gear that remains on the seafloor. We need to better understand the interactions between deep demersal target species, the gear types being used to fish them, and the types of corals and sponges occurring in fishing areas before we can develop optimal measures to protect these sensitive ecosystems

while maintaining sustainable fisheries.

A second unknown is the degree to which the closed areas aid the recovery of damaged deep corals and sponges. Few studies quantify the densities, diversities, and distributions of deep-sea corals and sponges before and after areas are closed. Althaus et al. (2009) studied stony coral habitats and associated megabenthic invertebrate assemblages on seamounts off Tasmania and found no clear signal of recovery after five years for habitats damaged by bottom-trawling; invertebrate communities remained impoverished, comprising fewer species at reduced densities than untrawled areas. Similarly, Williams et al. (2010) found no evidence of recovery in trawled seamount areas 5-10 years after protection in Australian and New Zealand. They concluded that the resilience of seamount ecosystems, dominated by corals, is low compared to most other marine systems disturbed by bottom-trawling. Studies to determine how quickly damaged ecosystems on the continental shelf and slope of the U.S. recover after a closure could inform optimal strategies for protecting areas and monitoring recoveries.

V. Future Research and Technology

Studies are needed that research pot and longline gear dynamics during deployment, fishing, and retrieval operations. These studies should be based on direct observation, remote sensing, or both. A number of new technologies may provide direct observations. Cameras on ROVs have been used to observe longline gear during fishing activities, but not during deployment or retrieval (K. L. Yamanaka, Department of Fisheries and Oceans, Canada, pers. comm.). Advances in camera technologies have also facilitated

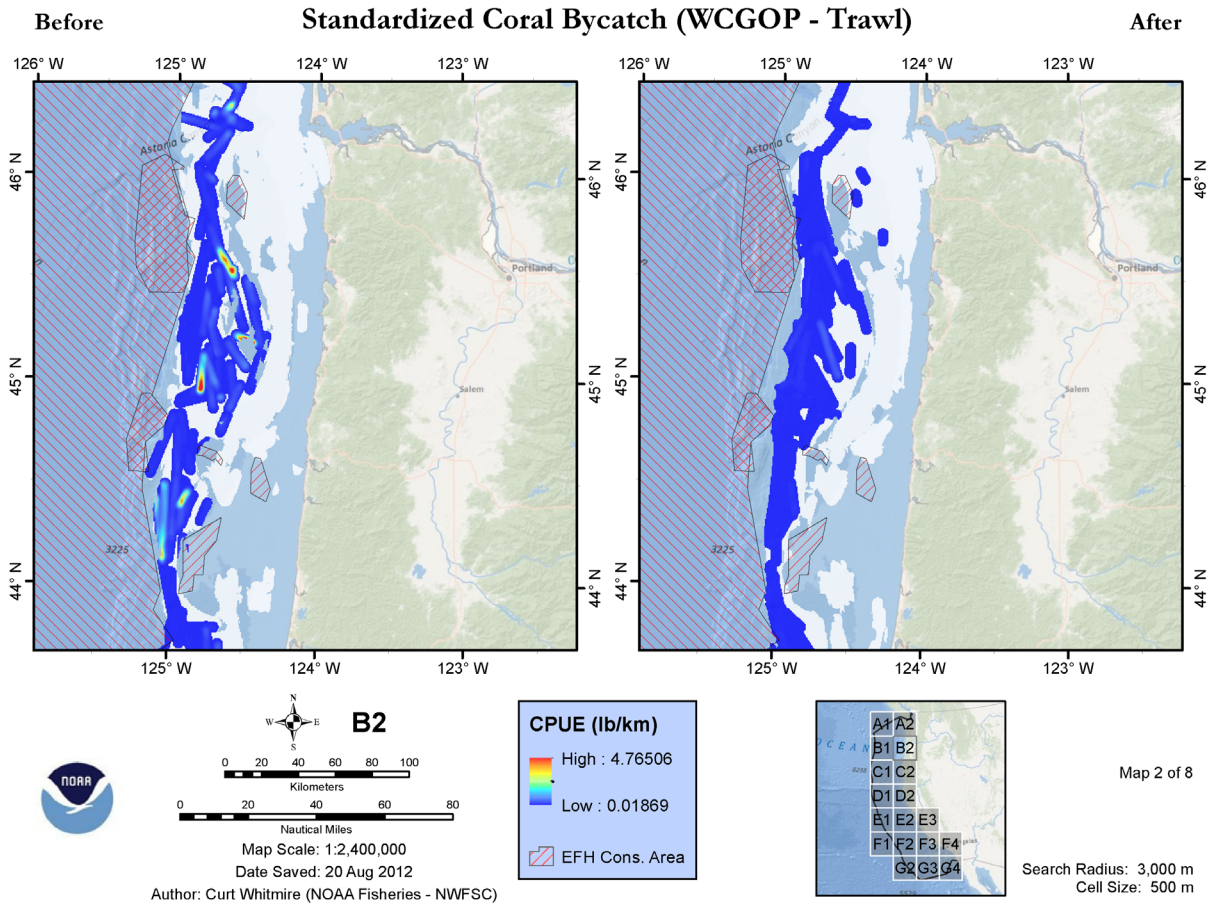


Figure 6. Coral bycatch (lb./km fished) from west coast trawl fisheries offshore Oregon state before (1 Jan 2002 - 11 Jun 2006) and after (12 Jun 2006 - 31 Dec 2010) essential fish habitat closures (PFMC 2012).

observations. For example, researchers in the Australian Antarctic Division developed a camera system to collect video images periodically during longline deployments and retrievals (Kilpatrick et al. 2011). A modified version of the camera system is being developed at the Alaska Fisheries Science Center to deploy on commercial longline and pot gear. The intention is to collect stereoscopic images to measure objects and fish, and estimate the area that is contacted by the fishing gear during setting, deployment, and retrieval.

Multiple studies examined changes in coral and sponge communities in closed areas

where trawling previously occurred (e.g. Freese 2001, Heifetz et al. 2009). In the Gulf of Alaska, there was no indication of sponge recovery after experimental trawling when the damaged sites were revisited a year later. These sites should be sampled on appropriate time and space scales to evaluate the recovery processes and periods. Following area closures off Oregon, the bycatch of coral appears to have declined for some fisheries (Fig. 6). However, it is unclear if bycatch reductions are due to area closures, gear restrictions, changes in abundances and distributions of coral and target species, or other factors that may influence fishing behavior (PFMC 2012). Few studies have examined differences in



the community structure of deep-sea corals and sponges “before and after” area closures, or demonstrated how long and how many of these closures are needed to maintain the ecosystem services that deep-sea coral and sponge ecosystems provide.

VI. Conclusion

Since publication of the report on the State of Deep Coral Ecosystems of the United States in 2007, there have been a limited number of studies of the effects of fishing activity on deep-sea corals and sponges. In the U.S., most studies have focused on the effects of mobile fishing gear. However, studies are also needed on the likely, but perhaps lesser, effects of fixed-gears. Information from observer programs and scientific surveys have been instrumental in the identification of areas where high coral and sponge bycatch is occurring and for designating closed areas. Bycatch of non-target species has driven the development of fishing gear modifications, which has reduced their impacts on deep-sea corals and sponges.

VII. Acknowledgements

Thanks to Curt Whitmire, Janet Mason, Wayne Palsson, David Demer, and Gerard DiNardo for helpful reviews of this manuscript. Stephanie Nehasil conducted the analysis of CDFW landings data used to create Figure 3. Thank you to Chris Lunsford and Cara Rodgveller for providing data from the AFSC longline survey, to Enrique Salgado for assistance with Figures 2, 3, and 4; John Butler and the SWFSC ROV team collected the images used in Figure 4. Special thanks to Catherine Polk for her gracious assistance with the document layout.

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Yellow Picasso sponge and white sponges on Davidson Seamount.
Courtesy of NOAA/MBARI.





STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. WEST COAST

1. Introduction

The U.S. Pacific coast marine region encompasses the continental margin off the coasts of Washington, Oregon, and California, and accounts for about 7% (778,628 km²) of the total area of the U.S. Exclusive Economic Zone (EEZ). The continental margin in this region is characterized by a relatively narrow (5-40 km) shelf and a steep continental slope, with the shelf break at approximately 200 meters water depth. This area is wholly within the California Current Large Marine Ecosystem (LME). The California Current LME is a transition ecosystem between subtropical and subarctic water masses and is characterized by seasonal upwelling. It encompasses portions of two marine biogeographic provinces – Oregon (cold-temperate) and California (warm-temperate [formerly San Diego]) – with a boundary between Point Conception and Los Angeles, CA (Allen and Smith 1988, McGowan 1971, Briggs and Bowen 2012). Relatively large estuaries border the area, including those associated with the Puget Sound, Columbia River, and San Francisco Bay. Fishing for salmon, groundfish, small coastal pelagic species, highly migratory species, and invertebrates (most notably squid, crab, shrimp, and sea urchins) is significant throughout this region.

Deep-sea corals and sponges are found throughout the area (Austin et al. 2007, Lee et al. 2007, Whitmire and Clarke 2007). Much of the information on the general zoogeography of corals in the region originated from taxonomic records collected from bottom trawl

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*Rockfish sheltering in a
glass sponge
(Aphrocallistes sp.) near
Grays Canyon off the coast
of Washington.*



surveys over the past century. Sea pens, black corals, and gorgonians were recorded coastwide in the catch of bottom trawl surveys and by fishery observers monitoring bycatch during commercial fishing operations. Our understanding of the distribution of corals has been informed by visual surveys using underwater vehicles (e.g., submersibles, remotely operated vehicles [ROVs] and autonomous underwater vehicles [AUVs]).

Whitmire and Clarke (2007) reported 101 species of corals from six cnidarian orders from the West Coast region. They highlighted significant coral communities at Davidson Seamount (DeVogelaere et al. 2005), Monterey Canyon, Cordell Bank (Pirtle 2005), the Olympic Coast National Marine Sanctuary (Hyland et al. 2005, Brancato et al. 2007), and on numerous rocky banks off southern California (Yoklavich and Love 2005, Tissot et al. 2006, Love et al. 2007).

Major stressors on deep-sea coral communities off the Pacific Coast included oil and gas development in the Southern California Bight, deployment of pipelines and communication cables, and marine pollution. Fishing operations, particularly bottom trawling, were identified as the most immediate and widespread threat to these communities. The risk posed by fishing activities was reduced by fishery management measures (e.g., area closures such as marine protected areas (MPAs) and gear restrictions) taken before 2007. In June 2006, the Pacific Fishery Management Council (PFMC), in cooperation with NMFS, implemented a comprehensive plan to protect

essential fish habitat (EFH) for west coast groundfish (PFMC 2005, 2006). This plan identified habitat areas of particular concern (HAPCs) that protect vulnerable biogenic habitats. The plan was developed in collaboration with non-governmental organizations, the fishing industry, and the National Marine Sanctuary Program, and addressed impacts from a broad range of human activities (fishing and non-fishing) and included procedures for review as new information became available.

As of 2007, MPAs were distributed along the length of the Pacific coast in both federal and state waters. Over 130,000 mi² (336,700 km²) had been designated as MPAs fully protected from impacts from bottom trawls, with selected vulnerable habitats protected from all fishing gears that contact the bottom. Additional MPAs and fishery closures were designated by the individual states, including bottom trawl prohibitions for the entire portion of Washington state waters and most of California state waters. Furthermore, there are five national marine sanctuaries in the region, all of which prohibit activities that may be harmful to corals, including but not limited to 1) new oil, gas or mineral exploration, development and production, 2) discharge of materials or substances except fish parts, bait, water or other biodegradable effluents, and 3) alteration of the seabed except for normal fishing activities and anchoring.

In this report, we highlight new scientific information on deep-sea corals uncovered since the 2007 report, and outline new management



measures that help protect these organisms on the Pacific coast. We also include new information on deep-sea sponges, which were not previously addressed in the 2007 report.

II. Update on Scientific Information

II.1. New Research – Overview

Several new studies on both deep-sea corals and sponges were initiated or completed since 2007 by researchers from NOAA and a variety of collaborative institutions. This includes research funded by NOAA's Deep Sea Coral Research and Technology Program, other targeted studies conducted by academic and non-governmental institutions, and work aboard ships of opportunity, all of which has yielded valuable information about corals, sponges and their habitats. The program also supported analysis of archived video or photographic surveys to assess the occurrence of deep-sea coral and sponge habitats. There also has been an expansion of regional bathymetric mapping of the seafloor (PFMC 2012), and of new methods to predict suitable habitats for corals. In addition, considerable attention has been given to the genetics of corals, which will assist in their identification and taxonomy. Opportunistic data collections continue, with coral and sponge specimens taken in the annual west coast groundfish bottom trawl survey and by observers monitoring the groundfish fishery.

New field research on deep-sea coral and sponge communities has been conducted coast-

wide, with many study sites located in and around the five national marine sanctuaries (Figure 1; Appendix Table A). Additional field expeditions, while not specifically targeting corals or sponges, also have provided information on these taxa.

II.1.i – NOAA's Deep Sea Coral Research and Technology Program

In 2010, NOAA's Deep Sea Coral Research and Technology Program launched a research initiative on the U.S. West Coast to locate, study, and provide information for the conservation of deep-sea coral and sponge habitats. The initiative was developed in consultation with the PFMC and targeted information that could inform management. Field research was conducted at various sites in and around four national marine sanctuaries and in sponge habitats offshore of Grays Harbor, Washington as well as at seamounts in Canadian and international waters to further the understanding of biogenic habitats and associated fishes (Figure 1). These areas were chosen based on expected suitability for deep-sea coral or sponge habitats and their potential to inform sanctuary management plans and the PFMC's five-year review of groundfish EFH. The field research, originally planned for three years (2010-2012), was extended to 2014 and has made substantial progress.

During this West Coast initiative, field research addressed one or more of the following specific goals:

1. Locate and characterize coral and sponge habitats, including the following:



- a. Collection of baseline data on abundance, size, condition, and distribution of deep-sea corals and sponges;
 - b. Mapping of targeted seabed and collection of environmental data associated with coral and sponge habitats (e.g., depth, sea floor substratum types, seawater temperature, salinity, pH, and dissolved oxygen) to help understand habitat factors that may influence species distribution.
2. Quantify fish and invertebrate associations with corals and sponges to help understand their potential value as habitat.
 3. Assess the condition of coral and sponge assemblages in relation to potential anthropogenic or environmental disturbances.
 4. Collect specimens of deep-sea corals, sponges, and associated organisms to confirm taxonomic identifications, and for genetic and reproductive analyses.

Program-funded surveys were conducted using remotely operated vehicles (ROVs), human occupied vehicles (HOVs), and an autonomous underwater vehicle (AUV). Observations of corals and sponges are being incorporated into NOAA's National Database for Deep-Sea Corals and Sponges.

II.1.ii – Additional field research

Researchers at a number of institutions conducted studies that contribute to our knowledge of deep-sea corals off Washington, Oregon and California (Appendix Table A). Of particular significance are deeper water surveys by the Monterey Bay Aquarium Research

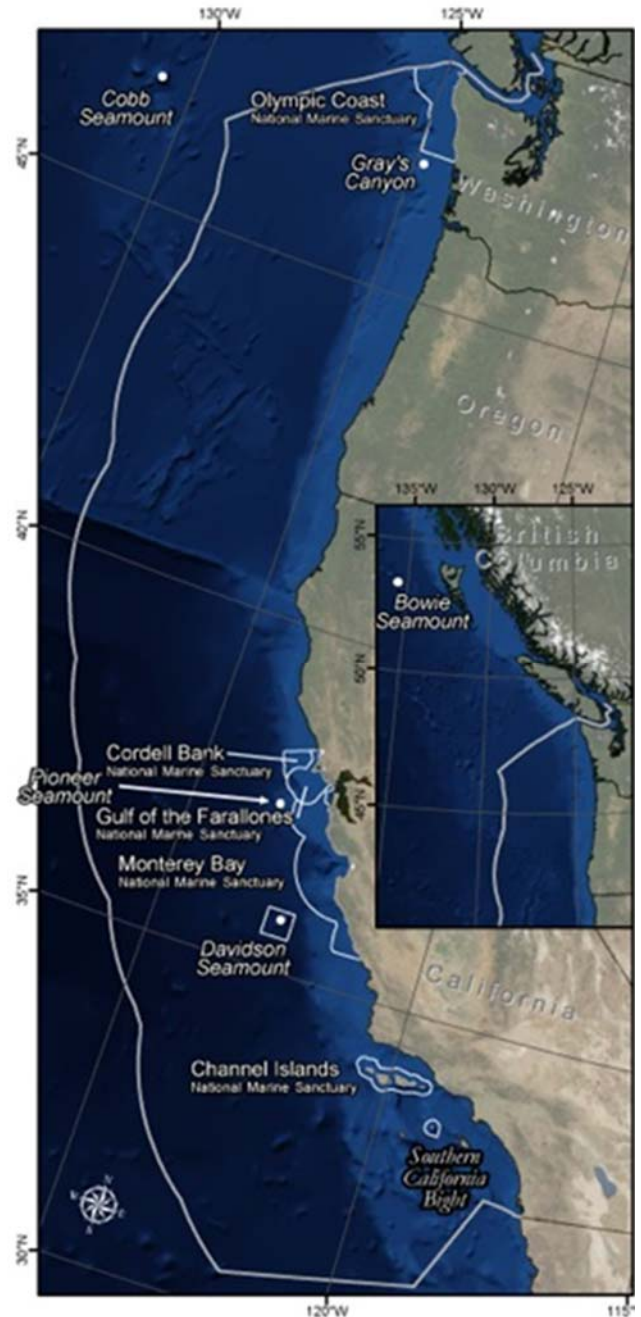


Figure 1. General locations of surveys of deep-sea corals and sponges off the Pacific coast from 2007 to 2013, including NOAA's Deep Sea Coral Research and Technology Program initiative. See Appendix Table A for details of individual surveys.

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. WEST COAST



Table 1. Summary of deep-sea coral and sponge taxa recorded during bottom trawl tows as part of the West Coast Groundfish Bottom Trawl Survey (2001-2012). “n” denotes number of tows with recorded bycatch; “FREQ” denotes ratio of tows with catch to total tows recorded; “Weight” denotes catch weight (kg); “FREQ Rank” and “Weight Rank” columns denote the rank of taxon by either frequency of occurrence or catch weight, respectively. Taxa are ranked by highest catch weight within major taxonomic groups.

	Taxon	Taxon Rank	n	FREQ	FREQ Rank	Weight (kg)	Weight Rank
Porifera	Porifera	Phylum	1,436	19.9%	1	11,035.01	1
	Hexactinosida	Order	512	7.1%	3	7,992.77	2
	Rosellinae	Subfamily	159	2.2%	8	1,328.24	3
	<i>Suberites</i> spp.	Genus	20	0.3%	19	1,073.27	4
	<i>Hyalonema</i> spp.	Genus	180	2.5%	7	561.63	5
	Hexactinellida	Class	17	0.2%	21	131.01	6
	<i>Farrea</i> spp.	Genus	11	0.2%	25	4.18	24
				1,869	25.9%		22,126.11
Pennatulacea	Pennatulacea	Order	926	12.8%	2	102.11	7
	<i>Anthoptilum grandiflorum</i>	Species	489	6.8%	4	97.89	8
	<i>Halipteris</i> spp.	Genus	211	2.9%	5	29.68	12
	<i>Ptilosarcus gurneyi</i>	Species	135	1.9%	10	21.09	14
	<i>Umbellula</i> spp.	Genus	141	2.0%	9	8.84	18
	<i>Anthoptilum murrayi</i>	Species	42	0.6%	15	3.00	25
	<i>Anthoptilum</i> spp.	Genus	5	0.1%	27	0.36	30
	<i>Pennatula phosphorea</i>	Species	15	0.2%	22	0.28	32
	<i>Halipteris willemoesi</i>	Species	5	0.1%	27	0.14	33
	<i>Halipteris californica</i>	Species	3	0.0%	28	0.05	34
			1,670	23.1%		263.44	
“Gorgonacea”	Gorgonacea	Order	197	2.7%	6	72.55	9
	<i>Paragorgia</i> spp.	Genus	26	0.4%	18	11.69	17
	<i>Isidella</i> spp.	Genus	12	0.2%	24	7.15	19
	<i>Callogorgia kinoshitae</i>	Species	29	0.4%	17	6.31	20
	<i>Keratoisis</i> spp.	Genus	5	0.1%	27	1.95	26
	<i>Callogorgia</i> spp.	Genus	5	0.1%	27	0.33	31
	<i>Leptogorgia chilensis</i>	Species	1	0.0%	30	0.04	35
	<i>Swiftia pacifica</i>	Species	2	0.0%	29	0.02	37
	Acanthogorgiidae	Family	1	0.0%	30	0.01	38
				253	3.5%		100.04
Antipatharia	Antipatharia	Order	126	1.7%	11	64.26	10
	<i>Chrysopathes</i> spp.	Genus	46	0.6%	13	44.45	11
	<i>Bathypathes</i> spp.	Genus	44	0.6%	14	1.37	27
	<i>Lillipathes</i> spp.	Genus	18	0.2%	20	1.01	28
				217	3.0%		111.09
Alcyonacea	<i>Heteropolypus</i> spp.	Species	104	1.4%	12	21.93	13
	<i>Anthomastus</i> spp.	Genus	39	0.5%	16	11.70	16
	Alcyonacea	Order	29	0.4%	17	6.11	21
	Nephtheidae	Family	1	0.0%	30	0.04	36
				168	2.3%		39.78
Scleractinia	Caryophylliidae	Family	7	0.1%	26	12.60	15
	Flabellidae	Family	13	0.2%	23	5.86	22
	Scleractinia	Order	7	0.1%	26	5.34	23
			26	0.4%		23.80	
Stylasteridae	Stylasteridae	Family	5	0.1%	27	0.53	29
ALL TAXA			3,182	44.0%		22,664.78	



Institute on a number of seamounts with rich deep-sea coral and sponge habitats. Additional field research has been conducted in the national marine sanctuaries (e.g., Etherington et al. 2011), by Oceana (Shester et al. 2012, Enticknap et al. 2013), as part of monitoring state MPAs (e.g., Yoklavich et al. 2010), and in association with other studies. Several graduate students at Washington State University summarized information on the spatial distribution and abundance of invertebrates and fishes that were quantified from archived videotape collected during visual surveys using ROVs or a submersible (e.g., Bright 2007, Graiff 2008, Bianchi 2011).

11.1.iii – Bottom trawl collections

The occurrence of deep-sea corals and sponges as catch in the NMFS West Coast Groundfish Bottom Trawl Survey remains the most comprehensive source of coast-wide information on the general distribution of higher-level coral and sponge taxa. These surveys are conducted annually in “trawlable” habitats coast-wide at depths from 55 to 1280 m. From 2001-12, sponges and pennatulaceans were the most abundant taxa observed in these surveys (Table 1), most likely because of the types of habitats (e.g., low relief) that are accessed by bottom trawls. Physical specimens were collected, with some sent to taxonomists for identification.

These data were summarized for the five-year review of Pacific Groundfish EFH conducted by NMFS and PFMC (PFMC 2012). This analysis focused on changes in bycatch before and after implementation of EFH regulatory measures in

June 2006. Although no significant difference in the total frequency of occurrence of corals and sponges is apparent, identification of species in the trawl surveys is improving and often samples are retained and sent to experts for taxonomic verification of species. Information collected by observers of the groundfish fishery provides only broad taxonomic resolution; however, these observers routinely collect specimens for species verification.

11.2. Taxonomy and Species Distributions

11.2.i – Corals

a. Coral taxonomy

Whitmire and Clarke (2007) reported 106 taxa of corals within the U.S. EEZ from the West Coast region (Table 2). The list included 52 taxa with incomplete taxonomy. Since 2007, there have been several additions to the number of deep-sea coral species documented on the west coast including range extensions of certain species (Tables 2 and 3; Whitmire et al. 2017, [Online Annex](#)). In addition, the relationships between species have been reviewed and several species have been synonymized.

With funding from the Deep Sea Coral Research and Technology Program, samples (vouchers) of deep-sea corals from the northeast Pacific Ocean have been identified to species using both morphology (form and structure) and DNA sequence bar codes (Everett et al. 2016). Coral samples have been collected during field research, research trawl surveys and by fishery observers. Genetic sequences for two mitochondrial genes – COI



Table 2. Number of coral taxa reported from the U.S. West Coast region in 2007 and in the present report. Increases include new species identifications and range extensions (Table 3), as well as species not included in the first report. Data sources and references online in Whitmire et al. 2017.

TAXON	Whitmire & Clarke 2007	Whitmire et al. 2017
Class Anthozoa		
Black corals (Order Antipatharia)	8	9
Stony corals (Order Scleractinia)	18	19
Gorgonian corals (Order Alcyonacea – in part [formerly Order Gorgonacea])	39	60
True soft corals and stoloniferans (Order Alcyonacea)	8	13
Sea pens (Order Pennatulacea)	28	28
Hydrozoa		
Stylasterid corals (Order Anthoathecata, Family Stylasteridae)	5	6
Total	106	135

and MutS – are linked to voucher specimens to create a resource for researchers of deep-sea corals. Microsatellite loci were also developed for the gorgonian *Primnoa pacifica* Morrison et al. 2015) and a species of sea pen in order to analyze genetic patterns in populations of deep-sea octocorals. By creating a voucher collection for deep-sea corals and linking those vouchers to species-specific genetic sequences, subsequent taxonomic identifications can potentially be made using DNA sequences rather than sending individual specimens to the few morphological taxonomists (Everett et al. 2017). The genetic information also will be useful in the identification of corals collected from fishery observers and bottom trawl

surveys, where poor condition of specimens makes morphological identifications difficult.

b. Coral distribution

Based on recent studies, an improved understanding of the distribution of coral species is emerging on the West Coast. With the exception of pennatulaceans, corals mostly occur on rocky substrata (e.g., boulders, pinnacles, rock outcrops). Region-wide, hard and mixed seabed types are relatively rare, representing only around 10% of the substrata from the shelf to depths of 3000 m (NMFS 2013). These seabed types are often associated with seamounts, banks, and canyons, which have been the focus of many recent studies.

Table 3. New coral species and range extensions reported from the U.S. West Coast region since 2007.

Order	Species	Reference
New species:		
Gorgonians	<i>Chrysogorgia pinnata</i>	Cairns 2007
	<i>Chrysogorgia monticola</i>	Cairns 2007
	<i>Calyptrophora bayeri</i>	Cairns 2007
	<i>Calyptrophora laevispinosa</i>	Cairns 2007
	<i>Narella alaskensis</i>	Cairns and Baco 2007
	<i>Narella bowersi</i>	Cairns 2007
	<i>Parastenella gymnogaster</i>	Cairns 2007
	<i>Parastenella pacifica</i>	Cairns 2007
	<i>Isidella tentaculum</i>	Etnoyer 2008
	<i>Sibogagorgia cauliflora</i>	Herrera et al. 2010
	<i>Leptogorgia filicrispa</i>	Horvath 2011
	<i>Swiftia farallonesica</i>	Williams and Breedy, 2016
Soft Corals	<i>Gersemia juliepackardae</i>	Williams and Lundsten 2009
Synonymized species:		
Gorgonians	<i>Euplexaura marki</i> = <i>Chromoplexaura marki</i>	Williams 2013
Soft Corals	<i>Gersemia rubiformis</i> = <i>Alcyonium</i> sp.	Williams 2013
Range Extensions:		
Scleractinians	<i>Caryophyllia diomedea</i>	Gonzalez-Romero et al. 2009
	<i>Caryophyllia quadragenaria</i>	Gonzalez-Romero et al. 2009
Gorgonians	<i>Paragorgia arborea</i> (CA Province)	Yoklavich et al. 2011
	<i>Paragorgia stephencairnsi</i> (CA Province)	Yoklavich et al. 2011
	<i>Parastenella ramosa</i> (CA Province)	Yoklavich et al. 2011
	<i>Swiftia pacifica</i> (CA Province)	Yoklavich et al. 2011
	<i>Eugorgia rubens</i> (OR Province)	M. Yoklavich (unpubl.)
Pennatulaceans	<i>Pennatula phosphorea</i> (CA Province)	Yoklavich et al. 2011
	<i>Umbellula lindahli</i> (OR Province)	M. Yoklavich (unpubl.)

Lundsten et al. (2009) described the abundance and distribution of benthic megafaunal invertebrates on Pioneer, Davidson, and Rodriquez seamounts off central and southern California. Coral diversity was relatively high with 23, 25, and 26 species identified, respectively on these seamounts. Davidson Seamount was the site for several detailed studies of community structure and endemism (McClain et al. 2009, McClain et al. 2010). From

these studies, there was little support for seamount endemism, but seamount communities may have unique structure that changes significantly with depth. The summit of Davidson Seamount (1299-1477 m) was characterized by the large bubblegum coral *Paragorgia arborea* and several hexactinellid sponge species (*Farrea occa*, *Heterochone calyx*, and *Chonelasma* sp.), while deeper zones (> 1600 m) were characterized by different corals (e.g.,



Corallium sp., *Chrysogorgia* spp., bamboo corals and black corals) and other abundant glass sponge species (McClain et al. 2010). Dense aggregations of large corals occurred on peaks and steep slopes, but were less abundant in valleys or on the flanks (Clague et al. 2010). Deep-sea coral records from Monterey Bay Aquarium Research Institute ROV surveys at San Juan and San Marco seamounts also revealed relatively high densities of gorgonian and antipatharian taxa that commonly reach large sizes (e.g., *Paragorgia* spp., certain isidid bamboo corals, and certain black corals).

In 2011 and 2012, two surveys were conducted on Canada's Bowie Seamount and on Cobb Seamount just outside the U.S. EEZ, by the Canadian Department of Fisheries and Oceans in collaboration with NMFS researchers. Information particularly on coral species occurring on Cobb Seamount was expanded during these cruises: 8 of the 11 species of gorgonians and soft corals (Order Alcyonacea) and all of the species of black corals (Order Antipatharia) were new records for Cobb Seamount (Curtis et al. 2015, Du Preez 2015).

In addition to seamounts, the Southern California Bight has varied topography with rocky banks, island flanks and ridges, and submarine canyons. A survey on Farnsworth Bank on the seaward side of Catalina Island revealed that much of the rocky area is covered by the purple hydrocoral, *Stylaster californicus*, at depths to 66 m (Love et al. 2010). Bright (2007) analyzed video from surveys conducted with a manned submersible in 1995-2004 at depths of 97-314 meters at the "Footprint," a

high-relief rocky bank south of Anacapa Island in the Channel Islands. Densities of corals > 20 cm in size were quantified. Gorgonians were relatively common (7/100 m²) with a mean size of 30 cm. Black corals, predominantly *Antipathes dendrochristos*, also were relatively abundant (4/100 m²). These densities were higher than reported by Tissot et al. (2006) for other banks in the region but much lower than more recent studies conducted in this area.

In 2010, deep-sea corals and sponges, along with fishes and seafloor habitats, were surveyed using the *Kraken II* ROV and the Seabed AUV at depths of 275-900 m on Piggy Bank near the Footprint Bank within the Channel Islands National Marine Sanctuary. At least 26 taxa each of corals and sponges were quantified (Yoklavich et al. 2011). This site comprised some of the highest densities of corals and sponges found in the West Coast region, ranging from 10-54 corals/100 m² and 22-97 sponges/100 m². The most abundant corals (depending on depth) included Christmas tree black coral (*A. dendrochristos*), mushroom soft coral (*Heteropolypus ritteri*), several species of Primnoidae and Plexauridae (*Swiftia* spp.), dense stands of *Lophelia pertusa* and cup corals (*Desmophyllum dianthus*), and the sea pen (*Halipteris californica*; only on soft sediment).

Visual surveys using a manned submersible in 2010 focused specifically on the biology and ecology of Christmas tree black corals on deep offshore banks within the Channel Islands National Marine Sanctuary (Yoklavich et al. 2013). This survey included habitats of high-



relief rock boulders and outcrops and steep slopes of soft sediments and rock rubble at depths 110-475 m. The 272 Christmas tree corals observed during 11 dives were 5-200 cm in height, and most were healthy with little or no evidence of damage.

Over 23,500 deep-sea corals and 23,800 sponges also have been identified from archived video transects conducted from a manned submersible while surveying fishes on rocky banks off southern California from 1995 to 2008 (M. Yoklavich, NOAA Deep-Sea Coral and Sponge Database). Various types of sea fans were among the most abundant corals, including golden corals (*Acanthogorgia* spp.), primnoids (*Plumarella longispina*), and plexaurids (*Swiftia* spp.). scleractinian cup corals and substantial colonies of *Lophelia pertusa* also were relatively abundant. Sponges from at least 18 taxa in a variety of shapes, sizes, and colors were observed. These data have been integrated into NOAA's National Database for Deep-Sea Corals and Sponges (<https://deepseacoraldata.noaa.gov/>).

A photographic database of 30,000+ images collected during ROV surveys 2003-2011 in the Southern California Bight recently has been reviewed (unpubl. data, P. Etnoyer and K. Stierhoff). Distinct depth-related patterns were observed in coral assemblage structure. Shallow depths (< 100 m) were dominated by *Leptogorgia chilensis*, *Stylaster californicus*, and *Eugorgia rubens*, while between 100 – 400 m *Plumarella* sp., *Lophelia pertusa*, *Acanthogorgia* sp., *Antipathes* sp., and *Paragorgia* sp. were the most abundant taxa.

Deep-sea corals also are associated with banks off Central California (e.g., Cordell Bank: Pirtle 2005, Etherington et al. 2011; Rittenburg Bank: Etnoyer et al. 2014) and Oregon (e.g., Coquille Bank: Strom 2006, Stierhoff et al. 2011, Enticknap et al. 2013). At Coquille Bank, the most abundant gorgonian was the small red *Chromoplexaura marki* (Stierhoff et al. 2011, Williams 2013). At least one specimen was observed with catshark egg cases attached.

Deep-sea corals are often observed on hard substrata in canyons. Bianchi (2011) assessed invertebrate composition, habitat complexity, and ecological associations with structure-forming invertebrates and fishes in three submarine canyons: Astoria Canyon off northern Oregon, and Carmel and Ascension canyons off the central California coast. There were two distinct habitat assemblages associated with soft and hard substrata in all three canyons, and deep-sea corals were mostly small species at relatively low densities (0.4-5 per 100 m²). In 2011, a survey was conducted using an AUV to assess the distribution of corals and sponges in Bodega Canyon, an area under consideration for possible expansion of the Cordell Bank National Marine Sanctuary. Much of this canyon had been categorized as hard substrata based on earlier multibeam sonar mapping. However, from the visual survey using the AUV, this area primarily was found to be mud draped rock with only occasional rocky outcrops and few small corals and sponges (Fruh et al. 2013).

Several studies have reported information on deep-sea coral and sponge habitats and

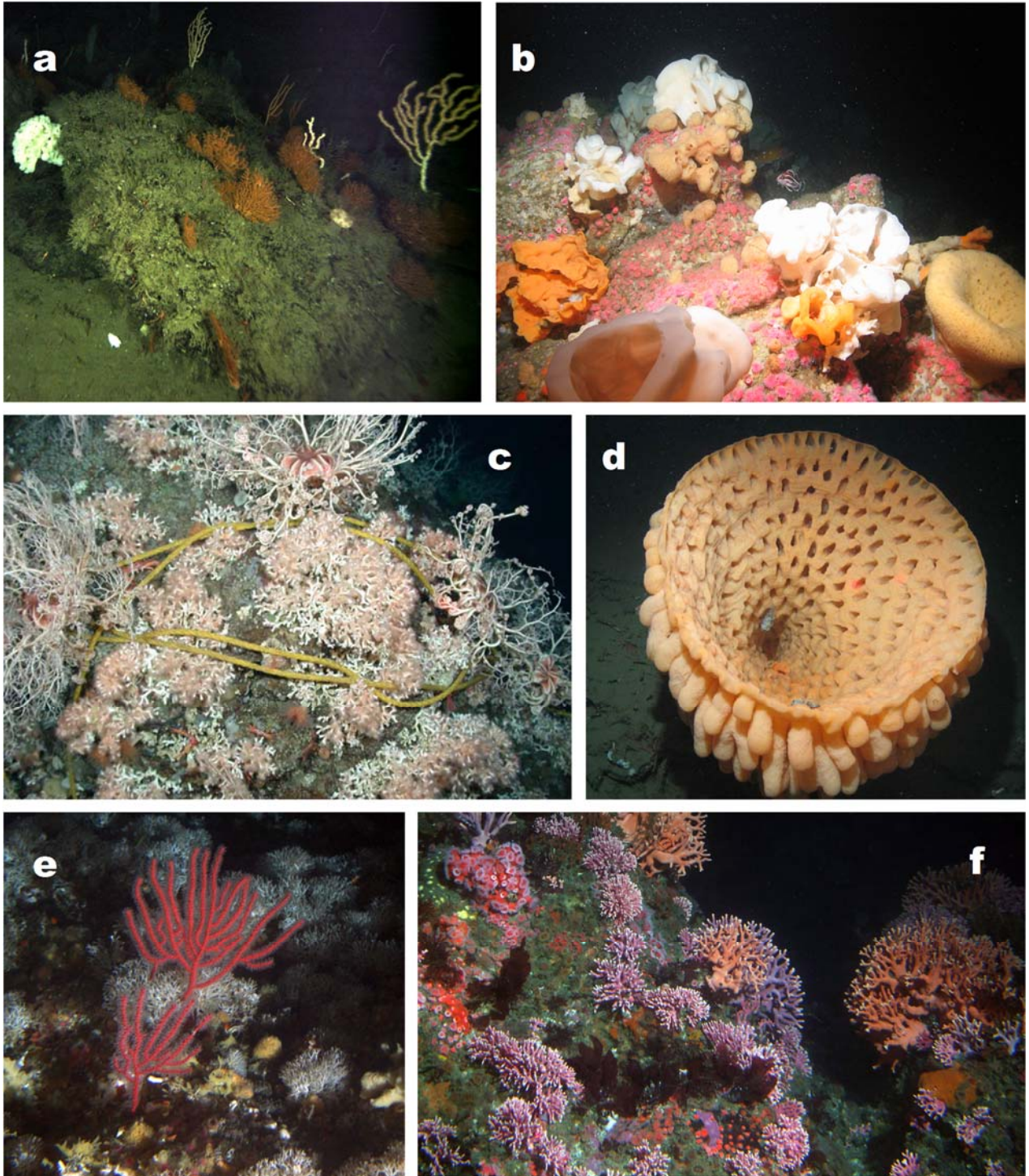


Figure 2. Corals and sponges of the West Coast: a) Deep-sea corals off Northern California at 750 m depth, including *Swiftia* sp., *Paragorgia* sp., *Parastenella* sp., and a hexactinellid sponge. b) Habitat dominated by deepwater sponges at Rittenburg Bank, Gulf of the Farallones National Marine Sanctuary. c) Fishing gear line wrapped around *Lophelia pertusa* coral on Seamount 109 in the Channel Islands. d) *Heterochone calyx* glass sponge from the Channel Islands National Marine Sanctuary. e) Small colonies of *Swiftia* sp. and *Lophelia pertusa* on Piggy Bank off Southern California. f) Stylasterid corals on rocky banks in the Channel Islands.



demersal fishes within Monterey Bay National Marine Sanctuary, including Graiff (2008), Starr and Yoklavich (2008), Yoklavich and Starr (2010), Bianchi (2011), Knight (2011), Stierhoff et al. (2011), and Shester et al. (2012). Most of

these studies were conducted in depths of 20-365 m using visual survey techniques from a manned submersible and ROVs. Scientists conducted baseline monitoring of seafloor communities in and out of eight newly

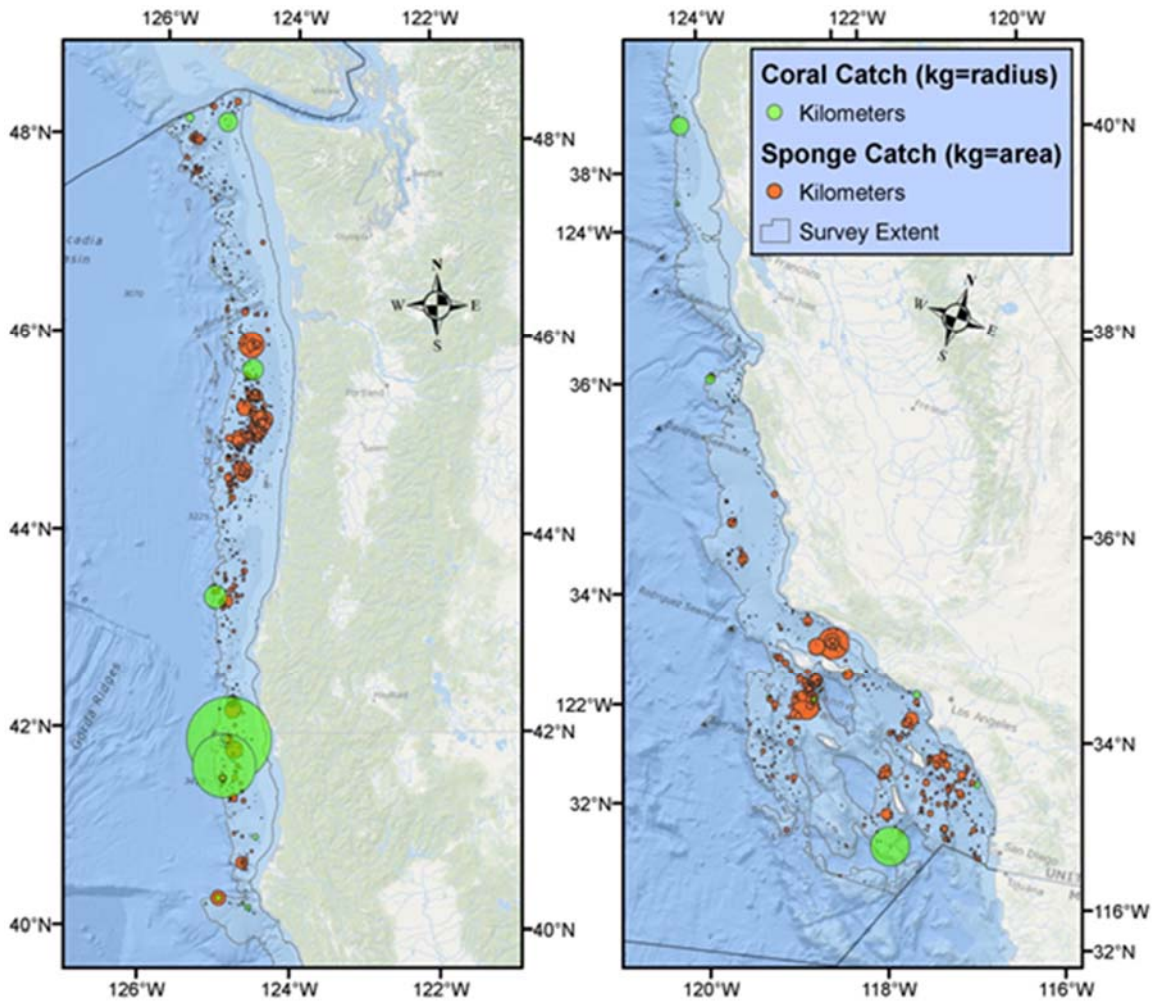


Figure 3. Distribution of coral (green) and sponge (orange) catch weights (kg) for tows conducted as part of the Northwest Fisheries Science Center's annual West Coast Groundfish Bottom Trawl Survey (2001-2012). Symbol sizes are proportional to size of catch for all coral (excluding pennatulaceans) and sponge taxa recorded in the trawl net. Maximum sponge catches per tow within the time period were significantly higher than coral catches, so circle size is equal to radius (km) for corals and area (km²) for sponges. The survey extent (irregular polygon) is bounded by the exclusive economic zone to the north and south and by the 30 and 700 fathom isobaths. Tows with no catch of either corals or sponges are not shown.



designated MPAs on the central California in 2007 and 2008 (Yoklavich and Starr 2010). Direct observations were made of 134,000 fishes and 42,098 structure-forming invertebrates in 341,000 m² of seafloor habitats that included deep rocky banks and outcrops, canyons, cobble fields and mud flats. At least 16 taxa of corals and 14 taxa of sponges have been cataloged; abundant corals were *Stylaster californicus*, *Leptogorgia chilensis*, and *Heteropolypus ritteri*. *Lophelia pertusa* was relatively common in rocky steep areas. ROV surveys on Rittenburg Bank, Farallon Escarpment, and Fanny Shoals in the Gulf of the Farallones National Marine Sanctuary revealed twenty taxa of corals and sponges (GFNMS 2013, Etnoyer et al. 2014).

Surveys of corals and sponges in Olympic Coast National Marine Sanctuary have received significant attention (Brancato et al. 2007; Bowlby et al. 2011a, 2011b). While the dominant corals in many areas were smaller species (e.g., *Swiftia* spp., *Calciogorgia beringi*, and *Stylaster* sp.), aggregations of larger species (*Paragorgia arborea* and *Primnoa pacifica*) also occurred in several locations.

The NMFS West Coast Groundfish Bottom Trawl Survey provides a broader view of deep-sea coral distributions at fishable depths (i.e., 55-1280 m) along the whole West Coast (Keller 2017). In these surveys, most corals were identified to order. The largest catches of corals by weight occurred in 800-1200 m of water near the Oregon-California border (Figure 3). Taxa in these high-weight catches included gorgonian, black, and cup corals. This area also

exhibited some areas of high bycatch of corals in the commercial trawl fishery as documented by the West Coast Groundfish Observer Program (PFMC 2012).

Several of these high-bycatch areas were subsequently surveyed by ROV, towed camera, and AUV, revealing both high densities of deep-sea corals, as well as evidence of damage from fishing gear (Yoklavich et al. 2016, Yoklavich et al. 2017).

c. Modeling distribution and abundance of corals

Modeling efforts relevant to the distribution and abundance of deep-sea corals on the West Coast are less than 10 years old, but the field is rapidly advancing. Five modeling efforts that incorporated either presence only or presence-absence data of various coral taxa and associated environmental factors off the west coast have been conducted recently. Bryan and Metaxas (2007) modeled habitat suitability for two gorgonian families (Primnoidae and Paragorgiidae) in the Northeast Pacific from northern California to Alaska. Guinotte and Davies (2012, 2014) used presence-only data and a variety of environmental factors to develop predictive models of habitat suitability for several broad taxonomic groups of deep-sea corals for the entire West Coast region (see Guinotte et al., this volume). Slope, temperature, salinity, and depth were important predictors for most taxa in their study. The majority of predicted suitable habitat for most taxa occurred within areas protected from bottom-trawling (e.g., 82% for



black corals and 66% for calcaxonian gorgonians); however, the majority of suitable habitat for holaxonian gorgonians (64%) was predicted to occur in unprotected areas. Both region-wide studies lacked high-resolution bathymetric and substratum data.

Deep-sea coral habitat modeling also has been conducted from data collected on Cordell Bank. Predictive models using presence-absence data and generalized linear models of *Stylaster* spp. and *Swiftia* spp. indicated that small-scale habitat features, including bathymetry, slope, and topographic position index, were important habitat predictors for both taxa (Etherington et al. 2011). Bathymetry and topographic position index had a positive influence, while slope had a negative influence on these taxa. Rugosity had a strong influence on the presence of *Stylaster* spp., which were associated with shallow, rocky habitats with high slope. Substratum type and aspect significantly contributed to the presence of *Swiftia* spp., which were predicted to be broadly distributed in deep water over a diversity of substratum types with low slope.

Krigsman et al. (2012) developed generalized linear models to predict the probability of occurrence of five commonly observed taxa (stony cup corals, hydroids, short and tall sea pens, and brittle stars) off southern California using presence-absence data from video transects in the Santa Barbara Channel. Predictive maps of probability of occurrence were produced using validated models and covariates of depth, location, and seafloor sediment types. Bottom habitat type was the

strongest predictor of the occurrence of stony cup corals, which occurred predominantly on mixed sediment and rugose rock. As expected, sea pens were predicted to occur on unconsolidated sediments, but high probabilities of occurrence were predicted only in areas where bottom trawling was relatively low.

Most recently, models have been developed to predict the densities of the black coral (*A. dendrochristos*) using environmental factors such as depth, ocean currents, and productivity throughout the Southern California Bight (Huff et al. 2013). Predicted densities have been mapped in relation to the extensive system of MPAs throughout the Bight.

II.2.ii – Sponges

a. Sponge taxonomy

There have been few systematic studies of sponge taxa for the U.S. West Coast. Austin et al. (2007) produced a list of sponges for the northeast Pacific, and Lee et al. (2007) compiled current information on the sponges of California. Many of the species from the region were described from collections conducted in the late 1800s and early to mid-1900s.

From surveys off southern California, a new species of carnivorous demosponge, *Cladorhiza pteron*, was collected from 1,442 m depth on San Juan Seamount, and also was seen at Rodriguez Seamount (Reiswig and Lee 2007). Lundsten et al. (2014) described three additional species of cladorhizid sponges off the west coast. Several of 13 sponges collected during an ROV survey on Piggy Bank off southern California were



new records for the northeastern Pacific and likely new species (pers. comm., W. Austin, Khoyatan Marine Laboratory, Sidney, BC; Yoklavich et al. 2011). In addition to new records and new species that have been reported since the 2007 report, several recently published taxonomic guides and compilations have improved the identification of sponges and corals on the West Coast and Alaska (Burton and Lundsten 2008, Stone et al. 2011).

b. Sponge distribution

Sponges occurred in about one quarter of all trawls by the NMFS West Coast Groundfish Bottom Trawl Survey (Table 1), though most could only be identified as “Porifera.” Compared to corals, the focus on identifying sponges is very recent. The identified sponges were predominantly glass sponges (Class Hexactinellida) and demosponges in the genus *Suberites*. The highest weight of sponges per tow occurred in relatively discrete areas, especially off the coast of northern Oregon and around the northern Channel Islands, CA (Figure 3).

In general, taxonomic information on sponges is lacking, and species identification of sponges from visual surveys is even more difficult than for corals. Consequently, much of the distributional information is based on morphotypes (e.g., vase, shelf, foliose). Sponges have been reported from nearly all the surveys in rocky habitats off the West Coast that reported deep-sea corals. In many cases sponges were larger and more abundant than corals (other than sea pens). Bianchi (2011)

reported higher densities and larger sizes for sponges than for corals in Astoria, Ascension and Carmel Canyons. Mean densities of sponges on southern California banks were reported to be 2.5 times higher than corals (Bright 2007). Sponges on Rittenburg Bank were particularly abundant, and occurred in larger sizes and densities than corals (GFNMS 2013). The most abundant sponges on Piggy Bank (Yoklavich et al. 2011) and other southern California banks (Yoklavich unpubl.) generally were mound, foliose, upright flat, vase, and barrel morphotypes.

A unique habitat dominated by hexactinellid sponges has been discovered in the vicinity of methane seeps off Grays Harbor, Washington (Salmi et al. 2011). NMFS bottom trawl surveys in this area in 1983 and 1985 reported significant catches of sponges, up to 907 kg in a single ~ 1.5 km trawl haul. Glass sponges identified from this survey included *Aphrocallistes vastus*, *Hyalonema* sp., and rossellid sponges. In 2010, the distribution of the sponges and associated fishes was quantified during an AUV survey (Clarke and Fruh 2012). The seafloor was of low relief and much of it was covered with sediment. On five dives the densities of sponges ranged from 10 to 99 sponges per 100 m² and included the structure-forming glass sponges *Heterochone calyx*, *Aphrocallistes* sp., and a demosponge, *Poecillastra* sp. Many of the rockfishes in the area were associated with sponges, and a high percentage of the fishes either were touching or within one body length of these structure-forming sponges.



Sponge reefs have been described in several areas of British Columbia (Conway et al. 2001). Similar to the area off Grays Harbor, *Heterochone calyx* and a species of *Aphrocallistes* are among the dominant species. However, the densities of sponges in the Grays Harbor area are much lower than found at the areas described as sponge reefs in British Columbia, Canada. In those areas, densities can typically be on the order of 2000 per 100 m² (Leys et al. 2004) while off Grays Harbor the densities ranged up to 99 sponges per 100 m².

II.3. Species Associations with Deep-Sea Corals and Sponges

While demersal fishes co-occur with various deep-sea corals and sponges, particularly in rocky areas, the extent and function of such relationships have yet to be fully described and quantified. Fishes occasionally have been seen resting inside, underneath, and beside corals and sponges during visual surveys conducted with manned submersibles, ROVs, and AUVs off the west coast (Brancato et al. 2007, Bianchi 2011, Clarke and Fruh 2012). Such associations, particularly of rockfishes (*Sebastes* spp.) with some of the same species of corals or sponges, have also been reported off British Columbia (Du Preez and Tunnicliffe 2011) and Alaska (Stone and Shotwell 2007, Stone 2014, Rooper et al. 2007). However, there was little evidence of a functional relationship between fishes and structure-forming invertebrates that co-occurred in various habitats throughout southern California (Tissot et al. 2006). Bright (2007) documented the co-occurrence of several

species of fishes with structure-forming invertebrates on the “Footprint” of the Channel Islands off southern California. In recent visual surveys conducted using an ROV and manned submersible on nearby seamounts in southern California, there were few instances of fishes associated with corals and sponges, and benthic invertebrates more commonly occurred on dead *Antipathes dendrochristos* (Christmas tree black corals) and *Heterochone calyx* (goblet sponges) than on living ones (Yoklavich et al. 2011, Yoklavich et al. 2013). Bianchi (2011) also reported few fishes in close proximity with structure-forming invertebrates (including corals and sponges) in submarine canyons off Washington and central California, with most fishes occurring ≥ 1 m away from the invertebrate. The extent of fish and invertebrate associations may depend on the densities of fishes and structure-forming invertebrates and on the local availability of rocky crevices in which fishes take shelter. Further research and critical evaluation are needed to clarify the role that corals and sponges serve as essential habitat for fishes in demersal communities off the West Coast.

II.4. Mapping Potential Distribution of Deep-Sea Corals and Sponges

One of the impediments to identifying areas that are likely to have abundant populations of corals and sponges is a lack of high-resolution bathymetry, backscatter, and associated interpreted substratum types on the seafloor in deep water on a coast-wide scale. A significant amount of new information on physical habitat



has been collected off the Pacific Coast over the last decade, including at least 261 sources of seafloor imagery compiled since the last regional habitat maps were published in 2005 (NMFS 2013). Some of this information has been used by NOAA to target coral and sponge surveys. Most of the new information has been consolidated into Pacific coast-wide comparative maps of bathymetry, acoustic coverage, seafloor substrata, and biogenic habitat observations in 2005 and 2011 for the EEZ off Washington, Oregon, and California in support of the PFMC 5-year review of EFH for Pacific coast groundfish (PFMC 2012).

The Office of Ocean Exploration mapped the Mendocino Ridge and specific areas in and around the Gulf of the Farallones, Cordell Bank, and Monterey Bay national marine sanctuaries. A new ridge southwest of Santa Rosa Island in the Channel Islands National Marine Sanctuary was identified during these multibeam surveys conducted from the NOAA R/V *Okeanos Explorer*. NOAA explored this newly charted ridge and to evaluate the depth stratification of deep-sea corals. Beginning in 2015, NOAA began a series of cruises designed to comprehensively map the deeper waters of the Channel Islands National Marine Sanctuary. NOAA has mapped additional areas in preparation for targeted ROV or AUV surveys. Additional bathymetric mapping in the Olympic Coast and Gulf of the Farallones National Marine Sanctuaries was completed. Multibeam surveys were conducted in preparation for AUV surveys of a sponge area off Grays Harbor, Washington and off Oregon.

In addition to these federally supported efforts, all of the seafloor within California's state waters (to 3 miles offshore) and large portions of Oregon state waters have been mapped with high-resolution multibeam sonar. These data have been coupled with predictive models to map the occurrence of deep-sea corals.

II.5. Research Priorities

Whitmire and Clarke (2007) identified a number of deep-sea coral research priorities for the region. In 2010, NOAA's Deep Sea Coral Research and Technology Program held a workshop (NOAA 2010) that supported and expanded on these research priorities for the West Coast (see below). While research since 2007 has made progress in many of these areas, most of the identified priorities remain.

- 1) *Identify deep-sea coral and sponge species, and map and characterize their distribution, abundance, densities, and diversity throughout the California Current LME.*
 - A great deal of new information is now available on coral presence, but very few studies report abundances and densities in ways that can be compared across studies. Information on the identification of sponges at the species level is particularly weak.
 - The lack of coast-wide seabed mapping information at a spatial scale relevant to demersal communities (i.e., meter resolution) remains an impediment for predictive models of habitat suitability



and of coral and sponge distribution and abundance. Improvements to seafloor maps also will yield efficient design of surveys to target areas with a high likelihood of containing abundant populations of corals and sponges. Additionally, much of the existing interpreted habitat mapping needs validation.

2) *Determine the ecological roles of deep-sea corals and sponges, especially the nature of associations between other invertebrates and fishes with deep-sea corals and sponges.*

- While co-occurrence of sponges and corals with some species of fishes and other invertebrates has been documented, the extent and nature of those associations has not been addressed. This is especially important from a management standpoint in relation to roles that structure-forming species might play as EFH for demersal fishes.

3) *Understand the basic biology of deep-sea corals, including taxonomy, age structure, growth, gender, population connectivity, and life histories.*

- There have been few new studies on the life history of west coast deep-sea corals. Flint et al. (2007) reported on the reproductive ecology of a deepwater solitary scleractinian coral, and Feehan and Waller (2015) examined reproduction of seven gorgonian species (*P. pacifica*, *Calcigorgia beringi* and five *Swiftia* spp.). Andrews et al. (2009) and

Hill et al. (2011) reported on growth and age of bamboo corals (Family: Isididae) from seamounts off California.

Estimates of bamboo coral ages ranged from 98 ± 9 years (Andrews et al. 2009) to over 300 years (Hill et al. 2011).

- As in most other areas, information on the biology of deep-sea sponges lags far behind that of deep-sea corals.

4) *Develop models to predict distribution and abundance of deep-sea corals and sponges.*

- There is a particular need to incorporate bottom-substratum information into region-wide models and to model corals at the species level (rather than broad groupings of species).
- To date there have been no models of deep-sea sponge distributions off the west coast.
- Better understanding of abiotic and biotic habitat requirements will not only improve habitat-suitability modeling, but will result in models that better predict impacts of changing ocean conditions due to acidification and climate change.

5) *Understand anthropogenic and natural impacts on deep-sea coral ecosystems.*

- Develop baseline indices of health and condition of corals and sponges at individual and community levels.
- Better quantify bycatch of corals and sponges in commercial fisheries.



6) *Further synthesize and understand existing information on deep-sea corals and sponges.*

- Bottom trawl surveys and fisheries bycatch provide valuable information on corals and sponges, but identification of these taxa is slow and inadequate. This will improve as progress is made in developing methods of genetic identification.

7) *Understand deep-sea corals' ability to recover from a variety of stressors.*

- The impacts and recovery rates of corals and sponges from various stressors are largely theoretical because it is difficult to conduct controlled experiments with these fragile deep-sea organisms. As methodologies improve, particularly relevant to climate change and ocean acidification, we are hopeful that experimental studies will offer valuable insight.

8) *Utilize deep-sea corals to discern past climate conditions.*

- There have been gains in determining paleoclimate information deep-sea corals (Prouty et al., this volume), but few studies on the west coast.

9) *Evaluate the efficacy of existing management measures.*

- Recent analysis suggests a majority of coral occurrences on the continental shelf and upper slope are outside existing conservation areas that are

meant to protect seafloor habitats from interactions with certain bottom-contact fishing gears (NMFS 2013). In contrast, MPAs on the lower slope appear to protect a large majority of known coral (excluding pennatulaceans) and sponge habitats from adverse impacts of bottom trawling. We need to evaluate the overall efficacy of all management measures meant to protect deep coral and sponge ecosystems.

10) *Improve tools and methods for studying deep-sea corals (e.g., new technologies; new applications for existing technologies; and develop best practices for research).*

- DNA analysis has become a standard tool to assist in species identification and collaborations between observer, survey and research programs are helping to increase the number of samples of corals and sponges available for analysis (e.g., Everett et al. 2016).

III. Update on Management of Deep-Sea Corals and Sponges

III.1. New Information on Impacts and Stressors

III.1.i – Fishing

Fishing activities were highlighted in the 2007 report as one of the most significant potential stressors to deep-sea coral and sponge communities, and impacts from bottom-contact gears, particularly bottom trawls and longlines,



remain the most significant documented threat. Recent and ongoing activities by management agencies have focused on minimizing these impacts; however, quantifying these impacts is difficult. Bycatch (e.g., NMFS 2016) and in situ evidence of fishing gears entangling corals and sponges (e.g., Brancato et al. 2007, Bowlby et al. 2011a, 2011b) continue to be the most direct evidence of adverse fishing interactions. As observer coverage increases and as fishery observers identify corals and sponges more consistently, bycatch data could be a reliable indicator of trends in fishing impacts.

There have been few in situ studies off the West Coast that relate observations of trawling to deep-sea coral or sponge habitats. Graiff (2008) analyzed the megafaunal invertebrate communities at three sites on the continental shelf and upper slope off central California, and examined the potential effects of fishing. It was difficult to discern fishing impacts from environmental effects on distribution of invertebrates in part because of the fairly coarse resolution of fishing effort information. Hixon and Tissot (2007) compared benthic communities in trawled and untrawled mud habitat off Oregon. Sea pens (*Stylatula* spp.) dominated untrawled bottoms, but were nearly absent on trawled bottoms. Hannah et al. (2010) also found that densities of sea pens (*Halipterus*

spp.) were significantly lower in areas off Oregon that were heavily-trawled for shrimp, compared to lightly-trawled areas. To more clearly quantify impacts, controlled in situ experimentation may be necessary.

Yoklavich et al. (2017) reported on visual surveys in areas of longtime bottom trawling off southern Oregon and northern California to evaluate the incidence of disturbance and damage to deep-sea corals and sponges. Overall frequency of disturbance was relatively low (2%). Most of the observed damage was to coral colonies, particularly to bamboo corals (family Isididae).

Deep-sea corals and sponges are recorded as bycatch in both the commercial trawl fishery and fixed gear fisheries (as documented by the West Coast Groundfish Observer Program). Taxonomic identification of commercial bycatch is usually limited to “sea pens and sea whips” (i.e., pennatulaceans), “other coral,” and “sponge.” These observations document ongoing interactions between commercial fishing gear and deep-sea corals and sponges.

Since June 2006, observers of the bottom trawl fishery have recorded a doubling of encounters with sponges and pennatulaceans, while the frequency of occurrence of other corals remained unchanged (Table 4, PFMC 2012).



Table 4. (Modified from PFMC 2012.) Summary of coral and sponge bycatch for observed tows using bottom trawls as part of the West Coast Groundfish Observer Program, comparing two time periods: “Before” (3 Jan 2002 – 11 Jun 2006) and “After” (12 Jun 2006 – 31 Dec 2010) implementation of Amendment 19 regulations. “#” denotes number of hauls; “FREQ” denotes ratio of hauls with positive catch of taxon to total hauls observed; “Weight” denotes catch (kg); “CPUE” denotes catch per unit effort (kg/km). Haul counts represent only those hauls where corals or sponges were present in the catch. Pennatulaceans are recorded separately from other corals, as they are relatively easy to distinguish and generally occur in different habitats. Annual Observer Program coverage of the limited-entry bottom trawl sector can be found online at: http://www.nwfsc.noaa.gov/research/divisions/fram/observer/sector_products.cfm.

TAXON	BEFORE				AFTER			
	#	FREQ	Weight	CPUE	#	FREQ	Weight	CPUE
coral	319	2.0%	4,223	2.2E-02	335	1.8%	997	4.1E-03
sea pen	198	1.3%	105	5.5E-04	474	2.5%	66	2.7E-04
sponge	469	3.0%	4,547	2.4E-02	1,444	7.6%	20,585	8.5E-02
Combined	903	5.7%	8,875	4.7E-02	2,003	10.5%	21,648	8.9E-02

Also, sponge bycatch appears to have increased corals from sponges. Other possible explanations of these bycatch patterns are changes in fishing patterns due to spatial management of the trawl fishery and better recording of bycatch due to increased interest in conservation of these organisms. Fixed bottom-contact fishing gears, such as bottom-set longlines and gill nets can also impact coral and sponge habitats, though the area contacted is likely to be much smaller than for bottom trawls. Surveys in the Olympic Coast National Marine Sanctuary have documented impacts to biogenic habitats from bottom longline fishing gear (Brancato et al. 2007, Bowlby et al. 2011a, 2011b). For fixed gear fisheries, corals and sponges are recorded in the catch infrequently by the West Coast Groundfish Observer Program (PFMC 2012), so it is difficult to

examine trends in bycatch. The transition to full observer coverage with implementation of catch shares in the groundfish fishery should someday afford a more meaningful analysis of bycatch trends.

For the five-year review of Pacific Groundfish EFH conducted by NMFS and the PFMC, data were compiled on fishing effort in three major gear sectors: bottom trawl, midwater trawl and fixed gears (see PFMC 2012). The intensity and extent of fishing effort for each gear type was mapped for two time periods bracketing implementation of EFH regulatory measures in June 2006. Mapping of bottom trawl intensity showed discrete areas where fishing effort either increased or decreased after June 2006, but in general effort appears to have moved from the continental shelf to deeper slope habitats. This shift in effort to deeper waters



was most likely caused not by EFH regulations but by the rockfish conservation area, a time-area closure designed to reduce bycatch of overfished groundfish. In fact, the analysis showed that EFH conservation areas did not significantly displace bottom trawling primarily because little (< 5% per year) bottom trawling occurred within these areas for the 4.5 years prior to implementation (NMFS 2013). In addition to the trawl restrictions in the rockfish conservation area, a footrope size restriction in late 2000 likely altered behavior of the bottom trawl fleet away from high-relief rocky habitats (Hannah 2003, Bellman et al. 2005). It is these types of habitats that many of the EFH closures were designed to protect.

Midwater, or pelagic, trawls do occasionally contact the seafloor, but observers have recorded very little bycatch of corals or sponges since records began in 2000. In fact, corals and sponges have been recorded in only 0.4% of tows between 2000 and 2010, totaling only 38.4 kg of bycatch over that time frame (PFMC 2012).

For fixed gears (e.g., longlines, pots, other hook-and-line), the annual proportion of effort within areas now closed to bottom trawls has fluctuated between 4 and 18% (NMFS 2013). This and the fact that observer coverage of many fixed gear sectors was relatively low compared to the trawl sector during this time period suggests it may be difficult to discern changes to fishing behavior due to implementation of EFH closures.

III.1.ii – Other Stressors

In addition to fishing, stressors such as sedimentation caused by oil and gas exploration, development and deployment of gas pipelines and communication cables, mining, pollution, and climate change were identified in the 2007 report. These continue to be important when considering the health and sustainability of deep-sea corals and sponges; however, little new information exists on specific impacts. A moratorium on new leases for offshore drilling for petroleum has existed in both federal (since 1984) and California state waters (since 1969); however, drilling continues on existing leases. A number of new submarine telecommunication cables have been installed in the region since 2007; however, the single study (Brancato and Bowlby 2005) and other anecdotal evidence suggest little impact on deep-sea corals and sponges. Finally, wind and wave energy projects have been considered along the West Coast, with a pilot wave energy facility permitted off Reedsport, Oregon. This facility underwent an extensive review by both state and federal agencies to ensure little impact to sensitive habitats. In the end, the installation company abandoned the project for lack of funding. Other sites would also be nearshore and should warrant a similar review, as deployment and operational aspects of these projects can have significant impact on the seabed, and should be evaluated for their potential impact on deep-sea corals and sponges (Boehlert et al. 2013). Despite growing interest from the energy sector, a moratorium on new federal wave energy permits for Oregon was put in place in 2008.



Since 2007, the specific role of climate change in ocean acidification has become more evident. Ocean acidification is predicted to affect corals worldwide, but maybe more immediately in the North Pacific (Guinotte et al. 2006). In the California Current System, upwelling brings acidified water up along the continental shelf, reaching the surface at some locations (Feely et al. 2008). Aragonite saturation levels (Ω_A) on the shelf may be among the lowest in the world (Manzello 2010), which is expected to impact calcification rates for many corals. There have, however, been no direct studies on the effects of acidification on west coast corals. Teck et al. (2010) surveyed 107 experts to quantitatively estimate the relative vulnerability of California Current ecosystems. For hard slope ecosystems, those most likely to support deep-sea corals and sponges, the stressors with the highest scores were ocean acidification and “demersal destructive fishing.” A recent threat assessment for the Davidson Seamount Management Zone identified ocean acidification, sea temperature rise, and vessel traffic (especially oil tankers) as the highest level threats to the seamount’s resources (NOAA 2012).

III.2. New or Planned Management Actions

Since 2007, a few management measures have been enacted to expand protection of areas where corals and sponges likely occur. The most significant action occurred in 2009, when the Monterey Bay National Marine Sanctuary was expanded to include Davidson Seamount off the coast of central California (15 CFR §

922.130). This undersea mountain, whose crest is approximately 1,250 m below the sea surface, is home to a diverse assemblage of dense, extensive deep-sea corals and sponges (Clague et al. 2010). The seamount was previously protected (in 2006) from fishing with bottom contact gear (or any other gear) below 3,000 feet (~ 1,000 m) by NMFS and the PFMC. Sanctuary designation provided additional protection against activities that might impact biological or non-biological sanctuary resources below 3,000 feet within the 2,006 km² Davidson Seamount Management Zone is prohibited without a permit.

In 2015, NOAA expanded the boundaries of Cordell Bank National Marine Sanctuary and Gulf of the Farallones National Marine Sanctuary (renamed Greater Farallones) to an area north and west of their old boundaries. This expansion eliminated the threat from petroleum development among other potential impacts to an area that includes major underwater features, such as Bodega Canyon, which could harbor significant coral and sponge resources.

The State of California, under the Marine Life Protection Act, has designated 94 MPAs in state waters with varying levels of protection, all of which comprise a network of protection along the entire California coast. These areas are enhancing the protection of corals and sponges in California State waters, and associated monitoring and research in these areas has added to our knowledge of the distribution of corals and sponges (Starr and Yoklavich 2008, Yoklavich et al. 2010).



As part of the PFMC 5-year review of Pacific coast groundfish EFH, a large amount of new data has been summarized and has greatly expanded our knowledge of the distribution of corals and sponges in the region (PFMC 2012, NMFS 2013). This review includes maps of the boundaries of current MPAs off the west coast. As part of this review, the Council received proposals from various sectors of the public to modify Pacific groundfish EFH. Most of these proposals include goals to protect deep-sea coral and sponge habitats.

The Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2006 (P.L. 109-479) directed NOAA to implement a Deep-sea Coral Research and Technology Program and allowed the designation of deep coral zones. It also gives regional fishery management councils new discretionary authority to protect corals and minimize interactions with fishing gears. This program funded research that has added to the information on corals and sponges on the West Coast. That information combined with a variety of continuing research projects conducted by other institutions has enhanced our knowledge of these resources. In addition, NMFS recently has developed a Habitat Assessment Improvement Plan (HAIP) (NMFS 2010) that outlines research priorities and procedures to improve habitat assessments. Many research activities associated with the HAIP will provide information to aid in our understanding and protection of deep-sea corals and sponges.

IV. Conclusions

Since 2007 there has been significant progress in gathering and organizing information on seafloor habitats and species, which has advanced our understanding of deep-sea coral abundance and distribution off the U.S. west coast. Most recently, much of this has been catalyzed by NOAA's Deep Sea Coral Research and Technology Program and data efforts associated with the PFMC 5-year review of Pacific coast groundfish EFH. Deep-sea corals on hard substrata are widely distributed and the composition of assemblages changes with depth. The dominant species in many areas are small and occur at relatively low densities, but in certain areas (e.g., ridges of seamount and certain banks, particularly in the Southern California Bight), larger gorgonian species may occur in patches of high density. Since 2007, there has been increased interest in sea pens, which occur on soft sediments and therefore are much more widespread than other corals.

Information on deep-sea sponges is much more rudimentary than our understanding of corals, and the data on sponges in this chapter is cursory at best. Most sponges, when recorded at all, are often not identified below the Phylum level. As elsewhere in the world, deepwater species are primarily glass sponges (Class Hexactinellida) and demosponges (Class Demospongiae). Still, it appears that in many hard-bottom habitats in deeper waters, sponges are more abundant than corals. Some habitats are dominated by sponges, such as glass sponge grounds, while corals are generally absent. The abundance of sponge habitats is reflected in their predominant occurrence in



catches from the NMFS West Coast Groundfish Bottom Trawl Survey and in bycatch in bottom trawl fisheries as recorded by the West Coast Groundfish Observer Program.

Fishing with bottom-contact gear, especially bottom trawls, remains the most immediate threat to both deep-sea coral and sponge ecosystems. While many areas expected to be prime habitat for corals and sponges were protected from trawling either indirectly in 2001 or directly in 2006, continued bycatch in commercial trawl fisheries indicates that significant interactions remain, and in many cases are restricted to relatively discrete areas (Figure 3). Among other stressors, ocean acidification will be a major long-term concern for some corals, although studies of specific impacts to corals in the region are lacking.

Since 2007, there have been very significant conservation actions in state waters (e.g., new MPAs) where corals and sponges are present. The expansion of Monterey Bay National Marine Sanctuary to include Davidson Seamount, and the expansion to create the Greater Farallones National Marine Sanctuary, represent the major management actions in the EEZ since 2007 that serve to protect deep-sea coral and sponge ecosystems.

V. Acknowledgements

We appreciate the thoughtful comments on earlier drafts of this chapter by our three colleagues: Tom Laidig (SWFSC), Aimee Keller (NWFSC) and Dan Howard (CBNMS).

Online Annex – Comprehensive list of deep-sea corals in the U.S. West Coast region linked here:

<https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>

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[Online Annex 1. Deep-sea Coral Taxa in the U.S. West Coast Region: Depth and Geographic Distribution](#)



Appendix

Table A. Sites of major research expeditions (2007-2014) referenced in the chapter that included deep-sea coral or sponge research. (DSCRTP = Deep Sea Coral Research and Technology Program; MBARI = Monterey Bay Aquarium Research Institute; NCCOS = National Centers for Coastal Ocean Research; NMS = National Marine Sanctuary; SWFSC = Southwest Fisheries Science Center; DFO Canada = Department of Fisheries and Oceans, Canada; BOEM = Bureau of Ocean Energy Management; COPC = California Ocean Protection Council; CDFW = California Department of Fish and Wildlife; USGS = United States Geological Survey; NWFSC = Northwest Fisheries Science Center; UW = University of Washington).

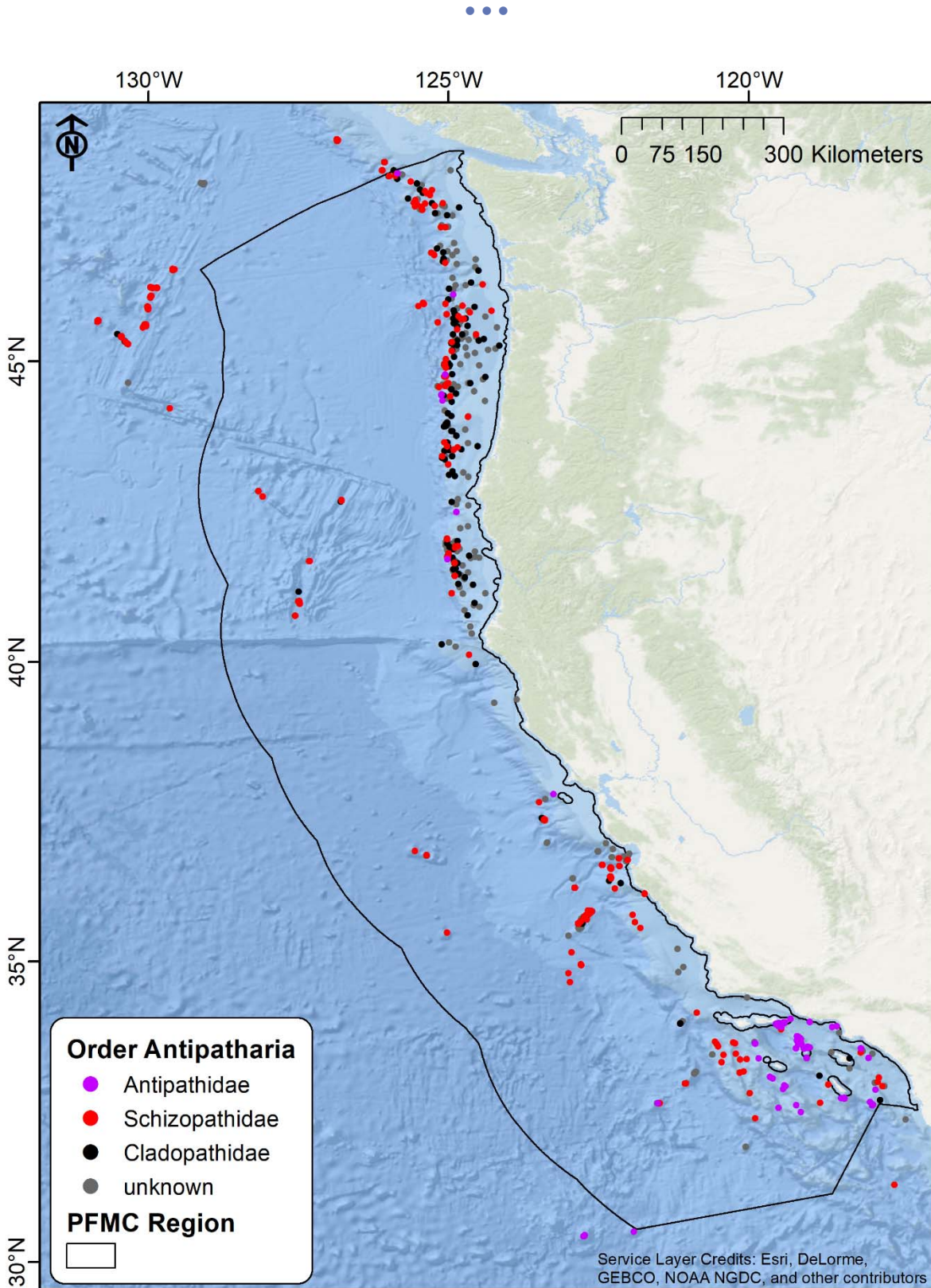
Location	Year	Vessel	Description	Program
Southern California Bight & Channel Islands NMS	2007	NOAA Ship	ROV photo surveys for ESA-listed abalone	NOAA SWFSC
	2008	<i>David Starr Jordan</i>	(subsequently analyzed for deep-sea coral occurrence) on several rocky banks. PI: J. Butler	
	2008	R/V <i>Velero IV</i>	Submersible video surveys for fishes and <i>Stylaster californicus</i> on Farnsworth Bank near Catalina Island. PI: M. Love	BOEM
	2010	NOAA Ship <i>McArthur II</i>	ROV and AUV surveys of Piggy Bank, Channel Islands NMS. PI: M. Yoklavich & M.E. Clarke	NOAA DSCRTP
	2010	R/V <i>Velero IV</i>	Submersible surveys of Christmas tree black coral habitats in Channel Islands NMS. PI: M. Yoklavich	NOAA DSCRTP
	2010	CPFV <i>Outer Limits</i>	ROV photo surveys of several rocky banks. PI: J. Butler & P. Etnoyer	NOAA SWFSC, NCCOS
	2011	R/V <i>Velero IV</i>	Submersible surveys of fishes and invertebrates on rocky banks in Channel Island NMS. PI: M. Yoklavich	NOAA SWFSC
Pioneer & Davidson Seamounts	2013	R/V <i>Shearwater</i>	ROV Surveys for deep-sea coral habitats in Channel Islands NMS. PI: S. Katz	NOAA DSCRTP
	2007	R/V <i>Western Flyer</i>	ROV surveys of Pioneer and Davidson Seamounts. PI: D. Clague	MBARI
Monterey Bay NMS	2009	R/V <i>Western Flyer</i>	ROV surveys of Davidson Seamount. PI: J. Barry	MBARI
	2008	R/V <i>Point Lobos</i>	ROV surveys of Monterey Canyon. PI: C. McClain	MBARI
	2007	R/V <i>Velero IV</i>	Submersible video surveys for fishes and invertebrates in and out of 8 offshore MPAs. PI: M. Yoklavich & R. Starr	COPC, CDFW
	2010	NOAA Ship <i>Bell M. Shimada</i>	ROV photo surveys of Sur Canyon. PI: J. Butler & P. Etnoyer	NOAA SWFSC, NCCOS
	2010	R/V <i>Derek M. Baylis</i>	ROV surveys at 17 sites in Monterey and Carmel Bays. PI: G. Shester	Oceana
	2013	R/V <i>Western Flyer</i>	ROV survey of Sur Ridge. PI: J. Barry & A. DeVogelaere	MBARI, NOAA MBNMS

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. WEST COAST

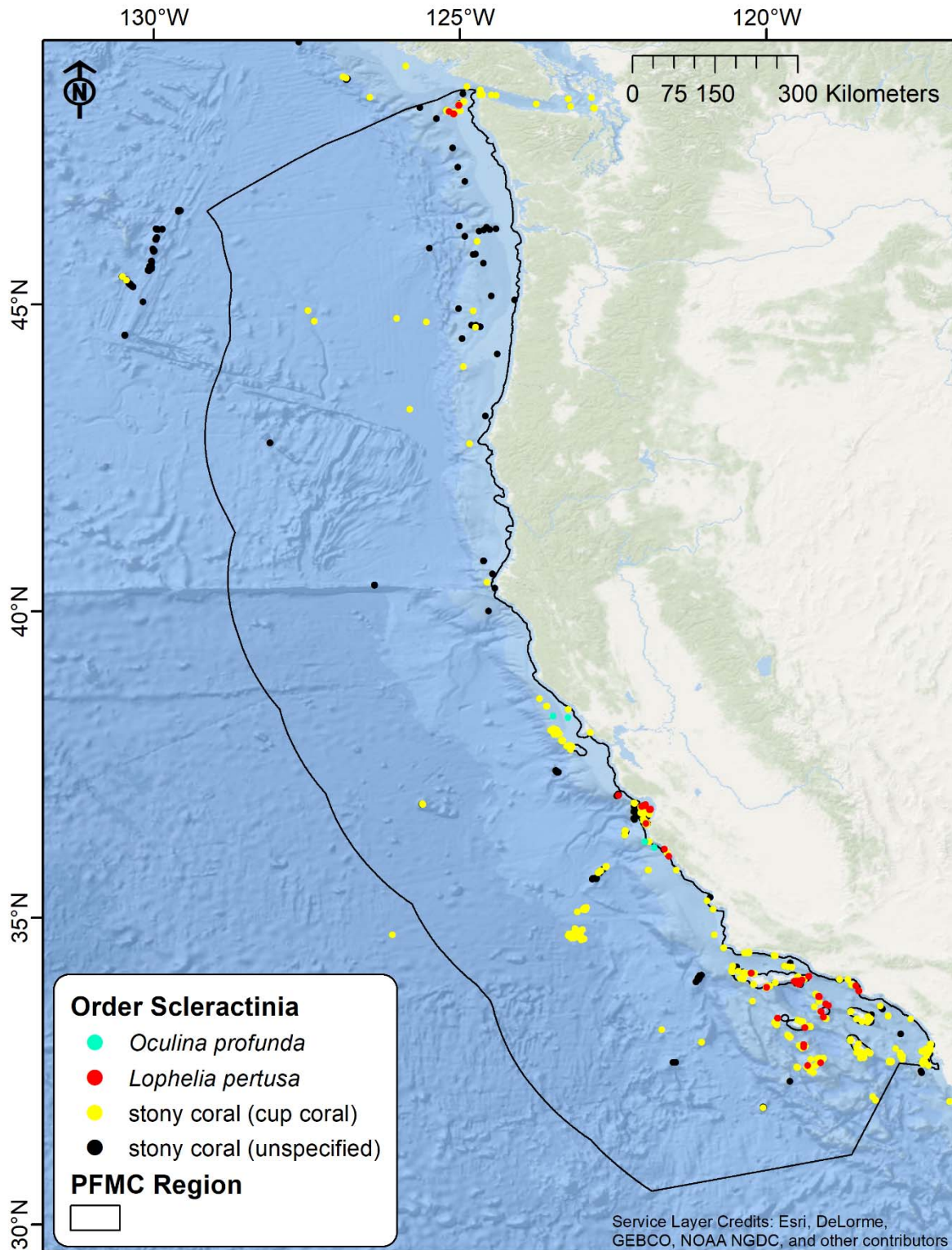


Table A. continued

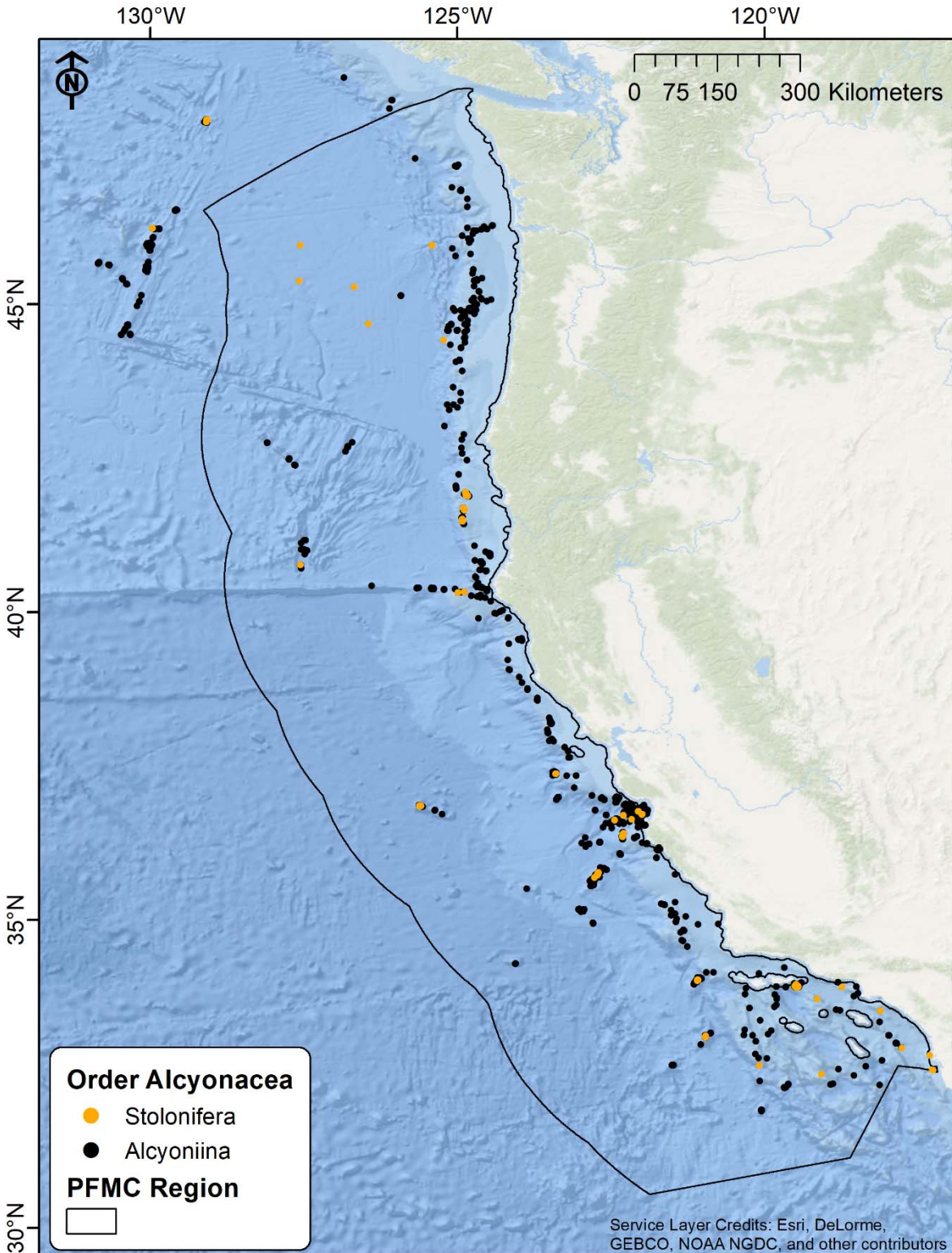
Location	Year	Vessel	Description	Program
Gulf of the Farallones NMS	2009	NOAA Ship <i>Okeanos Explorer</i>	Multibeam mapping survey of Gulf of the Farallones NMS and potential sanctuary expansion area. PI: M. Malik	NOAA Ocean Exploration
	2011	R/V <i>Fulmar</i>	Multibeam survey of potential deep-sea coral habitats on Rittenburg Bank and Farallon Escarpment. PI: J. Roletto	NOAA DSCRTP
	2012	R/V <i>Fulmar</i>	ROV survey of Rittenburg Bank, Cochrane Bank and Farallon Escarpment. PI: J. Roletto	NOAA DSCRTP
Cordell Bank NMS	2007	R/V <i>Fulmar</i>	Camera sled video surveys of deepwater habitats. PI: D. Roberts	NOAA CBNMS
	2009	NOAA Ship <i>Okeanos Explorer</i>	Multibeam mapping survey of Cordell Bank NMS and potential sanctuary expansion area. PI: M. Malik	NOAA Ocean Exploration
	2010	NOAA Ship <i>McArthur II</i>	ROV surveys. PI: D. Howard	NOAA DSCRTP
	2011	R/V <i>Fulmar</i>	AUV survey for potential deep-sea coral habitats. PIs: M.E. Clarke & D. Howard	NOAA DSCRTP
California Coast	2007-2012	R/V <i>Lakota & Coral Sea</i> ; R/V <i>Fulmar & Shearwater</i>	Camera sled video surveys of seafloor invertebrate communities in continental shelf habitats throughout California state waters. PI: G. Cochrane & L. Krigsmann	USGS, SWFSC
	2014	R/V <i>Point Sur</i>	AUV and towed camera surveys of areas of high bycatch of deep-sea corals off Northern California	NOAA DSCRTP
Oregon Coast	2010	NOAA Ship <i>Bell M. Shimada</i>	ROV photo surveys of Coquille Bank. PI: J. Butler & P. Etnoyer	NOAA SWFSC, NCCOS
	2011	R/V <i>Miss Linda</i>	ROV surveys at Cape Arago, Coquille Reef and Bank, Orford Reef. PI: B. Enticknap	Oceana
	2013	R/V <i>Miss Linda</i>	ROV surveys at Stonewall Bank, Hecata Bank, Daisy Bank, Siletz Hotspot, Siletz Reef/Cascade Head. PI: B. Enticknap	Oceana
Grays Canyon	2007	R/V <i>Thomas G. Thompson</i>	Side-scan sonar and Van Veen grab surveys of glass sponge grounds. PI: P. Johnson	UW
	2009	R/V <i>Kvichak Defender VI</i>	ROV survey of glass sponges and associated methane seeps and krill swarms. PI: P. Johnson	UW
	2010	R/V <i>Pacific Storm</i>	AUV surveys of glass sponges. PI: M.E. Clarke	NOAA DSCRTP
Olympic Coast NMS	2008	CCGS <i>John P. Tully</i>	ROV surveys. PI: E. Bowlby	NOAA OCNMS, DFO Canada
	2008	NOAA Ship <i>Okeanos Explorer</i>	Multibeam mapping survey. PI: M. Malik	NOAA Ocean Exploration
	2010	NOAA Ship <i>McArthur II</i>	ROV and AUV surveys. PI: E. Bowlby	NOAA DSCRTP
	2010	NOAA Ship <i>Bell M. Shimada</i>	ROV photo surveys. PI: J. Butler & P. Etnoyer	NOAA SWFSC, NCCOS
	2011	R/V <i>Pacific Storm</i>	Multibeam survey of potential deep-sea coral habitats. PI: E. Bowlby	NOAA DSCRTP
Cobb Seamount	2012	CCGS <i>John P. Tully</i>	ROV and AUV surveys of corals and sponges. PI: M.E. Clarke & J. Curtis	NOAA DSCRTP, NOAA NWFSC, DFO Canada
Bowie Seamount	2011	CCGS <i>John P. Tully</i>	ROV and AUV surveys for corals and sponges. PI: M.E. Clarke & J. Boutillier	NOAA DSCRTP, NOAA NWFSC, DFO Canada



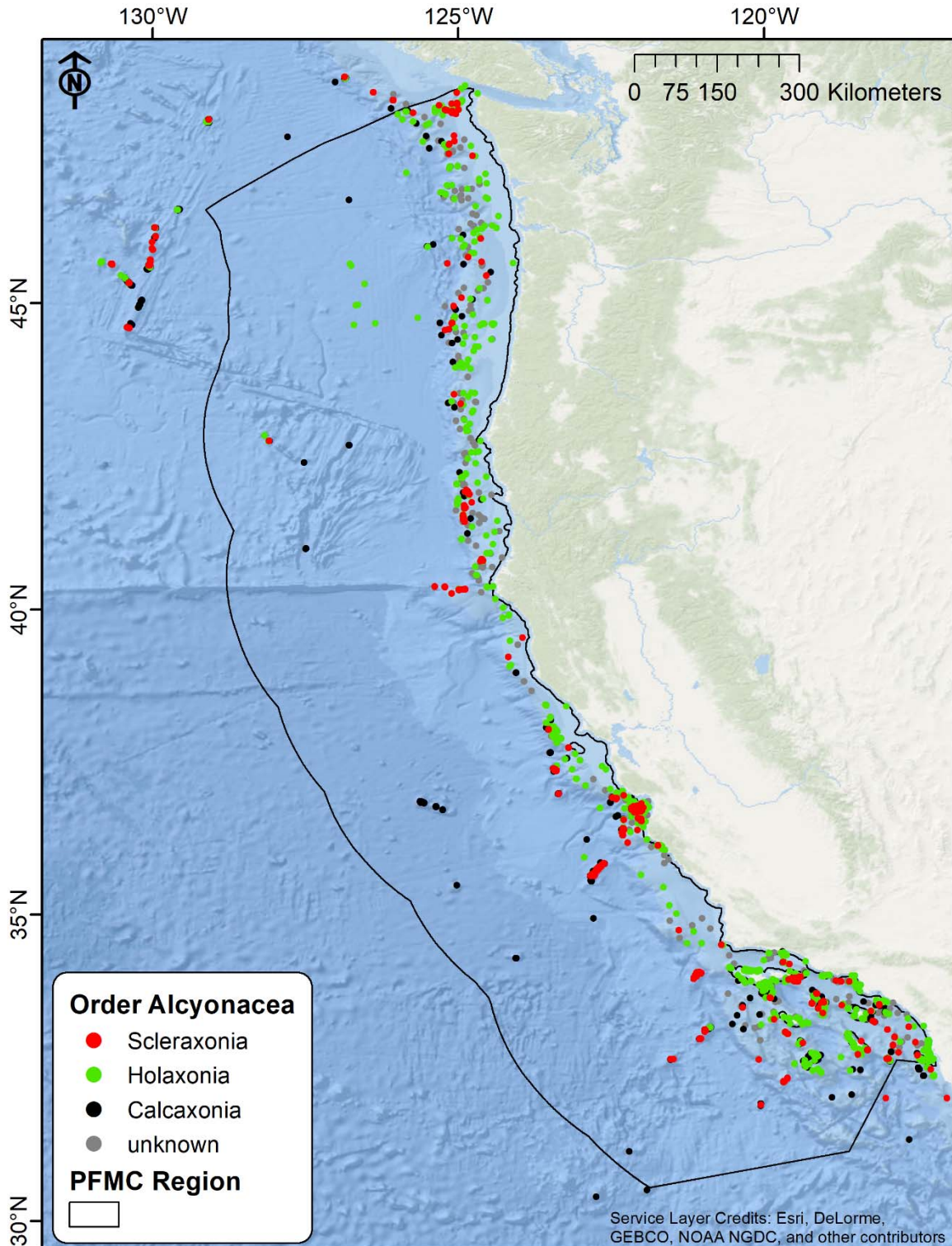
Map 1. Locations of black corals (Order Antipatharia) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017). PFMC = Pacific Fishery Management Council.



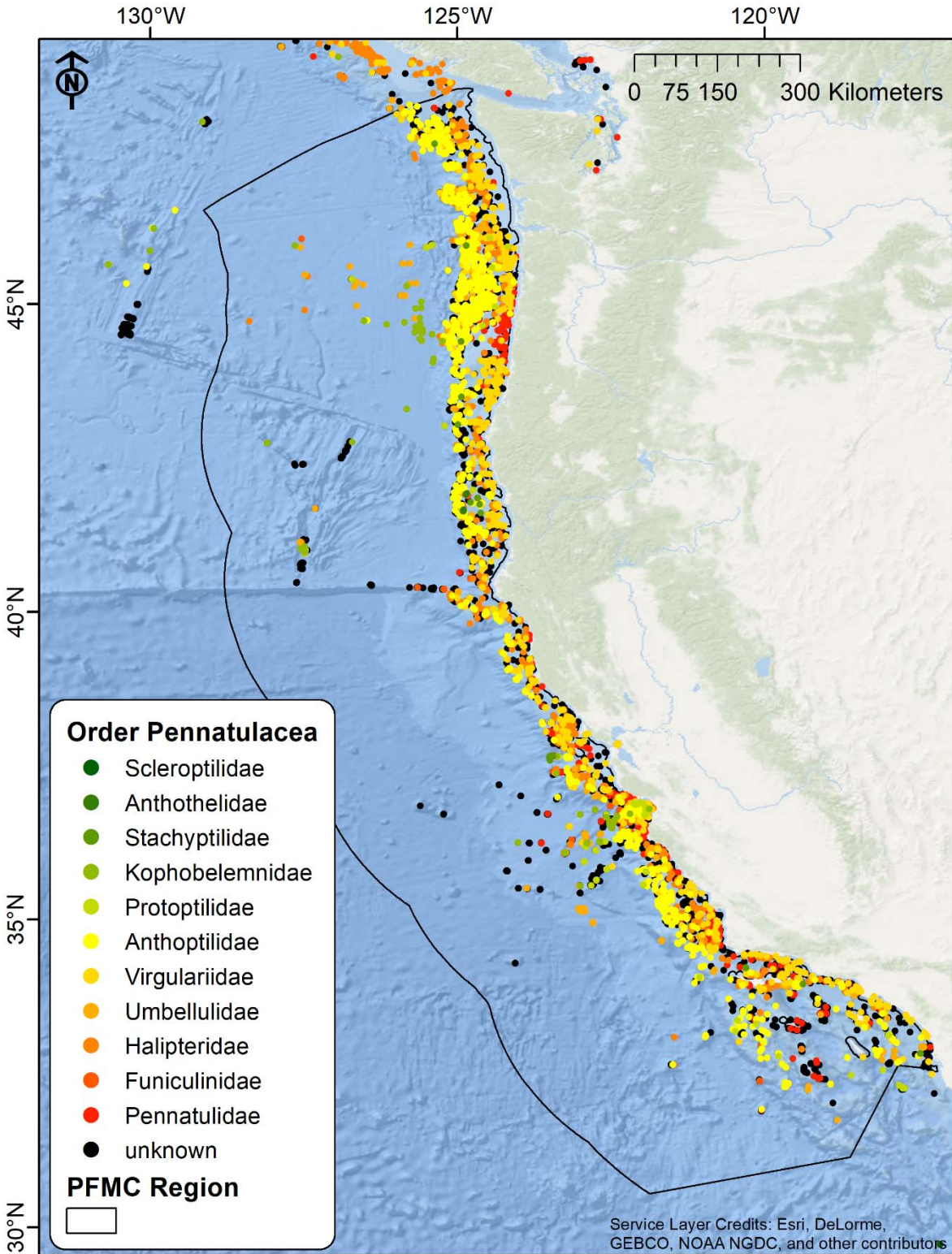
Map 2. Locations of stony corals (Order Scleractinia) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



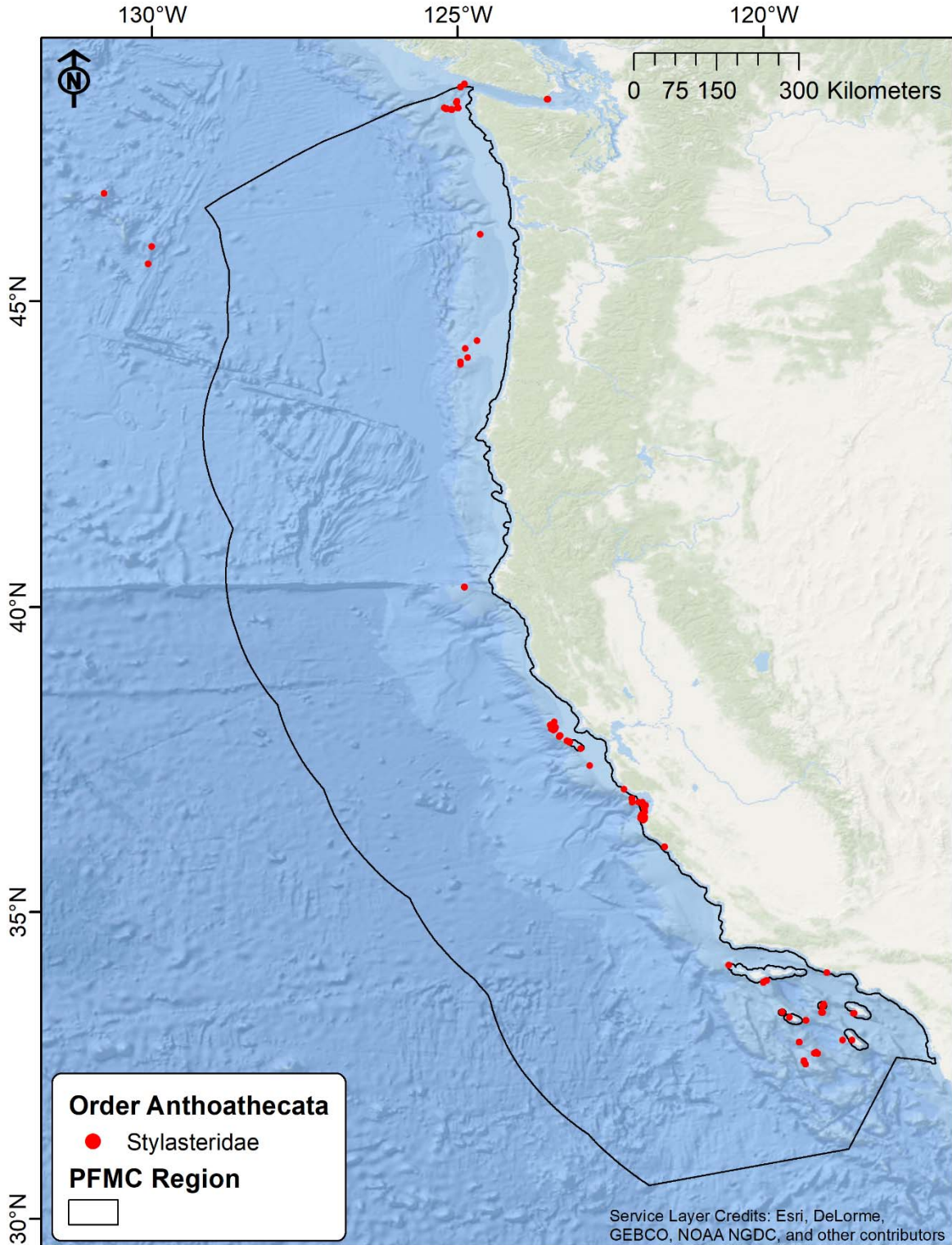
Map 3. Locations of non-gorgonian alcyonacean (true soft corals and stoloniferan corals; Order Alcyonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



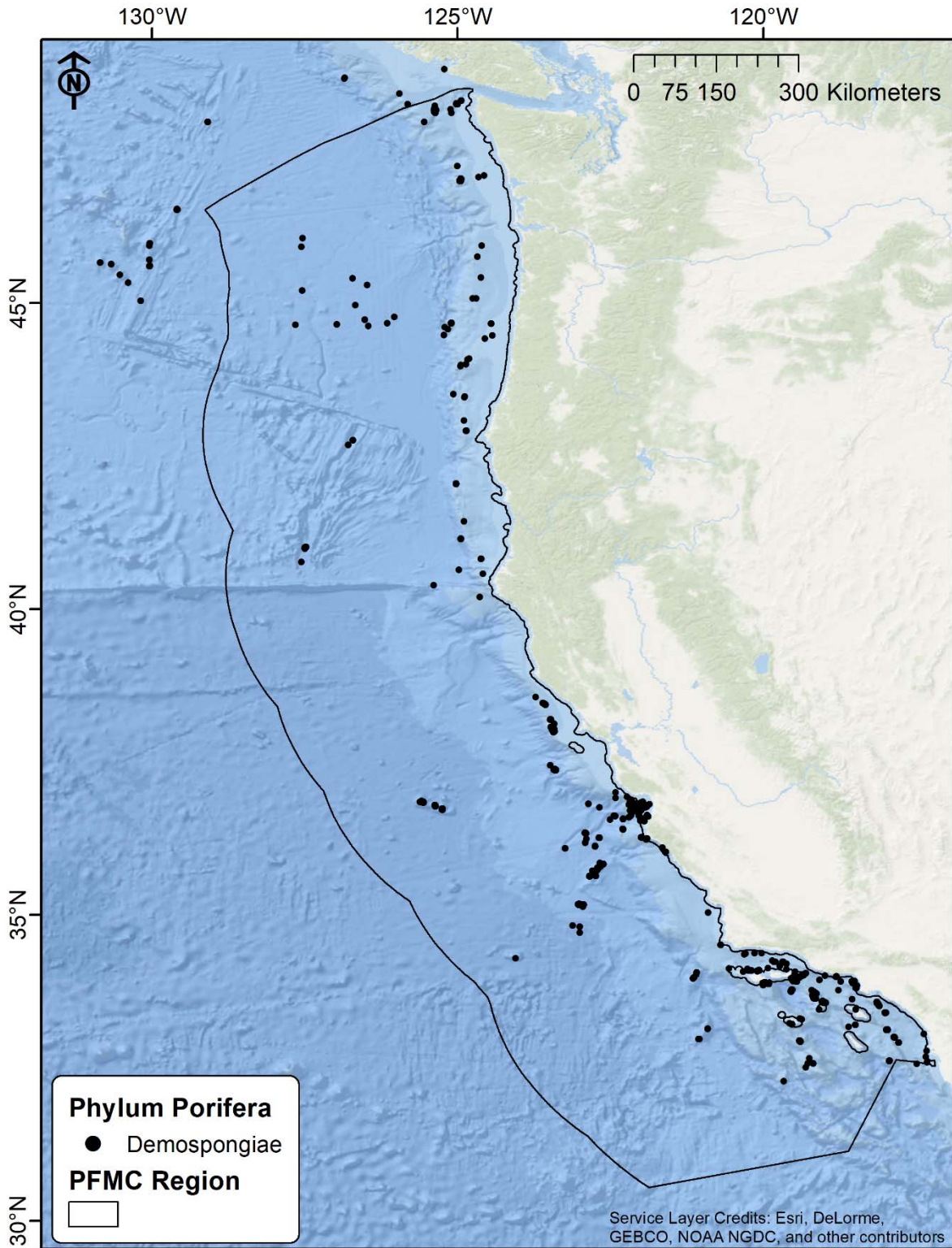
Map 4. Locations of gorgonians (formerly Order Gorgonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



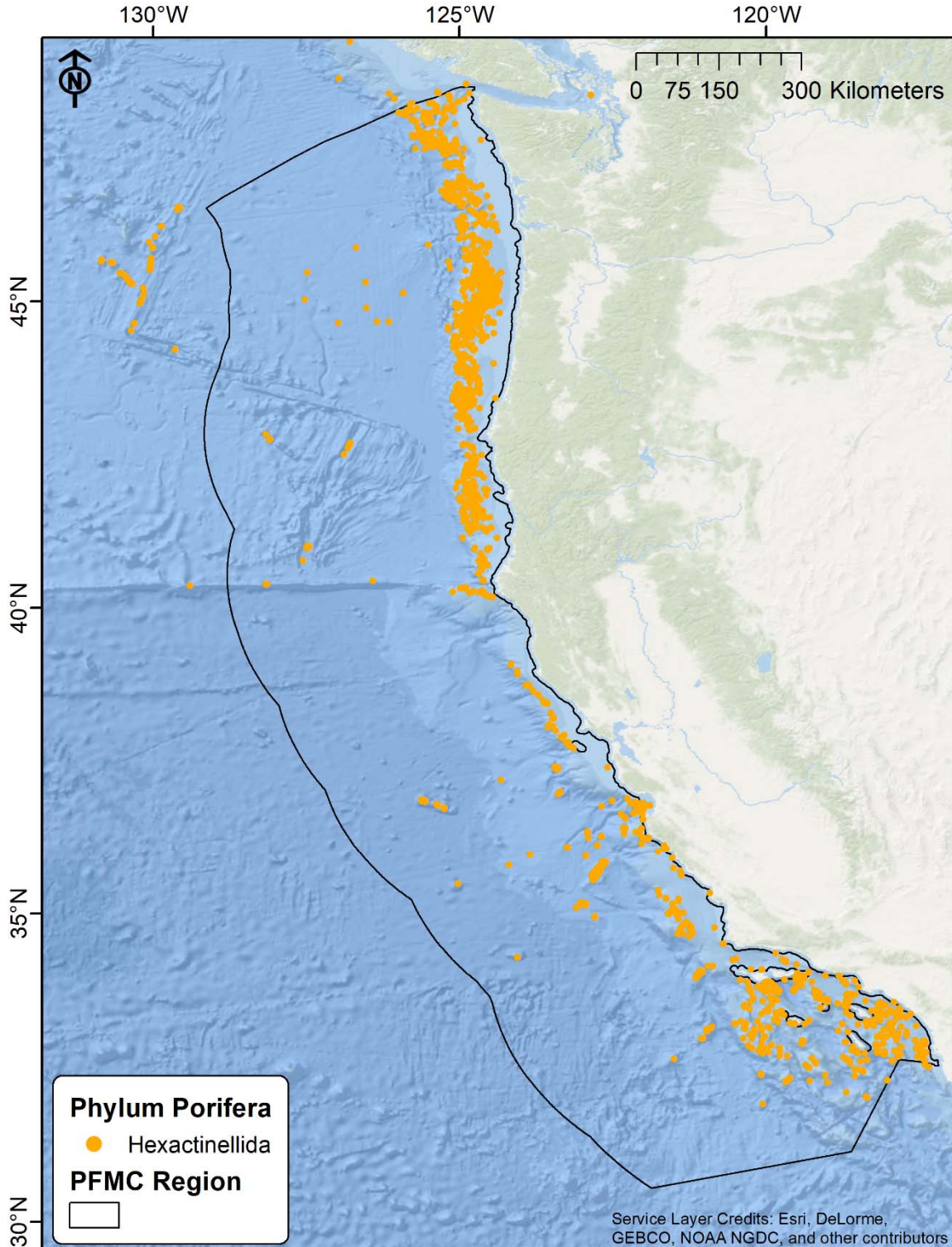
Map 5. Locations of sea pens (Order Pennatulacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



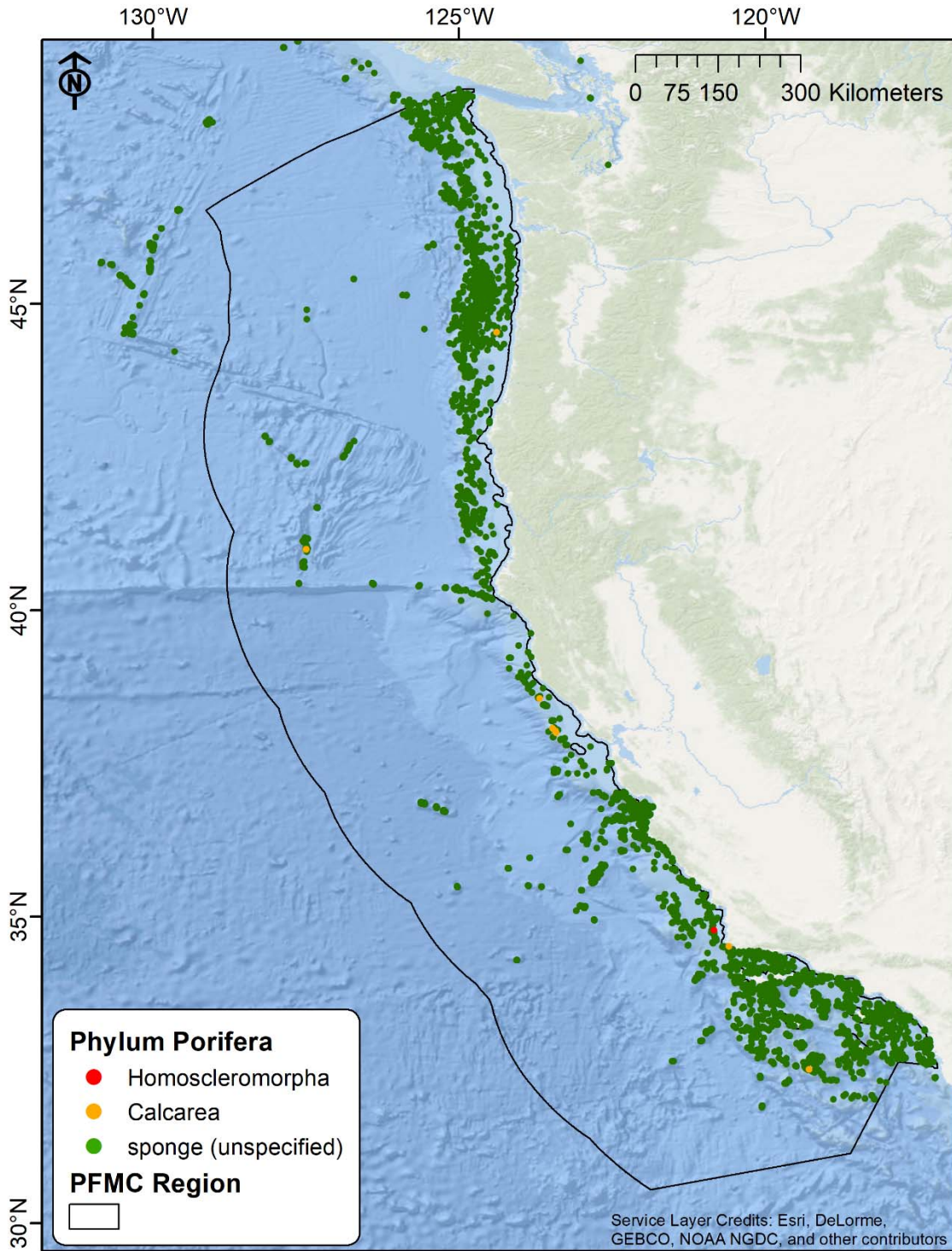
Map 6. Locations of lace corals (Order Anthoathecata, Family Stylasteridae) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



Map 7. Locations of demosponges (Class Demospongiae) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



Map 8. Locations of glass sponges (Class Hexactinellida) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



Map 9. Locations of sponges (Classes Homoscleromorpha, Calcareia, and unspecified) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).

Black coral *Bathypathes* on a rocky ridge crest
of Johnston Atoll. Courtesy of the NOAA
Office of Ocean Exploration and Research.





AN UPDATE ON RECENT RESEARCH AND MANAGEMENT OF HAWAIIAN BLACK CORALS

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Parrish⁴*



1. Introduction

Antipatharians, commonly known as black corals, are a little studied order of anthozoan hexacorals that currently encompasses over 235 described species (Cairns 2007, Daly et al. 2007, Bo 2008). Black corals occur worldwide in all oceans from polar to tropical regions, and have a wide depth distribution ranging from 2-8,600 m (reviewed by Wagner et al. 2012a). Despite this wide bathymetric range, black corals are primarily found in deeper waters below the photic zone, with over 75% of known species occurring exclusively below 50 m (Cairns 2007). At these depths, antipatharians are often abundant and dominant faunal components, and create habitat for a myriad of associated organisms (reviewed by Wagner et al. 2012a).

In Hawai'i black corals are particularly important, not just from an ecological perspective, but also from an economic and cultural one. First, black corals are the predominant habitat-forming species on Hawaiian deep reefs that are exposed to strong currents (50-150 m; Grigg 1965, Grigg 1976, Chave and Malahoff 1998, Parrish and Baco 2007). Second, Hawai'i is the only place in the United States, and only one of a few places in the world, where black coral is harvested commercially for the precious coral jewelry industry, a multi-million dollar business that employs close to 650 people in manufacturing facilities and retail stores statewide (Grigg 2001, Parrish and Baco 2007, Grigg 2010). Third, black corals are important culturally as they

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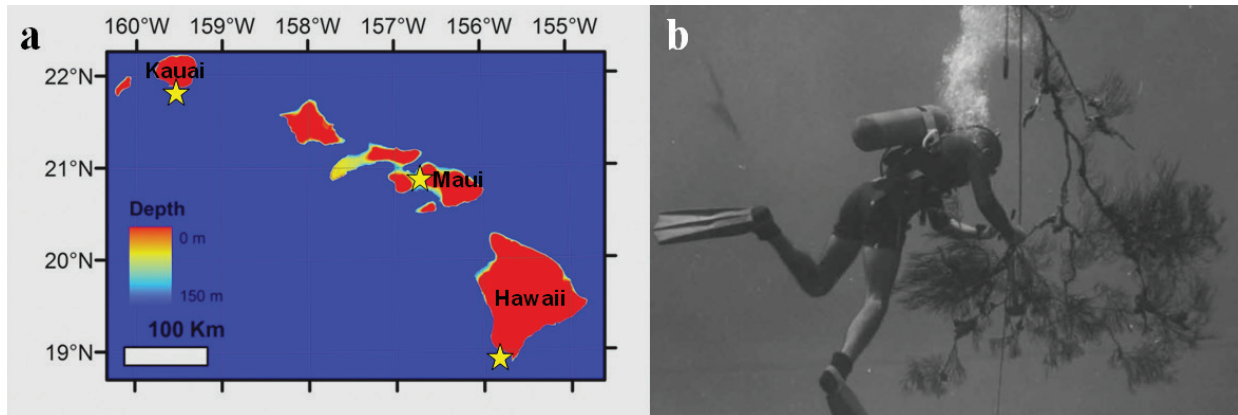


Figure 1. (a) Map showing the geographic locations of the three largest commercially valuable black coral beds in Hawai'i. (b) Diver attaching a black coral colony to an anchor line so it can be lifted to the surface (Photo by R. Grigg).

represent the official gemstone of the State of Hawai'i, and were traditionally used in Hawaiian culture for medicinal purposes (Kaaiakamanu and Akina 1922, Chun 1994). 'Ēkaha kū moana, as black coral is known in the Hawaiian language, has for a long time been cherished by native Hawaiians for its presumed therapeutic effects against lung diseases and mouth sores (Kaaiakamanu and Akina 1922, Chun 1994).

Despite the fact that native Hawaiians have used black corals for several centuries, Hawaiian antipatharians were only discovered by western scientists at the beginning of the 20th century. In 1902, the scientific expedition by the U.S. Fish Commission Steamer *Albatross* was the first to sample black corals from the Hawaiian Archipelago (Bayer 1961). Through the use of deep-sea trawls and tangle nets, the *Albatross* sampled black corals in Hawaiian waters at depths exceeding 2,000 m, although the majority of antipatharian specimens were collected at depths shallower than 500 m (Bayer 1961). Black coral specimens collected by the *Albatross* were deposited in the National Museum of Natural History, where they remained largely unexamined

until recent reexaminations of these collections led to the description of numerous new antipatharian species including several from Hawaiian waters (Opresko 2002, 2003c, 2005, Wagner and Opresko 2015, Wagner 2015a). In 1928, Verrill was the first to formally describe Hawaiian black coral species, when he described *Antipathes grandis* and *Antipathes irregularis* (Verrill 1928), the latter of which was later identified as a gorgonian (Grigg and Opresko 1977). In 1958, large aggregations of black corals were discovered off Maui (Gage 1962, Grigg 1964), a discovery that eventually led to the development of a local black coral fishery (Grigg 2001), as well as to numerous studies on this group of corals. Scientists, resource managers and fishermen have collaborated closely throughout the history of the fishery (Grigg 2001), and as a result, Hawaiian antipatharians are among the best studied on the globe (Etnoyer and Morgan 2005, Wagner et al. 2012a). The purpose of this article is to briefly summarize these collaborations, with an emphasis on black coral research and management activities that have occurred since the last synthesis on the state of the deep-sea coral ecosystems in Hawai'i (Parrish and Baco 2007).



II. The History of the Hawaiian Black Coral Fishery

Since its inception in 1958, the Hawaiian black coral fishery has been supplied by SCUBA divers that collect the coral at depths between 40-70 m, primarily in the Au'au Channel between the islands of Maui and Lāna'i, and to a lesser extent off the islands of Kaua'i and Hawai'i (Figure 1; Oishi 1990, Grigg 2001, Parrish and Baco 2007). Harvesting methods have remained essentially unchanged since start of the fishery, and involve fishermen descending to black coral beds using SCUBA, severing colonies from the substrate using axes or sledges, and then bringing coral trees back to the surface via lift bags or anchor lines (Figure 1; Oishi 1990, Grigg 2001). Three black coral species have been reported as being targeted by the Hawaiian precious coral fishery, and include *Antipathes griggi* Opresko, 2009 (formerly *A. dichotoma*), *Antipathes grandis* Verrill, 1928, and *Myriopathes* cf. *ulex* (Ellis and Solander, 1786) (formerly *Antipathes ulex*) (Figure 2; Grigg 1976, NOAA 1983, Oishi 1990, DLNR 1999, Grigg 2001, Parrish and Baco 2007, Grigg 2010). However, close to 90% of the coral harvested in Hawaiian waters consists of *A. griggi*, with *A. grandis* and *M.* cf. *ulex* representing 10% and 1% of harvested black coral, respectively (Oishi 1990).

III. Black Coral Fishery Management

The vast majority of commercially valuable black coral beds lie in waters that fall under the jurisdiction of the State of Hawai'i (< 3 nautical miles from shoreline), with a much lesser degree found in federal waters (3-200 nautical miles from shore) (Figure 1; Grigg 2001, Parrish and Baco 2007, Grigg 2010). The fishery is therefore managed through

both state and federal regulations, which are set by the Hawai'i Department of Land and Natural Resources (DLNR), and NOAA's National Marine Fisheries Service (NMFS) in consultation with the Western Pacific Regional Fishery Management Council (WPRFMC), respectively (NOAA 1983, DLNR 1999, NOAA 2002, DeMello 2006, NOAA 2007, 2008). State regulations came into effect in 1981 (DLNR 1999). Since then, all harvesters of black corals in Hawaiian state waters are required to purchase a state commercial marine license, and submit catch reports if the coral is sold (Oishi 1990). In 1999, the State of Hawai'i added size limits by which it prohibited harvesting of colonies with a base diameter of less than 1.905 cm (DLNR 1999), which corresponds to a colony height of 90 cm (Boland and Parrish 2005), or an age of 14-15 years using growth rate estimates (6.12-6.42 cm/yr; Grigg 1976). Federal regulations on the fishery became effective in 1983, which mandated domestic fishermen to report their catches in federal waters (NOAA 1983). In 2002, federal regulations added size harvesting limits, which prohibited harvesting of colonies with a base diameter of less than 2.54 cm or a colony height lesser than 122 cm (NOAA 2002). Additionally, the 2002 federal rule provided persons that had reported black coral landings between 1997 and 2002 the option to apply for an exemption, that allowed harvesting using the minimum base diameter of 1.905 cm (NOAA 2002). This exemption was removed in 2007, thereby effectively prohibiting all harvesting of colonies less than 122 cm in height or 2.54 cm in width from federal waters (NOAA 2007). In 2008, a harvesting quota of 5,000 kg/2 years was established for the Au'au Channel bed (Figure 1), where the vast majority of black corals have been harvested since 1980 (Parrish 2006, NOAA 2008). In 2012, an annual catch limit of



2,500 kg/year was set for the Au'au Channel bed (NOAA 2012). While this annual catch limit applies to the entire Au'au Channel bed, which extends through both state and federal waters, it is currently only enforced in federal waters (NOAA 2012). Additionally, the 2012 revisions set an annual catch limit of 1,000 kg/year for all precious corals in the Hawai'i exploratory area (NOAA 2012). This catch limit applies to all precious corals found in federal waters anywhere else outside the Au'au Channel bed in Hawai'i, and includes pink, red, bamboo, gold (currently under moratorium) and black corals (NOAA 2012).

IV. Recent Research

The recent revisions of fishery regulations (NOAA 2007, 2008, 2012), were the result of a number of deep-water surveys (40-110 m) that indicated a decline in the biomass of commercially valuable black corals (Grigg 2001, 2004). Surveys performed in the Au'au Channel in 1975 and 1998, showed similar colony size-frequency distributions, and thereby suggested a long-term stability in the recruitment and growth of black coral populations (Grigg 2001). In contrast, subsequent surveys performed in 2001, revealed a downward shift towards smaller sized colonies, as well as a 25% decline in the biomass of black corals since 1998 (Grigg 2004). Likely causes for these declining patterns included both increases in harvesting pressure, and overgrowth of black corals by the invasive octocoral *Carijoa* sp. (initially identified as *Carijoa riisei*; Grigg 2003, 2004, Kahng and Grigg 2005). Together, these developments raised questions about whether fishery regulations needed to be redefined in order to maintain a sustainable harvest (Grigg 2004). To address these concerns, the WPRFMC held a workshop to review the state

of the Hawaiian black coral fishery and to identify future research priorities (WPRFMC 2006). The workshop highlighted the need for studies on the (1) growth, (2) reproduction, (3) recruitment, (4) mortality, (5) fishing, and (6) geographical distributions of Hawaiian antipatharians (WPRFMC 2006). Motivated in large part by these recommendations, several studies have recently examined various aspects of the taxonomy, biology and ecology of commercially valuable Hawaiian black corals, and are briefly reviewed below.

IV.1. Taxonomy

In 1977, Grigg and Opresko (1977) published a taxonomic survey of Hawaiian antipatharians based on colony branching pattern. Since that study, skeletal spine morphology has become increasingly important in antipatharian taxonomy (Opresko 2001, 2002, 2003c, 2004, 2005, 2006, and references therein), because this character is thought to be largely independent of environmental cues, as compared to other more plastic morphological characters (Lapian et al. 2007, Wagner et al. 2010). Recent taxonomic studies using skeletal spine morphology have led to more detailed descriptions of several Hawaiian species, as well as to revisions of the species names that had previously been used in the literature (Opresko 2009, Wagner et al. 2010, Wagner 2011, Wagner et al. 2011a, Opresko et al. 2012, Wagner 2015a). While these recent revisions have provided better insights into what species are present in Hawaiian waters and how they compare to species found elsewhere, systematics of the entire antipatharian order are still in a state of revision.

Prior to recent revisions, the Hawaiian species *Antipathes griggi* (Figure 2) was known as *A. dichotoma* Pallas, 1766, a species originally described from off Marseilles in the

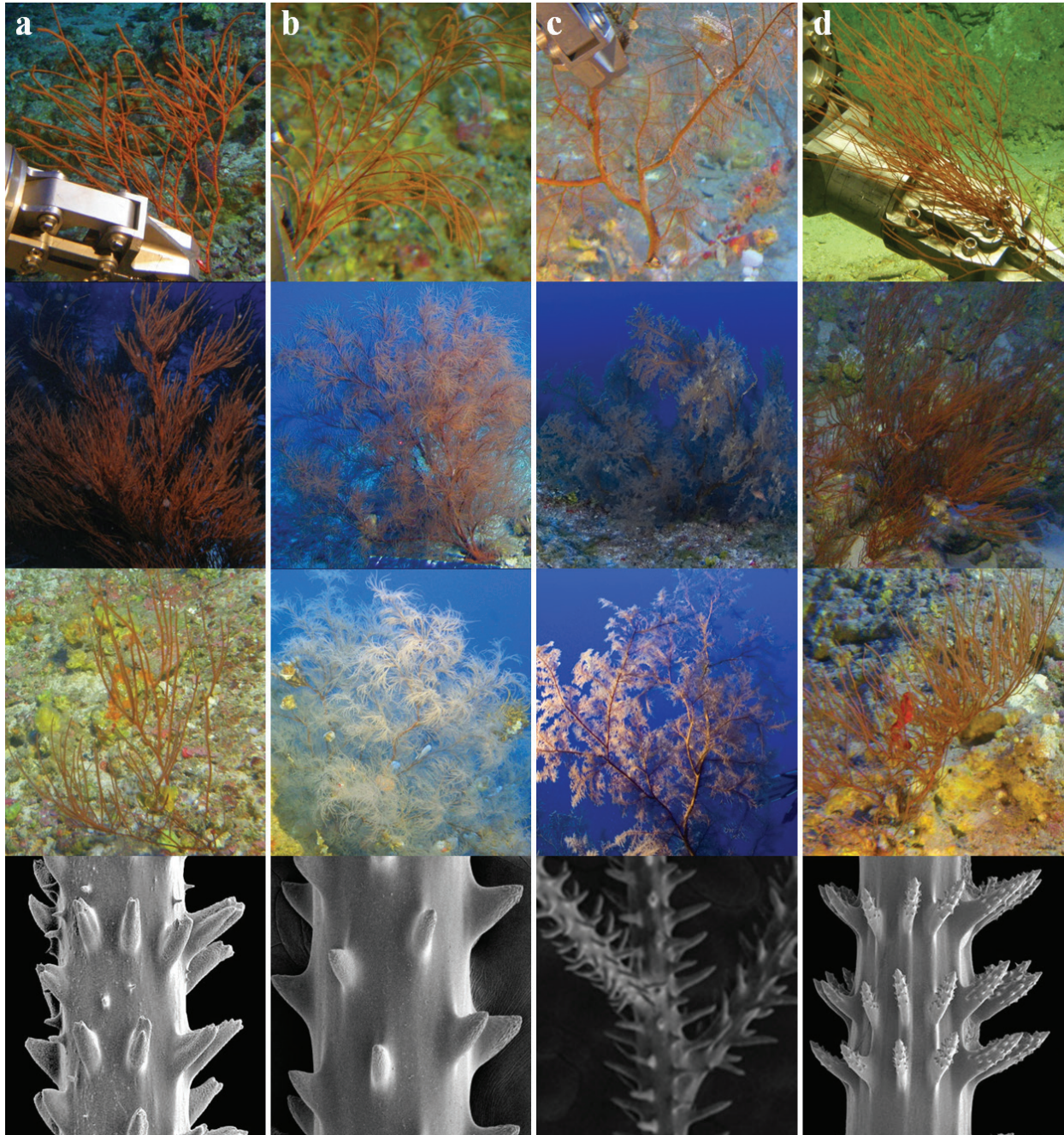


Figure 2. Hawaiian antipatharian species (a) Antipathes griggi, (b) Antipathes grandis, (c) Myriopathes cf. ulex, and (d) Aphanipathes verticillata (scale bars = 200 μ m). NOTE: With the exception of M. cf. ulex, species cannot be reliably differentiated based on colony morphology alone, and typically require microscopic examination of skeletal spines (bottom row). Photos courtesy of the Hawaiian Undersea Research Laboratory (HURL).



Mediterranean Sea (Pallas 1766). Subsequent comparisons between Hawaiian and Mediterranean specimens revealed substantial morphological differences (Opresko 2003a). As a result, the Hawaiian “*A. dichotoma*” was assigned the new name of *Antipathes griggi* and formally described (Opresko 2009).

Even though *Antipathes grandis* (Figure 2) was the first antipatharian species to be described from Hawai‘i (Verrill 1928), the original species description was very brief and the type material remained unexamined for a long period. Therefore, Wagner et al. (2010) redescribed *A. grandis* using morphological and molecular characters, in conjunction with *in situ* observations. These examinations revealed that *A. grandis* colonies can exhibit three different color morphotypes, at least one of which may have been confounded with *A. griggi* in the past (Figure 2).

Grigg (1964) presented the first published account of *Myriopathes* cf. *ulex* (Figure 2) from Hawai‘i (as *Antipathella* sp.), and Grigg and Opresko (1977) later identified this species as *Antipathes ulex* Ellis and Solander, 1786. In 2001, Opresko reassigned *A. ulex* to the newly established antipatharian family *Myriopathidae* and the new genus *Myriopathes*, resulting in the name *Myriopathes ulex*. The original species description of *M. ulex* is rather brief (Ellis and Solander 1786), and the type material has been lost (Opresko 2001). Thus, positive identification of *M. ulex* cannot be made until a neotype is designated. Pending such a taxonomic revision, the name *Myriopathes* cf. *ulex* is used here and elsewhere to refer to the species that is targeted by the Hawaiian black coral fishery (Wagner 2011, Wagner et al. 2012b, Wagner 2015b).

Besides these three species that had been known to exist in areas where black corals

have been harvested in Hawai‘i (*A. griggi*, *A. grandis* and *M. cf. ulex*), recent surveys have discovered a fourth species, *Aphanipathes verticillata* Brook, 1889 (Figure 2), which was previously unknown from Hawaiian waters (Opresko et al. 2012). While gross observations suggest that the skeleton of this species is suitable to manufacture jewelry and may therefore have been targeted by the fishery, all known records of Hawaiian *A. verticillata* come from depths that are slightly deeper (88-130 m) than the harvesting depth zone (40-70 m; Opresko et al. 2012). It is therefore unknown if, and to what extent, *A. verticillata* has been commercially harvested in Hawai‘i (Opresko et al. 2012).

IV.2. Geographic and Depth Ranges

Surveys for *A. griggi* have been particularly frequent in Hawai‘i, because it is the main fishery species. Based on field observations using colony morphology, *A. griggi* has been reported throughout the Hawaiian Archipelago to depths of 159 m (Chave and Malahoff 1998). However, recent taxonomic studies have shown that *A. griggi* can easily be misidentified as the sympatric species *A. grandis* or *Aphanipathes verticillata* (Figure 2). These recent taxonomic studies raise questions about the validity of many previous reports of *A. griggi* (as *A. dichotoma*), especially those at depths below 100 m. Additionally, colonies with similar morphologies to *A. griggi*, identified as *A. dichotoma*, have been reported from various Indo-Pacific locations including the Philippines, Indonesia, Palau, China, Guam and Johnston Atoll (Van Pesch 1914, Grigg 1975, Zhou and Zou 1984, Zou and Zhou 1984, Zhou and Zou 1992, Chave and Malahoff 1998, Paulay et al. 2003, Rogers et al. 2007, Qi et al. 2009). These locations all lie outside the range of *A. dichotoma*, which

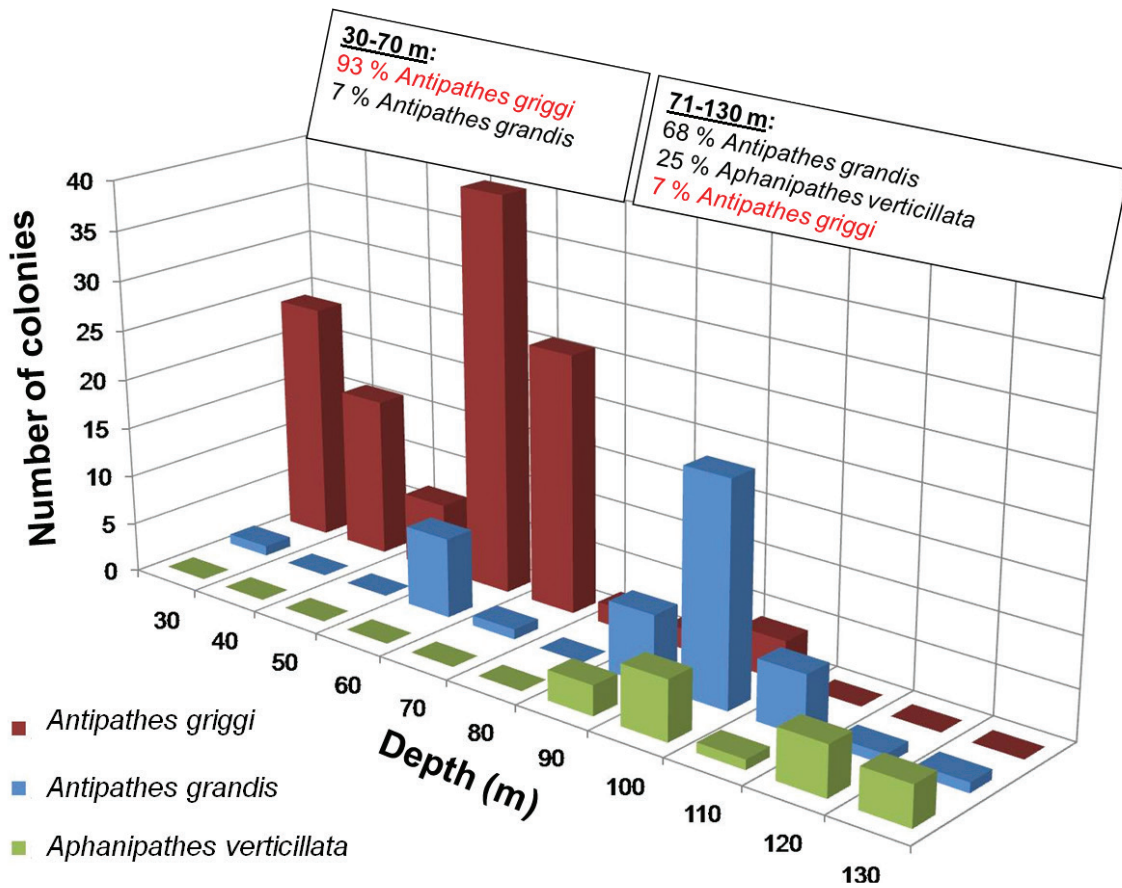


Figure 3. Depth distribution by species for 250 black coral colonies sampled at depths between 30-130 m in the Au'au Channel.

is only known from the Mediterranean and East Atlantic (Opresko 2003a, Bo 2008). Like the previous misidentification of *A. dichotoma* from Hawai'i, these misidentified *A. dichotoma* records may also be *A. griggi*. However, detailed taxonomic investigations of specimens from these Indo-West Pacific locations will have to be undertaken to confirm this. To date, specimens identified as *A. griggi* using all available diagnostic characters, have only been reported from the Hawaiian Archipelago from the islands of Hawai'i to Laysan at depths ranging between 10-110 m (Opresko 2009, Wagner 2011, Wagner et al. 2011a, Wagner 2015a,b).

A. grandis was originally described from a specimen collected off Maui (Verrill 1928), and subsequently reported throughout the Main Hawaiian Islands from Hawai'i to Ni'ihau at depths between 27-127 m (see Wagner et al. 2010). Additionally, there are two reports of this species from off China (Zhou and Zou 1984, Zou and Zhou 1984); however, these records cannot be confirmed until specimens from that locality are examined.

Myriopathes ulex was initially described from Indonesia (Ellis and Solander 1786), but subsequently reported throughout the Indo-West Pacific at depths ranging between 25-364 m (Blainville 1834, Gray 1857, Brook 1889,



Van Pesch 1914, Grigg and Opresko 1977, Chave and Malahoff 1998, Parrish and Baco 2007, Rogers et al. 2007, Bo 2008, Moon and Song 2008). However, a thorough taxonomic investigation is needed to verify whether these records all correspond to the same species that is present in Hawaiian waters. In the Hawaiian Islands, *Myriopathes* cf. *ulex* has been confirmed from Hawai'i Island to Pearl and Hermes Atoll at depths ranging between 41-326 m (Wagner 2011, Wagner et al. 2011a, Wagner 2015b).

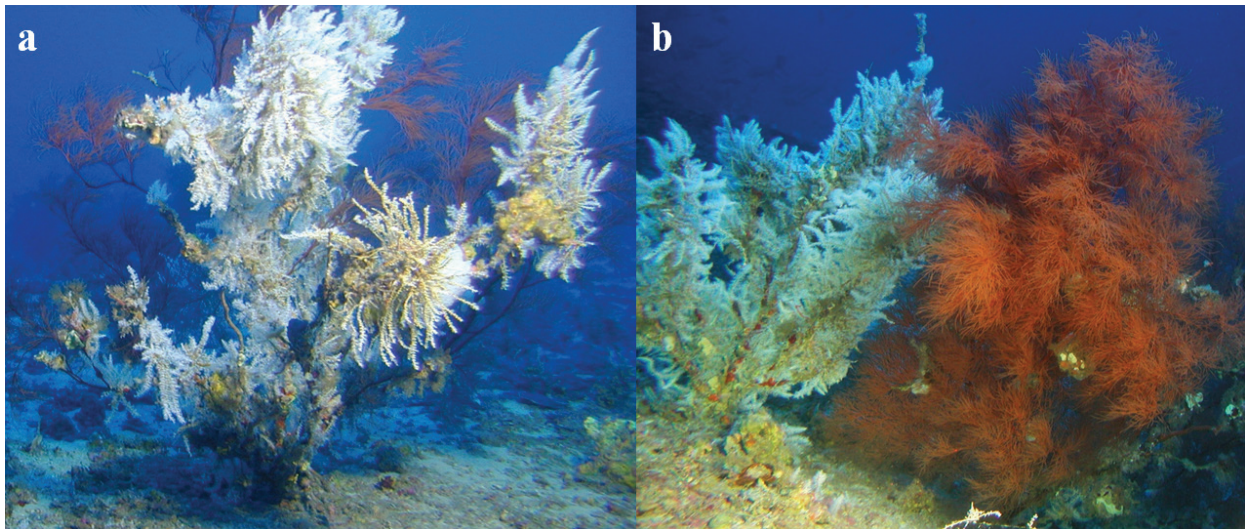
Up to now the black coral fishery has been managed under the presumption that a harvesting depth refuge exists; however recent studies have shown that there is no such depth refuge (Wagner et al. 2012b). Due to logistical constraints of SCUBA diving, fishermen have traditionally harvested black corals at depths between 40-70 m. However, dense black coral populations exist in the Main Hawaiian islands to depths of at least 110 m (Grigg 2001, Parrish and Baco 2007). It had previously been thought that colonies below the harvesting depth zone (> 70 m) provided a depth refuge from the fishery and were capable of reseeding fished populations in shallower water (< 70 m; Grigg 1976, 2001). However, recent surveys indicate that the majority of black corals below 70 m consist of *A. grandis* (68%) and *Aphanipathes verticillata* (25%), with *A. griggi* accounting for only 7% (Figure 3; Wagner et al. 2012b). Thus, the population size below the harvesting depth zone has been overestimated in the past and there is no real depth refuge from harvest (Wagner et al. 2012b).

IV.3. Sexual Reproduction and Histological Studies

As many other aspects of the antipatharian biology (see Wagner et al. 2012a), information on the sexual reproduction is scarce, and is

mostly limited to brief notes accompanying taxonomic descriptions (reviewed by Wagner et al. 2011b). Recent histological examinations of eight Hawaiian species, including the commercially valuable *A. griggi* and *A. grandis*, have revealed that there are several similarities in the sexual reproduction of black corals, even among distantly related species (Wagner et al. 2011b, Wagner et al. 2012a). First, of the six primary mesenteries only the two in the transverse plane bear gametes. Second, entire colonies are generally either female or male, although sequential hermaphroditism cannot be ruled out in most cases. Third, there is no evidence for internal fertilization within antipatharians, indicating that fertilization and larval development likely occur externally in the water column and not internally within polyps. Additionally, a more detailed study on the sexual reproduction of *A. griggi* has demonstrated that this species (1) is gonochoric with a 1:1 sex ratio, (2) has an annual reproductive cycle, and (3) spawns in multiple successive events with greatest intensities between November and December (Wagner et al. 2012b). Furthermore, this study revealed that ~80% of colonies meeting the state harvesting limit (90 cm) are sexually mature, whereas ~90% of colonies meeting the federal limit (122 cm) are sexually mature (Wagner et al. 2012b).

Apart from providing insights into the sexual reproduction of antipatharians, recent histological investigations have uncovered endosymbiotic algae of the genus *Symbiodinium*, also known as zooxanthellae, within a large proportion of Hawaiian black coral species (Wagner et al. 2011c). Due to the predominant occurrence of antipatharians in low-light environments that do not support photosynthesis (> 50 m; Cairns 2007), the absence of *Symbiodinium* within black corals has generally been inferred



*Figure 4. (a-b) Commercially valuable Hawaiian black corals, overgrown by the invasive octocoral *Carijoa* sp. in the Au'au Channel. Photos courtesy of HURL.*

rather than empirically demonstrated, and the whole taxonomic order has been considered azooxanthellate (see Wagner et al. 2011c). That said, close to a century ago several scientists noted round structures within the tissues of several black coral species, which they interpreted as symbiotic algae (Brook 1889, Van Pesch 1914, Buchner 1921). However, these early reports have been largely overlooked or dismissed as questionable. Supporting the tentative nature of these reports, numerous more recent studies using histological techniques (Grigg 1964, 1976, Goenaga 1977), chlorophyll measurements (Shick and Dykens 1985, Santiago-Vazquez et al. 2007) and molecular techniques (Santiago-Vazquez et al. 2007) have failed to detect *Symbiodinium* within antipatharians. In contrast, Wagner et al. (2011c) detected very low densities (0–92 cells/mm³) of endosymbiotic *Symbiodinium* within the majority of black coral species from Hawai'i, and down to a maximum depth of 396 m. While the physiological role of the endosymbiotic cells were not determined, their low densities coupled with the extreme

depths at which they were recorded, argue that they do not provide their antipatharian hosts with photosynthetic products and thus suggest an either parasitic or commensal association with black corals (Wagner et al. 2011c).

IV.4. Overgrowth by *Carijoa* sp.

The alcyonacean octocoral *Carijoa* sp. was first observed in Hawai'i in 1966 (Kahng et al. 2008) and the first published record of this species was in 1972, when it was discovered within the fouling community of Pearl Harbor, O'ahu (Evans et al. 1974). In 2001, black coral surveys in the Au'au Channel recorded *Carijoa* sp. overgrowing a large percentage of commercially valuable Hawaiian black corals at depths between 70-110 m (Figure 4; Grigg 2003). Due to the concerns about the effects of this invasion on the Hawaiian black coral fishery, several studies were initiated to characterize and monitor the impacts of *Carijoa* sp. on black corals (Kahng and Grigg 2005, Kahng et al. 2008, Concepcion et al. 2010, Kahng 2010). Initial surveys in the



Au'au Channel indicated that over 75% of the number of *A. grandis* and *A. griggi* colonies were overgrown by the octocoral at depths between 80-110 m (Kahng and Grigg 2005). However, subsequent monitoring efforts in the channel suggested that the impact of the *Carijoa* sp. invasion was not worsening with time, and that while still widespread and serious, the invasion was less severe than previously thought (Kahng 2010). These more recent surveys have determined that ~33% of black corals > 40 cm have *Carijoa* sp. overgrowth, with ~25% of colonies being completely overgrown and ~8% being partially overgrown (Kahng 2010). Furthermore, *Carijoa* sp. appears to settle on portions of black coral colonies where the bare skeleton is exposed, which can be created by abrasion or senescence (Kahng and Grigg 2005). There are no known natural predators of Hawaiian black corals (Wagner et al. 2012a), and therefore it is unknown whether predation facilitates *Carijoa* sp. overgrowth.

V. Future Management Directions and Implications for Other Coral Fisheries

While the latest surveys on the effects of *Carijoa* sp. on commercially valuable black corals indicate that the impacts are less severe than first assumed (Kahng 2010), recent studies also indicate that there is no depth refuge from harvest (Wagner et al. 2012b). Consequently, the biomass of commercially valuable black corals will likely continue to decline if no corrective management actions are undertaken (Grigg 2004). Specifically, three revisions in the management regulations should be pursued, including (1) increasing both the state and federal harvesting size limits to 130 cm to ensure that more colonies

have a chance to reproduce before being exposed to fishing mortality, (2) setting aside no-take areas to allow more colonies to continuously reproduce and reseed fished populations, and (3) limiting the entry of new fishermen. While there are only three permitted vessels in the Hawaiian black coral fishery (NOAA 2007), advances in diving technologies may attract more people into collecting black coral in the near future. Traditionally, diving for black corals has been a hazardous occupation due to the many inherent risks associated with deep SCUBA diving (Grigg 2001, 2010). However, as new diving technologies such as mixed-gas technical diving and closed-circuit rebreathers become more readily available, there will likely be an increased incentive for people to enter the fishery. Fetching over \$25/lb., harvesting black corals can be a lucrative enterprise (Grigg 2001). With novel technologies making black coral harvesting a safer practice, there will likely be a future increase in the fishing pressure on black corals. Thus, limiting the number of people entering the fishery should be pursued now before the resource becomes too depleted. Furthermore, creating no-take areas may allow for the reseedling of fished populations. With the exception of black corals found in federal waters around Hawai'i, there is currently no limit on the amount of black coral that can be harvested in Hawai'i. As black coral populations in federal waters get progressively depleted, fishermen might be pushed towards exploring black coral beds closer to shore. Without any other regulations, these beds are currently vulnerable to becoming overexploited, especially if new diving technologies attract more people to enter the fishery and allow for more efficient harvesting.



Besides Hawai'i, black corals have been commercially harvested in several other regions around the globe including throughout Asia, South America, the Caribbean, the Mediterranean and the Red Sea (Grigg 1975, Noome and Kristensen 1976, Castorena and Metaca 1979, Olsen and Wood 1980, Kenyon 1984, Grigg 1993, Romero 1997, Padilla and Lara 2003, Deudin et al. 2010, Tsounis et al. 2010). However, in contrast to the Hawaiian fishery, antipatharian fisheries in most other locations have remained largely unmanaged and thus exhibited a cyclic pattern of discovery of a population, exploitation, depletion, followed by exploration for new harvesting grounds, a boom and bust cycle that resembles strip mining more than a fishery (Noome and Kristensen 1976, Castorena and Metaca 1979, Grigg 1993, Romero 1997, Padilla and Lara 2003, Tsounis et al. 2010). In contrast, the Hawaiian black coral fishery has had a comparatively long history and serves as a commendable example of what can be achieved through close collaborations between resource managers, scientists and fishermen. Through continued research partnerships between different fishery stakeholders, black coral populations in Hawai'i have become some of the best studied in the world, and it is imperative that adaptive management strategies continue to be pursued as new scientific information becomes available.

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Iridogorgia soft coral located off the Northwest Hawaiian Islands. Courtesy of the NOAA Office of Ocean Exploration and Research.





STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION

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I. Introduction

The U.S. Pacific Islands Region consists of more than 50 oceanic islands, including the Hawaiian Archipelago, the Commonwealth of the Northern Mariana Islands (CNMI), and the territories of Guam and American Samoa, as well as the Pacific Remote Islands (Kingman Reef; Palmyra Atoll; Jarvis Island; Howland and Baker Islands; Johnston Atoll; and Wake Island) and Rose Atoll. The Pacific Island States in free association with the United States, including the Republic of Palau, the Federated States of Micronesia, and the Republic of the Marshall Islands, encompass additional large portions of the central and western Pacific with close ties to the U.S. This region includes some of the most remote, unpopulated islands in the Pacific, as well as many densely populated islands, and it extends from the South Pacific (e.g., American Samoa; 14° S latitude) to the North Pacific (Kure Atoll 28° N latitude; Fig. 1). Corals, sponges and other members of the deepwater community are found in patchy distribution on these oceanic ridges and have some of the highest levels of marine endemism recorded anywhere on earth.

The 2007 State of Deep-Sea Coral Ecosystems report (Parrish and Baco 2007) detailed discovery and history of harvesting deep water *Corallium* spp., *Kulamanamana haumea* (formerly *Gerardia* sp. (Sinniger et al. 2013)), *Isidella* sp., the mesophotic black corals



*Deep-sea coral
community on a
Northwestern Hawaiian
seamount.*

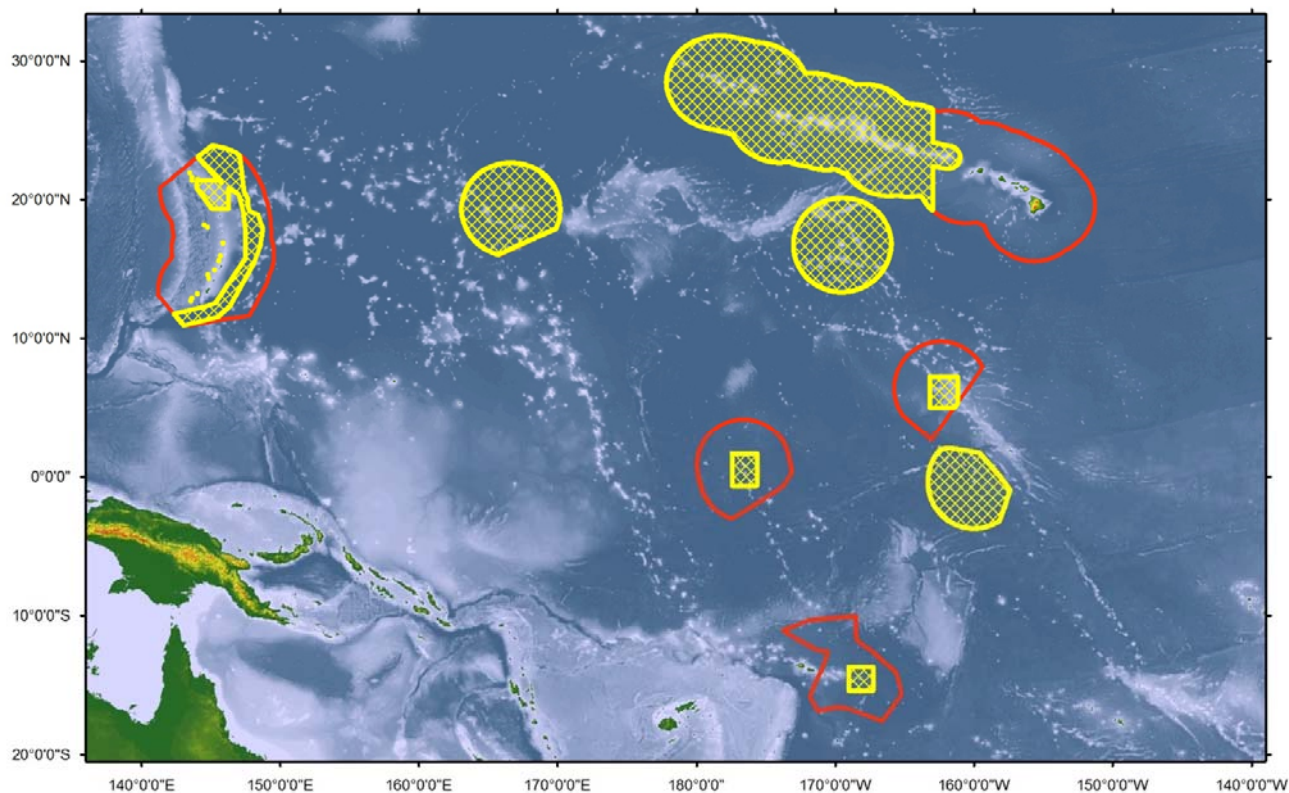


Figure 1. Map of the Pacific Basin showing U.S. islands, their Exclusive Economic Zones (EEZ), and Monument boundaries that comprise the Pacific Islands Region for the National Marine Fisheries Service. The yellow is the area of Marine National Monuments and the red is the U.S. EEZ. At the atolls of Johnston, Palmyra, and Wake the monument boundary is the same as the EEZ.

(antipatharians), and the associated development of a survey and monitoring program for the management of the “precious coral” fishery.

The chapter listed the inventory of the known structure forming corals and distinguished these colonies from the reef building cold-water coral complexes found in the Atlantic and the Gulf of Mexico. Also presented was information on the distribution of corals in the Hawaiian Archipelago and the absence of

survey effort in the wider expanse of the Pacific Islands Region. As the harvesting and surveys of corals relied on *in-situ* visual observations much was reported on the species associations with deep-sea coral communities including fish, invertebrates, and even visitation by monk seals. Aside from the limited activities of the precious coral fishery, the list of potential anthropogenic impacts to deep-sea corals in the region included impacts from placement of undersea cables and cold seawater pipes, and

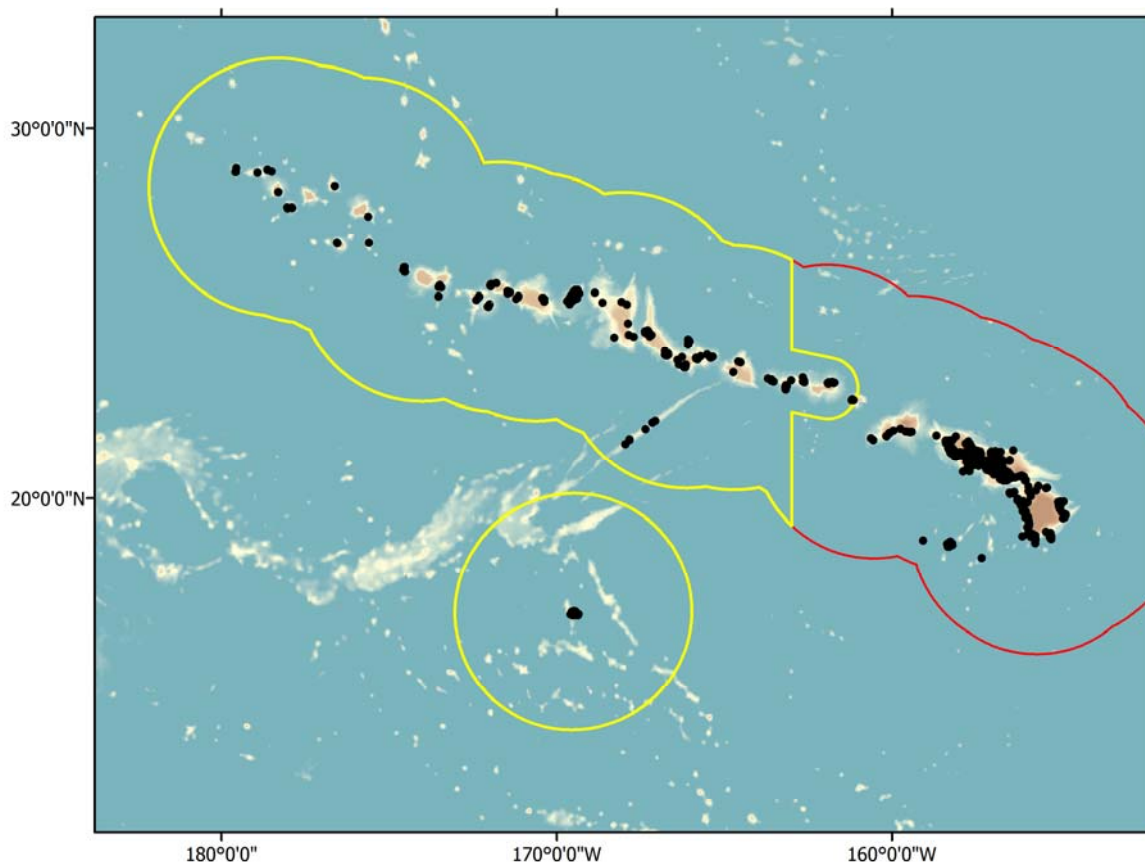


Figure 2. Map showing submersible (Pisces IV, Pisces V) and ROV (RCV-150) dive locations in the Hawaiian Archipelago and Johnston Atoll where deepwater corals and sponges have been found. The yellow line is the boundary of Marine National Monuments and the red is the U.S. EEZ. At Johnston Atoll the monument boundary is the same as the EEZ.

the potential destructiveness of future cobalt-rich manganese (Mn) crust mining.

Until 2015, deep-sea coral research in the Pacific Islands Region was still focused almost entirely in the Hawaiian Archipelago (Fig. 2). While coral fragments from incidental dredging and bycatch records indicates a wide distribution of deep-sea corals throughout the Pacific Island Region, Hawai'i is still the only location in the region with assets to conduct such studies, and even there the progress was sporadic,

dependent on when funding opportunities present themselves through various requests for proposals. Since the release of the 2007 national report the focus of deep-sea coral studies has shifted away from the intermediate depth range (300-500 m) where the commercial harvest of precious corals motivated most of the data collection, to coral/sponge communities that are both shallower and deeper, along with a greater emphasis on spatial modeling of existing data. Roughly half of the publications



produced since the 2007 report are taxonomic in nature. They include reviews of poorly understood families, some new descriptions, and some name changes. The rest of the papers are a mix of growth, distribution and life history studies. Work on the shallow water black corals was the best represented segment of the deep-sea coral community including both analysis of available data and some field surveys. New information on black coral and its history as a resource is presented in detail in chapter 6. This follow-up report differs from the 2007 report in that it includes information on deepwater sponges in the region that was not included in the first report.

II. Update on Scientific Information

II.1. New Research – Overview

Since the 2007 status report (Parrish and Baco 2007), there have been a number of research studies and publications on the region's deepwater corals. A complete list of new publications is included at the end of this chapter. Between 2007-2014, there were a number of deepwater coral and sponge field projects concentrated in the Hawaiian Archipelago, using the submersibles and remotely-operated vehicle (ROV) assets of the Hawai'i Undersea Research laboratory (HURL). These projects involved 15 cruises funded through HURL's grant program and through awards from the Papahānaumokuākea Marine National Monument (PMNM), NOAA's Center

for Sponsored Coastal Ocean Research (CSCOR), Western Pacific Fishery Management Council (WPFMC), and the National Marine Fisheries Service (NMFS). Research topics included precious coral age and growth, habitat, distributions of coral and sponges, use of corals for climate studies, studies of black coral density and distribution, and effects of invasive species on black coral populations. There was also some shore-based work conducted using charter boats and three annual (2008-2010) research cruises using NOAA vessels to support surveys of mesophotic coral communities using remote cameras and mixed gas divers that overlapped and contributed new information to the status of shallow black coral populations.

In addition to this fieldwork, analysis of data from past expeditions and collections has contributed to better understanding of deep-sea coral biology and ecology. Significant new insights have been gained into the genetics (Baco and Cairns 2012, Sinniger et al. 2013, Figueroa and Baco 2014a,b), reproductive biology (Waller and Baco 2007, Wagner et al. 2011c, Wagner et al. 2012), growth and age (Parrish and Roark 2009, Roark et al. 2009), and community structure (Long 2011, Long and Baco 2014, Parrish 2015) of precious coral and black coral species. Finally, international collaborative efforts through the Census of Marine Life Program, A Global Census of Seamounts (CenSeam) have also provided syntheses that provide a global context for the Hawaiian Archipelago fauna. These include analyses of global coral distributions and

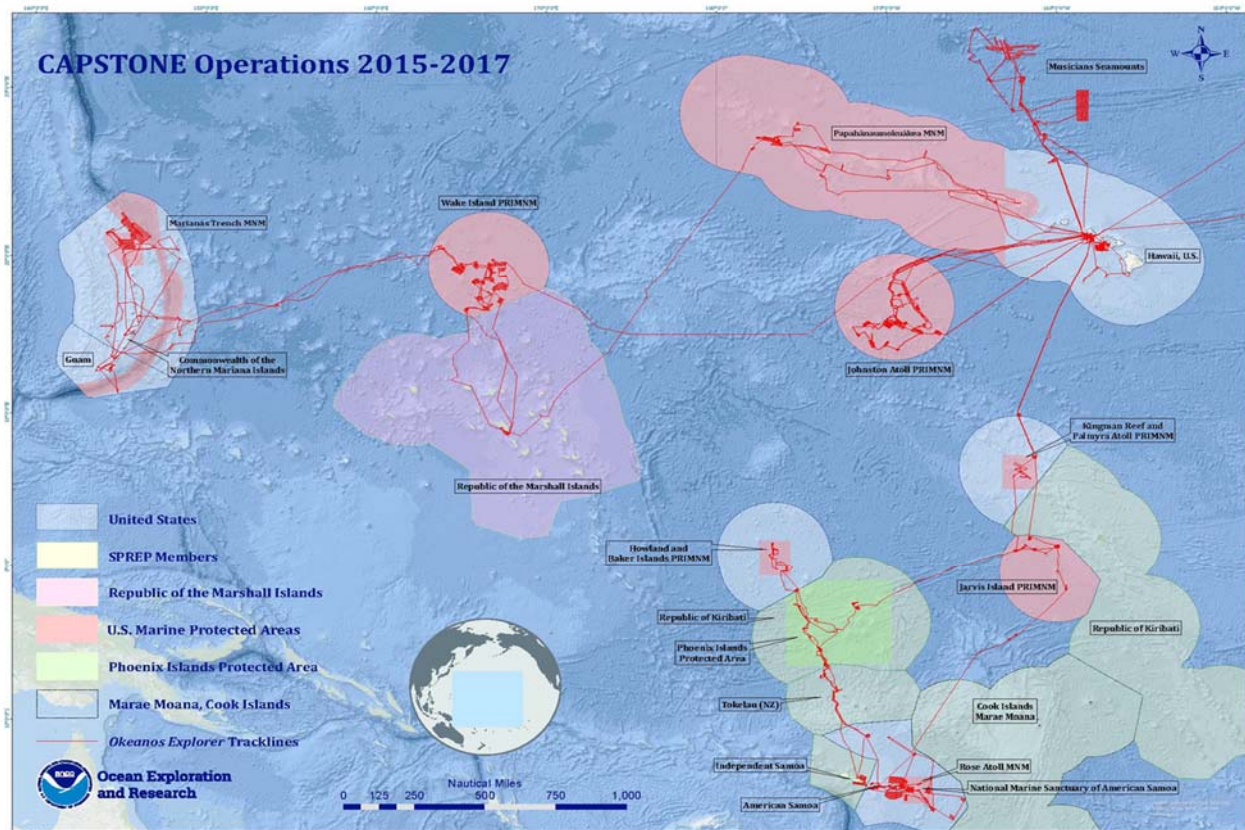


Figure 3. The three-year CAPSTONE expeditions conducted mapping and deep-sea surveys throughout the U.S. Pacific Islands region.

habitat suitability modeling of corals on a global basis (Rogers et al. 2007, Tittensor et al. 2009, Clark et al. 2011, Yesson et al. 2012, Schlacher et al. 2014).

In 2015, NOAA initiated CAPSTONE: the Campaign to Address Pacific monument Science, Technology, and Ocean Needs. This three-year campaign brought together resources from across NOAA to explore the nation's new central and western Pacific marine national monuments and national marine sanctuaries aboard NOAA Ship *Okeanos Explorer* (Fig. 3). The campaign, led by NOAA's Office of Ocean Exploration and Research,

provided foundational science by discovering and describing unknown deep-sea habitats.

Science themes included the following:

- Acquiring data to support priority monument and sanctuary science and management needs;
- Identifying and mapping vulnerable marine habitats – particularly high-density deep-sea coral and sponge communities;
- Characterizing seamounts in and around the Prime Crust Zone, the area of the Pacific with the highest concentration of commercially valuable deep-sea minerals;



- Investigating the geologic history of Pacific seamounts, including potential relevance to plate tectonics and subduction zone biology and geology; and
- Increasing understanding of deep-sea biogeographic patterns across the Central and Western Pacific.

This three-year campaign consisted of 23 cruises, 13 using the NOAA *Deep Discoverer* ROV. Over 600,000 km² of bottom was mapped using multibeam, and 188 ROV dives explored habitats between 240m – 6,000 m deep. More than 360 samples of deep-sea corals and sponges were collected, a large proportion of which are expected to represent new species.

These expeditions provided a first look at deep-sea coral and sponge habitats in U.S. Island regions outside the Hawaiian Archipelago. Among the most important initial discoveries was the occurrence of numerous extremely high-density coral and sponge communities. Initial information from the exploration is available on NOAA's [Ocean Explorer website](#). Scientific analysis of this rich trove of data and information has just begun, and is not yet reflected in following sections of this chapter.

II.2. Taxonomy and Species

Distributions

II.2.i – Corals

a. Coral taxonomy

Parrish and Baco (2007) reported 238 taxa of deepwater corals from the Hawaiian archipelago. The list included 75 taxa with incomplete taxonomy. A total of 6 new genera

and 20 new species of octocorals, antipatharians, and zoanthids have been discovered in Hawai'i since the 2007 report. These are either new to science, or new records for the Hawaiian Archipelago (Cairns and Bayer 2008, Cairns 2009, Opresko 2009, Cairns 2010, Wagner et al. 2011a, Opresko et al. 2012, Sinniger et al. 2013). Taxonomic revisions currently underway for several groups of corals, e.g., isidids, coralliids, plexaurids and paragorgiids, are also likely to yield additional species new to science and new records for Hawai'i.

Recent molecular phylogenetic and morphologic studies of the family Coralliidae, including Hawaiian precious corals, have illuminated taxonomic relationships. These studies synonymized *Paracorallium* into the genus *Corallium*, and resurrected the genera *Hemicorallium* (Ardila et al. 2012, Figueroa and Baco 2014, Tu et al. 2015) and *Pleurocorallium* (Figueroa and Baco 2014, Tu et al. 2015) for several species, including several species in the precious coral trade.

A molecular and morphological analysis of octocoral-associated zoanthids collected from the deep slopes in the Hawaiian Archipelago revealed the presence of at least five different genera including the gold coral (Sinniger et al. 2013). This study describes the five new genera and species and proposes a new genus and species for the Hawaiian gold coral, *Kulamanamana haumeaee*, an historically important species harvested for the jewelry trade and the only Hawaiian zoanthid that appears to create its own skeleton.

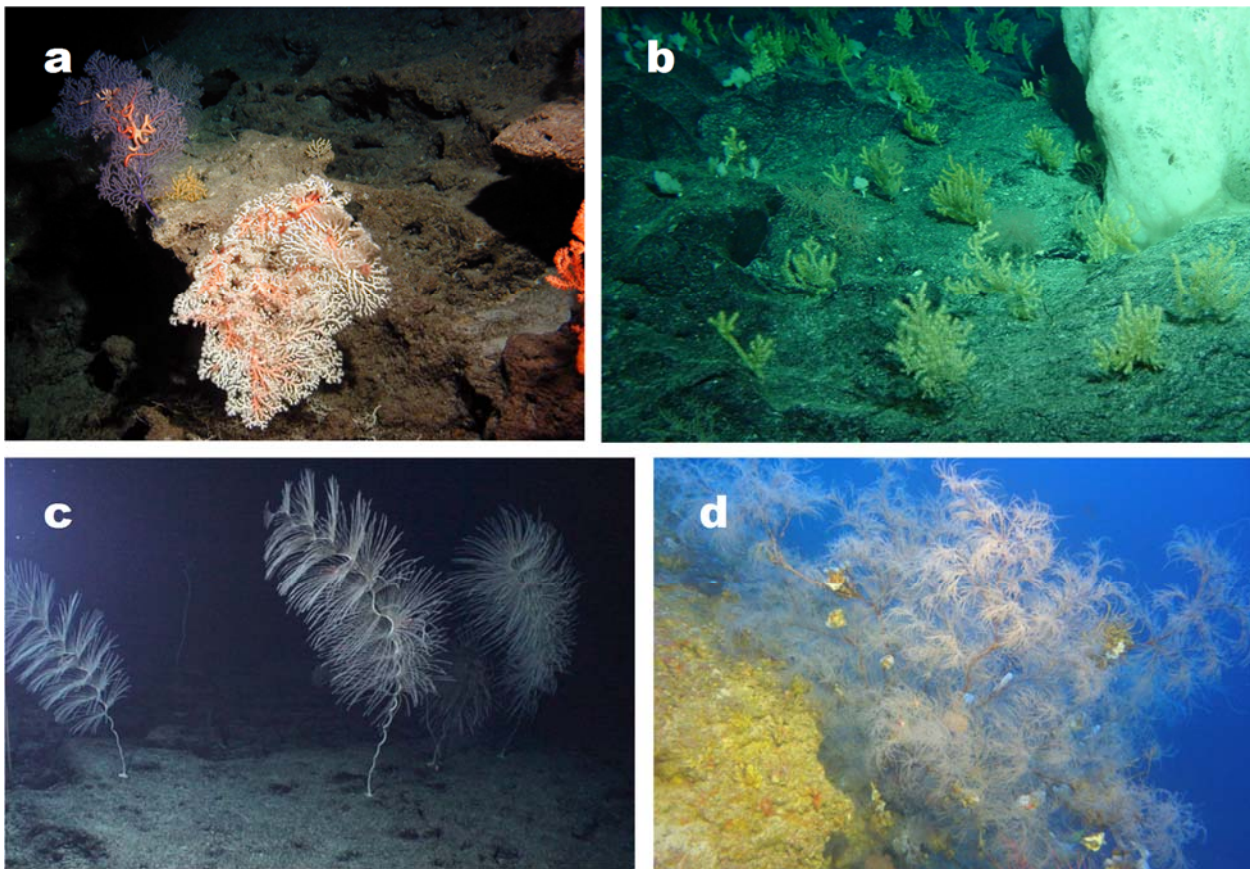


Figure 4. Examples of structure-forming deep corals found in the Hawaiian Archipelago. a) *Pleurocorallium secundum*, b) *Acanthogorgia sp.*, c) *Iridogorgia magnispiralis*, d) *Antipathes grandis*. Photo credit: HURL.

b. Coral distribution and community structure

Much of the funded work in the Hawaiian Archipelago in the last decade has been related to simply documenting species distributions. In the 2007 status report, the Hawaiian coral beds were divided into 2 zones, one at depths < ~600-700 m, and one > ~600-700 m. The shallower zone was dominated largely by precious corals, but with a high diversity of other octocoral and antipatharian species. The deeper zone was dominated by a broad array of octocoral

families. Scleractinians were relatively rare at all depths, and were primarily solitary (i.e. non-colonial) species. Records of colonial scleractinians in the Archipelago continue to be scarce. However, a large bed of dead scleractinian *Solenosmilia variabilis* was discovered in 2007 (Kelley unpubl. data), and live corals were collected from a seamount in the northwest end of the archipelago in 2016. Baco et al. (2017) have reported deep reef formations that appear to be constructed of this species (see below).



From 2007 to 2014, little field work was directed at deep-sea corals (Fig. 4) and much of it was in coral beds that had been documented years prior. Consequently there was limited new information on the spatial distribution of deep-sea coral in the Pacific Islands Region (Table 1). Work includes cross contour surveys contracted by the PMNM and climate-related coral work by universities that improved sampling on seamounts in the central part of the Northwestern Hawaiian Islands and conducted the first exploration of the Necker Ridge which extends south southeast from the central part of the Hawaiian Archipelago (Morgan 2013, Morgan et al. 2015). Habitat suitability modeling studies as outlined below also provide some insights onto potential locations of deep-sea coral abundance in the vastly underexplored areas of this region.

Additional explorations as well as continued analyses of pre-2007 cruise video data and sampling records, have provided more insights into coral distributions and discoveries of new species. A global synthesis of available data on seamount coral taxa found that the Hawaiian Archipelago is a diversity hotspot for deep-sea corals (Rogers et al. 2007).

The number of studies of the deep slopes of the Hawaiian Archipelago is also beginning to reach the critical mass needed to address broader-scale ecological questions in a more quantitative way. The availability of the HURL video archive as well as their video log

database have enabled these larger-scale efforts. The first of these efforts is a broad-scale synthesis of the HURL video log database, encompassing the Northwestern Hawaiian Islands and seamounts to the southeast of the Archipelago that have been sampled with the HURL submersible assets (Clark et al. 2011).

The goal of this study, funded by the International Seabed Authority, was to compare the megafaunal community structure of seamounts with cobalt-rich manganese (Mn) crusts to those lacking such crusts, with the southeast portion of the Hawaiian Archipelago falling into the “cobalt-rich” category. Over 30,000 records extracted from HURL’s database from the Northwestern Hawaiian Islands, Johnston Atoll, and Cross Seamount were analyzed. No correlation was found with cobalt or with feature type (island vs seamount, etc.), instead depth seemed to be the overriding factor related to the observed community structure, with communities distinguished into three depth groupings, those from dives with a median depth of 227-354 m, from dives with a median depth of 357-615 m and from dives with a median depth of 745-1799 m. Although this analysis focused on all megafaunal invertebrates, cnidarians made up about 30% of the total records and were the key species contributing to the differences among the 3 depth groups (Clark et al. 2011). Location was also a significant factor, but was a secondary factor to depth.

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION



Table 1. Primary structure-forming deep-sea corals and general attributes. The overall rating in the right column is a synthesis of the rest of the attributes.

Note: *Hydrodendron gorgonoide* is a chitinous hydroid, which while technically not a coral, nevertheless has similar characteristics.

Taxa	Reef-Building	Abundance	Maximum Colony Size	Morphology	Associations with other Invertebrates	Colony Spatial Dispersion	Overall Rating
<i>Acanella dispar</i>	No	High	Large	branching	many	clumped	high
<i>Acanella weberi</i>	No	High	Medium	branching		clumped	high
<i>Acanthogorgia</i> sp.	No	High	Small	branching		clumped	high
<i>Anthomuricea tenuispina</i>	No	Medium	Small	branching		clumped	medium
<i>Antipathes</i> sp.	No	Medium	Large	branching	few	both	medium
<i>Aphanipathes</i> sp.	No	High	Medium	branching	few	clumped	medium
<i>Callogorgia gilberti</i>	No	Medium	Large	branching		both	medium
<i>Calyptrophora</i> sp.	No	Medium	Large	branching		both	medium
<i>Chrysogorgia geniculata</i>	No	High	Small	branching		clumped	medium
<i>Pleurocorallium secundum</i>	No	High	Medium	branching	few	clumped	high
<i>Pleurocorallium niveum</i>	No	High	Small	branching	few	clumped	high
Coralliidae sp. (other)	No	High	Medium	branching	few	both	high
<i>Enallopsammia rostrata</i>	No	High	Medium	branching		clumped	high
<i>Enallopsammia</i> cf. <i>pusilla</i>	No	High	Medium	branching		clumped	high
<i>Eguchipsammia</i> sp.	No	Medium	Small	branching		clumped	medium
<i>Hemicorallium laauense</i>	No	High	Medium	branching	few	clumped	high
<i>Hemicorallium</i> near <i>laauense</i>	No	Medium	Large	branching		clumped	medium
<i>Hydrodendron gorgonoide</i> ^a	No	Medium	Medium	branching		both	medium
<i>Iridogorgia magnispiralis</i>	No	High	Large	branching		both	high
<i>Keratoisis</i> sp.	No	High	Large	branching		both	high
<i>Kulamanamana haumea</i>	No	High	Large	branching	many	clumped	medium
<i>Leiopathes</i> sp.	No	Low	Large	branching		dispersed	medium
<i>Lepidisis</i> sp.	No	High	Medium	non-branching		both	medium
<i>Madracis kauaiensis</i>	No	Medium	Small	branching		clumped	medium
<i>Madrepora oculata</i>	No	Medium	Medium	branching		dispersed	medium
<i>Narella</i> sp.	No	Medium	Medium	branching		both	medium
<i>Paracalyptrophora</i> sp.	No	High	Large	branching		clumped	high
<i>Paragorgia</i> sp.	No	Medium	Large	branching		clumped	medium
<i>Villogorgia</i> sp.	No	Medium	Medium	branching		clumped	medium
<i>Plumarella circumoperculum</i>	No	High	Small	branching		clumped	medium
<i>Solenosmilia variabilis</i>	Yes	Medium	Medium	branching		clumped	high
<i>Thouarella hilgendorfi</i>	No	Medium	Large	branching		clumped	medium



Another recent study synthesized ROV video from the Makapu'u precious coral bed on the island of Oahu (Long 2011, Long and Baco 2014). The bed extends from a depth of approximately 320 to 530 m. Despite the relatively narrow depth range, depth was again found to be the overriding factor correlated to community structure, with other physical parameters such as slope and rugosity also playing a minor role. Intriguingly, although this bed has always been referred to as a "precious coral bed", this quantitative assessment indicated that the octocoral family Primnoidae was actually the most abundant coral family overall within the bed area. Coralliids did dominate in one of the six depth bands, with *Corallium secundum* (= *Pleurocorallium secundum*) being the most abundant species there. Interestingly, the peak in abundance of *C. secundum* began about 400m, below the maximum depth of previous harvesting operations (Long 2011, Long and Baco 2014).

In contrast, surveys of deeper communities (1400-2000 m) on the Necker Ridge in 2011 revealed communities structured by factors other than depth (Morgan 2013, Morgan et al. 2015). This study surveyed 6 sites along the Ridge and found a significant difference in communities on the northern side of the ridge, which were dominated by octocorals, compared to the southern side of the ridge, which were dominated by crinoids. Diversity also increased from south to north along the ridge. A multivariate analysis of community structure in relation to environmental factors found that latitude, sediment cover, rugosity, oxygen, salinity, and temperature, but not

depth, were most strongly correlated with observed patterns.

Baco et al. (2017) recently reported the first observations of deep-sea scleractinian coral reefs (bioherms) from the central North Pacific. The reefs were found at depths of 535-732 m on six seamounts in the Northwestern Hawaiian Islands and Emperor Seamounts, three of which were within U.S. waters.

c. Coral population connectivity

While species lists and habitat suitability provide first order insights into potential connectivity of deep-sea coral populations, the real key to assessing connectivity is using genetic methods. Genetic methods for assessing connectivity are well developed in general, but the paucity of sampling makes them challenging to apply in the deep sea. The topic is covered more broadly by Morrison et al. (this volume). However, within the Hawaiian Archipelago, phylogeographic and phylogenetic work has focused primarily on the precious corals and also on the primnoid octocoral *Narella. Hemicorallium laauense* (Ardila et al. (2012); Figueroa and Baco (2014) formerly *Corallium laauense*) is the only Hawaiian deep-sea coral species that has published studies using population genetics.

Data from three microsatellite loci in *H. laauense* from 8 sites in the Main Hawaiian Islands and southern end of the Northwestern Hawaiian Islands indicated strong heterozygote deficiency and no pattern of isolation by distance (Baco and Shank 2005, Baco et al. 2006). The deepest site, at Kauai, in the middle



of the sampled locations, showed genetic structure when compared to just about every other site in the study. The Makapu'u bed on the Island of Oahu also had some indication of isolation for comparisons within the bed on the scale of 1.6 km and for comparisons to most other beds. These results indicate that the scale of genetic structure within the Archipelago may be very complex, and that the connectivity of each feature or location should be assessed for any management activities (Baco and Shank 2005).

Other types of genetic analyses such as DNA barcoding and phylogeography may also yield insights into connectivity, species distributions and species ranges of Hawaiian corals. A study designed to help develop barcoding markers for octocorals found that species in the primnoid genus *Narella* that occur in Hawai'i tend to have different haplotypes (DNA sequences) within a single species that is found at different depths. Of all the Hawaiian *Narella* haplotypes, only one haplotype (from the far Northwestern Hawaiian Islands) was also found on Derickson Seamount, a deep seamount south of the Aleutian Archipelago in Alaska (Baco and Cairns 2012).

Taken together, this review of distributions of Hawaiian corals from both genetics and species lists, indicates that depth is a very strong factor structuring deep-sea coral communities, potentially even over very small spatial scales. Therefore depth structuring should be taken into consideration in future management efforts.

d. Modeling distribution and abundance of corals

Although considerable effort has gone into exploration and description of species to help understand coral distributions in the Hawaiian Archipelago, the continued high rate of species discovery indicates that despite it being the best studied Island group in the Pacific region, it too is still drastically under-sampled for deep-sea corals and other taxa. Several global syntheses of coral distributions and habitat suitability modeling included data from prior collections in the Hawaiian Archipelago (Rogers et al. 2007, Tittensor et al. 2009, Tittensor et al. 2010, Yesson et al. 2012). These provide a context for results from Hawai'i and also insights into the likelihood of finding corals in the vast and unexplored areas of the U.S. Pacific Islands region (Tittensor et al. 2009, Davies and Guinotte 2011, Yesson et al. 2012) and the potential impacts of ocean acidification on deep-sea corals (Tittensor et al. 2010).

The first of these models relevant to corals was by Tittensor et al. (2009) and focused on scleractinians on seamounts. The results of this modeling effort indicate very low habitat suitability for scleractinians below 500 m across the entire geographic range of U.S. territorial waters in the Pacific Ocean. This work was later expanded to other submarine features by Davies and Guinotte (2011) and focused on five of the most broadly distributed scleractinian framework-forming species (including *Enallopsammia rostrata* and *Madrepora oculata*, known to occur in Hawaii). They also concluded that the North Pacific had very little



suitable scleractinian habitat but a few features that fall into U.S. waters in the southern hemisphere did have a narrow depth band of higher habitat suitability for certain species. Yesson et al. (2012) focused on octocorals, splitting them up into the seven major suborders, and based on their model virtually all of the sites within the U.S. Pacific Islands region have high habitat suitability for octocorals. The predicted lack of scleractinians and high abundance of octocorals are consistent with observations in this region (Baco 2007, Parrish and Baco 2007), however a strong caveat to these modeling efforts is that they are done at relatively coarse geographic and taxonomic resolution, and all of the models remain to be ground-truthed with in situ explorations.

Besides providing insights into potential distributions of corals, the models also provide insights into the environmental parameters that influence coral distributions. Recent modeling efforts indicate the distributions of scleractinian corals are related to depth, temperature, aragonite saturation state, salinity, oxygen concentration and saturation and dissolved nutrients (Tittensor et al. 2009, Davies and Guinotte 2011). Temperature, slope, salinity, surface productivity, currents, oxygen and calcite saturation state are correlated to the distribution of octocorals (Bryan and Metaxas 2007, Yesson et al. 2012).

Habitat suitability modeling for precious corals in the Main Hawaiian Islands was funded by

NOAA's Deep Sea Coral Research and Technology Program. The project "Predictive Modeling of the Distribution of Deep-Sea Corals in the Main Hawaiian Islands" (PIs John Rooney, Amy Baco and Michael Parke) used data from the Main Hawaiian Islands in attempt to identify suitable habitat of *Corallium secundum* (pink coral; =*Pleurocorallium secundum*) and *K. haumea* (gold coral), that are important targets in the precious coral fishery.

A total of 1227 observations of these taxa were made in the Main Hawaiian Islands during 102 of the more than 1100 submersible dives completed in the region by the Hawai'i Undersea Research Laboratory. An analysis of circulation data from ocean general circulation models and tidal models indicates that in this region, at depths below the main thermocline (300 to 500 m), tidal velocities are an order of magnitude larger than the general circulation flows. Deep-sea coral growth is thought to be enhanced in areas with higher current velocities that would increase the availability of food. Accordingly, maximum baroclinic tidal velocities at a depth of 400 m were calculated using output from a tide model developed by Carter et al. (2008) for a portion of the Main Hawaiian Islands on a one by one kilometer grid (Fig. 5). A high resolution grid of all available bathymetry data was also obtained from the Hawai'i Mapping Research Group at the University of Hawai'i. The modeling effort was unable to identify any significant

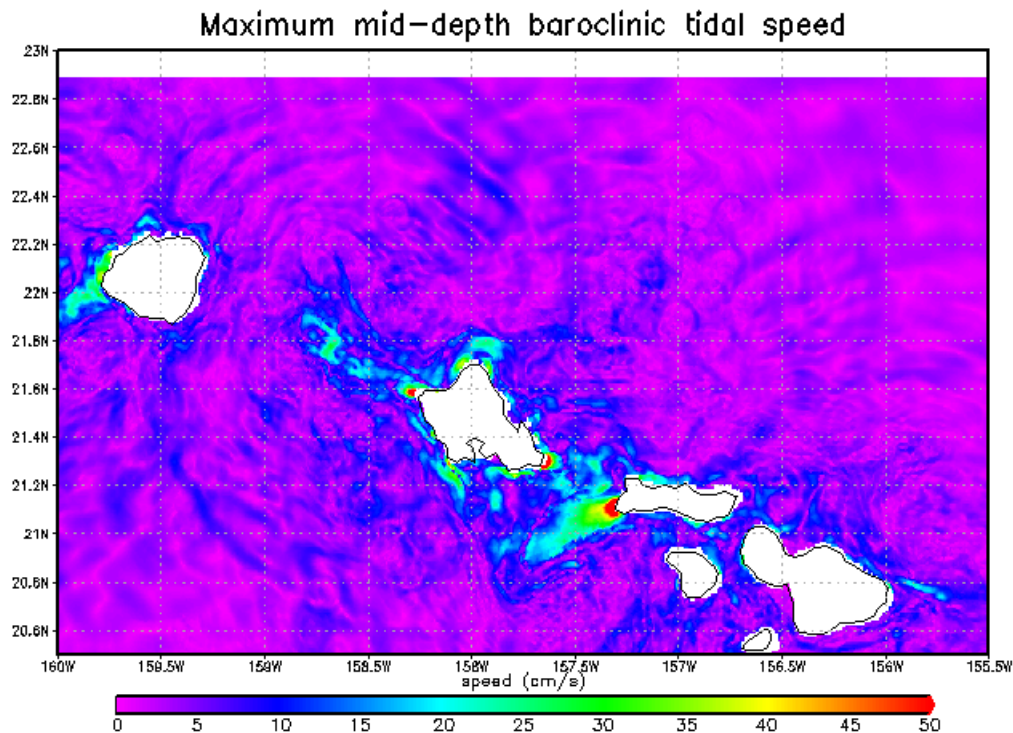


Figure 5. Maximum modeled current speeds at depth. The red end of the color spectrum indicates stronger currents.

predictions of coral occurrence but based on the observations it is hypothesized that these species of deep-sea corals prefer areas with current velocities 0.5 - 0.85 m/s (<https://deepseacoraldata.noaa.gov/other-studies/fy10-08>).

In a subsequent study, Bauer et al. (2016) modeled habitat suitability for 16 deep-sea coral groups, based on ecological importance, management considerations, and the number of presence records. Models included *Corallium* and the gold coral *K. haumea*. The *Corallium* model was among the best fits, with distance to shore, total curvature at 5 km scale, and annual bottom temperature as the most important predictor variables.

11.2.ii – Sponges

a. Sponge taxonomy and distribution

Sponges in the phylum Porifera are presently divided into 4 classes: Calcarea, Demospongiae, Hexactinellida, and the “revived” class Homoscleromorpha, which until recently has been considered to be an order of demosponges (Gazave et al. 2010). In general, most sponges in depths above 50 m are either demosponges, calcareans, or homoscleromorphans, whereas most sponges below 400 m are hexactinellids (Reiswig unpub. data, HURL database). Deepwater sponges in the Pacific Islands region are more poorly known than the deepwater corals and only those large enough to be considered structure-forming are included in this report (Table 2, Fig. 6). The major



transition between the hexactinellids and the other classes of sponges in this region appears to be below 200 m, perhaps as a result of higher water temperatures and light penetration above that depth (HURL database). However, this could also be a result of under-sampling within the 50-200 m depth zone, which for the most part falls between the routine operating depths of SCUBA and deepwater vehicles such as

submersible and ROVs. For simplicity, this first inclusion of deepwater sponges in the report for the Pacific Islands Region will focus on species found at depths below 200 m, and is largely derived from the HURL on-line Deepwater Animal Guide (<http://www.soest.hawaii.edu/HURL/>) and related database records (Fig. 6).

Table 2. Structure-forming attributes of deep-sea sponges in Hawaii. The overall rating in the right column is a synthesis of the rest of the attributes.

Taxa	Reef-Building	Abundance	Colony Size	Colony Shape	Spatial Dispersion	Overall Rating
<i>Bolosoma</i> sp. (all)	no	medium	large	pedunculate sphere	both	medium
<i>Farrea</i> near <i>occa</i>	no	high	medium	anastomosing tubes	clumped	medium
<i>Poliopogon</i> sp. (all)	no	high	large	hemispherical	clumped	high
<i>Regadrella</i> sp. 1	no	medium	medium	tube-like	clumped	medium
<i>Saccocalyx</i> cf. <i>pedunculatus</i>	no	medium	large	pedunculate cup	dispersed	medium
<i>Semperella</i> sp. (all)	no	high	medium	columnar	clumped	high
<i>Sericolophus hawaiiicus</i>	no	high	medium	pedunculate spoon	clumped	high
<i>Tretopleura</i> sp. 1B and sp. 2	no	medium	large	elongated plate	both	medium
<i>Walteria</i> sp. (all)	no	medium	medium	tube-like	both	medium

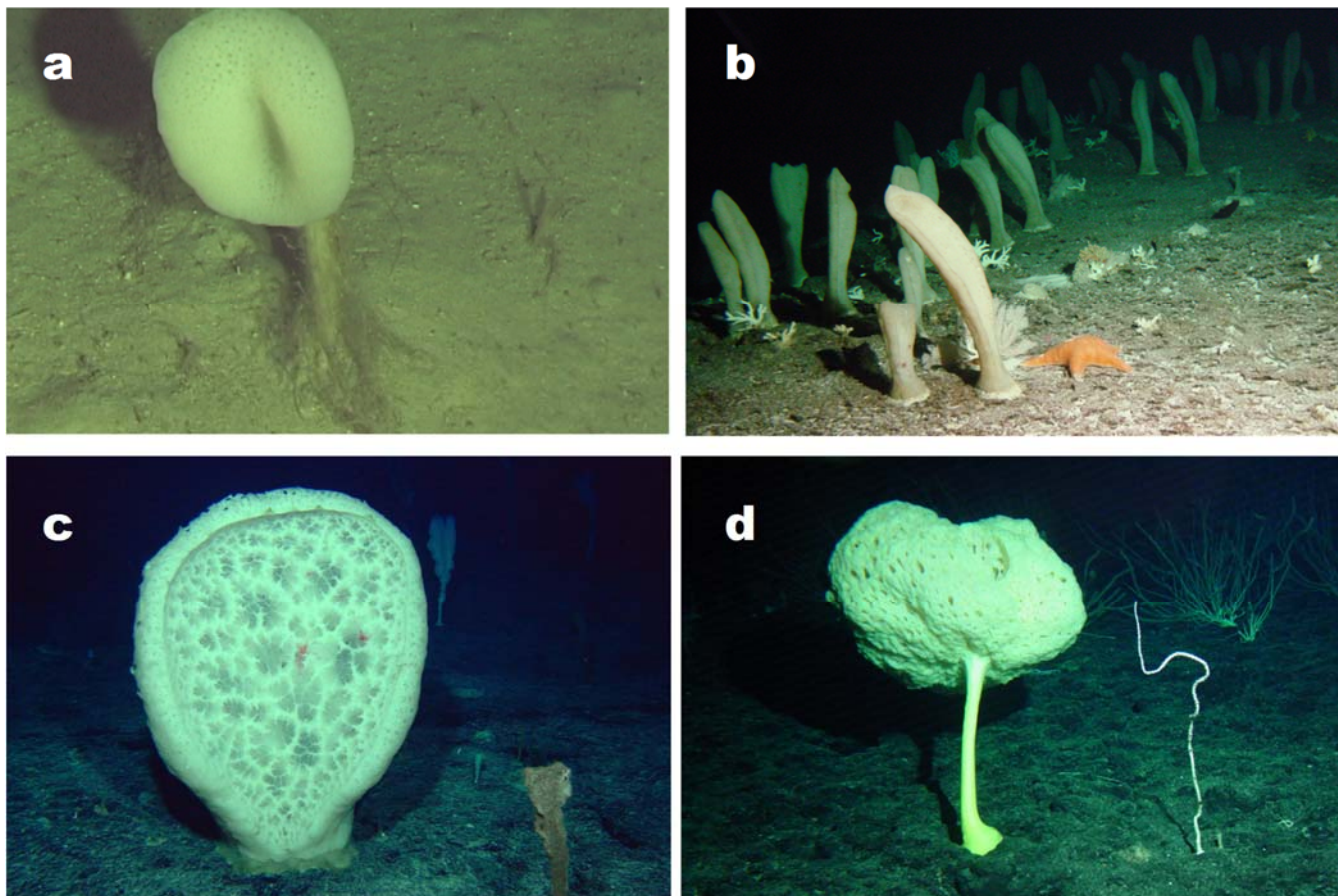


Figure 6. Examples of structure forming deep sponges found in the Hawaiian Archipelago: a) Sericolophus hawaiiicus, b) Poliopogon sp4, c) Poliopogon sp1, d) Bolosoma sp2. Photo credit: HURL.

a. (i) Calcareans and Demospongiae below 200 m

A single colony identified from a photograph as a calcarean species in the genus *Clathrina*, has been included in the HURL database and online identification guide for many years. In 2017, this rare species was encountered and collected during an *Okeanos Explorer* cruise to the Johnston Atoll monument area. Microscopic examination determined that it was actually a misidentified and potentially new species of hexactinellid in the family Tretodictyidae. Therefore, at the present time, there are no

confirmed published or unpublished accounts of deepwater calcareans being found in the Pacific Islands region.

Chave and Malahoff (1998) listed seven species presumed to be demosponges that have been photographed from submersibles operated by HURL. One of these has subsequently been collected and identified as a species of hexactinellid. Another of these, *Corallistes* sp., has been only identified from photographs but is similar to confirmed species so is listed in the appendix as cf. *Corallistes* sp. The remaining



five species were described with only descriptive names so are not included.

The HURL database has 9 species of demosponges including cf. *Corallistes* sp. that occur below 200m in Hawai'i. Of these, 5 were collected and identified by spicule examination: *Penares* sp., *Poecillastra* sp. 1, *Poecillastra* sp. 2, *Hamacantha (Vomerula)* n. sp. and *Stelodoryx* sp. The remaining 4, cf. *Corallistes* sp., cf. *Petrosia* sp., cf. *Polymastia* sp. 1 and cf. *Polymastia* sp. 2 were identified from images only but all show clear similarities to confirmed species in those genera. During the preparation of this report, additional demosponge specimens were collected during HURL submersible and *Deep Discoverer* ROV dives that have not as yet been entered into the HURL or National Deep-Sea Coral and Sponge databases. These include a *Geodia* sp., an unidentified species in the order Haplosclerida, another *Poecillastra* sp., an unidentified species of *Characella*, an unidentified species of *Desmacella*, a dendrocellid in the genus *Pylocleroma*, and several species in the family Cladorhizidae, . All were identified from spicules or spicule images by Dr. Rob van Soest in the Netherlands. Of these 18 total species, cf. *Corallistes* sp., *Penares* sp., *Poecillastra* sp. 2, *Polymastia* sp. 1, *Characella* sp., *Stelodoryx* sp. *Pylocleroma* sp. were found in discrete beds that may have formed from localized settlement events. While several of these can found in moderate to high abundance, the colony sizes of these sponges are relatively small and few if any have been observed with associated fauna. None are therefore considered to be major structure forming species, however it is worth

noting here that based on these new collections, there may be a greater prevalence of demosponges below 200 m than previously thought.

a. (ii) Hexactinellida below 200 m

Prior to 2015, 118 hexactinellid specimens had been collected in Hawaiian waters dating back to the Albatross expedition in 1902. Three of the five currently recognized orders (Amphidiscosida, Lyssacinosa, and Sceptulophora) and seven of the currently recognized families (Phoronematidae, Uncinateridae, Euretidae, Farreidae, Tretodictyidae, Euplectellidae, and Rossellidae) are represented in these collections. At least 49 distinctly different taxa are among the specimens. However, to date, only three have been identified to the species level: *Sericolophus hawaiiicus* Tabachnick and Levi 2000, *Walteria flemmingi* Schultze 1886, and *Farrea occa* Bowerbank 1862. Seven types are listed as being "near" a previously described species because spicule examination has shown they are close to but not an exact match and therefore may be different. The remaining 42 types are believed to be potentially new, undescribed species, which are the most of any region in the U.S. or for that matter, in the world (Reiswig unpub. data). A collaborative effort that includes two of the authors of this report (Kelley and Reiswig) in addition to Dr. Craig Young and Dr. Martin Dohrmann is now underway to publish species descriptions for this somewhat "neglected" fauna. In addition to the collections, at least 8 additional distinctly different hexactinellids have been captured on video during HURL dives and are included in this report's online



species list but have not as yet been collected. At the preparation of this report, there are believed to be at least 57 species of hexactinellids in Hawaiian waters that have been recorded from 330 m to over 2,000 m. However, recent CAPSTONE collections (that included from waters deeper than 2,000 m, as well as from U.S. Pacific Island areas outside the Hawaiian Archipelago) will significantly increase these numbers once the specimens have been carefully examined.

1.0 Order Amphidiscosida

1.1 Family Hyalonematidae

Chave and Jones (1991) and Chave and Malahoff (1998) reported the presence of two families of Amphidiscosida in Hawai'i: Hyalonematidae and Pheronematidae. However, further investigation determined their unidentified species of *Hyalonema* was actually a pheronematid that was subsequently named *Sericolophus hawaiiicus* (Tabachnick and Levi 2000). Two species of hyalonematids were recently collected during CAPSTONE dives around Hawai'i. Therefore even though the initial report of this family being in Hawai'i was found to be incorrect, its presence has now been confirmed.

1.2 Family Pheronematidae

All other Hawaiian amphidiscosidans identified to date are pheronematids, with representatives from three genera: *Poliopogon*, *Semperella*, and *Sericolophus*. Pheronematids have been both collected and recorded on video between 338 m and the 2000 m maximum operating depth of the Pisces submersibles. This

group no doubt extends much deeper. While most species are found attached to hard rocky substrates, *S. hawaiiicus*, the shallowest species, is found exclusively on soft substrates. *S. hawaiiicus* has an elongate tuft that both anchors the sponge into the sediment as well as serving as a stalk (Fig. 6a). This species is considered to be structure forming because it is typically found in very high density beds and with a variety of commensals since it often provides the only firm elevated surfaces in the area. Some of the other pheronematids are both large and also form beds with densities close to 1/m². Large lateral oscula in many of these species attract commensal crabs and ophiuroids that appear to use them for shelter. Until the taxonomy of family is completely worked out, all species of pheronematids in Hawai'i should be considered as structure forming due to both their size and abundance (Fig 6b,c).

2.0 Order Sceptrulophora

The order Sceptrulophora (formerly Hexactinosida, in part) is represented in this region by four families: Euretidae, Farreidae, Tretodictyidae, and Uncinateridae.

2.1 Family Euretidae

Three different species of euretids have been identified from specimens collected during HURL dives in Hawai'i. The latest of these, a suspected new species of *Lefroyella*, was collected in 2013 and like its New Zealand congener, *Lefroyella decora*, was found to have a large number of commensal anemones growing through its framework. These anemones are believed to be in the family Edwardsiidae



(Fautin, pers comm.), but this has not as yet been confirmed. Additional euretids were collected during CAPSTONE dives bringing the total number of species tentatively identified as being euretids to 9. However, these are all relatively uncommon and therefore are not considered major structure forming sponges in this region.

2.2 Family Farreidae

All of the farreid specimens collected during HURL submersible dives around Hawai'i have similarities to *Farrea occa*, which has been tentatively identified as being in this region from a single specimen. These species are therefore described as *Farrea* near *occa* or *Farrea* near *occa erecta* based on whether their colony is bushy (the former) or taller and more upright (the latter). Farreids have been recorded from 350-2400 m in Hawai'i and are relatively common. In some locations *F. near occa*, but not *F. near occa erecta*, can be found in beds of modest densities. Another interesting distinction between the two types is the presence of a commensal antipatharian found growing on *F. near occa* but not on *F. near occa erecta*. This antipatharian appears to be a new species and is presently under investigation. Other colonies of *F. near occa* have been seen completely covered with zoanthids which again has not been observed with colonies of *F. near occa erecta*. Collections of farreids during CAPSTONE have revealed the presence of at least 2 other genera around Hawai'i: *Aspidoscopulia* and *Lonchiphora* as well as a possible third new genus that presently doesn't match any of the known genera in this family.

Aspidoscopulia colonies are large and can be found in relatively dense beds. However, until these new specimens can be examined more carefully, *F. near occa* will be listed here as the only structure forming farreid in this region.

2.3 Family Tretodictyidae

Although two species in this family are listed in this report's online species list, only one has been positively identified in this region and has been assigned to the genus *Tretodictyum*. The specimen is vase-shaped and was collected on hard substrate at a depth of 687 m. This species is neither large nor abundant and therefore is not considered to be structure forming. As mentioned previously, a potentially new species of branching tretodictyid was collected several months ago, which had been previously identified from photographs as a calcarean. Colonies were moderately abundant at the CAPSTONE dive site and were furthermore found to have large numbers of what appeared to be commensal zoanthids. This is likely a new species however that determination requires additional investigation.

2.4 Family Uncinateridae

The presence of this order in Hawai'i was unknown until 2011 when the identification of four specimens collected in 2003 were assigned with several other specimens collected in 2007 and 2009 to the genus *Tretopleura* in the family Uncinateridae. Three additional specimens do not fit into any known genera and are therefore listed as "Uncinateridae new genus new species." All of the species in this family attach to hard substrates at depths of 685-1850 m.



Commensal crabs and ophiuroids are typically observed on the *Tretopleura* colonies, which can reach over a meter in height. *Tretopleura* sp. 1B and sp. 2 are relatively common and are therefore considered structure forming.

3.0 Order Lyssacosida

Lyssacosidans are relatively common in this region of which all have been assigned to one of two families: Euplectellidae and Rossellidae.

3.1 Family Euplectellidae

Euplectellids are the most diverse family of hexactinellids in Hawai'i with 18 potential species having been identified from specimens and video images. Thirteen genera have been identified to date and include one in the lophophytous subfamily Euplectellinae, four in the pedunculate subfamily Bolosominae and 8 in the vase-like and tube-like subfamily Corbitellinae. While *Dictyocalyx gracilis* was reported to have been collected near Hawai'i (Tabachnick 2002), the 2 specimens of this genus actually collected in Hawai'i are not the same and are believed to be a new species. Euplectellids are found from 330 m to over 4,000 m, with those in the genus *Regadrella* being observed in the shallowest depths while pedunculate euplectellids only appearing at depths below 500 m. All species attach to hard substrates and several have been observed in aggregations. Some species in both the Bolosominae and Corbitellinae can grow to relatively large sizes (Fig. 6d). Most euplectellids are inhabited by commensals such as ophiuroids and crustaceans. In some species

with small or covered primary oscula, early colonization leads to commensal shrimp becoming "trapped for life" inside their atrial cavities (Baba 1983). For the purpose of this report, several species of euplectellids found in the genera *Bolosoma*, *Saccocalyx*, and *Regadrella*, and *Walteria* are considered structure forming in this region.

3.2 Family Rossellidae

Until CAPSTONE, rossellids were represented in Hawai'i by 9 species, 7 of which have been placed into two genera: *Bathydorus* and *Caulophacus*. The two species of *Bathydorus* are vase-like, with the specimen of *Bathydorus* near *laevis* being a huge caldron sized sponge while the specimen of *Bathydorus* sp. was not. These two species, along with other similar looking vase sponges identified from video as only rossellids, have been recorded at depths of 350-1760 m. The five species of *Caulophacus* are pedunculate with small bodies supported above the substrate by a relatively long stalk. Both pedunculate and non-pedunculate rossellids can be found in small aggregations but none are considered structure forming in this region. CAPSTONE collections of rossellids around Hawai'i included members in additional genera of both pedunculate and non-pedunculate species. The most noteworthy of these was a specimen from an extremely large colony of an undescribed genus in the subfamily Lanuginellinae. While this colony had numerous associated fauna, the species is rare and therefore is therefore not considered to be structure forming at this time.

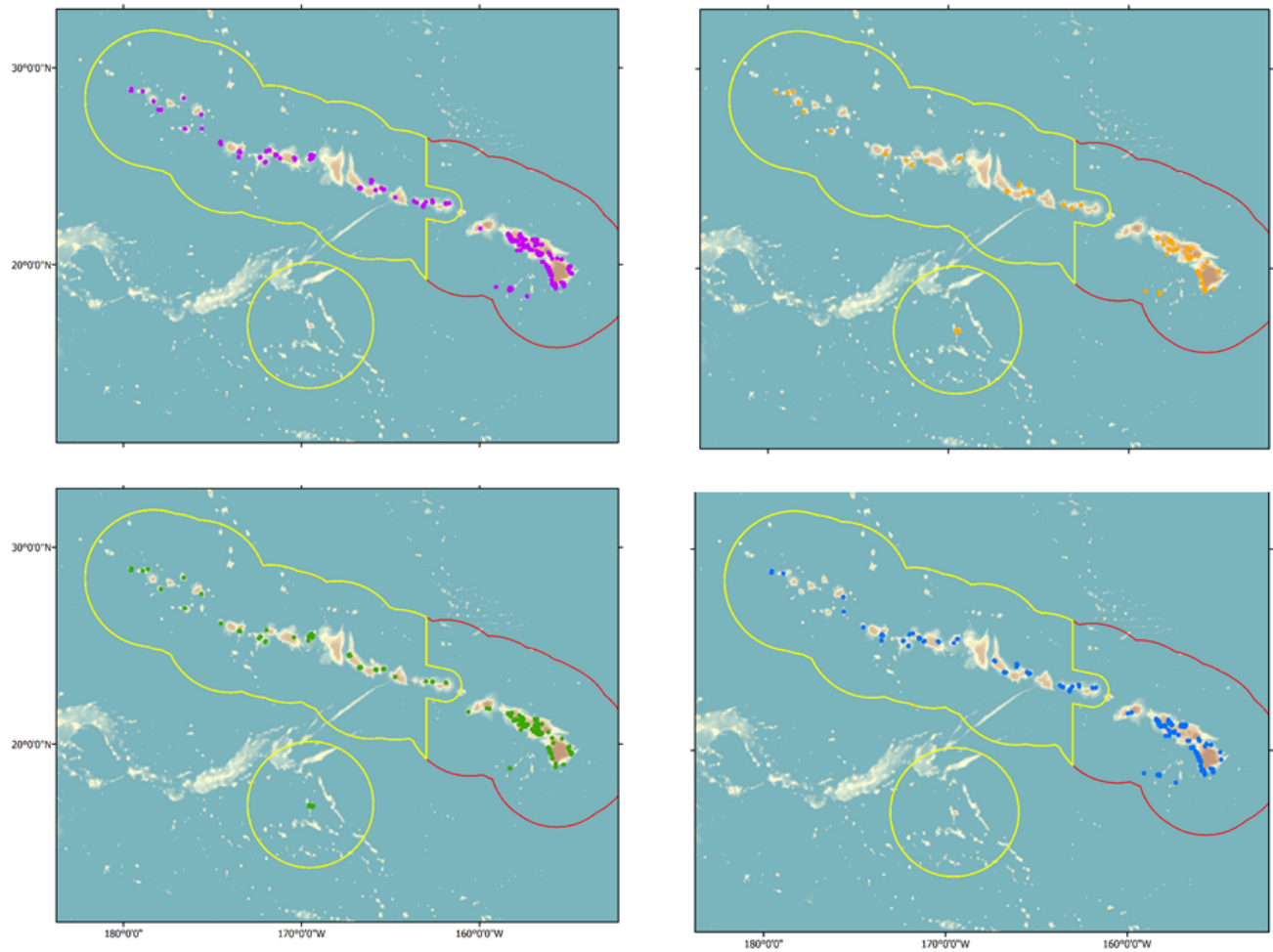


Figure 7. Maps of the Hawaiian Archipelago and Johnston Atoll showing the locations where deepwater octocorals (purple, upper left), scleractinians (orange, upper right), antipatharians (green, lower left), and sponges (blue, lower right) have been found. For additional detail see maps in Appendix. The yellow line indicates the monument boundaries and the red line is the EEZ boundary. The two are the same around Johnston Atoll.



II.3. Coral Growth, Biology and Reproduction

The Western Pacific Fishery Management Council placed a moratorium (2007) on the harvesting of gold coral (*K. haumea*) (Fig. 8) for the precious coral fishery until a validation study of conflicting growth estimates could be conducted. Gold coral colonies that were measured and marked up to 9 years earlier were revisited and re-measured (Parrish and Roark 2009). The measured change in growth was statistically indistinguishable from zero, indicating that gold coral growth is much slower than the annual growth estimate derived from basal stem ring-counts previously relied on for the fishery. The duration of the re-measurement period was too short to effectively evaluate the validity of longer lifespan estimates from radiocarbon dating that yielded a linear growth rate of 2.2 ± 0.2 mm yr⁻¹ but clearly indicated that gold coral growth was very slow. The main criticism of using radiocarbon measurements to determine the

lifespan of *K. haumea* and *Leiopathes* sp. (estimated at up to 2,742 years and 4,265 years, respectively) was that the corals might be feeding on old dead carbon thereby giving unrealistically old ages. By reproducing the radiocarbon bomb curve in a Hawaiian *K. haumea* specimen (Roark et al. 2009) and a Gulf of Mexico *Leiopathes* sp. specimen (Prouty et al. 2011) these studies clearly demonstrate that these deep-sea corals are feeding on recently exported young fresh particulate organic carbon from surface waters clearly demonstrating the validity of the extreme longevity and slow radial growth for both species (see Prouty et al., this volume, on age, growth rates, and paleoclimate studies). U-Series dating of stony coral *Enallopsammia rostrata* specimens from 480 to 788 m water depth in the Line Islands indicate life spans ranging from 209 ± 8 to 605 ± 7 years, radial growth rates ranging from 0.012 to 0.073 mm yr⁻¹ and with linear growth rates ranging from 0.6 to 1.9 mm yr⁻¹ (Houlbrèque et al. 2010). These



Figure 8. The purple stoloniferan *Clavularia grandiflora* growing on a *Kulamanamana haumea* colony. Photo credit: HURL.



Figure 9. The invasive *Carijoa riisei* growing on shallow water black coral. Photo credit: HURL.



results show *E. rostrata* is relatively slow growing deep-sea coral.

Recent reproductive studies on Hawaiian deep-sea corals includes work on the morphological structures of precious gold coral (*K. haumea*), pink coral (*Pleurocorallium secundum*), and red coral (*Hemicorallium laauense*) (Waller and Baco 2007). All 3 species appear to be gonochoric broadcast spawners. The reproductive biology of the shallow water black corals (including *Antipathes grandis*, *Antipathes griggi*, *Cirrhopathes* cf. *anguina*, *Stichopathes echinulata*, *Stichopathes* sp., *Aphanipathes verticillata*), and deepwater corals (*Leiopathes* sp. and *Alternipathes alternata* [= *Bathypathes alternata*]) (Wagner et al. 2011c, Wagner et al. 2012) has also been examined.

Wagner et al. (2011b) found that 10 out of 14 Hawaiian black coral species collected between 10 and 396 m contained the symbiotic algae *Symbiodinium* and thus perhaps should not be considered strictly azooxanthellate. Histological examination of five species showed low densities of *Symbiodinium*-like cells inside gastrodermal tissues. The authors concluded that the *Symbiodinium* were unlikely to play a significant role in the nutrition of the black corals.

II.4. Species Associations with Deep-Sea Corals and Sponges

The 2007 report summarized information on species associations with deep-sea corals and highlighted concerns over the colonization of shallow water black coral by the parasitic

octocoral *Carijoa* sp. (originally identified as *Carijoa riisei*; Fig. 9). Wagner et al. (this volume) discuss the improved understanding of this parasitic association. Many additional associations of invertebrate species with deep-sea corals and particularly with sponge communities (Fig. 10) have been documented. The exceptional imagery collected during the CAPSTONE cruises have expanded the number of observed associations and along with collected samples will be a future area of research focus.

II.5. Research Priorities

The priorities for future work in the region on both deep-sea corals and sponges remain largely the same as those identified for deep-sea corals in the 2007 report, and can be divided into: 1. Exploration and mapping, 2. Taxonomy and connectivity, 3. Biology, ecology and environmental parameters, and 4. Resilience of deep-sea coral communities. In 2014, NOAA brought together over 20 researchers and resource managers to identify and prioritize information needs to increase our understanding of deep-sea coral and sponge ecosystems in the U.S. Pacific Island Region. The workshop participants identified priority research questions and specific information needs and activities (Parrish et al. 2014). The results of the workshop informed NOAA's Deep-Sea Coral and Sponge Fieldwork Initiative and the CAPSTONE expeditions, and are reflected in the priorities below:

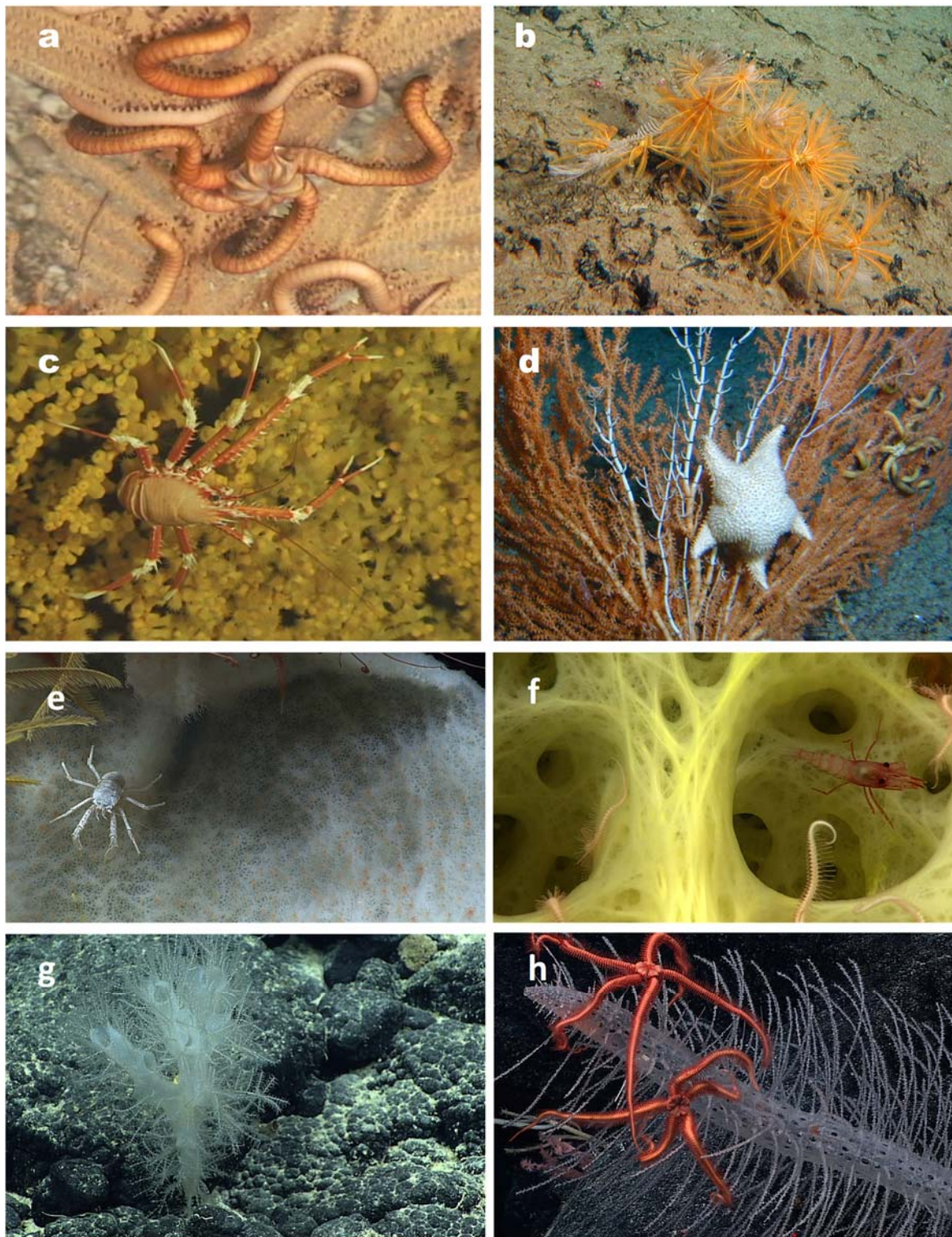


Figure 10. Examples of invertebrates found associated with Hawaiian deep-sea corals (a-ophiuroid, b-crinoid, c-squat lobster, d-asteroid feeding on a bamboo coral; Photo credit: HURL) and sponges (e-squat lobster, f-shrimp and ophiuroids, g-antipatharian growing out of sponge, h-ophiuroids; Photo credit: NOAA).



1. *Exploration and mapping*

Prior to 2015, there had been little or no exploration of the U.S. Pacific Islands Regions except for the Hawaiian Archipelago. There is a need to expand surveys to under sampled regions in the U.S. Pacific including the Marianas, American Samoa and the Pacific Remote Islands Marine National Monument. Exploring the rest of the U.S. Pacific is the highest priority for the region and represents a real challenge. Applying consistent taxonomy, and where possible, collecting genetic samples in order to evaluate the degree to which various assemblages are connected, will begin to elucidate biogeographic patterns at the Pacific basin scale. Even within the Hawaiian Archipelago, where research tools are available, most information on the distribution of deep-sea corals and sponges was restricted to depths shallower than 2000 m and little was known about the deep-sea fauna found below this depth.

2. *Taxonomy and connectivity*

Taxonomy using both traditional morphological methods and recently developed genetic methods continues to be a high priority for all deep-sea coral and sponge work because so many of the specimens are new to science. While gene flow in shallow water ecosystems is relatively well-understood, the gene flow in deep-sea coral ecosystems is poorly understood and their role in connectivity is an obvious emphasis for future work in the U.S. Pacific Islands region. CAPSTONE collected numerous samples of corals and sponges (including genetic sampling) that have already begun to

identify new species (e.g., Cairns 2017), however, population-level studies were constrained by limited sample sizes.

3. *Biology, ecology, and environmental parameters*

Much of the basic biology and ecology of major structure-forming deep-sea corals and sponges in the region are poorly known, as are the environmental variables that govern where deep-sea coral and sponge communities colonize and develop into mature assemblages. Having information on the conditions needed to support these ecosystems is valuable, as this provides the parameters needed for planned modeling activities and contributes to the growing body of climate research. To date there are no published habitat suitability models for deep-sea sponges. The Pacific Islands, with its large protected areas in the form of marine national monuments, is an ideal place to look for environmental change using data loggers at established study sites.

4. *Resilience of deep-sea coral communities*

It is not known how long it takes for deep-sea coral or sponge individuals or communities to recover following disturbance. Deep-sea corals and probably many sponges can grow extremely slowly and are vulnerable to impacts from activities that disturb the seafloor. Additionally, ocean acidification may affect corals' ability to grow and maintain their structures. There is a need to understand community development that considers overall natural recruitment, growth, and mortality over large spatial scales.



Opportunities for addressing these research priorities need to take into account the loss of research and monitoring assets in the region. In 2013 NOAA discontinued funding for the Hawai'i Undersea Research Laboratory, which operates the *Pisces 4* and *Pisces 5* submersibles, ROV, and support vessel. These have been the key and nearly exclusive assets for in situ explorations in the U.S. Pacific Islands Region. Loss of these assets will severely impact deep-sea coral and sponge work in Hawai'i and the U.S. Pacific Islands Region. The availability of other similar assets typically requires that highly competitive proposals based on hypothesis-driven research be submitted to funding entities. The success of CAPSTONE highlights the value of exploratory work, however it may be incredibly challenging to bring submersible and ROV assets here on a sustained basis in the future.

III. Update on Management of Deep-Sea Coral and Sponge Habitats

III.1. New Information on Impacts and Stressors

III.1.i – Precious coral fishery

Hawai'i has had the only significant black and precious coral fisheries in the U.S. There have been no reported commercial catch reports for precious coral since the 2007 report. Harvest of the precious coral (e.g., *Corallium* spp., *Hemicorallium* spp., *Pleurocorallium* spp, *K. haumea*) has been dormant since 2000 although a permit was obtained in 2012 for

harvesting in the Makapu'u bed using a small ROV system but is as yet unused. In 2011 sales reports of shallow water black coral were filed but cannot be described in detail because the number of participants is too small to report publicly due to confidentiality requirements. Robin Lee, long time black coral diver and key participant in the fishery passed away in 2012, and recently submitted landing logs indicate new participants have joined the fishery.

III.1.ii – Undersea cables

The laying of undersea cables in the channels of the Hawaiian Islands to deliver power from planned wind and solar farms on outer islands (e.g., Molokai, Lanai) is the region's most immediate potential impact concern. Most of the known shallow-water black coral population is found in these channel waters and are the focus of harvesting by divers. Tracts of zooxanthellate scleractinian corals (e.g., *Montipora capitata*, *Leptoseris hawaiiensis*) also occur at the mesophotic depths between 30-150 m and are fragile, growing on the slopes and the submerged land bridge that connects the islands and could incur some damage if cables are laid on them. Azooxanthellate corals in the deeper channels between Oahu and Molokai are also at risk of damage from cables.

However, at the moment, the state has taken the effort to survey potential cable routes and has already diverted proposed routes around known coral beds such as that off Makapu'u.

III.1.iii – Undersea mining

The interest in mining cobalt-manganese crust from the seafloor between 400-4000 m in the



U.S. Pacific was identified in the 2007 report and continues to be discussed as an option for the future. Although this is unlikely to occur in areas such as the Hawaiian Archipelago due to its young age and the fact that much of the archipelago has been designated as a marine national monument, other, older island groups in the U.S. Pacific may be more likely targets. However, Cretaceous seamounts (i.e., 60-120 ma) with presumed extensive Mn crusts do exist in the vicinity of the archipelago and could be targeted by the industry in the future. There is enough concern about the impacts of mining that the International Seabed Authority (ISA) funded data syntheses to provide the first ever comprehensive description of taxa present on cobalt-rich crusts (see Clark et al. (2011) and Schlacher et al. (2014)). Additional studies of this kind are clearly warranted, particularly in light of the fact that 3 exploratory leases have already been issued by the ISA on prospective Mn crust mining sites in the Western Pacific.

III.2. New or Planned Management Actions

III.2.i – Precious coral fishery

The only change in federal regulation for the precious coral fishery is a 5-year moratorium on the harvest of live gold coral due to its reported slow growth rate (Roark et al. 2006). A subsequent study (Parrish and Roark 2009) using mark and re-measurement techniques reported similar findings and the moratorium was extended until 2018. Other proposed actions relevant to the coral fishery included a proposal in 2009 to list the genera *Corallium* and *Paracorallium* under the Convention on

International Trade in Endangered Species of Fauna and Flora (CITES) Appendix 2 but this proposal did not pass.

III.2.ii – Designation of new Marine National Monuments

In January 2009, Presidential proclamations 8335-8337 designated waters off CNMI as the Marianas Trench Marine National Monument; Kingman Reef, Palmyra Atoll, Jarvis, Howland, Baker, Johnston and Wake Islands were designated the Pacific Remote Islands Marine National Monument; and Rose Atoll was made the Rose Atoll Marine National Monument under the Antiquities Act. These new Monuments added to the existing Papahānaumokuākea National Marine Monument (est. 2006) to form the largest network of marine monuments in the U.S. Their mandate is to protect the unique natural and cultural resources within the region through the advancement of scientific research, exploration and public education. Combined this area encompassed a total 800,076 km² with each marine national monument extending seaward 50 nm from mean low water the seabed. They are co-managed between the Department of Interior and the Department of Commerce in coordination with federal partners (e.g., Department of Defense) and the State/Territorial governments. No commercial fishing is allowed in any of the monuments, which precludes the expansion of the precious coral fishery into these areas.

In 2014, the boundaries of the Remote Pacific Islands National Marine Monument around Jarvis, Wake and Johnston Atoll were expanded



out to the 200 nautical mile U.S. EEZ by Presidential Proclamation 9173. The newly protected areas contain additional seamounts that have since been confirmed to include important deep-sea coral and sponge resources. The monument now encompasses an area of 1,057,494 km² (308,316 square nautical miles). These virtually unexplored areas were the target of mapping and ROV surveys by NOAA ship *Okeanos Explorer* under CAPSTONE.

The Papahānaumokuākea Marine National Monument management plan was finalized in 2008, and in 2010 the area was inscribed as a natural and cultural World Heritage Site. The Monument was expanded by Presidential Proclamation 9478 to 1,508,870 km² (582,578 square miles), making it the largest protected area - terrestrial or marine - on the planet.

III.3. New Priorities for Management

III.3.i – Alternative Energy

Hawai'i's push for alternative energy has prompted a number of feasibility studies including some initial surveys of potential cable-laying routes. Management groups involved in these plans are studying the potential impacts and examining the best alternatives. An example is the Hawaiian Islands National Humpback Whale Sanctuary, which spans the channel waters of the Main Hawaiian Islands, partnering with NOAA scientists and the University of Hawai'i to spatially model data from their studies on mesophotic coral ecosystems in the Au'au channel between the islands of Maui and Lanai

(Costa et al. 2012). The Bureau of Ocean Energy Management also supported modeling of shallow, mesophotic and deep-sea corals (Bauer et al. 2016) in order to inform potential future alternative energy development. There has also been an interagency meeting to look at potential impacts of implementing Ocean Thermal Energy Conversion (OTEC) using intake pipes laid down slope 800-1000 m to bring deep cold water to the surface for energy production.

III.3.ii – Ocean cage aquaculture

Limited offshore cage aquaculture of fishes has occurred on the leeward coast of a couple of the Main Hawaiian Islands and there is interest in expanding this activity, which could involve use of mooring anchors potentially at deeper depths. It is not known if this type of development would impact deep-sea coral communities significantly.

IV. Conclusions

In the first seven years since the 2007 report, deep-sea coral research focused on using available data from Hawai'i to study the biology, reproduction and growth of select coral taxa – especially antipatharians. Notable advances included taxonomy, preliminary habitat suitability models for deepwater corals, and the first steps in the characterization of the sponge community. Hawai'i's deep-sea sponges are far less well studied than are the deep-sea corals. Much of the U.S. Pacific Islands has been recently designated as new Marine National Monuments and yet still little or no



information had been collected on the deep-sea coral and sponge communities in areas outside of the Hawaiian Archipelago. The monument designations will limit expansion of domestic commercial harvesting especially for precious coral resources that are protected as part of the seafloor. However, much of this area is remote making it difficult to monitor the degree of illegal fishing by foreign fleets. Other potential impacts include cable-deployment and development of oceanic cage aquaculture, and for the adjacent high seas region, deep-sea mining. Finally, the region's ability to continue and expand studies of deep-sea corals in support of management using the submersible and ROV assets operated by the Hawai'i Undersea Research Laboratory has been jeopardized if not ended as a result of budget cuts.

Beginning in 2015, NOAA's Deep Sea Coral Research and Technology Program, in partnership with NOAA's Office of Ocean Exploration and Research, National Marine Sanctuary Program, and NMFS, began a major three-year field research initiative, CAPSTONE, in the Pacific Islands region. This campaign conducted the first major biogeographic exploratory work on deep-sea coral and sponge ecosystems outside the Hawaiian Archipelago, as well as ecological studies off Hawai'i, where the infrastructure and technical capacity exist to support this type of field work. The results will provide information on monument resources and increase scientific understanding of these unique deep-sea ecosystems.

Online Annex – Comprehensive list of deep-sea corals in the U.S. Pacific Islands region linked here:

<https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>

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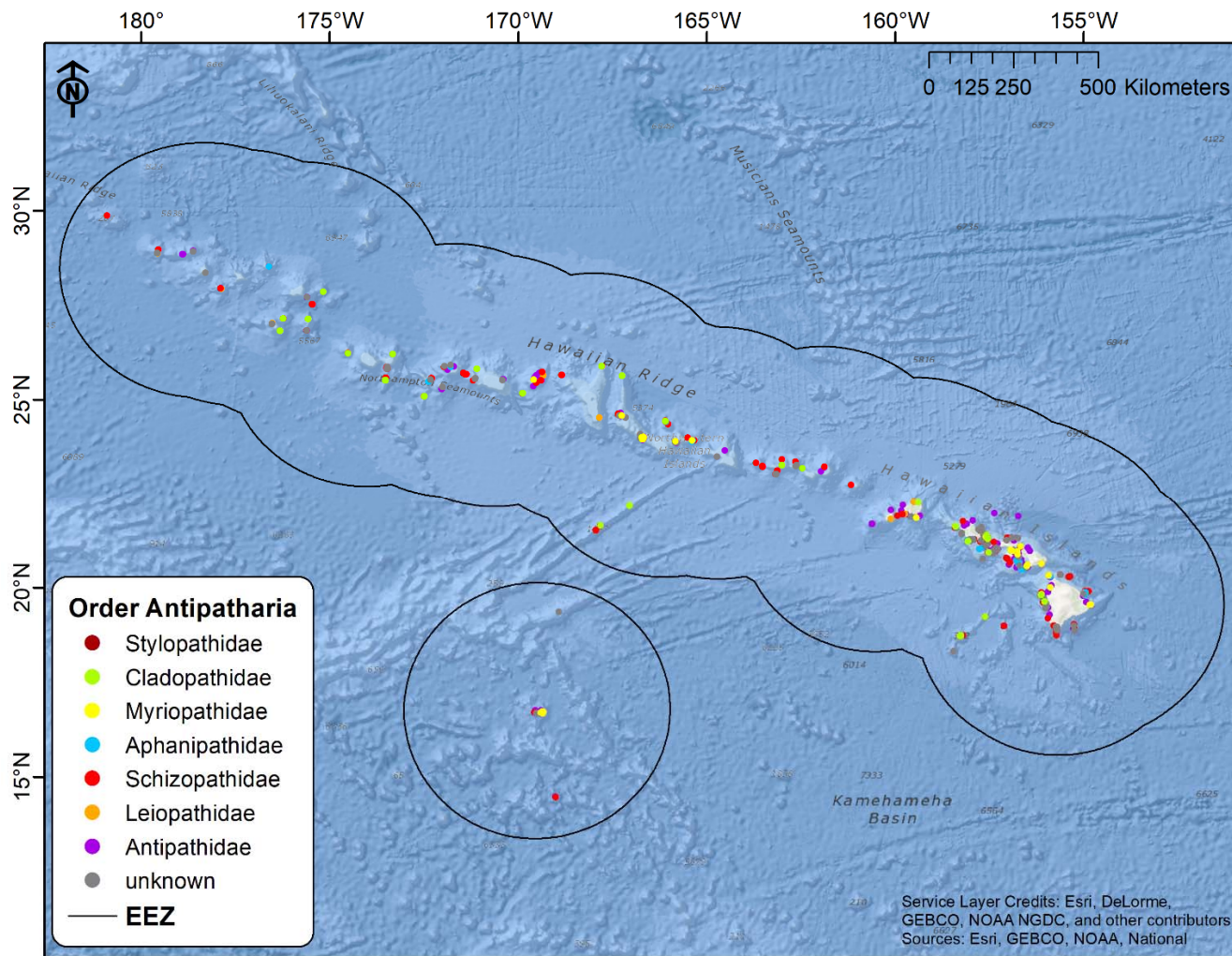
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[Online Annex 1. Deep-sea Coral Taxa in the U.S. Pacific Islands Region: Depth and Geographic Distribution](#)

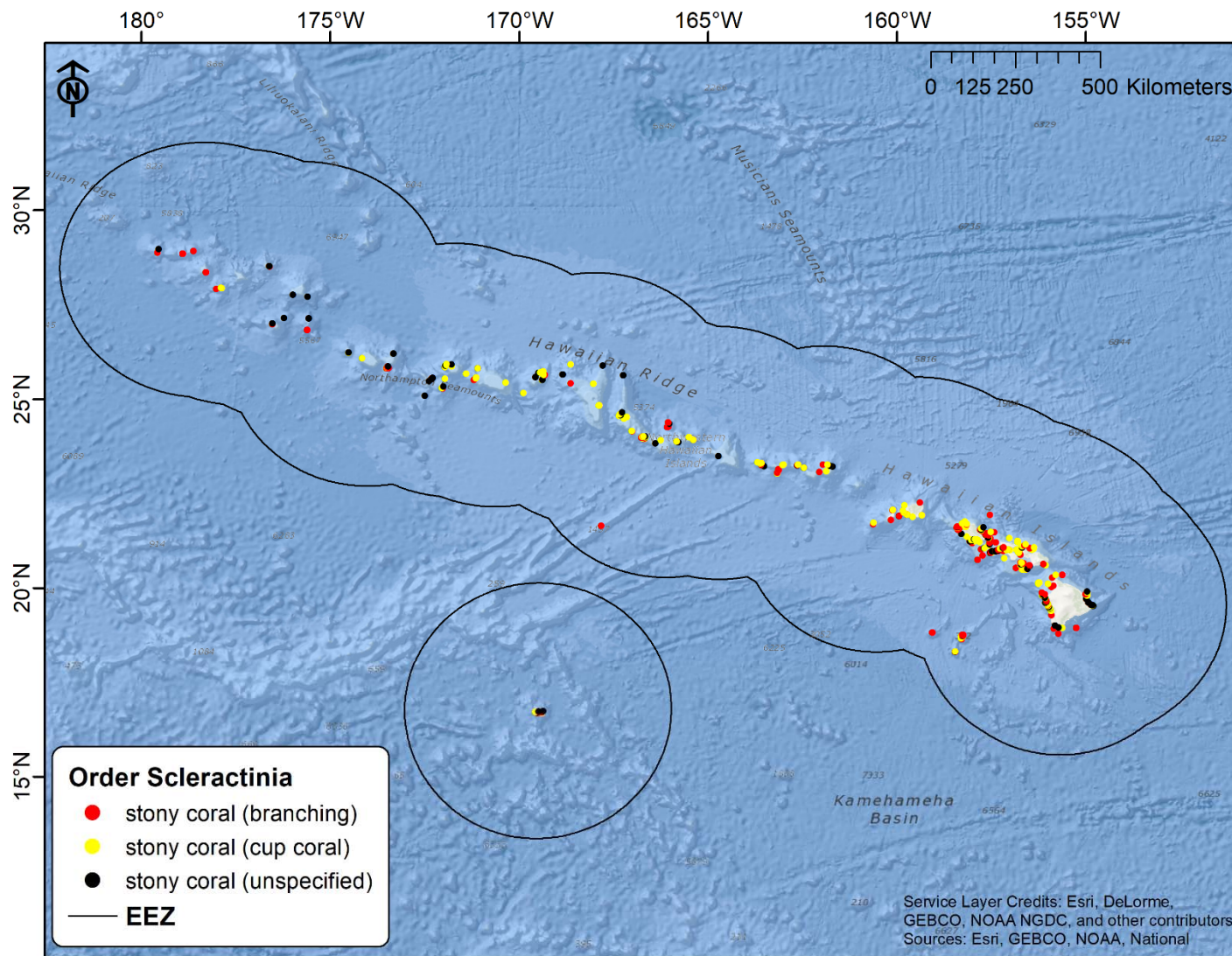


Appendix – Distribution maps for the Hawaiian Archipelago and Johnston Atoll



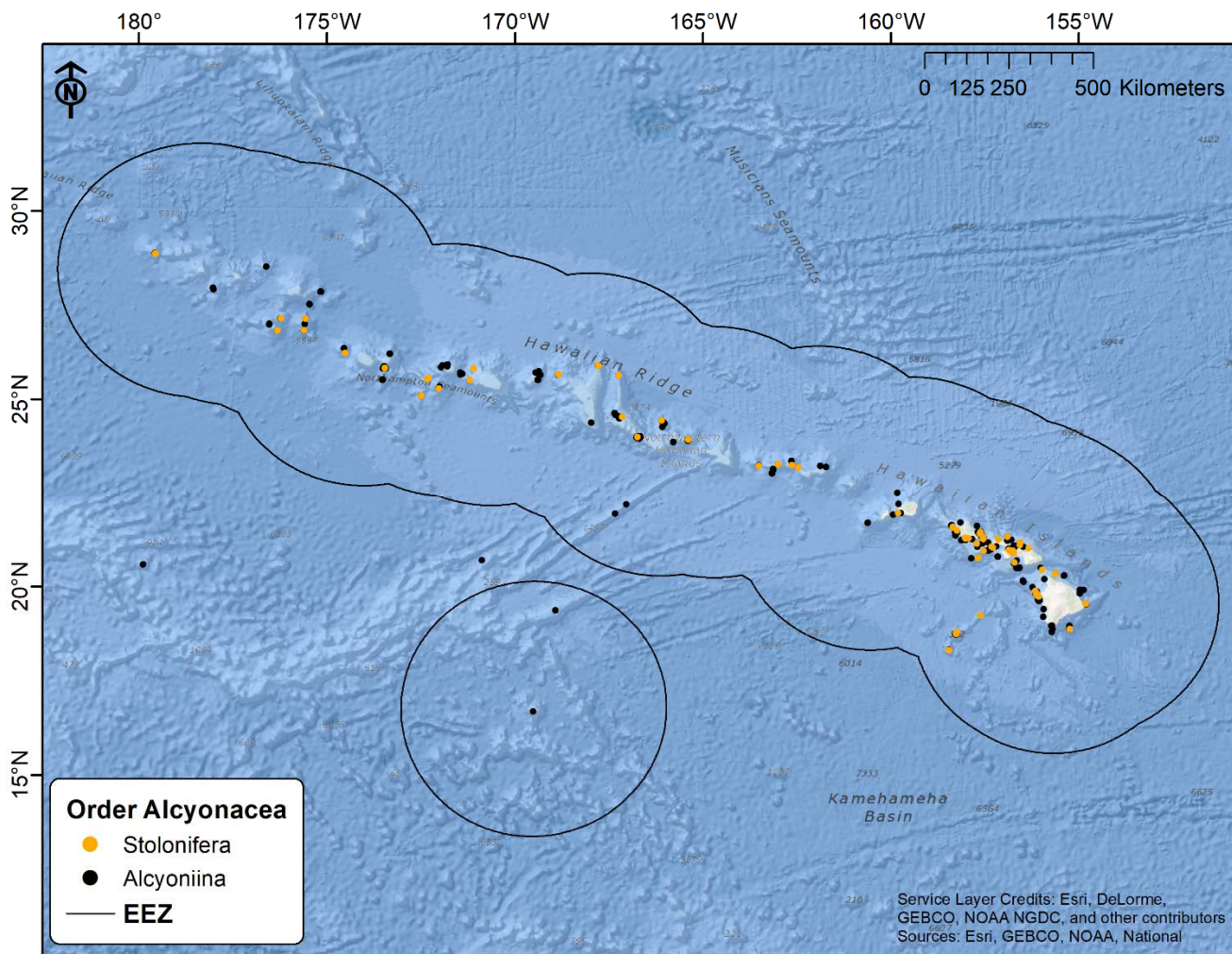
Map 1. Locations of black corals (Order Antipatharia) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION



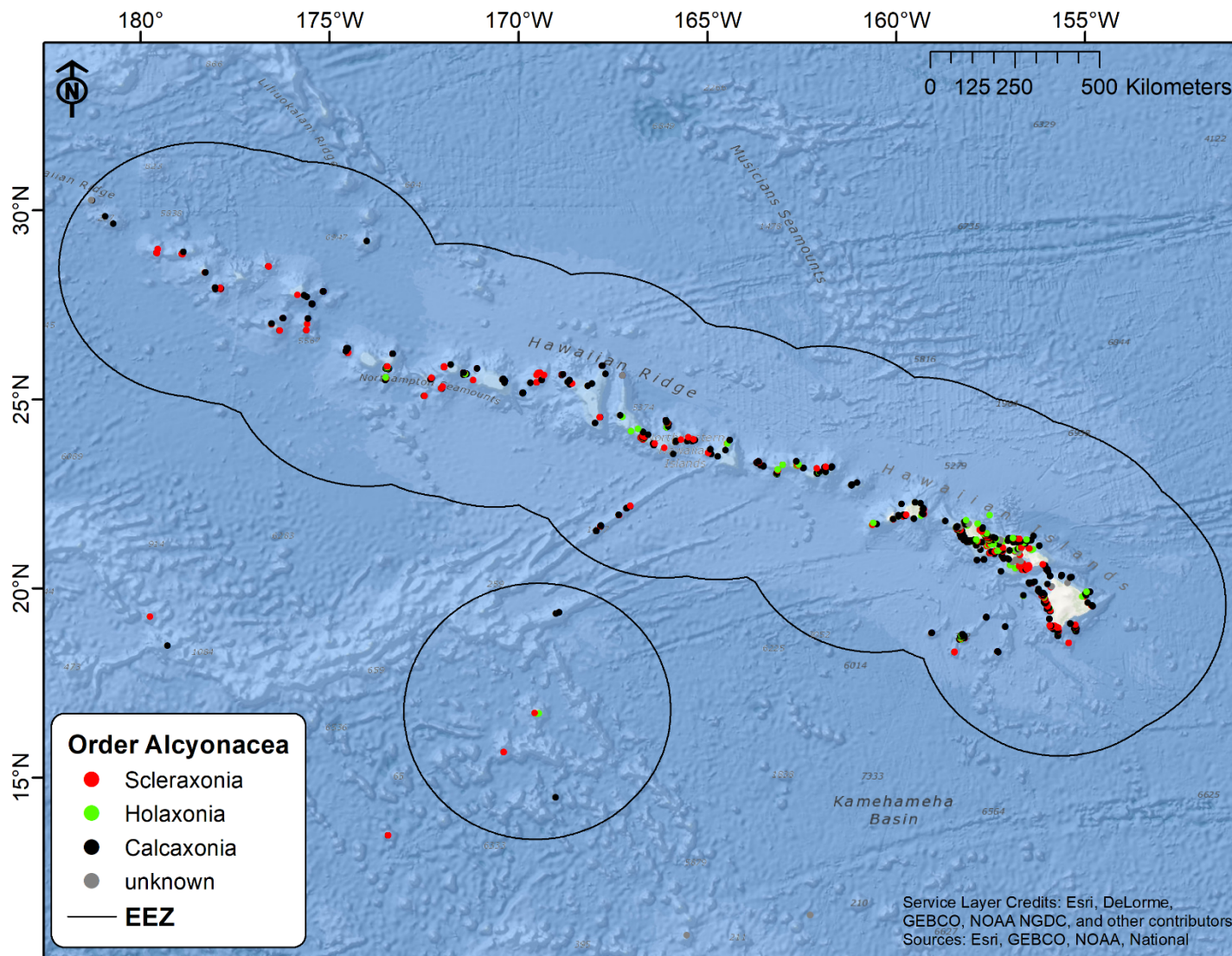
Map 2. Locations of branching stony corals (Order Scleractinia) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION



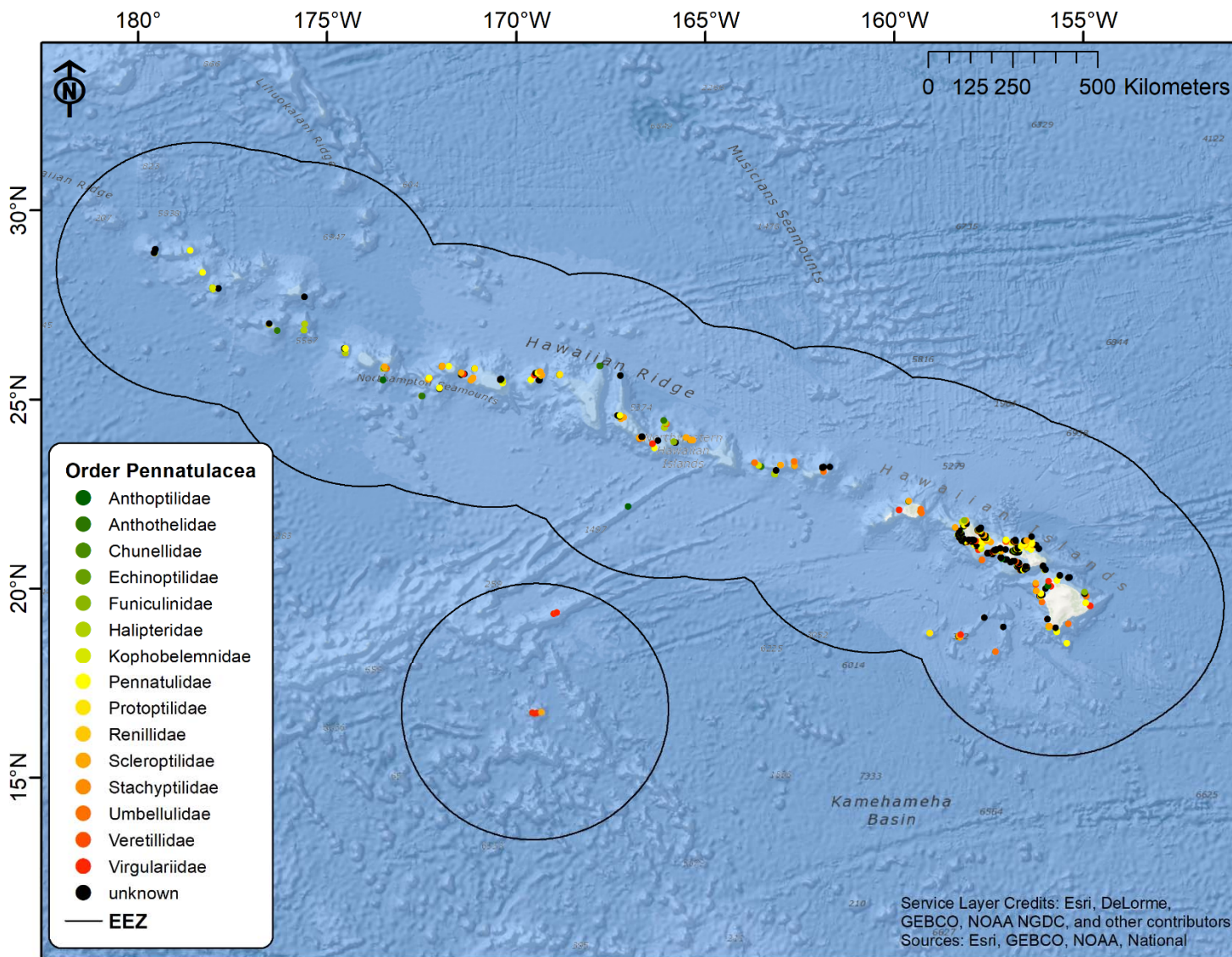
Map 3. Locations of non-gorgonian alcyonaceans (Order Alcyonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION



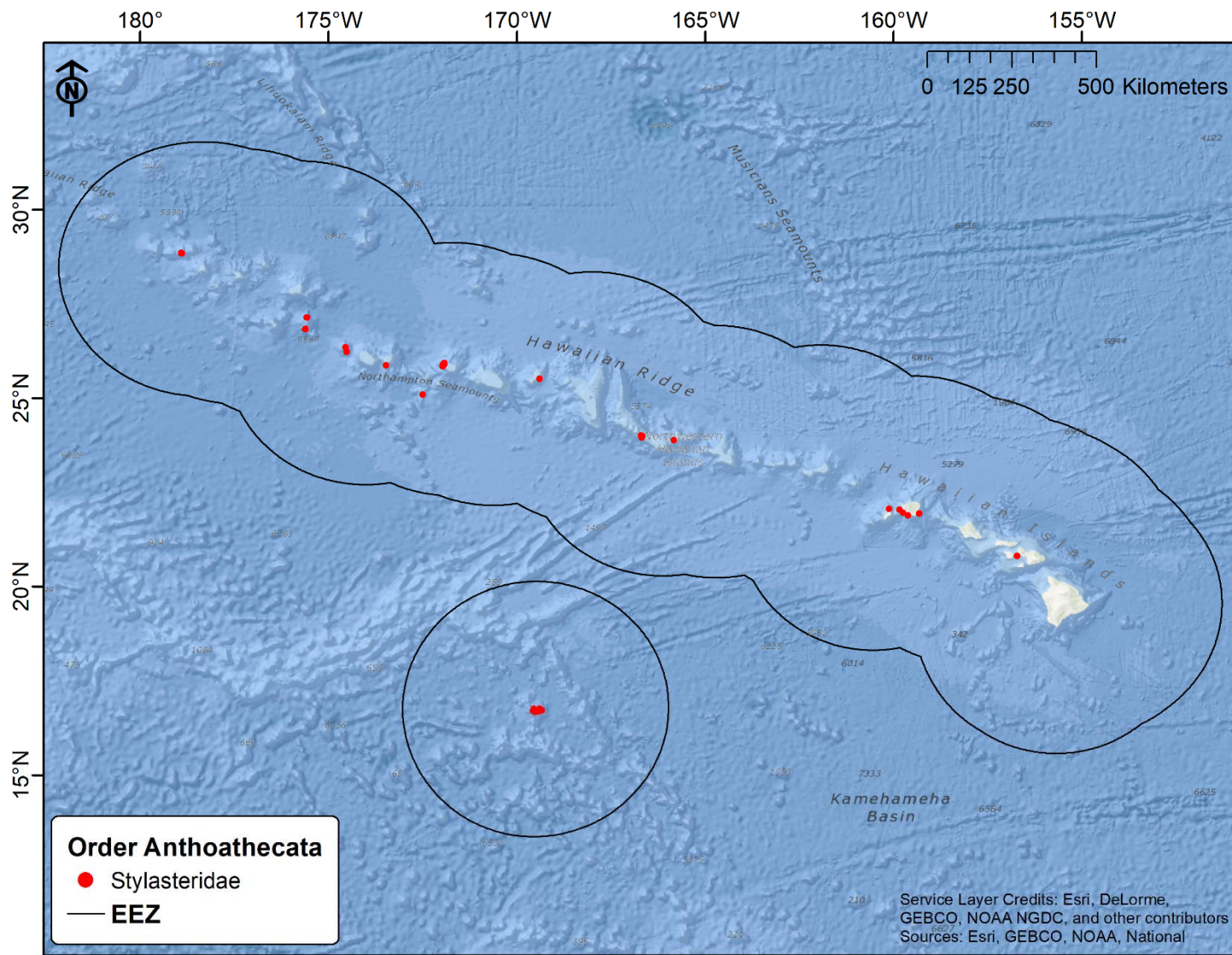
Map 4. Locations of gorgonians (formerly Order Gorgonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION



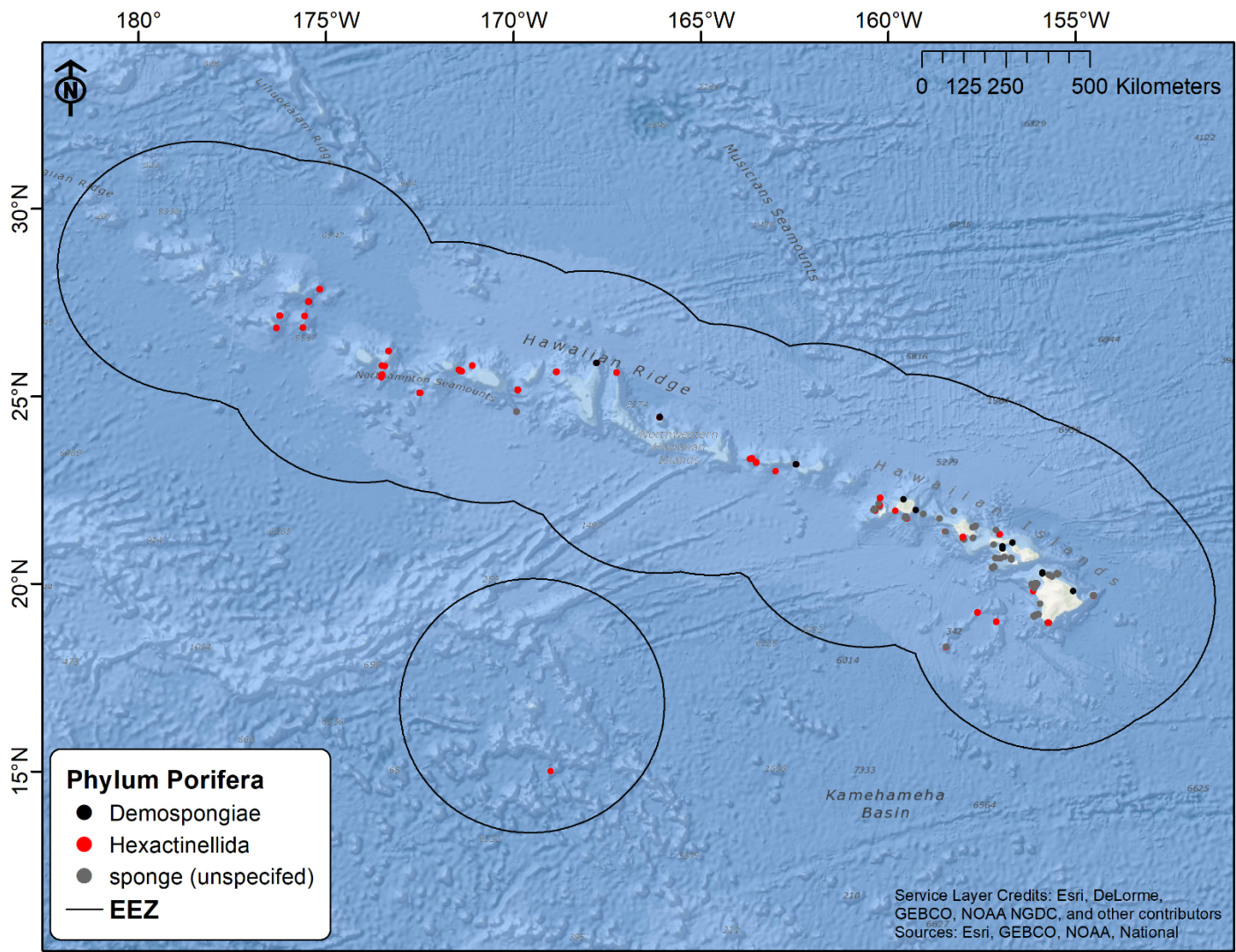
Map 5. Locations of sea pens (Order Pennatulacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION

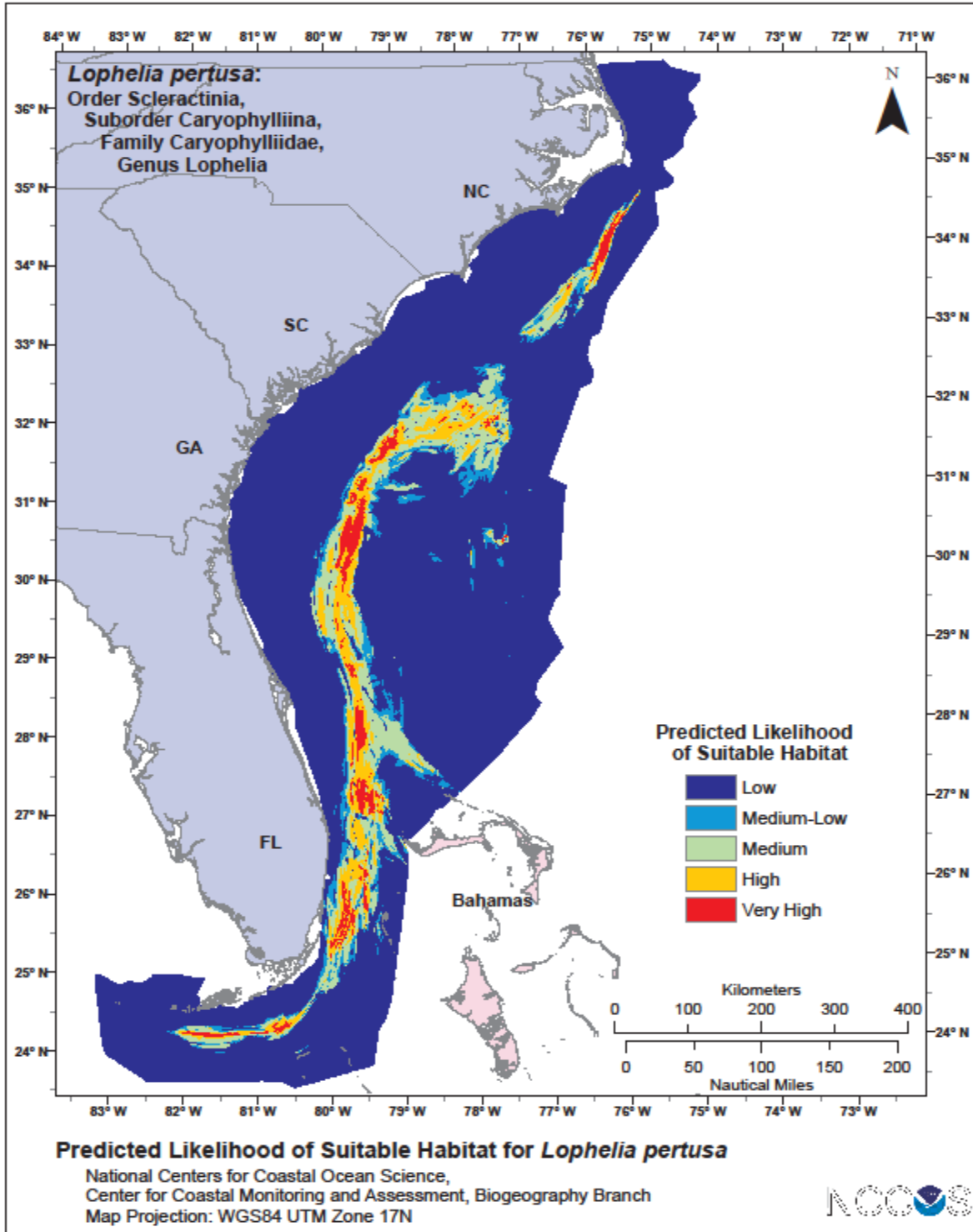


Map 6. Locations of lace corals (Family Stylasteridae) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).

STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE U.S. PACIFIC ISLANDS REGION



Map 7. Locations of sponges recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017). Note: This does not include additional HURL records shown in Figure 6.



Maxent predictive habitat model for the primary framework-forming deep-sea coral in the Southeast U.S., *Lophelia pertusa*. Warmer colors indicate greater likelihood of suitable habitat, determined by a cross-validation method that determined likelihood thresholds using the ratio of false positive to false negative classification results when the model was tested on data left out of the fitting process (Kinlan et al. 2012a).



PREDICTIVE HABITAT MODELING FOR DEEP-SEA CORALS IN U.S. WATERS

I. Introduction

Predictive habitat modeling (PHM) is a cost-effective method for extending the range and utility of expensive and time consuming field efforts to identify deep-sea coral habitat in locations that have not been sampled. PHM is not intended and should not be used as a substitute for field surveys via remotely operated vehicles (ROVs), submersibles, and similar instruments. Instead, modeling is one component of a highly integrated process that includes biological surveys, oceanographic data gathering efforts, management and conservation actions, and new exploration and scientific efforts. New data collection and verification of model results generates feedback that allows for the creation of better models (as illustrated by the conceptual model in Figure 1). Recognition of the utility of regional-scale habitat suitability models for deep-sea corals is increasing both in domestic and international waters and the models have become accepted as a useful indicator of vulnerable marine ecosystems.

PHM complements field efforts by facilitating habitat predictions across large regions, and this method can be used to help focus limited resources in areas that have the highest probability of supporting deep-sea coral ecosystems. Predictive habitat models also provide important insights into the environmental conditions controlling deep-sea coral distribution (feedbacks in Figure 1). Threats to deep-sea coral habitats such as climate change and the looming threat of ocean acidification reinforce the need to gain a better understanding of the physical, chemical, and oceanographic conditions that influence deep-sea coral survival.

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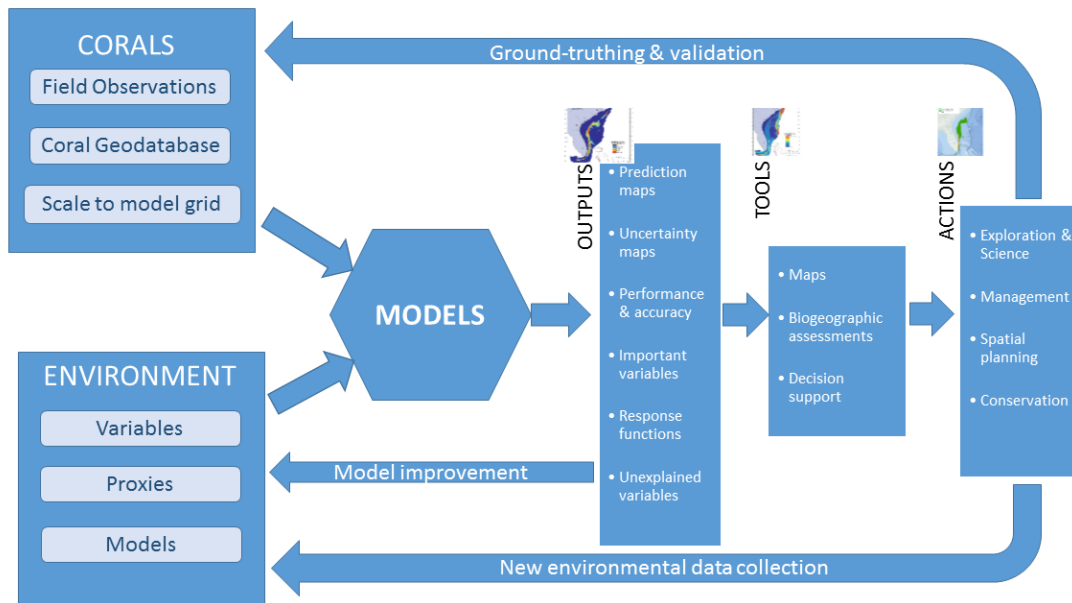


Figure 1. Conceptual process diagram showing the inputs and outputs of predictive habitat models for deep-sea corals, including feedbacks from model outputs to exploration and scientific efforts that lead to continual improvement in model quality, as well as informed management, conservation, and spatial planning actions.

In this spotlight we provide an overview of regional-scale modeling efforts in U.S. waters, some of the methods used to determine predicted habitat for deep-sea corals, the utility of these efforts for researchers and resource managers, and the limitations of such models.

II. Model Methodology

Predictive habitat modeling (often called habitat suitability modeling, ecological niche modeling, or species distribution modeling) integrates the spatial distribution of coral colonies with environmental data (including geomorphology of the seafloor and physical, biological, and chemical variables) to estimate the potential niche and distribution of deep-sea corals.

Most deep-sea coral PHM studies to-date have used “presence-only” approaches, as the vast majority of data on coral distribution consists only of records of presence (occurrence). The range of environmental conditions for known coral locations is used to determine an “environmental envelope” which is then mapped across the entire region, including areas where no sampling has taken place. This process results in an index of relative habitat suitability, typically ranging from 0-1 or 0-100, that predicts the relative likelihood that a given area harbors deep-sea coral habitat. Presence-only modeling approaches that have been commonly used have included maximum entropy modeling (Maxent; e.g., Davies and Guinotte 2011, Rengstorf et al. 2012, Yesson et al. 2012, Rengstorf et al. 2013,

Recent trends in deep-sea coral modeling

1. Predictive habitat modeling for deep-sea corals has increased in the last ten years due to: a) improved resolution and availability of environmental data, b) increased quality and quantity of coral data, c) increased recognition that modeling is a useful and cost-effective means to identify vulnerable benthic habitats and d) increased computational power and the availability of appropriate algorithms and software for predictive habitat modeling.
2. For the first time, global and regional modeling efforts can predict habitat at scales that are biologically relevant as well as practical for resource management (10s of meters to 10s of kilometers).
3. Presence-only modeling approaches (e.g., Maxent, ENFA) have been the most frequently used method to model deep-sea coral habitat at regional scales, but they do not show probability of occurrence. Improved sampling and analysis methods are required to allow for presence/absence models in the deep-sea. The next generation of models should incorporate measures of abundance (e.g., biomass, number of colonies, percent cover), and move beyond presence-absence approaches.
4. Modeling has helped identify important environmental correlates of deep-sea coral distribution, which is useful for forecasting areas where corals are most at risk from climate change and ocean acidification.

Georgian et al. 2014), Ecological-Niche Factor Analysis (ENFA; eg., Leverette and Metaxas 2005, Bryan and Metaxas 2007, Davies et al. 2008, Dolan et al. 2008, Tittensor et al. 2009, Taylor et al. 2013), and Genetic Algorithm for Rule Set Production modeling (GARP; e.g., Guinan et al. 2009, Tong et al. 2013). Of these, Maxent is becoming increasingly common, as it has consistently outperformed other presence-only techniques (Elith et al. 2006, Tittensor et al. 2009, Tong et al. 2013).

Models that incorporate known absences in addition to known presences are being increasingly used to predict deep-sea coral habitats. These “presence/absence” approaches have included Boosted Regression Trees (BRT; Tracey et al. 2011), Generalized Linear Models (GLM; e.g., Woodby et al. 2009), Generalized Additive Models (GAM; e.g., Ross and Howell 2013, Rooper et al. 2014), and logistic regression and Generalized Estimating Equation models (GEE; e.g., Woodby et al. 2009). When both presences and absences are recorded with reasonable certainty, presence/absence models can produce more accurate and therefore, more useful habitat predictions. It is important to note however, that absence data can be misleading in models with coarse spatial resolutions (> 200 m), as it cannot be assumed that coral is absent from a large area unless the entire area has been surveyed. Current sampling methods in the deep-sea often give us confirmation of coral absence in only a small portion of each modeled cell. In addition, absence data may be misleading if the species’ distribution is not in equilibrium, if dispersal is limiting, or due to historical artifacts including population losses due to human activities (Hirzel et al. 2002).

Difficulties in determining ‘true’ absences have led researchers to generate ensemble



models produced by using a combination of presence-only and presence/absence approaches (e.g., GAMs and Maxent; Ross and Howell 2013) to identify potential habitat. In the future, as databases improve, more data on deep-sea coral presence/absence and abundance (e.g., biomass, number of colonies, percent cover) will facilitate more sophisticated models (e.g., Guinan et al. 2009). Models that can predict areas of high abundance or biodiversity hotspots are of particular importance to conservation and resource managers, who must weigh the biological and ecological value of different areas against economic costs associated with their protection (Ardron et al. 2014).

Field survey efforts offer critical support to these improved datasets and help to avoid one of the primary pitfalls of presence-only models: important, undiscovered coral habitats can easily be missed because the presence locations are unlikely to fully represent the range of possible deep coral habitats. Verified absence data should always be preferred over a model prediction of “unsuitable habitat.” The collection of georeferenced, verified absence data with broad spatial coverage would greatly reduce sampling bias and help to improve the next generation of models. Yet, due to the time and expense involved, deep-sea field surveys are rarely randomly distributed spatially, introducing sampling bias that will always be an important consideration in the interpretation of model results. The adage by Carl Sagan that “absence of evidence is not the evidence of absence” is especially critical in interpretation of deep-sea field survey data and model outputs (discussed in Etnoyer and Morgan 2007). Habitat suitability models can influence spatial management decisions, so they should be tested for their validity, updated, and improved periodically.

Models also differ in the types of environmental data they use to make predictions. At a minimum, environmental data usually include bathymetry (depth) and statistics derived from bathymetry that characterize the topography of the seafloor, generally referred to as terrain metrics. Other types of environmental variables often included in models are substrate (benthic sediment types and the distribution of hard bottom) and oceanographic data. Oceanographic data encompasses physical variables (e.g., temperature, salinity, and currents), biological variables (e.g., surface productivity and particulate organic carbon flux to the seafloor), and chemical variables (e.g., pH, dissolved oxygen, and carbonate chemistry). The importance of individual environmental variables in determining the distribution of deep-sea corals appears to vary considerably both among taxa and among regions (Table 1).

Seven environmental variables that are consistently strong predictors across regions and taxa include: depth, seafloor geomorphology (slope, curvature, roughness, changes in slope), sediment/substrate type, carbonate chemistry, temperature, salinity, indices of near-bottom current velocity, and food flux to benthic environments. The regional variation in approach and data priority in modeling efforts often depends in part on the types of data available. For example, carbonate chemistry has been found to be among the most important predictor variables for the global occurrence of both scleractinian reef-forming corals and octocorals (Davies and Guinotte 2011, Yesson et al. 2012), but deep-water carbonate chemistry data are limited or non-existent in many regions. Other variables are proxies for the actual processes driving coral distribution; for example, near-bottom currents are thought

Table 1. Summary of key features of the regional and global-scale deep-sea coral predictive habitat models discussed in this chapter, including the taxa modeled, the modeling approach used, the spatial resolution, and the environmental variables used as predictors. Environmental variables that were significant in models are italicized. Abbreviations: ENFA=Environmental Niche Factor Analysis, Maxent=Maximum Entropy, GAM=Generalized Additive Models. Variable abbreviations: *Chl. a*=chlorophyll a, CPI=Chlorophyll Persistence Index, BPI=bathymetric position index, POC=particulate organic carbon, ΩA =aragonite saturation state, ΩC =calcite saturation state, TPI=topographic position index, AOU=apparent oxygen utilization, TA=total alkalinity, $[CO_3^{2-}]$ =carbonate ion concentration, DIC=dissolved inorganic carbon, lat./long.=latitude/longitude, TRI=terrain ruggedness index, DO=dissolved oxygen, SL=slope, SL-of-SL=slope of slope, PLC=plan curvature, PRC=profile curvature, LonC=longitudinal curvature, LatC=latitudinal curvature, GC=general curvature, FF=Framework Forming. Variables are at-depth unless otherwise indicated (i.e., surface chlorophyll a, surface primary production, surface turbidity).

Study	Model	Taxa	Resolution	Terrain	Substrate	Chemical	Physical	Biological
Northeast and Mid-Atlantic U.S.								
Kinlan et al. in press	Maxent	Alcyonacea, Gorgonacea, Pennatulacea, Sessiliflorae, Scleractinia, Caryophylliidae, Flabellidae	370 m	Aspect, <i>depth, SL, SL-of-SL, rugosity, PLC, PRC, BPI</i>	Mean grain size, % sand, %mud, %gravel	–	Temperature, salinity, surface turbidity, DO	Surface chl. a
Bryan and Metaxas 2007	ENFA	Paragorgiidae, Primnoidae	5 km	Depth, SL	–	–	Current velocity, temperature	Surface chl. a
Southeast U.S.								
Davies (unpublished), Mienis et al. 2014	Maxent	<i>Lophelia pertusa, Madrepora oculata, Enallopsammia profunda, Solenosmillia variabilis, Oculina varicosa</i>	90 m, 1 km	Depth, SL, rugosity SL-of-SL, PLC, PRC, BPI	–	ΩA , nitrates	Temperature, salinity, DO	POC
Kinlan et al. 2012a	Maxent	<i>Lophelia pertusa, Madrepora oculata, Enallopsammia profunda</i> , FF Scleractinia (exc. <i>Oculina</i> spp.), Non-FF Scleractinia, Antipatharia, Stylasteridae, Pennatulacea, Alcyonacea, Gorgonacea, Holaxonia, Calcaxonia	370 m	Depth, SL, SL-of-SL, aspect, rugosity, PLC, PRC, BPI	Mean grain size, % sand, %mud, %gravel	–	Temperature, salinity, surface turbidity	Surface chl. a
Gulf of Mexico								
Guinotte and Davies (in prep)	Maxent	<i>Lophelia pertusa, Madrepora oculata, Enallopsammia profunda, Solenosmillia variabilis, Oculina varicosa</i>	~90 m	Depth, SL, rugosity	To be determined	ΩA , ΩC	Temperature, salinity, DO, surface turbidity	Export POC
Georgian et al. 2014	Maxent	<i>Lophelia pertusa</i>	5 m, 25 m	Depth, SL, roughness, TPI, LonC, LatC, GC, eastness, northness	Potential hard-bottom locations from 3D seismic data	ΩA	–	Export POC
Kinlan et al. 2012b	Maxent	<i>Lophelia pertusa, Madracis, Madrepora, Bebyrce, Callogorgia, Hypnogorgia, Paramuriceidae, Plexauridae, Isididae, Ellisellidae, Chrysogorgiidae, Antipatharia, Alcyonacea, Gorgonacea, Scleractinia, FF Scleractinia, Non-FF Scleractinia, All FF taxa</i>	370 m	Depth, SL, SL-of-SL, aspect, rugosity, PLC, PRC, BPI	Mean grain size, % sand, % mud, % gravel, potential hard-bottom locations interpreted from 3D seismic data	–	Temperature, salinity, surface turbidity, DO	Surface chl. a
West Coast U.S.								
Guinotte and Davies 2012, 2014	Maxent	Antipatharia, Scleractinia, Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia	500 m	Depth, SL	–	ΩA , ΩC , nitrate, phosphate, silicate	Temperature, salinity, DO	Export POC
Huff et al. 2013	GAM, GLM	<i>Antipathes dendrochristos</i>	90 m	Depth, SL, PRC	–	–	Temperature, salinity, DO, current velocity, current direction	Surface primary productivity (CPI)

Bryan and Metaxas 2007	ENFA	Paragorgiidae, Primnoidae	5 km	Depth, SL	–	–	Current velocity, temperature	Surface chl. a
Alaska								
Guinotte and Davies 2013	Maxent	Alcyoniina, Antipatharia, Calcaxonia, Filifera, Holaxonia, Scleractinia, Scleraxonia, Stolonifera	700 m	Depth, SL, rugosity, BPI, PLC, PRC, tangential curvature, aspect, northness, eastness, TRI, TPI, roughness	–	ΩA, ΩC, nitrate, phosphate, silicate	Temperature, salinity, DO	Export POC
Bryan and Metaxas 2007	ENFA	Paragorgiidae, Primnoidae	5 km	Depth, SL	–	–	Current velocity, temperature	Surface chl. a
Rooper et al. 2016	GAM	Primnoidae, Stylasteridae, all corals combined, Porifera	100 m (Aleutian Islands), 1km (Bering Sea)	Depth, SL, rugosity, lat./long., aspect	Sediment type	–	Temperature, mean ocean current, maximum tidal current	Surface primary productivity
Sigler et al. 2015	GAM	Plexauridae, Primnoidae, Isididae, Paragorgiidae, Antipatharia, Penatulacea, Porifera	1 km	Depth, SL, lat./long.	Grain size, sediment sorting	–	Temperature, current velocity	Surface primary productivity
Hawaii and U.S. Pacific Territories								
Bauer et al. 2016	Maxent	Calcaxonia, Holaxonia, Scleraxonia, gold corals, red and pink corals, black corals, bamboo corals, bubblegum corals, FF and non-FF stony corals, gorgonian and non-gorgonian soft corals	360 m	Depth, SL, SL-of-SL, aspect, rugosity, total curvature, PLC, PRC, BPI, distance to shore, distance to seamounts	–	–	Temperature, salinity, turbidity, current velocity, current direction, mixed layer depth	Surface chl. a
Global								
Davies and Guinotte 2011	Maxent	FF deep-sea corals (<i>Enallopsammia rotata</i> , <i>Goniocorella dumosa</i> , <i>Lophelia pertusa</i> , <i>Madrepora oculata</i> , <i>Solenosmillia variabilis</i>)	~1 km	Depth, SL, rugosity	–	TA, pH, [CO ₃ ²⁻], ΩA, ΩC, nitrate, phosphate, silicate, DIC	Regional current flow, vertical flow, salinity, temperature, DO, % oxygen saturation	AOU, surface POC, surface primary productivity, POC export
Yesson et al. 2015	Maxent	Antipatharia (Antipathidae, Aphanipathidae, Cladopathidae, Leiopathidae, Myriopathidae, Schizopathidae, Stylopathidae)	1 km	Curvature, SL	–	TA	Temperature, % oxygen saturation	Surface chl. a
Yesson et al. 2012	Maxent	Alcyoniina, Calcaxonia, Holaxonia, Scleraxonia, Sessiliflorae, Stolonifera, Subselliiflorae	~1 km	Depth, SL, rugosity	–	TA, pH, [CO ₃ ²⁻], ΩA, ΩC, nitrate, phosphate, silicate, DIC	Temperature, regional current flow, vertical flow, DO, % oxygen saturation, salinity	POC, surface primary productivity, POC export, AOU
Tittensor et al. 2009	Maxent, ENFA	Scleractinia corals on seamounts	~130 km	Depth	–	TA, ΩA, nitrate, phosphate, silicate, total DIC	Temperature, salinity, DO, regional current velocity, % oxygen saturation	Surface primary productivity, export POC
Davies et al. 2008	ENFA	<i>Lophelia pertusa</i>	0.25°, 1°	Depth, aspect, SL	Hydrocarbon seeps and pockmarks, iceberg ploughmarks	TA, ΩA, DIC, nitrate, phosphate, silicate	Current velocity, temperature, salinity, DO	Surface primary productivity



to be very important determinants of particle flux, coral distribution and abundance (White et al. 2007, Mienis et al. 2012), but data on bottom currents are limited. Terrain metrics may therefore serve as proxies for currents. Moreover, the importance of geomorphological variables such as slope and curvature appears to be highly scale-dependent, with high-resolution multibeam bathymetry often required to reveal fine-scale seafloor features associated with suitable coral habitat. More in situ observation and experimentation, more consistent collection and integration of high-resolution bathymetric and seafloor characterization products, and better data-assimilating deep ocean biophysical and chemical models are necessary to better resolve questions about the primary drivers of deep-sea coral distribution and abundance.

Finally, models vary in the level of spatial and taxonomic detail, or resolution, they convey. The spatial resolution of predictive habitat modeling is often limited by the availability of fine-grained spatial data for environmental variables. For example, the spatial scales of environmental data may be coarse (1,000-10,000 meters resolution) compared to the resolution of multibeam bathymetry available in the same study area (2-40 m resolution, depending on depth). This issue, combined with the reality that high-resolution multibeam does not exist across entire study areas, often leads modelers to predict habitat at coarser resolutions than the multibeam bathymetry. Regional fisheries management councils, conservation organizations, and habitat suitability modelers seek to manage areas larger than the extent of fine-scale data that are available, so such a compromise is

necessary. There is a need for more extensive spatial coverage of fine-scale resolution environmental data, and conversely, a need for more habitat suitability studies that operate over smaller extents. Local-scale studies with fine-resolution data allow researchers to incorporate locally important drivers of species distributions, like bottom hardness and local relief. One large boulder, or one meter of vertical relief can make a considerable difference in habitat quality for deep-sea corals and sponges.

Difficulties with species identification can inhibit taxonomic resolution: it is not always possible to model habitat for a single coral species because the observations are recorded at the genus or family level. In many cases, useful models are created by grouping coral species at higher taxonomic levels, ranging from genus to family, suborder, or order. Grouping to high taxonomic levels is often necessary from a practical resource management perspective when managers cannot deal with hundreds of species models. However, careful interpretation and assessment of predictions should be exercised when members of those taxa occupy very different environmental niches (e.g., Quattrini et al. 2013). In other cases, corals may be grouped for modeling by their functional similarity, for example, branching stony corals that form a rigid framework and thus form habitat for fishes and invertebrates (e.g., Dolan et al. 2008).

Below, we review recent and ongoing predictive habitat modeling efforts in different regions of the U.S.,¹ providing a brief overview of approaches, data, taxa modeled, resolution, results, and management/conservation applications in each region.

¹There are many fine-scale PHM efforts underway or completed for deep-sea coral habitat for specific sites in U.S. waters. These efforts are not reviewed here.



III. Predictive Habitat Modeling in U.S. Regions

III.1. Northeast and Mid-Atlantic

Over the past 5 years, NOAA's Deep-sea Coral Research and Technology Program has supported development of a geospatial database of known coral presence locations in the Northeast and Mid-Atlantic regions (e.g., Packer et al. 2007, Scanlon et al. 2010, Packer and Dorfman 2012, Packer and Drohan 2012, NOAA 2015). The New England Fishery Management Council has used these locations, in conjunction with primary literature, expert opinion, and geomorphological characteristics of canyons, to help identify and prioritize known and potential areas of deep-sea coral habitat (NEFMC 2012). This constitutes a first step toward predictive modeling and has helped the Council as they consider various alternatives for coral habitat protection.

NOAA scientists also produced a suite of moderate resolution (~370 m) models for multiple deep-sea coral taxonomic groupings in the northeast and Mid-Atlantic region (Kinlan et al. in prep; Figures 2 and 3). The inclusion of multiple spatial scales was designed to capture biologically-relevant features ranging from relatively fine-scale topography, the presence of deep-water canyons, and the continental shelf break. Maxent models were constructed using presence-only data and environmental variables including depth, terrain metrics calculated at multiple spatial scales (slope, slope-of-slope, rugosity, plan curvature, profile curvature, and bathymetric position index), substrate (mean grain size and percent sand/mud/gravel of benthic sediments), and physical (bottom temperature, salinity, and surface turbidity), biological (surface chlorophyll-*a*), and chemical (dissolved oxygen) oceanographic variables.

In order to improve model parsimony while maintaining predictive power, a stepwise model selection process was employed to reduce the final number of environmental variables included in the models by removing the most redundant variable remaining at each step. The model runs from the model selection process were ranked from best to worst by model performance and by model complexity, and the model run with the best average rank was selected as the final model. To generate model predictions in a format that can be directly compared across taxonomic groups and regions, Maxent outputs were classified into habitat suitability likelihood classes using breakpoints corresponding to ratios of the cost for false positive errors versus the cost for false negative errors.

Three major taxonomic groups were modeled: stony corals (order Scleractinia), sea pens (order Pennatulacea), and other octocorals (orders Alcyonacea and Gorgonacea combined). For each major taxonomic group, two subgroups were also considered based on suborder or family-level taxonomy. The Gorgonacea subgroup incorporates most of the potential habitat-forming species in this region (Packer et al., this volume).

The models predicted extensive areas of potential habitat on the continental slope for all major taxonomic groups and subgroups modeled. Highest suitability values were concentrated in submarine canyon areas at depths of 300-2000 m. Results were used to identify several unexplored potential hotspots of deep coral habitat suitability in the Mid-Atlantic and New England canyons, and subsequent ground-truthing cruises from 2012-2015 aboard NOAA Ship *Henry Bigelow* and NOAA Ship *Okeanos Explorer* (Nizinski and Shank 2012, NOAA OER, 2013, 2014, NRDC 2014, Quattrini et al. 2015) confirmed the existence of these hotspots (e.g., Figure

PREDICTIVE HABITAT MODELING FOR DEEP-SEA CORALS IN U.S. WATERS

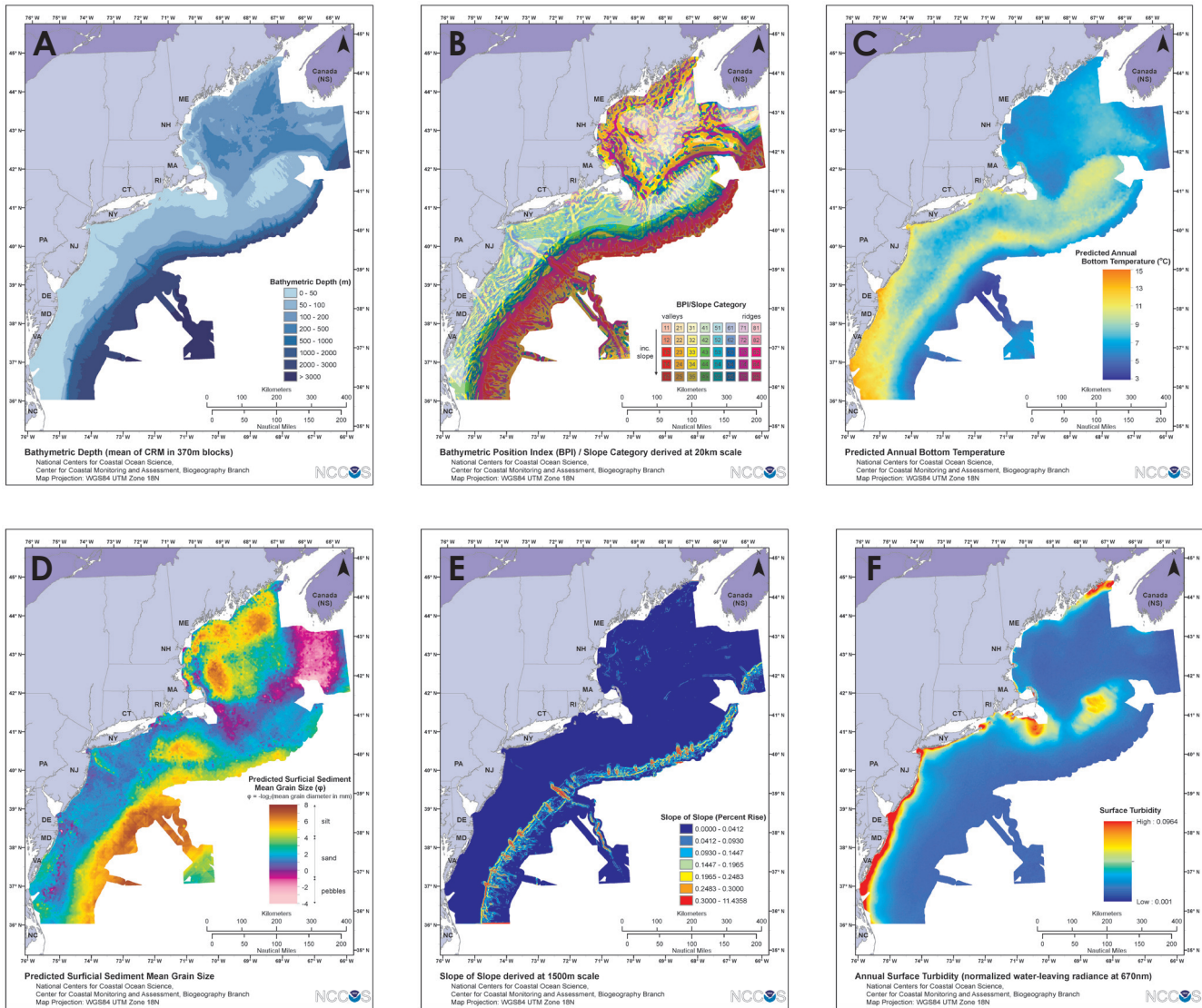


Figure 2. Environmental layers used in the creation of Maxent deep-sea coral predictive habitat models for the Northeast U.S. region. A) bathymetric depth, B) bathymetric position index (BPI) calculated at a 20 km scale, C) predicted annual bottom temperature, D) predicted surficial sediment mean grain size, E) slope of slope, F) surface turbidity.

3). Efforts are underway to improve the resolution and accuracy of this model using coral data collected during these field efforts and multibeam bathymetry collected as part of the Atlantic Canyons Undersea Mapping Expeditions (ACUMEN) project (NOAA OER 2012), in a direct application of the process model illustrated in Figure 1.

Predictive habitat modeling helped guide BOEM-funded field surveys of canyons in the

Mid-Atlantic region in 2012 (Ross and Brooke 2012). Using archived historical observations from surveys in the 1980s in conjunction with modern state-of-the-art multibeam, areas of potential hard ground and coral habitat were modeled from a suite of terrain and environmental variables within Mid-Atlantic canyons using the Maxent approach. This approach highlighted the value of local-scale, high-resolution models in guiding and focusing



Gorgonian Alcyonaceans in Oceanographer, Gilbert, Lydonia Canyon Complex

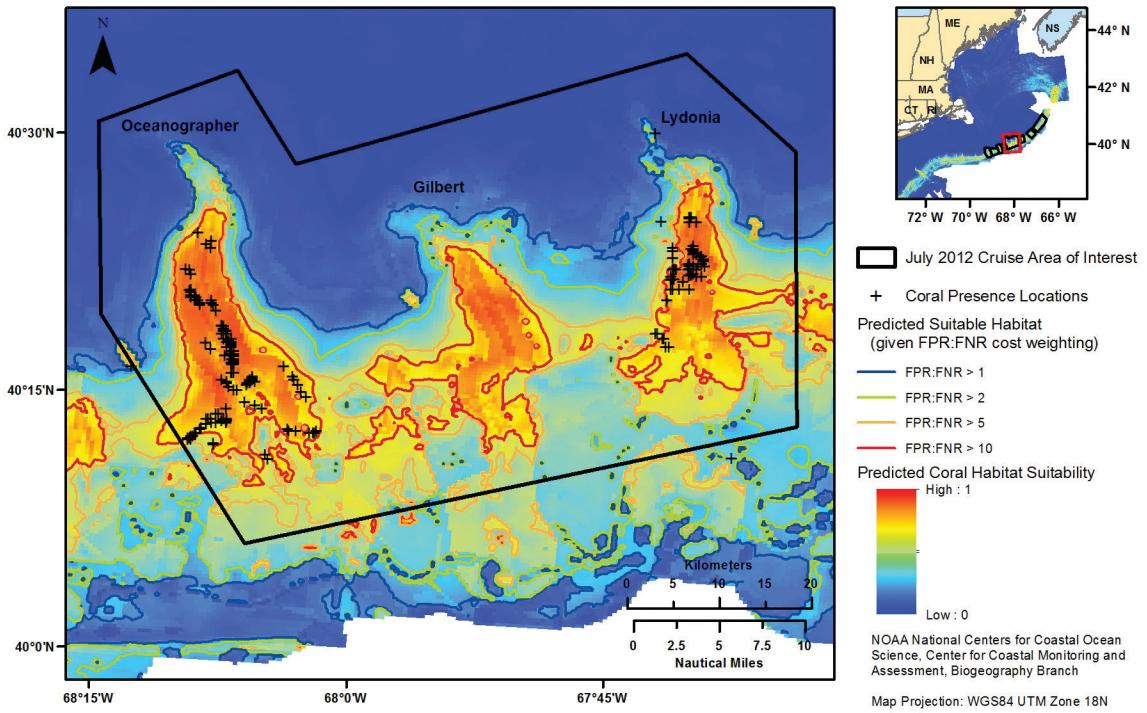


Figure 3. Maxent predictive habitat model for Gorgonian Alcyonaceans in the Oceanographer, Gilbert, and Lydonia Canyon Complex in the Northeast U.S. region. Black crosses indicate locations of known coral locations discovered during a 2012 ground-truthing cruise aboard the NOAA Ship Henry Bigelow (Nizinski and Shank 2012). FPR=False positive rate. FNR=false negative rate.

research effort within a clearly defined area whilst utilizing past observations. The models have been validated in the field and visual observations collected during subsequent cruises will be used to enhance the local-scale model.

All of the models described will continue to be developed and refined, however they have already played a seminal role in regional fishery management. In 2015, the Mid-Atlantic Fishery Management Council (MAFMC 2015) recommended establishment of “deep-sea coral zones” to protect deep-sea corals from the impacts of bottom-tending fishing gear. This fishery management plan amendment

was recently approved by the National Marine Fisheries Service, and will protect over 98,000 km² of habitat in canyons and deep-water areas where corals have been observed or where they were predicted to occur based on NOAA Maxent models. This was among the first explicit examples of deep-sea coral predictive habitat models playing a major role in U.S. fishery management conservation decisions, confirming the utility of PHM for future conservation and management efforts. The New England Fishery Management Council is expected to use similar approaches in a planned deep-sea coral amendment.

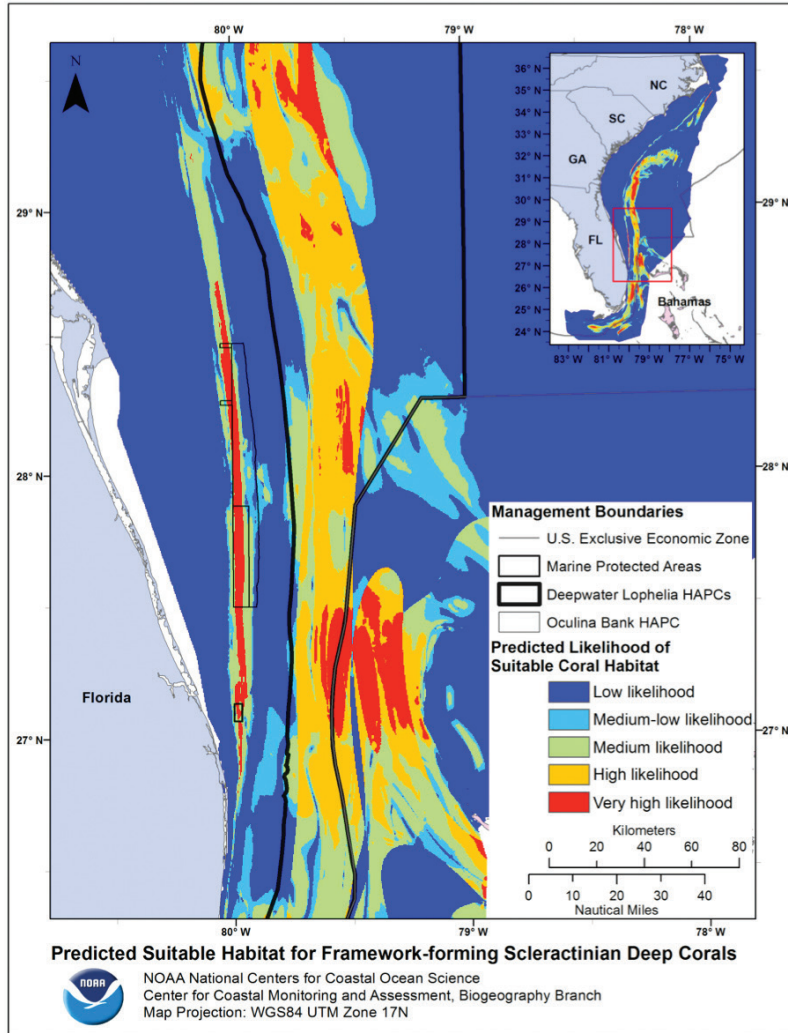


Figure 4. Maxent predictive habitat model for all framework-forming Scleractinian deep-sea corals in a subset of the U.S. Southeast Atlantic. Warmer colors indicate greater likelihood of suitable habitat, determined by a cross-validation method that determined likelihood thresholds using the ratio of false positive to false negative classification results when the model was tested on data left out of the fitting process (see Kinlan et al. 2012b and David et al., this volume for details).

III.2. Southeast

In 2009, Davies (unpublished) created the first Maxent predictive habitat model in the Southeast U.S. Atlantic region for framework-forming scleractinian corals (including records for *Lophelia pertusa*, *Madrepora oculata*, *Enallopsammia profunda*, *Solenosmilia variabilis* and *Oculina varicosa*). Environmental variables were created following procedures later described in Davies and Guinotte (2011) using the highest resolution bathymetry available including the National Geophysical Data Center’s Coastal Relief Model at 3 arc second (~90 meter) resolution and global bathymetry available at 30 arc second (~1 km) resolution

(Becker et al. 2009). Relevant environmental layers were selected for the model, including omega aragonite (Orr et al. 2005), depth (Becker et al. 2009), dissolved oxygen (Garcia et al. 2006), salinity (Boyer et al. 2009), nitrate concentrations (Garcia et al. 2006), temperature (Boyer et al. 2009) and rugosity (Wilson et al. 2007). Model results from this effort were overlaid with existing fishery closures to identify areas with high habitat suitability that remain at risk from destructive fishing practices.

In 2012, NOAA produced a set of 370 meter resolution regional predictive habitat models for deep-sea coral taxonomic groups in the



Southeast U.S. (Kinlan et al. 2012a). Example outputs from this model are shown in Figure 4 and in Hourigan et al. (this volume). Using a similar approach to that employed in the Northeast region, Maxent models were constructed using presence-only data and environmental variables selected from a set of candidate predictors. A total of 14 taxonomic groups were modeled, including three important species of framework-forming stony corals (*Lophelia pertusa*, *Madrepora oculata*, and *Enallopsammia profunda*), an important framework-forming genus (*Oculina* spp.), all framework-forming stony corals as a group (Figure 4), non-framework-forming stony corals, black corals, lace corals, sea pens, gorgonian and non-gorgonian soft corals, and two suborders of gorgonian corals (*Holaxonia*, *Calcaxonia*). The models predicted extensive areas of potential framework-forming deep coral habitat, concentrated at depths of 100-1000 m. Results confirmed that existing coral protection areas covered the majority of likely framework-forming deep coral habitat (Figure 4). The models were provided to the South Atlantic Fishery Management Council to support discussions of Ecosystem Based Management measures including a recent amendment to the Fishery Management Plan for Coral, Coral Reef, and Live/Hardbottom Habitats in the South Atlantic Region (SAFMC 2013).

The two Southeast models highlight the issue that model results can vary considerably in both the extent of highly suitable habitat and in the suitability scores of individual grid cells, even when similar modeling methods are used (i.e., Maxent). Predictor variables used as input in the models are likely responsible for these differences (e.g., seafloor substrate type), but the coral records used to determine the environmental niche also play an important role in determining final model results. Multiple independent modeling

efforts are useful because they can highlight areas of high certainty (where multiple models agree), reveal sensitivity of model predictions to different assumptions, methods, and input data, and improve future model iterations. Determination of which model(s) more accurately predicts reality can only be accomplished through field validation efforts.

III.3. Gulf of Mexico

Marine Conservation Institute and Bangor University are currently developing Maxent models for both deep-sea and mesophotic coral habitat in the Gulf of Mexico. The spatial resolution of model results is based on the National Geophysical Data Center's Coastal Relief Model at 3 arc second (~90 meter) resolution. Modeling methods are similar to the approach used in the Southeast U.S., U.S. West Coast, and Alaska. The objectives of this work are to identify both deep-sea and mesophotic reef habitat that are not currently under protection from human activity including oil and gas production/accidents, bottom trawling, and climate change.

The Gulf of Mexico presents unique challenges and opportunities for predictive coral habitat modeling. High-resolution seismic data that can be used to detect potential hard-bottom patches are lacking in most of the U.S. Exclusive Economic Zone (EEZ), but this is not the case in the Gulf of Mexico due to a long history of oil and gas exploration in the region. Extensive 3D seismic surveys conducted over several decades in large areas of the Gulf have recently been interpreted to provide high-resolution information on potential hardground areas that are helping to improve predictions of coral habitat suitability (Boland et al., this volume).

In 2012, scientists at NOAA applied the Maxent modeling approach used in the Northeast and Southeast regions to develop



moderate spatial resolution (370 meter) regional models for deep-sea coral taxonomic groups in the northern Gulf of Mexico (Kinlan et al. 2012b). Maxent models were constructed using presence-only data and environmental variables selected from a suite of terrain, substrate (including potential hardground locations), and physical and biological oceanographic variables. Taxonomic groups similar to those used in the Southeast region were used for modeling, with an emphasis on predictions of key framework-forming species. This work has already been used in targeting exploration surveys and is expected to contribute to efforts at habitat protection, spatial planning, and fishery management in the Gulf of Mexico.

In 2014, Georgian et al. developed high-resolution (25 m) Maxent models predicting the distribution of *Lophelia pertusa* across a large region of the northern Gulf of Mexico. The authors used a suite of 11 environmental variables including depth, a number of terrain metrics, omega aragonite, substrate type, and export productivity. Substrate type consisted of potential hardground areas developed by the Bureau of Ocean Energy Management (Boland et al., this volume) and was highly predictive of *L. pertusa* distribution, demonstrating the utility of these type of data for future PHM efforts. The model was tested during a field survey aboard EV Nautilus by Ocean Exploration Trust in 2013 and successfully predicted the location of two large *L. pertusa* mounds.

III.4. U.S. Caribbean

There have been no predictive habitat models for deep-sea corals in the U.S. Caribbean (Puerto Rico, U.S. Virgin Islands, and Navassa Island), despite their relatively high diversity in the region (Cairns 1979, 2007). While several global-scale modeling efforts have included

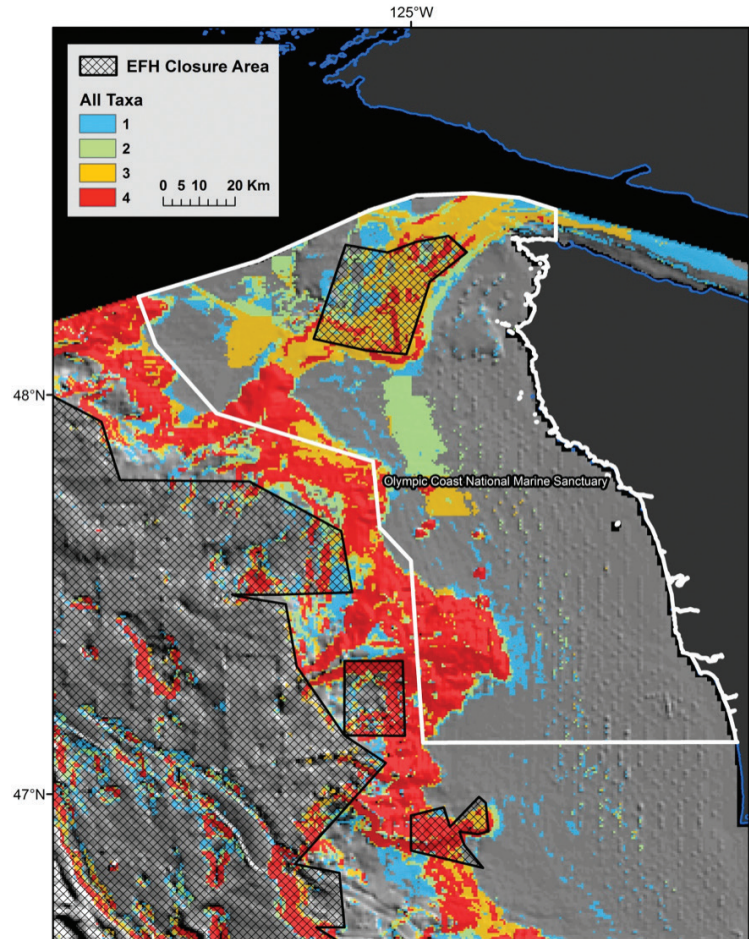
parts of the Caribbean (e.g., Tittensor et al. 2009, Davies and Guinotte 2011), there is an urgent need to better characterize the distribution of cold-water corals throughout the region.

III.5. West Coast (Washington, Oregon, California)

Bryan and Metaxas (2007) published the first predictive habitat models for deep-sea corals (Families Paragorgiidae and Primnoidae) for the West Coast and Alaska. Four years later, in 2011, predictive habitat models were developed for six taxonomic groups of deep-sea corals (Orders Antipatharia and Scleractinia, Suborders Alcyoniina, Calcaxonia, Holaxonia and Scleraxonia) in the waters of Washington, Oregon and California (Guinotte and Davies 2012, 2014). The objectives of this effort were to: 1) aid future research and mapping efforts for deep-sea coral habitats, 2) Assess potential coral habitat suitability both within and outside existing bottom trawl closures (e.g., to inform designation and protection of essential fish habitat – EFH), and 3) identify suitable habitat in and around the region’s six National Marine Sanctuaries. Maxent was used to model deep-sea coral habitat at a 500 m spatial resolution using coral records collected from a variety of sources and a regional database of 30 physical, chemical and environmental variables. Figure 5 shows the model results for Washington waters with overlays of existing fishing closures and the Olympic Coast National Marine Sanctuary. These modeling results will be used to assess gaps in protection afforded by existing fishery management closures through the Pacific Fishery Management Council’s periodic review of essential fish habitat (Huff et al. 2013; Guinotte and Davies, 2014).



Figure 5. Maxent predictive habitat model for all taxa (Orders: Antipatharia and Scleractinia; Suborders: Alcyoniina, Calcaxonia, Holaxonia, and Scleraxonia) for the Olympic Coast National Marine Sanctuary. Warmer colors indicate greater likelihood of suitable habitat across all taxa modeled (see Guinotte and Davies 2012 for details on likelihood). Hatched areas are existing trawl closures (EFH).



III.6. Alaska

Several regional-scale predictive habitat-modeling efforts have been conducted or are currently underway for deep-sea coral and sponge habitats in Alaskan waters. Guinotte and Davies (2013) developed Maxent models for the Alaska EEZ at a spatial resolution of ~700 m using 30 environmental, physical, and chemical predictor variables. Models at the Suborder and Order levels revealed that the majority of predicted suitable habitat for gorgonians and lace corals (Family Stylasteridae) occurs in the Aleutian Islands, and to a lesser extent the eastern Bering Slope, Gulf of Alaska seamounts, and the Fjord region and shelf break of Southeast Alaska. Soft corals (Suborders Alcyoniina and Stolonifera) additionally had predicted

suitable habitat on the eastern Bering Sea Shelf. Guinotte and Davies (2013) also modeled a complex habitat type, coral and sponge “gardens” (Stone and Shotwell 2007) in the Aleutian Islands. While some coral and sponge gardens are currently protected from bottom-contact fishing, other areas of predicted suitable habitat remain open to such fishing. Results from this modeling effort will be combined with new information on the skeletal mineralogy of Alaska’s deep-sea corals (Stone et al. in prep.) and predicted changes in carbonate chemistry through 2100 to produce a spatially explicit ocean acidification risk assessment for Alaska’s coral resources.

NOAA’s Alaska Fisheries Science Center has also developed generalized additive models (GAMs) for coral and sponge habitat in Alaska

that use data from bottom trawl surveys. Rooper et al. (2014) presented models that predicted presence or absence, abundance, and family diversity of corals and sponges (as opposed to presence-only models) for the Aleutian Islands. The predictor variables included remotely-sensed data, predictions from oceanographic models, and location-specific data collected during trawl surveys. The PHM objective was to develop and parameterize a spatially explicit model to predict coral and sponge presence, abundance, and diversity at 100 m spatial resolution for the Aleutian Islands. Field validation surveys using towed camera systems and a stratified-random station selection were conducted in 2012-2014 and data are in the process of being analyzed. Similar models based on bottom trawl survey data have also been produced for corals and sponges in the Gulf of Alaska (Rooper et al. 2017). These models will be ground truthed using available underwater image data.

Using catches from trawl surveys and similar GAM techniques, Sigler et al. (2015) developed models of coral (excluding Pennatulacea), sea whip (Pennatulacea), and sponge distribution for the outer shelf and slope of the eastern Bering Sea. In 2014, randomized camera surveys were conducted to verify these distribution models (Rooper et al. 2016). Coral densities were low, but the model based on trawl survey data was generally reliable for predicting coral presence or absence in the camera survey. The bottom trawl survey models also successfully predicted sponge and sea whip presence or absence, but to a lesser degree than for coral. Presence or absence models of corals, sponges and sea whips were also constructed from the camera survey data. Combining these models with the distribution models constructed from bottom trawl survey data predicted the distribution of corals,

sponges, and sea whips with better accuracy than the individual models did during cross-validation. These models and associated data are being used by the North Pacific Fishery Management Council in deliberations on potential additional habitat protections in the Eastern Bering Sea.

III.7. Hawaii and U.S. Pacific Territories

In 2015, scientists at NOAA National Centers for Coastal Ocean Science applied the same Maxent modeling approach used in the Northeast, Southeast, and Gulf of Mexico to develop moderate resolution (360 meter) regional models for deep-sea coral taxonomic groups in the Main Hawaiian Islands (Bauer et al. 2016). Maxent models were constructed using presence-only data and a suite of environmental variables including depth, terrain metrics calculated at multiple spatial scales, proximity to seamounts, and physical and biological oceanography. A total of 16 taxonomic groups were modeled, including gold corals, red and pink corals, black corals (separated into distinct groups by depth), bamboo corals, bubblegum corals, framework-forming and non-framework-forming stony corals, gorgonian and non-gorgonian soft corals, three suborders of gorgonian corals (Calcaxonia, Holaxonia, Scleraxonia), and sea pens (separated into distinct groups by substrate). In addition, models were constructed to predict high diversity areas likely to support ≥ 4 and ≥ 7 genera of deep-sea corals. For many of the taxonomic groups, predictions of potential habitat were driven by depth. These models were part of a comprehensive marine biogeographic assessment to provide data products to inform the Bureau of Ocean Energy Management's renewable energy policy decisions in Hawaii.



While there are many coral occurrence records in the Hawaiian archipelago, information from other U.S. Pacific Territories is sparse (Parrish et al., this volume). The only modeling results for these areas are from global-scale efforts for 6 species of scleractinian reef formers (Davies and Guinotte 2011), octocorals (suborders *Alcyoniina*, *Calcaxonia*, *Holaxonia*, *Scleraxonia*, *Sessiliflorae*, *Stolonifera*, and *Subselliflorae* (Yesson et al. 2012)), and black corals (Yesson et al. 2017). Both efforts modeled deep-sea coral habitat at a ~1 km spatial resolution using Maxent, global databases for coral locations, and 30 environmental, physical, and chemical predictor variables.

IV. Application of Predictive Habitat Models to Fishery Management

In addition to helping researchers identify areas where coral habitat is most likely to be found, modeling results can be used in conjunction with existing fisheries management boundaries to help resource managers identify areas where potential deep-sea coral habitat remains at risk from human activity. Figure 5 shows the predicted distribution of several taxa of deep-sea corals and existing areas closed to bottom trawls to protect essential fish habitat for groundfish off Washington (Guinotte and Davies 2012, 2014). Commercial fishing using bottom-contact gear is a common practice in most U.S. regions, but field surveys for deep-sea corals are limited by the expense and extent of area that can be surveyed. Predictive habitat modeling represents a potential cost-effective means to fill these gaps.

Modeling results can also be overlaid with coral bycatch maps to test the accuracy

of model results. However, this type of comparison can give conflicting results when commercial fishers actively avoid high-relief areas (most likely to harbor most deep-sea corals) in order to minimize gear damage and/or loss. Modeling results can and should be incorporated into U.S. regional Fishery Management Councils' fisheries review processes to help determine areas where additional management measures may be warranted or where existing boundaries need to be amended.

For example, regional PHM results in the Southeast U.S. Atlantic contributed to discussions of alternatives in the development of the SAFMC's Coral Amendment 8 to the Fishery Management Plan for Coral, Coral Reef, and Live/Hardbottom Habitats in the South Atlantic Region. This outcome resulted in both the expansion of some Habitat Area of Particular Concern (HAPC) boundaries (Figure 4) to capture more high-likelihood coral habitat, and opening of some flat bottom areas of low likelihood to support coral habitat (SAFMC 2013). In 2015, the Mid-Atlantic Fishery Management Council approved the closure of 15 submarine canyon and slope areas to almost all bottom-contact fishing gear specifically to protect deep-sea coral habitats (MAFMC 2015). The results of the NOAA deep-sea coral PHM were included in the closure proposal and specifically used in the identification of boundaries for these discrete areas. Decisions like these are difficult to make based on spatially limited field sampling efforts alone; comprehensive regional maps of habitat suitability produced by PHM can greatly assist in developing and prioritizing spatial boundaries. Similar discussions are underway to varying degrees in other Fishery Management Councils, including the New England, Pacific and North Pacific Councils, and PHM results are likely to be a useful tool



for shaping and evaluating alternative spatial management and conservation measures in these regions.

V. Limitations of Predictive Habitat Modeling Results

There are several limitations to predictive habitat modeling. Many of the variables that are important for coral settlement, growth and survival cannot be incorporated into the models because data on these variables do not exist at sufficient resolutions or are limited in geographic extent. This is particularly true for data on high-resolution current direction/velocity, water-column data (e.g., turbidity, temperature, salinity, saturation state), and benthic substrate type (Davies and Guinotte 2011). These variables, particularly hard substrata, can be patchy at small scales, and these alone may determine whether or not deep-sea corals inhabit a given location. In addition to predictor variables, there are limitations with the coral records used in models. The taxonomy of deep-sea coral records can be highly uncertain. This is particularly true for deep-sea coral records obtained from video and/or images when no specimens were collected for expert examination. Coral records obtained from trawl/bycatch surveys are associated with inherent spatial uncertainty as trawls can be several kilometers in length and precise georeferencing can be difficult depending on the technology used.

Perhaps the most important question that arises pertains to the accuracy of these models for deep-sea corals. The preferred method to assess model accuracy is to perform robust field validation surveys to assess model performance. Field validation efforts must be conducted to assess the accuracy of the models, enable model refinement, and gauge

the utility of these methods for determining deep-sea coral habitat in unsurveyed areas, as illustrated in Figure 1. Rooper et al. (2016) demonstrated a systematic field validation for a U.S. deep-sea coral predictive habitat model for the Eastern Bering Sea, and similar efforts are currently underway in the Aleutian Islands, Gulf of Mexico and Northeast U.S. Field validation of models should be integrated into the cruise plans of existing/future NOAA deep-sea exploration and research. These surveys should record both georeferenced locations of coral presence (identified to the best taxonomic resolution possible) as well as locations of areas where corals have been confirmed to be absent. They should also be appropriately stratified so that areas predicted to have low, intermediate, and high habitat suitability are sampled adequately to support model calibration and validation. These accuracy assessments will guide refinement of future deep-sea coral predictive habitat modeling efforts, and also shape the appropriate use of such models for conservation and management purposes. If field validation is not possible, cross-validation methods can be used to aid in the assessment of predictive model results (e.g., Huff et al. 2013).

VI. Conclusions and Recommendations

Predictive habitat modeling is increasingly used to help identify areas that are most likely to harbor deep-sea coral taxa. The growth and adoption of these techniques in most U.S. regions are primarily due to improvements in input data quality/quantity, the low cost of producing the models, and the need to identify habitat across large spatial extents for management. The spatial resolution of model results has improved in the last five



years to the point where model outputs can be used to aid management decisions, and this is also spurring an increase in their development and subsequent use. Some of the regional examples reviewed here have been used to help target areas for field sampling efforts and others have been used to help inform U.S. regional Fishery Management Councils' EFH/HAPC review processes. High-resolution substrate data (e.g. backscatter, side scan sonar) can be used in conjunction with model results to identify areas with the highest probability of finding deep-sea corals, but the limited availability of substrate data at regional scales continues to hinder the accuracy of predictive habitat models. Model results tend to over predict suitable deep-sea coral habitat in many regions due to the absence of high-quality substrate data and this issue will likely persist as the distribution of substrate is highly variable over small spatial scales.

VII. Acknowledgments

Marine Conservation Institute and Bangor University would like to thank the Ittleson Foundation, Oak Foundation, NOAA's Deep-Sea Coral Research and Technology Program, and ESRI's Conservation Program for providing funding and software support for modeling efforts. We also would like to thank Bob Stone and Chris Rooper for their input on Alaskan modeling efforts. BPK would like to thank Matt Poti, Chris Caldwell, Dave Packer, Martha Nizinski, Amy Drohan, Richard Langton, Vincent Guida, Peter Etnoyer, Andrew David, Thomas Hourigan, Gregory Boland, William Shedd, James Sinclair, Christopher Jenkins, and Laughlin Siceloff for helpful discussions, data and technical assistance. BPK was supported under NOAA Contract No. DG133C07NC0616 with Consolidated Safety Services, Inc.

Recommendations to NOAA Deep-Sea Coral Research and Technology Program:

1. Encourage all Program funded cruises to provide presence *and* absence data at relevant spatial scales to help validate and improve predictive habitat models.
2. Develop and improve the publicly available national database of coral occurrences and absences for the U.S. EEZ, including in situ environmental data where possible.
3. Support the development of a publicly available database for high-resolution substrate data for the U.S. EEZ.
4. Ensure that the modeling results funded by the Program are incorporated into U.S. regional Fishery Management Councils' EFH/HAPC reviews and other relevant Council processes.
5. Provide support to make the best regional predictive habitat model maps broadly available to the public and federal agencies for marine spatial planning purposes.
6. Convene regular working groups to compare and synthesize the results of modeling efforts in each region. Multiple modeling efforts lead to more robust understanding, but require expert review, comparison, and synthesis to identify strengths and weaknesses of different approaches as well as areas of consensus and disagreement among models.
7. Ensure that field surveys, habitat modeling, and management efforts are efficiently integrated to take advantage of the feedback loops illustrated in Figure 1.
8. Improve mapping and modeling of real and potential human impacts and integrate these maps with deep-sea coral PHM to identify and prioritize high risk areas.



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An octopus hides in a rock wall dotted with cup coral and soft coral in Welker Canyon off New England. Courtesy of the NOAA Office of Ocean Exploration and Research.



STATE OF DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE NORTHEAST UNITED STATES

1. Introduction

The Northeast region extends from Maine to North Carolina ends at the U.S. Exclusive Economic Zone (EEZ). It encompasses the continental shelf and slope of Georges Bank, southern New England, and the Mid-Atlantic Bight to Cape Hatteras as well as four New England Seamounts (Bear, Physalia, Mytilus, and Retriever) located off the continental shelf near Georges Bank (Fig. 1). Of particular interest in the region is the Gulf of Maine, a semi-enclosed, separate “sea within a sea” bounded by the Scotian Shelf to the north (U.S. jurisdiction ends at the Hague Line), Georges Bank to the south, and Cape Cod to the southwest. Diverse benthic habitats are found on the rocky ledges, soft sediment banks, and within the 21 deep basins (the largest and deepest being Jordan, Wilkinson, and Georges) of the Gulf. Georges Bank, another prominent feature in the region, is a shallow elongate extension of the continental shelf bounded by the Gulf of Maine to the north, Great South Channel and Nantucket Shoals to the west and south, and the Northeast Channel/Scotian Shelf to the east and north (U.S. jurisdiction ending at the Hague Line). The central portion is shallow, consisting mostly of larger grain-sized sediments, ranging from sand to gravel to boulders depending on location. Numerous submarine canyons, found near the shelf break from Georges Bank down to Cape Hatteras (Fig. 1), cut into the slope and occasionally into the shelf. They were formed by erosion of sediments and

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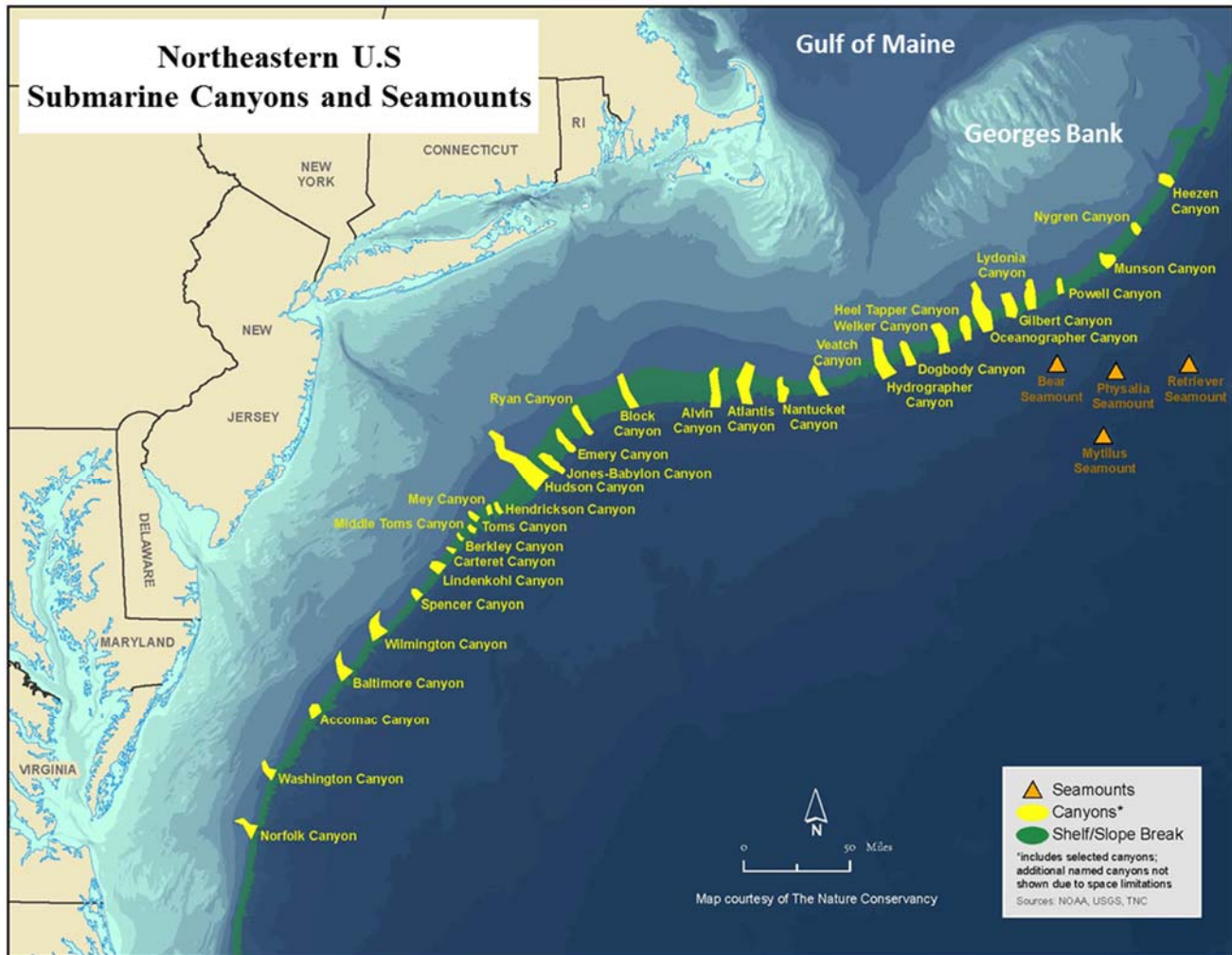


Figure 1. The major submarine canyons and seamounts (within the EEZ) off the Northeast coast of the U.S.

sedimentary rocks of the continental margin and are classed as deep (V-shaped from erosion by rivers, mass wasting, and turbidity currents) or shallow (shallowly eroded into the continental margin, or U-shaped canyons). The Mid-Atlantic Bight includes the shelf and slope from Georges Bank to Cape Hatteras. Many hard-bottom topographic features characteristic of other deep-sea coral habitats (e.g., boulders, bedrock, etc.) are absent here. The relatively small amount of hard substrate in deeper water

available in this area occurs in conjunction with submarine canyons or is anthropogenic in origin (e.g., artificial reefs, shipwrecks). The shelf topography is relatively smooth and sediments are rather uniform, mostly consisting of sand with some gravel, with finer sediments occurring toward the outer shelf, shelf break, and deeper parts of canyons. The Hudson Shelf Valley and Canyon, off NY/NJ is the main physiographic feature in the Bight, extending from the inner shelf to slope.



Packer et al. (2007) extensively reviewed most of the major coral groups of the Northeast (the exception was sea pens or pennatulaceans; see below), including gorgonians and true soft corals (alcyonaceans), black corals (antipatharians), and certain stony corals (scleractinians). However, much of the information needed to assess the status of the deep-sea coral habitats was unavailable or incomplete at the time of that review. There was missing or inadequate information on deep-sea coral distribution, abundance, natural history, taxonomy, and overall population status and trends, as well as a lack of high-resolution bathymetry data. Available information on deep-sea corals from shelf, slope, and canyon locations was compiled from historical databases (see Packer et al. 2007). These data were mainly presence-only or occurrence records. The canyons where the majority of the survey work had been done were Heezen, Lydonia, Oceanographer, Hendrickson, Baltimore, and Norfolk canyons.

A few patterns or trends were suggested or apparent (Watling and Auster 2005; Packer et al. 2007). For the gorgonians and true soft corals, species composition varies with depth. The suite of species that occurs at depths less than 500 m (shelf and upper slope) is different than that which occurs at depths greater than 500 m (lower slope and rise) (Watling and Auster 2005). Some other species (e.g., the stony coral *Astrangia poculata*) can also be found in nearshore waters less than 50 m deep. Corals occurred in higher densities and were more diverse in canyons, and some species, such as those restricted to hard substrates, were found

only in canyons while those utilizing soft substrata were found both in canyons and on the continental slope (see discussions of Hecker and colleagues surveys in Packer et al. 2007). Surveys conducted prior to 2012 (Moore, Watling, Auster, Shank, and colleagues) showed that deep-sea corals are major components of benthic communities of the New England Seamounts. At the time, the black corals (antipatharians) in this region appeared to be primarily confined to the seamounts. Sea pens (pennatulaceans) were not discussed in detail. However, the most common and widespread sea pens (*Pennatula aculeata* and *Stylatula elegans*) are found on the continental shelf in soft sediments, with most other species recorded on the slope and in canyons.

In addition, little was known about the fauna associated with deep-sea coral habitats. For example, debate continued on the role of deep-sea corals as essential fish habitat (EFH) in this region. Although redfish (*Sebastes* spp.) commonly occur in the vicinity of deep-sea corals in the Gulf of Maine and corals may provide important structural attributes of habitat that can affect the distribution and abundance of fishes, it was suggested that corals may not be functionally different from other structure available to fishes (e.g., Auster 2005). There was also little information available about associations between invertebrate species and deep-sea corals in this region, except for nearby studies in Canada (e.g., Northeast Channel: Metaxas and Davis 2005). Studies on invertebrate species associations with octocorals on the seamounts were ongoing.



The effects of fishing efforts on deep-sea corals and coral habitats in this region were not quantified. Quantitative information on the extent of other anthropogenic impacts to corals was also not available. The types of bottom-contact fishing gear used in the Northeast include fixed gear such as longlines, gillnets, pots and traps, as well as mobile gears such as trawls and dredges. Most fishing is conducted on the shelf, or along the shelf break, and in the Gulf of Maine.

The fisheries that have the highest likelihood of occurring near concentrations of known deep-sea coral habitats in canyon and slope areas are the bottom trawl fishery for monkfish (or goosefish, *Lophius americanus*) and the bottom longline fishery for tilefish (*Lopholatilus chamaeleonticeps*, *Caulolatilus microps*), and the pot fisheries for Atlantic deep-sea red crab (*Chaceon quinqueedens*) and offshore lobster (*Homarus americanus*). Bottom trawl fisheries for squid (*Doryteuthis* [*Amerigo*] *pealeii* and *Illex illecebrosus*), whiting (includes silver hake, *Merluccius bilinearis* and offshore hake, *Merluccius albidus*), and butterfish (*Peprilus triacanthus*), and pot fisheries for Jonah crab (*Cancer borealis*) occur along the shelf break. In the Gulf of Maine, lobster fishing occurs in all known coral habitats, and gillnet and bottom trawl fisheries for groundfish such as pollock (*Pollachius virens*), redfish (*Sebastes* spp.), and white hake (*Urophycis tenuis*) occur offshore.

In terms of fishery management actions, in 2005, NOAA's National Marine Fisheries Service (NMFS), on the advice of the New England and Mid-Atlantic Fishery Management Councils (NEFMC, MAFMC), closed portions of Oceanographer and Lydonia canyons indefinitely to vessels fishing with bottom trawls or bottom gillnets during a monkfish "day-at-sea" in order to minimize impacts of the monkfish fishery on EFH. Although corals were not included in the EFH descriptions for any fisheries species in the Northeast region, a number of federally-managed species had EFH defined as hard substrates in depths greater than 200 m (e.g., redfish), and the abundance of structure-forming organisms, especially deep-sea corals in these canyons was a major driver for the protection of these hard bottom habitats.

In this chapter we highlight new scientific information on deep-sea coral ecosystems that has become available since the publication of Packer et al. (2007), both from the analysis of samples collected before 2007 (e.g., seamount expeditions conducted from 2003-2005 and described in Packer et al. 2007) and major new mapping and research initiatives since 2011. This new information has resulted in major new management measures established or under development to help protect these habitats in the region. We also include information on deep-sea sponges, which were not addressed in the 2007 report.



II. Update on Scientific Information

II.1. New Research – Overview

In 2010, the Bureau of Ocean Energy Management (BOEM), in partnership with the U.S. Geological Survey (USGS) and the National Oceanic and Atmospheric Administration (NOAA) initiated a major study: Exploration and Research of Mid-Atlantic Deepwater Hard Bottom Habitats and Shipwrecks with Emphasis on Canyons and Coral Communities (BOEM 2010). Between 2012 and 2015, NOAA conducted a series of exploratory surveys of coral habitats in the Gulf of Maine, additional Northeast canyons, and New England seamounts, which have significantly expanded our knowledge of deep-sea coral and sponge habitats in the region. While analysis of information from many of these surveys is ongoing, several publications and reports have already come out (cited and discussed below), and the higher-level identification of deep-sea coral and sponge habitats has already been used by the Regional Fishery Management Councils in development of coral protection zones and by the Obama Administration to inform designation of the Northeast Canyons and Seamounts Marine National Monument (discussed below).

II.1.i – BOEM Atlantic Deep-water Canyons Study 2010-2017

This multi-year study focused on Baltimore and Norfolk canyons in the southern mid-Atlantic

Bight, and was designed to understand the distribution and complexity of hard bottom communities in the region. The study was funded by BOEM and awarded to Continental Shelf Associates, Inc. Partners included NOAA, USGS, North Carolina Museum of Natural Sciences, European agencies, and several U.S. universities. The study area was originally selected based on the potential oil and gas lease sales in federal waters within the BOEM mid-Atlantic planning region.

Specific coral related objectives included characterization of the canyons' physical environments, habitats, and associated communities, and included documenting deep-sea coral distribution and diversity, developing predictive habitat models of deep-sea coral distributions, evaluating sensitivity of communities to disturbance, and understanding population connectivity between canyons. The study mapped Baltimore, Accomac, Washington, and Norfolk canyons, with subsequent remotely operated vehicle (ROV) surveys, collections, and studies focused on Baltimore canyon and Norfolk canyon.

For example, see Brooke et al. 2017 for deep-sea corals specifically, as well as other studies by Ross et al. 2015; Prouty et al. 2016; Bourque et al. 2017, etc. See also:

<http://oceanexplorer.noaa.gov/explorations/12/midatlantic/welcome.html> and <http://oceanexplorer.noaa.gov/explorations/13/midatlantic/welcome.html>.

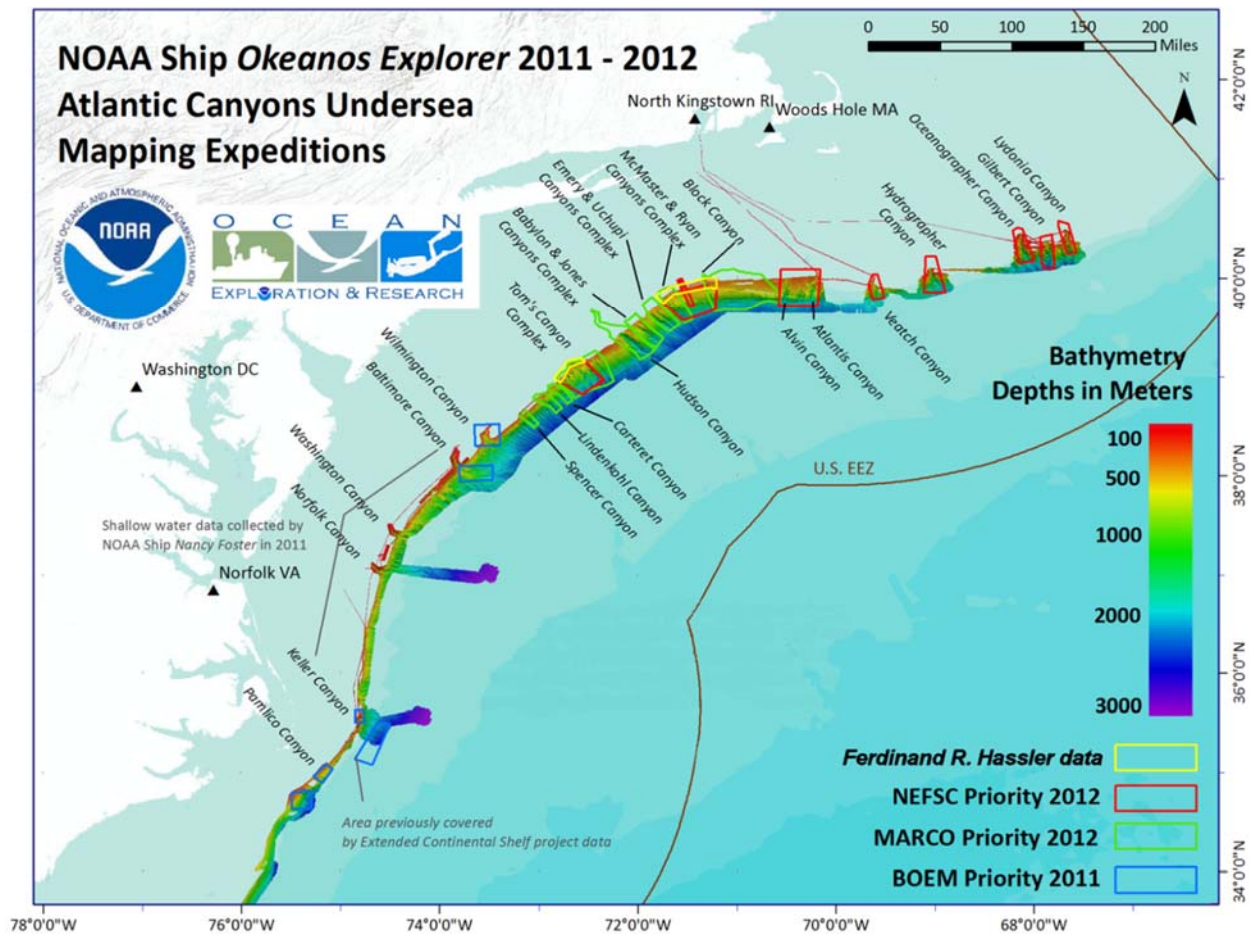


Figure 2. ACUMEN priority areas selected by NOAA and external partners. Mapping efforts by NOAA Ship Okeanos Explorer depicted as color swaths; NOAA Ship Ferdinand Hassler as yellow boxes.

II. 1.ii – ACUMEN (Atlantic Canyons Undersea Mapping Expeditions) 2012

Because the submarine canyons on the Northeast continental shelf and slope are diverse and unique habitats that contain a variety of fauna, they are of great interest to federal and state management agencies. However, most are poorly known, due to the costs and logistical difficulties of surveying these areas. A partnership among NOAA line offices, the Atlantic Canyons Undersea

Mapping Expeditions (ACUMEN) was established to make efficient use of research ships’ multibeam mapping resources, allowing for effective and efficient data collection and capitalizing on complementary capabilities of NOAA assets to produce an integrated, coherent dataset. ACUMEN’s goals included field efforts to support the NOAA Habitat Blueprint Northeast Regional Initiative (NOAA 2012a), support of NOAA Integrated Ocean and Coastal Mapping efforts, prioritization of



canyons for conservation goals as suggested by state and regional constituents (e.g., NEFMC Habitat Plan Development Team [Habitat PDT], the Mid-Atlantic Regional Council on the Ocean [MARCO]), and sharing of data and products across platforms to guide and refine expedition plans in near real-time. A working relationship was also established with scientists in charge of the BOEM Atlantic Deep-water Canyons study mentioned above.

Priority areas along the continental shelf/slope from Virginia to Rhode Island were initially identified for exploration and mapping by ACUMEN to gather baseline information in support of science and management needs. Between February and August 2012, five expeditions conducted a mapping ‘blitz’ focused on the submarine canyons (Fig. 2). The expeditions highlighted the complementary capabilities of three NOAA ships: *Okeanos Explorer* (Office of Ocean Exploration and Research), *Ferdinand R. Hassler* (Office of Coast Survey), and *Henry B. Bigelow* (NMFS, Northeast Fisheries Science Center). The *Hassler* and *Okeanos Explorer* collected high-resolution bathymetry data that were quickly processed into mapping products that guided the majority of subsequent habitat modeling and deep-water surveys (discussed below).

The 2012 ACUMEN field efforts finished with a July survey aboard the FSV *Henry B. Bigelow*. Overall goals of the mission were to survey and ground-truth known or suspected deep-sea coral habitats associated with the submarine canyons off the edge of the Northeastern U.S continental shelf/slope. Activities included: (1)

characterizing benthic habitats and identifying areas where deep-sea corals and sponges were present; (2) initial ground-truthing of areas predicted to be coral “hotspots” based on data and outputs from a deep-sea coral habitat suitability model; and, (3) ground-truthing newly collected high-resolution (25-50 m) continental slope bathymetric maps created from multibeam data collected during ACUMEN cruises. Using the Woods Hole Oceanographic Institution’s (WHOI) towed camera system (*TowCam*), three main canyon areas were targeted: Toms Canyon complex in the mid-Atlantic (Toms, Middle Toms, and Henderickson canyons; Toms-Hendrickson inter-canyon area), Veatch Canyon and the rim of an unnamed canyon northeast of Veatch, and Gilbert Canyon off New England (Fig. 3). Gilbert Canyon in particular was identified as a deep-sea coral “hotspot” by the habitat suitability model. All three main canyon areas were either under-explored or unexplored with regards to deep-sea coral and sponge occurrences. Thus, these areas were of particular interest to the regional Fishery Management Councils.

II.1.iii – Physalia Seamount Expedition 2012

In October 2012, the Waitt Institute funded a cruise with their two REMUS 6000 autonomous underwater vehicles (AUVs; operated by Woods Hole Oceanographic Institution to investigate deep-sea corals on *Physalia* Seamount (summit depth approximately 1880 m), a previously unexplored member of the western New England Seamount chain within

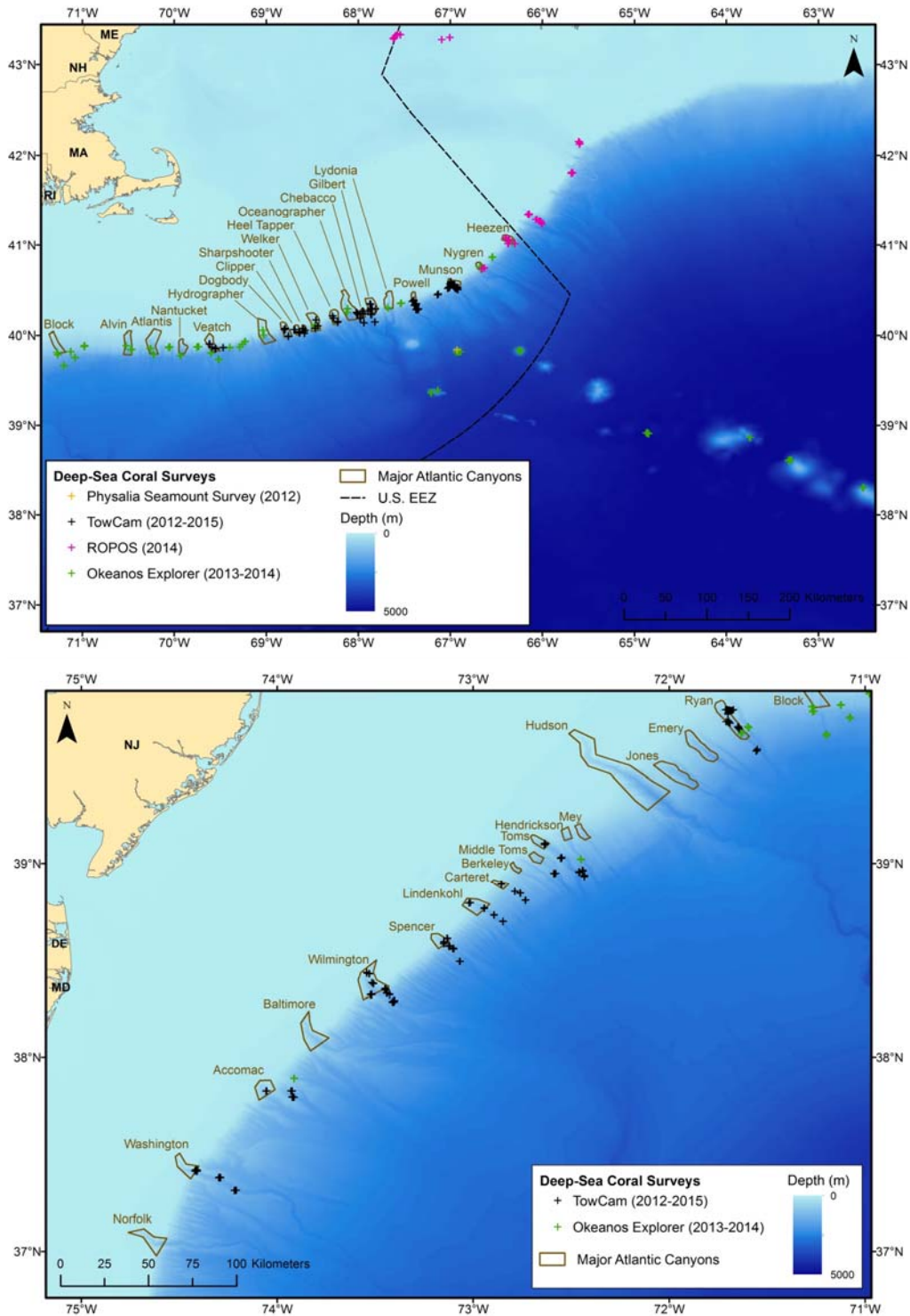


Figure 3. Map of 2012-15 NOAA expeditions (dives and tows) of the continental slope, canyons, and Mytilus, Physalia, and Retriever Seamounts using either the Woods Hole Oceanographic Institute’s TowCam towed camera system or the Canadian ROV ROPOS onboard NOAA ship Henry Bigelow, and exploratory surveys by ROV Deep Discoverer onboard NOAA ship Okeanos Explorer. BOEM funded surveys of Baltimore and Norfolk canyons are not included. A) New England region. B) Mid-Atlantic region.



the U.S. EEZ (Kilgour et al. 2014; Fig. 3). The vehicles collected 2956 color seafloor images as well as 120 kHz (low-frequency) and 420 kHz (high-frequency) sidescan sonar. The cruise demonstrated that AUVs are suitable for the rapid assessment of the presence and distribution of deep-sea corals. This "high and fast" sampling strategy was appropriate for the spatial resolution of current management approaches that essentially propose broad geomorphic features (e.g., discrete submarine canyons, seamounts) as deep-sea coral protection zones. The geo-referenced images provided fine scale distribution information, which is optimal for surveying the large areas required for tactical management needs (Kilgour et al. 2014). This project demonstrated that AUVs could be ideal tools for linking fine-scale spatial distribution of deep-sea corals to meso-scale patterns and variation in landscape features, flow regimes and other oceanographic attributes. Such information is of particular benefit for improved deep-sea coral habitat suitability modeling to predict distribution of deep-sea coral taxa across regional landscapes (Kilgour et al. 2014). The results from the AUV deep-sea coral surveys at Physalia Seamount were provided to the NEFMC for use in their regional deep-sea coral management zone determinations.

II. 1.iv – NOAA Ship Okeanos Explorer Atlantic Canyon and Seamounts Expeditions 2013 & 2014

In 2013 and 2014, NOAA Ship *Okeanos Explorer* surveyed canyons off New England and the Mid-Atlantic as well as three seamounts off

New England using the ROV *Deep Discoverer* (Fig 3). Areas for exploration were prioritized prior to the cruise by resource managers, federal and state partners, and through broad participation of the marine science community. The ship also conducted additional multibeam mapping.

In 2013, surveys were conducted in 11 submarine canyons and Mytilus Seamount (Quattrini et al. 2015; also: <http://oceanexplorer.noaa.gov/okeanos/explorations/ex1304/welcome.html>). The New England areas surveyed in 2014 included Physalia and Retriever Seamounts, Nantucket Canyon, an unnamed, minor canyon east of Veatch Canyon. Mid-Atlantic areas surveyed in 2014 included the Mey-Linden Kohl Slope (Linden Kohl and Hendrickson canyons) and Washington, Norfolk, Phoenix, McMaster, and Ryan canyons. Full descriptions of the 2014 dives can be found at:

<http://oceanexplorer.noaa.gov/okeanos/explorations/ex1404/welcome.html>.

II. 1.v – NOAA Northeast Deep-sea Coral and Sponge Initiative 2013-2015

The Deep Sea Coral Research and Technology Program funded a Northeast fieldwork initiative from 2013 to 2015 to locate, survey, and characterize deep-sea coral and sponge communities in this region (NOAA 2016). The fieldwork initiative was implemented by NOAA scientists in collaboration with other government agencies (including the Canadian Department of Fisheries and Oceans), and



researchers from academic institutions. The projects were designed with the participation of the Regional Fishery Management Councils. The emphasis during the 3-year initiative was on baseline coral and sponge habitat characterization, while trying to survey as many areas as possible in order to provide information and contribute to management decisions by the Fishery Management Councils and other regional partners (e.g., Mid-Atlantic Regional Council on the Ocean, [MARCO]). Thus, the Initiative was designed to satisfy resource management needs while significantly increasing our understanding of the region's deep-sea coral and sponge ecosystems.

By combining Program resources with other partners within and outside of NOAA, leveraging funding, and employing a wide range of research tools, the initiative advanced deep-sea coral science and management through three major fieldwork projects:

1. Exploratory surveys of coral/sponge habitats in submarine canyons, slope areas, and seamounts off New England and the Mid-Atlantic (Fig 3). Surveys off New England and the Mid-Atlantic were conducted every summer from 2013-2015 using towed cameras, targeting areas in and around submarine canyons from approximately 300+ m to 2100 m. The Deep Sea Coral Research and Technology Program was also a partner on the *Okeanos Explorer* expeditions. Surveys contributed to groundtruthing and refining the next iterations of the Northeast's deep-sea coral habitat suitability model.

2. Characterizations of seafloor communities in the U.S. and Canadian cross-boundary Gulf of Maine region and on the U.S. and Canadian continental margin (ROV *ROPOS* dives, 2014; Fig 3).
3. Exploratory surveys of northern Gulf of Maine (U.S.) habitat areas for deep-sea corals and sponges. This component also included collecting specimens of the common sea pen (*Pennatulula aculeata*) to determine if they are being used by fish larvae (perhaps redfish, *Sebastes* spp.) as nursery habitat, as has been observed in Canada (Baillon et al. 2012).

II.2. Taxonomy and Species Distributions

II.2.i – Corals

a. Coral taxonomy

Deep-sea corals in the Northeastern U.S. belong to four orders: Order Scleractinia (the stony corals), Order Antipatharia (black corals), Order Alcyonacea (including gorgonians [formerly in the order Gorgonacea], true soft corals, and stoloniferan corals), and Order Pennatulacea (sea pens) (see Packer et al. 2017 online). Sea pens were not covered in detail by Packer et al. 2007; however, they may play an important role in benthic communities (Buhl-Mortensen et al. 2016) and provide nursery habitat for some commercial fish species (see below, re: Baillon et al. 2012) Thus, sea pens are now included in the species list and summaries of deep-sea corals in this region. NOTE: Gorgonians are the most important structure-



Table 1. Number of coral species reported from the Northeast U.S. in 2007 and in the present report (including taxa with incomplete taxonomy – e.g. taxa reported only to genus level). Increases include new species identifications and range extensions, but principally represent species not included in the first report. The lower number of sea pen taxa reflects a number of synonymized species. Data sources and references online in Packer et al. 2017: <https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>.

TAXON	Packer et al. 2007	Packer et al. 2017
Black corals (Order Antipatharia)	2	6
Stony corals (Order Scleractinia)	16	17
Gorgonian corals (Order Alcyonacea – in part [formerly Order Gorgonacea])	17	32
True soft corals and stoloniferans (Order Alcyonacea)	9	9
Sea pens (Order Pennatulacea)	17	14
Total	61	78

forming corals in the Northeast region, and for the purposes of this chapter, they will generally be treated separately from other alcyonaceans. Current taxonomic recognizes gorgonians, true soft corals, and stoloniferans under order Alcyonacea (Bayer 1981; Daly et al. 2007; McFadden et al. 2010).

Packer et al. (2007) reported 61 species of corals from the Northeast region (Table 1). Since 2007, the systematic compilation of coral records in the National Deep-sea Coral and Sponge Database, along with new descriptions and range extensions, has increased this number to 78 (Table 1; see Packer et al. 2017 online). The largest increase in numbers was among the gorgonian corals, reflecting new species descriptions by Cairns (2006, 2007), Pante and Watling (2011), and Simpson and Watling (2011), as well as new additions to the species

list. Many of the new species descriptions resulted from analysis of specimens collected during 2003-2005 seamount expeditions (described in Packer et al. 2007).

For sea pens, there have been several new additions and name changes; e.g., *Protoptilum aberrans* Kölliker 1880 has been removed from the current list as it is now considered a junior synonym of *Protoptilum carpenteri* Kölliker, 1872 (Mastrototaro et al. 2015), *Funiculina armata* Verrill, 1879 has been added, etc. (see Packer et al. 2017 online).

b. Coral distribution

Data Sources: The primary sources of historical (i.e., prior to 2007) deep-sea coral records and observations in this region are discussed and referenced in Packer et al. (2007). There are two main types of deep-sea coral data in the



Northeast region: geo-referenced presence records, and presence records with no accompanying geo-referenced information, or only general location information, which we call “observations.” (The latter most often comes from the historical deep-sea coral survey literature.) There is too little deep-sea coral density or abundance data to be useful for either scientific or management purposes, especially in aggregate with other occurrence data. A database of Northeast deep-sea corals, based largely on historical geo-referenced presence records from the late 1800s to the present, was updated by incorporating taxonomic changes made between 2007 and 2013 and adding “new” presence records gleaned from museum collection databases (e.g., the Smithsonian Institution’s National Museum of Natural History collection, which includes records of coral taxa collected from various research surveys/expeditions from 1873 through to the present), other data mining activities, the literature, and new records from expeditions in the 2000s (e.g., the NOAA-Ocean Explorer 2001 “Deep East” expeditions to Oceanographer, Hydrographer, and Hudson Canyons and 2003 “Mountains in the Sea” expeditions to the New England Seamounts). Additional records of sea pens (especially *Pennatulula aculeata*) collected from 1956-1984 were compiled from various sources (e.g., Langton et al. 1990). Records of new species of octocorals, mostly from Bear and Retriever Seamounts with some from the submarine canyons off New England (e.g., *Thouarella grasshoffi* Cairns 2006 from Bear Seamount and Oceanographer Canyon) were obtained from

recently published literature (Cairns et al. 2007; Thoma et al. 2009; Pante and Watling 2011; Watling et al. 2011). New records of antipatharians were also obtained from recently published seamount literature (Thoma et al. 2009). These records have now been incorporated into NOAA’s National Database on Deep-Sea Corals and Sponges (www.deepseacoraldata.noaa.gov; Hourigan et al. 2015).

Deep-sea Coral Habitat Suitability Modeling:

Because of the prohibitive costs and logistical difficulties of surveying for deep-sea corals and their associated habitats, geo-referenced deep-sea coral location data are often limited and patchy, and are mostly of presence-only. This makes it difficult for resource managers trying to identify and implement deep-sea coral habitat management areas to develop spatially contiguous measures for coral conservation in the absence of comprehensive surveys.

Habitat modeling for deep-sea corals has become a cost effective approach to predict locations of deep-sea corals and other benthic species, and aid managers in developing deep-sea coral management zone alternatives (Leverette and Metaxas 2005; Bryan and Metaxas 2007; Davies et al. 2008; Tittensor et al. 2009; Davies and Guinotte 2011; Guinotte and Davies 2012; Yesson et al. 2012; Vierod et al. 2013). Habitat suitability modeling examines the associations between the presence and/or absence of organisms and their relevant environmental or habitat variables such as depth, slope, temperature, and related measures.



NOAA developed a set of deep-sea coral predictive habitat models for this region for a set of taxonomic groups (Kinlan et al. 2013; Kinlan et al., in review). The spatial domain of the models includes the continental shelf and canyons in New England and the Mid-Atlantic. Seamounts are not included, because the model is based on the footprint of the coastal relief digital elevation model, which does not include the seamounts. A machine-learning technique called Maximum Entropy modeling, or MaxEnt, was used to predict suitability of unexplored habitats based on locations and environmental characteristics of known deep-sea coral presence (Guinotte et al., this volume).

The MaxEnt models were run with selected predictor (environmental) variables and presence data for four taxonomic orders of deep-sea corals represented in the Northeast historical database (Alcyonacea, [formerly] Gorgonacea, Scleractinia, and Pennatulacea). Data included in the models were: 1) Northeast coral presence records from the Cold Water Coral Geographic (CoWCoG) database (Scanlon et al. 2010; NOAA 2011a) supplemented with additional records from the region (Packer and Dorfman 2012); 2) high-resolution bathymetry data from the NOAA Coastal Relief Model (NOAA 2011b); and, 3) environmental predictors (seafloor terrain statistics; physical, chemical, and biological oceanographic data, and sediment/substrate information).

Habitat suitability maps and model evaluation methods predicted suitable habitat in the vicinity of known deep-sea coral presence locations, as well as in unsurveyed areas (for

more detailed discussion of model results, see Guinotte et al. 2016, Guinotte et al., this volume, Kinlan et al., in review). Some model outputs are better predictors of coral presence than others, in part due to the number of coral records for each order in the historical database. The model outputs for alcyonacean (= gorgonian and true soft) corals is based on a sizeable number of data points and is the model with the best predictive ability. Therefore, these model outputs were used by the MAFMC and NEFMC to evaluate deep-sea coral habitat suitability of each proposed broad and discrete deep-sea coral management zone (see discussion, below). Conversely, the model for scleractinians is based on a smaller number of records, mostly of solitary, soft-sediment dwelling cup corals (e.g., *Dasmomilia lymani* and *Flabellum* spp.). The scleractinian model is likely to under-predict the likelihood of suitable habitat for this coral taxon. Sea pens were modeled, based mostly on records from the continental shelf (e.g., *Pennatula aculeata* from New England/Gulf of Maine and *Stylatula elegans* from the Mid-Atlantic) but are not currently used by the Fishery Management Councils. These corals occur in soft bottoms, are more widespread in distribution, and the contribution of these two species, especially *P. aculeata*, as structure-forming habitat for other species is still poorly understood or open to question (see discussion below). Black corals were not included in the modeling study due to insufficient data on their distribution when the study commenced. Future incorporation of recent data for structure-forming scleractinians and black corals in the Northeast region will

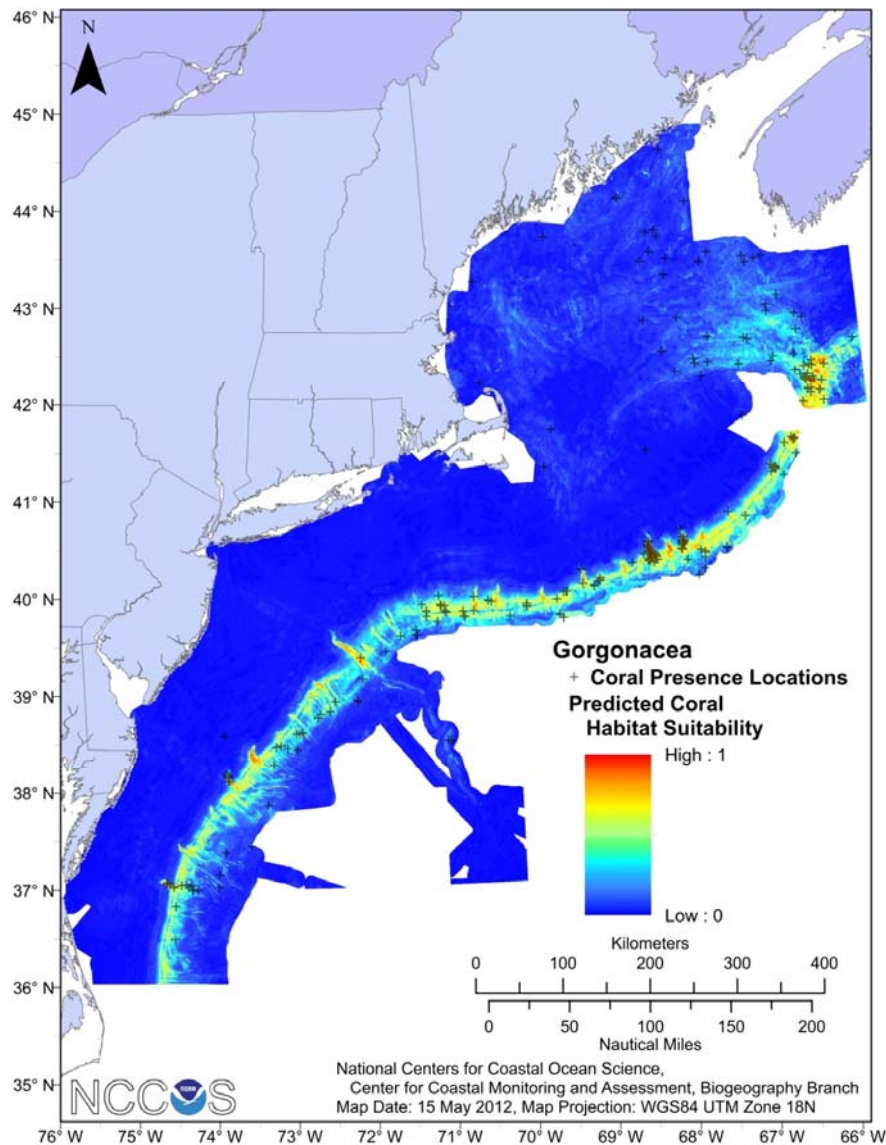


Figure 4a. Example of MaxEnt Predictive Habitat Model (PHM) for gorgonians in the Northeastern U.S. region (Kinlan et al. 2013). Warm colors (e.g., red) denote areas predicted to be more suitable gorgonian habitat and cooler colors (e.g., blue) denote areas predicted to be less suitable gorgonian habitat. Crosses represent coral presence records used in generating the model.

likely improve the predictive ability of models for these taxa.

An example of model outputs for gorgonians are shown in Fig. 4a,b. The outputs show the predicted likelihood of deep-sea coral habitat in a given area. The predicted likelihood of coral

habitat suitability is displayed in “thresholded logistic” maps; i.e., the likelihood values are displayed by the following likelihood scale: cooler colors (e.g., blue) denote areas predicted to be less suitable habitat for gorgonians, while warmer colors (e.g., red) denote areas predicted

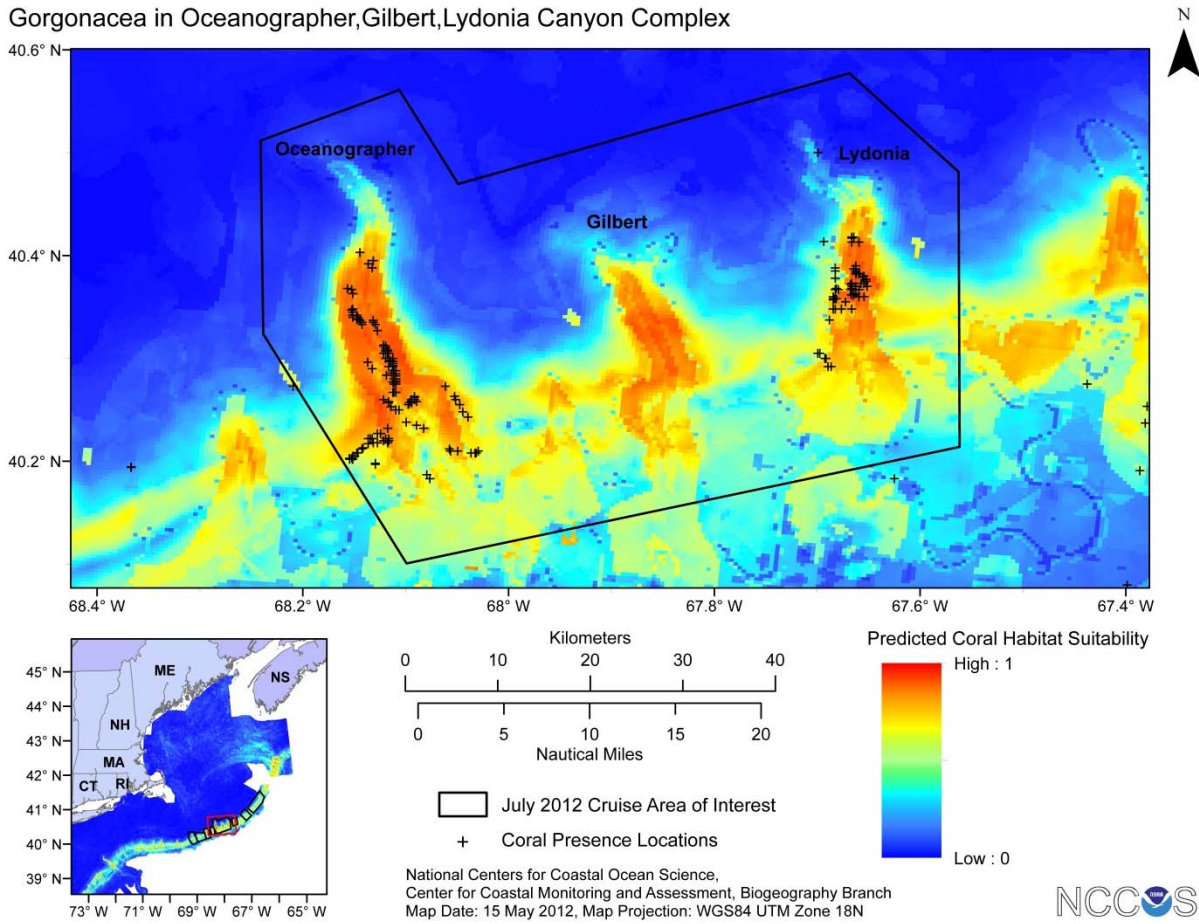


Figure 4b. Close-up of predicted gorgonian habitat suitability in the Oceanographer-Gilbert-Lydonia canyon complex. Crosses represent historical coral presence records. Polygon boundary shows area of interest identified for exploration and groundtruthing for July 2012 DSCRTP/NEFSC R/V Bigelow cruise.

to be more suitable habitat. The models predict that the canyons represent “hot-spots” for gorgonian coral presence.

After the surveys designed to ground-truth the model were conducted (see below), the Northeast’s habitat suitability models, along with distribution data from historical and recent deep-sea coral surveys, became essential components of the deep-sea coral protection zone decision-making process by the two Regional Fishery Management Councils. This

includes the decision by the MAFMC in 2015 to approve an amendment to protect deep-sea corals in their region from the impacts of bottom-tending fishing gear along the edge of the continental shelf and slope and in the submarine canyons (discussed, below).

Mid-Atlantic and New England Continental Slope and Canyons Exploratory Surveys: The continental slope off the Northeast U.S. is incised by numerous submarine canyons,



which contain extensive hard-bottom habitat, which is needed for the attachment of most deep-sea corals (Packer et al. 2007). Prior to 2010, most information on deep-sea coral habitats within Northeast canyons came from the surveys of Hecker et al. during the 1980s (see Packer et al. 2007 for discussions and references, and B. Hecker presentation in NEFMC 2011). Based on these historical surveys, some general patterns in deep-sea coral distribution were suggested. As stated above, deep-sea corals were generally more densely distributed and diverse in the canyons than on the adjacent slope owing to steep canyon topography, accelerated currents, and heterogeneous sedimentary geology. Some species, such as those restricted to hard substrates, were only found in the canyons while other species that frequently occur on soft substrates, such as *Acanella arbuscula*, were found both in canyons and on the slope. There appeared to be two distinct distributional patterns for the gorgonians and true soft corals (Watling and Auster 2005). Most were deep-water species that occurred at depths > 500 m (gorgonians in the genera *Acanthogorgia*, *Acanella*, *Anthothela*, *Lepidisis*, *Radicipes*, *Swiftia*; the alcyonacean soft coral *Anthomastus*, and the stoloniferan *Clavularia*). Other species appeared to occur throughout shelf waters to the upper continental slope (gorgonians *Paragorgia arborea*, *Primnoa resedaeformis*, *Paramuricea* spp.) (Watling and Auster 2005). The larger northern canyons such as Lydonia and Oceanographer have hard substrates along most of their axes and walls that support many deep-sea corals and sponges. The slope south of Georges Bank

appeared to be mostly soft substrate, supporting mainly solitary stony (cup) corals on the upper slope (e.g. *Flabellum* sp., *Dasmosmilia lymani*) and sea pens deeper than about 1500 m, with some exceptions (NEFMC 2011). Some harder substrate was found at depths greater than 1400 m depth on the Mid-Atlantic slope off New Jersey. Sparse coral populations were found at these deeper depths; sea pens and stony corals appeared to be sparse or common on the upper slope; sea pens and *A. arbuscula* were found on the lower slope. The larger, southern canyons like Baltimore and Norfolk canyons appeared to have less hard substrate than the northern canyons (NEFMC 2011), although some hard substrate that supports coral and sponges was found in shallower depths (300-550 m). There were also sea pens at upper slope depths and sea pens and *A. arbuscula* at lower slope depths.

Recent towed camera and ROV surveys (most without associated specimen collections) were conducted in almost all of the major canyons in the Mid-Atlantic and New England regions (Fig. 3). Several minor canyons and slope areas were also surveyed. The surveys revealed significant inter-canyon variability, even between neighboring canyons. Canyon morphology, habitat heterogeneity, the amount and type of substrate, depth, environmental conditions, and currents appear to play a role in the biodiversity of corals, sponges, and fishes observed in each canyon. Corals were observed in every canyon, however, abundance and diversity of corals varied dramatically. For example, only a few colonies of widely dispersed corals were observed in Washington



Canyon (off Virginia) whereas a “coral forest” of the bubblegum coral (*Paragorgia arborea*) was observed in Heezen Canyon (near Hague Line). The surveys also revealed unique areas; e.g., discovery of coral biodiversity hotspots in relatively shallow (300-500 m) depths at the head of Wilmington Canyon, as well as Baltimore and Norfolk canyons (Brooke et al. 2017), and observations of corals in minor canyons.

Colonial stony corals, the solitary stony cup coral *Desmophyllum dianthus*, black corals, most alcyonaceans, and the majority of sponges observed were on hard substrates, whereas other solitary stony corals (e.g., *Flabellum* sp.), sea pens, and the bamboo coral *Acanella* sp. were common on soft sediments (Fig. 5). Throughout the Mid-Atlantic and New England canyons, gorgonians were the dominant structure-forming corals. The large gorgonians, *Paragorgia arborea*, *Paramuricea* spp. (including *P. placomus*), *Primnoa resedaeformis*, and *Acanthogorgia* spp. were generally most abundant in canyons from Virginia to the Hague Line at depths shallower than 1000 m. Gorgonians in the genus *Anthothela* were also abundant. The bubblegum coral (*P. arborea*) reached the largest sizes. As for the true soft corals, *Anthomastus* is probably the numerically dominant species, while *Duva florida* can be extremely locally abundant (hundreds of colonies) but distribution is patchy (Sandra Brooke, Florida State Univ., pers. comm.). The first observations of black corals in a number of the canyons were made during recent surveys. These included species in the genera *Bathypathes*, *Parantipathes*, *Stauropathes*, and the

recently described *Telopathes magna* (Quattrini et al. 2015; Brooke et al. 2017) (Fig. 5).

Stony corals (Order Scleractinia) were not especially abundant or diverse at large spatial scales (although they were patchy and dense within particular areas of canyons). The solitary cup coral, *Desmophyllum dianthus*, was the most often observed stony coral, usually seen on canyon walls and in dense aggregations along ledges or overhangs (Quattrini et al. 2015, Brooke et al. 2017). The branching colonial corals *Lophelia pertusa* and *Solenosmilia variabilis* were also observed in the canyons. Both corals occurred as small, individual colonies, with *L. pertusa* generally observed between 300-1000 m and *S. variabilis* generally deeper than 1000 m. *Lophelia pertusa* is the most important reef-forming deep-sea coral in the Atlantic, and forms large reefs (bioherms) in the southeast U.S. (Ross and Nizinski 2007; Hourigan et al., this volume) and the Northeast Atlantic (Roberts et al. 2009). There was no evidence of large bioherm formation by either species in the Northeast region.

Quattrini et al. (2015) reported at least 58 coral taxa representing 20 families in 11 New England canyons and adjacent slope habitats. Quattrini et al. (2015) found that the type of broad-scale habitat feature and high habitat heterogeneity in this region was an important factor that influenced the diversity of coral assemblages. There were no significant differences between deep-sea coral assemblages occurring in the two different types of canyons (continental shelf-breaching canyons vs. canyons confined to the continental slope).

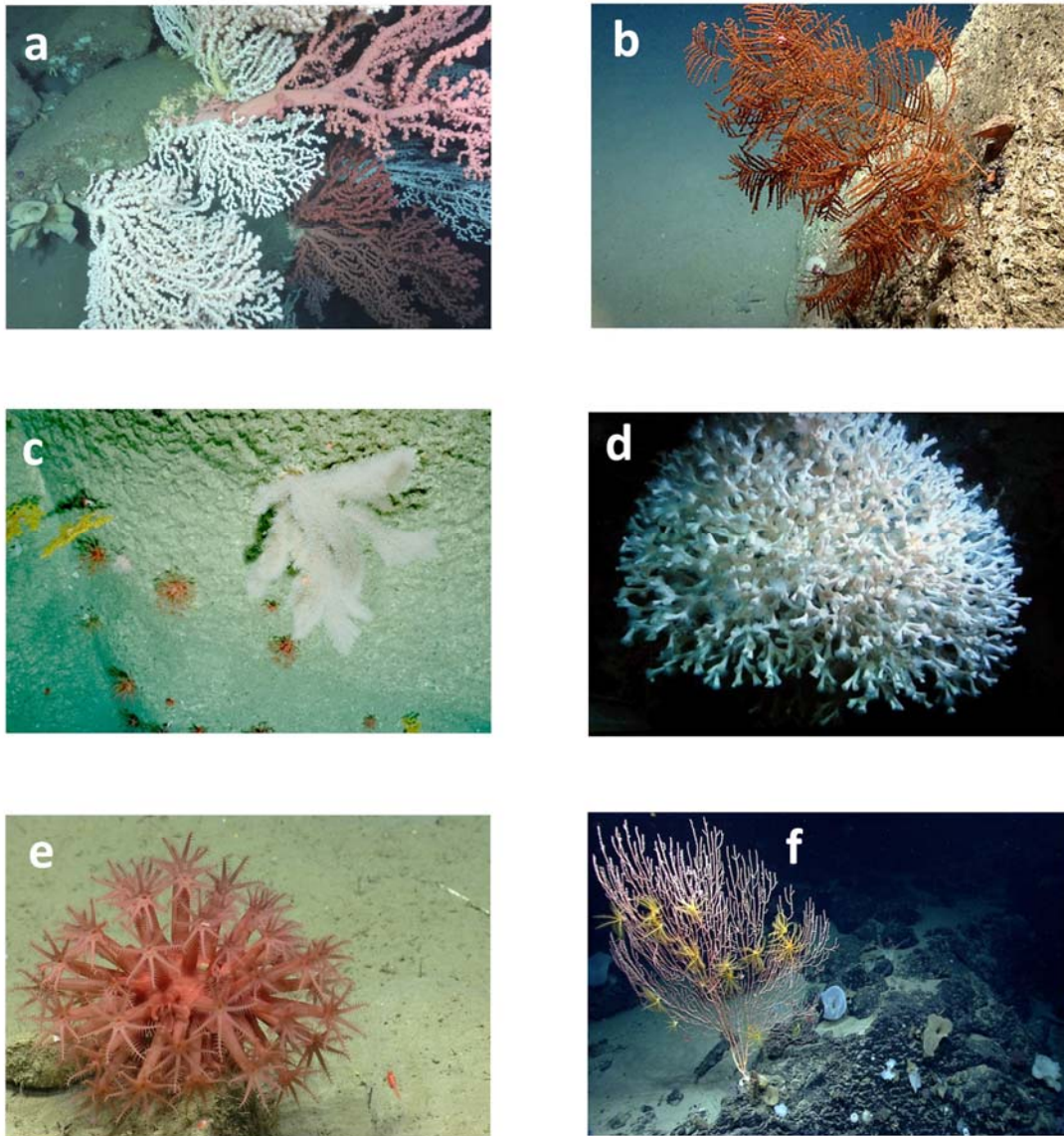


Figure 5. Examples of Northeast deep-sea corals from the submarine canyons and seamounts during the 2012-2015 expeditions. Coral identifications in the images may be tentative. *a*) Various color morphs of gorgonian bubble gum coral (*Paragorgia arborea*), Heezen Canyon (656 m) (ROPOS). *b*) Black coral *Telopathes magna*, Block Canyon (1345 m) (Deep Discoverer). *c*) Gorgonian *Thouarella grasshoffi* (white), soft coral *Anthomastus* (red), gorgonian *Paramuricea* (yellow); Powell Canyon (1300-1770 m) (TowCam). *d*) Scleractinian colonial coral *Lophelia pertusa*, Baltimore Canyon (381 m) (Kraken 2). *e*) Soft coral *Anthomastus*, Oceanographer Canyon (Deep Discoverer). *f*) Gorgonian bamboo coral *Jasonisis*, with numerous crinoid associates, Mytilus Seamount (Deep Discoverer).

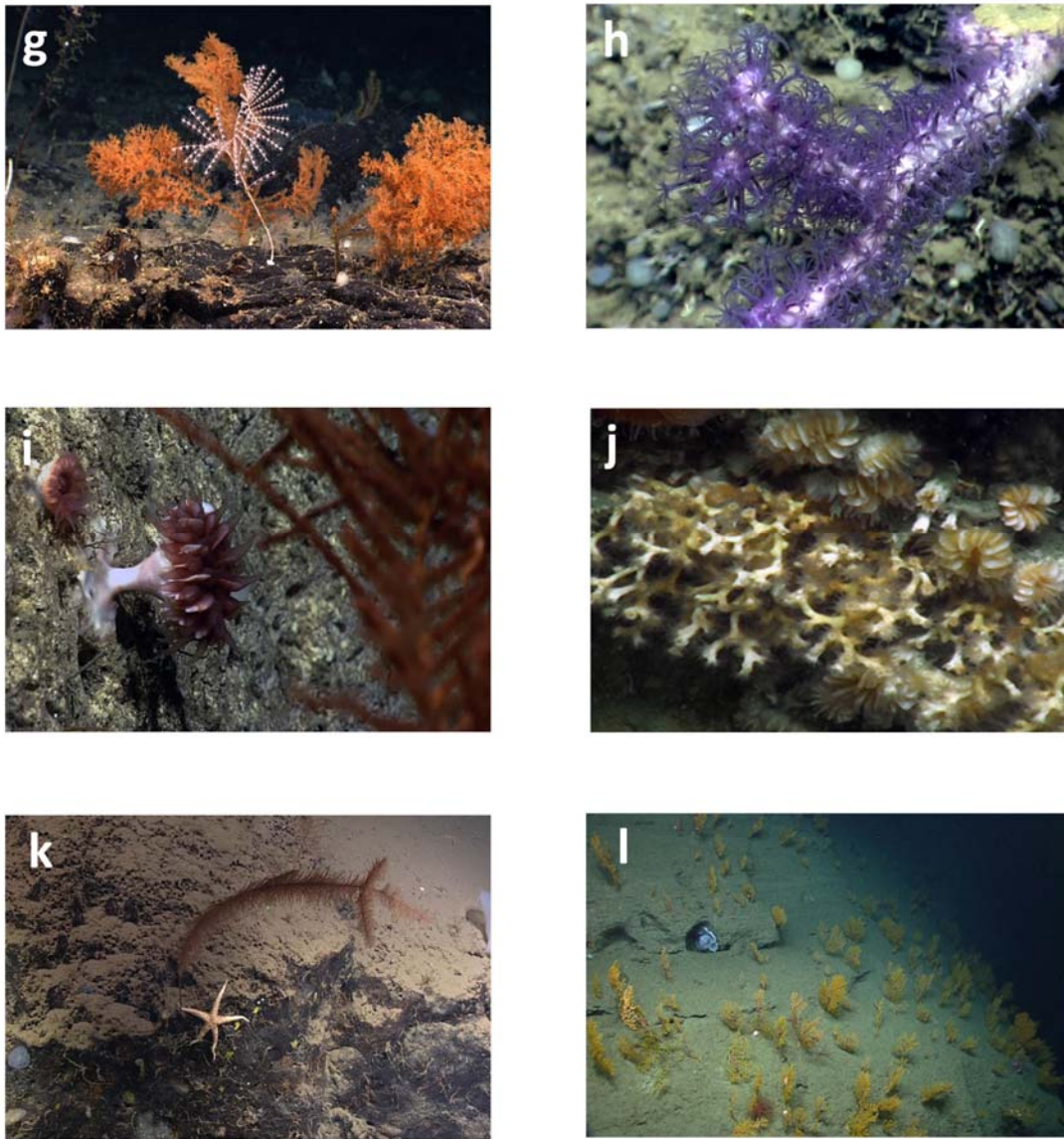


Figure 5 (cont.). Examples of Northeast deep-sea corals from the submarine canyons and seamounts during the 2012-2015 expeditions. Coral identifications in the images may be tentative. (g) Two colonies of black corals and spiraled gorgonian *Iridogorgia* sp., Retriever Seamount (Deep Discoverer). (h) Stoloniferan coral *Clavularia* sp., Nygren Canyon (Deep Discoverer). (i) Scleractinian cup corals and black coral (foreground), wall of unnamed canyon east of Veatch Canyon (1480 m) (Deep Discoverer). (j) Scleractinian colonial coral *Solenosmilia variabilis* and solitary cup coral (above) *Desmophyllum dianthus*, Baltimore or Norfolk Canyon (Brooke et al. 2017). (k) Black coral *Parantipathes* sp., Nygren Canyon (ROPOS). (l). Gorgonian *Paramuricea* sp., Welker Canyon (Deep Discoverer).



However, different, less diverse faunal assemblages were observed at cold seeps (areas on the seafloor where hydrocarbon-rich fluid seeps up from below) and soft bottom open slope sites. The canyons often had large patches of hard bottom deep-sea coral habitat, which also included bivalves, anemones, and sponges. Stony corals (e.g., the solitary cup coral *Desmophyllum dianthus* and the colonial *Solenosmilia variabilis*) and octocorals were often abundant on long stretches of canyon walls and under and around overhangs; the colonial stony coral *Lophelia pertusa* was particularly noted in canyons at depths from 733-1030 m. Coral communities were uncommon on the open slope, except on the channel floor of Veatch Canyon where sea pens and bamboo corals in soft sediments were frequently observed. Corals and sponges were also observed on boulders and outcrops in some open slope and inter-canyon areas. At Veatch seeps and the canyon wall adjacent to the seep community in Nygren Canyon, octocorals and stony cup corals (*D. dianthus*) were found attached to authigenic carbonates (carbonate precipitated in-situ at the sediment–water interface and/or within the sediment).

Quattrini et al. (2015) also found that depth was a significant factor influencing the coral assemblages. Although species richness did not change significantly with depth over the range explored by the surveys (494-3271 m), species composition changed at ~1600-1700 m. Species composition in the canyons and other areas with hard substrates were significantly dissimilar across this depth boundary. Stony corals and the gorgonians *Anthothela* spp.,

Keratoisis sp. 1, and *Paragorgia arborea*, occurred at depths < 1700 m, whereas gorgonians from the family Chrysogorgiidae (chrysogorgiids) and sea pens were more common at depths > 1700 m. Overall, depth, habitat, salinity and dissolved oxygen explained 71% of the total variation observed in coral assemblage structure (Quattrini et al. 2015).

The surveys of both Baltimore and Norfolk canyons discovered that deep-sea corals were patchily distributed and locally abundant and large gorgonians were the dominant structure-forming species on exposed hard substrates (Brooke et al. 2017). Several species of stony corals were also present, including new records of *Solenosmilia variabilis* on deep walls (~1400 m) in Norfolk Canyon, and the structure-forming *Lophelia pertusa* on shallower (381-434 m) walls of both Baltimore and Norfolk canyons (Brooke and Ross 2014; Fig. 5d). A new record of the black coral *Telopathes magna* was also reported for Norfolk Canyon. The diversity of structure-forming corals was low, but several areas in both canyons had high coral abundances and diverse coral communities, dominated by large octocoral species (Brooke et al. 2017). Coral distribution varied within and between the two canyons, with greater abundances of the bubblegum coral *Paragorgia arborea* in Baltimore Canyon than in Norfolk Canyon, but higher occurrences of stony corals in Norfolk Canyon than in Baltimore. The gorgonians *P. arborea*, *Primnoa resedaeformis*, and *Anthothela grandiflora* had a wide distribution within these canyons, whereas *Paramuricea placomus* and the branching stony corals *L. pertusa* and *S. variabilis* were limited to certain habitat types and/or depth zones (Brooke et al. 2017).



The Northeast deep-sea coral habitat suitability models generally predict that the canyons are highly suitable habitat for the gorgonian and soft coral groups. Surveys of the canyons allowed independent ground-truthing of the models, which were qualitatively validated: all sites observed to be areas of high coral abundance and diversity were also areas predicted to have a high likelihood of suitable habitat based on the regional model. The habitat suitability models performed well in predicting areas of likely deep-sea coral habitat, as well as predicting areas where corals are unlikely to be found. However, the exact location of areas of high deep-sea coral density and diversity often depends on fine-scale seabed features (e.g., ridges or ledges of exposed hard substrate) that are smoothed over in this regional-scale model. The current resolution of the model is grid cells of approximately 370 m² (although there are plans to improve the model by increasing resolution to 25 m², as well as incorporating more recent multibeam bathymetry and coral observations with higher taxonomic specificity). Habitat suitability maps based on this model should be viewed as representing only the general locations of predicted suitable coral habitat (within a distance of approximately 350-740 m, the dimension of one to two model grid cells). For this reason, the total area of high/very high habitat suitability is an approximation using the best available data. Quantitative ground-truthing of the model includes assessment of the prediction skill of the model and correlation between predicted habitat suitability and coral frequency/abundance observations.

New England Seamounts Exploratory Surveys: Bear Seamount was discussed in Packer et al. (2007).

Physalia Seamount (summit depth ~ 1,880 m) was explored by AUVs in 2012 (Kilgour et al. 2014) and an ROV in 2014 (*Okeanos Explorer* 2014 expedition). The AUV surveys revealed the presence of octocorals, with sea pens generally found in flat, soft sediments, and most other octocorals found at either the transition between soft sediment and hard bottom, or on hard bottom features such as walls, ledges, and gravel/bedrock pavement (Kilgour et al. 2014). The more detailed ROV survey revealed relatively low abundances and low diversity of corals. The gorgonian *Chrysogorgia* sp. and sea pen *Anthoptilum* sp. were seen most commonly. Of particular note, *Anthoptilum* sp. was seen in typical sea pen habitats embedded in soft sediments but also on hard substrates; Williams and Alderslade (2011) described species in this genus from the Pacific with the unusual adaptation of the peduncle that acts as a holdfast for attachment to rocky substrata. Occasionally, the bamboo coral *Lepidisis* sp. was observed. Other corals reported from Physalia Seamount include the black corals *Telopathes* sp. and *Bathypathes* sp., the soft coral *Anthomastus* sp., and stony cup corals.

Mytilus Seamount has the deepest summit (~2,500 m) of all New England seamounts in U.S. waters. The first ROV surveys of Mytilus (Quattrini et al. 2015) revealed a diverse assemblage of taxa, including gorgonians (Fig. 5f) and especially black corals, and numerous



hexactinellid sponges and demosponges. The corals observed (> 2600 m) were significantly different from those observed in Northeast canyon sites at similar depths by Quattrini et al. (2015). Differences in species composition between Mytilus Seamount and other sites were primarily due to the presence/absence of numerous species. For example, *Chrysogorgia* spp., *Convexella? jungerseni*, *Corallium? bathyrubrum*, *Paranarella? watlingi*, and *Paragorgia/Sibogorgia* sp. 1 were observed on Mytilus Seamount, while *Acanthogorgia* spp., *Anthothela* spp., *Clavularia? rudis*, *P. arborea*, and *Paramuricea* spp. were not seen on Mytilus Seamount, but occurred at other sites. No stony corals were observed here. Quattrini et al. (2015) suggest that the deeper depths (2600 to 3200 m) are beyond the bathymetric limits of stony corals.

Retriever Seamount is the farthest-offshore seamount within the U.S. EEZ. It is about 2000 m high, 7 km in diameter, and has three main summits. Thoma et al. (2009) reported the occurrence of gorgonians in the genera *Chrysogorgia*, *Iridogorgia*, *Metallogorgia*, *Acanella*, and *Paramuricea*; as well as black corals in the genera *Bathypathes* and *Parantipathes*. A single ROV dive in 2014 (Fig. 5g) between 2142 to 2003 m depth revealed sandy slopes, boulders and a rock outcrop. Many sea pen colonies, with *?Anthoptilum* sp. more common than *Pennatula* sp., as well as stony cup corals (*Caryophyllia* sp.) were seen in sedimented areas. Colonies of the chrysogorgiid gorgonian, *Metallogorgia melanotrichos* were very abundant on the rock outcrops; several “sub-adult” colonies were observed, suggesting multiple recruitment

events in the area. Other corals observed on the outcrop included the gorgonians *Hemicorallium? bathyrubrum* (= *Corallium? bathyrubrum*) and *H. ?niobe*, *Paramuricea* sp., *Iridogorgia splendens* (at least one with shrimp associate) and *I. magnispiralis*, *Candidella imbricata* and an unidentified primnoid coral, bamboo corals (*Lepidisis* sp. and *Acanella* sp.), and black corals in the genera *Parantipathes* (branched), *Stauropathes*, and, seen further upslope on isolated rocks, *Bathypathes*.

Gulf of Maine Exploratory Surveys: Deep-sea corals in the Gulf of Maine have been reported since the 19th century, both as fisheries bycatch and from naturalist surveys. At one time, deep-sea corals may have been considered common on hard bottoms in the region. However, after a century of intensive fishing pressure using mobile bottom gear such as trawls and dredges as well as fixed gear such as lobster traps, the denser populations of deep-sea corals and coral habitats are now confined to small areas where the bottom topography makes them mostly inaccessible to these fisheries (Auster 2005; Watling and Auster 2005; Cogswell et al. 2009; Auster et al. 2013).

Previous studies, including work on the Canadian side of the Gulf (e.g., Northeast Channel: Buhl and Buhl-Mortensen 2004; Watanabe et al. 2009) do show that deep-sea corals have a patchy distribution that is correlated with environmental factors such as slope, sediment, current, temperature and depth. Nevertheless, the information needed to assess their overall status in the U.S. Gulf of Maine has been lacking. Additionally,



information on deep-sea coral distribution in relation to habitat and landscape features, abundance, natural history, associated species, and human impacts has been inadequate.

Previous deep-sea coral exploratory surveys and seafloor mapping in the region guided the selection of survey sites in 2013. Initial deep-sea coral surveys using ROVs in 2002 and 2003 documented a limited number of locations in Western Jordan Basin and around Mount Desert Rock with dense coral garden communities at around 200 m (Auster 2005; Watling and Auster 2005). Deep-sea corals were found on rocks, boulders, ridges and walls extending above the surrounding fine-grained sediments. During a cruise aboard NOAA Ship *Ronald H. Brown* in 2005, multibeam bottom sonar data collected in Western Jordan Basin revealed that hard bottom in the immediate area around “114 Bump” (one of the sites surveyed for corals in 2002-2003) was more spatially extensive than previously suspected (see Fig. 2 in Auster et al. 2014). Thus, the potential for suitable deep-sea coral habitat in the area was more likely.

Results of the recent Gulf of Maine exploratory surveys (2013-15) revealed extensive coral aggregations at depths around 200-250 m in the five primary survey sites: Western Jordan Basin, Central Jordan Basin, near Mount Desert Rock, on Outer Schoodic Ridge, and on Lindenkohl Knoll in Georges Basin (Fig. 6) (Auster et al. 2013, 2014; Packer et al., unpublished data). Structure-forming corals on hard substrate at all sites were predominantly gorgonians, although a few tiny, stony

scleractinian cup corals were seen on some dives. Coral occurrences were classified as either coral present (sparse to medium density) or coral garden (high density patches).

Coral gardens are defined as areas where non-reef-forming corals are among the dominant fauna and occur at densities higher than surrounding patches (Bullimore et al. 2013). Dense and extensive gorgonian coral gardens were seen in Western Jordan Basin, Outer Schoodic Ridge, and near Mount Desert Rock, especially in areas of high vertical relief. Outer Schoodic Ridge especially was a unique area, with topography reminiscent of narrow slot canyons on land (e.g., western U.S., in southern Utah). Based on preliminary analyses of 2013 images (Auster et al. 2013), these steeper areas had some of the highest densities, with about 16-39 colonies/m², well above the threshold of 0.1 colonies/m² used by ICES (2007) to define coral garden habitat. Central Jordan Basin and Georges Basin also contained coral communities, but these assemblages were more patchy, less dense, and occurred in lower relief environments than the aforementioned areas.

The dense corals on the steep vertical walls and cliffs of Outer Schoodic Ridge and Mount Desert Rock were primarily *Primnoa resedaeformis*, with lower abundances of *Paramuricea placomus* (both in two color morphs of yellow and purple color morphs). On some of the tall, narrow canyon-like walls and cliffs of Outer Schoodic Ridge, *P. resedaeformis* colonies were so densely packed it was impossible to identify and count individual colonies (Fig. 7a,b), some were likely 1 m tall.

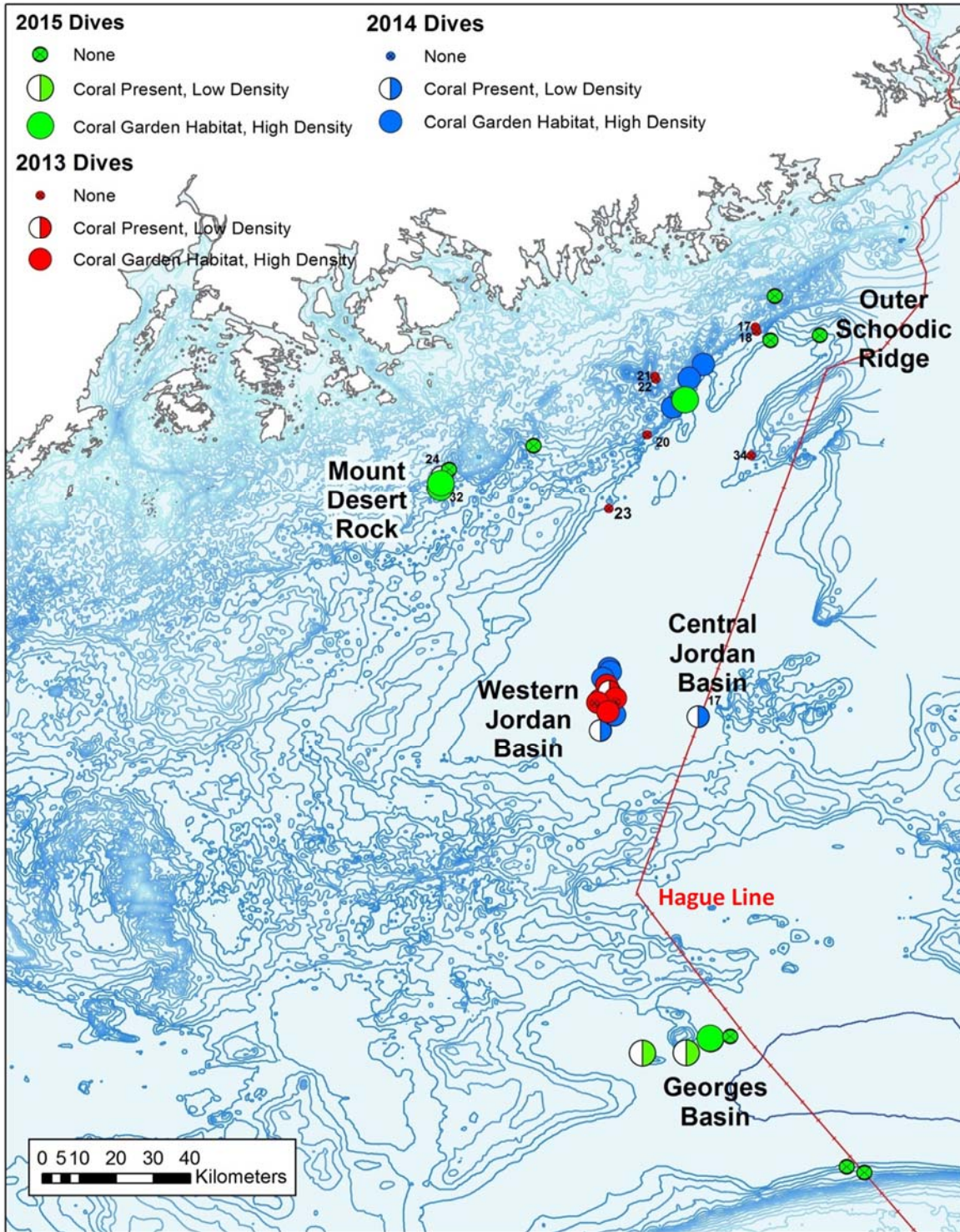


Figure 6. Gulf of Maine deep-sea coral exploratory survey locations and results (2013-2015). Modified from Auster et al. (2014).



Conversely, the major coral species found in Western and Central Jordan Basin and Georges Basin was *P. placomus*, with lower abundances of *P. resedaeformis* and *Acanthogorgia cf. armata* (Fig. 7c-e). *Paramuricea placomus* was found in higher densities on steeper hard-bottom areas. Open areas adjacent to steeper features including muddy areas containing gravel, sand-gravel, and emergent rock outcrop features (with shallow expressions above the fine-grain sediment horizon) supported lower densities of coral, primarily *P. placomus*. This was also true for Outer Schoodic Ridge and Mount Desert Rock. Based on multivariate analyses of eight 2013 transects in Jordan Basin with coral garden habitat (Martin 2015), temperature and depth were primary environmental factors and sediment type, rock outcrop, and topographic rise were primary sedimentary factors that correlated with coral distributions.

Of note were the first observations of *Anthothela (grandiflora?)* in the relatively shallow waters of the Gulf of Maine (Auster et al. 2014). A couple of colonies were seen at Outer Schoodic Ridge (Fig. 7f) around 200 m. This species is most common at 400-1600 m depth in Northeast canyons (Hecker et al. 1983; Quattrini 2016; Brooke et al. 2017) and off the Northeast Channel along the continental margin (Cogswell et al. 2009). *Paragorgia arborea*, both pink and white forms, which was noted at 114 Bump in Western Jordan Basin during the 2003 survey, was not seen in the more recent exploratory dives.

The most common and ubiquitous sea pen species found in the Gulf of Maine, *Pennatula*

aculeata was also found in dense patches in mud and gravel/mud habitats adjacent to hard-bottom habitats (Fig. 8e,f). Highest densities were observed in the Mount Desert Rock region (Packer et al., unpublished data). *Pennatula aculeata* became a focus of the surveys because Baillon et al. (2012) found convincing evidence that several species of sea pens were directly utilized as shelter by fish larvae, particularly by those of redfish (*Sebastes* spp.; see below, and Dean et al. 2016).

The results from these Gulf of Maine exploratory surveys have provided the NEFMC with improved information to inform conservation and management decisions for these unique deep-sea coral and sponge habitats. Currently the Council is using these data to revise and develop new deep-sea coral management zone alternatives for the northern Gulf of Maine region. The large-sized, structure-forming gorgonians *P. resedaeformis* and *P. placomus*, occurring in such high densities in the relatively shallow waters of the Gulf of Maine, as compared to the submarine canyons and seamounts, is unique in the Northeast. The proximity of these habitats to shore and their association with commercially important fish and shellfish increases the potential role of these habitats as EFH (e.g., Auster 2005, 2007). Finding these unique deep-sea coral habitats, especially the spectacular walls of corals at some sites, for the first time after 40-plus years of previous underwater surveys, illustrates how much remains to be discovered about the Gulf of Maine ecosystem in order to better conserve and protect its living marine resources.

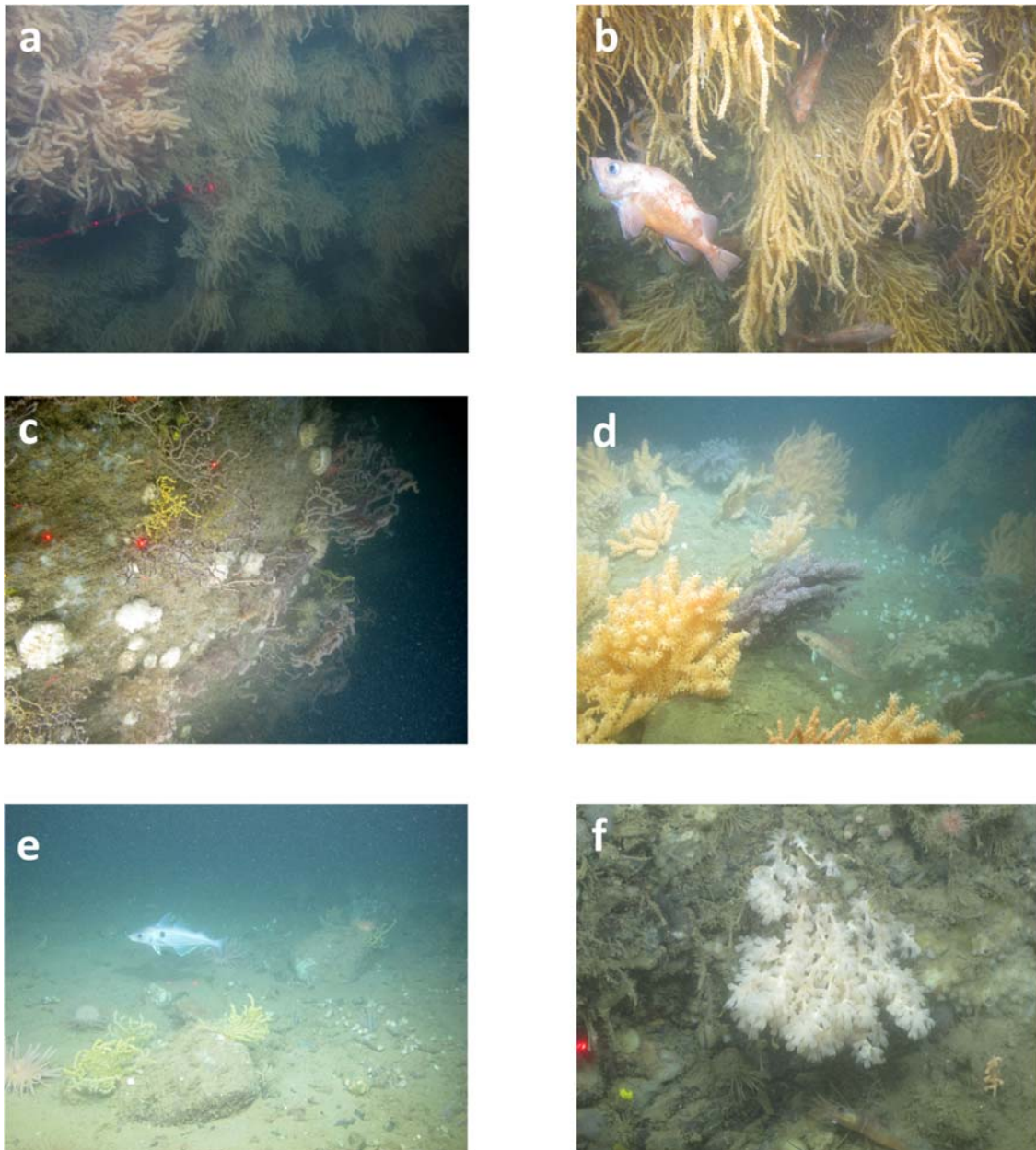


Figure 7. Examples of Gulf of Maine deep-sea coral habitat seen during 2013-14 exploratory surveys (Auster et al. 2014 and unpublished images). (a) Dense colonies of *Primnoa resedaeformis* on a near vertical rock wall along Outer Schoodic Ridge. (b) Acadian redfish and *P. resedaeformis* on a near vertical rock wall along Outer Schoodic Ridge. (c) Purple and yellow forms of *Paramuricea placomus* and *Polymastia* sponge along a steep escarpment in Western Jordan Basin. (d) *P. placomus*, *P. resedaeformis*, and juvenile cod in Western Jordan Basin. (e) *P. placomus* and haddock, Central Jordan Basin. (f) *Anthothela* sp. at around 200 m on a near vertical rock wall along Outer Schoodic Ridge.

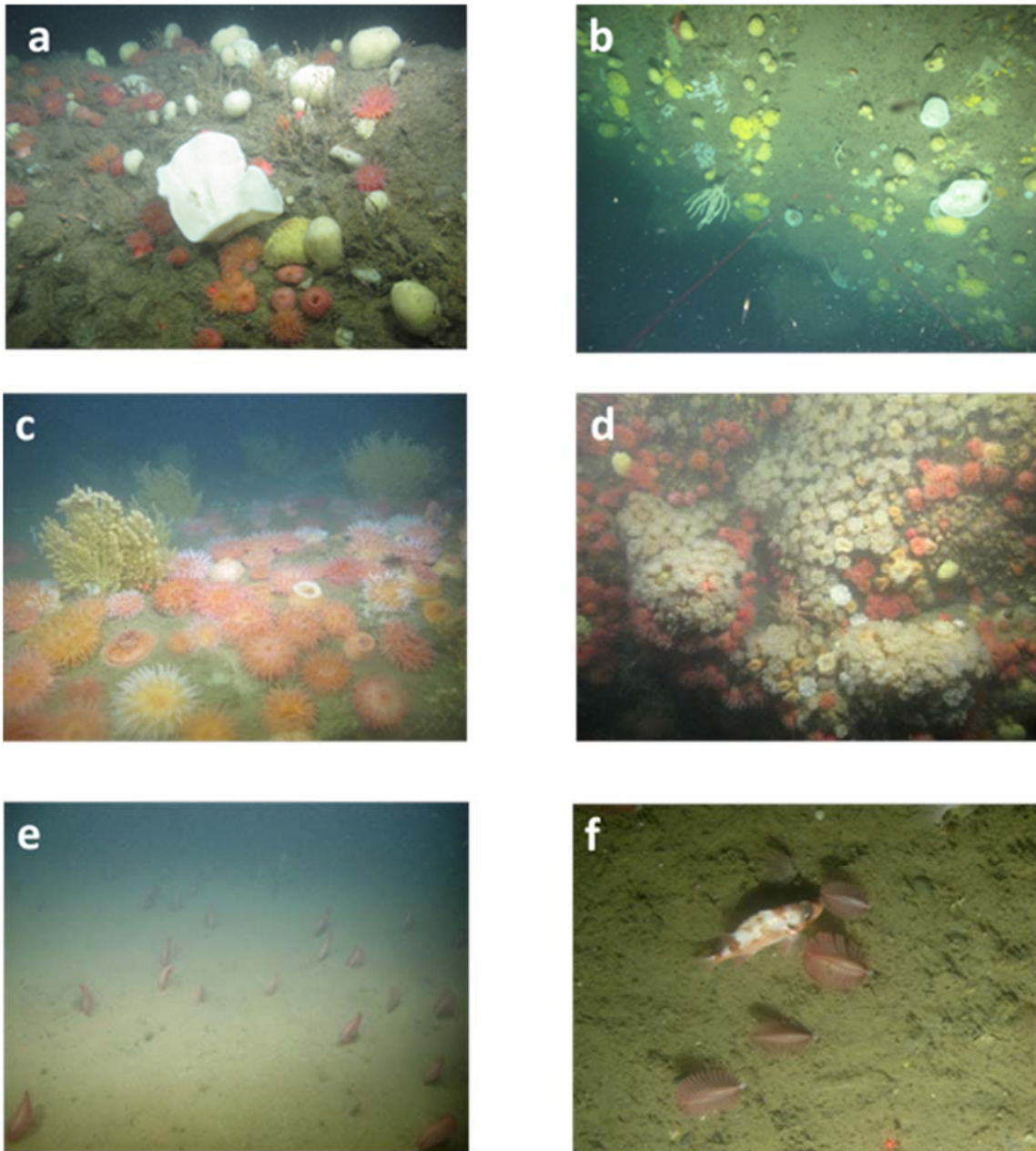


Figure 8. Examples of dense sponge, anemone, and sea pen habitats in the Gulf of Maine (Auster et al. 2014 and unpublished images). (a) Sponge (including vase sponge *Phakellia?* sp. and *Polymastia* sponge sp.) and anemone habitat along Outer Schoodic Ridge. (b) Sponge (including vase sponge *Phakellia?*, *Polymastia* sponges, and finger sponges) habitat along Outer Schoodic Ridge. (c) Anemone and coral habitat in Western Jordan Basin. (d) Anemone habitat (with king crab, *Lithodes maja*) on near vertical rock walls along Outer Schoodic Ridge. (e) Sea pens, *Pennatula aculeata*, in soft substrate in Western Jordan Basin. (f) *P. aculeata* and Acadian redfish in an area of Jordan Basin known as 91 Bump.



11.2.ii – Sponges

Information on the regional sponges and their habitats is severely lacking. Deep-sea sponges in the Northwest Atlantic in general have been the subject of relatively few studies or surveys. However, most of these studies, both historically (e.g., Lambe 1896, 1900) and more recently (e.g., Fuller 2011; Beazley et al. 2013, 2015, 2016), have been conducted in Canada. In the Northeast U.S., Theroux and Wigley (1998) reported on extensive surveys of invertebrates collected by grab samplers. They reported that sponges constituted a small proportion of the observed fauna, and were “generally uncommon on the continental shelf and uncommon to rare on the continental slope and rise.” Larger specimens included *Polymastia* sp. and *Myxilla* sp. usually found on cobbles and boulders. Sponges were more abundant off Nova Scotia and in the Gulf of Maine than elsewhere in the region. However, it is likely that sponges were underrepresented in their samples, as benthic grabs cannot adequately sample hard substrates where most sponges occur, especially if they are mostly found on vertical surfaces (e.g., Miller and Etter 2011). Documenting the diversity and distributions of sponges in this region is still in the preliminary stages. Difficulties with taxonomy and identifications (especially via photographs or video alone) and lack of expertise hamper these efforts. Thus far, presence records from the Smithsonian Institution’s database and other limited data have been used to create an initial species list. Most geo-referenced records that have been entered in the National Deep-Sea Coral and Sponge Database are listed simply as

“Porifera.” New geo-referenced records of sponges from the photographic images obtained from recent 2012-2015 surveys will be added to the database after processing.

Sponges that are of conservation interest are the large, structure-forming sponges that, like deep-sea corals, provide habitat for managed species of fish (especially juveniles that seek refuge from predators), increase biodiversity of local fauna, or are susceptible to fishing gear impacts (e.g., Auster and Langton 1999; Fuller 2011; Beazley et al. 2013; Maldonado et al. 2016). Preliminary, historical information on the geographic range (or locations where present), size, morphological form, and habitats (depth and substrates) was compiled for 12 structure-forming species that are found on the continental shelf in the region (Table 2). Encrusting species or species that would not be considered structure-forming are not included. Information sources for Table 2 include the Marine Life Information Network, the Stellwagen Bank National Marine Sanctuary (Gulf of Maine) (on-line), the European Marine Life Network, the Marine Life Encyclopedia website, Georgia Southern University (on-line), the Chesapeake Bay Program website, Hartman (1958), Gosner (1978), Witman and Sebens (1988), Fuller et al. (1998), Steimle and Zetlin (2000), and Stokesbury and Harris (2006).

On Georges Bank, species of interest include *Suberites ficus*, *Haliclona oculata*, *Halichondria panicea*, *Isodictya palmata*, *Clathria prolifera* (= *Microciona prolifera*), and *Polymastia robusta* (Almeida et al. 2000; Stokesbury and Harris 2006). The larger species are probably the most



susceptible to the adverse effects of fishing. These would include *S. ficus*, *H. oculata*, *H. panicea*, and *I. palmata* as well as *Mycale lingua* and the large form of *Cliona celata*. All of these species attach to some form of hard substrate including shells. *Suberites ficus* attaches to small shell fragments on sandy bottom habitats on Georges Bank. These relatively rare microhabitats provide cover for fishes and crustaceans (Lindholm et al. 2004). As this sponge grows, the substrate on which it originally attached is covered over and the sponge often is rolled along the bottom by currents and wave action. The other species of structure-forming sponges are more common on hard bottom habitats. Based on the available information, only two of the species listed in Table 2, *C. celata* and *H. oculata*, are known to occur south of southern New England (see also Van Dolah et al. 1987). This may reflect the fact that natural rocky bottom habitats on the shelf are rare south of New York Harbor (Steimle and Zetlin 2000). Other structure-forming species of sponge are undoubtedly present in the Mid-Atlantic region, but are either found on hard substrates on the continental slope and in the canyons or on the shelf attached to gravel, scallop shells, and shell fragments in predominantly sandy habitats.

Fuller (2011) also created a species list of sponges, as documented in published reports, for the entire Gulf of Maine, including the Bay of Fundy (Fuller 2011 Appendix III). Sixty-seven species were recorded; the Gulf of Maine Census of Marine Life listing 32 in the Gulf of Maine. The North Atlantic Fisheries Organization (NAFO) also published a sponge

identification guide for eastern Canada, with some overlap into the U.S. Gulf of Maine (Best et al. 2010).

The species list presented here focuses mostly on the shallower species. Thus, the list is preliminary and incomplete. Analysis of recent deep-sea surveys will add many additional species including some new to science. For example, not listed here are the vase/basket demosponges (*Phakellia/Axinella* spp.). *Phakellia ventilabrum* has been found in Stellwagen Bank National Marine Sanctuary in the Gulf of Maine (< 100 m; Tamsett et al. 2010), and several large vase/basket demosponges have been recently seen in the Gulf of Maine surveys at around 200 m (Packer et al. unpublished). However, Fuller (2011) does not list *Phakellia/Axinella* as even occurring in the Gulf of Maine. This type of conflicting information highlights just how little is truly known about the deep-sea sponges in this region.

Hecker et al. (1980, 1983) indicated that sponges, along with corals, were frequently the dominant epifaunal organisms observed during submersible surveys on exposed hard substrate in Northeast submarine canyons. Both sponges and corals were consistently more abundant in the canyons compared to adjacent slope areas. The demosponge, *Asbestopluma* sp. occurred on walls of consolidated clay in Lydonia Canyon and accounted for more than half the invertebrates observed between 800-950 m



Table 2. Preliminary list of structure-forming sponges of the U.S. Northeast continental shelf.

Species	Range	Height	Form	Habitats
<i>Cliona celata</i> Grant, 1826	Gulf of Mexico to Long Island Sound, locally to Gulf of St. Lawrence	Up to 1 m, 60 cm diameter	Two growth forms, boring into shells and large "barrel" shape, firm with tough outer layer, embeds rocks and sediments into tissue	On rock to 200 m; begins life by boring into limestone, shells, or calcareous red algae
<i>Halichondria (Halichondria) panicea</i> (Pallas, 1766)	Arctic south to Cape Cod, rarely beyond	Up to 30 cm	Encrusting, globular, or branched	Cobbles, boulders, bedrock, shells, algae down to 80 m (570 m in Europe), esp. abundant in strong tidal flows
<i>Haliclona (Haliclona) oculata</i> (Linnaeus, 1759)	Labrador to Long Island, rarely to North Carolina, but present in Georgia	Up to 45 cm	Short stalk with flat to rounded finger-like branches, very flexible, not fragile	Sandy, rocky substrates, often attached to stones, to 150 m
<i>Haliclona (Haliclona) urceolus</i> (Rathke and Vahl, 1806)	Range unknown, found in Bay of Fundy	To 15 cm, stalk typically < half body length	Tubular, even bell shaped, with thin, hard, flexible stalk	On rock, shell fragments, etc.
<i>Isodictya deichmannae</i> (de Laubenfels, 1949)	Newfoundland to Rhode Island	Often confused with <i>I. palmata</i>		To 110 m
<i>Isodictya palmata</i> (Ellis and Solander, 1786)	Nova Scotia to Gulf of Maine, Georges Bank	Up to 35 cm	Large, palmate with finger-like branches	Deep water on rocks, 52-70 m in sand and gravel on Georges Bank
<i>Clathria (Clathria) prolifera</i> (Ellis and Solander, 1786) (= <i>Microciona prolifera</i>)	Nova Scotia to Florida and Texas	Up to 20 cm	At first encrusting, then forms small clumps with fingerlike branches	Shells, pilings, hard surfaces, in shallow to moderate depths (52-70 m on Georges Bank)
<i>Mycale (Mycale) lingua</i> (Bowerbank, 1866)	Range unknown, found in the Gulf of Maine	Up to 30 cm high with variable width and depth	In mounds, sometimes in erect, flattened form with base narrower than apex	Between 30-2460 m on rocky bottom
<i>Myxilla (Myxilla) fimbriata</i> (Bowerbank, 1866)	Range unknown, found in GOM		Mounds	To 78 m
<i>Polymastia boletiformis</i> (Lamarck, 1815) (= <i>Polymastia robusta</i>)	Range unknown, found on Georges Bank, in the Gulf of Maine and southern New England	Volume of 40 cm ³	Globular with thick base, body is soft	Most common on upward facing rock or boulder tops, as deep as 2300 m (in Europe)
<i>Suberites ficus</i> (Johnston, 1842)	Arctic south to Rhode Island, possibly to Virginia	10-40 cm diameter	Variable, lobed or globular cushion, rolls over bottom if it outgrows its substrate	Attaches to rocks and to small stones, empty shells, in sandy or muddy bottom, from 15 to 200 m

(Hecker et al. 1983). This species was also common in Baltimore Canyon. Brooke et al. (2017) reported that sponges were commonly observed on hard substrata in Norfolk and

Baltimore canyons, and that their species richness exceeded that of corals, with more than 30 different morphotypes of hexactinellid and demosponges.



Sponges are often a major component of the epibenthic organisms found on the hard substrates that dominate seamounts (Samadi et al. 2007). Cho (2008) reported that the phylum Porifera represented the most abundant megabenthic fauna in the New England Seamount chain (surveys did not include the four seamounts in U.S. waters). As noted previously, (Quattrini et al. 2015) observed numerous and diverse hexactinellid sponges and demosponges on Mytilus Seamount. Moore et al. (2003) reported six taxa of sponges on Bear Seamount, including glass sponges and the demosponge *Geodia* sp. The latter forms major sponge grounds elsewhere in the North Atlantic, including along the continental slopes of the Grand Bank and Flemish Cap and northward along the Labrador Slope to the southern Davis Strait off Canada (Murillo et al. 2012; Knudby et al. 2013; Kenchington et al. 2014), but high density aggregations have not been reported in the U.S. Northeast.

II.3. Species Associations with Deep-Sea Corals and Sponges

Packer et al. (2007) summarized information on species associations with deep-sea coral habitats off the Northeast U.S. While there were numerous examples of invertebrate associations with deep-sea corals in the region, the role of deep-sea corals as habitat for commercially important fish species was unclear.

Recent studies in this region highlight relationships of invertebrate symbionts and their octocoral hosts at deep-sea coral habitats on the seamounts (Watling et al. 2011). In an

extreme case of host fidelity, Mosher and Watling (2009) showed that the ophiuroid *Ophiocreas oedipus* was found only on the chrysogorgiid *Metallogorgia melanotrichos*. The young brittle stars settle on young corals and the two species then remain together. The brittle star may receive some refuge and feeding benefits from the coral, but the coral's relationship to the brittle star appears to be neutral (Mosher and Watling 2009). Within the EEZ, these two species were collected from Bear Seamount at 1491 and 1559 m. Another ophiuroid, *Asteroschema clavigerum*, has a close relationship with *Paramuricea* sp. and *Paragorgia* sp. on both the seamounts and the continental slope (Cho and Shank 2010). The shrimp *Bathypalaemonella serratipalma* as well as the egg cases of an unknown octopus were found on *Chrysogorgia tricaulis* on the seamounts (Pante and Watling 2011). Additionally, older colonies of *Acanella arbuscula* collected from the seamounts were host to a scale worm (Watling et al. 2011). De Clippele et al. (2015) reported on associations of invertebrate fauna with three gorgonian species (*Paragorgia arborea*, *Primnoa resedaeformis*, and *Paramuricea placomus*) in Norway, which are also dominant coral species in the U.S. Northeast. All hosted numerous associates, with *P. arborea* colonies having the most associated taxa and numbers of individuals. Cho (2008) found that corals were the dominant living substrate for other macroinvertebrates on the New England Seamount chain; sponges were the second most important host. See Watling et al. (2011) for reviews and lists of known invertebrate symbionts and their octocoral hosts worldwide.



Quattrini et al. (2015) noted that the presence of certain deep-sea coral species may influence crustacean assemblage patterns. For example, the squat lobster *Uroptychus* sp. was only observed on the black coral *Parantipathes* sp. In contrast, *Munidopsis* spp. (squat lobsters in a different superfamily) utilized a variety of different coral species as habitat, particularly those with structurally complex morphologies. Many other observations suggesting possible species associations between deep-sea corals and other invertebrates are recorded in the various dive logs and summaries from the recent *Okeanos Explorer* surveys.

In all areas explored in the Gulf of Maine, sponges (e.g., in the genera *Polymastia*, *Iophon*, *Phakellia*/*Axinella*) and anemones (e.g.; *Metridium*, *Urticina*) often occurred in high-density patches amongst the more extensive corals on walls and on steep features without corals (Fig. 8a-d) (Auster et al. 2014). Crustaceans such as shrimp, amphipods, aggregations of krill (*Meganyctiphanes norvegica*), and the king crab (*Lithodes maja*; Fig. 8d) were commonly associated with coral communities along steep walls and were seen foraging amongst structure-forming organisms, including corals, on the seafloor.

A number of commercially important fish and shellfish species were observed at the Gulf of Maine coral sites, including Acadian redfish (*Sebastes fasciatus*; juveniles, adults, and pregnant females; Fig. 7b), haddock (*Melanogrammus aeglefinus*; Fig. 7e), pollock (*Pollachius virens*), cusk (*Brosme brosme*), monkfish (*Lophius americanus*), Atlantic cod

(*Gadus morhua*; juveniles, adults; Fig. 7d), silver hake (*Merluccius bilinearis*), Atlantic herring (*Clupea harengus*), spiny dogfish (*Squalus acanthias*), squid (*Illex illecebrosus*), and lobster (*Homarus americanus*). The fish were observed searching for and catching prey that were also found among the coral, including shrimp, amphipods, krill, and other small fish (Auster et al. 2014). The corals also appeared to provide refuge from the strong, tidally-generated bottom currents.

A cause and effect relationship between coral/sponge presence and fish populations is difficult to determine. Our understanding of relationships between deep-sea corals and fishes is both situational and inferential (e.g., Baker et al. 2012). This may be particularly true with regard to the seamount habitats (Auster 2007), although it has been shown, for example, that false boarfish, *Neocyttus helgae*, were associated with basalt habitats colonized by gorgonian corals and sponges (on both nearly horizontal basalt sheets and steep cliffs) on Bear and other seamounts (Moore et al. 2008). Aggregates of dead coral debris on seamounts also served as habitat for juveniles of deep-sea fish, but observations have been limited (Moore and Auster 2009). In Norway, Foley et al. (2010) applied the production-function approach to estimate the link between *Lophelia pertusa* deep-sea coral reef habitat and redfish (*Sebastes* spp.). Both the carrying capacity and growth rate of the redfish were found to be functions of deep-sea coral habitat. Thus, the authors concluded that deep-sea coral reef habitat can be considered as essential fish habitat. They also estimated a facultative relationship between



deep-sea coral and *Sebastes* spp. stocks. Deep-sea coral reef (bioherm) habitats do not occur in the U.S. Northeast, and comparable quantitative studies on gorgonian-dominated habitats have not been carried out.

Recent surveys in the region addressed the functional role deep-sea corals play in fish life history and ecology. Demersal fish distributions and habitat associations, including the influence of deep-sea corals and sponges, were assessed for Baltimore and Norfolk canyons (Ross et al. 2015). Although deep-sea coral and sponge presence did not significantly influence fish assemblages in the two canyons, deep-sea coral and sponges did increase habitat complexity, which is an important factor in determining habitat use for deep-sea fishes (Ross et al. 2015). Some of the fishes were closely associated with the corals, including *Dysommima rugosa* (cutthroat eel), *Benthocometes robustus* (robust cusk-eel), and *Brosme brosme* (cusk) (Ross et al. 2015). Ross et al. (2015) also noted unidentified shark egg cases were frequently entangled in octocorals, especially the bubblegum coral *Paragorgia arborea*, while eggs of snailfish (Liparidae) were also found in *Anthothela* sp. and *Acanthogorgia* sp. Quattrini et al. (2015) did find that deep-sea coral species richness was an important variable in explaining demersal fish assemblage structure. These authors hypothesized that corals may increase fish diversity because the fish use the corals as habitat, or corals may increase food resources for fishes. However, Auster (2005, 2007 and references therein) also hypothesizes that some fish co-occur with deep-sea corals because both taxa do better in areas of

enhanced flows that advect food, and not because the fish need the corals per se.

Baillon et al. (2012) reported that several species of sea pens, including *Anthoptilum grandiflorum*, *Pennatula aculeata*, *P. grandis*, and *Halipterus finmarchica* from the Laurentian Channel and southern Grand Banks in Canada were utilized as shelter by fish larvae, mainly by those of redfish (*Sebastes* spp.). *Anthoptilum grandiflorum* may have been of particular importance to redfish larvae in that study. Both redfish and these species of sea pens also co-occur in the U.S. Northeast region (e.g., Fig. 8f). These discoveries could have significant research and management implications for sea pens and redfish in the Northeast.

The Baillon et al. (2012) study collected sea pens as trawl bycatch during their routine multispecies research surveys. A relatively small number of *P. aculeata* collected via ROV from different sites in the U.S. Gulf of Maine in July/August 2014 yielded no fish larvae. In 2015, 186 individual *P. aculeata* were collected as bycatch from the 2015 NMFS Gulf of Maine northern shrimp survey and subsequently examined in the laboratory. Redfish larvae were found on *P. aculeata* at four stations, either adhering to the exterior of the colony, or entrapped within the arms or polyps (Dean et al. 2016). However, the source of the sea pen samples for both the Baillon et al. (2012) and this study was from trawl survey bycatch. Thus, the possibility that fish larvae were actually extruded in the net by viviparous ripe and running redfish, or when the catch was emptied on the deck, and the larvae then



subsequently adhered to the sea pens must be explored. In June 2016, some stations in the Gulf of Maine where a positive association had been found between redfish larvae and *P. aculeata* were resampled. This time a small beam trawl was used as the sampling gear, increasing the probability that only sea pens, and not adult redfish, would be captured, thus eliminating the potential cross contamination described above. Over 1400 sea pens were collected over two days of beam trawling over soft bottoms at 150-180 m depth. No larval redfish were found associated with the sea pens. However, ~80 to 85% of the sea pens collected were quite small, < 25-50 mm total length (adults are upwards of 200-250 mm). This suggests a recent recruitment event occurred, and therefore colonies collected were probably too small to serve as possible nursery habitat for larval redfish. Very few larger sea pens were captured, and those that were caught were generally tangled in the chain rather than caught in the net. The beam trawl likely did not dig deep enough into the sediment to dislodge these larger animals. Thus, the role of *P. aculeata* as possible nursery habitat for larval redfish in the Gulf of Maine remains uncertain.

II.4. Other new information from published studies since 2007

Other new findings from the region include information on coral growth and life history. For example, *Metallogorgia melanotrichos* colonies change form as they grow (Mosher and Watling 2009). Young colonies have lateral

branches coming off the central axis, while older colonies lose these branches as the colony senesces, leaving only a dense crown of branches.

Life history studies (e.g., reproductive strategies) on several species of corals found on both the eastern Canadian shelf and slope (Newfoundland, Labrador) and off the Northeastern U.S. (e.g., *Acanella*, *Anthomastus*; see Watling et al. 2011 for review) were also conducted. The bamboo coral, *Acanella arbuscula*, which is abundant in canyons and slope areas of the Northeast U.S., has separate sexes (gonochoric) and is likely a broadcast spawner (Beazley and Kenchington 2012). Colonies reached sexual maturity at a small size (~3 cm, corresponding to an age of 3 years) and larger colonies appeared to be relatively fecund compared to other gorgonians (Beazley and Kenchington 2012). The authors nevertheless concluded that its longevity and the uncertainty surrounding its dispersal and recruitment, combined with its vulnerability to bottom-contact fishing gear, warranted considering *A. arbuscula* as an indicator species or vulnerable marine ecosystems.

Lawler et al. (2016) reported on the microbial assemblages of two species of the octocoral *Anthothela* from Norfolk and Baltimore canyons, and Kellogg et al. (2016) examined *Paramuricea placomus* bacterial community diversity in Baltimore Canyon, providing insights into the functional roles that these bacteria may play in corals.



II.5. Research Priorities

Packer et al. (2007) identified a number of deep-sea coral research priorities for the region. In 2011, NOAA convened a group of federal, state, academic, and non-governmental organization scientists to identify exploration and research priorities for deep-sea coral and sponge ecosystems in the Northeast region (NOAA 2012b). Key priorities identified, which continue to be our major priorities going forward, included the following:

- Locate and characterize deep-sea coral and sponge communities:
 - Collect and analyze existing data, and evaluate data gaps
 - Develop and refine predictive models for coral and sponge distribution
 - Conduct multibeam sonar surveys to improve bathymetry data to guide field research and for use in spatially-explicit models (canyons and deepwater areas of the Gulf of Maine)
 - Conduct site-specific research designed to locate and characterize deep-sea coral and sponge habitats
- Understand the biology, biodiversity and ecology of deep-sea corals and sponges, including:
 - Species identification
 - Population connectivity
 - Age and growth rates
 - Functional role
- Understand natural and human impacts on deep-sea coral and sponge ecosystems:
 - Disturbance effects and recovery

- Economic and social values associated with these coral and sponge communities

New research conducted since 2011 has addressed a number of these priorities for deep-sea corals, resulting in extensive multibeam mapping of the shelf-edge and slope, the first comprehensive predictive habitat models for deep-sea corals, extensive new exploratory surveys, and studies of community ecology (trophic and population structure) and coral biology (age, growth, life histories). Studies of various aspects of the biology and ecology of key species (e.g., *Primnoa resedaeformis*) are underway. However, much additional work remains to be done. Studies on deep-sea sponges, including taxonomy, distribution, life history, and habitat functions, are almost totally lacking.

III. Update on Management of Deep-Sea Corals and Sponges

III.1. New Information on Impacts and Stressors

III.1.i – Fishing

Fishing impacts to deep-sea corals in the Northeast region were discussed previously (Packer et al. 2007), but this is an active field of research, and new field and modeling studies have been published since 2007. Much of this work is applicable to the Northeast region and informs interpretation of observations of obvious gear impacts to regional deep-sea coral



and sponge habitats. In any case, the conclusions about the nature of these impacts are generally similar to earlier work. Because the predominate industrial use of the deep-sea in the Northeast is fishing, impacts from bottom-contact fishing are still considered the greatest and most immediate threat to deep-sea corals and sponges in this region. The seriousness of the threat is reflected in the proactive work of the Fishery Management Councils in pursuing the current management options, discussed below.

Most bottom-contact fisheries in the Northeast U.S. are conducted on the continental shelf, including the Gulf of Maine and Georges Bank, with some fishing effort around the shelf/slope break. Considering the major areas of coral distribution described above, the Gulf of Maine and the upper portion of canyons and slope are subject to the highest fishing pressures. Fishing for monkfish (largely by trawl, with some gillnet fishing) and tilefish (predominantly by bottom longlines) occurs predominantly on the shelf, but can extend into deeper waters, as can the squid, whiting, and butterfish trawl fisheries. Lobster pots are used to harvest American lobster, as well as Jonah crab, along the shelf break. A small deep-sea red crab (*Chaceon quinquegens*) fishery is active in deeper waters, deploying strings of 90-120 pots primarily at depths from 400-800 m (NEFMC 2002), targeting approximately the 640 m depth contour.

During the 2012-2015 Gulf of Maine exploratory surveys, areas exhibiting direct impacts from fishing activities were observed at sites in

Western and Central Jordan Basin, Outer Schoodic Ridge, and Georges Basin (Auster et al. 2014). In steep areas, paths or tracks, consistent with the setting or recovery of trap gear, were denuded of corals and associated fauna (Fig. 9a). The peaks of some ridges and nearly horizontal sections of wider rock outcrops were also denuded. Tracks observed here were consistent with impacts from mobile fishing gear (Fig. 9b,c). Some coral patches exhibited damage in the form of live colonies with disjunct size class structure, suggesting past impacts (Fig. 9d). In areas such as Georges Basin, colonies of *Paramuricea placomus* and associated species were often small and virtually all occurred in physical refuges such as cracks and crevices of outcrops and along the sediment-rock interface of large cobbles and boulders. Of note is that the sea star *Hippasteria phrygiana* was observed eating or preying on *P. resedaeformis* colonies at the Outer Schoodic Ridge site. These sea stars were seen on living coral colonies that had been detached from rock walls and were laying on the seafloor, possibly due to fishing activity, as one was seen next to an abandoned fishing net. Opportunistic predation by *H. phrygiana* has also been noted in Alaska on *Primnoa pacifica* that had been injured or detached by fishing gear (Stone et al. 2015). This may indicate that coral damaged by fishing gear interactions are at an increased risk of predation by sea stars, thus further reducing the chances that a coral colony will recover from gear-related injuries and impacts.

Knight et al. (2006) analyzed recovery of epibenthic megafauna in predominantly soft-

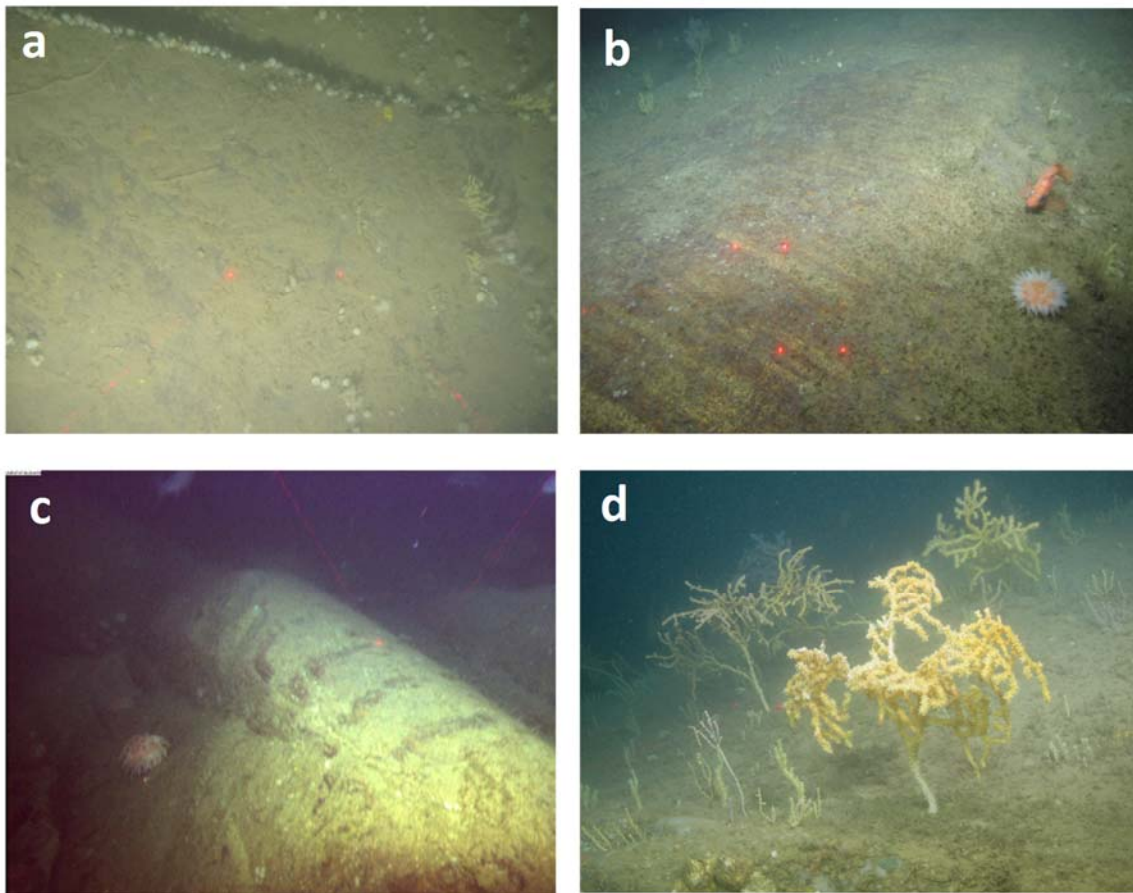


Figure 9. Examples of fishing gear impacts to coral habitats in the Gulf of Maine (Auster et al. 2014 and unpublished images). (a) Denuded bottom (sediment covered hard bottom) in Western Jordan Basin (114 Bump) consistent with fixed gear impacts. (b) Denuded ridge in Central Jordan Basin consistent with mobile gear impacts. (c) Denuded ridge in Georges Basin consistent with mobile gear impacts. (d) Example of oddly shaped corals with disjointed size class structure, possibly due to damage, in Western Jordan Basin.

sediment shelf areas in the Western Gulf of Maine that had been closed to fishing for 6 years. The closed sites showed higher average taxonomic abundance than fished sites – with unidentified sponges and a tunicate (*Mogula* sp.) responsible for approximately 83% of the difference. This suggests that sponges are susceptible to impacts from bottom-contact fishing, and at least certain species may recover more quickly than corals.

The annual number of interactions between fishing gear and deep-sea corals and sponges is not known, but bycatch data indicate that a relatively small number of trips interact with deep-sea corals. In 2011 NOAA’s National Marine Fisheries Service (NMFS) granted the Maine Department of Marine Resources an exempted fishing permit for redfish in order to conduct a baseline catch and bycatch evaluation in and around Wilkinson Basin and elsewhere



in the central Gulf of Maine. Many smaller individuals escape from the 6.5 inch mesh nets required by groundfish regulations. The experimental fishing used nets with smaller, 4.5 inch mesh liners in the cod end and targeted schools of redfish that congregate on "bumps" or pinnacles that occur in the normally deep, muddy areas in the central Gulf of Maine. Since redfish seek shelter near structure-forming organisms such as deep-sea corals and sponges, as well as boulder reefs (Packer et al. 2007), concerns were raised by NMFS that the smaller mesh nets would increase the probability of bycatch of deep-sea corals. NMFS determined that the project could have an adverse effect on EFH, particularly on any deep-sea corals found there. Therefore, they requested that deep-sea coral bycatch be carefully monitored to enhance the understanding of deep-sea coral distribution in the Gulf of Maine and the potential effects of an expanded redfish fishery on deep-sea corals. However, by the end of the project the only coral by-catch was that of a single specimen of the common sea pen, *Pennatula aculeata*, which, as stated previously, is ubiquitous in muddy areas of the Gulf of Maine. It seems that none of the project tows overlapped with any known soft coral habitats, even though the current redfish fishery appears to operate in the vicinity of these habitats.

Several years ago, NMFS Northeast Fisheries Science Center's (NEFSC) fishery independent surveys and Northeast Fisheries Observer Program (NEFOP) were assessed for potential coral bycatch. As discussed previously (Packer et al. 2007), the spring/fall NEFSC groundfish

trawl and scallop dredge surveys conducted in the region do not "catch" deep corals in any meaningful quantities, nor is any deep coral that may be brought on deck recorded in a significant quantitative way. The NEFSC groundfish trawl surveys loosely describe and roughly quantify any substrate (rock, shell, etc.) or non-coded invertebrate species. Although this bycatch information could possibly be useful as presence/absence data, since deep-sea corals are not the focus of the bottom trawl surveys, these data should of course be used with caution (John Galbraith, NMFS, NEFSC, Woods Hole Laboratory, Woods Hole, MA, pers. comm.).

Outside the Gulf of Maine, the general lack of deep-sea coral in both the groundfish trawl and scallop dredge surveys may be a function of the surveys fishing in waters shallower than where the larger deep-sea coral species are likely to occur; i.e., the groundfish survey fishes from about 9-366 m depth, while nearly all the scallop surveys fish < 100 m and all are < 140 m. In some areas in the Gulf of Maine and Georges Bank, these larger corals (e.g., *Paragorgia arborea*, *Primnoa resedaeformis*) may have already been "fished out" in the survey areas during the 19th and 20th centuries (Packer et al. 2007). In Canadian waters near the Northeast Channel, but within the survey region, there is a deep-sea coral protection area that is closed to fishing. J. Galbraith (NEFSC, pers. comm.) stated that this was the only area he could remember where any amount of coral was encountered. Anecdotal accounts from the time period before the groundfish survey began



(1950's or early 60's) reference an area on Georges Bank called "The Trees" where large corals existed in shallower water before being eventually cleared out, supposedly by foreign trawling vessels. There are also anecdotal accounts from Gloucester fishermen who said that they used bottom gear on Georges Bank to first knock down the "trees" before fishing for large adult redfish.

The fishery dependent deep-sea coral bycatch data collected from the NEFOP used to suffer many of the same problems as the groundfish trawl and scallop dredge surveys. First, it should be noted that only 10-40% of all fishing effort is observed by "observers" onboard vessels, depending on the fishery, and a grand average may be somewhere around 10%. A small NEFOP database of coral bycatch collected from 1994-2009 showed only 39 confirmed coral entries. Two of these entries were labeled '*Astrangia*' (a solitary stony cup coral) and 10 additional entries were labeled stony corals. Basic information about the haul (gear type, year, month, depth, and geographic coordinates) was included. Gear used included otter trawls, scallop dredges, and gill nets, at depths from 5.5-253 m (depths were taken at the beginning of a tow or set). Estimated or actual weights for the coral in a given haul ranged from 0.05 – 22.7 kg. No specimens or photographs were included.

In 2013, the NEFOP training curriculum and associated sampling protocols were changed to improve deep-sea bycatch identification, retention, enumeration, and documentation (Lewandowski et al. 2016). This included the

use of a Northeast deep-sea coral identification guide for the onboard observers, and standardized recording, sampling, and preservation procedures. Since implementation of the new protocols, although deep-sea coral bycatch is still low, the number of recorded and verified samples has increased, and photographic records and samples are being stored via the NEFOP Species Verification Program (Lewandowski et al. 2016). These were recently reviewed and classified by Northeast deep-sea coral experts. Several structure-forming gorgonians, as well as sea pens, were documented in bycatch by at-sea observers. Improved NEFOP fishery dependent deep-sea coral bycatch data will lead to a better understanding of fisheries and deep-sea coral interactions and impacts, and guide conservation efforts of deep-sea corals habitats in the Northeast. Of course, bycatch only reveals what is not lost below the net, or not lost through the mesh, or not destroyed within the net (see Auster et al. 2011 on this issue).

III. 1.ii – Other stressors

Oil and gas drilling, while currently not conducted within the region, took on an added urgency with the lifting of the ban on oil drilling off Virginia in 2010; hence, the BOEM-funded study discussed above. The Mid-Atlantic was removed from the 2017-2022 Outer Continental Shelf Oil and Gas Leasing Proposed Program (BOEM 2016), but this decision could be revisited. On June 29 2017, the Secretary of the Interior announced a review of the 2017-2022 Program to include all 26 planning areas. Ocean acidification, although



not discussed in Packer et al. (2007), is obviously a major threat to all corals worldwide (e.g., for tropical coral reefs, see Kleypas and Yates 2009). Research on ocean acidification in relation to deep-sea corals has begun (e.g., Form and Riebesell 2012; Lunden et al. 2014), but has focused primarily on stony corals (i.e., *Lophelia pertusa*). There have been no studies on the dominant coral species in the Northeast region.

Other activities that impact the seafloor and pose potential threats to deep-sea corals and sponge habitats in the region include deployment of seafloor cables and offshore renewable energy installations. New York is a major hub for underwater communication cables, but there is little information on impacts to biogenic habitats. Potential offshore wind development has become a major driver for more comprehensive ocean planning within the region. The Bureau of Ocean Energy management (BOEM) has awarded leases in specific areas from Massachusetts to Virginia. In 2016, the Block Island Wind Farm off Rhode Island began operations as the nation's first offshore wind installation. This and future wind development is likely to be conducted on the continental shelf relatively close to shore, and thus less likely to impact major deep-sea coral and sponge habitats, although it could affect shallower water sponge populations.

Marine debris and trash are also a threat to corals in this region, and have been noted in

some of the recent surveys. Quattrini et al. (2015) found an estimated 0.002-0.130 items/10 m², including derelict fishing gear (ghost traps, lines, hooks) and trash (cans, bottles, plastic bags, etc.). The highest numbers came from one of the minor, unnamed canyons. At least 12 deep-sea coral colonies were tangled in debris, including five gorgonian colonies (*Paramuricea* spp., *Thouarella grasshoffi*) that suffered varying degrees of injury or death. Brooke et al. (2017) noted marine debris on almost every dive in Baltimore and Norfolk canyons, often near the canyon heads on rock outcrops; canyon heads are where most fishing activity would take place. During the Gulf of Maine exploratory surveys, little debris was seen, which was surprising considering the number of vessels traversing the survey areas. Debris observed included lines, nets, trash, and in one instance in Western Jordan Basin, a large piece of plastic sheeting that covered a boulder with several large colonies of *Paramuricea placomus*.

Packer et al. (2007) discussed potential impacts of an invasive colonial tunicate (*Didemnum* sp. A) found on gravel and cobble substrates on Georges Bank. This species has since been identified as *Didemnum vexillum* (Lengyel 2009). The progress of this species is being monitored, as it can have a major effect on the benthic invertebrate communities of Georges Bank (Kaplan et al. 2017a, b), but it has not been reported in the primary habitats of high-density deep-sea coral or sponge communities (e.g., Bullard et al. 2007).



III.2. New or Planned Management Actions

III.2.i – Northeast Canyons and Seamounts Marine National Monument

On September 15, 2016, President Obama designated the first marine national monument in the Atlantic Ocean, the Northeast Canyons and Seamounts Marine National Monument, using his authority under the Antiquities Act of 1906. The monument consists of two units (Fig. 10), representing distinct geological features that support vulnerable ecological communities, including deep-sea coral and sponge communities. The Canyons Unit covers approximately 2,437 km² (941 square miles) on the edge of Georges Bank, including Oceanographer, Gilbert, and Lydonia submarine canyons. The Seamounts Unit encompasses 10,287 km² (3,972 square miles) and includes the four New England Seamounts in the U.S. EEZ: Bear, Mytilus, Physalia, and Retriever. The presidential proclamation specifically referenced deep-sea corals, along with “other structure-forming fauna such as sponges and anemones,” as resources that “create a foundation for vibrant deep-sea ecosystems” and are extremely sensitive to disturbance from extractive activities.

The new monument will be managed jointly by the Department of the Interior and the Department of Commerce (through NOAA). The proclamation creating the Monument identifies a number of prohibitions designed to help protect monument ecosystems, including prohibiting oil, gas, and mineral exploration and development. Commercial fishing in the

monument is prohibited with the exception of existing red crab and lobster fisheries, which were granted a grace period for up to seven years. Other activities, such as cable deployment and maintenance, scientific activities, and recreational fishing will be permitted as long as they are determined to be consistent with the conservation goals of the Monument. The Department of the Interior and NOAA will jointly develop a management plan for the Monument within three years. Recent marine national monument designations are undergoing review by the Department of the Interior and NOAA, in response to an April 26, 2017 Executive Order.

III.2.ii – Fisheries management

In the Northeast region, fisheries in Federal waters are primarily managed by NOAA’s National Marine Fisheries Service (NMFS) under fishery management plans (FMPs) developed by the New England and Mid-Atlantic Fishery Management Councils (NEFMC, MAFMC). Recent work by both regional Councils has been facilitated by the new exploratory surveys and data on the distribution of deep-sea corals. As described above, most of these data were collected between 2012 and 2015. The Councils, in collaboration with NMFS, recommended priority targets to ensure that results would be relevant to managers. Additionally, in 2011, NMFS, in collaboration with the two regional Councils, initiated a partnership to develop and implement a strategy for deep-sea coral conservation as part of NOAA’s Habitat

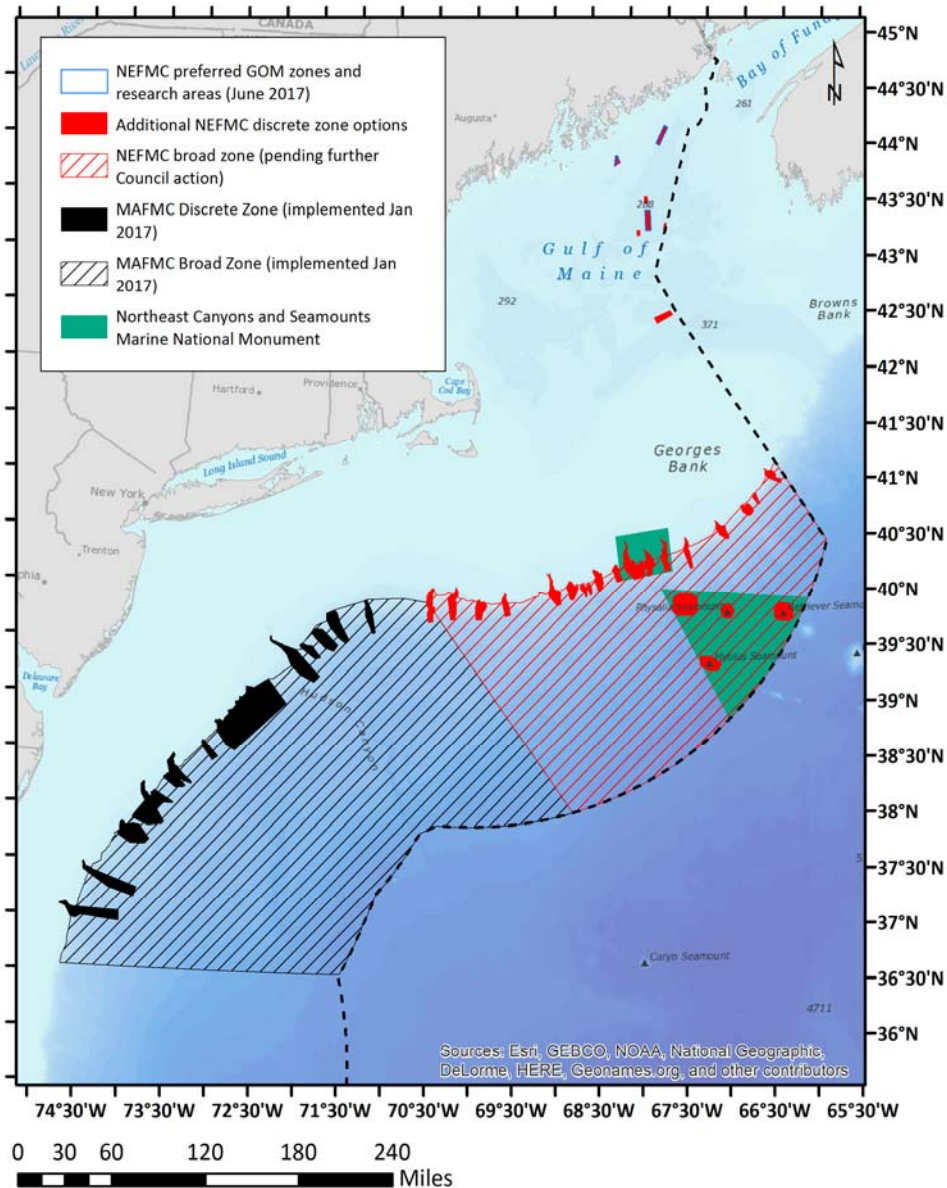


Figure 10. Deep-sea coral protection zones for the Northeast region enacted in the Mid-Atlantic and being considered for New England. Broad zones are shaded; discrete zones on seamounts, in canyons, and in the Gulf of Maine, are outlined. Alvin Canyon straddles the New England/Mid-Atlantic inter-council boundary. New England zone boundaries will likely change as the amendment is finalized based on stakeholder feedback.



Blueprint program. The goal was to ensure effective, long-term conservation of deep-sea coral habitats with existing management and scientific resources as well as provide a template to integrate habitat conservation and science into the Council process. This program took advantage of deep-sea coral science and management activities that were already underway in the region, including the 2013-2015 NOAA Northeast Deep-sea Coral and Sponge Initiative. Another objective of this program was to implement a coral conservation strategy with federal offshore energy licensing agencies (e.g., BOEM) using existing coordination and consultation procedures.

There are two primary authorities in the Magnuson Stevens Fishery Conservation and Management Act (MSA) that can be used to protect deep-sea coral and/or sponge habitats. Under the Essential Fish Habitat (EFH) authority, fishing restrictions should be enacted to minimize, to the extent practicable, the adverse effects of fishing on corals or sponges that are considered a component of EFH for a managed fisheries species (MSA section 305(b)). Actions taken under the EFH authority generally occur within areas that are designated as EFH. The NEFMC used this authority in 2005 to protect deep-sea corals and associated habitat features in Lydonia and Oceanographer canyons from fishing activity occurring under a monkfish “days-at-sea” permit. The MAFMC used the same authority in 2008 to close these two canyons to bottom trawling by vessels in the squid, mackerel, and butterfish fisheries via Amendment 9 to that FMP. In 2009 the MAFMC closed Lydonia, Oceanographer,

Veatch, and Norfolk Canyons (as tilefish Gear Restricted Areas) to mobile bottom tending gear through Amendment 1 to the tilefish FMP, with the intention of protecting vulnerable tilefish habitat (clay outcroppings also known as “pueblo” habitats).

Areas outside designated EFH may also be managed under the EFH authority, but the scope of this authority is presumably not limitless. In the Northeast region, coral distributions extend into waters deeper than the bounds of managed species and their designated EFH. The deep-sea coral discretionary provisions (MSA Section 303(b)) from the 2007 MSA reauthorization provide an additional and more flexible mechanism by which to protect deep-sea corals from physical damage by fishing gear. This discretionary authority allows Councils to designate protection zones anywhere corals have been identified by the Deep Sea Coral Research and Technology Program and implement measures to protect corals within those zones, provided that long term sustainable use of fishery resources has been considered, and there is a nexus to Council-managed fisheries (NOAA 2010; Sutter 2014). This authority has become the primary basis for a range of coral protection measures enacted by the MAFMC and currently under development by the NEFMC (Fig. 10). The measures define the boundaries of coral protection zones and implement fishing restrictions within them. In addition to the EFH and discretionary authorities, National Standard 9 of the MSA requires federal fishery management plans to minimize bycatch to the extent practicable.



Substantial spatial overlap exists between continental slope fisheries managed by the NEFMC and MAFMC. This overlap affects the range of coral alternatives developed and their potential impacts on fishing activities. The NEFMC began development of a deep-sea coral amendment in 2010 that included coral areas from the Gulf of Maine to Norfolk Canyon, off Virginia. In 2012, the MAFMC decided to initiate their own FMP amendment to protect deep-sea corals in the Mid-Atlantic region (roughly south of Alvin Canyon). These two Councils, along with the South Atlantic Fishery Management Council, then drafted a memorandum of understanding (MOU) to coordinate deep-sea coral management activities. Also during 2012, the NEFMC decided to develop their deep-sea coral management measures in a standalone coral-focused amendment, independent from a much more comprehensive omnibus EFH amendment.

In 2015, the MAFMC recommended specific proposals to NMFS to prohibit the use of most types of bottom-tending fishing gear within a 99,000 km² (~38,000 square miles) area on the outer continental shelf, slope, and canyons to the outer boundary of the EEZ. This was approved by NOAA in 2016, marking the first use of the MSA deep-sea coral discretionary authority. The new management zones are officially known as the “Frank R. Lautenberg Deep-Sea Coral Protection Area.” Senator Lautenberg, a senator from New Jersey, was responsible for, and authored, several important pieces of ocean conservation legislation, including several provisions in the

reauthorized MSA, including the discretionary provisions described above.

The Frank R. Lautenberg Deep-Sea Coral Protection Area includes two types of zones. ‘Discrete’ zones protect defined areas of canyons and canyon complexes based on the best available information on known coral distributions or outputs of predictive models that rank the likely presence of suitable coral habitats. A precautionary ‘broad’ zone protects a large area of deepwater habitats extending from approximately 450 m on the slope to the outer limits of the U.S. EEZ (Fig. 10). The objective is to protect corals by limiting future expansion of bottom fishing in an area that is largely outside the footprint of current fishing activity. Both zones restrict most bottom-tending gears, but the red crab fishery is exempted for a period of at least two years in the discrete zones and indefinitely in the broad zones, and the action does not restrict lobster/Jonah crab traps in either type of coral zone. The lobster fishery is primarily managed by the Atlantic States Marine Fisheries Commission. This dual discrete/broad framework follows the approach of NOAA’s *Strategic Plan for Deep-Sea Coral and Sponge Ecosystems* (NOAA 2010), and provides flexibility to revise fishing restrictions independently in the various areas.

The NEFMC is still developing and evaluating management approaches and will likely make final recommendations to NMFS during late 2017 or early 2018. The council has taken a similar approach to that of the MAFMC, including a precautionary ‘broad’ zone in



deeper water. Discrete area options that are being considered in New England include seven areas in the Gulf of Maine, a number of submarine canyons and canyon complexes, and the four New England Seamounts in the U.S. EEZ southeast of Georges Bank.

III.2.iii – Other Resource Management and Ocean Policy Efforts

The Mid-Atlantic Regional Council on the Ocean (MARCO) was created by the Governors of five Mid-Atlantic States (NY, NJ, DE, MD, VA) to improve regional coordination of shared ocean issues and to address the ocean environment across the states as a whole ecosystem, through the principles of ecosystem-based management (Capobianco 2011). The first MARCO priority is to coordinate the protection of important habitats and sensitive and unique offshore areas, such as the submarine canyons and deep-sea coral and sponge habitats, on a regional scale. To facilitate habitat protection actions by its partners, MARCO developed an online portal (<http://midatlanticocean.org/data-portal/>) that displays geospatial information obtained from sources such as NOAA's deep-sea coral and sponge database to aid in identifying regionally-important habitats such as the canyons (Capobianco 2011). The high-resolution multibeam bathymetric surveys of the slope and canyons conducted by NOAA were done in part to support MARCO's habitat mapping and protection goals. MARCO has been following the work of the two Councils in protecting submarine canyon habitats, and facilitated the engagement of multiple federal

entities and stakeholders with an interest in these habitats to ensure that all existing resources and authorities were leveraged. Similar planning and geospatial data gathering efforts are underway in New England as well, and coral-related data products including habitat suitability model outputs are available through the Northeast Ocean Data Portal (<http://www.northeastoceandata.org>). In December, 2016, the National Ocean Council certified the Northeast and Mid-Atlantic Ocean Plans.

NOAA's National Marine Sanctuary Program also received nominations from communities for new National Marine Sanctuaries for Baltimore Canyon and Hudson Canyon (<http://www.nominate.noaa.gov/nominations/>). In both cases, deep-sea coral resources were identified in the justification for consideration for sanctuary status. The Baltimore Canyon proposal was withdrawn in January 2017, but the Hudson proposal was moved into candidate status at NOAA during February 2017.

V. Conclusions

Mapping and exploratory surveys since 2010 have covered almost all the submarine canyons off the Northeast coast as well as areas of the continental slope, the seamounts within the EEZ, and significant areas in the Gulf of Maine. Considering the state of our knowledge of deep-sea coral and sponge habitats prior to these surveys, the results documented herein have increased our knowledge base of



Northeast deep-sea coral and sponge habitats exponentially. They have also generated much interest from the public and media (e.g., see NRDC 2014 for some 2011-2014 canyon and seamount expedition highlights). However, knowledge gaps still exist for many of these organisms, especially for the sponges, and some basic questions about distribution, abundance, taxonomy, connectivity, life history, population biology, functional role, effects and scale of disturbance, ecological resilience, etc. remain unanswered. Nevertheless, the new surveys have contributed greatly to our regional knowledge of deep-sea coral diversity, distribution, and habitat characteristics.

From a management perspective, these results prompted the NEFMC and MAFMC to revisit their previous lists of potential deep-sea coral protection zones, especially those for the submarine canyons and the Gulf of Maine. Now that most of these areas have been surveyed and deep-sea corals were observed in almost all of them, these areas can be confidently classified as “assessed” and as “suitable” deep-sea coral habitat. The Councils, therefore, were then able to recommend additional areas for consideration as deep-sea coral protection zones/ management areas. Having this information led directly to the creation of the Frank R. Lautenberg Deep-Sea Coral Protection Area in the mid-Atlantic, will support the decision-making process for the creation of deep-sea coral protected areas by the NEFMC, and was one of the major factors behind the creation of the Northeast Canyons and Seamounts Marine National Monument. In addition, a high correlation between recent

coral observations and locations predicted to be suitable coral habitat has increased confidence in using the regional deep-sea coral habitat suitability model to inform current and future management decisions of the Councils. Both the NEFMC and MAFMC have used and continue to use the information and results gathered from the recent exploratory surveys, the historical database, and the habitat suitability model to draft management alternatives to designate deep-sea coral zones in the Northeast and Mid-Atlantic and implement fishing restrictions necessary to protect the deep-sea corals within those zones.

V. Acknowledgements

The authors thank those people from other NOAA Line Offices that were either part of the *Bigelow/Okeanos/Hassler* mapping/survey cruises and/or led and provided assistance/funding for modeling, surveys, etc. including Mashkoor Malik, Jeremy Potter, Elizabeth Lobecker, Nathan Keith, LCDR Ben Evans, LT Sam Greenway, and Tim Shank from WHOI. The authors also thank the Gulf of Maine survey scientists, including Peter Auster, Rhian Waller, Rich Langton, and Steve Auscavitch; the crew and engineers of the *Connecticut*, *ISIS2*, and *Kraken 2*, including Ivar Babb; and the Sandy Hook folks who help get the data out there: Donna Johnson, Jeff Pessutti, Barry Shafer, Christine Shafer, and Caren Martins. Additional thanks to Tania Lewandowski (NEFOP). Finally, we thank Rich Langton (NEFSC), David Stevenson (GARFO), Stephen Cairns (Smithsonian NMNH), Andrea Quattrini



(Harvey Mudd College), Sandra Brooke (Florida State Univ.), Rhian Waller (U. Maine), Peter Auster (U. Conn.), Kiley Dancy (MAFMC), and especially Tom Hourigan for helpful reviews and comments. Figure 5d courtesy of Source: Deepwater Canyons 2012 Expedition NOAA-OER/BOEM/USGS. Figures 5e,f,l courtesy of NOAA *Okeanos Explorer* Program, 2013 Northeast U.S. Canyons Expedition. Figures 5g,h,i courtesy of NOAA *Okeanos Explorer* Program, Our Deepwater Backyard: Exploring Atlantic Canyons and Seamounts. Gulf of Maine Figures 7-9 courtesy of NOAA/UConn. – NURTEC/UMaine.

This chapter is dedicated to the memory of Brian Kinlan, whose presence is deeply missed but whose ideas and passion live on.

Online Annex – Comprehensive list of deep-sea corals in the U.S. Northeast region link:
<https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>

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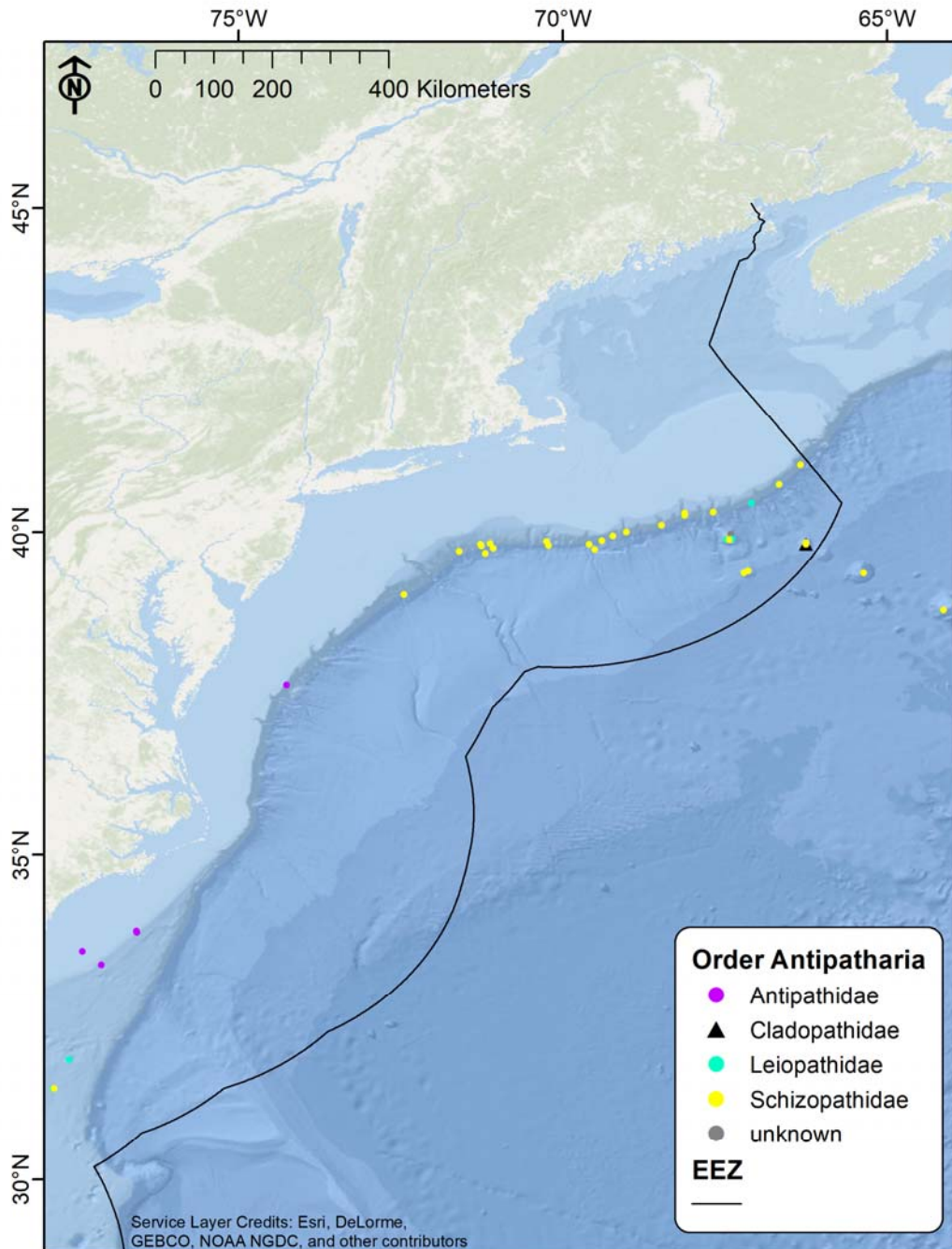


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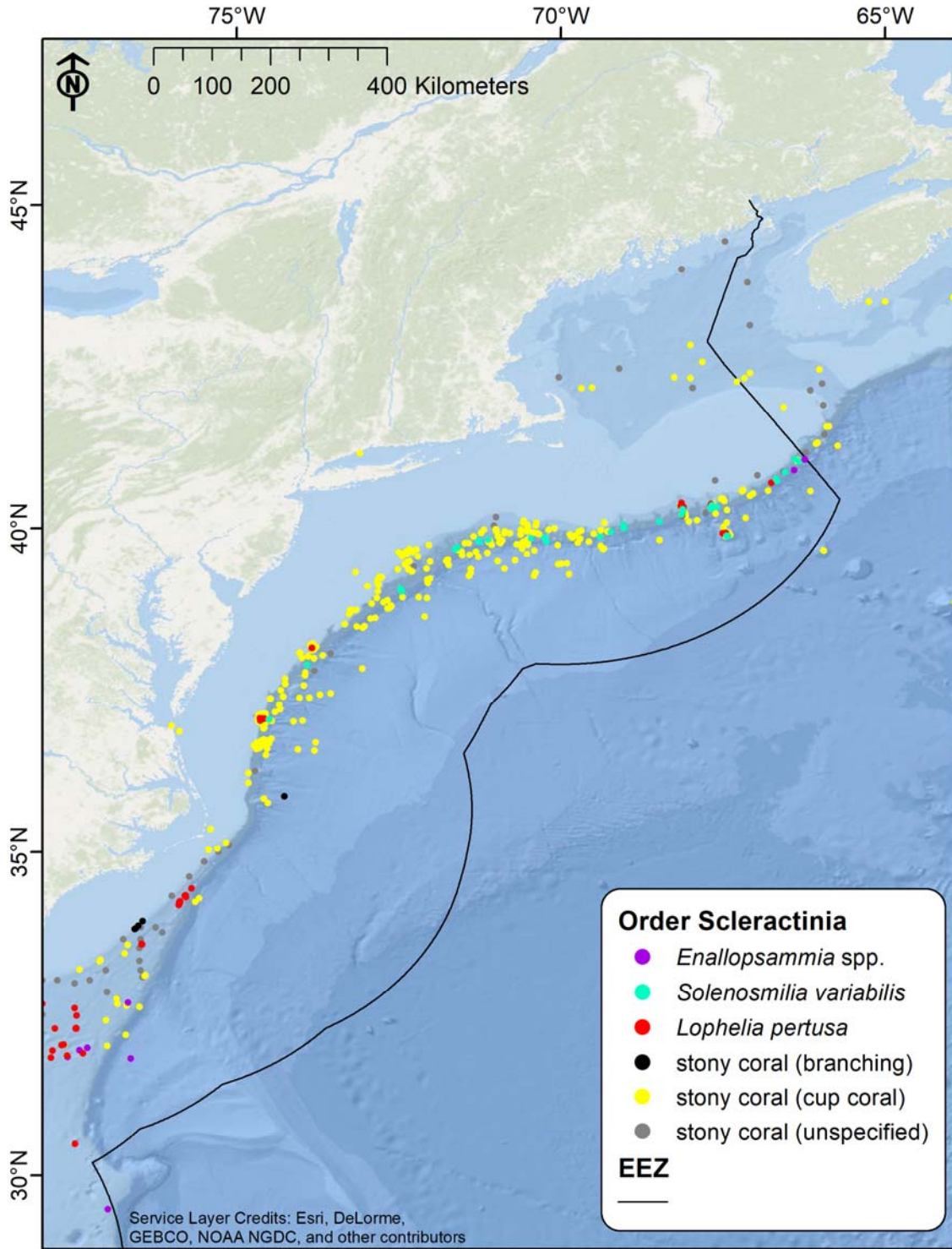
[Online Annex 1. Deep-sea Coral Taxa in the U.S. Northeast Region: Depth and Geographic Distribution](#)



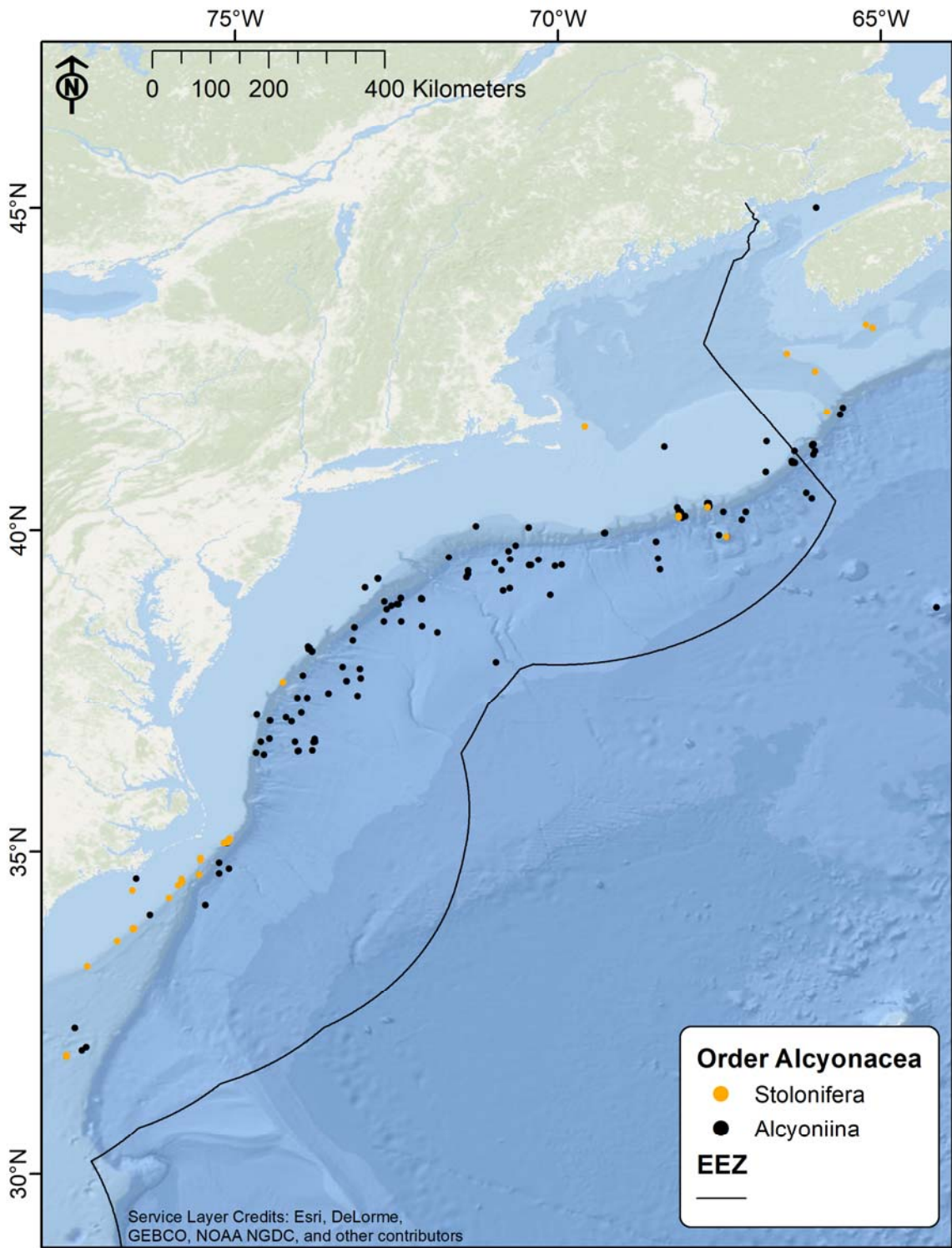
Appendix – Deep-Sea Coral and Sponge Distribution Maps



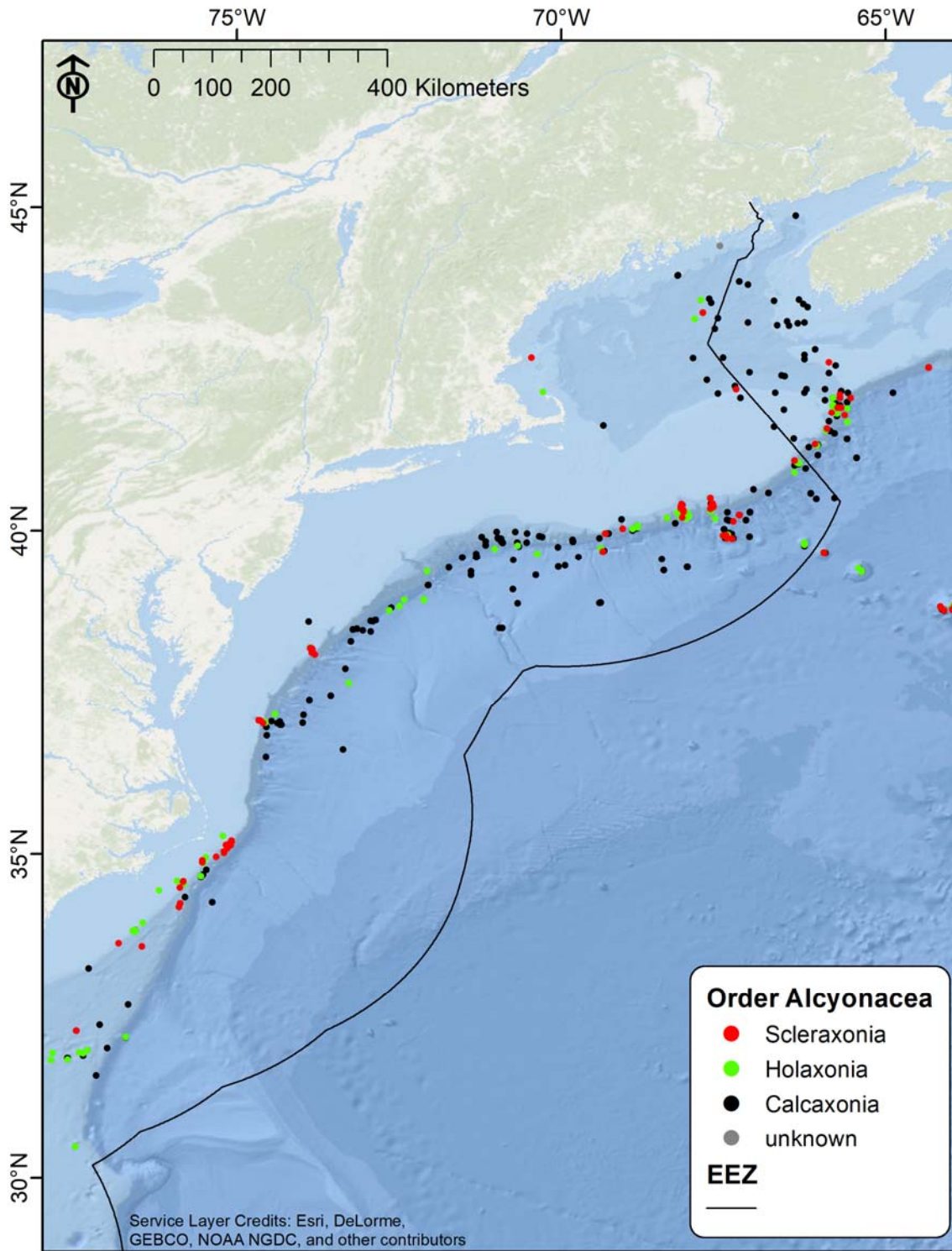
Map 1. Locations of black corals (Order Antipatharia) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



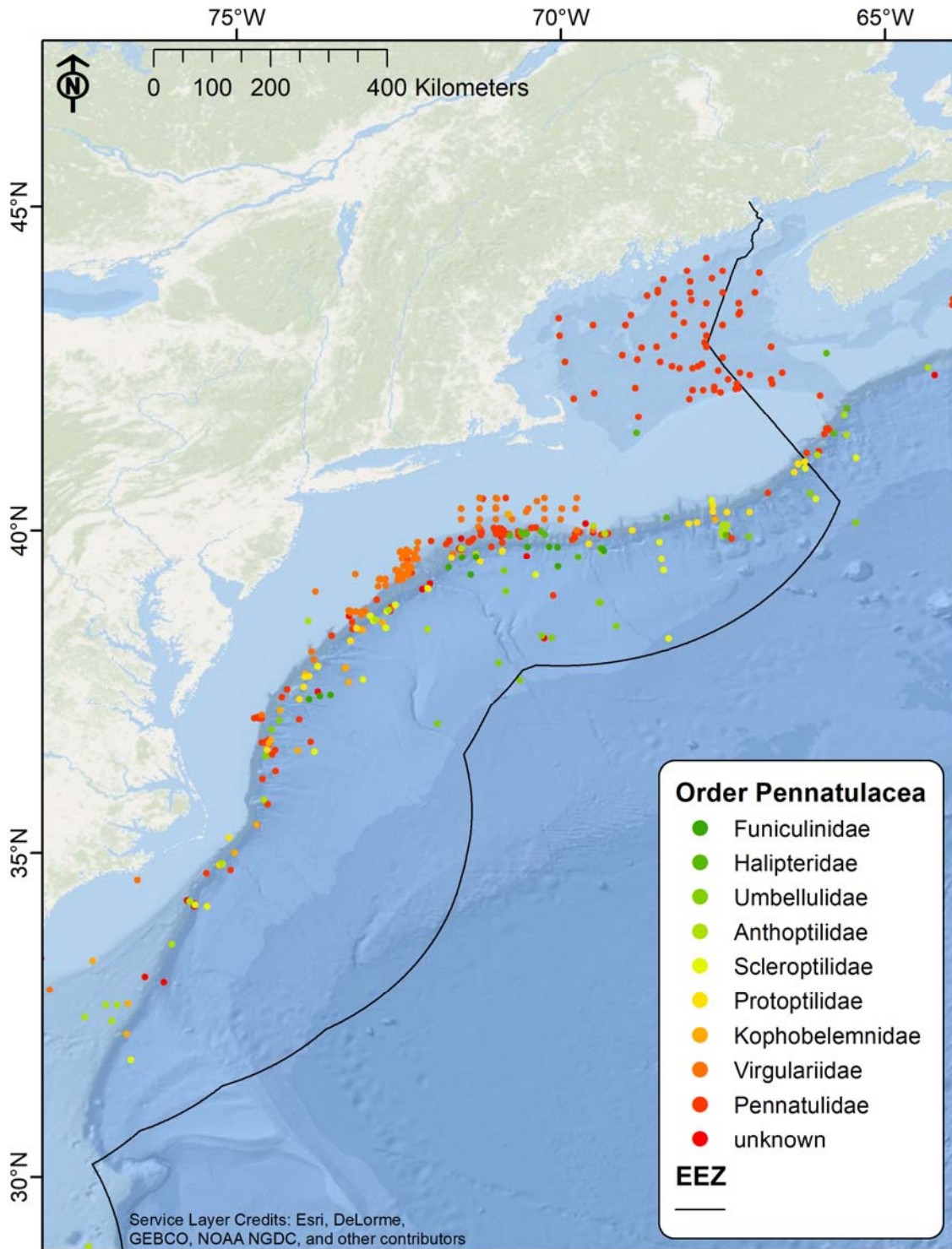
Map 2. Locations of stony corals (Order Scleractinia) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



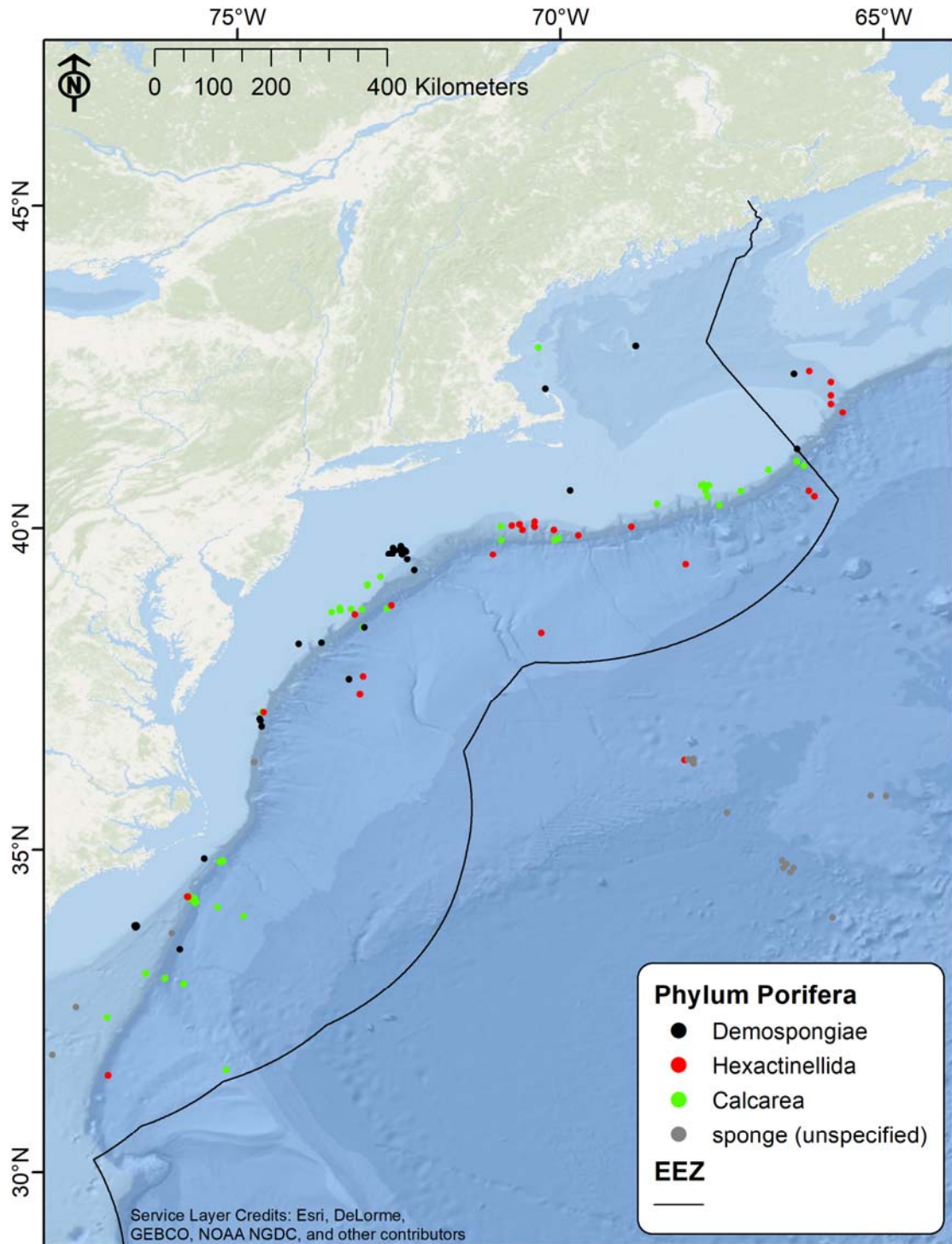
Map 3. Locations of soft corals (Order Alcyonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



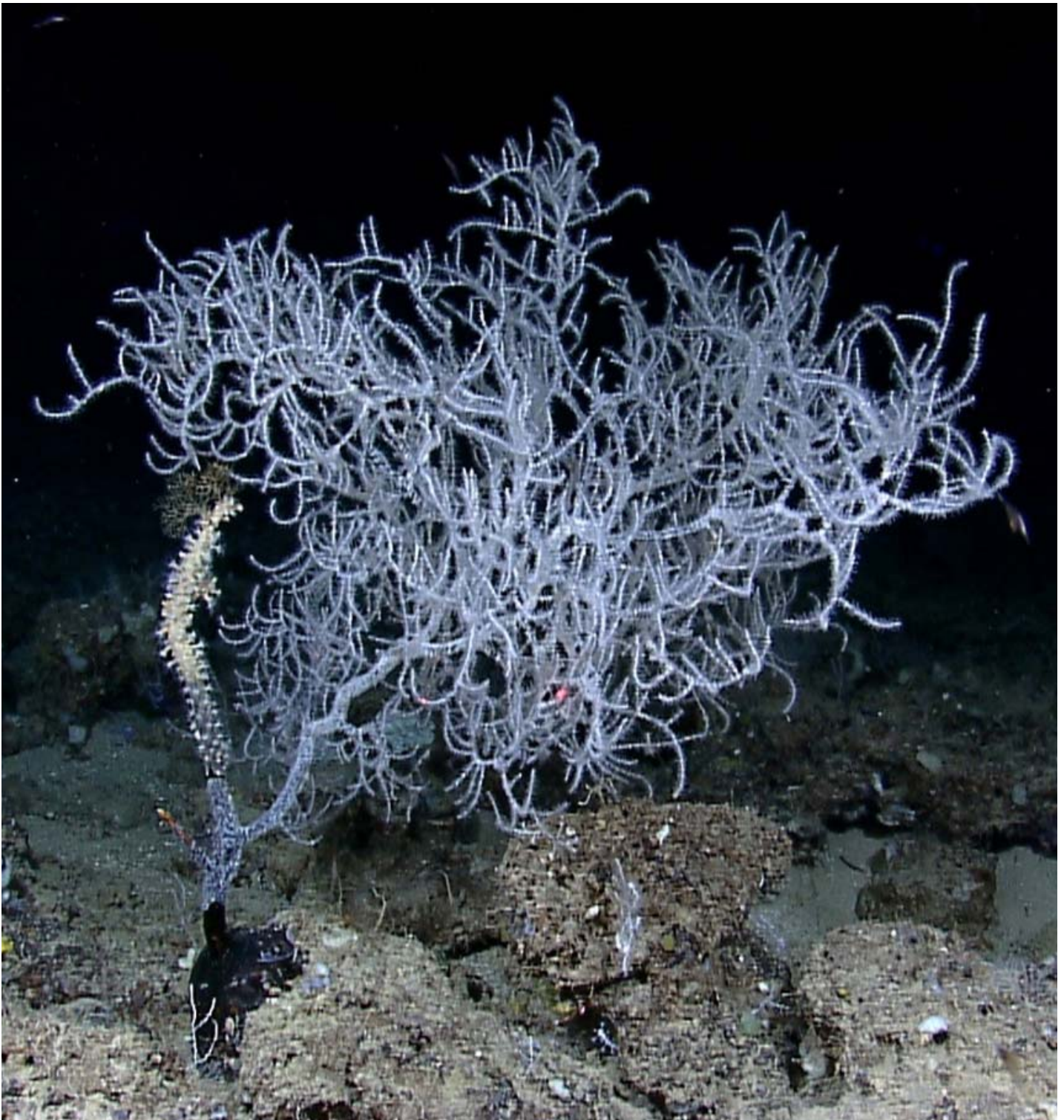
Map 4. Locations of gorgonians (Order Alcyonacea, in part – formerly Order Gorgonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



Map 5. Locations of sea pens (Order Pennatulacea) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017).



Map 6. Locations of sponges (*Phylum Porifera*) recorded in the National Deep-Sea Coral and Sponge Database (as of October 2017). Although sponges occur throughout the region, observations have not been systematically recorded and organized, so records in the database are currently limited.



Leiopathes black coral colony on the West Florida escarpment in the Gulf of Mexico. Red lasers visible near the middle of the image indicate that the basal axis of the colony is about 1.7 cm in diameter. This measurement suggests the coral colony is between 400-1000 years old, based on published growth rates for black corals in the Gulf of Mexico (Prouty et. al, 2011). Black corals in the genus *Leiopathes* are among the longest-lived marine organisms, reaching ages of thousands of years. Courtesy of the NOAA Office of Ocean Exploration and Research.



AGE, GROWTH RATES, AND PALEOCLIMATE STUDIES IN DEEP-SEA CORALS OF THE U.S.

I. Introduction

Deep-water corals are some of the slowest growing, longest-lived skeletal accreting marine organisms. These habitat-forming species support diverse faunal assemblages that include commercially and ecologically important organisms. Therefore, effective management and conservation strategies for deep-sea corals can be informed by precise and accurate age, growth rate, and lifespan characteristics for proper assessment of vulnerability and recovery from perturbations. This is especially true for the small number of commercially valuable, and potentially endangered, species that are part of the black and precious coral fisheries (Tsounis et al. 2010). In addition to evaluating time scales of recovery from disturbance or exploitation, accurate age and growth estimates are essential for understanding the life history and ecology of these habitat-forming corals. Given that longevity is a key factor for population maintenance and fishery sustainability, partly due to limited and complex genetic flow among coral populations separated by great distances, accurate age structure for these deep-sea coral communities is essential for proper, long-term resource management.

The importance of accurate age and growth characteristics has another important utility in marine sciences. Many deep-sea corals have been useful as

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biogeochemical proxies that provide a unique view of marine climate and environmental change over time (e.g., Adkins et al. 1998, Robinson et al. 2005, LaVigne et al. 2011). Similar to trees on land, many corals have concentric growth rings that allow scientists to track growth patterns, which can be used to look back into climate history over the coral's lifespan using stable and radio-isotope techniques. Here we summarize recent developments in determining age and growth characteristics for structure-forming deep-sea corals, many of which are vulnerable to disturbance, with highlights on recent advances in paleoclimate reconstruction efforts using deep-sea corals.

II. Age and Growth Rates

Age and growth rates of deep-sea corals have been determined by methods that differ greatly in approach and experimental design. These methods include tagging and outgrowth observations (often limited to shallower depths; Grigg 1976, Stone and Wing 2001, Peck and Brockington 2013), sclerochronology (counting of growth rings in the axial skeleton; Grigg 1974, Wilson et al. 2002, Marschal et al. 2004, Tracey et al. 2007, Aranha et al. 2013), and by radiometric techniques (Uranium/Thorium, Lead-210 and radiocarbon (^{14}C) dating; Cheng et al. 2000, Adkins et al. 2002, Andrews et al. 2009, Roark et al. 2009, Carreiro-Silva et al. 2013, Aranha et al. 2014).

When evaluating reported age and growth rates, it is important to evaluate the strengths and weakness of each method along with its applicability to the potential lifespan (Figure 1). These may include the limits of methodological dating and precision, as well as skeletal morphology and mineralogy. For example, in traditional tagging studies it is

difficult to get accurate in-situ measurements and it can take many years to see measurable growth (Grigg 1976). Sclerochronology can provide estimates of age from visible growth rings in the skeletal structure (Figure 2), but this approach requires validation of the ring formation periodicity (Andrews et al. 2002; Sherwood et al. 2005). Radiometric techniques have different ranges for effective dating and usually require assumptions. With recent advances in Uranium/Thorium dating, it is possible to determine the age of aragonitic (a form of calcium carbonate) corals from less than a few decades old up to 600,000 years in age (Cheng et al. 2000). Typical uncertainty is variable and dependent upon various factors, but recent developments have reduced the uncertainty (Edwards et al. 1987, McCulloch and Mortimer 2008). Lead-210 dating is typically applicable to the last ~100 years with uncertainties as low as ± 10 years and is most applicable to determining a mean growth rate for the entire colony (Andrews et al. 2009). The range of conventional radiocarbon dating is from modern time (defined as 1950 AD) to ~50,000 years BP. While the method is effective, challenges exist in most applications because the atmospheric concentration of radiocarbon has varied over time (Stuiver and Braziunas 1993, Reimer et al. 2009). In the marine environment, radiocarbon ages are also corrected for the difference between the atmospheric radiocarbon content and the local radiocarbon content of the surface ocean, also known as a "reservoir correction." Age determination in deep-sea corals using radiocarbon dating is most applicable to growth occurring over centuries to millennia for living specimens, and extends into fossil specimens in the tens of thousands of years (Guilderson et al. 2005). A second form of radiocarbon dating for some living deep-sea corals involves the identification of the

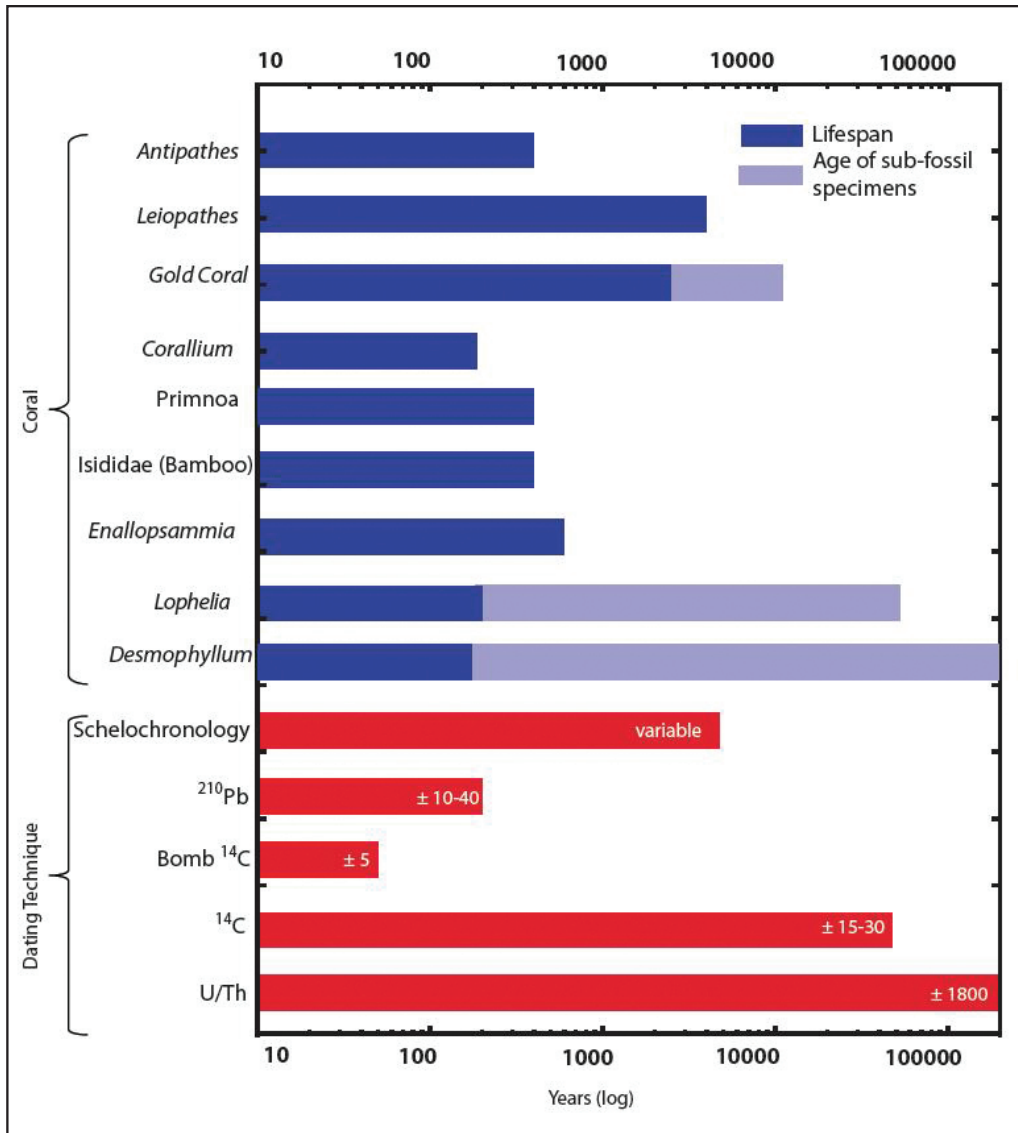
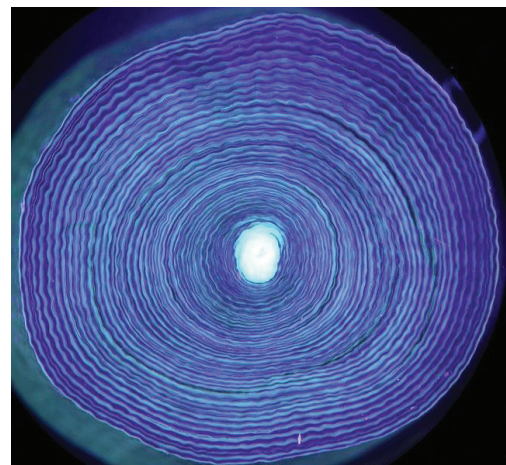


Figure 1. Maximum lifespan (years) of several key deep-sea corals (blue), and the relative time span of efficacy for different dating techniques (red). Typical dating uncertainties listed for dating techniques.

Figure 2. Ultraviolet light illuminates the growth rings in a cross-section of a 44-year-old deep-sea coral (*Primnoa resedaeformis*) collected off the coast of Newfoundland at 400 meters. Similar to trees, cross-sections reveal coral-growth rings (photo by Owen Sherwood).



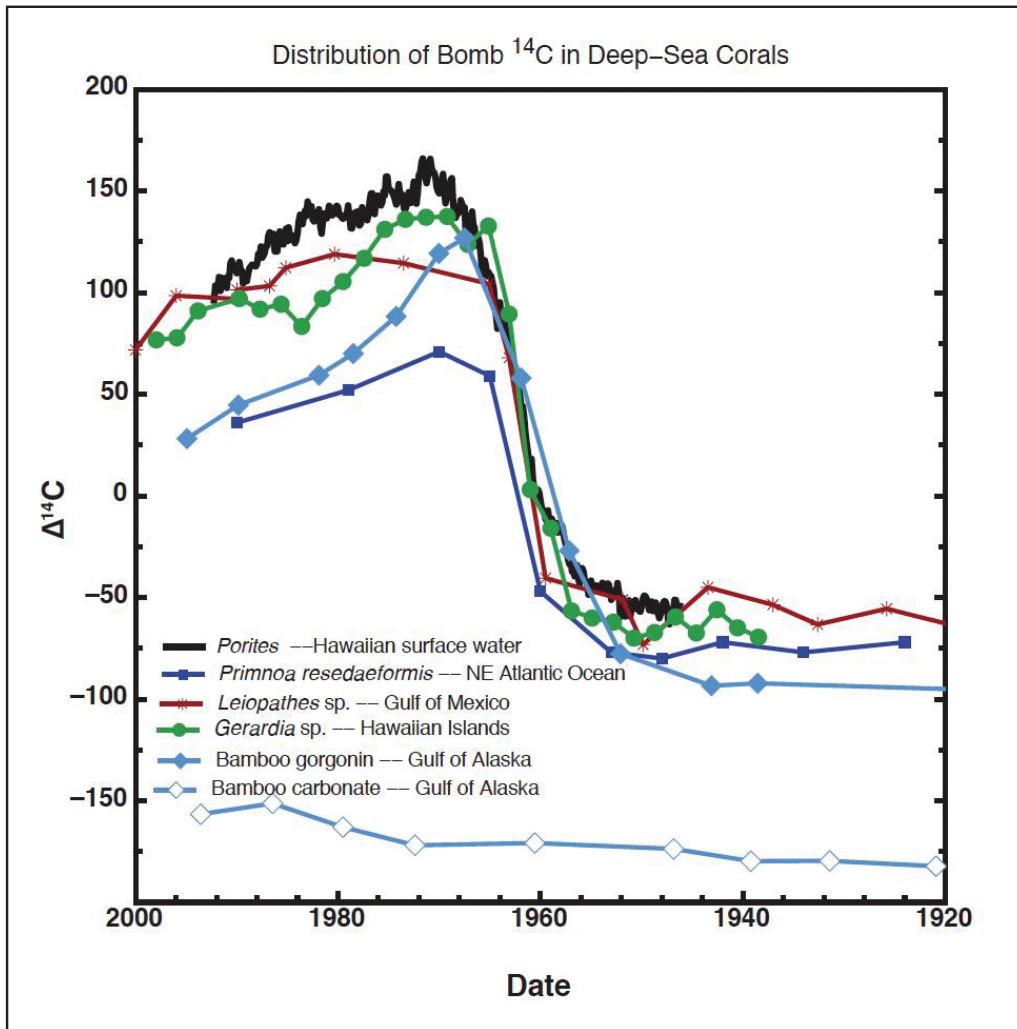
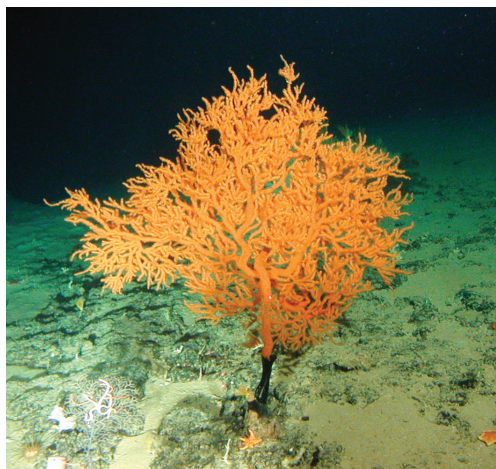


Figure 3. Distribution of bomb-derived radiocarbon ($\Delta^{14}\text{C}$) in proteinaceous deep-sea corals illustrating the uptake and delivery of elevated $\Delta^{14}\text{C}$ in food sources (e.g., rapidly exported surface derived organic matter) to the deep-sea coral community. In comparison, the $\Delta^{14}\text{C}$ of the carbonate portion of the bamboo coral is not elevated and reflects the influence of ambient water with a $\Delta^{14}\text{C}$ signature equivalent to the surrounding dissolved inorganic carbon pool.



*Figure 4. Hawaiian black coral *Leiopathes annosa*. This species includes the oldest known coral. Photo credit: Hawaii Undersea Research Laboratory (HURL).*



anthropogenic bomb-radiocarbon signal from the testing of thermonuclear devices in the 1950s and 1960s. This method is sometimes referred to as bomb radiocarbon dating (Figure 3; Roark et al. 2005, Sherwood et al. 2005), which also has applications in the validation of fish age (Andrews et al. 2012).

II.1. Black Coral

Black coral (Figure 4) represent a group of organisms that are some of the deepest dwelling and longest-lived species. Several species live in U.S. territorial waters and most have been long lived (centuries to millennia). Wagner et al. (2012) summarized information on black coral growth and longevity. Longevity is particularly important within the black coral fishery (Parrish et al. and Wagner et al., this volume) because age and growth rates are needed to determine sustainable yields. These typically shallower dwelling species appear to be faster growing than deeper species and growth rates have been measured based on axial extension rates, growth rings, radiocarbon (^{14}C) and lead-210 dating (Grigg 1976, Roark et al. 2006, Love et al. 2007, Risk et al. 2009). Estimated longevity for sampled *Antipathes* spp. ranged from ~ 12 - 140 years (Wagner et al. 2012).

In contrast, deepwater black corals from Hawaii (*Leiopathes annosa*, reported as *Leiopathes* spp.) were found to have a potential lifespan in excess of 4000 years with a radial growth rate of less than $10 \mu\text{m}\cdot\text{yr}^{-1}$ (Roark et al. 2006, 2009). Similar estimated growth rates and longevity (400 – 2100 years) have been reported for *Leiopathes* from the Gulf of Mexico (Prouty et al. 2011) and the southeastern United States (Williams et al. 2007), with variable growth rates documented from populations in the Azores (Carreiro-Silva et al. 2013).

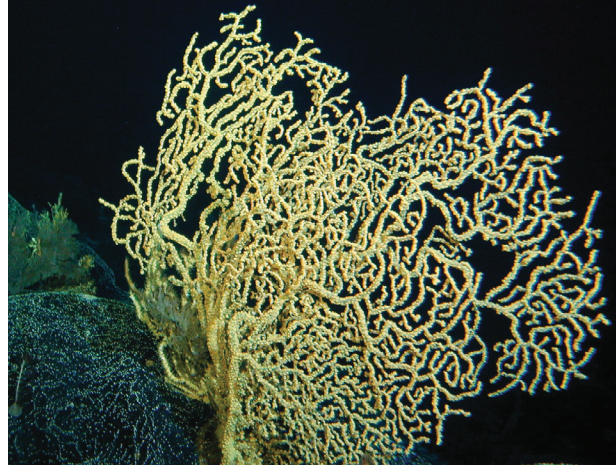


Figure 5. The Hawaiian gold coral *Kulamanamana haumea*. Photo credit: HURL.

II.2. Gold Coral

The proteinaceous colonial parazoanthids (formerly known as *Gerardia* spp.), commonly referred to as gold corals, have similar longevity to that of *Leiopathes*. Numerous specimens ($n = 23$) of the Hawaiian gold coral (*Kulamanamana haumea*) (Figure 5) dated by radiocarbon show lifespans up to 2740 years with an average radial growth rate of $41 \pm 20 \mu\text{m}\cdot\text{yr}^{-1}$ (Roark et al. 2006, 2009, Parish and Roark 2009). These results are not in agreement with shorter lifespan estimates (max age ~70 years) and faster radial growth rates ($\sim 1 \text{ mm}\cdot\text{yr}^{-1}$) from presumed annual growth rings (Grigg 1974). A gold coral (identified as *Gerardia* sp.) specimen from Little Bahamas Bank in the Atlantic Ocean dated by amino acid dating ($\sim 250 \pm 70$ years; Goodfriend et al. 1997) and by radiocarbon (1800 ± 300 years; Druffel et al. 1995) also revealed similar age and growth discrepancies. Using radiocarbon and stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), Roark et al. (2009) showed that *K. haumea* are feeding almost exclusively on recently transported particulate organic carbon from surface waters and that skeletal growth utilizes this carbon. An in

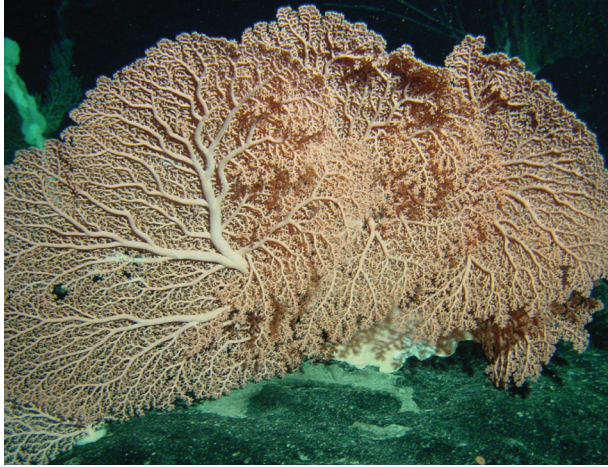


Figure 6. The Hawaiian precious coral *Corallium laauense* (= *Hemicorallium laauense*). In the past, this species has been harvested for jewelry in Hawaii. Photo credit: HURL.

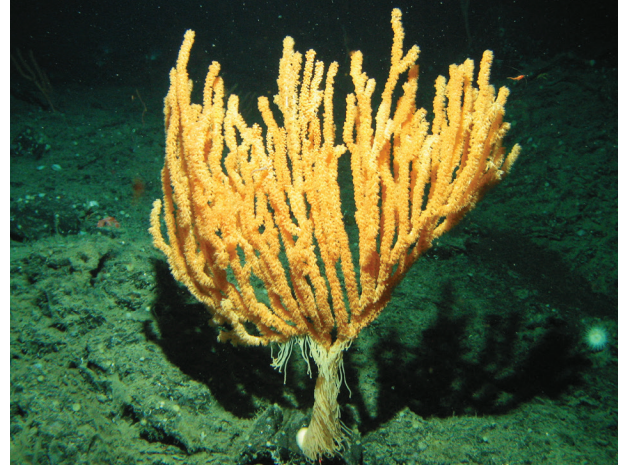


Figure 7. The bamboo coral, *Isidella tentaculum*, from Giacomini Seamount in the Gulf of Alaska. Photo credit: NOAA and the Woods Hole Oceanographic Institution Alvin Group.

situ tagging study by Parrish and Roark (2009) observed no measurable change in the size of Hawaiian gold coral colonies over nine years, which is consistent with the slow growth, long-lived age estimates using radiocarbon dating. Based on radiocarbon results, and counter indicative to sclerochronology estimates, the Western Pacific Fishery Management Council implemented a 5-year moratorium on gold coral harvesting in 2008, which was subsequently extended through 2018.

II.3. Precious Coral

Corals in the Family Coralliidae (e.g., pink and red corals in the genus *Corallium*) have been a historical part of the precious coral (Figure 6) fishery in many parts of the world, primarily in the Mediterranean and western north Pacific (Bruckner and Roberts 2009). Most of these fisheries have been strongly impacted by fishing effort that exceeds sustainable growth. Age estimates based on a variety of petrographic (carbonate structure) and organic band counting are generally consistent with

ages estimated using radiometric techniques. Colony age estimates range between 50 and 180 years, with radial growth rates less than $1 \text{ mm}\cdot\text{yr}^{-1}$ (Druffel et al. 1990, Marschal et al. 2004, Andrews et al. 2005, Roark et al. 2006, Luan et al. 2013). In addition, deeper water *Corallium* species appear to grow more slowly than shallower species (Roberts et al. 2009), making them more vulnerable to exploitation. This has led to cautionary measures in some regions where deep-water *Corallium* is known to exist (DeVogelaere et al. 2005).

II.4. Bamboo & Other Octocoral

Radiocarbon and bomb-radiocarbon dating of living bamboo corals (Family Isididae) (Figure 7) range from 50 to 420 years and radial growth rates ranging 50 to $100 \text{ }\mu\text{m}\cdot\text{yr}^{-1}$ (Roark et al. 2005, Sherwood et al. 2009, Hill et al. 2011, Sinclair et al. 2011, Thresher et al. 2011, Farmer et al. 2015). Based on the timely response of the bomb radiocarbon signal, it is likely that there is a correspondence of growth with surface water productivity. A recent innovation in lead-210 dating using a higher



resolution approach provided age estimates of 50 to 100 years for bamboo coral in the NE Pacific (Andrews et al. 2009). Given that radial growth rates for this group appear to be less than $200 \mu\text{m}\cdot\text{yr}^{-1}$, this group is susceptible to disturbance and removal because recovery would take decades.

Red tree corals (Family Primnoidae) can reach over 2 m in height and are among the most important habitat-forming gorgonian corals in the Northeast Pacific and Northwest Atlantic. Maximum ages of live-collected red tree coral specimens from Eastern Canada (*Primnoa resedaeformis*) were ~ 78 -100 years (Sherwood et al. 2005, Sherwood and Edinger 2009) and from the Northeast Pacific (*Primnoa pacifica*) were ~ 119-185 years (Andrews et al. 2002, Aranha et al. 2014). Estimated average radial growth rates of *P. pacifica* of $320\text{-}360 \mu\text{m}\cdot\text{yr}^{-1}$ were faster than those of the sister species, *P. resedaeformis*, in the Atlantic (Aranha et al. 2014). Sub-fossil (i.e., dead corals whose remains are not fully fossilized) specimens of *P. resedaeformis* were estimated to be at least 700 years old (Sherwood et al. 2006).

Ages and radial growth rates of other deepwater gorgonian corals have been reported for *Muricella* sp. (Family: Acanthogorgiidae; ~50 and 100 years; $100\text{-}200 \mu\text{m}\cdot\text{yr}^{-1}$) from the 100 m depth range in the tropical Pacific (Williams and Grottoli 2010); and from the Northeast Atlantic, *Paramuricea* sp. (Family: Plexauridae; ~ 70 – 100 years; $92\text{-}205 \mu\text{m}\cdot\text{yr}^{-1}$; depth 814-850 m) and *Paragorgia arborea* (Family: Paragorgiidae; 80 years; $830 \mu\text{m}\cdot\text{yr}^{-1}$; depth 814-850 m) (Sherwood and Edinger 2009). From the Gulf of Mexico, Prouty et al. (2014b) reported life spans of over 600 years for *Paramuricea biscaya*, with radial growth rates between $0.34 \mu\text{m yr}^{-1}$ and $14.20 \mu\text{m yr}^{-1}$ and linear growth rates from 0.019 cm yr^{-1} to over 1 cm yr^{-1} .

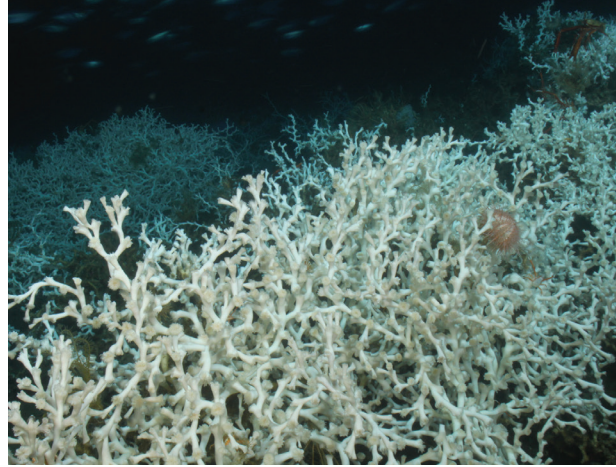


Figure 8. Stony coral Lophelia pertusa in the Gulf of Mexico. Photo credit: NOAA and Bureau of Ocean Energy Management Lophelia II Project.

II.5. Stony Coral

A few species of scleractinian corals, especially *Lophelia pertusa* (Figure 8), *Solenosmilia variabilis*, and *Oculina varicosa*, (and to a lesser extent *Enallopsammia rostrata*, *E. profunda*, *Madrepora oculata* and *Goniocorella dumosa*) create deepwater coral reefs or bioherms. These massive and ancient structures can be up to 30 m high and 10's of kilometers in length (Reed 2004, Roberts et al. 2009). *Lophelia* reefs from lower latitudes, like those off of NW-Africa, the Mid-Atlantic Ridge and the Western Mediterranean Sea, indicate their structural growth represents 50,000 years of accumulation, according to U/Th dating (Schroder-Ritzrau et al. 2005). Higher latitude *Lophelia* carbonate mounds, appear to have gone through alternating cycles of accumulation and die off over periods of centuries that appear to be tied to changes in oceanographic conditions associated with glacial-interglacial cycles (Roberts et al. 2009) and the North Atlantic sub-polar gyre (Douarin et al. 2013). Individual colonies of *L. pertusa* from bioherms in the northeastern



Atlantic exhibited axial growth rates of 5-26 mm·yr⁻¹ based on in situ measurements, aquaria observations, isotopic analyses and estimates of age inferred from growth on artificial structures (Mortensen and Rapp 1998, Mortensen 2001, Gass and Roberts 2006). Results with transplanted *L. pertusa* in the Gulf of Mexico exhibited axial growth rates of up to 16 mm·yr⁻¹ with new polyps exhibiting higher growth rates and more mature polyps at rates of ≤5 mm·yr⁻¹ (Brooke and Young 2009). Observations of *L. pertusa* colonies on oil rigs and shipwrecks in the northern Gulf of Mexico (320-995 m depths) yielded minimum calculated growth rates ranging from 3.2 to 32.3 mm·yr⁻¹ (Larcom et al. 2014).

Azooxanthellate *Oculina varicosa* has a geographically restricted distribution and forms reef-like structures in relatively shallow water (70 – 100 m). An axial branch growth rate of 16.1 mm·yr⁻¹ was measured in-situ for *O. varicosa* at 80 m depth (Reed 1981). Similar axial growth rates were found for *Madrepora oculata* (14.4 ± 1.1 mm·yr⁻¹) using lead-210 dating for samples collected off Norway (Sabatier et al. 2011).

Solenosmilia variabilis is the dominant reef-building coral on seamounts in the southwest Pacific, where it occurs at depths significantly deeper than the Northern hemisphere *L. pertusa* reefs. Fallon et al. (2014) reported growth rates of from 0.84 – 1.25 mm·yr⁻¹ linear extension for colonies collected between 958 and 1,454 m. The authors estimated a coral accumulation rate of ~ 0.27 mm·yr⁻¹, indicating that recovery from trawl damage would likely be extremely slow. Neil et al. (2011) found similar linear growth rates for *S. variabilis* in on Chatham Rise in New Zealand (ranging from 0.3 to 1.3 mm·yr⁻¹) and estimated that it could take 380 to 1,700 years for colonies to grow to a maximum height of 1 m.

Enallopsammia rostrata (Family Dendrophylliidae) is an aborescent stony coral that creates massive dendritic colonies up to 1 m wide and 0.5 m tall. Uranium-thorium dating of specimens from the Line Islands (Houlbreque et al. 2010), and lead-210 dating of a single North Atlantic specimen, have documented longevity up to ~600 years with axial extension rates of 5 mm·yr⁻¹ a radial growth rate of ~0.07 mm·yr⁻¹ near its base (Adkins et al. 2004). The structure of *E. rostrata* is prone to 'shedding' (natural limb loss) and as a consequence accurate estimates of axial growth rates are difficult to determine.

Other members of the stony corals have different growth structures. The solitary cup coral *Desmophyllum dianthus* has a slow axial extension rate of 0.5-2.0 mm·yr⁻¹ based on lead-210, radiocarbon, and U/Th dating techniques (Cheng et al. 2000, Adkins et al. 2002, 2004).

III. Paleoclimate and Paleoenvironmental Studies using Deep-Sea Corals

The utility of deep-sea corals in understanding past climate variability is closely tied to accurately dating the corals specimens (Robinson et al. 2014). Equally important is the development of environmental proxies for the temperature and elemental composition of the water in which the coral grew. As such, a fundamental goal in deep-sea coral paleoclimate research has been to determine how environmental conditions are captured in the coral skeleton records. Both solitary and colonial, as well as calcitic and proteinaceous deep-sea coral species, are being used for climate change studies. Increased geographic distribution of sampling, coupled with advances in micro-analytical sampling techniques and recognition of novel



biogeochemical proxies, have advanced the field and are providing insights on climate variability at century to millennial time-scales.

III.1. Paleothermometry

Deep ocean circulation plays a vital role in modulating and stabilizing the Earth's climate system, because the deep ocean stores and transports heat. Using radiocarbon captured within the skeletons of deep-sea corals, researchers have examined how the ocean has behaved in the past, in terms of rates of circulation and carbon exchange between different water bodies (e.g., Mangini et al. 1998, Frank et al. 2004). Evidence from deep-sea coral records indicate that the deep ocean circulation can change abruptly, on timescales as short as 10 years (Adkins et al. 1998, Eltgroth et al. 2006). Such changes may have a major impact on global temperatures (Robinson et al. 2005), atmospheric carbon concentrations (Burke and Robinson 2012), and deep-sea organisms (Sutherland et al. 2012). Recent studies also indicate that tracers, such as the isotopic composition of neodymium from living and fossil deep-sea coral species (*L. pertusa*, *D. dianthus* and *M. oculata*), may have value in reconstructing ocean circulation patterns, particularly those operating during the last 10,000 years (van de Flierdt et al. 2006, 2010, Copard et al. 2012, Lopez Correa et al. 2012, Montero-Serrano et al. 2013).

To understand historical climate and ocean circulation changes, it is critical to reconstruct changes in seawater temperature. Ocean temperature reconstructions are challenging because biological processes also affect skeletal chemical compositions. The chemical composition of the skeleton is thus controlled by two main factors: 1) the external environment (e.g., temperature),

and 2) biological activity (referred to as 'vital' effects). In deep-sea corals, these vital effects may be larger than environmental controls in elemental tracers, such as oxygen isotopes ($\delta^{18}\text{O}$) or trace metal ratios (e.g., Mg/Ca), which are typically used as temperature proxies in other marine organisms. However, by taking an average of multiple analyses it is possible to calculate environmental temperatures from single specimens based on direct and indirect comparisons (Smith et al. 2000, Adkins et al. 2003, Hill et al. 2011). Additional methods that show promise for temperature reconstruction include the ratio of Mg/Li in coral skeletons (Case et al. 2010, Montagna 2014) and "clumped" carbon and oxygen isotopes that act independently of vital effects (Thiagarajan et al. 2011). One important caveat for all of these methods is that calculated uncertainties for the paleothermometry estimates can range from 0.5 to 2°C. The utility of reconstructing small-scale temperature changes in the deep-sea is limited by the precision of the technique as well as temporal precision and accuracy. Efforts are underway by a number of research groups to increase the precision and resolution with which deep-water temperatures can be reconstructed.

III.2. Nutrient and Trophic Level Proxies

Proteinaceous deep-sea corals, such as black corals, gorgonians (e.g., *Primnoa* spp.), and the colonial zoanthids gold corals (formerly known as *Gerardia* sp.), derive their skeletal protein from recently exported particulate organic matter from the surface. From a compositional perspective, these corals are somewhat analogous to sediment traps, integrating the geochemical signature of recently exported organic matter into their slow growing skeletal structure. Useful



geochemical signatures captured in skeletal protein include radiocarbon and stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes, which can be used to reconstruct nutrient sources and cycling as well as food web (trophic) dynamics through time. Elemental composition, such as phosphorus and barium, in both stony corals and gorgonians, can also be used in studies of seawater nutrients variability.

III.2.i – Nitrogen

With sufficient understanding of the nitrogen dynamics of a particular region, including the $\delta^{15}\text{N}$ of sinking and suspended particulate organic matter, skeletal $\delta^{15}\text{N}$ may be used in reconstructions of local trophic and/or nutrient dynamics. In the Gulf of Mexico and the South Atlantic Bight, marked increases over the past 75 years in coral skeletal $\delta^{15}\text{N}$ exceed 3‰, indicating there has been a higher contribution of terrestrial effluent to the deep sea (Williams et al. 2007). In the western tropical Pacific, multi-decadal decreases in $\delta^{15}\text{N}$ values from specimens at the base of the euphotic zone suggest a gradually shallowing of the nutricline (nutrient gradient) (Williams and Grotolli 2010). Off Tasmania, records of bulk $\delta^{15}\text{N}$ indicate relatively stable nutrient and trophic conditions over the past 250 years (Sherwood et al. 2009). In instances where the cause of skeletal stable isotopic variability is ambiguous, analysis of the $\delta^{15}\text{N}$ of amino acids ($\delta^{15}\text{N-AA}$) has emerged as a powerful tool to separate and independently track the effects of source nutrients, trophic transfers and microbial activity (McCarthy et al. 2007, Prouty et al. 2014a). Using *Primnoa resedaeformis* samples from Nova Scotia, Canada, Sherwood et al. (2011) pioneered the application of $\delta^{15}\text{N-AA}$ to deep-sea corals, demonstrating a nutrient regime shift in the western North Atlantic since the 1970s. These studies underscore the broad

potential for proteinaceous deep-sea corals in paleoceanographic studies linking nutrient and trophic variability to changes in global climate.

III.2.ii – Phosphorous and Barium

In addition to using isotopic studies from proteinaceous corals as proxies for nutrient input to the deep sea, two elements that have also been used are phosphorus and barium. Phosphorus is a key nutrient in global primary productivity. It is used by organisms at the ocean surface and concentrates at depth. As a result, variations in seawater phosphorus reflect changes in surface ocean biological production and cycling (Montagna et al. 2006). As a proxy for seawater phosphate, phosphorus to calcium (P/Ca) ratios have been studied in the deep-sea coral *D. dianthus* (Montagna et al. 2006, Anagnostou et al. 2011). These global studies have shown a relationship between seawater phosphate and coral skeletal P/Ca ratios (Montagna et al. 2006, Anagnostou et al. 2011), suggesting that coral P/Ca has the potential to reconstruct variations in biological productivity on annual to decadal time-scales. Seawater barium, which also displays nutrient-like behavior in seawater, such that coral Ba/Ca ratios have the potential to trace the history of intermediate and deep-water refractory (slowly decomposed) nutrients, such as silica (Anagnostou et al. 2011, LaVigne et al. 2011, Sinclair et al. 2011).

III.3. Ocean Acidification

Ocean acidification is predicted to have profound implications for marine ecosystems partly because carbonate ions are an essential part of coral calcification. Changes to carbonate ion chemistry may particularly affect deep-water corals because carbonate



levels are already low (Guinotte et al. 2006, Turley et al. 2007, Thresher et al. 2011). Instrument and modeling studies indicate that seawater carbonate chemistry (carbon dioxide, pH, total dissolved inorganic carbon and alkalinity) is changing due to uptake of anthropogenic carbon dioxide (CO₂) from the atmosphere. In addition, it is likely that there were large changes during major climate events of the past. One way to examine the response of the ocean and deep-sea corals to large perturbations to the carbon cycle is to use geochemical proxies that record pH within the coral skeletons.

Boron isotopes ($\delta^{11}\text{B}$) in biogenic carbonates have been established as a proxy for seawater pH due to preferential uptake of the borate ion relative to boric acid as a function of pH (Vengosh et al. 1991, Hemming and Hanson 1992). Experimental relationships between pH and $\delta^{11}\text{B}$ have been determined in both surface and deep-water scleractinian corals, indicating a relationship between carbonate $\delta^{11}\text{B}$ and seawater pH (Reynaud et al. 2004, Blamart et al. 2007, Maier et al. 2009, Trotter et al. 2011, McCulloch et al. 2012a). However, $\delta^{11}\text{B}$ values higher than predicted for seawater pH have been observed in these studies (e.g., Vengosh et al. 1991, Blamart et al. 2007, Trotter et al. 2011). In an effort to reconcile these observations, scientists have found that aragonitic (CaCO₃) forming corals (e.g., stony corals) are able to regulate internal pH at the site of calcification (McCulloch et al. 2012a, 2012b). This may explain how some deep-sea corals can calcify at levels below the aragonite saturation horizon, which suggests deep-sea corals may be influenced less by decreasing seawater pH than originally thought (McCulloch et al. 2012a, 2012b, Hennige et al. 2015). Therefore, one must be cognizant of the fact that the research is evolving and presently there are conflicting results.

III.4. Challenges

The geochemical archives derived from deep-sea corals have enormous potential to help scientists decipher and describe changes and variability of paleoenvironmental and paleoceanographic conditions through time. However, it is inherently difficult to determine the accuracy of predictive relationships in the coral skeleton relative to the seawater environment from field data. Analyses of deep-water taxa are constrained by the challenges of collecting and sampling the organisms and sparse environmental data for use in validating relationships in ambient deep-sea environmental conditions. Deep-sea coral research is still in its infancy in terms of understanding variability between locations, depth strata, as well as taxonomic orders. For example, Thresher et al. (2010) suggest that adaptation to local conditions and hence a role for physiology at higher taxonomic levels may occur in deep-sea corals. Therefore challenges still exist to better constrain the species-dependent effect and to identify the causes of inter-species differences and intra-colony age and growth variability (Carreiro-Silva et al. 2013).

Studies employing advanced micro-analytical techniques have confirmed that micrometer scale heterogeneity influences the geochemical signal in deep-sea corals. Recent studies on stony corals show that the main differences in minor/trace element compositions, stable isotopes and organic compounds occur between calcification centers and fibrous aragonite (Gagnon et al. 2007, Rollion-Bard et al. 2009, López Correa et al. 2010). Biomineralization processes exerting a strong biological control on the skeletal formation can overwhelm signals caused by environmental conditions (Adkins et al. 2003, Gagnon et al. 2007). Systematic studies of the isotopic and



trace metal variation in various biocarbonates, combined with detailed studies of deep-sea coral skeletal structure are critically needed to decipher the role of “vital effects” on the application of these proxies to paleoclimate studies.

IV. New Directions

There are several new directions being pursued in an attempt to successfully use deep-sea corals as reliable archives of seawater chemistry and oceanographic proxies to climate change research. Given that many common tracers in the carbonate skeletons of deep-sea corals are strongly affected by physiological processes during biomineralization (i.e., “vital effects”), there is a need to increase our knowledge of the characteristics and mechanisms of vital effects. In other words, how can we tease apart the strong biological fractionation that is superimposed on the environmental signal? Focused studies, such as addressing the question of how the fluid reservoir from which calcification occurs is linked to the surrounding seawater, are becoming increasingly important as we refine our understanding of the various coral calcification models and strategies to reduce bias from vital effects. The introduction of micro-analytical sampling techniques, such as micromilling, ion microprobes, laser-ablation and highly focused synchrotron radiation, has made it possible to investigate coral intraskeletal variability of trace element and stable isotopic compositions directly related to the ultra-structure of the skeleton (Rollion-Bard et al. 2009, Thresher et al. 2009, 2010, Case et al. 2010, López Correa et al. 2010, Sinclair et al. 2011). Therefore, we need to couple these high-resolution measurements to increase knowledge of present day processes affecting the coral communities.

As previously mentioned, from a compositional perspective, proteinaceous corals are somewhat analogous to sediment traps since they depend on surface-derived particulate organic matter. Therefore, age and growth studies should be accompanied by sediment trap studies that can clarify how the elemental and isotopic composition of particulate organic matter (i.e., food source) is captured or represented in the deep-sea coral skeletal chemistry. Additional focused studies should include the collection of appropriate coral specimens along with food sources and particulate and dissolved nutrients from the same location to clarify our understanding of feeding habits, prey type, timing and seasonality, as well as the impact of microbial activity of food sources on geochemical signatures encoded in corals. Examination of new specimens from different nutrient and oceanographic regimes, integration of isotopic and trace elemental geochemical signals, and use of new techniques such as the $\delta^{15}\text{N}$ of skeletal amino acids will aid in understanding past nutrient and trophic dynamics in the oceans, including reconstructions of source nitrogen variability and phytoplankton trophic and community structure.

A paramount challenge to the application and utilization of paleoenvironmental reconstructions using deep-sea corals is the precision, fidelity, and resolution of independently derived age-models (e.g., Komugabe et al. 2014), regardless of whether they are radiometric or based on sclerochronology. A particularly challenging time period is the ‘near instrumental’ period of the last several hundred years where radiocarbon is insensitive and sample size requirements make Th/U, in general, untenable for a well resolved chronology. Anthropogenic tracers with known or reconstructed emission histories (e.g., Pb, Pb-isotopes, As, Cd, Hg) and proxies of



disturbance events of known age may provide regional tie points (e.g., Schuster et al. 2002, Kelly et al. 2009) that could be coupled to radiometric chronologies. For example, Andrews et al. (2009) applied a refined lead-210 dating technique to yield relatively high-precision growth rate and age determinations for bamboo corals living during the last 100 years. Inter-disciplinary studies that use multiple chronological approaches with cross-validation of sclerochronological features are also necessary. Validation of the timing and cause of sclerochronological features have the potential to refine chronologies. Advances in deep-sea coral research continue to highlight the growing importance of deep-sea corals as reliable marine archives of climate change and other environmental cycles. Like their shallow-dwelling counterparts, deep-sea corals have also proven to be important archives of past ocean variability. While challenges still exist to providing reliable, reproducible records of climate variability, recent advances provide new opportunities and directions to close this gap.

Information on growth rate and life span of deep-sea corals is essential for conservation and management because the life history of these prominent organisms is either poorly understood or unknown. Validated age and growth of these organisms is the most fundamental information on susceptibility to disturbance or removal. Early estimates of age and longevity have been roughly determined, but more advanced techniques hold promise in not only determining longevity, but variations in growth through ontogeny (Andrews et al. 2009, Roark et al. 2009, Carriero-Silva et al. 2013). Assessment of the vulnerability of these long-lived, habitat-forming organisms to both natural and anthropogenic perturbations is of paramount importance because recovery may involve life history aspects that are not currently

considered. Once some or many of these coral species are lost to damage or removal, many are not likely to return within our lifetime. Even in terms of minor damage, some arborescent corals have shown little to no recovery in nearly a decade of no disturbance (Krieger 2002, Williams et al. 2010). In addition, there is evidence that energy may be focused on regenerative growth within the broken colony in lieu of reproductive effort (Waller and Tyler 2005). For the longest-lived members of the deep-sea corals, perhaps it is prudent to take on a perspective of value in terms of world heritage, analogous to ancient terrestrial forests.

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Euplectella aspergillum glass sponge in the northwestern Gulf of Mexico. Courtesy of the NOAA Office of Ocean Exploration and Research.



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1. Introduction

This chapter provides an update and summary of the current state of knowledge of deep (> 50 m) azooxanthellate coral and sponge communities on hard-bottom habitats in the northern Gulf of Mexico (GoM) from the U.S.-Mexico border to the Florida Straits. This is an update since the first State of Deep-Sea Coral Ecosystems of the U.S. report (Lumsden et al. 2007) on the GoM by Brooke and Schroeder (2007)¹. The chapter will focus on new material but also touch on some additional background information important in the context of deep corals and sponges not presented in 2007.

The GoM is unique in many ways, partly due to unusual geological history and resulting physiographic features that provide substrate for deep corals and sponges. The deep Gulf, from the outer portions of the continental shelf near 150 m depth across the continental slope to some of the deepest portions near 3,000 m depth, is

¹The 2007 GoM report (Brooke and Schroeder 2007) also included information on the Florida Straits up to Biscayne Bay on the east coast of Florida. This geographic area is covered in the Southeast U.S. chapter of the current volume.

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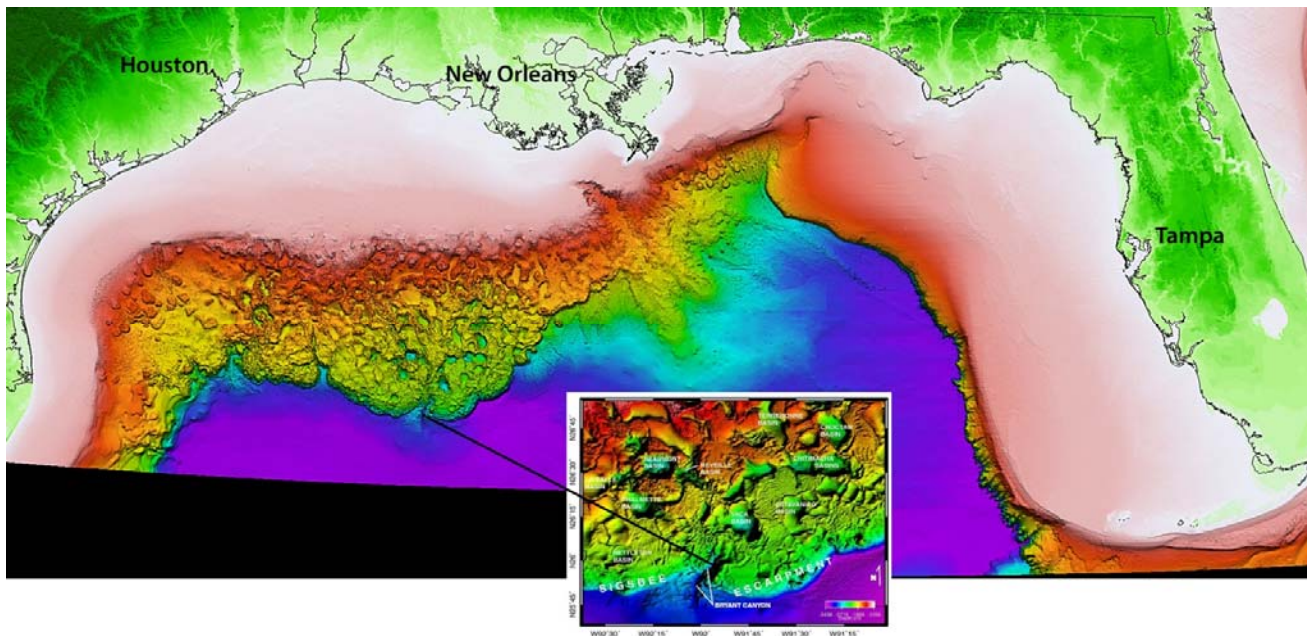


Figure 1. Multibeam bathymetry of the northern Gulf of Mexico with depth shading of continental slope below 100 m showing the complexity of the slope. Created from industry-acquired 3-D seismic data processed at 50 foot bin size by the Bureau of Ocean Energy Management. Inset shows the Sigsbee Escarpment.

generally considered one of the most geologically complex continental slopes in the world (Figure 1). The geological complexity of the GoM supports a high diversity of deep corals, each adapted to different environmental conditions (described broadly in Roberts et al. 2009). The vast majority (> 99%) of the substrate in the central and western portion of the deep northern GoM is composed of soft sediments in mixtures of fine sand, silt and clay (Rowe and Kennicutt 2009). Sea pens, cup corals and bamboo corals can occur in soft sediments, occasionally in high abundance over a large area (Gallaway et al. 1988, Rowe and Kennicutt 2009). However, the highest diversity of large structure-forming coral and sponge epifauna tends to occur on hard bottom. In the mesophotic zone (30-150 m), some of the

limited hard substrate is of biogenic origin (e.g. drowned Pleistocene coral reefs). Many other areas on the continental shelf are influenced by movement of underlying salt deposits that can raise the seabed to form banks or mounds where in some cases, such as the Flower Garden Banks, diverse zooxanthellate coral communities can develop. In one location, the only known example, basalt spires form a volcanic chimney that is exposed at Alderdice Bank. Hard-bottom habitats below 200-300 m are primarily the result of diapirism of Jurassic-age salt associated with trapping and migration of hydrocarbons.

Salt diapirism or 'salt tectonics' produced hundreds of banks and mounds along the continental slope in the northern region (west



of the Florida Escarpment), because salts typically are buoyant relative to overlying sediments. Fissures in sediment overlying salt domes can allow trapped hydrocarbons to seep upwards to the seafloor which become a food source for bacterial chemosynthesis at the seep interface resulting in deposition of authigenic (generated in place) carbonates which can form large rocky features with moderate relief and patchy distribution. Carbonates either develop above the soft bottom substrate or become exposed over time. Carbonate structures associated with former and extant hydrocarbon seeps provide substantial habitat for deep corals and sponges in the northern GoM shelf and slope region (CSA 2007, Brooks et al. 2016).

In contrast, the Florida platform and escarpment along the eastern Gulf were formed by deposition and consolidation of sediments created by a variety of mechanisms including deposition by carbonate-producing organisms such as corals and mollusks (Hine 2009). The Bureau of Ocean Energy Management (BOEM) subdivides the GoM into three operational areas; Western, Central and Eastern (termed Planning Areas), each with different levels of industrial development and agency mission-oriented research investment (although many studies are ecosystem-based and include Gulf-wide locations and objectives). The northern central GoM (Central Planning Area) is historically the most active for research and exploration. Due to a moratorium on drilling offshore, the eastern GoM is less explored.

Since the last State of Deep-Sea Coral Ecosystems report (Brooke and Schroeder 2007)

there has been an increase in exploration and research of the deep coral and sponge assemblages of the West Florida shelf and slope. Although data are limited, explorations to date suggest that the extent of hard-bottom habitat is large and the abundance and diversity of corals and sponges is high.

II. New Exploration and Research

Research on deep corals in the GoM has intensified substantially over the last decade. Since 2007, at least 52 research cruises have taken place in this region (Tables 1-2). A number of large multidisciplinary interagency projects have greatly expanded the number of known deep coral habitats in the GoM, and increased our knowledge of their distribution and community structure, as well as dispersal, growth and reproduction of key species.

Federally sponsored explorations of the deep GoM were planned for 2008-2012, but the 2010 GoM oil spill resulting from the blowout of the Macondo well and the sinking of *Deepwater Horizon* (DWH) drilling platform at a depth of 1,522 m was a major environmental event with profound ramifications for research and management. One effect of the spill was a dramatic increase in research effort as part of the federally mandated Natural Resource Damage Assessment (NRDA) for DWH. NRDA conducted multi-year investigations of deep corals in the mesophotic zone (depth range 65-90 m), and in the deep-sea (depth 1500 m and more). These studies included investigations of

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Table 1. Research expeditions targeting deep-sea coral and sponge habitats in the Gulf of Mexico since 2007.

Date	Vessel	Underwater vehicle	Sites	Notes
Mesophotic Coral Habitat Exploration by Flower Garden Banks National Marine Sanctuary				
Mar. 2007	M/V <i>Carolyn Choest</i>	HOV <i>Argus/NRI</i>	Horseshoe, Rankin/Bright, EFG and WFG,	Secrets of the Gulf Expedition - Dr. Robert Ballard
May 2009	R/V <i>Manta</i>	ROV <i>Phantom</i>	Stetson, McGrail and MacNeil Banks	
May 2010	R/V <i>Manta</i>	ROV <i>Phantom</i>	EFG and WFG	NCCOS
May 2011	R/V <i>Manta</i>	ROV <i>Phantom</i>	EFG and WFG	NCCOS
Aug.-Sep. 2012	R/V <i>Manta</i>	ROV <i>Phantom</i>	EFG and WFG	NCCOS
Oct. 2013	R/V <i>Manta</i>	ROV <i>Mohawk</i>	EFG	
Jul. 2015	R/V <i>Manta</i>	ROV <i>Mohawk</i>	McGrail, Bright and Geyer Banks	FAU/CIOERT/Voss Lab
Jul. 2015	R/V <i>Manta</i>	ROV <i>Mohawk</i>	Stetson Bank	Stetson Bank LTM
Jul. 2015	R/V <i>Manta</i>	ROV <i>Mohawk</i>	EFG, Horseshoe, Rankin, Bright, Rezak, Elvers, Sidner, Bouma, Bryant, Alderdice and Parker Banks	
BOEM/NOAA OER; Chemo III 3rd Field Sampling Expedition				
Jun.-Jul. 2007	R/V <i>Ronald H. Brown</i>	ROV <i>Jason II</i>	Chemo III primary sites, GB697, AT320, GC852, GB647, GC645, AC601	Spectacular <i>Madrepora</i> colonies at 1,400 m at GC852
BOEM/NOAA OER; Lophelia II				
Sep.-Oct. 2008	R/V <i>Nancy Foster</i>	ROV <i>Sea Vision</i>	4 shipwrecks, 13 coral sites	
Jun.-Jul. 2009	R/V <i>Brooks McCall</i>	AUV <i>Sentry</i>	8 coral sites	
Aug.-Sep. 2009	R/V <i>Ronald H. Brown</i>	ROV <i>Jason II</i>	5 shipwrecks, 12 coral sites	10 new coral sites
Oct.-Nov. 2010	R/V <i>Ronald H. Brown</i>	ROV <i>Jason II</i>	2 shipwrecks, 15 coral sites	5 new coral sites, first observation of corals impacted by <i>Deepwater Horizon</i> spill at block MC294.
Jul. 2012	R/V <i>Brooks McCall</i>	ROV <i>Kraken II</i>	5 deep-water oil and gas structures	4 surface structures, 1 subsea installation
USGS Collaboration Expeditions for Lophelia II				
Oct. 2008	R/V <i>Nancy Foster</i>	ROV <i>Sea Vision</i>	VK826, 862/906, West Florida Shelf	
Sep. 2009	R/V <i>Seward Johnson</i>	HOV <i>Johnson Sea Link</i>	VK826, 862/906, West Florida Shelf	
Sep.-Oct. 2010	R/V <i>Cape Hatteras</i>	ROV <i>Kraken II</i>	VK826, 862/906, West Florida Shelf	
Oct. 2010	R/V <i>Arctic Sunrise</i>	HOV <i>Dual DeepWorker</i>	VK862/906	Lander deployment
Oct.-Nov. 2011	R/V <i>Ronald H. Brown</i>	ROV <i>Jason II</i>	West Florida Shelf	
Oct.-Nov. 2011	R/V <i>Tommy Munroe</i>	ROV <i>Global Explorer</i>	VK862/906	Lander recovery
Florida Shelf Edge Exploration (FloSEE); NOAA OER, Cooperative Institute for Ocean Exploration, Research and Technology				
Jul. 2010	R/V <i>Seward Johnson</i>	HOV <i>Johnson Sea Link</i>	West Florida Shelf to Alabama	
Sep. 2011	R/V <i>Nancy Foster</i>	ROV <i>Kraken II</i>	West Florida Shelf to Alabama	
Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG); Ocean Exploration Trust				
Jul. 2013	E/V <i>Nautilus</i>	ROV <i>Hercules</i>	All Gulf	
Jun. 2014	E/V <i>Nautilus</i>	ROV <i>Hercules</i>	All Gulf	
Apr.-May 2015	E/V <i>Nautilus</i>	ROV <i>Hercules</i>	All Gulf	
BOEM study; Deep-Water Reconnaissance of Potentially Sensitive Biological Features				
Oct. 2011	R/V <i>Manta</i>	ROV <i>Phantom</i>	Horseshoe and 29 Fathom Banks	
Sep. 2012	R/V <i>Manta</i>	ROV <i>Phantom</i>	Rankin and 28 Fathom	
Sep. 2012	R/V <i>Manta</i>	ROV <i>Phantom</i>	28 Fathom, Bright, Geyer	
Apr. 2013	R/V <i>Manta</i>	ROV <i>Phantom</i>	Alderdice and Rezak	
Apr.-May 2013	R/V <i>Manta</i>	ROV <i>Phantom</i>	Rezak, Bouma, Sonnier	
Jun. 2013	R/V <i>Manta</i>	ROV <i>Phantom</i>	Elvers and McGrail	
Jun. 2013	R/V <i>Manta</i>	ROV <i>Phantom</i>	Sidner and Parker	

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Table 1. continued.

Date	Vessel	Underwater vehicle	Sites	Notes
Gulf of Mexico Exploration; NOAA OER				
Apr. 2012	E/V <i>Okeanos Explorer</i>	ROV <i>Deep Discoverer</i>	Northwest Gulf	EX1202
May 2012	E/V <i>Okeanos Explorer</i>	ROV <i>Deep Discoverer</i>	Florida Escarpment and Straits, Northeast Gulf	EX1203
Apr. 2014	E/V <i>Okeanos Explorer</i>	ROV <i>Deep Discoverer</i>	All Gulf	EX1402
Gulf of Mexico Exploration; Alvin				
Apr.-May 2014	R/V <i>Atlantis II</i>	HOV <i>Alvin</i>	North central Gulf	Science mission on deep coral and chemosynthetic community sites
Schmidt Ocean Institute Exploration, Mapping and Long-Term Effects of the DWH Spill				
Aug. 2012	R/V <i>Falkor</i>	ROV <i>Global Explorer</i>	Northeast Gulf	Deep-sea coral shakedown expedition
Sep. 2012	R/V <i>Falkor</i>	ROV <i>Global Explorer</i>	Northwest Gulf, Texas Banks	Mapping of South Texas Banks
Nov. 2012	R/V <i>Falkor</i>	ROV <i>Global Explorer</i>	Northwest Gulf	Long-term effects of DWH spill
General Exploration; Ocean Exploration Trust				
Mar. 2012	R/V <i>Maria S. Merian</i>	ROV <i>Cherokee</i>	West and southwest Florida slope	General cold-water coral ecosystem exploration including other areas in southern GoM and outside GoM
Jul. 2014	E/V <i>Nautilus</i>	ROV <i>Hercules</i>	All Gulf	Exploring the unknown Gulf of Mexico

Table 2. Research expeditions after Deepwater Horizon spill to assess deep-water coral damages.

Date	Vessel	Underwater Vehicle	Sites	Notes
Natural Resources Damage Assessment Cruises				
Jul. 2010	R/V <i>Nancy Foster</i>	ROV <i>Global Explorer</i>	VK sites and MC751	
Aug. 2010	R/V <i>Nancy Foster</i>	ROV <i>Global Explorer</i>	Alabama Alps, Roughtongue Reef, Coral Trees Reef	Mesophotic reef assessment
Nov. 2010	R/V <i>Brooks McCall</i>	Drift Camera	Well site and MC334	MC344 corals discovered
Mar. 2011	HOS <i>Sweetwater</i>	Industry ROV	MC294 and MC118	
Apr. 2011	R/V <i>McArthur</i>	AUV <i>Sentry</i>	Well site vicinity	5 new sites found
Aug. 2011	M/V <i>Holiday Choest</i>	UHD Shilling Robotics	Alabama Alps, Roughtongue Reef, Yellowtail Reef, Coral Trees Reef, Madison-Swanson South Reef	Mesophotic reef assessment
Oct. 2011	M/V <i>Holiday Choest</i>	UHD Shilling Robotics	previously discovered sites	
Jun.-Jul. 2014	R/V <i>Walton Smith</i>	ROV <i>Global Explorer</i>	Alabama Alps, Roughtongue Reef, Yellowtail Reef, Coral Trees Reef, Madison-Swanson South Reef, Madison-Swanson North Reef	Mesophotic reef assessment
ECOGIG Expeditions (Ecosystem Impacts of Oil and Gas Inputs to the Gulf - Part of Gulf of Mexico Research Initiative)				
Nov. 2012	R/V <i>Falkor</i>	ROV <i>GE</i>	Impacted and control sites	Additional exploration
Jun. 2013	R/V <i>Nautilus</i>	ROV <i>Hercules</i>	Impacted and control sites	Additional exploration
Jun.-Jul. 2014	R/V <i>Nautilus</i>	ROV <i>Hercules</i>	Impacted and control sites	Additional exploration
Other Cruises Associated with Damage Assessment				
Dec. 2010	R/V <i>Atlantis</i>	HOV <i>Alvin</i> , AUV <i>Sentry</i>	Return to MC294 and MC344	
Mar. 2012	E/V <i>Okeanos Explorer</i>	ROV <i>Deep Discoverer</i>	Portion of virtual cruise, previous coral sites	Additional exploration



coral associated communities of fish, red crabs, infaunal and epifaunal invertebrates in surrounding soft sediments. Each of the relevant major developments will be discussed in more detail below. New deep coral research since 2007 can be divided into three broad categories.

- Continental slope studies; applied science and exploration missions (Table 1);
- Continental shelf studies of mesophotic reef habitats (Table 1);
- DWH-related response and NRDA cruises (Table 2).

II.1. Continental Slope Studies

II.1.i – Large federal interdisciplinary studies

Two large federal multidisciplinary deep-water studies have been completed since 2007, sponsored by the National Oceanographic Partnership Program (NOPP) and funded by BOEM and the National Oceanic and Atmospheric Administration (NOAA) through the Office of Exploration and Research (OER). The intention of these studies was to conduct research that addresses the needs of BOEM, which is charged with regulating the development of oil and gas resources in the deep GoM in an environmentally sound manner. The exploratory mission and other agency objectives of NOAA OER were also met. These studies had complimentary projects separately funded by United States Geological Survey (USGS), and are briefly described below:

a. Investigations of chemosynthetic communities on the lower continental slope of the GoM, (Chemo III): 2005-2009

This multidisciplinary study was initiated by partners BOEM and NOAA OER in 2005 to investigate both chemosynthetic and coral communities at depths below 1,000 m. This depth zone had received little research effort because regional submergence facilities (e.g., the *Johnson Sea Link* submersibles) were limited to ~1,000 m depth. Three major cruises were conducted during the Chemo III study including the use of the *Alvin* manned submersible and the remotely operated vehicle (ROV) *Jason II*. At most of the 13 primary study sites there were observations of at least a few large colonial cnidarians; however, only one site (in lease block GC852) visited during this study was found to have a diverse coral community. This site included three species of scleractinian structure-forming corals (*Madrepora oculata*, *Enallopsammia rostrata* and *Solenosmilia variabilis*) at a depth of 1,435 m (Brooks et al. 2014, Brooks et al. 2016).

In a related study, USGS partners conducted a series of cruises (2006–2009) visiting a subset of Chemo III stations. This research incorporated a variety of additional research topics, including tropho-dynamics of fish populations and mid-water trawl collections above deep coral communities to investigate connectivity. USGS researchers also returned to a shallower deep coral site within Viosca Knoll lease block 826 (VK826, 500-700 m). This is a well-known deep coral site that was a primary focus during the earlier *Lophelia I* research program (funded by

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BOEM) from 2004-2007 (CSA 2007). The USGS cruises included additional study sites at Viosca Knoll, Atwater Canyon, Alaminos Canyon, and Green Canyon (Demopoulos et al. 2010, Ross et al. 2012).

b. Exploration and research of northern GoM deep-water natural and artificial hard-bottom habitats with emphasis on coral communities: reefs, rigs and wrecks (Lophelia II): 2008-2012

Lophelia II was the second of the BOEM and NOAA OER studies on deep coral ecosystems in the GoM, and this represented a continuation and expansion of Lophelia I. As with the previous BOEM studies, Lophelia II brought together numerous collaborating groups and again partnered with USGS to continue the exploration and research of deep coral communities in the deep GoM (Brooks et al. 2016). Lophelia I spanning 2004-2007 was referenced in Brooke and Schroeder (2007) but the report was final in July 2007 (CSA 2007).

The partnership between federal and academic scientists included exploration and research at three different types of deep-water habitats: natural reefs, shipwrecks and offshore energy platforms in water depths ranging from 300 to 2,700 m. One primary goal of the study was to develop a robust capability for predicting the occurrence of rich cnidarian hard-bottom communities in the deep GoM, with emphasis on scleractinian coral assemblages. In addition, long-term monitoring stations were established

to study change over time along with laboratory experiments to provide a more comprehensive understanding of the processes that control the occurrence and distribution of *Lophelia pertusa* in the GoM (Larcom et al. 2014, Lunden et al. 2014, Brooks et al. 2016).

A total of five Lophelia II cruises (eight including USGS cruises) were completed between 2008 and 2012 (Table 1). During these cruises, researchers discovered new coral-dominated sites on the northern GoM slope and the west Florida Escarpment, documented coral colonization of shipwrecks and deep-water offshore platforms, and documented changes at sites discovered during Lophelia I. The shipwreck and platform components of the Lophelia II study represented important additions to the understanding of coral habitats. Eight wreck sites were surveyed to depths of over 2,100 m, in addition to those described previously (Brooke and Schroeder 2007, Church et al. 2007). Many had extensive coral cover (Larcom et al. 2014, Brooks et al. 2016). A total of 24 natural habitat study sites were surveyed with an ROV during the project. Community structure, biodiversity and biogeography of corals and associates were addressed by different techniques including photographic transects, photo mosaics, quantitative collections of community components and molecular methods.

Lophelia II had strong collaboration with USGS scientists, which was highlighted on the USGS DISCOVRE Program website.² A series of

²<http://fl.biology.usgs.gov/DISCOVRE/gom.html>

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reports were produced summarizing the Lophelia II findings beginning with a final BOEM interim report in 2012 (Brooks et al. 2012) followed by the BOEM final report in 2016 (Brooks et al. 2016). Numerous blogs, mission essays, images, video clips, and other information were also made available from expedition webpages for each cruise in 2008, 2009, 2010, and 2012 on the NOAA Ocean Explorer website. The USGS final report is in revision (Demopoulos et al. in revision) but other publications were completed and are available (e.g., Morrison et al. 2011, Prouty et al. 2016).

II.1.ii – Other deep-sea expeditions in the GoM since 2007

In addition to the Lophelia II studies, several other deep coral explorations have taken place in the Gulf since 2007 (Table 1). The *Johnson-Sea-Link II* manned submersible supported the Florida Shelf Edge Expedition (FloSEE) in 2010 and followed up one year later aboard NOAA ship *Nancy Foster* in 2011 deploying the *Kraken II* ROV. The R/V *Seward Johnson* and *Johnson-Sea-Link II* submersible concluded its legacy in the GoM in 2010. Harbor Branch Oceanographic Institute (HBOI) operated the vessel since 1985, but the vessel was sold in 2010. The NOAA ship *Okeanos Explorer* (2012 and 2014) and Ocean Exploration Trust's E/V *Nautilus* (2013, 2014, and 2015) engaged in telepresence cruises that provided shore-based observers real-time remote access to images of deep coral habitats using fiber-optic ROV feeds from the GoM seafloor.

Two new research platforms had maiden dives to deep coral and sponge habitats in the GoM. The R/V *Falkor* (Schmidt Ocean Institute) conducted ROV dives during its Deep-Sea Coral Shakedown Expedition in August 2012, with subsequent cruises to the South Texas Banks (September 2012) and other previously explored sites (November 2012). The R/V *Falkor* and E/V *Nautilus* both supported deep coral investigations by the Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG) consortium funded through the Gulf of Mexico Research Initiative. The *Alvin II* submersible (Woods Hole Oceanographic Institution) also conducted its first science dives in the GoM (March – June 2014, dives no. 4679-4737) on a science verification cruise focusing on deep-water seep habitats in the northwestern GoM and the Florida Escarpment, funded by the National Science Foundation (NSF).

II.1.iii – Highlights of research findings from the continental slope

Valuable new information has become available from the many field and experimental studies, including data on the survival and growth rate of *L. pertusa* (Brooke and Young 2009, Larcom et al. 2014, Lunden et al. 2014), the extreme longevity of black corals in the genus *Leiopathes* (Prouty et al. 2011) and gorgonian octocorals in the genus *Paramuricea* (Prouty et al. 2016), as well as the vulnerability of these corals to pollution and disturbance (Hsing et al. 2013, DeLeo et al. 2016). The branching stony coral *L. pertusa* was found to grow in thickets on offshore energy platforms and shipwrecks with



linear extension rates of 1-2 cm/yr on average (Larcom et al. 2014). Large *Paramuricea* and *Leiopathes* colonies (> 1 m) between 300-1,500 m depth were found to reach ages of 660 years for *Paramuricea* and as old as 2,100 years for *Leiopathes* (Prouty et al. 2016). The growth rates of these corals may depend on their proximity to major nutrient resources like the Mississippi River (Prouty et al. 2011) or the Loop Current. Because these corals are heterotrophic suspension feeders, it is worth noting that resource availability is likely to vary on finer scales as well, for example on different sides of a mound or canyon feature which may also contribute to different growth rates.

A few long-term monitoring studies measured bottom currents over extended (one year) and short-term periods in the northern Gulf. Long-term studies showed maximum bottom currents peaked at only 22.6 cm/s at the 1,420 m GC852 site, but a substantial peak of 60 cm/s occurred at the shallower 440 m site at Viosca Knoll (VK826, Brooks et al. 2016). Average current speed at VK826 was 8 cm/s, but there were periodic shifts in the current from west to east, corresponding with a decrease in temperature and salinity (Mienis et al. 2012) that suggest two alternating water masses impinging on the reef. Sediment traps were deployed at VK826 as well to identify and quantify sources of nutrition to the suspension feeding benthic assemblage. Two food pathways to *Lophelia* were identified from trap samples: sinking organic matter (phytodetritus) from the Mississippi River and vertically migrating zooplankton (Mienis et al. 2012).

Significant contributions were made regarding the associations and limits of temperature, salinity, dissolved oxygen and aragonite saturation states for *L. pertusa* at natural reefs (Davies et al. 2010, Davies and Guinotte 2011, Mienis et al. 2012, Lunden et al. 2013) and in aquaria (Brooks et al. 2012, Lunden et al. 2014, Brooks et al. 2016). The environmental conditions at natural reefs were similar to those recorded for *Lophelia* reefs in the eastern North Atlantic, though dissolved oxygen and density were lower in the GoM (Davies et al. 2010). Interestingly, the aragonite saturation state was found to be lower at sites where *L. pertusa* was present than at sites where it was absent, suggesting that this factor was likely not an exclusive control of *L. pertusa* presence in the deep GoM (Lunden et al. 2013). The thermal tolerance of *L. pertusa* was also investigated. Experimental studies suggest that a temperature threshold occurs near 12 °C (Brooks et al. 2016). These results will help scientists and managers to understand the effects of climate change on deep coral habitats now and in the future.

II.2. Continental Shelf Studies of Mesophotic Habitats

The mesophotic zone is a transition zone between shallow reefs in the photic zone and deep coral and sponge ecosystems in the aphotic zone. These habitats occur between 30 and about 130 m depths on the continental shelf (this report includes heterotrophic corals in this zone at depths \geq 50 m under the broad term deep corals). Reefs occur on substrate related to

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salt domes fossil structures and other hard bottom features in the northern and eastern GoM on the Florida Shelf. The total area of mesophotic seafloor habitat in the GoM is vast, estimated by Locker et al. (2010) to be 178,885 km² (between 30-100 m), an order of magnitude larger than that depth zone of the U.S. Caribbean or the main Hawaiian Islands, at 3,892 km² and 3,299 km², respectively. The GoM continental shelf is broad and slopes gently, allowing mesophotic ecosystems to occur further offshore than in other parts of U.S. waters. These reefs may be more isolated from nearshore effects, like fishing intensity and nutrient runoff (Locker et al. 2010).

Epicenters of new research in the GoM mesophotic zone since 2007 were in three primary regions: (1) the Northwestern GoM, including the Flower Garden Banks National Marine Sanctuary (FGBNMS) and the South Texas Banks off the coast of Texas, (2) the Pinnacle Trend in the northern Gulf off Louisiana, Alabama and Mississippi, and (3) Pulley Ridge in the southeastern Gulf off Florida. Research on these ecosystems since the late 1970s has focused on exploration of hard bottom banks and mounds elevated above surrounding soft-bottom substrate in order to understand the character and abundance of the associated biological communities. Manned submersibles (Bright and Rezak 1978, Reed et al. 2005, 2006) and ROVs (Gittings et al. 1992, Weaver et al. 2002, Schmahl and Hickerson 2006) were used to explore and characterize dozens of pinnacles, banks and mounds in the Gulf's mesophotic zone, and most were

reported as good habitat for scleractinian, antipatharian, stylasterid and gorgonian corals.

The purchase of a Forum Energy Technologies Mohawk ROV by the National Marine Sanctuary Foundation (NMSF) in 2013 has increased the exploration and characterization capabilities of the region. This science class ROV is operated by the University of North Carolina at Wilmington, Undersea Vehicle Program through an NMSF agreement. The vehicle is depth rated to 600 m and currently outfitted for operations down to 365 m.

II.2.i – New research in the northwestern GoM

The FGBNMS has conducted biological surveys since 2001 on reefs and banks in the Northwestern GoM to document the occurrence of deep corals and sponges within and outside the Sanctuary. The FGBNMS and partners have conducted 17 ROV cruises to visit a total of 16 banks between 2007-2015. Octocoral and black corals are abundant and diverse components of the benthic assemblages explored by these ROV expeditions. Survey photos and videos since 2003 were analyzed as part of a doctoral dissertation on octocorals (Etnoyer 2009) and a master's thesis on mesophotic black corals (Nuttall 2013) at Texas A&M University. The deep coral assemblages of the nearby South Texas Banks were mapped, surveyed and explored as well (Rodriguez 2015). Additionally, Dr. Suzanne Fredericq from the University of Louisiana – Lafayette, is investigating algae populations on the Northwestern GoM reefs and banks, including

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comparisons of areas affected by DWH (Felder et al. 2014). The information on the complexity of shelf-edge habitats from these surveys, and the imagery data obtained by FGBNMS and USGS, has helped to support management planning and development of proposed

extensive numbers of features with significant relief revealed by multibeam data that lie outside No Activity Zones. This collaborative project began in 2011 in partnership with Louisiana Universities Marine Consortium, FGBNMS, and the University of North Carolina

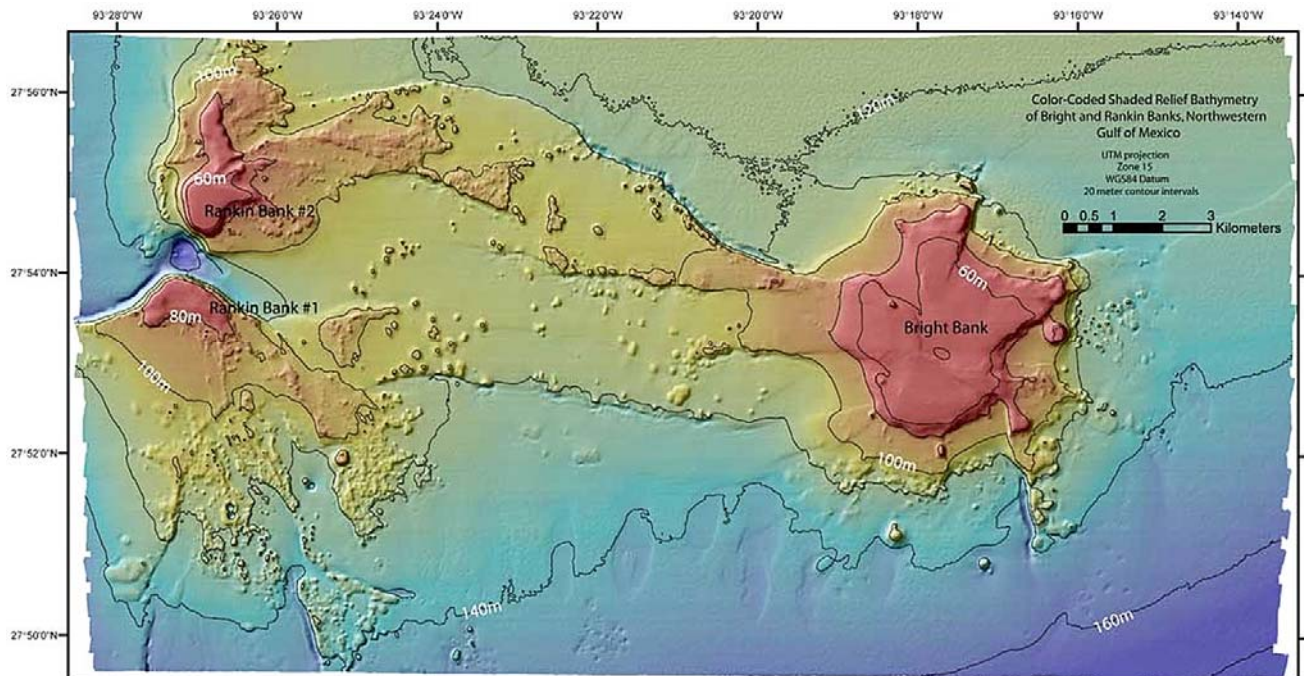


Figure 2. High-resolution multibeam bathymetry map of the Bright and Rankin Banks showing complex topography and features. Red shaded areas represent BOEM no activity zones above a depth of 85 m. (Images courtesy of USGS, <http://walrus.wr.usgs.gov/pacmaps/wg-index.html>).

sanctuary expansion plans. The investigations described above and the multibeam surveys of numerous GoM topographic features published by Gardner et al. (1998, 2002; Figure 2) prompted a broad new study awarded by BOEM in 2011. The purpose was to investigate the significance of features outside of existing BOEM environmental protection areas called No Activity Zones that prohibit all energy development activities. Figure 2 illustrates

at Wilmington Undersea Vehicle Program. The objective of this project was to survey outside No Activity Zones and inside core-biological zones to investigate habitat and species composition at these newly discovered bathymetric features (Sammarco et al. 2016). The first ROV cruises took place in October 2011, and continued through 2013 with two cruises in September 2012, two cruises in April 2013 and two cruises in June 2013 (see Table 1).

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Results of continued research will lead to more refined adaptive management and protective measures for these Potentially Sensitive Biological Features including the potential expansion of No Activity Zones.

In addition to the efforts by FGBNMS, NOAA's National Center for Coastal Ocean Science (NCCOS) conducted quantitative surveys in the mesophotic depth ranges of the Sanctuary. The project was titled "Fish and Benthic Communities of the FGBNMS: Science to Support Sanctuary Management" (Clark et al. 2014). The Cooperative Institute for Ocean Exploration, Research and Technology (CIOERT) also initiated investigations of hermatypic corals in the mesophotic depth ranges at the FGBNMS and Bright and McGrail Banks. In 2011, the NOAA ship *Nancy Foster* mapped Elvers Bank over an area of 30 km². Mapping has also taken place at Parker, Ewing, and Claypile Banks by FGBNMS and Texas A&M University. An online GIS-based mapping tool was developed to allow for virtual exploration of these deep-water habitats.³ Catalogs of the major biological components are available through this portal.

The FGBNMS is actively pursuing an expansion plan that draws on these studies to support the incorporation of additional mesophotic reefs and banks in the northwest region. A draft environmental impact statement addressing

sanctuary expansion was released on June 10, 2016, and presents a range of alternatives, including a preferred alternative recommending the addition of fifteen banks to the Sanctuary, which would increase the protected area from 56.21 miles² to 383.19 miles². This recommendation stemmed directly from the mapping, exploration and characterization activities in the region.

II.2.ii – New research in the Pinnacle Trend region

In the Northeastern GoM, mesophotic reef research has focused on the deep-water reefs of the Pinnacle Trend off Mississippi, Alabama and Louisiana (Alabama Alps, Roughtongue Reef and Yellowtail Reef) and on Coral Trees Reef and Madison Swanson Marine Reserve reefs south of the Florida panhandle. The Pinnacle Trend reefs were below the oil slick created by DWH spill for a period of several weeks (Figure 3). These surveys commenced in August 2010, three months after the spill, following a period of little research activity on deep corals and sponges in that area since 2003. New studies reported on the density, health and condition of gorgonian and black corals in relation to days below the oil slick, polyaromatic hydrocarbons (PAHs) in tissues and sediments, as well as fishing gear impacts (Silva et al. 2015, Etnoyer et al. 2016), in a 20-year retrospective analysis of ROV surveys.

³http://www.ncddc.noaa.gov/website/google_maps/FGB/mapsFGB.htm

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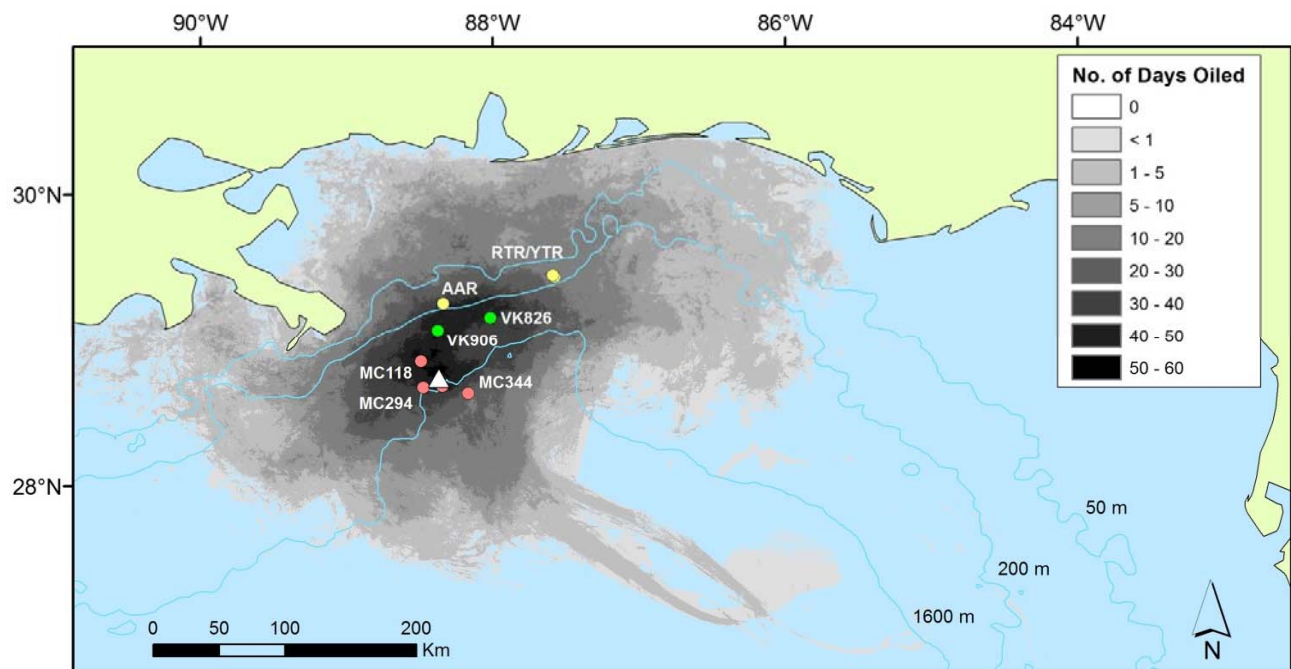


Figure 3. Map showing known deep-sea coral aggregations (colored circles) in relation to the extent and duration of the surface oil slick produced by the Deepwater Horizon blowout at Macondo wellhead in lease MC252 (white triangle). Yellow circles represent mesophotic reefs at Alabama Alps Reef (AAR), Yellowtail Reef (YTR) and Roughtongue Reef (RTR); green circles represent *Lophelia pertusa* reefs at Viosca Knoll; red circles represent deep gorgonian sites near Macondo wellhead (MC) at 850-1,850 m.

II.2.iii – New research in the GoM including Pulley Ridge

Research since 2007 in the Eastern GoM has focused on Pulley Ridge and Tortugas reefs, and shelf-edge habitats at Sticky Grounds, Madison-Swanson and Steamboat Lumps. These are true mesophotic reefs of zooxanthellate corals (*Leptoseris* and *Agaricia*) in deep-water to 90 m (Collier et al. 2015).

Harbor Branch Oceanographic Institute at Florida Atlantic University (HBOI-FAU) led the Florida Shelf Edge Ecosystem (FloSEE) cruises in 2010 and 2011 under the auspices of CIOERT (Table 1). Results were detailed in reports by Reed and Rogers (2011), Reed and Farrington

(2012), and Reed et al. (2012 a, b, c). One focus of the FloSEE work was in response to DWH, but the original intent of the effort was to characterize poorly known mesophotic and deep-water habitats on the West Florida Shelf using the *Mohawk* ROV, operated by UNCW-Undersea Vehicles Program.

Another project in the Eastern GoM mesophotic zone was titled “Connectivity of the Pulley Ridge – South Florida Coral Reef Ecosystem.” Field expeditions took place in August 2012 and 2013 (Reed et al. 2014), sponsored by NOAA’s NCCOS Center for Sponsored Coastal Ocean Research (CSCOR) and NOAA OER. The 5-year, \$5 million project focused on population



connectivity, specifically the role that mesophotic reefs may play in replenishing corals, fish and other organisms in downstream reefs of the Florida Keys and Dry Tortugas. The studies were primarily concerned with zooxanthellate corals and fishes in the mesophotic zone, but deep-water heterotrophic octocorals were documented as well (Table 1).

II.3. Research associated with the DWH Oil Spill

The DWH oil spill in April 2010 catalyzed a large number of assessment and research activities, including substantial new research on deep corals. The total volume of oil entering the GoM was approximately 651.85 million liters (172,200,000 gallons) after subtracting the volume of oil captured by various techniques (McNutt et al. 2011). This represents the second largest human-caused oil spill into the environment after the intentional 1991 Kuwait oil field destruction. During the DWH spill, the oil escaped at a depth of 1,500 m for a period of 100 days, and took the form of a submerged plume and an oil slick that was present on the sea surface and tracked by satellite for a period of several weeks (Figure 3). Deep corals were among the first benthic organisms targeted for assessment and linked to the DWH spill.

Damaged corals were discovered in lease block MC294, 11 km southwest of the Macondo well site (White et al. 2012). The area was identified as good potential for coral development by BOEM and NRDA investigators using industry 3D seismic seabed anomaly data, and

discovered during the final dive of the previously scheduled Lophelia II field sampling cruise on November 2, 2010. The main area reported in White et al. (2012) measured 10 x 12 m, and about 43 gorgonian octocorals, primarily *Paramuricea biscaya*, were documented in this area or within 10 m.

Impacts to gorgonian live tissue were observed using high-definition video from the *Jason II* ROV, and a month later, from the manned submersible *Alvin*. Injuries were observed to 86% of the corals. Analysis of hopanoid petroleum biomarkers isolated from the brown floc on the damaged corals provided strong evidence that this material contained oil from the Macondo well (White et al. 2012). A calculation based on the age of the corals and the odds of the impact happening coincidentally at this location and time (and not at any of the other 20 coral sites visited during that time period), yielded a probability of this being due to a different coincidental cause of about 0.001 (White et al. 2012). One follow-up study identified the anionic surfactant dioctyl sodium sulfosuccinate (DOSS), a component of the dispersant applied during the spill, in floc removed from one of the corals (White et al. 2014). Another recent laboratory study experimentally exposed deep-water corals (*Paramuricea* type B3, *Callogorgia delta* and *Leiopathes glaberrima*) to oil, the dispersant Corexit 9500A and mixtures of the two (Deleo et al. 2016). Under the conditions of this experiment the authors report the most severe declines in health were after exposure to dispersant alone and the oil-dispersant mixture.

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The mechanism of the impact from the spill was not determined, but White et al. (2012) suggested a possible link to the subsurface hydrocarbon plume that was detected by fluorescence and predicted from deep current models. The principal origins of the plume remain controversial and the divergent origins are discussed in most publications dealing with subsurface hydrocarbon dispersion (e.g. Hazen et al. 2010, Camilli et al. 2010, Ryerson et al. 2012, Reddy et al. 2012). In a follow up study,

along with a healthy colony. Hydroid colonization occurred on some branches originally covered with the oil-containing floc and the probability of hydroid colonization was directly proportional to the original level of impact to the colony (Hsing et al. 2013). These authors emphasize the patchy nature of the impact on both the community and individual colony scale and suggest that the impacting agent may not have been evenly dispersed in the water at the time of impact.

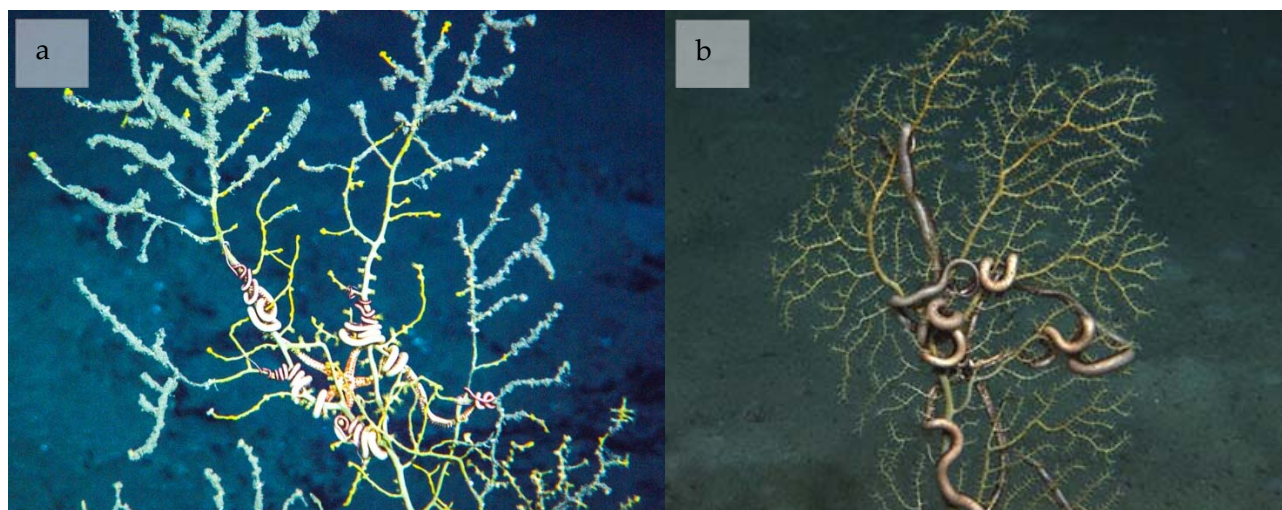


Figure 4. a) Impacted Paramuricea sp. gorgonian with symbiotic brittle star Asteroschema sp. discovered in lease block MC294 at a depth of 1,370 m, 11 km southwest of the Macondo well site on November 2, 2010. Brown floc covering coral tissue contained hopanoid petroleum biomarkers consistent with oil from the Macondo well. b) Healthy Paramuricea sp. observed in October 2010 at a depth of 360 m over 450 km away from the spill site. (Images courtesy of Lophelia II, NOAA-OER/BOEM).

Hsing et al. (2013) found that the median level of impact to coral colonies decreased over the next 17 months as some areas originally covered with floc appeared to recover. One of the impacted *Paramuricia* gorgonians discovered 6 km southeast of the Macondo well at a depth of 1,370 m is depicted in Figure 4

Fisher et al. (2014a) reported the discovery of two additional coral sites impacted by the DWH spill. One community located 6 km from the Macondo wellhead (MC297) was heavily impacted, with 49 of 68 corals showing impact to over 5% of colonies in November 2011. Another site surveyed at that time, 22 km



distant from the Macondo wellhead (MC344) and in much deeper water (1,850 m), was more lightly impacted with only 7 of 30 colonies showing some evidence of impact from the blowout. However, the depth of this site suggests that either the deep-water plume impacted the seafloor at greater depths than either models or the empirical evidence suggested, or that the impacting agent may have been oil or dispersant containing marine snow originating from the sea surface. Data on the oil content in sediment cores taken from these sites, as well as studies of the meiofauna and macrofauna present in the cores, are consistent with the coral data showing impacts to these sites resulting from the DWH blowout (Fisher et al. 2014b).

Additional studies conducted by NRDA focused on the health and condition of black corals and octocorals on mesophotic reeftop biotopes between 65-75 m depth, in relation to the number of days below the oil slick and evidence of exposure to PAHs. Pathologies in more than 400 octocoral and antipatharian corals were quantified using methods consistent with deep-water studies (Silva et al. 2015). The researchers found elevated PAHs in coral tissues and sediments, as well as demonstrable evidence of injury to corals located below the oil slick at higher frequencies than ever reported (Silva et al. 2015).

Another study with a Before-After-Control-Impact research design using video taken since 1985 showed a significant decline in octocoral health and condition at Alabama Alps Reef, Roughtongue Reef and Yellowtail Reef,

positioned directly below the oil slick (Etnoyer et al. 2016). Less than 10% of colonies exhibited injury before the oil spill, while nearly 50% of colonies exhibited injury after the oil spill, with no significant corresponding change at reference sites (Etnoyer et al. 2016). Odds of encountering injury after the spill were up to 10 times higher compared to odds of encountering injured octocorals before the spill. Although proportions could not be determined, some injuries were attributed to visible interactions with fishing line or sedimentation, while others were attributed to the effects of surface oiling and dispersants (Silva et al. 2015, Etnoyer et al. 2016). These mesophotic studies extend the potential footprint of the DWH impacts to sites nearly 100 km distant from the wellhead.

The NRDA program, and subsequently the GoM Research Initiative, supported several years of research into mesophotic and deep coral habitats to document any potential injuries to coral associated with the spill. The principal cruises that contributed information to and subsequent work on these habitats are listed in Table 2.

II.4. New Information on the Distribution of Deep-Sea Corals

Research since 2007 has expanded knowledge that mesophotic reefs and deep coral habitats are widespread throughout the GoM (although generally restricted to relatively rare hard substrates). Maps showing the locations of deep-sea coral records in the GoM are presented in the Appendix. Several new large



aggregations of corals and sponges were documented between depths of 50-2,000 m. New information has come to light showing changes with species assemblages on fine depth scales, over 10s of meters in the mesophotic zone and over 100s of meters in the deep-sea. There is also increased awareness about the mesophotic diversity of octocorals and black corals, which has been documented before (Rezak et al. 1986), but developed further using molecular techniques. Scleractinian corals have been shown to occur in zooxanthellate, azooxanthellate and apo-zooxanthellate forms, with the capacity to switch back and forth between forms (reviewed by Kahng et al. 2010).

Newly identified species in the GoM include *Oculina varicosa* aggregations near the Twin Ridges, south of Apalachicola, Florida (Barnette 2006) and a number of *Paragorgia* bubblegum corals when few, if any had been known from the Gulf before. In deeper waters (300-1,000 m), *L. pertusa*, *Leiopathes* spp. and *Madrepora* spp. have been found to be locally abundant. Primnoid octocorals (*Callogorgia* spp.) are also common in this depth range (Quattrini et al. 2013) and sometimes have catshark egg cases. Many new observations were made of *Paramuricea* octocorals, precious corals like *Corallium*, gold corals (family Chrysogorgiidae) and bamboo corals (family Isididae), which may occur in abundance as deep as 1,800 m or more (Doughty et al. 2014).

Habitat suitability models have added new insight to species distributions, and refined understanding of how depth and substrate have a significant influence on deep coral

distributions (Davies et al. 2010, Kinlan et al. 2013, Georgian et al. 2014). New models of surface productivity, particle flux and bottom currents are available as well. One previously established pattern that is well reinforced is that large, structure-forming deep corals generally prefer hard bottom substrates with moderate to high relief. In the GoM, these substrates can take the form of banks and mounds, or authigenic carbonates near hydrocarbon seeps, or artificial substrates like shipwrecks, as well as oil and gas platforms. At the time of the last report (Brooke and Schroeder 2007), the wreck of oil tanker *Gulfpenn* was considered one of the largest aggregations of *L. pertusa* in the GoM (Church et al. 2007). Its sister ship, *The Gulfoil*, was discovered during Lophelia II in 2010 and this supported a similar luxuriant community of *L. pertusa* (Figure 5). Yet, research since that time has found even larger aggregations of *L. pertusa* in natural environments, including the largest *L. pertusa* reef known to date, called Robert's Reef.

II.5. Detection of Hard-Bottom Habitats using Seismic Anomalies

New coral habitats are being discovered routinely in the GoM, because new types of information are improving researchers' abilities to detect and predict deep coral habitat. With the continued refinement of industry-acquired 3D seismic seabed anomaly locations and new exploration (ground-truthing) of these anomalies using ROVs and autonomous underwater vehicles (AUVs), it is clear now that there are many thousands of additional habitats

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with high probability for the presence of corals. The total number of positive seismic reflectivity anomalies at the seabed (representing hard substrate within about 9 m of the seafloor) is now in the vicinity of 23,000 for the northern GoM (Figure 6). These discontinuous features range in size from hundreds of meters in diameter to many kilometers. However, it cannot be assumed that all of these seafloor anomalies correlate to coral and sponge communities or even that a hard substrate is exposed on the seabed. The presence of living

of science expeditions for all the BOEM/NOAA/USGS studies between 2002-2012, including many sites chosen for the 2011 and 2012 NOAA *Okeanos Explorer* missions, and sites explored around the Macondo well during the NRDA effort (Fisher et al. 2014a).

11.5.i – Search for Lophelia Reefs using seismic anomalies

Seabed acoustic anomaly data has been relied upon heavily in recent years, directing numerous missions towards the location of

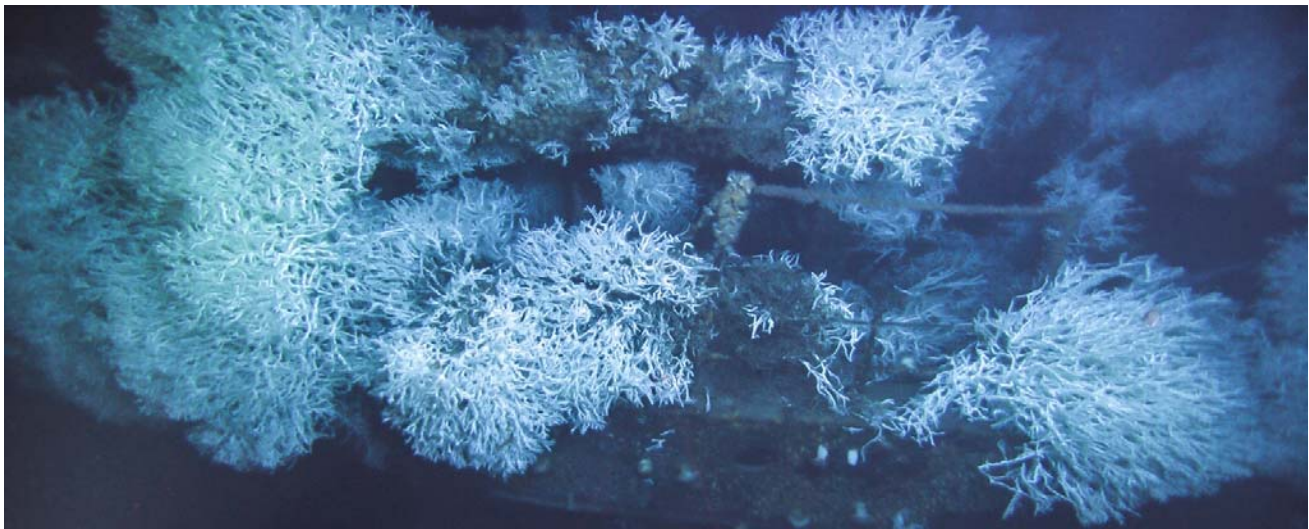


Figure 5. Extensive Lophelia growth on shipwreck Golfoil at 534 m. This ship sunk in 1942 resulting in 56 years of colonization when first surveyed in 2008. (Image courtesy of Lophelia II, NOAA-OER/BOEM).

coral or dense hardground communities on seafloor anomalies needs verification with visual exploration. Less than 100 sites (less than 0.5% of total) have visual confirmation of exposed carbonate primarily colonized by deep corals (although the success rate of finding living coral habitats is very high as a proportion of selected anomaly targets). The seismic targeting process has been a foundational part

deep coral habitat. One example can be illustrated through the story of a *Lophelia* location surveyed in 1955 by Moore and Bullis (1960). The position of the trawl catch with 300 pounds of *Lophelia* was reported to the nearest minute (29° 5' N, 88° 19' W), but there were no features in this area that could support any substantial *Lophelia* habitat. The depth of the collection in the publication correlates almost

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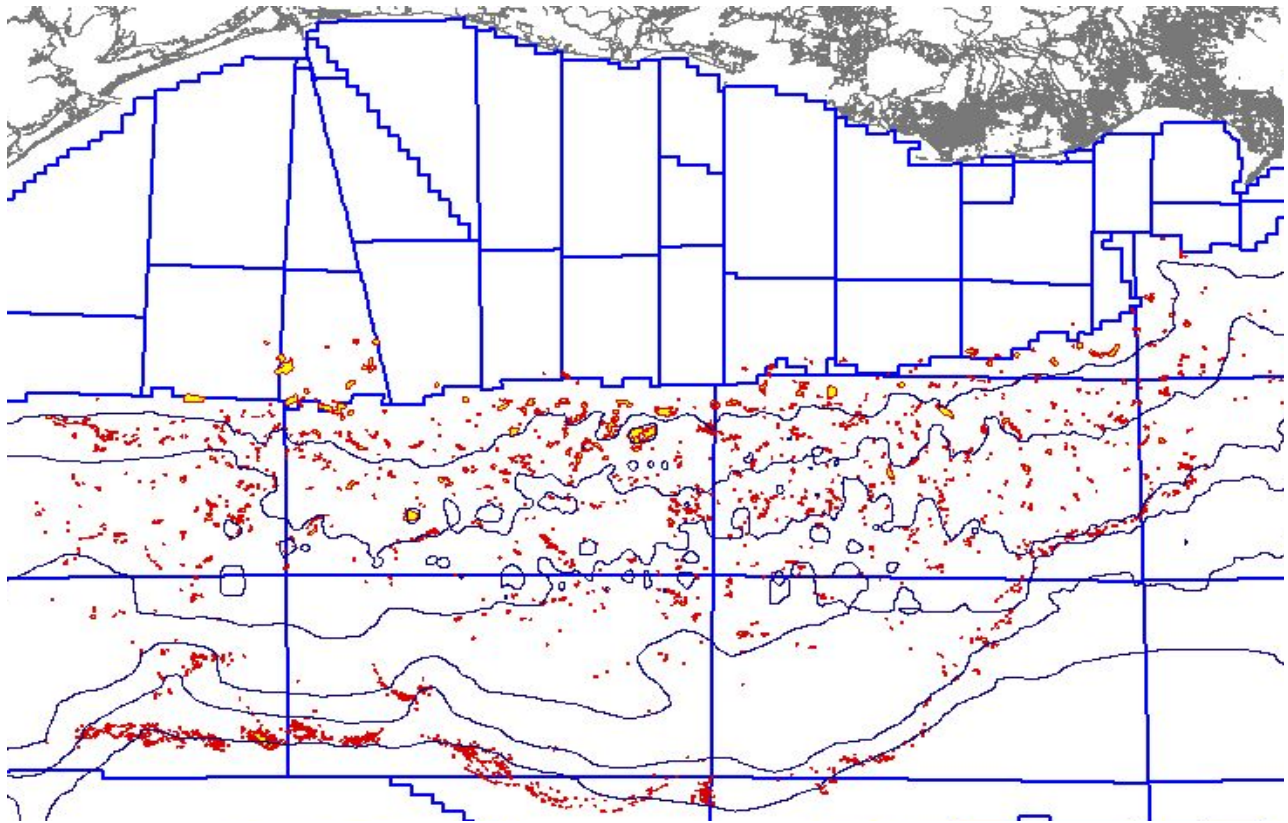


Figure 6. Continental slope of the northern Gulf of Mexico with a variety of seabed anomalies. The source 3-D seismic data are extracted for the water bottom and can represent features up to 9 m below the surface. Red polygons represent interpretation and some consolidation of complex positive reflectivity features. Other features include pockmarks from gas expulsions and negative reflectivity (potential seeps). (Image courtesy of BOEM analysis of industry-acquired 3-D seismic data).

exactly with seabed 3D seismic anomaly data (and bathymetry) of a prominent feature located about 4 miles to the west of the discovery (or rediscovery) of lush *L. pertusa* sites at Viosca Knoll 906 (Schroeder 2007).

Seismic anomalies are publicly available on a website hosted by BOEM⁴. GIS shapefiles for more than 32,000 anomalies are now available.

These data have been used to facilitate field explorations, as well as state-of-the-art habitat suitability models (Kinlan et al. 2013, Georgian et al. 2014). The most recent addition to the seismic anomaly collection is a new category for Cretaceous-aged platform-derived carbonate along the Florida Escarpment posted in 2012. One category includes talus detected on the lower Florida Escarpment. Future explorations

⁴<http://www.boem.gov/Oil-and-Gas-Energy-Program/Mapping-and-Data/Map-Gallery/Seismic-Water-Bottom-Anomalies-Map-Gallery.aspx>



Figure 7. Newly discovered expansive Lophelia community at Viosca Knoll lease block 906 (VK906) at a depth of 390 m. (Image courtesy of Lophelia II, NOAA-OER/BOEM).

off West Florida can access this information to guide their surveys.

One of the remarkable deep coral discoveries in the GoM since 2007 was a discovery in 2009 of a spectacular accumulation of *L. pertusa* and abundant black corals (*Leiopathes glaberrima*) at Robert's Reef. The location of the mound was associated with a negative seismic anomaly (Lunden et al. 2013), a short distance from earlier surveys in lease block VK862 and adjacent to the same large area of seabed

anomalies associated with most of lease blocks VK862 and VK906. The Robert's Reef site showed that *L. pertusa* can form large mounds in the northern GoM (Figure 7), not just thickets of corals. Age-dating of piston cores from Robert's Reef reaching a depth of 16 m showed the presence of *Lophelia* coral throughout the core dated by a variety of methods to span approximately 300,000 years (Brooks et al. 2016). This is important because the smaller thickets known to researchers before 2009

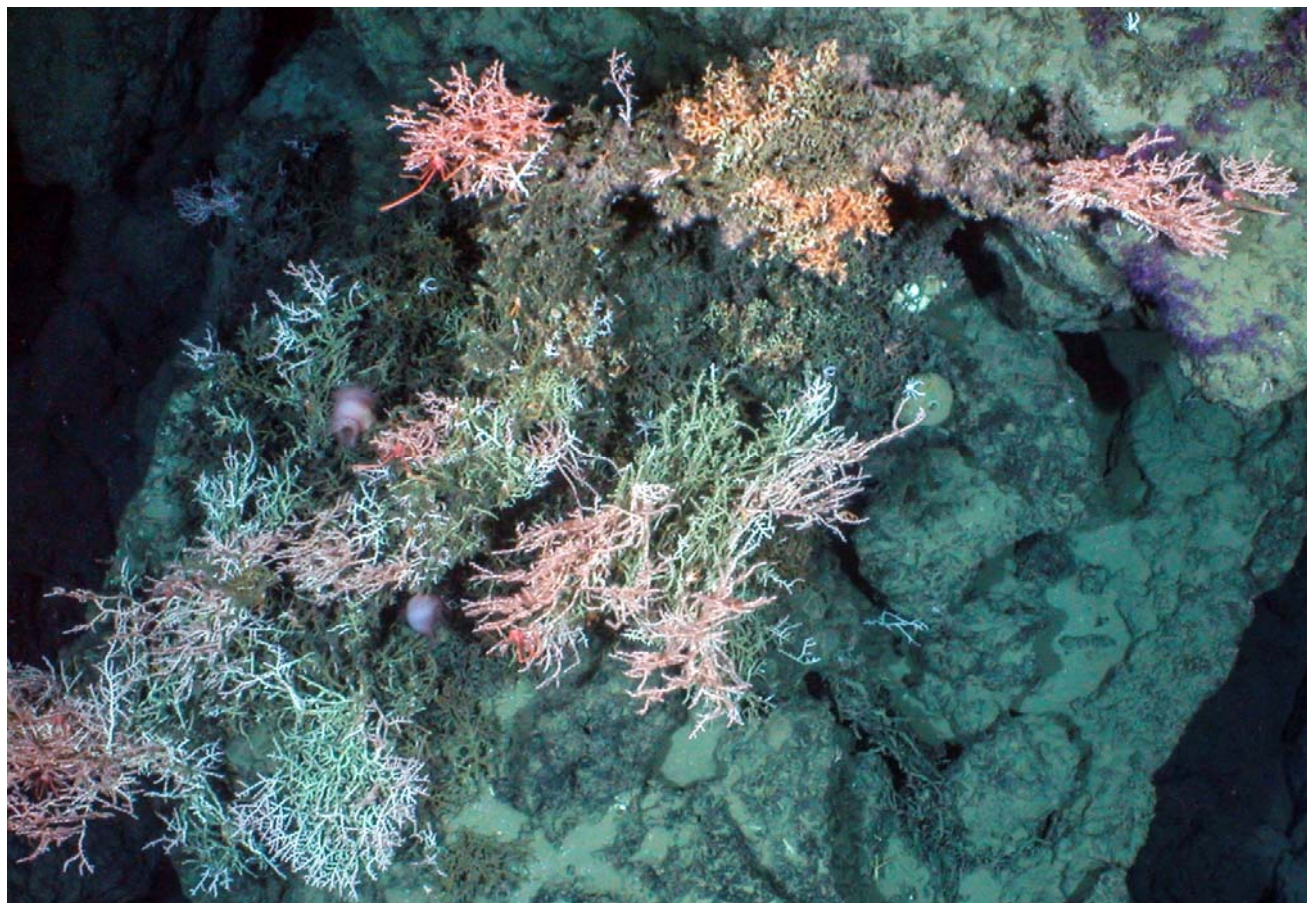


Figure 8. Extensive Madrepora oculata with its pink and white skeleton, and other species of corals including Enallopsammia rostrata and Solenosmilia variabilis from the Green Canyon 852 site at a depth of 1,410 m. (Image courtesy of Chemo II, BOEM/NOAA-OER).

suggested the Gulf may be suboptimal habitat for *L. pertusa* compared to the North Atlantic.

II.5.ii – Discovery of Madrepora Reefs from seismic anomalies

Another remarkable discovery since 2007 is that the branching stony coral *Madrepora oculata* is the dominant framework-forming scleractinian coral at depths below 800 m (Figure 8). This is in contrast to shallower depths where *M. oculata* occurs primarily as solitary colonies (Brooke and Schroeder 2007). In these deeper sites at

GC852, *Madrepora* colonies were found at 1,410 m depth, in a framework with other structure-forming corals including *Enallopsammia profunda* and *Solenosmilia variabilis*.

A second *Madrepora* site occurs at a depth of 886 m in the Mississippi Canyon (lease block MC118). This site was explored during the Lophelia II project, and hosts numerous large thickets. A third site at 1,050 m depth in lease block AT357 hosts the largest deep-water coral assemblage currently known in the central



Figure 9. Dense colony of Madrepora oculata with commensal squat lobsters at a depth of 1,050 m in Atwater Valley lease block 357 (AT357). (Image courtesy of Lophelia II, NOAA-OER/BOEM).

GoM including *Madrepora oculata* (Figure 9) and thousands of colonies of large gorgonian octocorals *Paramuricea* sp. with numerous associated species of epifauna.

II.6. Artificial Hard-Bottom Substrates; Stepping-Stones for *Lophelia* corals?

New information since 2007 suggests that artificial substrates like shipwrecks and energy platforms for offshore oil and gas may

represent important habitat and are potentially stepping-stones that connect populations of some deep corals (Brooks et al. 2016). To date, 533 structures are known from depths ≥ 50 m and 53 structures at depths ≥ 300 m. *L. pertusa* was first recognized on the deep-water

Pompano platform at a depth of 400 m during a NOAA OER cruise in 2003⁵ (Figure 10). The Lophelia II program subsequently found *L. pertusa* on three shipwrecks and all seven energy installations investigated (Brooks et al.

⁵<http://oceanexplorer.noaa.gov/explorations/03bio/welcome.html>



2016). Figure 11b is an example of a thriving *Lophelia* habitat that developed on a subsea manifold structure in lease block MC355 at a depth of 443 m from the installation date of 1991 to the time of observation in 2012. This study extended the known depth range for *L. pertusa* from 201 to 801 m depth, with the highest densities occurring near 500 m. Calculated growth rates on platforms were higher (≤ 3.2 cm/yr) than those measured using other methods at natural sites (Larcom et al. 2014). No large gorgonian or black corals were seen on the platforms, although large octocorals were present on some of the deeper and older shipwrecks investigated.

A total of seven wreck sites were investigated as part of Lophelia II. One site, the tanker *Gulfpenn* was once regarded as one of the

largest aggregations of *L. pertusa* in the GoM (Church et al. 2007, Figure 11a). The *Gulfpenn* survey was repeated from Church et al. (2007), but several new wrecks were documented in detail for the first time. Spectacular *Lophelia* coral communities were also discovered on the *Gulfoil* shipwreck, which were only distantly seen by Church et al. (2007), and another shipwreck that was named the *Ewing Bank* wreck.

II.7. Detection of *Lophelia* Reefs off Western Florida using Multibeam Data

A large extent of the west Florida shelf and slope has been mapped since 2007 using high-resolution multibeam echosounders aboard NOAA ships *Nancy Foster* (Naar 2010) and

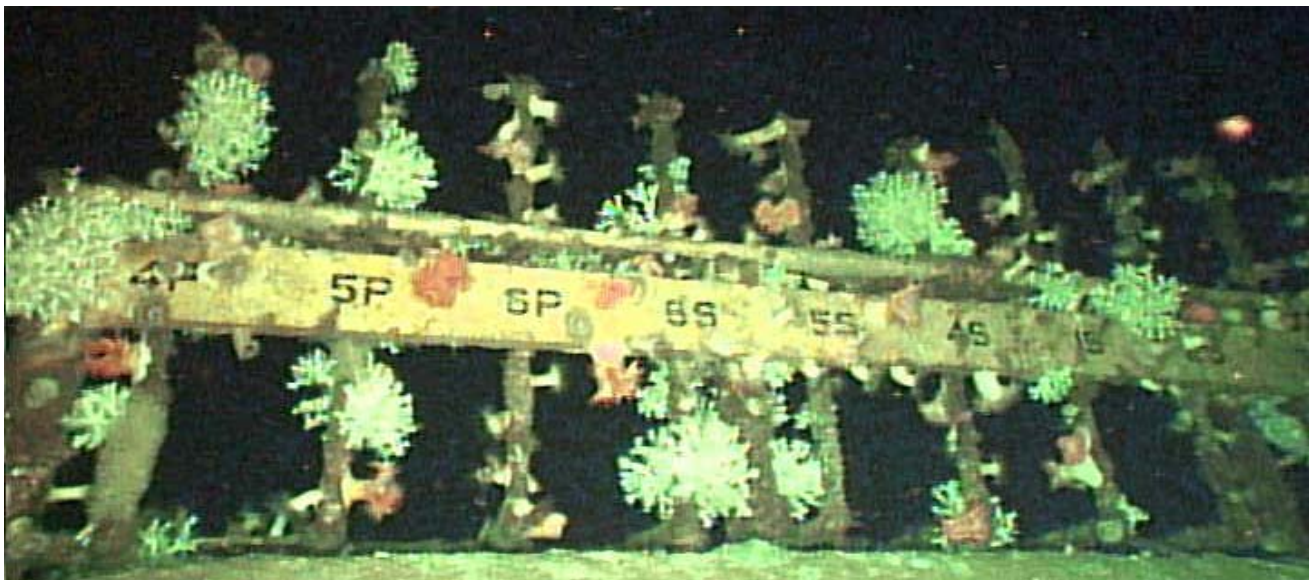


Figure 10. Numerous colonies of Lophelia coral on a portion of the Pompano platform observed in 2003, representing maximum potential development of nine years since installation in 1994 at a depth of approximately 305 m. (Image courtesy of John Reed, Harbor Branch Oceanographic Institute).

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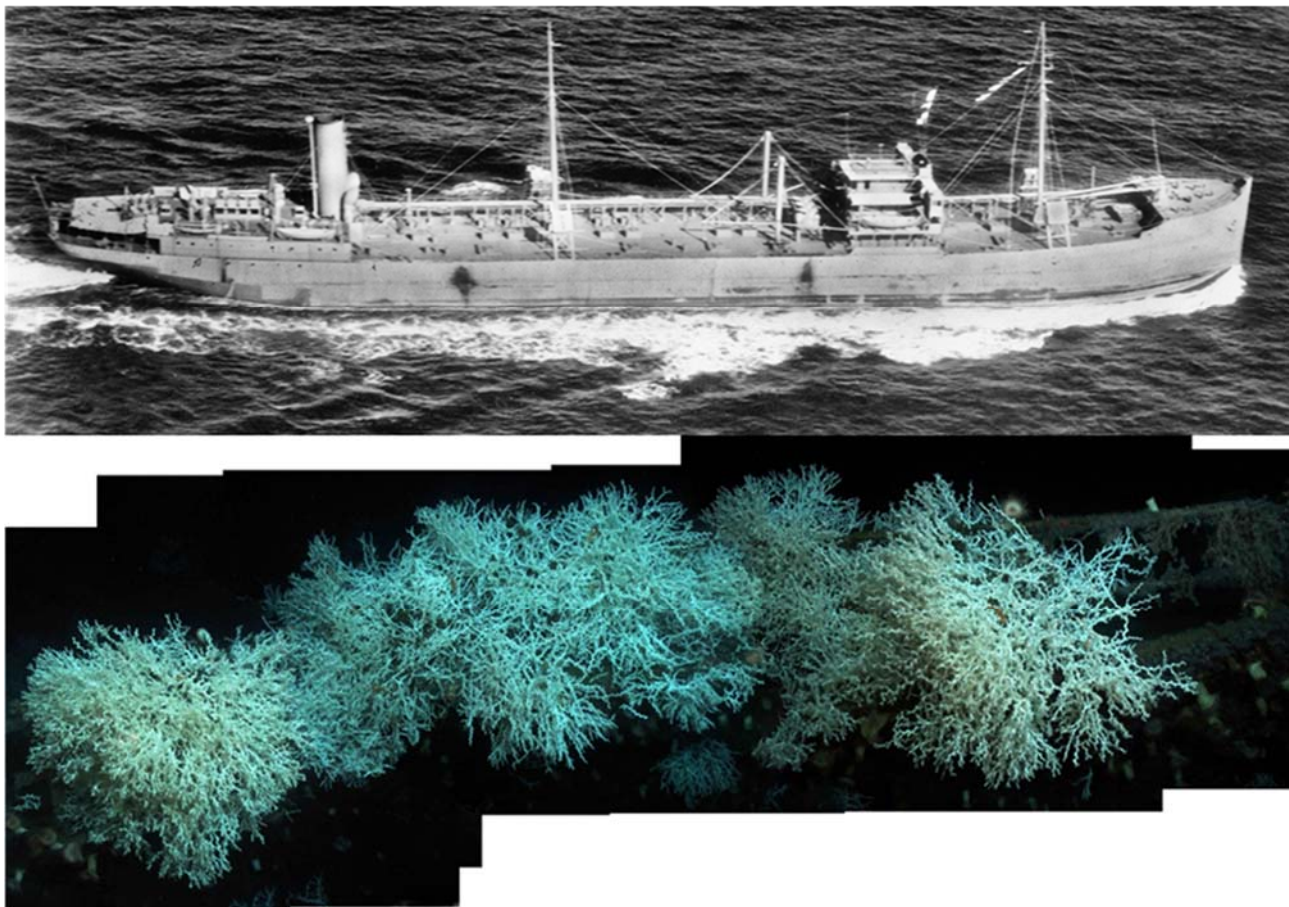


Figure 11. a) The Gulfpenn, an oil tanker sunk by a German U-Boat in 1942 (Image courtesy of Mariner's Museum, Newport News, Virginia). b) Example of Lophelia coral development on the wreck. Photomosaic depicts numerous colonies nearly completely obscuring the upper bow with some ship structure visible in the upper right (Image courtesy of Lophelia II, NOAA-OER/BOEM and S. Lessard-Pilon).

*Okeanos Explorer*⁶, as well as the Schmidt Ocean Institute's R/V *Falkor*⁷. The German expedition on the R/V *Maria S. Merian* in 2012 also mapped the area. The new maps revealed hundreds of mounds and ridges, some of which were subsequently surveyed using submersibles and ROVs. Maps and data from these expeditions revealed a long continuous escarpment near 400 m depth, many mound features with 10 m

relief or more, and a few isolated ridges with high vertical relief. Many features are within the *Lophelia* depth range (300-800 m).

The first reports of *Lophelia* aggregations on the west Florida slope were published by Reed et al. (2006) based on observations from the *Johnson Sea Link* submersible. Extensive hard bottom ecosystems were documented on the

⁶<http://oceanexplorer.noaa.gov/okeanos/explorations/ex1202/welcome.html>

⁷ <http://www.schmidtocean.org/story/show/906>



west Florida slope during several research cruises between 2008 and 2014. These included two European cruises that conducted seafloor mapping, water column profiling and documented *L. Pertusa* and other corals using underwater vehicles (Hübscher et al. 2010, Hebbeln et. al. 2012). Demopoulos et al. (in revision) describe the physical and oceanographic characteristics of these deep reefs and provide estimates of the accumulations from six cruises (2008-2012). The surveys identified mounds and ridges in < 525 m depths capped with living coral colonies, dominated by *L. pertusa*. A rocky scarp, running north-south for at least 229 km, supported lower abundances of scleractinian corals than the mounds and ridges, despite an abundance of settlement substrata. Several of these *Lophelia* aggregations were recommended for protection to the Gulf of Mexico Fishery Management Council (GMFMC) (Reed and Farrington 2014).

II.8. Advances in Understanding Population Connectivity

Although the advancing field of genetics applies to a wide spectrum of subjects related to deep corals, it fits well within the discussion of distribution. Recent advances have been largely due to the exponential growth in capabilities to perform genetic analyses. In the deep GoM, genetic techniques have been used to identify new coral species (Cairns et al., this volume) and provide estimates of population connectivity for the scleractinian coral *L. pertusa* (Morrison et al. 2011, Morrison et al., this volume), the black coral *Leiopathes glabberima*

(Ruiz-Ramos et al. 2015) and the octocoral *Callogorgia delta* (Quattrini et al. 2015).

Consideration of connectivity among coral habitats is fundamental to the understanding of basic ecology, and also critical for consideration of the sensitivity of populations with respect to anthropogenic impacts and potentials for recolonization. Predictions of larval dispersal for deep corals are difficult due to a lack of information on timing of reproduction, deep-water currents, larval longevity and behavior.

Research since 2007 has shown that *L. pertusa* occurs from the deep Garden Banks in the western Gulf to the deep Pulley Ridge in the eastern Gulf. Morrison et al. (2011) investigated the population genetics of North Atlantic and GoM *L. pertusa*. That paper presented patterns of connectivity among *L. pertusa* populations at various scales and across a large portion of the species' Atlantic range from the GoM to Norway. Using a modeling approach, Morrison et al. (2011) found four distinct genetic groupings corresponding to ocean regions: GoM, coastal southeastern U.S., New England Seamounts, and eastern North Atlantic Ocean. In some regions, including the GoM, connectivity across larger geographic distances suggests that some larvae are broadly dispersed. Gene flow within the GoM indicates high connectivity. Thus, there is high potential for larvae to repopulate new areas following impact. However, Morrison et al. (2011) reported gene flow between ocean regions to be restricted, indicating more isolation and concluding that the most effective management approach for *L. pertusa* would include regional



conservation networks. *L. pertusa* in the GoM were also evaluated for effects from manipulation, acidification, warming and deoxygenation with implications of population genetic variability being responsible for variable responses (Lunden et al. 2014). Additional information can be found in the connectivity spotlight article in this report (Morrison et al., this volume).

II.9. Distribution of Gorgonian and Black Coral Communities

Since 2007, black corals and gorgonians are increasingly recognized as key species within deep coral ecosystems that provide structure and habitat, much like branching stony corals (Etnoyer and Warrenchuk 2007). A comprehensive study of species diversity across the entire GoM was published by the Harte Research Institute (Felder and Camp 2009), along with a public database curated by more than 140 taxonomic experts from 15 countries around the world, titled Biodiversity of the Gulf of Mexico. Data from this study indicates that the combined species richness of octocorals and black corals is higher than scleractinian richness at all but the shallowest depth in the GoM (Figure 12). Another specimen-based study drawn from museum collections showed that octocoral diversity peaks at depths between 50 and 800 m and the assemblage varies over a broad vertical range down to 2,500 m (Etnoyer 2009, Figures 13 and 14), indicating that depth gradients contribute to patterns of biodiversity for deep corals in the GoM.

Other field studies since 2007 indicate that *Leiopathes* black corals, *Callogorgia* and *Paramuricea* octocorals are widespread in waters deeper than 200 m. *Antipathes*, *Cirripathes*, and *Tenacetipathes* are among the most commonly reported black corals from the mesophotic zone (50-200 m), whereas *Nicella*, *Ellisella*, *Hypnogorgia*, *Thesea*, *Scleracis*, *Bebryce*, *Swiftia* and *Placogorgia* are common gorgonian genera found in depths between 50-200 m (NOAA 2012).

These corals can occur in high densities, sometimes over large extents. Previous research has shown that both black corals and octocorals provide structure and refuge for demersal fishes in the mesophotic zone (Weaver et al. 2002). New information is available regarding the biogeography and vertical distribution of octocorals in the GoM. Etnoyer (2009) combined records from national and regional museums with field samples and cruise reports to identify hotspots of biodiversity. The study compared rates of species accumulation for octocorals in five depth zones: 0-50 m, 51-200 m, 201-800 m, 801-1600 m and 1600-3800 m. The highest rates of species accumulation were between 50-200 m and 200-800 m. Highest average diversity (Simpson's D) was in the 50-200 m depth range. The study identified some dissimilarity in the octocoral species assemblage between the northern GoM and the Florida platform (Etnoyer 2009). The findings contrast the hypothesis that deep coral assemblages are homogenous among the subregions of the Gulf.

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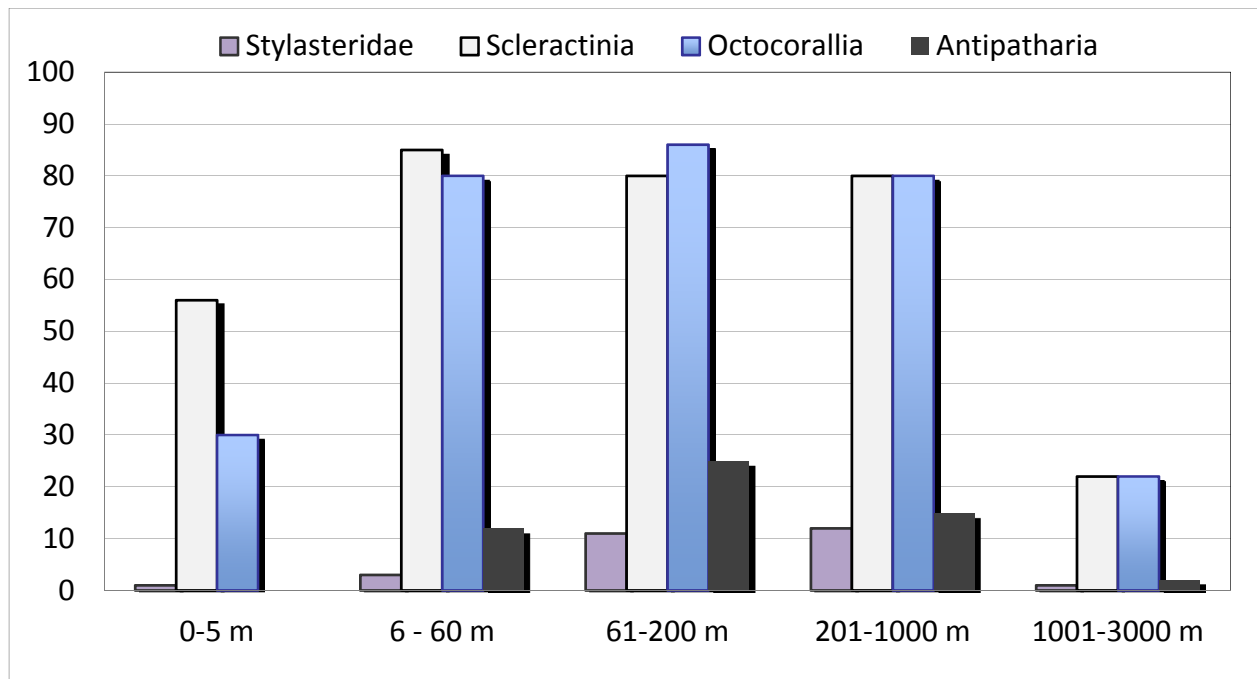


Figure 12. Coral species richness by taxa and depth strata showing relatively high richness of deep-water taxa. (Graph courtesy of Peter Etnoyer and Fabio Moretzsohn using the Biodiversity of the Gulf of Mexico database at the Harte Research Institute).

Quattrini et al. (2014)'s study, based on samples collected during Lophelia II expeditions, supported the idea of two biogeographic regions in the GoM using measures of phylogenetic diversity, and extended this concept into deeper waters. Highest species richness for octocorals occurred at the shallowest sites (< 325 m) and the deepest sites surveyed (1,800-2,500 m). Specimens were collected from 31 hard bottom sites in the northern and eastern GoM between 2008-2011. This pattern was different from that of museum samples, and opposite of the typical pattern of deep-sea diversity in the GoM, which is expected to peak at mid-slope depths (Gallaway et al. 1988, Rowe and Kennicutt 2009).

The research described transitions in octocoral assemblages at depth breaks near 325, 425, 600, 1,100 and 2,100 m. Octocoral assemblages on the west Florida slope represented a separate biogeographic group within the 425-600 m depth range compared to other groups located in the north central GoM. Using molecular tools, these authors also report on 12 species never before collected in the GoM, including three that are likely new to science.

Species within the genus *Callogorgia* are the most common and abundant gorgonian octocoral taxa reported from the upper continental slope (200-1,000 m) in the GoM (NOAA 2015). Quattrini et al. (2013)

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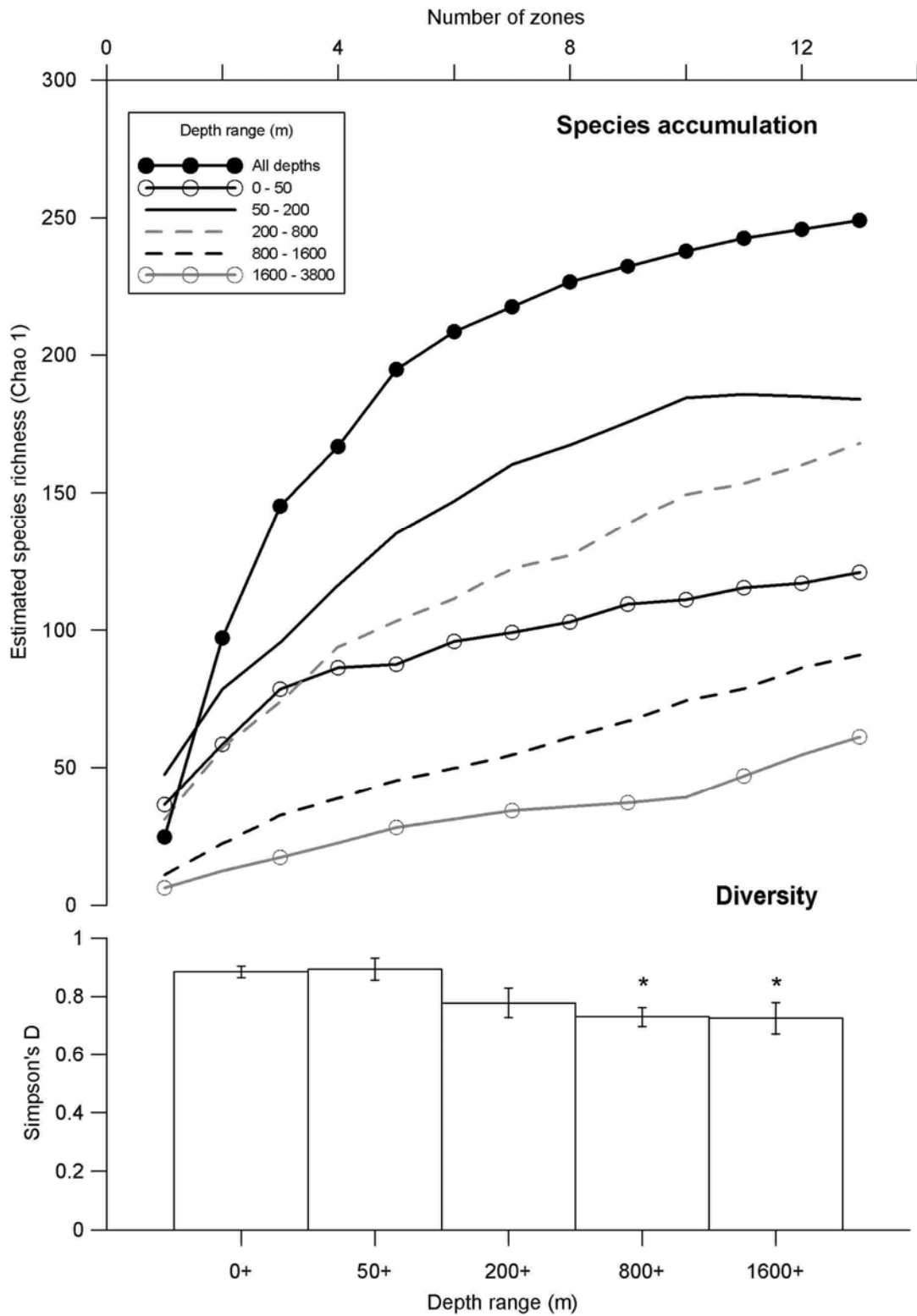


Figure 13. Analysis of gorgonian species diversity by depth range from Gulf of Mexico museum collections showing high diversity in the 50-200 m depth range. The number of zones on the species accumulation curves correspond to regional zones defined in Etnoyer (2009). (Graphic reprinted from Etnoyer 2009).

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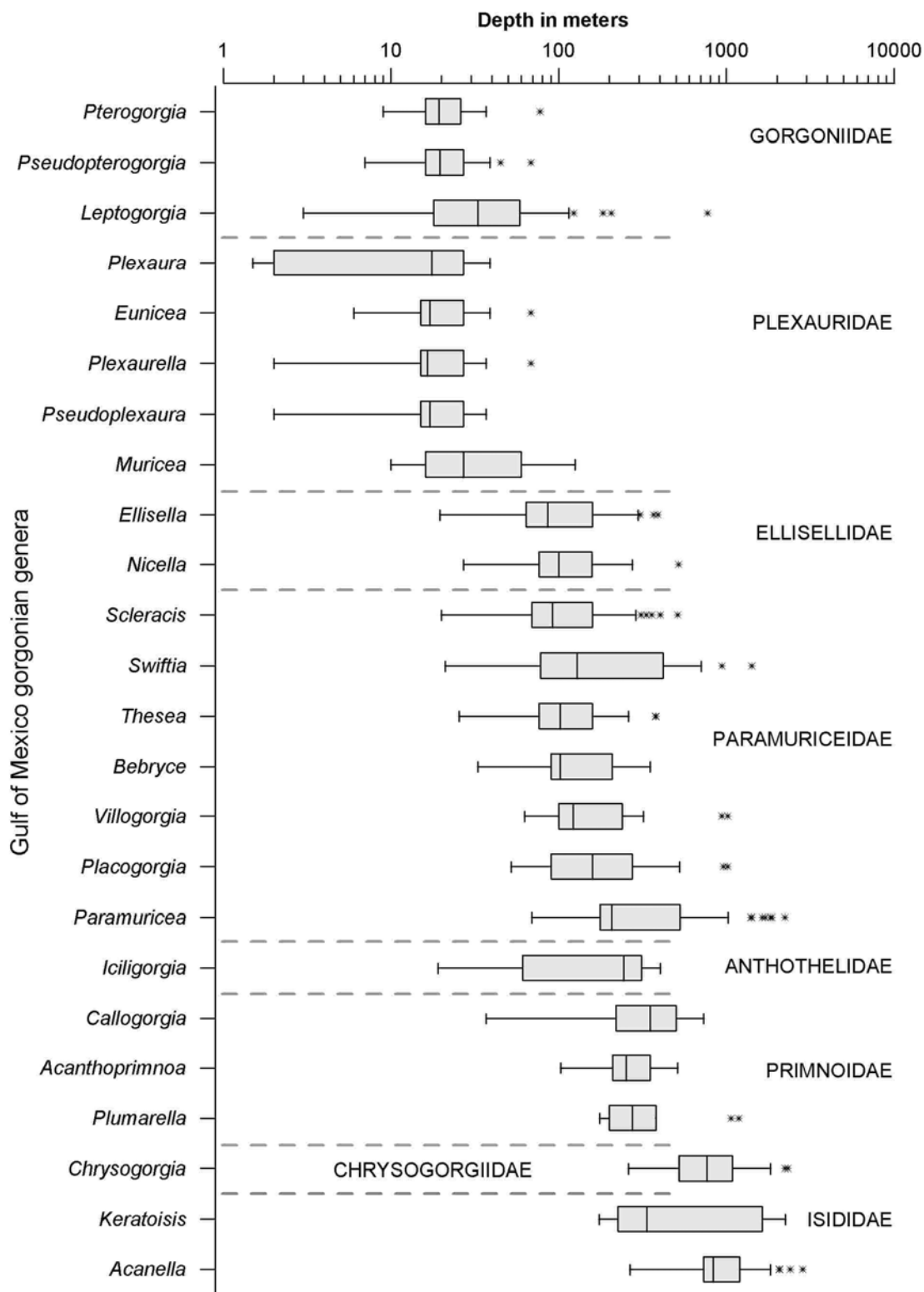


Figure 14. Analysis of the vertical distribution of Gulf of Mexico gorgonian families and genera, as derived from museum collections. (Graphic reprinted from Etnoyer 2009).



documented strong niche segregation with depth in the genus using specimen collections, video data, environmental niche modeling and DNA barcoding. *C. gracilis* occurred at the shallowest sites (depths up to 320 m), *C. americana* was found in mid-depths (339-384 m) and *C. delta* was found at the deepest depths (403-914 m) surveyed. *C. delta* was also associated with cold seeps, indicating that this species may have adaptations to living in areas of increased hydrocarbon seepage.

Following this study, Quattrini et al. (2015) examined whether depth could serve as an isolating factor in populations of *C. delta*. Significant genetic differentiation occurred across seven sites spanning 400 km of distance and 400 m of depth. Greater genetic differentiation was observed with vertical distance, rather than geographical distance; however, geographical distance may also play a role in limiting gene flow. The study concluded that water mass boundaries isolate populations across depth, subsequently leading to adaptive divergence with depth (Quattrini et al. 2015).

Another recent study examined the population structure of the black coral *L. glaberrima* in the deep Gulf (Ruiz-Ramos et al. 2015). These authors found that although different color morphotypes of this coral could not be distinguished genetically, they did show distinct differences in distribution. The study also found evidence of two distinct populations of *L. glaberrima*, one of which showed evidence of the ability for long range dispersal (and was present at all sites examined) and another

which was restricted to VK826 and VK906 where it occurred sympatrically with the other lineage. These results indicate that coupled ecological and evolutionary processes are important in structuring the distribution of deep corals in the GoM.

Doughty et al. (2014) investigated the occurrence, density and size distributions of one of the most common gorgonian octocorals in the Gulf below 200 m (*Paramuricea* spp.). Similar to the results of Quattrini et al. (2015), the species of *Paramuricea* present in the GoM (based on molecular haplotypes) were partially segregated by depth. The authors concluded that as a result of their sparse distribution, low recruitment rates and slow growth rates, these deep-sea gorgonian octocorals are highly susceptible to anthropogenic threats.

NOAA's Deep Sea Coral Research and Technology Program (DSCRTP) has developed a national database of deep-sea corals and sponges with nearly 300,000 coral records including black corals and octocorals. This has greatly broadened the number of records of deep coral locations (see annex to this chapter). Habitat suitability models were developed from these occurrences to help fill gaps in the survey extent and to increase the reliability of predictions of coral locations that have never been surveyed before (Kinlan et al. 2013). Habitat suitability models have contributed immensely to a better understanding of the true extent of potential deep coral habitats at broad regional scales, as well as the mesoscale (Georgian et al. 2014).



II.10. Continental Shelf Mesophotic Habitats

II.10.i – Northwestern GoM

An updated biological habitat characterization scheme was released for the reefs and banks on the outer continental shelf of the northwestern GoM, including FGBNMS (Hickerson et al. 2008, Schmahl et al. 2008), based on the results of sampling efforts since 2003. Nuttall (2013) compared field identifications of black coral species (collected from the FGBNMS and other historical data) with laboratory identifications, and showed that species-level field identifications are not reliable and genus level identifications are more accurate. Nuttall (2013) also contains habitat suitability maps for antipatharians. Wicksten et al. (2014) described crustaceans associated with black corals, including a new species of crustacean, the squat lobster *Uroptychus marissae* (Baba and Wicksten 2015). Rodriguez (2015) studied black corals on nearby South Texas Banks showing highest abundance and diversity of black corals on the tops of banks compared to the flanks. An isolated observation of the antipatharian *Plumapathes pennacea* was reported by Boland and Sammarco (2005) on the crest of the East Flower Garden Bank at a depth of 22 m. Opresko et al. (in press) provided a guide to the antipatharians of the FGBNMS, which is useful throughout the region.

On the Flower Garden Banks, octocorals are absent shallower than 50 m (Bright et al. 1984), but a total of 24 species were documented in 16 genera (Etnoyer 2009) in deeper waters (52-130 m). The octocoral assemblage was stratified by

depth, with a shallow group (50-70 m) and a deeper group (70-125 m). Hotspots of octocoral species richness and abundance were identified at the base of East and West Flower Garden Banks. Furthermore, four different octocoral assemblages were recognized at among six banks within a similar depth range, including Flower Gardens. Thus, nearby features 20-40 km apart may have very different species composition. One surprising result of the study was a high diversity of octocorals on low relief hard-bottom habitats between East and West Flower Garden Banks, on a feature now referred to as Horseshoe Bank.

The publications resulting from BOEMs Potentially Sensitive Biological Features investigations will provide insights into the distribution, diversity, dominance and structure of the mesophotic communities in the region, as well as the fine-scale geomorphology of a set of 14 banks in the northern GoM (Sammarco et al. 2016). This will also contribute to our understanding of the relationship between the fine-scale geomorphology and species richness in these habitats at a variety of spatial scales (Sammarco et al. 2016). Considerable range extensions of fish populations have resulted from the investigations in this region. An effort is currently underway to organize and publicize this data.

II.10.ii – Pinnacle Trend Region

Considerable new research occurred since 2010 on the mesophotic reefs at Alabama Alps, Roughtongue, and Yellowtail in the Pinnacle



Trend region off Louisiana, Alabama and Mississippi (Figure 3), as well as on Coral Trees Reefs and Madison Swanson Marine Reserve off Florida. These studies also found differences in species composition between the two groups of reefs at similar depths (Etnoyer et al. 2016). Pinnacle Trend sites were dominated by the octocorals *Swiftia* sp., *Thesea nivea* and *Hypnogorgia* sp., while at the Florida sites, *Thesea rubra* and *Placogorgia* sp. were most common. These differences in species composition are consistent with the idea of a biogeographic boundary for deep corals between the northwestern and the eastern GoM. Differences could be driven by differences in seasonal temperatures, salinity, productivity or underlying substrate. In contrast, habitat suitability models developed for *Swiftia*, *Thesea* and *Hypnogorgia* indicate that these taxa are broadly distributed (Kinlan et al. 2013), but models can widen distributions beyond direct observations and rely on ground-truthing. Much remains to be explored in terms of population connectivity and environmental tolerances for the mesophotic sea fans and black corals.

II.11. Species Range Extensions

Many species of habitat-forming deep corals were encountered in the GoM for the first time (Figure 15), or in exceptional abundance, since the last report in 2007. Bubblegum corals (Paragorgiidae) were thought to be rare in the GoM, but they have been sampled and observed numerous times since 2008, at depths

ranging from 360-1,800 m depth, in both the northwestern and eastern parts of the Gulf (Brooks et al. 2016). Precious corals (Corallidae) and *Iridogorgia* spiral corals (Chrysogorgiidae) have also been observed. A list of species discovered during Lophelia II or Chemo III, but not included in Cairns and Bayer (2009) is shown in Table 3. A comprehensive list of deep coral species in the GoM is provided in an annex to this chapter. This annex is modified from Cairns and Bayer (2009) to include newspecies occurrences and range extensions since the original publication. Clearly, the more we explore, the more we discover and observe.

II.12. Occurrence and Distribution of Deep-Sea Sponges

Limited data still exist on sponges in the deep GoM despite intense research over the last ten years. A map showing the locations of deep-sea sponge records in the GoM is presented in the Appendix. The paucity of research on these important taxa was identified but not fully addressed in the 2007 volume (Lumsden et al. 2007). Rützler et al. (2009) indicated the presence of 66 taxa for the deep-sea from 12 orders with three orders representing the majority of the total; Lithistida (15), Poecilosclerida (14) and Hexactinosida (12). No annotations or references in that summary are dated after 2004. The last comprehensive study of the deep GoM by Rowe and Kennicutt (2009) consisted of widely separated sampling stations ranging in depth from 200 to 3,750 m spanning across most of the northern GoM and also

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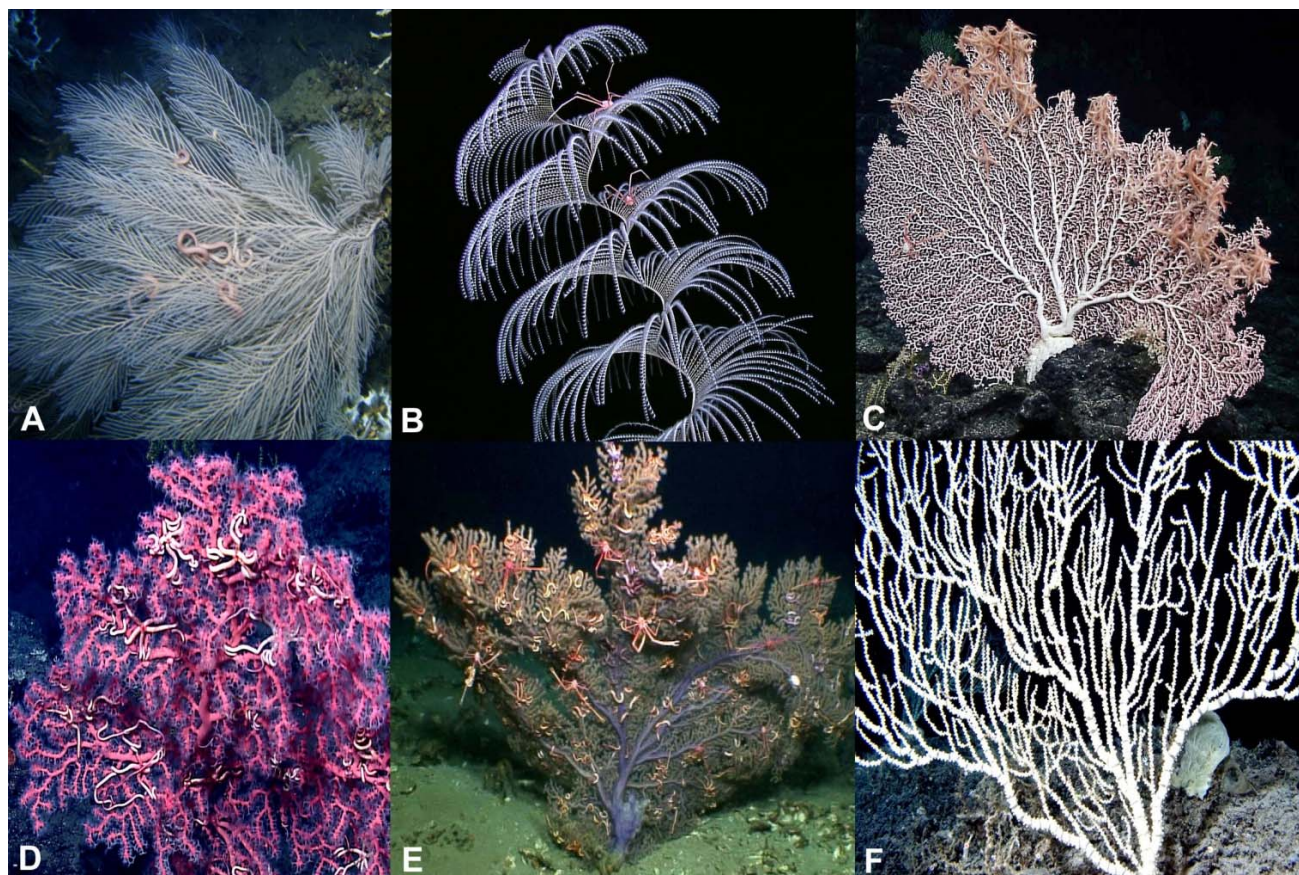


Figure 15. Several species and genera of deep-sea gorgonian octocorals were recorded in the Gulf of Mexico for the first time since 2007, including species in the genera a) *Callogorgia*, b) *Iridogorgia*, c) *Corallium*, d) *Paragorgia*, e) *Paramuricea*, and f) *Keratoisis* (see annex list of deep-sea coral species).

Table 3. Octocoral range extensions documented from the Chemo III and Lophelia II study. (*Confirmed by taxonomic experts S. Herrera and J. Sanchez. Designations of new species await additional genetic data and morphological confirmation).

Family	Species
Paragorgiidae	<i>Sibogorgia cauliflora</i> *, <i>Paragorgia wahine</i> *, <i>Paragorgia johnsoni</i> , <i>Paragorgia regalis</i>
Corallidae	<i>Hemicorallium niobe</i> (= <i>Corallium niobe</i>), <i>Corallium medea</i>
Primnoidae	<i>Callogorgia delta</i>
Chrysogorgiidae	<i>Iridogorgia splendens</i> , <i>Iridogorgia magnispiralis</i>
Plexauridae	<i>Paramuricea biscaya</i>
Clavulariidae	<i>Clavularia rudis</i>
Aquaurmbriidae	(new family described in 2012 from the tropical eastern Pacific)



included some stations in Mexican waters. However, not much was reported on sponges and results were primarily qualitative.

A prior Gulf-wide study (Gallaway et al. 1988) was conducted in the mid-1980s and represents a more significant body of data on GoM deep-water sponges and also includes one of the few records of a high-density sponge area on the GoM slope. This study included 60 stations that spanned most of the northern GoM ranging in depth from 300 to 3,000 m. Gallaway et al. (1988) report 39 taxa of Porifera with 22 identified to species. Densities of small sponges from boxcore transects ranged from 0-137/m² with the maximum density observed at a single site at Station E5 during the fourth of five cruises at a depth of 2,902 m. However, the species observed were not reported (Gallaway et al. 1988). The ten most abundant taxa identified from boxcore samples as part of the macrofauna category, and mostly small in size and not structure forming, were only identified to genus or family. These included the genera *Stelletta*, *Sycon*, *Thenea*, *Stylocordyla*, *Thenea*, *Mycale* (species A and B) and *Microciona*, as well as the families Suberitidae and Suberotodae.

Sponges were also reported as part of the quantitative benthic photography component of Gallaway et al. (1988) using a drift camera maintained 2 m off the bottom at the same 60 stations. Hard bottom was not targeted. Densities from imagery exceeded densities from trawling at all stations. Maximum sponge

density from imagery was 16,514 per hectare at one station at a depth of 1,400 m. Overall density of Porifera from benthic photography was approximately 450 individuals per hectare.

In the mesophotic region, research conducted by the FGBNMS has collected about 50 sponge samples in the 50-150 m depth range in the NW GoM. These samples were identified with the help of Dr. Christi Savarese, and Klaus Rützler at the Smithsonian National Museum of Natural History. An interesting glass sponge habitat was identified at Elvers Bank and warrants further investigation. Results from these efforts are available in poster form.⁸

II.13. New Information of Species Associations and the Role of Corals and Sponges as Habitat

Work has been done on deep coral associates including results from earlier studies (*Lophelia* I) ranging from microsymbionts to crustacea and fish. Wicksten et al. (2014) described crustaceans associated with black corals, as well as a new species of crustacean, the squat lobster *Uroptychus marissae* (Baba and Wicksten 2015). Giarad et al. (2016) reported on the benefits provided by the commensal ophiuroid *Asteroschema clavigerum* living on *Paramuricea* colonies impacted by the DWH spill. Recovery from visible impact and hydroid colonization of *Paramuricea* colonies was negatively correlated with distance from the ophiuroid. Branches within the area of influence of the ophiuroid

⁸http://flowergarden.noaa.gov/document_library/scidocs/spongeposter.pdf



were also more likely to recover, indicating likely benefits from its association with *A. clavigerum* through the physical action of ophiuroids removing material depositing on polyps. Cordes et al. (2008) reported 68 invertebrate taxa that were identified in close association with the *L. pertusa* coral framework in the northern GoM. Lessard-Pilon et al. (2010) report high diversity of fish and invertebrates in *L. pertusa* structure and that the highest diversity is associated with thickets containing high proportions of dead *L. pertusa*. Because *L. pertusa* in the central and northern GoM are often associated with current or historical seeps through colonization of derived carbonates, Becker et al. (2009) used stable isotopes to investigate a potential relation between *L. pertusa* communities and seep primary production. With the exception of a single gastropod (of 33 species tested), the authors found no evidence for a nutritional dependence of *L. pertusa*, or the fauna associated with the coral colonies, on seep primary production. Much of the work of the USGS Lophelia II team is contained in the regional publication list including Kellogg et al. (2009), Ross et al. (2012) and Demopoulos et al. (2010). Final reports from this suite of major studies also contain significant new information on deep coral associates, trophic relationships of associated species groups, substrate infauna and new results from microsymbiont studies.

II.14. New Research Priorities

Research priorities for deep coral in the GoM are many. There continues to be a need for baseline data in preparation for future catastrophic incidents and potential habitat impacts due to ecosystem impacts from climate change. The DWH incident clearly illustrates this need. Additionally, it is necessary to understand long-term responses to major environmental events. Below we outline several research priorities to increase knowledge on deep-sea and mesophotic habitats in the region.

- Known deep coral and sponge sites need to be mapped at high resolution. This is the first step in exploration and characterization of these resources.
- Continued exploration and characterization of known sites in order to manage and protect resources.
- Long-term monitoring of deep coral habitats at a variety of sites throughout the GoM, including but not limited to, the sites impacted by the DWH incident.
- Growth rates, damage and aging of deep corals, as well as the natural abundances of fauna both directly and indirectly associated with deep corals.
- Enhance the predictive capability (i.e., use of remote sensing rather than visual detection) for identifying the distribution of deep coral including a modeling approach. NOAA's DSCRTP has begun a modeling project for the GoM. Additional ground-truthing and other research could be required. Ideally this would overlap with other research priorities.



- Understand two major components that determine the success of recolonization of potentially impacted habitats; 1) reproduction and development of species of concern (e.g., *Lophelia*, *Madrepora*, *Leiopathes* and *Paramuricea*) and 2) physical factors determining the transport of reproductive propagules of species of concern (both gametes and larvae).
- Investigations of genetic connectivity between populations are needed to effectively manage these resources.
- Archiving of invertebrate specimens including corals and related community species will continue with an ongoing contract between BOEM and the Smithsonian National Museum of Natural History. Additional scope of this program will include tissue archiving in their recently completed biorepository, as well as potential genetic barcoding. This effort should be expanded as much as possible and extended to other agencies involved in collection of deep-sea coral specimens.

II.15. Update on Management: New Information on Stressors

II.15.i – Oil and gas development

Brooke and Schroeder (2007) reviewed the stressors on deep coral communities in the northern GoM. Oil and gas development was identified as having a perceived medium level of threat to these communities – the highest relative threat level for human activities in the

Gulf. As part of continued offshore development in the GoM, a total of 1,906 wells were drilled in water depths below 50 m from January 2007 to August 2015. Of that total, 1,066 were at depths below 300 m. Information on wells can be accessed through a variety of query options at a regularly updated internet site at BOEM.⁹ Other than some visible linear physical impacts from anchor cables reported in Schroeder (2007), there have been no documented impacts to deep coral habitats from routine oil and gas activities.

The DWH oil spill and associated use of oil dispersants showed how a major accident could affect deep coral communities. Numerous additional research publications directly involving deep corals and the associated communities will become available over the next few years as a direct result of research funded through federally required oil spill damage assessment, the GoM Research Initiative, as well as a spectrum of additional research funding related to the DWH event. One thing that is clear from NRDA benthic studies is that deep corals are important sentinel species that are useful for monitoring and vulnerable to oil pollution impacts.

II.15.ii – Fishing threats

Bottom longlines for reef fish are a potential threat to corals and sponges in shelf-edge depths, because these fisheries target the same complex reef habitats where the target species of groupers and snapper occur including

⁹<https://www.data.boem.gov/Well/Borehole/Default.aspx>

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snowy grouper, Warsaw grouper and tilefish. Lost longline gear has been observed throughout the mesophotic reefs of the Northwestern GoM. Abandoned fishing lines have been observed with some frequency near Coral Trees Reef and Madison Swanson South Reef (MSSR), sometimes wrapped in and around gorgonian corals. The reefs are situated in an offshore region between Pensacola and Tampa, Florida known as the northern grounds for the GoM bottom longline fishery and the area of the Gulf where fishing for reef fish actually began in the 1800's (Prytherch 1983). Intense fishing pressure at MSMR led to closure in 2000, when the GMFMC prohibited all bottom contact gear in the reserve. Low levels of bottom longline fishing effort were reported from the Pinnacles region in 2001, but the majority of effort was concentrated in the eastern GoM, near Tampa, Florida (Scott-Denton et al. 2011). Observations of fishing line on Pinnacle Trend sites were few compared to Coral Trees Reef and MSSR (Etnoyer et al. 2016). Anchoring associated with specific types of fishing, such as bandit reel fishing, is also a threat to mesophotic reef systems.

There is little available information regarding new fisheries operating deeper than 300 m in the GoM that could significantly impact deep corals. An overview of this subject was a component of the *Lophelia* II project and is presented in Brooks et al. (2016). Commercial fishing pressures on deep coral in the GoM remain low compared to other regions;

however, discarded fishing line has been documented in deep coral communities and may pose a threat to these coral communities (Fisher et al. 2014a). The only two fisheries identified as having some potential impact to deep-water scleractinian coral habitats, such as *Lophelia* and *Madrepora*, are limited to golden crab (*Chaceon fenneri*) and royal red shrimp (*Pleoticus robustus*). A fishery for the deep-sea golden crab has not developed since its early description in the literature (Brooks et al. 2016). However, this pot and trap fishery does come in contact with the bottom near 500 m depth where deep corals occur. The pots are strung together and retrieved by grappling hook before being dragged to the surface, so there is some potential for severe bottom disturbance in sensitive coral habitats. Golden crab is not currently a managed fishery in the GoM, but there is a small fleet operating off the southeastern U.S. coast.

There is some evidence of a golden crab fishery operating in and around *Lophelia* aggregations off the west coast of Florida. Golden crabs, a discarded crab pot, and broken *Lophelia* coral rubble were observed in 2012.¹⁰ The feature has not been revisited since that time. There are only eight reports of golden crab landings in the NMFS fishery logbook databases from 1995 to 2004.¹¹ Landings data include small catches, some likely as by-catch, ranging from 25-641 MT over a period of eight years. The last reported data for golden crab landings in the GoM from the National Marine Fishery Service

¹⁰<http://www.schmidtocean.org/story/show/915>

¹¹http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html



(NMFS) reference site for annual commercial fishery landings was 2004.

Royal red shrimp are fished in the GoM using bottom-contact trawling on the continental slope. The vessels target soft bottoms, but are occasionally close to known deep coral ecosystems including those in VK862/906. This species represents a small portion of the overall U.S. shrimp fishery (Stiles et al. 2007). The shrimp are sometimes observed close to and in association with deep corals (Ross 2005). Landings data from the last available NOAA data records for this species in 2014 is recorded for the Gulf States of Alabama (59.7 MT). A small catch was also reported in 2014 for the west coast of Florida (17.8 MT). The most recent data from Louisiana was in 2013 (2.8 MT). Texas reported relatively small royal red shrimp catches of less than 1 MT only in 2004 and 2012. Alabama landings diminished from 141 MT in 2009 to 102 MT in 2010, but rose to 159 MT in 2011 and 144 MT in 2012, remaining relatively consistent since the 1990s.

II. 15.iii – Invasive species

The invasion of the Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) also poses a different kind of threat to GoM deep coral and sponge habitats. Lesser and Slattery (2011) report loss of biodiversity and resilience of nursery areas (mangroves), coral reefs, mesophotic ecosystems and artificial reefs, as well as cascading impacts across food webs. Based on the gut content analysis, and the size of potential prey, it should be acknowledged that the lionfish invasion poses a threat to prey in

deep coral habitats, and this may have cascading effects throughout the lionfish depth range. One potential impact is that the reduction of herbivorous fish species abundance, indirectly impacts corals by fostering algal growth (Albins and Huxon 2013).

Invasive lionfish have been reported down to depths of 300 m (Albins and Hixon 2013). Lionfish were first captured off the northern Yucatan peninsula in December 2009 and in the northwestern GoM in September of 2010. Numbers of sightings have been increasing exponentially in the northern Gulf since 2011. Since lionfish were first observed in the FGBNMS in 2011, 2,614 lionfish sightings have been reported at depths ranging from 17-96 m, inclusive of both the shallow reef cap and mesophotic habitats through 2015. From this total, 1,484 (56.8%) have been removed. To date approximately 600 lionfish have been reported from other reefs and banks in the northern GoM, outside of the FGBNMS, primarily during ROV surveys at depths ranging between 50-177 m (Nuttall et al. 2014).

While lionfish were first observed by divers on all three banks of the FGBNMS in 2011, they were not recorded in long-term monitoring surveys until 2013, most likely due to the limited number of lionfish present during the first two years (Johnston et al. 2016a). Lionfish sightings from these surveys, occurring on the shallowest portion of the reef caps (17–27 m), varied among the three banks. In 2013, lionfish sighting frequency at East Flower Garden Bank was 25%, 33% at the West Flower Garden Bank



and 5% at Stetson Bank. Sighting frequency in 2014 doubled at East Flower Garden Bank (50%) and increased at West Flower Garden Bank (40%), but decreased at Stetson Bank (2.9%). In 2015, sighting frequency decreased at East Flower Garden Bank (17%), increased at West Flower Garden Bank (60%), and was below 1% at Stetson Bank (Johnston et al. 2016 a, b). In 2015 long-term monitoring surveys, average lionfish density was 0.55 per 100 m² at the East and West Flower Garden Banks.

II.16. Management Actions

Much has happened in the GoM since 2007, particularly with regard to the management of the energy industry. Some new policies preceded the DWH oil spill, and it is likely that more management actions will result from ongoing reviews and research. Numerous reforms to the offshore oil and gas industry were also enacted in response to the DWH blowout and resulting oil spill in 2010.

II.16.i – Management of oil and gas development

BOEM manages the exploration and development of the nation's offshore energy resources. Since 2007, the agency made changes to two specific regulatory policies for the oil and gas industry dealing with biological communities in the GoM, in addition to numerous changes in regulatory policies related to drilling safety.

BOEM supplements regulations that govern energy development operations on the Outer Continental Shelf through a regulatory mechanism called Notices to Lessees (NTL¹²). For example, NTL 2009-G40, titled Deepwater Benthic Communities, became effective in January 2010 and it increased the distance of avoidance from sensitive deep-water biological communities, including both chemosynthetic communities and deep coral habitats, for drilling discharges (610 m) and anchoring (152 m). This effectively doubled the distance of avoidance from prior NTL regulations. NTL 2009-G40 applies to all oil and gas activities, including exploration and production drilling plans, as well as pipeline applications, in water deeper than 300 m (the depth was raised from 400 m to encompass newly discovered deep coral communities). As described in Schroeder (2007) there was some evidence of physical impacts to deep corals from anchoring activities in the past, specifically at the coral communities in lease block VK826. There have been no similar impacts observed to deep coral sites related to energy development activities on deep corals since 2002, with the exception of the DWH incident.

A second NTL (NTL 2009-G39, effective date January 2010), titled Biologically-Sensitive Underwater Features and Areas, applies to water depths shallower than 300 m and protection to sensitive biological features. In addition to previously established protective measures for topographic features and live bottom areas including the Pinnacle Trend

¹²<http://www.boem.gov/Notices-to-Lessees-and-Operators>

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region, a new avoidance category of bottom feature was created for this NTL. This new category, titled potentially sensitive biological features, is defined as features of moderate to high relief (about 2 m) that are not protected by other biological lease stipulations. This addressed the increasing awareness that extensive areas of exposed hard bottom and associated communities (including corals) were not included in No Activity Zone boundaries of named topographic features (e.g., Bright Bank, Geyer Bank and Sonnier Bank) or within the defined areas of high diversity features in the Pinnacle Trend. Although this major shift in protection for continental shelf features was first implemented in 2005 (part of earlier NTL 2004-G05), it was not addressed in Brooke and Schroeder (2007) and is continuing to evolve with extensive field research efforts in these habitat areas.

Comprehensive reforms and fundamental changes were made to offshore oil and gas regulation and oversight in response to the DWH explosion and resulting oil spill in the GoM to maintain responsible oil and gas drilling and production on the U.S. Outer Continental Shelf. Beyond the fundamental reorganization of the former regulatory agency, Minerals Management Service (MMS) into two new, independent bureaus – the Bureau of Safety and Environmental Enforcement (BSEE) and BOEM, numerous regulatory policies have also been enacted since 2010. With consideration of the impact to deep corals, the following new policies have a direct influence on the increased safety of deep-water drilling

and future accident events. Other new policies such as more exacting inspection criteria and heightened standards for well design, casing and cementing are also indirectly tied to the issue but will not be detailed here.

- 1) One NTL was implemented shortly after the DWH spill, NTL 2010-N06 now updated to NTL 2015-N01, “Information Requirements for Exploration Plans, Development and Production Plans, and Development Operations Coordination Documents on the OCS” requires operators to demonstrate they are prepared to deal with the potential for a blowout and worst-case discharge.
- 2) A drilling safety rule implemented in 2010 makes mandatory several requirements for the drilling process that enhance safety of oil and gas drilling operations on the Outer Continental Shelf. It addresses both well bore integrity and well control equipment and procedures requiring two independent test barriers across each flow path during well completion activities. BSEE inspectors must now be on location and observe the Blow Out Preventer (BOP) testing prior to drilling commencing at the rig site.
- 3) Before receiving approval for deep-water operations, all operators now must demonstrate the capability to contain a subsea blowout like the one seen in the DWH spill. Operators demonstrate that they have access to all necessary equipment for subsea well control and containment, including a capping stack. As a result, there is now containment equipment available for industry deployment.

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The most recent five-year leasing plan for GoM energy development (2017-2022) is described on the BOEM website. The five-year program consists of a schedule of oil and gas lease sales indicating the size, timing and location of proposed leasing activity that will best meet national energy needs for the five-year period following its approval. A total of ten separate lease sales have been proposed that will include the entire available GoM leases as opposed to separate sales for the Central, Western and Eastern Planning areas. The total submerged lands incorporated in the next five-year cycle include an area of approximately 647,499 km² (160 million acres).

Potential future management actions include the consideration of expanded No Activity Zones for the more formal inclusion of densely spaced habitat features adjacent to existing banks (potentially sensitive biological features).

II. 16.ii – Other management actions

In June, 2016, the FGBNMS released a draft environmental impact statement outlining a range of alternatives for boundary expansion, including five alternatives ranging from no action (current sanctuary area of 56.21 miles²) to a comprehensive plan to protect known high value benthic habitats and cultural resources in the north-central GoM. A preferred alternative was identified, which proposes an expansion to 383.19 miles², and includes Horseshoe (between East and West Flower Garden Banks), MacNeil, Rankin, 28 Fathom, Bright, Geyer, Elvers, Sonnier, McGrail, Rezak, Sidner, Bryant,

Bouma, Parker and Alderdice Banks. All of these banks harbor significant habitats that include deep corals and sponges. In addition to these proposed expansion sites, the document also proposes to amend the boundaries of the three banks currently in the sanctuary (East and West Flower Garden and Stetson), to better encompass and therefore protect the deep coral habitats. After a period of public scoping, a Final Environmental Impact Statement will be developed and likely released in 2018.

NOAA's NMFS and the GMFMC have authority over fisheries in federal waters of the GoM. There have been no major changes in federal fishing regulations affecting deep coral areas since essential fish habitat designations in 2006. In June 2015, the GMFMC considered recommendations from its coral advisory bodies to evaluate 47 sites for Habitat Areas of Particular Concern designations and to protect them from fishing gear impacts (DSCRTP 2016).

These sites are distributed throughout the GoM from Texas to Florida, and all have confirmed presence of multiple deep-sea coral taxa including the South Texas Banks, shelf and slope sites in the northern GoM and west Florida Platform including sites in Mississippi Canyon, Green Canyon, Garden Banks, Pinnacle trend and Viosca Knoll. The GMFMC plans to seek input from the fishing community on this proposal before officially starting a process to amend the Fishery Management Plan for Coral and Coral Reefs with new Habitat Areas of Particular Concern designations.



II.17. New Management Priorities

Following on from the ongoing Potentially Sensitive Biological Features shelf-edge study described above, additional high-resolution mapping will be needed for GoM topographic features where only low-resolution bathymetry is known (most from early 1970s). Additional mapping will lead to further investigations of any relevant benthic features and consideration of additional management protective measures. Results from this study will allow refinement of avoidance of energy development activities from benthic features occurring outside of No Activity Zones established by BOEM, as well as help guide development of other potential protective measures by other agencies.

If future oil and gas leasing moves farther east in the GoM, additional investigations on the west Florida shelf and slope will become a higher priority to inform management decisions for protective measures within this area that is much different than authigenic carbonate features of the rest of the GoM. Newly released BOEM shape files of water bottom seismic anomalies in this area will be very informative in the future, by allowing targeted research. Additionally, these files will be fundamental for management decision-making related to avoidance criteria of hard substrate depicted in survey databases.

III. Conclusion

An extensive amount of research on deep corals has been performed in the GoM since 2007, both prior to the DWH incident and afterwards, leading to increased awareness among managers and the public. This awareness has resulted in significant management actions to protect deep coral habitats in the mesophotic zone and deeper waters. Even though much less targeted research has been devoted to deep-water sponge ecosystems, it appears sponge communities (at least high-density communities) are relatively rare in the GoM compared to corals. The DWH incident was a landmark event with major revelations related to deep spill impacts including the unclear dynamics of deep plumes, extensive subsurface and surface dispersant use, the potential for impacts to deep-water habitats from horizontal transport of hydrocarbon plumes and from oiled marine snow. Increased understanding of genetic diversity, age, growth, reproduction and distribution of deep corals will greatly benefit management efforts, but much remains to be discovered and described. The availability and interpretation of GoM seismic reflectivity data have greatly facilitated discovery of new deep coral habitats throughout the northern GoM. The addition of more sophisticated modeling and ground-truthing efforts has greatly enhanced our understanding of deep

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coral distribution in the GoM. New multibeam data and exploration efforts along the West Florida Shelf has led to the subsequent discovery of large aggregations of sensitive coral habitats, and these should be investigated in the future to determine their extent and degree of vulnerability to climate change and other anthropogenic impacts. There continues to be a need to map, explore and characterize vast areas of the GoM and to better understand the biology and ecology of deep corals and sponges in order to provide the understanding necessary for the development of appropriate regulatory and protective measures.

IV. Acknowledgements

We thank Sandra Brooke, Cynthia Cooksey, Andrea Quattrini and Paul Sammarco for their thoughtful reviews and expert comments on an earlier draft of this chapter. Their contributions and in-depth suggestions greatly enhanced the quality of the final product. Reviewers in BOEM included Brad Blythe, Rodney Cluck and William Brown. We also thank Robert McGuinn for generating maps. Tom Hourigan provided helpful guidance through the lengthy period of early writing and development. We thank Daniel Wagner for his assistance in final formatting and layout of this chapter.

Online Annex – Comprehensive list of deep-sea corals in the U.S. Gulf of Mexico region link: <https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>

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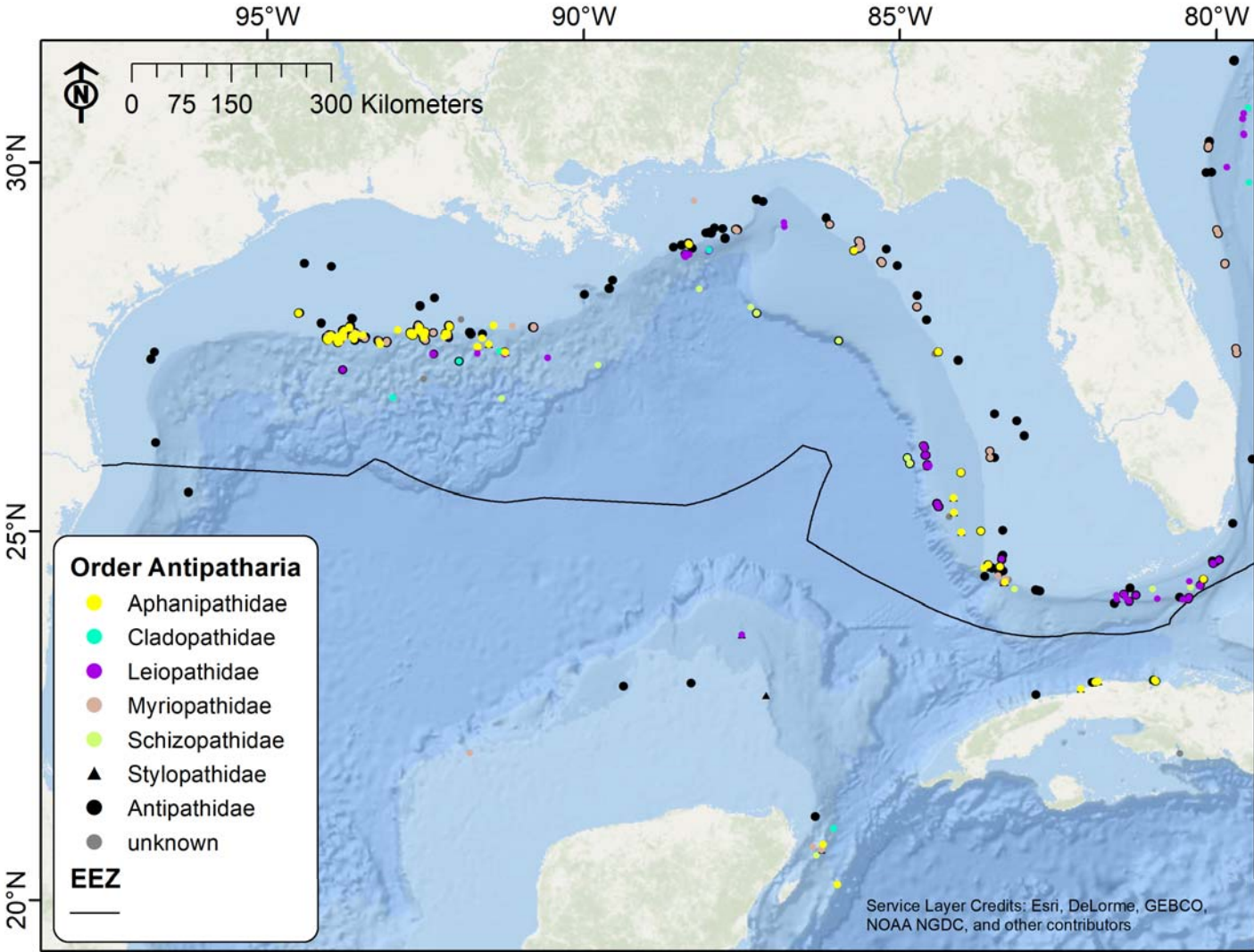


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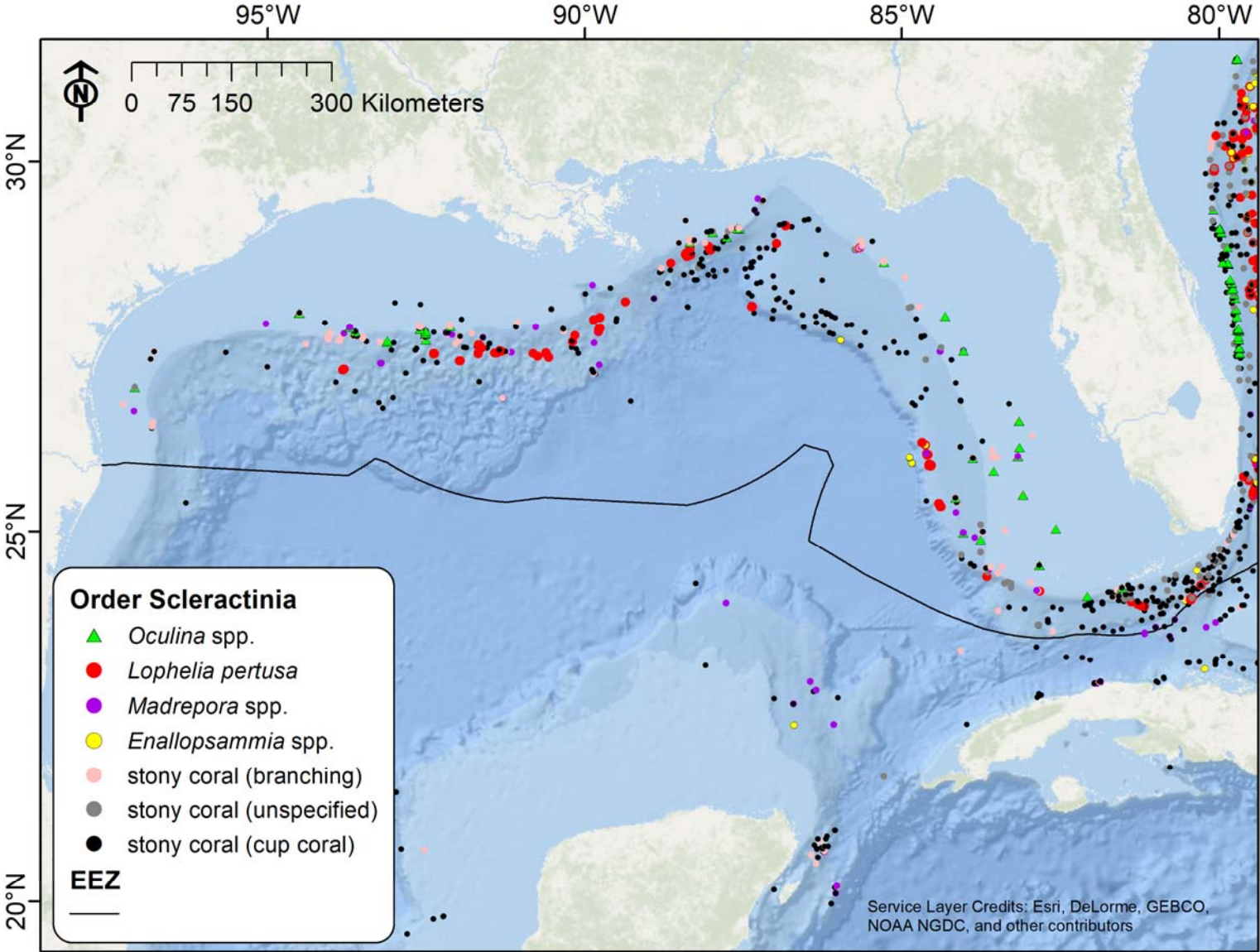
[Online Annex 1. Deep-sea Coral Taxa in the U.S. Gulf of Mexico Region: Depth and Geographic Distribution](#)



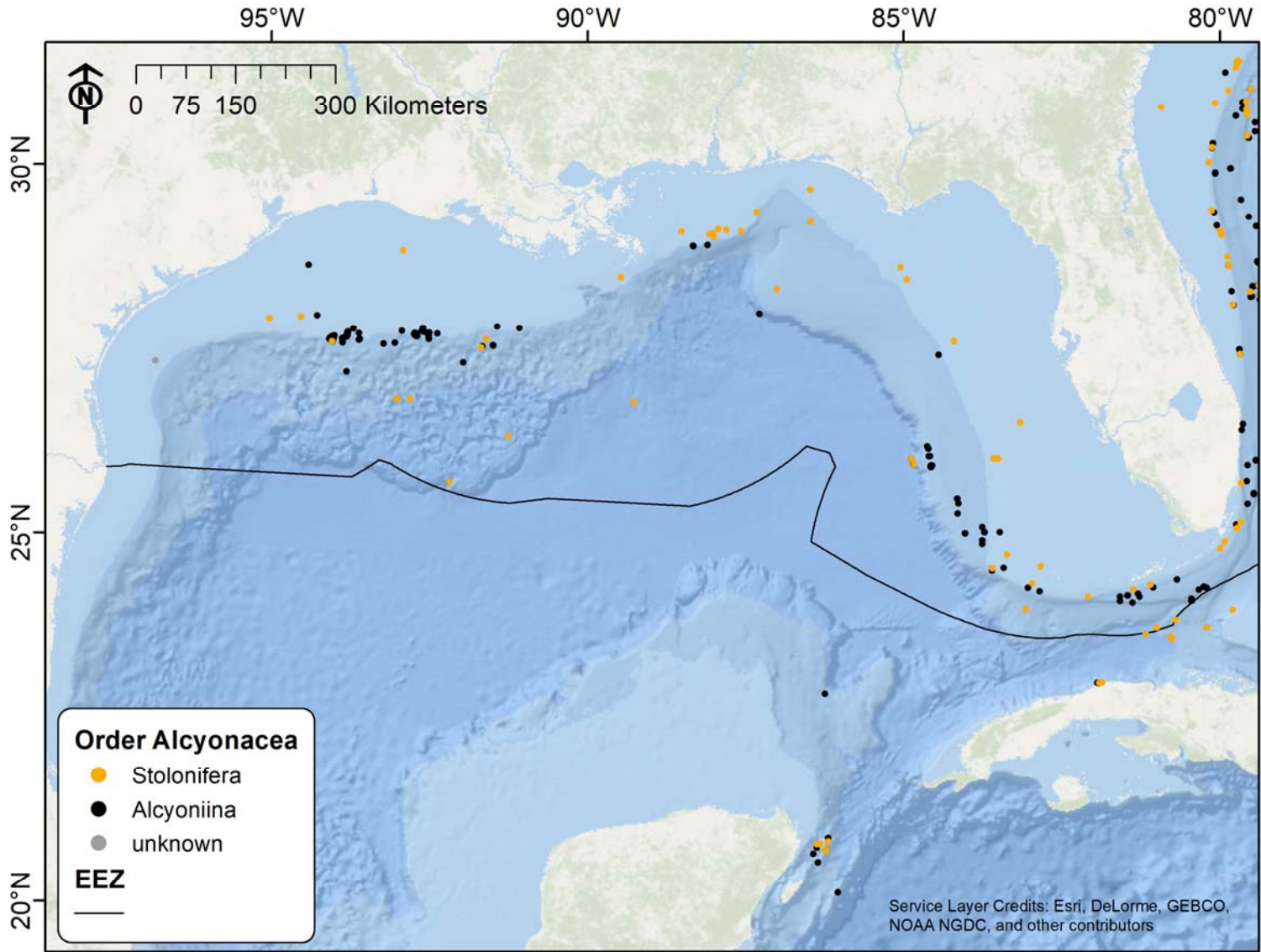
Appendix



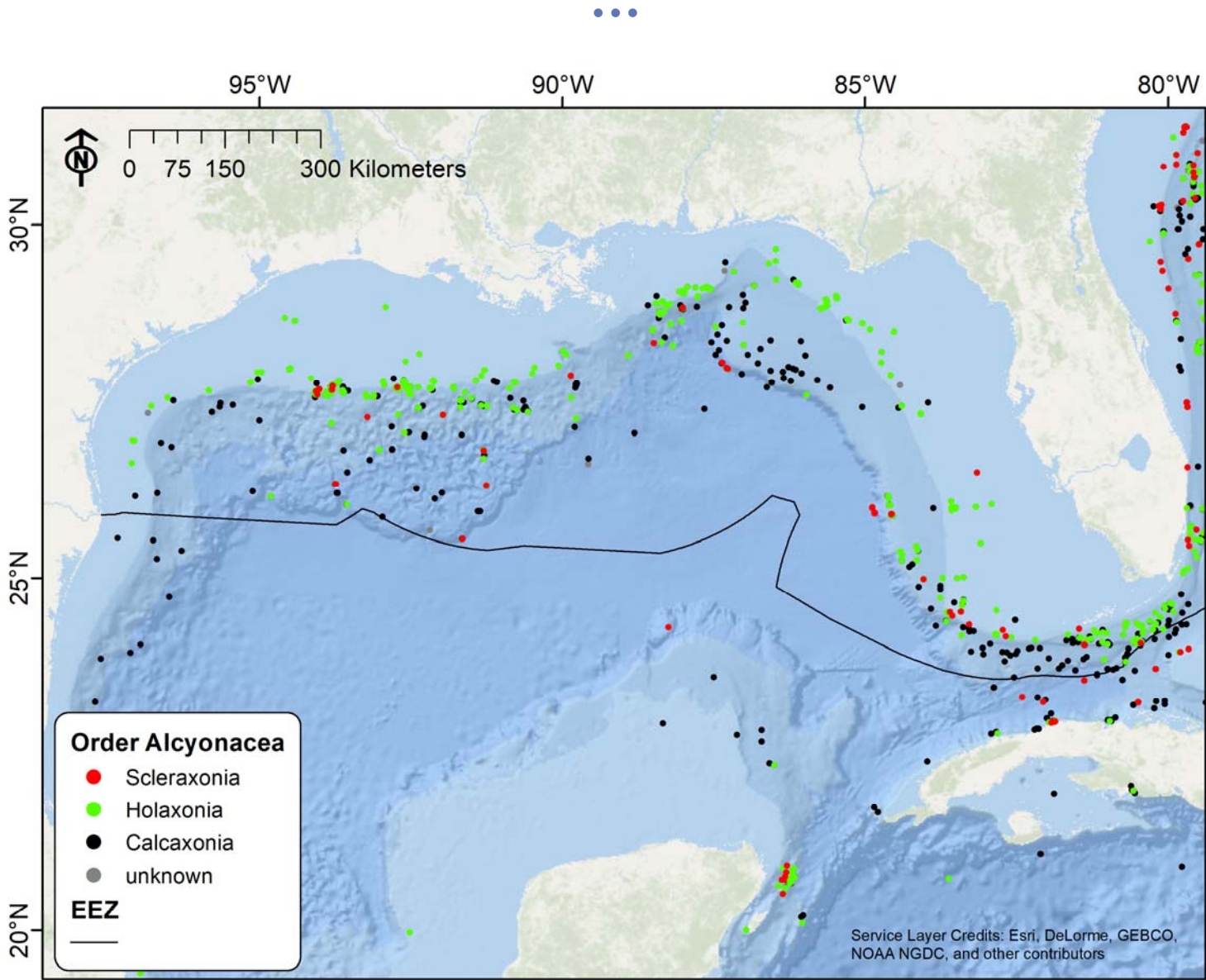
Map 1. Locations of black corals (Order Antipatharia) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



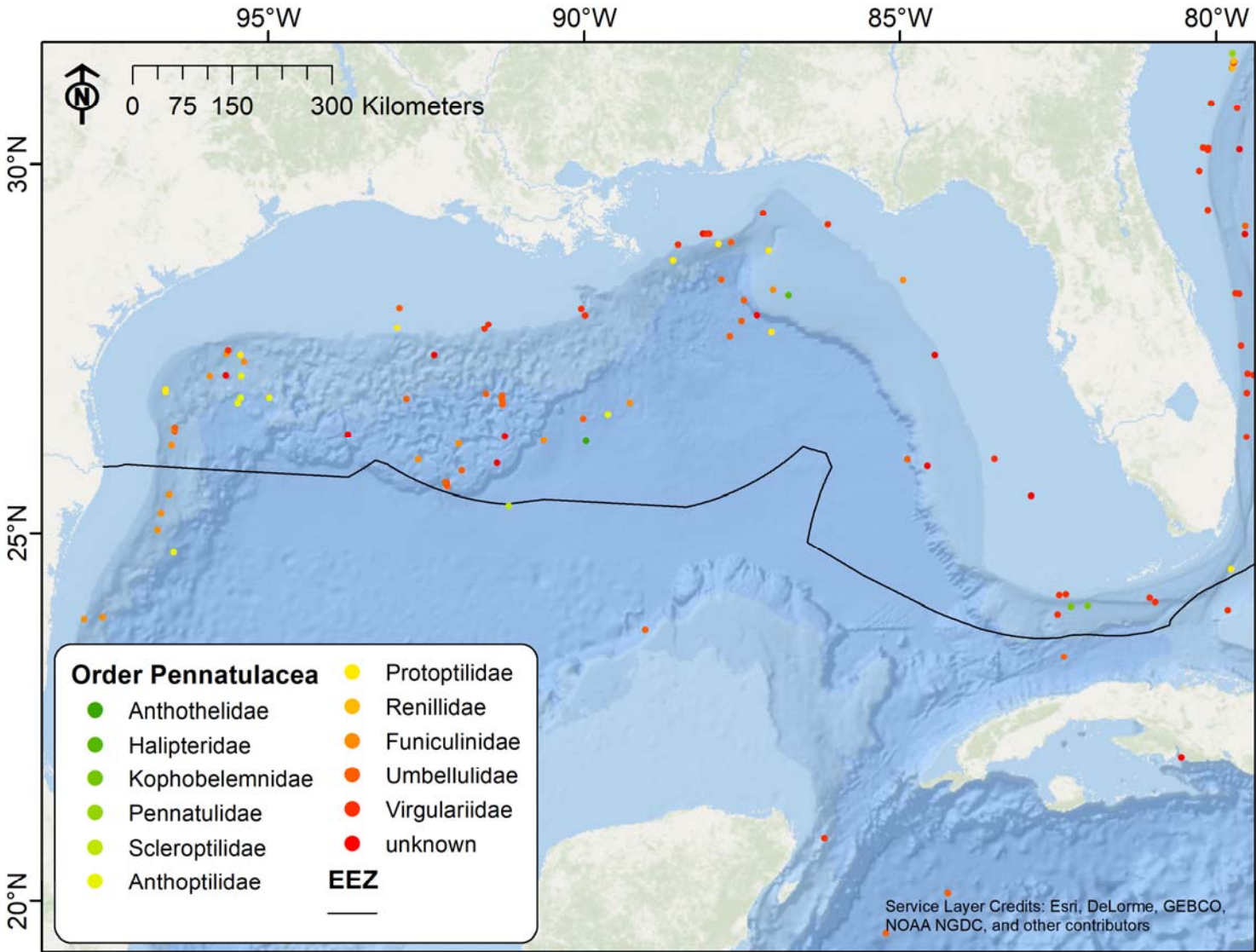
Map 2. Locations of stony corals (Order Scleractinia) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



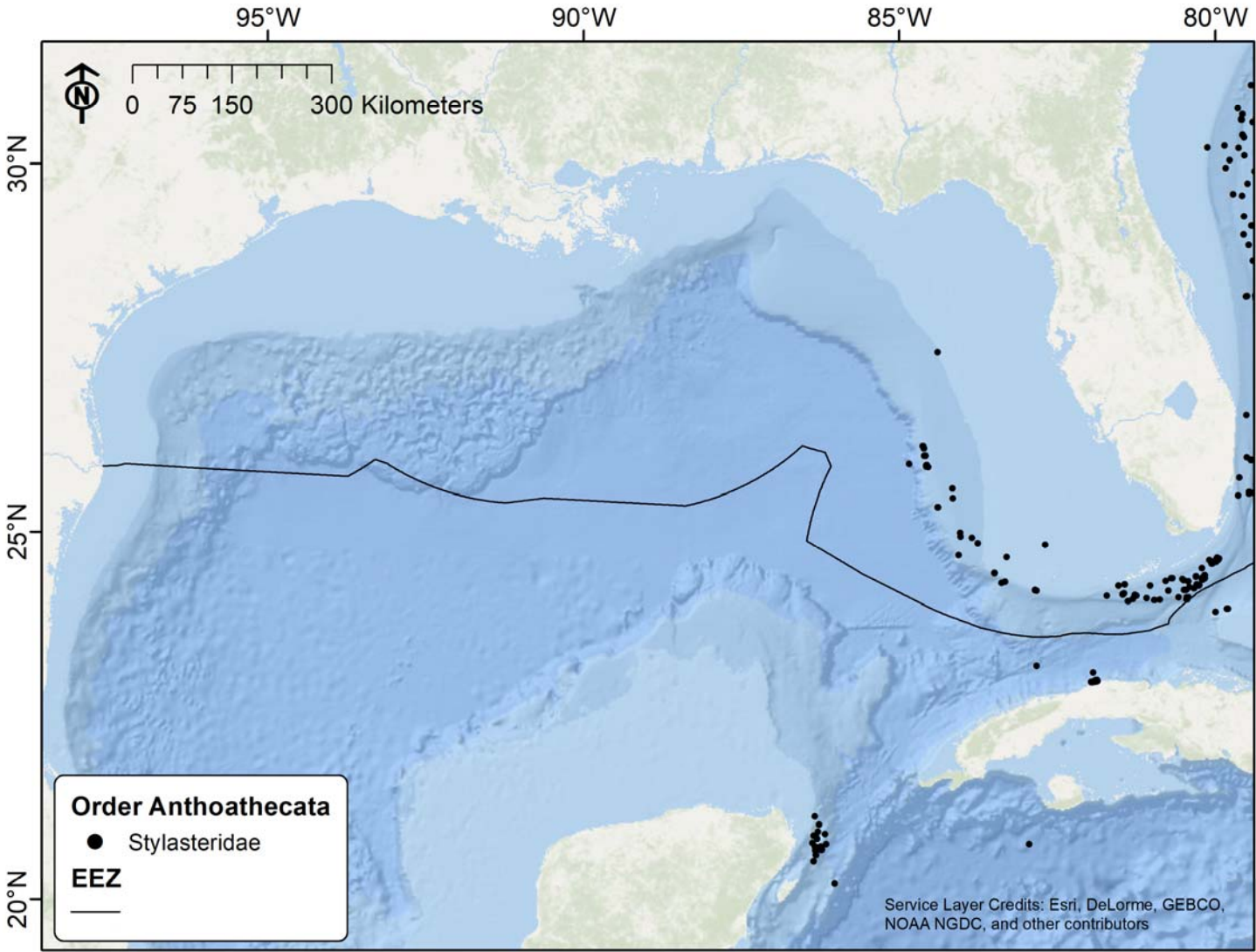
Map 3. Locations of true soft corals (Order Alcyonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



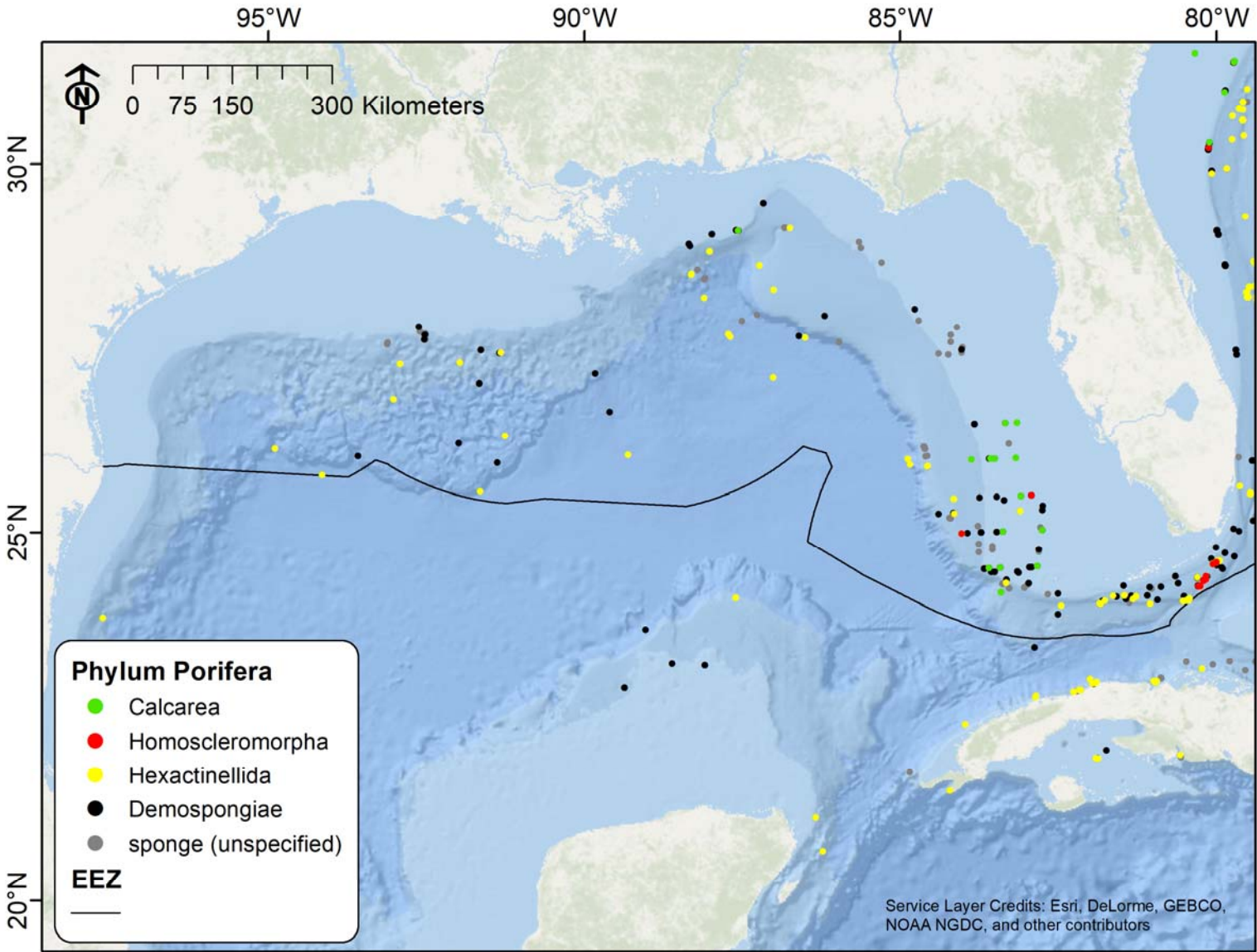
Map 4. Locations of gorgonian corals (Order Alcyonacea, in part – formerly Order Gorgonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



Map 5. Locations of sea pens (Order Pennatulacea) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



Map 6. Locations of lace corals (Order Anthoathecata, Family Stylasteridae) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



Map 7. Locations of sponges (Phylum Porifera) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



POPULATION CONNECTIVITY OF DEEP-SEA CORALS

I. Introduction

Identifying the scale of dispersal among habitats has been a challenge in marine ecology for decades (Grantham et al. 2003, Kinlan and Gaines 2003, Hixon 2011). Unlike terrestrial habitats in which barriers to dispersal may be obvious (e.g. mountain ranges, rivers), few absolute barriers to dispersal are recognizable in the sea. Additionally, most marine species have complex life cycles in which juveniles are more mobile than adults. As such, the dynamics of populations may involve processes in distant habitats that are coupled by a transport mechanism. Studies of population connectivity try to quantify the transport, or dispersal of individuals, among geographically separated populations. For benthic marine species, such as corals and demersal fishes, colonization of new populations occurs primarily by dispersal of larvae (Figure 1; Shank 2010). Successful dispersal and recruitment, followed by maturation and reproduction of these new migrants ensures individuals contribute to the gene pool (Hedgecock 2007). Thus, successful dispersal links and cohesively maintains spatially separated sub-populations. At shorter time scales (tens to hundreds of years), connectivity regulates community structure by influencing the genetic composition, diversity and demographic stability of the population, whereas at longer time scales (thousands of years), geographic distributions are affected (McClain and Hardy 2010). Alternatively, populations may become extinct or speciation may occur if connectivity ceases (Cowen et al. 2007). Therefore, the genetic exchange of individuals between populations is fundamental to the short-term resilience and long-term maintenance of the species. However, for the vast majority

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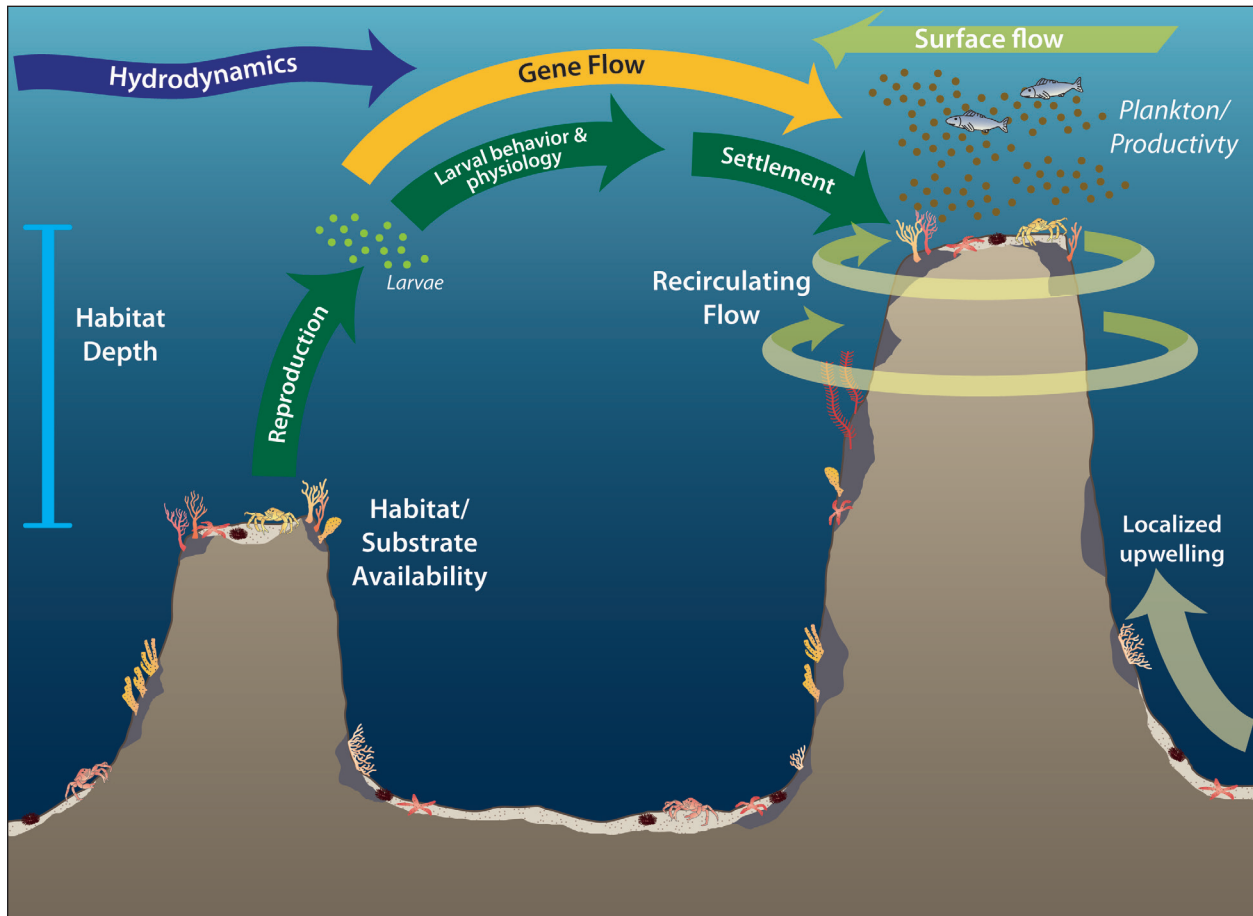
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POPULATION CONNECTIVITY OF DEEP-SEA CORALS



*Figure 1. Diagrammatic representation of potential physical (hydrodynamics, depth) and biological (reproduction, larval behavior, settlement) forces that may influence dispersal, colonization, and genetic connectivity among deep-sea coral populations. (reprinted from Shank 2010, *Oceanography*; 1).*

of marine species, population connectivity remains poorly understood.

To effectively manage marine species, knowledge of the spatial scale at which populations are connected is beneficial (Palumbi 2003, Fogarty and Botsford 2007). Ecosystems within the deep sea often occur over large geographic scales, yet are spatially fragmented across the entire range with stretches of unsuitable habitat separating prime habitat patches (e.g. cold-water coral reefs, methane seeps, hydrothermal vents). Habitat fragmentation may escalate with increasing resource exploitation (e.g. Hilário et al. 2015). The ecological patterns observed in

many deep-sea ecosystems can be explained by metapopulation dynamics as conceived by Levins (1969). Under this scenario, species occur within patchy habitats that undergo local extinction and recolonization and those patches are connected via dispersal and migration. The persistence, or viability, of the metapopulation increases as the availability of suitable habitat patches increases, local extinction decreases, and migration/dispersal between patches increases. In local deep-sea communities, the regional distributions of each species may be composed of metapopulations that are influenced by a balance among global-scale, landscape-scale and small scale dynamics (Levins et al. 2001).

Spatial management tools, such as networks of marine protected areas or reserves have the potential to protect the entire ecosystem, including nursery grounds, adult habitats, food sources, etc. Success of these protective measures relies at least partially upon estimates of dispersal rates across reserve boundaries (Botsford et al. 2003, Hilborn et al. 2004). For example, a population may be more vulnerable to human activities if it is not likely to receive recruits from other populations (e.g., self-sustaining populations, where only larvae produced within the population settle in the population). Alternatively, if larvae produced within a given population disperse to other populations, that population may be an important larval “source” that could rescue depleted populations (Pulliam 1988). Identifying source sub-populations is vitally important to management and conservation plans. Estimates of connectivity provide the relative scale at which a protected area may function. Such information may be utilized to optimize the placement of protected areas and to estimate the potential impacts to recruitment outside protected area boundaries (Palumbi 2001, Gaines et al. 2010).

Biological and physical processes influence larval dispersal (Cowen et al. 2007, Paternello et al. 2007, Galarza et al. 2009, Cowen and Sponaugle 2009, Sivasundar and Palumbi 2010, Mokhtar-Jamaï et al. 2011, Woodson et al. 2012). While biological attributes, such as timing of reproduction, larval behavior (e.g., swimming, vertical migrations), buoyancy, and physiology (e.g., feeding), affect larval survivorship and dispersal distances, physical processes, such as prevailing currents, eddies, recirculating flows, bottom topography and upwelling, can enhance or constrain larval movement (Figure 1; Shank 2010). Factors such as distance from a spawning site, advection and diffusion, and high mortality rates, all

influence the number of larvae present in the water column (Cowen and Sponaugle 2009, Rosser 2015). The combined influences of these biological and physical parameters may either promote dispersal of larvae over great distances (i.e. create dispersal corridors), or constrain population connectivity by isolating some populations from others (i.e. create barriers to dispersal).

Due to small larval sizes and the immense volume of the oceans into which larvae disperse, measurements of dispersal distances are difficult and tracking of spawning events can be quite challenging (Gawarkiewicz et al. 2007). Life history traits, such as pelagic larval duration, have been used as a proxy for dispersal distances. Pelagic larval duration correlated well with estimates of dispersal for some species (Bohonak 1999, Shanks et al. 2003). However, there are numerous examples where no relationship between pelagic larval duration and dispersal distance was observed (e.g. Severance and Karl 2006, Miller and Ayre 2008, Weersing and Toonen 2009, Galarza et al. 2009). Although the validity of correlation between pelagic larval duration and dispersal potential remains equivocal, it may at least set an upper bound on dispersal distance (Selkoe and Toonen 2011). For the cold-seep dwelling mussel “*Bathymodiolus*” *childressi* and an associated gastropod, *Bathynnerita naticoidea*, larvae were detected in surface currents, suggesting larvae migrate hundreds of meters above the sea floor, allowing greater dispersal in faster surface currents (Arellano et al. 2014). Unfortunately, for the majority of deep-sea coral species, knowledge of larval duration and behavior such as swimming ability is completely absent. In a review of data on pelagic larval durations in deep-sea taxa, a total of 21 species have been characterized. Of these, only three were cnidarian species (Hilário et al. 2015). In fact, knowledge of basic

types of reproduction in deep-sea cnidarians is scarce. For example, of the 615 known deep-sea scleractinian coral species (Cairns 2007), reports on various aspects of reproduction have been ascertained for only 15 species (Waller 2005, Mercier et al. 2011). The structure-forming scleractinian corals *Lophelia pertusa* and *Oculina varicosa* are seasonal broadcast spawning species that release gametes into the water column (Brooke and Young 2003, Waller and Tyler 2005, Brooke and Järnegen 2013). In contrast, hydrocorals in the family Stylasteridae, often an important structural component of deep-sea coral gardens (Stone 2006, Lindner et al. 2008), have a reproductive strategy that involves brooded larvae with a short planktonic duration, which may limit larval dispersal potential (Brooke and Stone 2007). Similarly, *Corallium rubrum*, a precious coral with a wide bathymetric distribution, also broods larvae and releases well-developed, competent larvae (Abbiati et al. 2010). In accordance with brooded larvae, effective dispersal appears restricted (Ledoux et al. 2010a, Constantini and Abbiati 2015), and shallow water populations are genetically structured at a scale of tens of meters (Ledoux et al. 2010b, Abbiati et al. 2010, Aurelle et al. 2011, Aurelle and Ledoux 2013). Many octocorals broadcast gametes into the water column annually, relying on external fertilization and larvae with an extended planktonic development phase (Waller and Baco 2007, Kahng et al. 2011, Mercier and Hamel 2011, Watling et al. 2011, Waller et al. 2014, Nonaka et al., in press, Feehan and Waller 2015), so greater dispersal potential may be expected. Identification of newly-settled individuals is also extremely difficult, and *in situ* measures of recruitment in deep sea corals are limited (Grigg 1988, Thresher et al. 2011, Lacharite and Metaxas 2013).

Traditional methods such as stock assessments or analysis of morphological differences between populations have been used to define conservation management units and potential larval sources. However, *potential* for connectivity between geographically separated populations that do not appear to differ morphologically does not mean active exchange of larvae is occurring. In fact, populations may have been isolated for thousands of years or more yet remain morphologically similar, resulting in genetically differentiated sibling species (see Knowlton 1993). Thus, sampling organisms from different sites and indirectly measuring connectivity using genetic techniques may be the only practical way to understand past and present connections (Palumbi 2003, Shank 2010).

II. Genetic Methods

Use of molecular techniques has changed our view of population structuring and management. Molecular data have demonstrated that a single management unit with a homogeneous, wide-ranging distribution is not necessarily the best management/conservation model (Ayre and Hughes 2000, Swearer et al. 2002, Jones et al. 2005, Almany et al. 2007). For example, the scale over which populations of shallow-water scleractinian corals are differentiated can range from 25 to 7,500 km (Baums 2008), and may involve differentiation with depth (Serrano et al. 2014). A heterogeneous spatial mosaic of multiple units with varying amounts of genetic structure may better describe what is found in nature. Researchers must properly sample geographic populations, consult taxonomists, use appropriate genetic markers (e.g., mitochondrial or nuclear DNA), and consult theoretical models to ascertain the

genetic structure of a species' populations (Pante et al. 2015a).

Over broad geographic scales (e.g., entire ocean basins), mitochondrial DNA markers are often employed to assess connectivity. For most animals, mitochondrial DNA is inherited maternally. Thus, only one copy of each gene exists in an individual. Mitochondrial DNA markers provide some of the most well-known examples of geographic breaks in population connectivity among shallow water marine species such as oysters, horseshoe crabs, and black sea bass along the east coast of Florida (Avisé 1992). Mitochondrial DNA markers have also been useful in identifying closely related (sibling) or morphologically similar (cryptic) species, both of which commonly occur in the deep sea (Rogers 2002). However, mitochondrial DNA evolves at a slow rate in corals (50-100 times slower than most animals) and generally does not provide species-level resolution (France and Hoover 2002, Shearer et al. 2002, Hellberg 2007, McFadden et al. 2011, Baco and Cairns 2012). This slow rate of mitochondrial DNA sequence evolution has impeded studies of connectivity in corals (e.g., van Oppen and Gates 2006, Eytan et al. 2009), where more variable nuclear DNA markers are necessary to assess connectivity.

Realized average dispersal of an organism over its entire life cycle (planktonic larval stage, settlement, maturation) can be estimated from nuclear markers such as microsatellites (Neigel 2002). Microsatellite markers refer to regions of DNA that include adjacent repeats of several nucleotide bases. Microsatellites have a higher mutation rate than mitochondrial DNA, so often reflect connectivity on more recent time scales. However, unlike mitochondrial DNA, nuclear markers like microsatellites are inherited from both parents, so individuals

have two copies of each nuclear gene, called alleles, which are the building blocks that populations utilize to adapt and evolve in changing environments. These alleles may differ in length due to differences in the number of times the nucleotide bases are repeated. When the alleles are identical, they are termed homozygous, different alleles are heterozygous. Often, these population-level molecular markers are species-specific and highly variable. Utilization of rapidly-evolving genetic markers with many alleles allows one to decipher the unique genetic makeup of each individual. Although the initial cost of analysis is higher, results with resolution to the level of individuals and parentage is often worth the expense. Markers with high specificity and variability are utilized to assess family relationships and clonality in organisms, two attributes that complicate the genetic signatures of cold-water coral populations.

One of the most important applications of population genetic data is to determine the level of genetic structuring within and between populations. Genetic structure within a species can range from very weak, where exchange of individuals is common (i.e., high connectivity), to strong genetic structuring, where exchange of individuals is more rare (i.e., low connectivity, moving toward isolation of populations; reviewed by Palumbi 2003, Hedgecock 2007, Cowen and Sponaugle 2009). Genetic estimates of connectivity result from counting differences in DNA sequences or examining the variance in allele frequencies between populations that accumulate when connectivity is low or nonexistent (see below). When genetic structuring is detected, examination of the physical or biological parameters that may be correlated to genetic differentiation may provide clues to the processes that act to determine spatial connections among populations.

Population geneticists also attempt to decipher patterns of genetic connectivity indirectly through the application of theoretical models of population structure (Hedgecock 2007). The stepping-stone model assumes neighboring populations are more likely to exchange migrants amongst themselves than with populations further away (Kimura and Weiss 1964). Thus, genetic distance should increase with geographic distance, populations in closer proximity will be genetically more similar to each other than to populations farther away. This pattern of connectivity, referred to as isolation-by-distance (Wright 1943), creates a highly structured, genetically complex system (Rousset 1997). For example, an isolation-by-distance pattern was confirmed for *Porites lobata* populations inhabiting shallow reefs in the Hawaiian Archipelago (Polato et al. 2010). If an isolation-by-distance pattern of connectivity is detected, estimation of dispersal distances may be biologically meaningful (Rousset 1997, Palumbi 2003).

An indirect measure of the persistence of a metapopulation is genetic diversity. Genetic diversity covaries with the number of patches (sources) that can supply migrants (Maruyama and Kimura 1980, Vrijenhoek 2010). Therefore, estimating genetic diversity within metapopulations is a proxy for the vulnerability of a species to extinction.

III. Connectivity in the Deep Sea

The majority of studies of marine connectivity focus on shallow-water environments, particularly tropical reef fishes (Hixon 2011). Although shallow marine habitats were once considered open systems with ample exchange of larvae over large distances, it is now accepted that local recruitment and small-scale

population structure are common despite the lack of obvious physical barriers (Cowan and Sponagule 2009). Genetic data have suggested similar results for shallow-water corals, in that most recruitment is local, yet occasional long-distance dispersal can occur across tens to hundreds of kilometers (Ayre and Hughes 2000, Miller and Ayre 2008, Gorospe and Karl 2013).

Although less is known about patterns of connectivity in the deep sea, recent studies have suggested common themes. First, similar to shallow populations along coastlines, including many coral species along the Great Barrier Reef (Ayre and Hughes 2004), the stepping stone model may be appropriate for many deep-sea populations, particularly those arranged linearly along continental margins (LeGoff-Vitry et al. 2004, Smith et al. 2004), mid-oceanic ridge axes (Coykendall et al. 2011, reviewed by Vrijenhoek 2010) or linear arrays of seamounts (Samadi et al. 2006).

In contrast, stretches of open ocean that interrupt a linear array of reefs (Ayre and Hughes 2004) or vent populations (Vrijenhoek 2010) may create an effective barrier to dispersal, and connectivity may decrease abruptly, creating regionally isolated populations. Regional differentiation of deep-sea fauna that inhabit continental slope habitats may not be limited to benthic organisms such as corals. Even mobile species, such as fishes (e.g. *Helicolenus dactylopterus* (Aboim et al. 2005), squid (Shaw et al. 1999), scavenging isopods (France and Kocher 1996), and red crabs (Weinberg et al. 2003), show regional structuring (see Rogers 2002). Suggested mechanisms that may prevent panmixia of continental slope species include physical barriers (continents and large expanses of deep water, deep water sills (Coward et al. 2013), or among back-arc

basins (Thaler et al. 2014)), structuring of the water column (density layers), rugged topography (canyons and seamounts) and oxygen minimum zones (Rogers 2002). In addition, species-specific life history strategies, especially related to spawning, may also act to limit exchange of individuals between populations (Rogers 2002).

Shared patterns of species diversity and genetic structuring across unrelated but co-distributed species may indicate that oceanographic features affect connectivity of many species in similar ways (Cunningham and Collins 1998). For example, the deep-sea scleractinian coral species *Desmophyllum dianthus*, as well as two antipatharian species, *Antipathes robillardii* and *Stichopathes variabilis*, exhibited genetic subdivision across large ocean expanses in the southern Pacific Ocean (Miller et al. 2010). Concordance among regional connectivity patterns of these co-distributed species indicates that physical forces (e.g., prevailing currents, eddies, upwelling) may restrict larval dispersal among regions. However, no genetic subdivision was detected for two other coral species (*Solenosmilia variabilis*, *Madrepora oculata*) using the same mitochondrial and nuclear gene regions (Miller et al. 2010). Conversely, using microsatellites instead of mitochondrial DNA, Becheler et al. (in review) identified distinct genetic populations of *Madrepora oculata* among canyons in the Bay of Biscay (Eastern North Atlantic Ocean), yet co-occurring *Lophelia pertusa* were panmictic. Clearly, no generalized connectivity pattern applies to all coral species.

A factor that may uniquely influence connectivity among deep-sea organisms is depth. Pronounced physiological gradients occur as depth increases, which could result in locally adapted populations and enhanced

genetic differentiation (Rogers 2002, Zardus et al. 2006). This concept, known as the depth-differentiation hypothesis (Rex and Etter 2010), suggests that the divergent selection across environmental gradients may cause population differentiation, leading to new and/or cryptic deep-sea species. Depth-related divergence has been identified in molluscs (e.g. Chase et al. 1998, Etter et al. 1999, Goffredi et al. 2003, Etter et al. 2005, Zardus et al. 2006, Jennings et al. 2013), polychaetes (Lundsten et al. 2010, Schüller 2011, Cowart et al. 2014), amphipods (France and Kocher 1996, stylasterid corals (Lindner et al. 2008), primnoid octocorals (Baco and Cairns 2012), and the red coral *Corallium rubrum* (Constantini et al. 2011). In other deep-sea corals, limited vertical larval dispersal has been suggested the solitary coral *Desmophyllum dianthus*, a scleractinian coral with a cosmopolitan distribution. Genetic differentiation with depth in *D. dianthus* was consistent with the stratification of deep water masses that entrain larvae and do not allow mixing among depth strata (Miller et al. 2011). In a study that included three species of octocorals in the Gulf of Mexico, an ecological niche model revealed little overlap among *Callogorgia* species occupying different depths (Quattrini et al. 2013). The depth differentiation hypothesis was tested of these species, *Callogorgia delta*, using microsatellite data, and isolation by depth was confirmed (Quattrini et al. 2015). Rex et al. (2005), using deep-sea molluscan fauna with bathyal and abyssal distributions as examples, postulate that the abyssal environment may create population sinks due to a decrease in organic carbon influx from more productive coastal systems. These isolated populations rely on bathyal populations for immigrants. Conversely, nine genetic breaks were detected in the cosmopolitan deep-sea

POPULATION CONNECTIVITY OF DEEP-SEA CORALS



REFERENCE	SPECIES	REGION	MARKERS	CONNECTIVITY	IBD
Eytan et al. 2009	<i>Oculina varicosa</i>	WNAntlantic	4 nuclear DNA genes	Depth structured	No
Thoma et al. 2009	6 octocorals, 2 antipatharians	WNAntlantic, NE Seamounts	mtDNA	No structuring, high connectivity	NA
Cho and Shank 2010	<i>Asteroschema clavigerum</i> <i>Ophiocreas oedipus</i> <i>Ophioplinthaca abyssalis</i> <i>Ophioplinthaca chelys</i>	WNAntlantic, NE Seamounts	2 mtDNA genes	Regional seamount structure, depth	Yes
Morrison et al. 2011	<i>Lophelia pertusa</i>	North Atlantic	9 microsatellites	Regional structure, moderate connectivity within regions	Yes, broad scale
Baco and Shank 2005 Baco et al. 2006	<i>Corallium lauuense</i>	Central Pacific	3-6 microsatellites	High connectivity, structure between sites and depths	No
Baco and Cairns 2012	Several <i>Narella spp</i>	North Pacific	6 mtDNA markers	Narrow geographic and depth ranges for haplotypes	NA
Herrera et al. 2012	<i>Paragorgia arborea</i>	North Pacific, South Pacific, North Atlantic	7 mtDNA genes	Regional structure	NA
Quattrini et al. 2015	<i>Callogorgia delta</i>	Gulf of Mexico	10 microsatellites	Depth structured	Yes, depth > distance

Table 1. Studies examining connectivity among deep-sea corals and/or deep coral communities in U.S. waters.

amphipod *Eurythenes gryllus*. In this instance, higher diversity was observed at abyssal rather than bathyl depths, thus reflecting a pattern contrary to the depth-differentiation hypothesis (Havermans et al. 2013). Clearly, environmental factors associated with depth may create important abiotic gradients that may influence population structuring in the deep sea (Quattrini et al. 2015).

IV. Connectivity Among Deep-Sea Corals in U.S. Waters

IV.1. North Atlantic Ocean

Genetic methods were used to assess connectivity patterns in several North Atlantic deep-sea coral species (Table 1). In the first of these studies, connectivity among shallow and deep populations of the structure-forming coral *Oculina varicosa* was examined using three nuclear DNA sequence markers (Eytan et al. 2009). *Oculina varicosa* occurs most commonly at shallow depths (< 30 m). However, azooxanthellate colonies grow at 70 to 100 m depth along the *Oculina* Banks off the Florida east coast (Reed 2002). Despite Federal protection, the *Oculina* Banks have been negatively impacted by illegal trawling and dredging (Reed et al. 2007). The *Oculina* Banks population was found to be distinct from shallow populations; therefore, depth was considered an important factor structuring the pattern of connectivity in *O. varicosa* (Eytan et al. 2009).

Lophelia pertusa, a structure-forming coral species commonly found on the continental slope off the southeastern U.S. coast (Ross and Nizinski 2007) and Gulf of Mexico (Brooke and Schroeder 2007), has a nearly cosmopolitan distribution, suggesting substantial dispersive ability. *Lophelia pertusa*

is a broadcast spawner that was originally thought to produce non-feeding larvae (Waller and Tyler 2005). Yet a recent study suggests larvae may feed and actively swim upwards during the first weeks after fertilization, a behavior that may allow larvae to rise above the benthic boundary layer and promote advection in stronger currents (Larsson et al. 2014). Swimming behavior as well as an estimated three to five week larval duration imply high dispersal potential. However, the spatial scales that *L. pertusa* larvae travel remains unknown, making accurate predictions of realized larval dispersal challenging. Nine microsatellites were used to examine patterns of genetic connectivity across a large portion of the geographic range of *L. pertusa* in the North Atlantic Ocean (Morrison et al. 2011). Four distinct genetic groupings corresponding to ocean regions were identified: Gulf of Mexico, coastal southeastern U.S., New England Seamounts, and eastern North Atlantic Ocean (Figure 2). It is known that reproductive timing is offset between the eastern North Atlantic (Waller and Tyler 2005) and Gulf of Mexico (Brooke et al. 2007) *L. pertusa* populations. Whether or not regionally isolated *L. pertusa* populations represent cryptic species will require further morphological examination and biological evidence. Interestingly, similarities exist between zoogeographic patterns of deep-sea scleractinian corals (Cairns and Chapman 2001) and regional *L. pertusa* genetic differentiation (Morrison et al. 2011), suggesting that similar mechanisms (see above) may constrain coral larvae within regions.

Although the populations of *L. pertusa* at the New England seamounts occur in a geographic location that could be a corridor, or stepping stone, for connectivity across the Atlantic Ocean, the seamount populations

POPULATION CONNECTIVITY OF DEEP-SEA CORALS

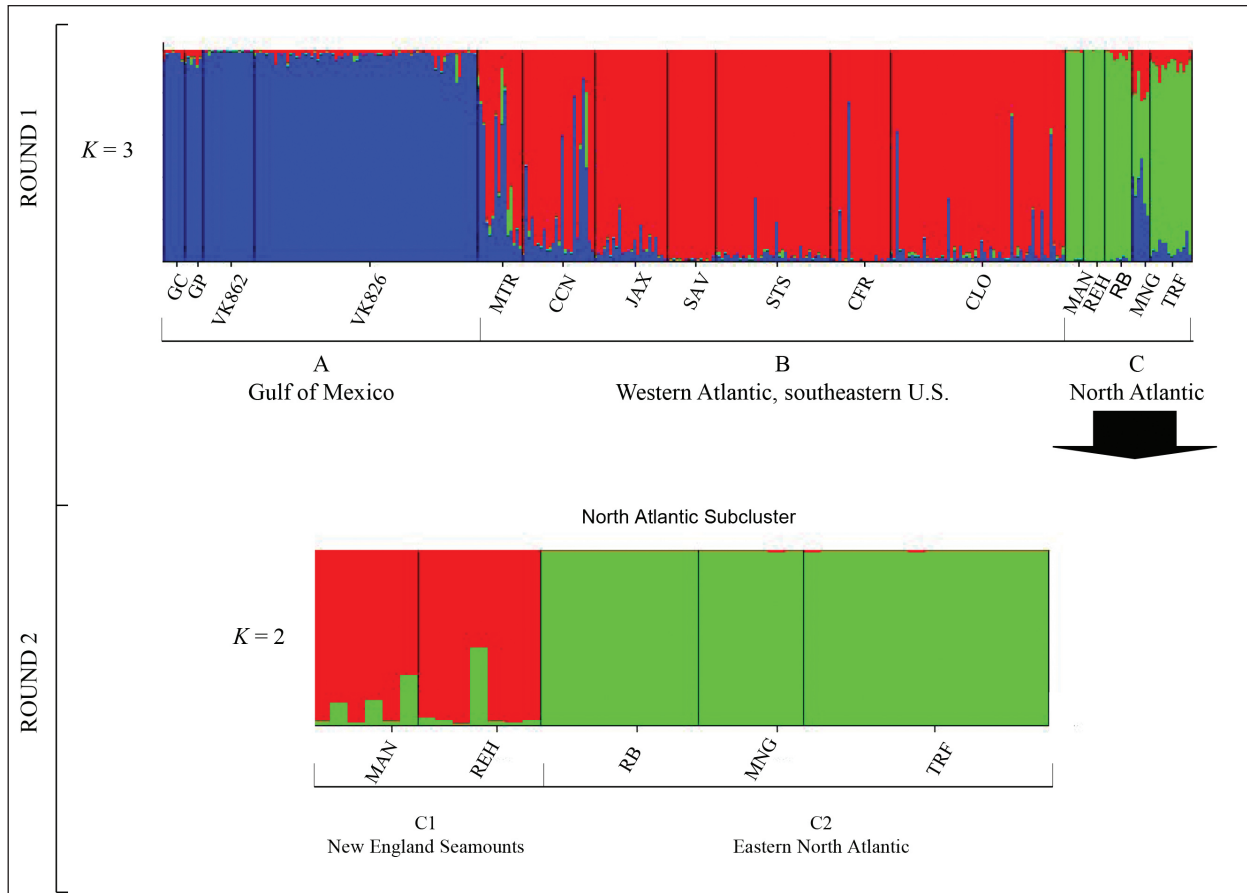


Figure 2. Probability of assignment of *Lophelia pertusa* individuals, represented by colored vertical bars, to four groups based upon multi-locus genotypes using the program STRUCTURE. Populations are arranged from west (left) to east (right). The top bar (round 1) represents an initial run including all *L. pertusa* samples. The lower bar represents additional structuring between New England Seamounts and Eastern North Atlantic populations detected during a subsequent run of STRUCTURE. (Reprinted from Morrison et al. 2011, *Conservation Genetics*; 37).

were the most genetically differentiated based upon microsatellites, suggesting little connectivity (Morrison et al. 2011). The seamount populations appeared more genetically similar to populations from the eastern rather than western North Atlantic Ocean, despite occurring in closer proximity to the latter. These seamount populations occur deeper (1418-1679 m) than other populations sampled (140-740 m) and therefore differing water masses and circulation patterns may act as a barrier to gene flow.

For North Atlantic Ocean *L. pertusa* populations, a positive correlation between genetic and geographic distance was detected at broader scales (thousands of km), but not at smaller scales (Morrison et al. 2011). Since regional breaks in connectivity were also detected, deductions regarding dispersal distances may be compromised due to the likely violation of the stepping-stone model assumption of on-going dispersal at these large scales (Slatkin 1993, Garnier et al. 2004). However, results suggest moderate connectivity within each of the regions. A

previous study of *L. pertusa* in the eastern North Atlantic Ocean also reported moderate connectivity (genetic cohesion) among European continental margin populations and no correlation between genetic and geographic distance (Le Goff-Vitry et al. 2004). Levels of both inbreeding and asexual reproduction (clones) varied among European margin *L. pertusa* populations, suggesting that most dispersal is spatially restricted, yet occasional long-distance dispersal is adequate to maintain genetic cohesion (Le Goff-Vitry et al. 2004). While both studies detected genetic structuring (i.e., decreased connectivity) between continental slope and Norwegian fjord *L. pertusa* populations in the eastern North Atlantic, results from Morrison et al. (2011) suggest the magnitude of differentiation is less than that observed across the North Atlantic Ocean.

Lophelia pertusa populations surveyed in both the eastern and western North Atlantic Ocean using microsatellites have shown heterozygote deficiencies (Le Goff-Vitry et al. 2004, Morrison et al. 2011, Dahl et al. 2012). Similarly, heterozygote deficits have been detected in the majority of population genetic studies of corals (Ayre and Hughes 2000, van Oppen and Gates 2006, Selkoe and Toonen 2006), including cold-water corals (Baco and Shank 2005, Baco et al. 2006). Occurrence of heterozygote deficits in nature is often explained as a violation of the concept of the 'ideal population' assumed by the Hardy-Weinberg principle. For instance, a subset of the population could contribute the most genetic material to the next generation (non-random mating). Studies have shown a propensity for clonal reproduction via fragmentation in most *L. pertusa* populations surveyed (Le Goff-Vitry et al. 2004, Morrison et al. 2011, Dahl et al. 2012).

Clonal reproduction can cause heterozygote deficits due to deviation from random mating (Dahl et al. 2012, van Oppen et al. 2008). In fact, asexual reproduction via fragmentation may play a key role in the establishment and maintenance of deep *L. pertusa* reefs (Dahl et al. 2012). For example, few genetic individuals become dominant at a reef site and skew opportunities for mating. Additionally, the lifespan of a genetic individual may be quite long (thousands of years; Dahl et al. 2012), therefore, this life history trait may be important to both estimates of connectivity and to the evolution of the species.

Seamounts are hypothesized to be locations of isolation in the deep-sea, resulting in high levels of speciation and endemism (e.g. Hubbs 1959, Rowden et al. 2010, Pante et al. 2015b). Three studies (Thoma et al. 2009, Cho and Shank 2010, Herrera et al. 2012) have addressed connectivity along the New England and Corner Rise Seamounts. Thoma et al. (2009) investigated isolation among individual seamounts by testing the hypothesis that corals occurring at isolated seamounts would possess unique mitochondrial DNA haplotypes. Variability in the mitochondrial mismatch repair gene homolog (*mutS*) was assessed for five octocoral genera. Nine markers for antipatharians as well as an intergenic spacer for bamboo corals were also incorporated into the data set.

The Thoma et al. (2009) study found four haplotypes unique to the seamounts, as well as two haplotypes from the adjacent margin that were widespread, consistent with the possibility of seamounts being hotspots for divergence of species. A caveat of this work is that the unique haplotypes discovered at the seamounts were not necessarily the result of endemism, but could be due to small



sample sizes. This work, however, is based on the assumption that *mutS* haplotypes were species-specific. Subsequent work has shown this is not the case. Rather, some species of octocorals have multiple haplotypes for *mutS*, which can lead to underestimating species ranges, while other *mutS* haplotypes are shared between multiple species, resulting in overestimating species ranges (McFadden et al. 2010, McFadden et al. 2011, Baco and Cairns 2012, Pante et al. 2015b). These same studies show that only about 50% of species could be resolved using the *mutS* marker. Thus the single-marker approach of Thoma et al. (2009) likely does not provide sufficient power to resolve the connectedness of the New England and Corner Rise seamounts at the species level.

In contrast, data from seven mitochondrial gene regions and nuclear genetic variants of the deep-sea bubblegum coral *Paragorgia arborea* revealed basin-wide and global patterns of genetic variation correlated with historical migrations and connectivity from the Western Pacific into the Atlantic (Herrera et al. 2012). Prior to this study, diversity throughout the entire known distribution of a cold-water coral species had not been evaluated. Herrera et al. (2012) utilized mitochondrial and nuclear genetic variants in a phylogeographic context to examine the compatibility of *P. arborea* with the genealogical-phylopecies concept by examining specimens collected over its known distribution. The multi-marker use demonstrated that the global morphospecies *P. arborea* can be defined as a genealogical-phylospecies hosting differing levels of connectivity around the world's oceans. Global genetic variation among populations of this species revealed significant basin scale differences. These phylogeographic data suggest a scenario in which *P. arborea*

originated in the North Pacific, possibly in the Western North Pacific, followed by colonization of the South Pacific and spreading eastward around the Southern Hemisphere in a stepping stone fashion (possibly via the Antarctic Circumpolar Current). The colonization of the North Atlantic seems to have occurred through a more recent dispersal event from the South Pacific, via the Central American Seaway, or from the South Atlantic. Notable is that despite the finding of significant geographic variation over the geographic range, no significant correlation with depth was observed.

A study by Cho and Shank (2010) demonstrated the impact host-specific symbiotic relationships may have on the genetic connectivity of fauna associated with cold-water corals. Deep-sea corals provide habitat for many species that have developed symbiotic relationships with varying degrees of specificity to their host corals (Shank 2010, Buhl-Mortensen et al. 2010). The co-evolution of host-associate relationships may affect the genetic connectivity of these coral associates. Cho and Shank (2010) studied the patterns of dispersal and genetic connectivity of four brittle star species (*Asteroschema clavigerum*, *Ophiocreas oedipus*, *Ophioplinthaca abyssalis* and *Ophioplinthaca chelys*; Figure 3) that display differing levels of associative specificity to deep-sea coral hosts inhabiting the New England and Corner Rise seamounts.

Analyses of two mitochondrial markers, mt16S and mtCOI, revealed species-specific genetic differentiation based on geography and depth. *Asteroschema clavigerum* and *O. oedipus* showed significant isolation by distance, significant genetic differentiation by depth, and predominantly westward historical migration. *Asteroschema clavigerum*

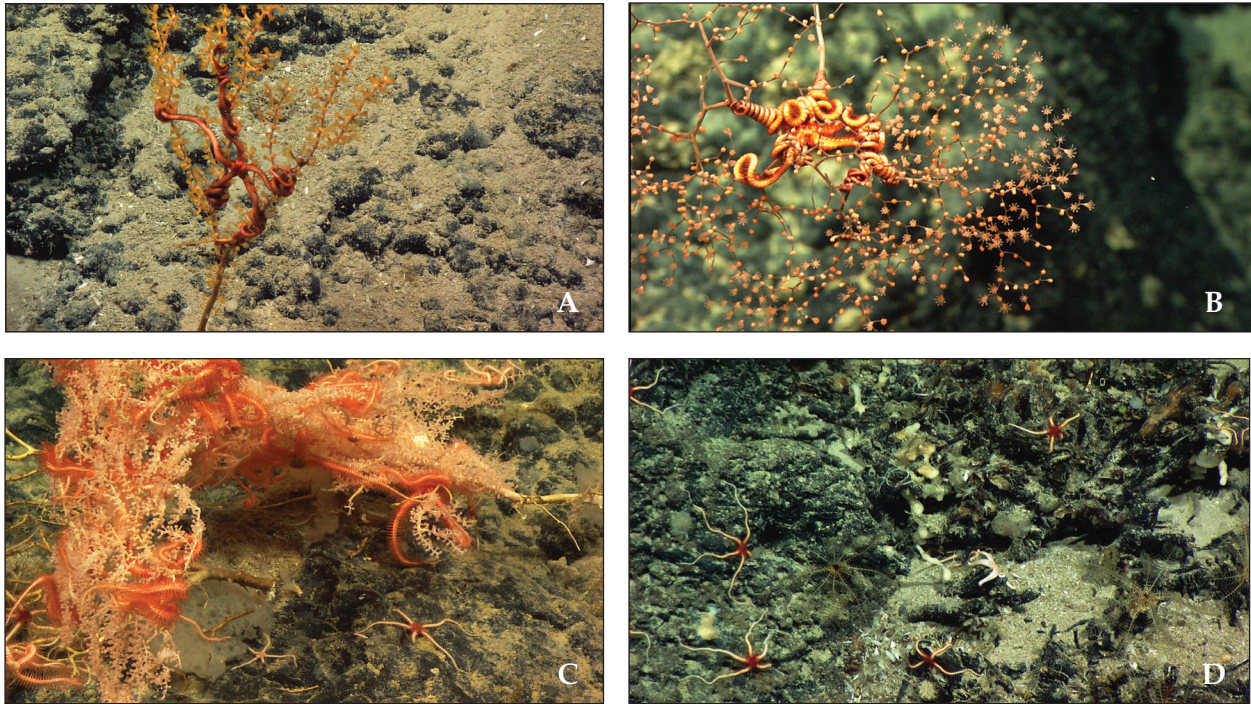


Figure 3. Images of four brittle star species studied by Cho and Shank (2010). A) Brittle star *Asteroschema clavigerum* found on the deep-sea coral *Paramuricea* sp. B) Brittle star *Ophiocreas oedipus* found on the deep-sea coral *Metallogorgia melanotrichos*. C) Brittle stars *Ophioplinthaca abyssalis* found on the deep-sea coral *Candidella imbricate*. D) Brittle stars *Ophioplinthaca chelys* found on the sea floor. Image credit: WHOI; DASS 2005 Expedition; IFE; NOAA OE.

had significant genetic differentiation by geographic region. In contrast, *O. abyssalis* and *O. chelys* displayed predominantly eastward historical migration and *O. chelys* displayed significant genetic differentiation within individual seamounts. The patterns of genetic differentiation shared by *A. clavigerum* and *O. oedipus* may be correlated with species-specific host specificity and dispersal strategies. Both of these species have seemingly obligate symbiotic relationships to their specific coral hosts and are broadcast spawners, while the other two species studied, *O. abyssalis* and *O. chelys*, have lower or no fidelity to their coral hosts and are potentially brooders.

IV.2. North Pacific Ocean

Although scleractinian reefs are not common in the North Pacific Ocean, dense deep-sea coral assemblages, dominated by octocorals and antipatharians, are found throughout the region (Baco 2007, Hourigan et al. 2007). Despite the high diversity and abundance of corals, population genetics analysis of only one species has been published. *Hemicorallium laauense* (= *Corallium laauense*), a commercially important octocoral in the family Coralliidae, harvested periodically as part of the precious coral fishery (reviewed in Grigg 2002), is numerically dominant in the Hawaiian Archipelago at 350-575m depth (Parrish and Baco 2007, Baco 2007). *Hemicorallium laauense* appears to spawn with a periodic or quasi-continuous reproductive strategy (Waller and Baco 2007).



Because of the relatively linear nature of the Hawaiian Archipelago, one would expect a classic isolation-by-distance signature in the genetic data for most species. However, results from an analysis of three microsatellite loci in *H. laauense*, collected from eight sites in the Main Hawaiian Islands and southern end of the northwestern Hawaiian Islands, indicated no isolation-by-distance pattern (Baco and Shank 2005). Instead, results indicate that the scale of genetic structure on isolated features such as oceanic islands and seamounts may be more complex than a simple stepping-stone model. For example, the deepest site, located off Kauai in the middle of the sampling area, was quite different genetically compared to the majority of sites sampled during the study. Also, there was significant variation within the continuous Makapu'u bed (on the scale of 1.6 km) off the Island of Oahu. The fairly high heterozygote deficiency found for this species based on six microsatellite markers (Baco and Shank 2005, Baco et al. 2006) could indicate a high degree of inbreeding for this species, implying significant isolation for each of the precious coral bed locations investigated, with only occasional long distance dispersal events. These results suggest connectivity within and between each feature on or each location along a seamount chain should be assessed when considering any management actions.

Analyses based upon mitochondrial DNA also provide some insight into connectivity along North Pacific seamounts. Previous studies of seamount octocorals indicated widely distributed mitochondrial haplotypes and counter the idea that seamounts may be isolated (Smith et al. 2004, Thoma et al. 2009). However, each of these studies cautions that mtDNA markers were not morphologically ground-truthed to determine the level of genetic variation which corresponds to a species. A recent study of the octocoral genus

Narella (Family Primnoidae) examined the variability of six mtDNA regions relative to species designations in this genus (Baco and Cairns 2012). The results of this study indicated that the markers used in previous studies could not distinguish individuals at the species level (*mutS*) and two markers (indel regions) could not distinguish between genera (Smith et al. 2004) based on mtDNA haplotypes. Thus, the fact that haplotypes were widespread is not sufficient evidence to disprove isolation of seamount features. Using all six mtDNA markers on specimens collected on North Pacific seamounts, the results of the *Narella* study indicate that geographic and bathymetric ranges of seamount species may be much narrower than previously thought.

V. Future Directions

Whereas the examples discussed above provide insights into patterns of connectivity for several abundant and important deep-sea coral species in U.S. waters, much work remains before we can achieve a fundamental understanding of the factors that control connectivity among coral species and their diverse associated fauna. Several specific research questions that may guide future studies of connectivity among deep-sea corals are suggested below.

V.1. How Far do Larvae of Deep-Sea Corals and Associated Organisms Disperse?

A basic understanding of distributions of deep-sea coral species and associated fauna, coupled with a thorough taxonomic evaluation, is necessary to address this research question (see Pante et al. 2015a). Although general ranges for many deep-sea coral species are known, the need exists to

fine-tune estimates and fill in information gaps by visiting unexplored areas. Exploratory cruises are necessary to locate populations, assess abundances, and collect samples. Success in locating and sampling deep-sea corals and associated organisms during exploratory cruises will depend upon access to deep-submergence technologies (see below). Additionally, such explorations may be guided by predictive biophysical modeling, which may help locate where previously unknown coral habitats occur (e.g. Yearsley and Sigwart 2011). Predictive modeling involves methods that produce distribution maps from limited sampling data, as interpreted through remote sensing information such as multibeam bathymetry, substrate and geomorphology, rugosity, slope and aspect (e.g., Howell et al. 2011) and/or aspects of the environmental tolerances of corals compared with physical, chemical and biological variables at the geographic locations being studied (Davies et al. 2008, Guinotte et al., this volume)). The effective use of biophysical models for deep-sea organisms is hampered by knowledge gaps in both physical and biological parameters (Hilário et al. 2015

While sampling deep-sea organisms can be labor intensive and expensive, obtaining sufficient numbers of individuals per population for statistical testing has strongly impeded progress to date. Need for adequate numbers of samples is regarded as essential and of critical importance. A balance between adequate sampling of local populations and sampling broadly throughout the geographic range of the species is imperative (Pante et al. 2015a). Therefore, funding agencies and science parties need to appreciate the value of connectivity studies and dedicate dive time specifically for sampling spatially structured populations. Much can be gained through collaborative efforts in large-scale and multi-

species connectivity studies if adequate time for intensive sampling of individual species is included in the sampling plan.

With the advance of new genetic tools and the unknown scales of dispersal for almost all deep-sea corals and their symbionts, fine-scale (spatial and temporal) studies are now needed. For example, genetic structure was found at very small spatial scales (within a reef) but disappeared or became negative at larger scales in Hawaiian *Pocillopora* corals (Gorospé and Karl 2013). Clonal reproduction through fragmentation in scleractinian corals may be key to extreme longevity of a genetic individual (clone), and may skew chances for reproduction to a few individuals (Dahl et al. 2012). Therefore, sampling should address fine-scale structuring adequately. The feasibility of such a sampling scheme has been demonstrated (Becheler et al., in review). Larger sample sizes and additional markers are necessary to obtain the statistical power necessary to distinguish small but important genetic distinctions (Waples 1998, Hedgecock 2007).

V.2. Can Larval Dispersal Distances be Accurately Estimated Given Current Knowledge of Early Life Histories?

Early life history traits, such as timing and potential seasonality of reproduction, reproductive output and success, planktonic duration, and recruitment, all influence connectivity (e.g. Underwood and Fairweather 1989, Rosser 2015). Reproductive periodicity, larval type and behaviors are fundamental processes that need further investigation (Hilário et al. 2015). In the few species that have been studied, nearly all modes and patterns of reproduction have been observed



(Patarnello et al. 2007, Metaxas and Kelly 2010, Mercier et al. 2011). Thus, making predictions on dispersal, based upon taxon, depth, or location, is extremely difficult.

Assessing patterns of connectivity among organisms associated with deep-sea coral habitats will expand understanding of the functioning of and potential sensitivities to disturbance of these ecosystems. By comparing patterns of genetic connectivity between different species within the same habitat, we gain insight into what drives migration and dispersal in these ecosystems (community genetics). Contrasting patterns of population structure observed among species within the same habitat indicates different life histories are driving resultant dispersal patterns (i.e., vagile vs sessile, lecithotrophic vs planktotrophic larvae) whereas similar patterns of population structure among species within the same habitat indicate larger forces, such as deep ocean current circulation that entrain larvae, are acting on organisms similarly. For example, Samadi et al. (2006) examined connectivity among populations of several squat lobster species and two gastropod species along the Norfolk ridge seamounts. Results suggested that connectivity is restricted only for species with limited dispersal ability. Thus, life history is an important factor shaping connectivity patterns along this seamount chain.

V.3. To What Extent do Patterns of Connectivity Relate to Hydrodynamics?

For shallow-water marine taxa, integration of genetic, biological, geographic and hydrodynamic data into dispersal models has provided both estimates of connectivity as well as descriptions of physical forces that likely shape connectivity patterns (Manel et

al. 2003, Galindo et al. 2006, Cowen et al. 2006, Baums et al. 2005, Baums et al. 2006, Werner et al. 2007, Mokhtar-Jamaï et al. 2011, Foster et al. 2012). Hydrodynamic patterns surrounding deep-sea coral areas are less known (see Hilário et al. 2015, for review). However, physical data are now being collected in some deep-sea regions through the deployment of instrumentation that sequentially collects environmental data over either short (autonomous underwater vehicles) or long periods of time (benthic landers; e.g. Davies et al. 2010, Yearsley et al. 2011). Integration of ocean circulation and larval transport models (based upon laboratory tested larval durations of seven deep-sea invertebrates) exemplified the various patterns of dispersal possible (Young et al. 2012). General conclusions from this study were that most larvae are retained in the same geographic location as adults, but when there is net transport of larvae out of an area, it is unidirectional in an eastward and northward trajectory in Intra-American seas (Young et al. 2012). The combination of genetic connectivity and hydrodynamic data at key time periods (i.e., coral spawning) should allow for better precision in predictive modeling of both dispersal potential and coral presence.

V.4. What Research Tools May be Useful for Studies of Connectivity in the Deep Sea?

Continued development of genetic tools is necessary to fill large knowledge gaps regarding evolutionary processes that shape diversity in the deep sea. Through the application of genetic techniques, patterns and limits of species distributions as well as patterns of dispersal, migration, recruitment and clonality can be described. Choosing the most appropriate genetic tools is project-

specific, dependent upon the question driving the research. For poorly characterized taxa, DNA sequence data is necessary to identify and refine species boundaries and relationships between closely related taxa prior to further analyses (Knowlton 2000). For example, examination of morphological and phylogenetic data is necessary prior to population genetic analyses for most octocoral species (McFadden et al. 2010). Given the prevalence of regional and bathymetric cryptic species (France and Kocher 1996, Etter et al. 1999, Etter et al. 2005, Chase et al. 1998, Vrijenhoek 2009, Miller et al. 2010, Miller et al. 2011, Puillandre et al. 2011, Mantelatto et al. 2014, Pante et al. 2015a), it is likely that the number of deep-sea species has been underestimated (Rogers 2002). Broad-scale sampling and DNA sequencing of few samples can address the taxonomy as well as provide a first order understanding of relationships among geographically distant populations. Adequate sampling, plus simultaneous molecular and traditional systematic investigations may eventually produce more accurate species lists and better evolutionary descriptions of the evolutionary relationships among them (Vrijenhoek 2009, Pante et al. 2015a). These kinds of results would provide the foundation for future population genetic studies. Sampling of this nature should be incorporated into cruise objectives. Additionally, continued database development, promotion of data and sample sharing, plus synthesis and collaboration, should allow for advancements in understanding (McClain and Hardy 2010).

Inexpensive production of large volumes of sequence data for any organism is now possible using next-generation sequencing technologies (NGS). These new sequencing technologies offer exciting prospects for marker development in deep-sea

coral taxa. Researchers using NGS can identify microsatellites more quickly and inexpensively (e.g. Coykendall and Morrison 2013, Morrison et al. 2015). Additional types of molecular markers, such as single-copy nuclear genes (e.g. Concepcion et al. 2008), and single-nucleotide polymorphisms (SNPs, e.g. Baird et al. 2008), may now be developed without prior knowledge of the genome (Reitzel et al. 2013). SNPs are often numerous (hundreds to thousands) and may provide higher genome coverage than microsatellites (tens of markers). The utility of SNPs for delimiting recalcitrant species of octocorals in the genera *Chrysogorgia* (Pante et al. 2015c) and *Paragorgia* (Herrera and Shank 2015) was recently demonstrated. Whether or not differentiation is detected using neutral genetic markers as discussed thus far, populations may be adapted to local environmental conditions. By sequencing coding regions of the genome, genes that may underlie functional variation can be identified and surveyed through gene expression analyses (e.g. Vera et al. 2008). As such, advances in both sequencing technologies and statistics for population genomics may allow researchers to identify genome-wide signatures of adaptation (Baums 2008, Ledoux et al. 2015). Collection of environmental data that may be correlated with differences in gene expression will add value to population genomic studies and may help to identify the mechanisms that generate and maintain diversity.

For certain deep-sea coral associates, chemistry of calcified structures (e.g., fish otoliths and molluscan statoliths) can be used to assess natal origins of individuals and help define geographic scale of dispersal and connectivity. These metabolically inert structures record the chemistry of the environment in which the animal lives.



Natural tags are derived from variation in environmental conditions, including temperature, salinity, dissolved oxygen, and other chemical parameters. If the environmental chemistry is distinct, then these chemical tags provide a record that chronicles spatial separation during spawning, and differences between populations (Campana et al. 1994). While connectivity in shallow-water environments has been addressed using this technique (Thorrold et al. 2007, Eldson et al. 2008), application in the deep sea has been limited to a few studies focused on stock assessments of commercially exploited fishes (Hauser and Carvalho 2008). Combined approaches using microsatellite markers and otolith chemistry can help assess fine scale genetic structure in deep-sea fishes, because these tools document both the ecological and evolutionary timescales appropriate for assessing dispersal (Carlsson et al. 2011)

Working in the deep-sea environment is challenging and costly, and the advancement of connectivity research and exploration is intimately tied to advancements in deep-submergence technologies. Future technological achievements will be those that comprehensively expand our ability to characterize factors fundamental to understanding connectivity, including refining distributions of subpopulations and habitats, obtaining co-located oceanographic data over relevant temporal and spatial scales of connectivity, confirming the presence of fauna and habitat availability, and collecting sufficient numbers of population-level samples for taxonomy and connectivity studies. Improved AUVs offer long-range multi-sensor platforms for spatially-expansive survey coverage, precise dynamic navigation, fine-scale bathymetric mapping, high-resolution photographic and chemical laser imaging (e.g., detecting

species-specific chemicals secreted by corals), coupled with coincident oceanographic data. The use of remotely-deployed cameras (e.g., drop cameras and towed camera sleds) allows for rapid ground-truthing of habitats and targeting of prime habitat for further observation, exploration, and sampling using Remotely Operated Vehicles (ROVs) and/or submersibles. Development of novel sampling gear for ROVs and submersibles that allows many discrete samples to be collected per dive will increase sampling resolution and extent. Lastly, strategically-placed long-term monitoring instrumentation, including time-lapse cameras, oceanographic data samplers, plankton samplers and non-lethal sample collection devices, will help resolve long-term oceanographic patterns as well as provide insights into species behaviors and larval transport. Advancing technological capabilities, including autonomous oceanographic characterization of seafloor habitats, expands our fundamental understanding of benthic processes and their link to coral community connectivity.

VI. Conclusions

Understanding connectivity and the processes that influence connectivity can enhance the conservation of deep-sea coral diversity through science-based stewardship. Connectivity through exchange of larvae among populations should be one of the factors considered during the planning and design phases of deep-sea coral protection areas. Combining estimates of genetic connectivity with physical oceanographic data will lead to a better understanding of processes that underlie larval dispersal and, therefore, connectivity. Population connectivity data among deep-sea coral populations is slowly becoming available. However, more work is needed and research



must continue as scientists and managers work toward protecting and conserving these ecologically valuable ecosystems.

VII. Acknowledgements

The authors would like to thank Rhian Waller (University of Maine), Than Hitt (USGS), Tom Hourigan (NOAA), and Peter Etnoyer (NOAA) for helpful comments on earlier drafts.

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POPULATION CONNECTIVITY OF DEEP-SEA CORALS

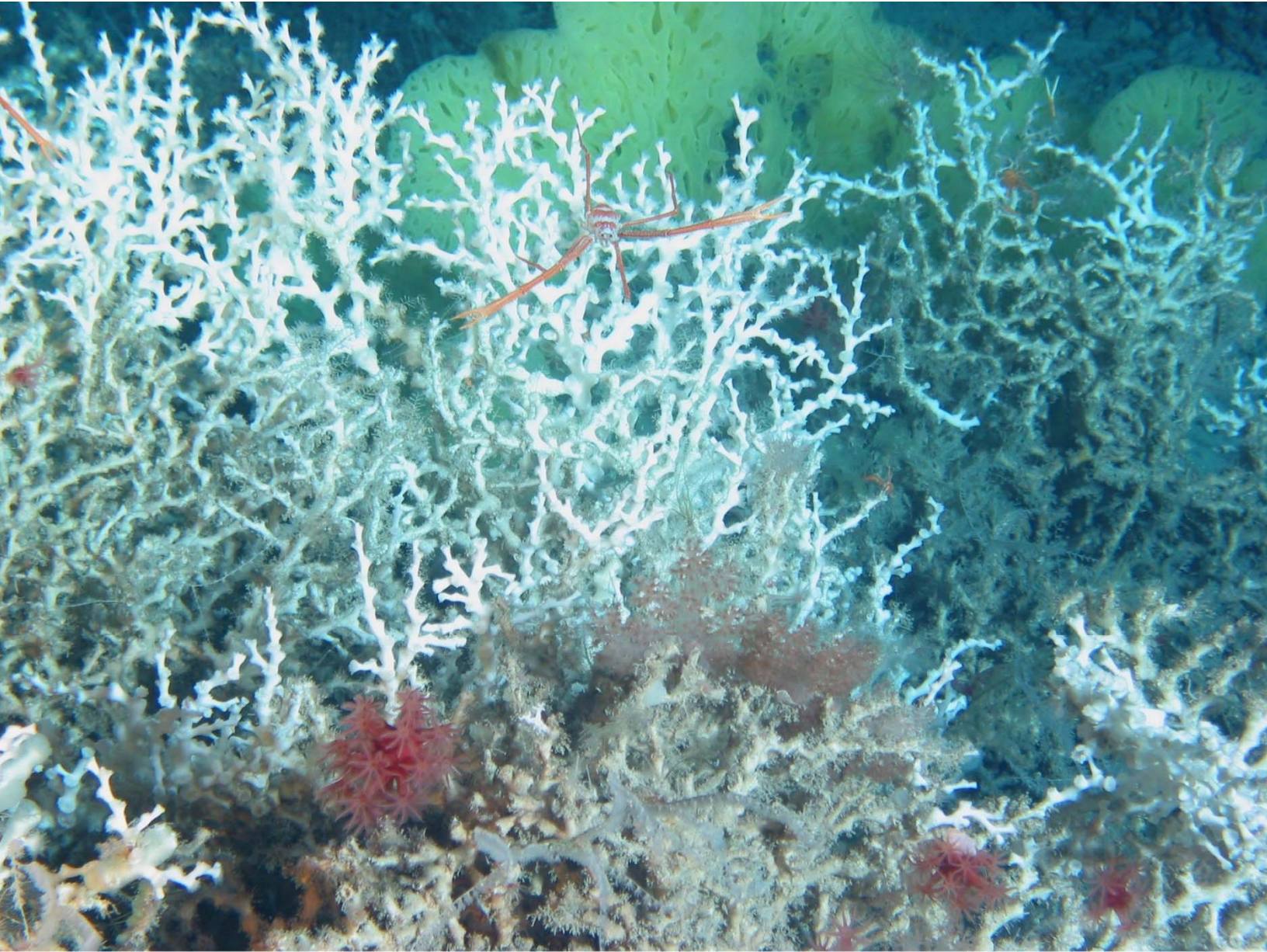


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Squat lobster perched on *Lophelia pertusa* colonies with a sponge in the background. Courtesy of NOAA/USGS.



STATE OF THE DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE SOUTHEAST UNITED STATES

1. Introduction

The Southeast U.S. region stretches from the Straits of Florida north to Cape Hatteras, North Carolina, and encompasses the Southeast U.S. Continental Shelf large marine ecosystem (LME; Carolinian ecoregion) and associated deeper waters of the Blake Plateau, as well as a small portion of the Caribbean LME off the Florida Keys (eastern portion of the Floridian ecoregion). Within U.S. waters, deep-sea stony coral reefs reach their greatest abundance and development in this region (Ross and Nizinski 2007). This warm temperate region is strongly influenced by the northern-flowing Gulf Stream.

Along with the Gulf of Mexico, this region has been the focus of some of the most extensive U.S. deep-sea coral research, yet many of the region's deeper waters remain poorly explored. The South Atlantic Fishery Management Council (SAFMC) has authority over most fisheries in Federal waters in this region, which includes the waters off North Carolina, South Carolina, Georgia, and the Atlantic coast of Florida, including the Florida Keys. In 1984 the SAFMC recommended, and NOAA's National Marine Fisheries Service (NMFS) established, the Oculina Bank Habitat Area of Particular Concern (HAPC) —the world's first marine protected area specifically designed to protect deep-sea corals. Over the last decade, NOAA and the Council have built on these initial steps to craft a truly comprehensive approach to conserving vulnerable

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deep-sea coral habitats by expanding the Oculina Bank HAPC and establishing five additional deepwater Coral Habitat Areas of Particular Concern (C-HAPCs) on the southeastern U.S. continental margin covering 59,560 km² (see <http://safmc.net/managed-areas/deep-water-corals>).

In this chapter, we highlight new scientific information on deepwater coral ecosystems that has become available since the 2007 deep-sea coral status report, and review new management measures that help protect these habitats in the region. We also include information on deepwater sponges, which were not addressed in the 2007 report.

II. Update on Scientific Information

II.1. New Research – Overview

Since the research summarized by Ross and Nizinski (2007), there have been a number of surveys of deep-sea coral habitats in the region (Figure 1; Appendix Table A). Much of this effort has focused on deep-sea coral mounds off eastern Florida, which are dominated by the coral *Lophelia pertusa*. There have also been significant new surveys of shallower shelf-edge habitats associated with new snapper-grouper marine protected areas (MPAs). These areas contain rocky hardgrounds with coral (primarily gorgonian) and sponge assemblages that were not included in the 2007 report and are quite different from those that occur in deeper water.

In 2009, NOAA's Deep Sea Coral Research and Technology Program chose the southeast region for its first 3-year field research initiative to locate, study, and provide information for the conservation of deep-sea coral and sponge habitats. The initiative was developed in consultation with the SAFMC and surveys targeted information needed for management. From 2009 – 2011, fieldwork employed a three-tiered approach: 1) systematic reconnaissance mapping using multibeam sonar to provide the physical context for deep-sea coral habitats; 2) targeted high-resolution mapping; and 3) *in situ* ground-truthing and multidisciplinary research using submersibles or remotely operated vehicles (ROVs) to understand the distribution and ecological role of deep-sea corals. The Southeast Deep-Sea Coral Initiative, in partnership with numerous research institutions, supported seven major research cruises, including two dedicated solely to multibeam mapping, two dedicated to remotely-operated vehicle (ROV) or submersible surveys, and three combined ROV and mapping missions (Figure 1; Annex 1). Over 10,000 km² of seafloor were mapped. There were also 22 submersible dives, 36 ROV dives, numerous midwater and benthic samples and oceanographic measurements collected. The initiative also developed predictive habitat models for deep-sea corals (see below), which complemented the field research.

In addition to the Deep Sea Coral Research and Technology Program, NOAA's Coral Reef Conservation Program supported annual research cruises from 2012-2015 designed to



Table 1. Number of coral species reported from the Southeast U.S. in 2007 and in the present report. Increases include new species identifications and range extensions, but principally represent species not included in the first report. *Not confirmed from U.S. waters.

Taxon	Ross and Nizinski 2007	This Report
Class Anthozoa		
Black corals (Order Antipatharia)	4	16
Stony corals (Order Scleractinia)	57	77
Zoanthid gold coral (identified as <i>Gerardia</i> sp.)	1	0*
Gorgonian corals (Order Alcyonacea – <i>in part</i> [formerly Order Gorgonacea])	30	68
True soft corals and stoloniferans (Order Alcyonacea)	12	15
Sea pens (Order Pennatulacea)	1	10
Class Hydrozoa		
Stylasterid corals (Order Anthoathecata, Family Stylasteridae)	7	15
Total	112	201

characterize the benthic habitat and fauna of the SAFMC’s new Snapper-Grouper MPAs from North Carolina to Florida (Harter et al. 2015; Figure 1; Appendix Table A). A total of 122 ROV dives surveyed 35 sites at depths between 50-200 m. Multibeam sonar surveys mapped 574 km² of benthic habitats. Other studies in the region that shed light on deep-sea coral and sponge resources during this period included exploration supported by NOAA’s Office of Ocean Exploration and Research, Harbor Branch Oceanographic Institute at Florida Atlantic University, a Dutch/U.S.-led cruise on the R/V *Pelagia* (Mienis et al. 2014), and surveys associated with proposed pipeline, cables and offshore energy projects that

provided additional information on benthic habitats of the Miami Terrace region (Messing et al. 2012). Additional mapping of deep-sea habitats was conducted by the NOAA Ship *Okeanos Explorer* and the U.S. Navy.

II.2. Taxonomy and Species Distributions

II.2.i – Corals

a. Coral taxonomy

Ross and Nizinski (2007) reported 112 species of corals from seven cnidarian orders from the U.S. Southeast region (Table 1). Since 2007, the systematic compilation of coral records in the National Coral and Sponge Database, along

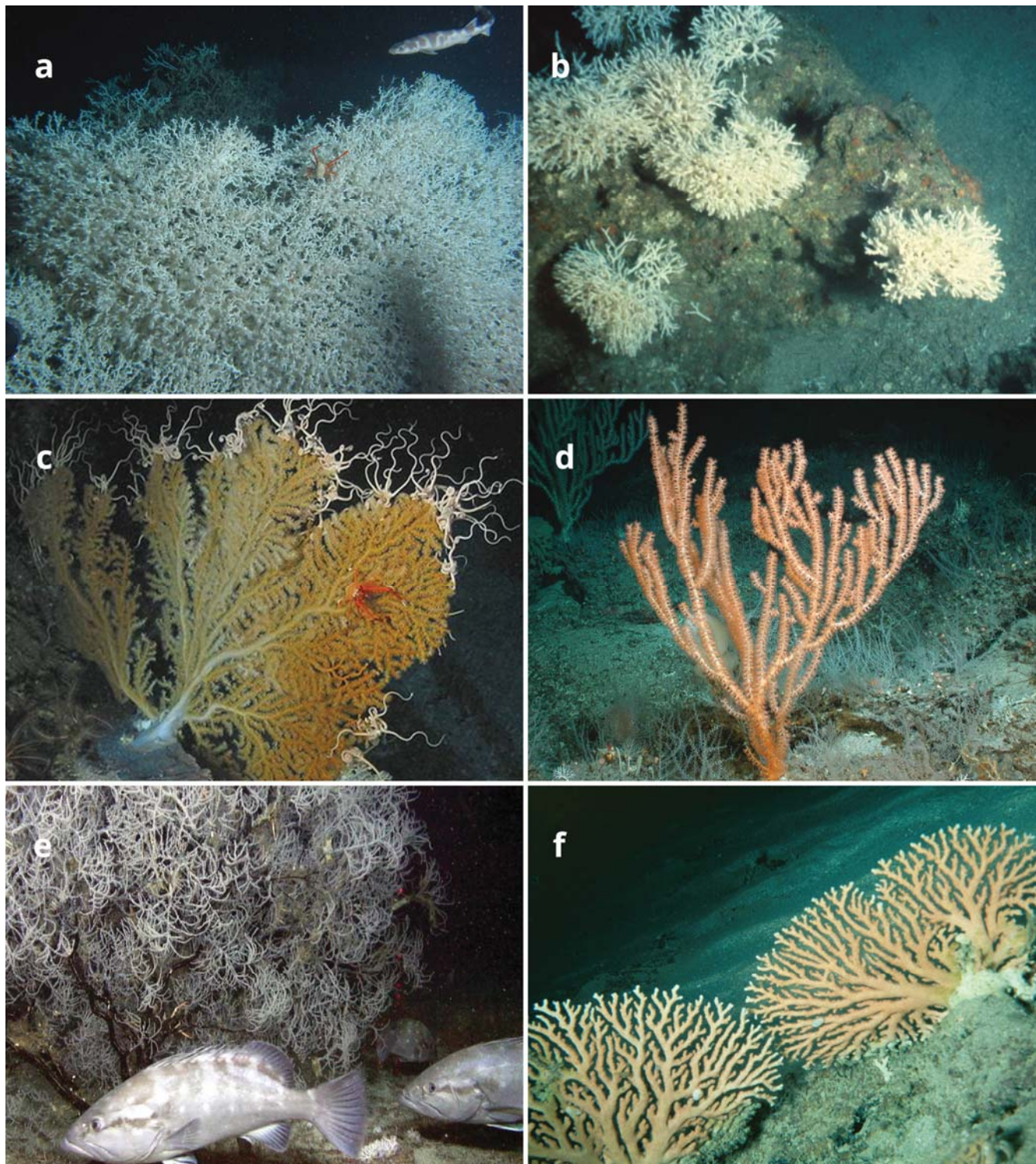


Figure 2. Important structure-forming deep-sea corals of the Southeast U.S. a) Lophelia pertusa; b) ivory tree coral (Oculina varicosa); c) large paramuriceid gorgonian coral with squat lobster and brittle stars; d) bamboo coral (Keratoisis flexibilis); e) black coral (Leiopathes sp.); f) Stylasterid coral.



with new descriptions and range extensions, has nearly doubled this number to 201 (Table 1; [Online Annex 1](#); Cairns et al., this report). The biggest increase in numbers of species was among the gorgonian corals, reflecting reviews by Cairns and Bayer (2009), DeVicor and Morton (2010), and Watling et al. (2011). Calder and Cairns (2009) described several new stylasterid species from the region.

b. Coral distribution

Research over the last ten years has expanded our understanding of the distribution of deepwater scleractinian coral habitats in the region. Partyka et al. (2007), Harter et al. (2009), Ross (2012), Reed et al. (2013a, 2014, 2015) and David et al. (in prep.) summarized results of numerous deepwater surveys from 2001 – 2011. Ross et al. (2012) reviewed museum records of dominant scleractinian corals from the region and evaluated their utility for documenting distributions. They cautioned that often such records are misleading and in many cases are incorrect. [NOAA's Database for Deep-Sea Corals and Sponges](#) (Hourigan et al. 2015) has instituted protocols to address these limitations when possible. In addition, taxonomic and field surveys of the shallower hard-bottom habitats (50-150 m; DeVicor and Morton 2010, Harter et al. 2015) have provided information on components of the coral fauna that were not addressed by Ross and Nizinski (2007). In both the shallower and deep-sea habitats, a number of deepwater coral species, including reef-building stony corals, black corals, gorgonian corals and stylasterid corals represent important structure-forming species – growing

to relatively large sizes and occurring in aggregations (Figure 2).

Most deep-sea corals (aside from pennatulaceans) and sponges require hard substrate for attachment. Thus the underlying geology in the region determines the distribution of such habitat, and along with oceanographic conditions (especially those generated by the Gulf Stream), influences the distribution of deep-sea corals (Ross and Nizinski 2007, Reed et al. 2013a). Ross and Nizinski (2007), Reed et al. (2013a) and others have identified the following major deepwater concentrations of hard-bottoms in the Southeast U.S. that support coral and sponge communities:

- 1) *Shelf and shelf break*: The continental shelf is wide and shallow through most of the region from Cape Hatteras to central Florida. Hard-bottoms are most common near the shelf break (~ 55-110 m depths) and below the shelf break (110-183m; see SEAMAP-SA 2001).
- 2) *Oculina coral mounds*: Off Florida, near the shelf edge at depths of 70 – 100 m, are large bioherms (10-30 m relief) built by the azooxanthellate form of the ivory tree coral, *Oculina varicosa* (Reed 1980, 2002a,b, Reed et al. 2007, Ross and Nizinski 2007, Maness 2011).
- 3) *Continental slope and Blake Plateau*: This is a complex region with numerous hard-bottom and coral mound features (lithoherms and bioherms). The continental slope around Cape Hatteras is incised with



several canyons. South of Cape Hatteras, the continental slope broadens from central North Carolina into the Blake Plateau, a broad depositional feature formed by the Gulf Stream (400-1250 m depths, Popenoe and Manheim 2001). Major coral habitats in this region include the North Carolina *Lophelia* mounds, the Charleston Bump, Stetson and Savannah banks, and extensive *Lophelia pertusa* and *Enallopsammia profunda* mounds off eastern Florida.

- 4) *Miami and Pourtalès Terraces and Escarpments*: The Miami and Pourtalès terraces are large limestone features bordering the Florida Straits that provide hard-bottom habitat for deep-sea corals and sponges.

Shelf and shelf break: High relief ridges and rock outcrops at the shelf break and on the upper slope are often heavily encrusted with sponges and gorgonians. These extensive hard-bottom habitats are also recognized as essential fish habitat (EFH) for the snapper, grouper, porgy species complex. In 2009, the South Atlantic Council established seven deepwater marine protected areas (MPAs) to help maintain these stocks (see below and <http://safmc.net/managed-areas/marine-protected-areas>; an eighth MPA, the Charleston Deep Reef MPA is primarily sandy bottoms, but has two large artificial reef sites).

Recent surveys of shelf-edge MPAs by NOAA have resulted in a better understanding of the numerically dominant corals species present (Harter et al. 2015). A total of 31 species of

corals were recorded from these habitats. These were dominated by gorgonians (including, *Bebryce* sp., *Diodogorgia* sp., *Ellisella* spp., *Iciligorgia schrammi*, *Leptogorgia* sp., *Muricea* sp., *Nicella* sp., *Plumarella* sp., *Swiftia exerta*, and *Titanideum frauenfeldii*), which can reach moderate sizes and occur in locally high-density patches (Fig. 3a). Several azooxanthellate colonial stony corals also occurred (*Oculina varicosa*, *Madracis myriaster*, *Madrepora oculata*), but no bioherm formation has been observed aside from the *Oculina* bioherms off central Florida (see below). Other coral species observed include black corals (*Antipathes atlantica*, *Antipathes* spp., *Stichopathes* sp., *Tanacetipathes hirta*), and soft corals (including *Anthomastus* sp., *Chironophthya caribaea*, *Nidalia occidentalis* and *Telesto* sp.).

***Oculina coral mounds*:** The *Oculina* reefs (bioherms) off eastern Florida are unique coral habitats (Reed 1980, 2002a,b, Reed et al. 2013b). These bioherms also serve as habitat for gorgonians, soft corals, black corals and stony cup corals (Fig. 3b,c). Recent work has increased our understanding of the extent and importance of these habitats. Harter et al. (2009) reported on surveys of benthic habitat and fish assemblages conducted inside and outside the *Oculina* Bank Habitat Area of Particular Concern (HAPC) in 2003 and 2005. They found that the percentage of intact coral, fish diversity, and densities of groupers were higher inside the area closed to fishing.

In 2011, multibeam sonar and ROV surveys discovered additional, previously unknown

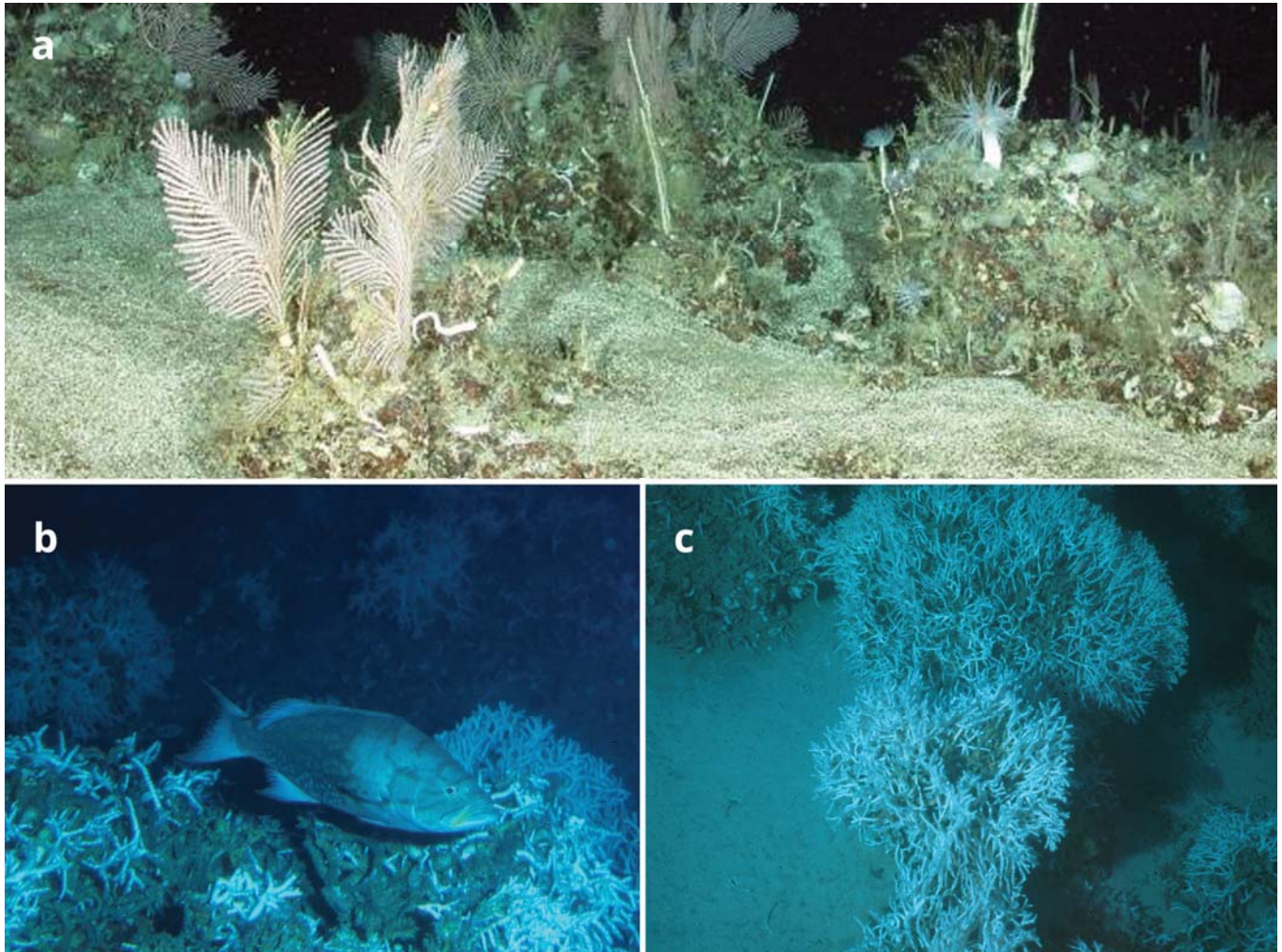


Figure 3. a) Shelf-edge hard-bottom habitat with *Plumarella* spp. octocoral colonies; b) supermale scamp grouper (grey head color phase) on *Oculina* bioherm; c) large *Oculina varicosa* colonies.

Oculina coral mounds with live *O. varicosa* stretching north of the then boundaries of the *Oculina* Bank HAPC (Reed et al. 2013b). In addition to the mounds, surveyed sites also included smaller coral thickets, isolated live colonies, and coral rubble on hard-bottom. These newly-discovered and unprotected coral mounds were similar in size to those within the *Oculina* Bank HAPC; however, these mounds had only 4.4-5.5% cover of standing coral

framework, compared to 28.6-37.8% cover within the HAPC (Reed et al. 2013b). Most live *O. varicosa* colonies at these unprotected sites were much smaller in size compared to those within the HAPC, perhaps reflecting recovery following previous damage. Densities of live *O. varicosa* and gorgonian colonies, sponges, and fishes were also higher in the protected HAPC. While there is some evidence that the *Oculina* Bank HAPC has been effective in protecting



coral habitat, benthic biota, and fish populations in recent years (Harter et al. 2009), coral and fish densities remain severely depleted from what they used to be in the 1980's prior to the reefs being decimated by trawling gear.

Oculina varicosa occurs as both shallow-water zooxanthellate and deepwater azooxanthellate forms. Only the deepwater azooxanthellate corals form bioherms. Eytan et al. (2009) provided evidence from mitochondrial DNA that *O. varicosa* corals from the Oculina Banks were genetically isolated from the shallow-water zooxanthellate populations that occur from North Carolina to the eastern Gulf of Mexico. Genetic population separation by depth has also been found in gorgonians in the Gulf of Mexico (see Morrison et al. and Boland et al., this volume).

Continental slope and Blake Plateau: The dominant framework-forming scleractinian corals in waters deeper than 200m are *Lophelia pertusa* and, to a lesser extent *Enallopsammia profunda*. Both species form deepwater coral mounds or reefs, including bioherms and consolidated limestone lithoherms, which are a dominant feature on the Blake Plateau from North Carolina to south Florida and the Bahamas (Brooke 2007, Ross and Nizinski 2007 - and references therein; Grasmueck et al. 2007, Ross and Quattrini 2007, Messing et al. 2008, Correa et al. 2011, 2012, Reed et al. 2013a). *Madrepora oculata* occurs commonly in smaller colonies, but does not appear to contribute

substantively to the reef framework. Partyka et al. (2007) and Ross (2012) summarized habitat information from submersible and ROV dives from North Carolina to southeast Florida. Reed et al. (2013a) compiled information on over 400 sites at depths between 200 and 900 m with high-relief bathymetry, from northeastern Florida (31°N) through the Straits of Florida, of which 147 sites were groundtruthed with submersible or ROV dives. Ross et al. (2012) analyzed museum specimens of four species of deepwater branching stony corals (*L. pertusa*, *E. profunda*, *E. rostrata* and *M. oculata*) from the region.

The Cape Lookout and Cape Fear *Lophelia* mounds off North Carolina appear to be the northernmost bioherms in the U.S. Atlantic (Reed et al. 2006, Ross and Nizinski 2007, Partyka et al. 2007, Roberts et al. 2009). These are extensive high profile (up to 80-100 m tall) bioherms almost entirely composed of dead *L. pertusa*, entrapped sediments, and capped with living and dead *L. pertusa* (Ross and Quattrini 2009, Mienis et al. 2014). These bioherms have less cover of *Enallopsammia* spp. than do the bioherms off the east coast of Florida. The North Carolina mounds also appear to have fewer black corals and octocorals compared with regions to the south and the Gulf of Mexico. Mienis et al. (2014) deployed landers to measure near-bottom environmental conditions on coral mounds near Cape Lookout. They found that the corals were exposed to large temperature and current fluctuations related to Gulf Stream

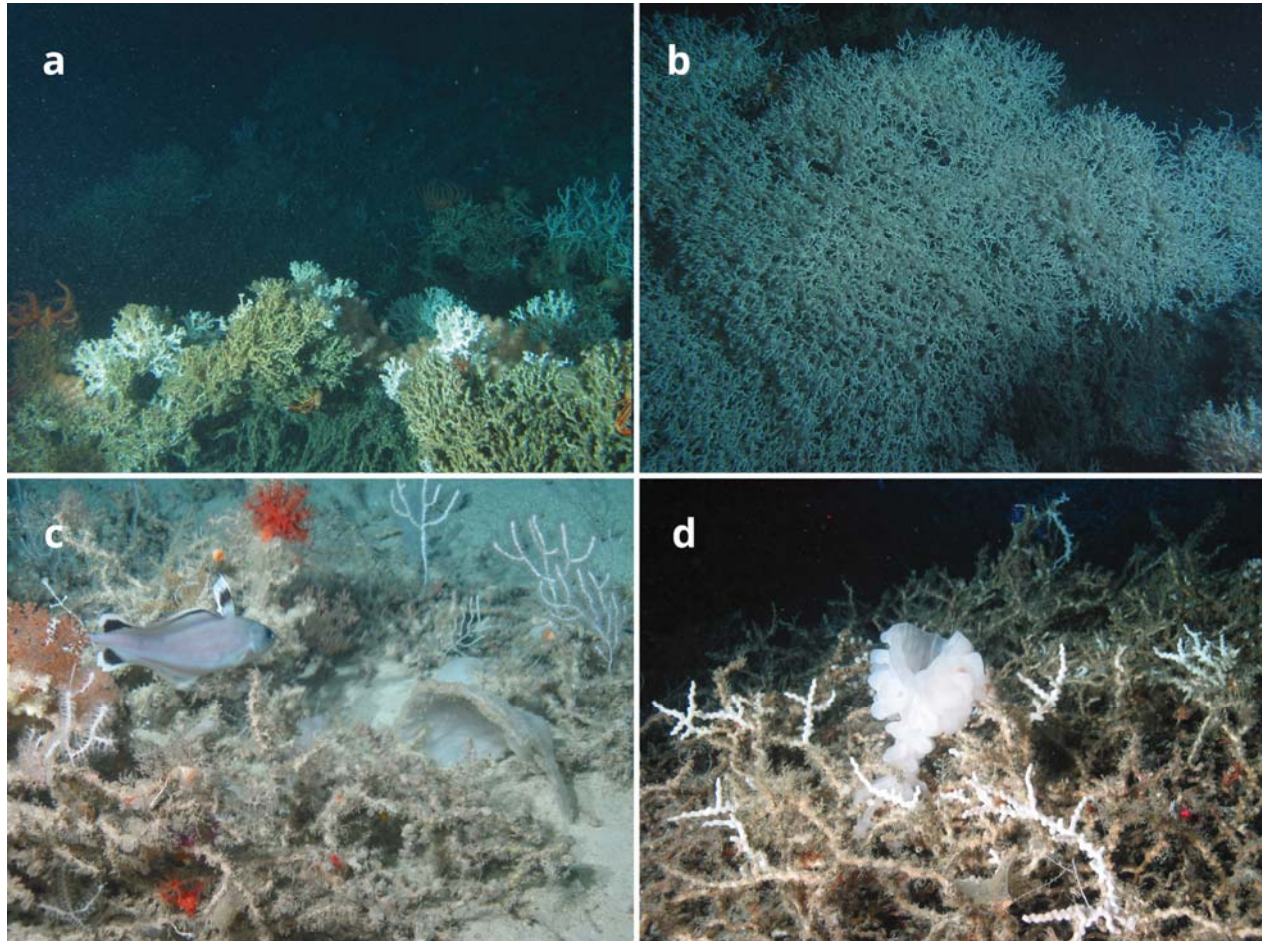


Figure 4. *Lophelia coral bioherms: a) Cape Lookout Lophelia pertusa habitat; b) dense live Lophelia pertusa off E. Florida; c) codling (Laemonema melanurum) on coral habitat; d) Enallopsammia profunda coral and a hexactinellid sponge (Aphrocallistes beatrix).*

meanders, and concluded that *L. pertusa* live under extreme conditions that may limit present mound growth. However, in the same area Brooke et al. (2013) noted that *L. pertusa* survived these extreme and variable temperatures, indicating resilience in this species. Matos et al. (2015) investigated the age of the Cape Lookout coral mounds using cores and U-series dating and concluded that mound growth primarily occurred during interglacial periods, most recently during the last 7,000 years. In contrast to North Carolina, southern Georgia and Florida, coral habitats of the central Blake

Plateau region appear to have mostly smaller aggregations of live corals occurring both on coral mounds and attached to abundant rocky substrata. Off South Carolina and Georgia, Stetson and Savannah banks and the Charleston Bump represent major areas of high relief, hard bottom topography with significant coral habitats, including *Lophelia* mounds (Partyka et al. 2007, Ross and Quattrini 2009, Sedberry et al. 2010). The Charleston Bump rises from 700m to 400m and has a varied topography ranging from flat hard bottom to rugged relief and near vertical scarps (Sedberry 2001). Corals in the



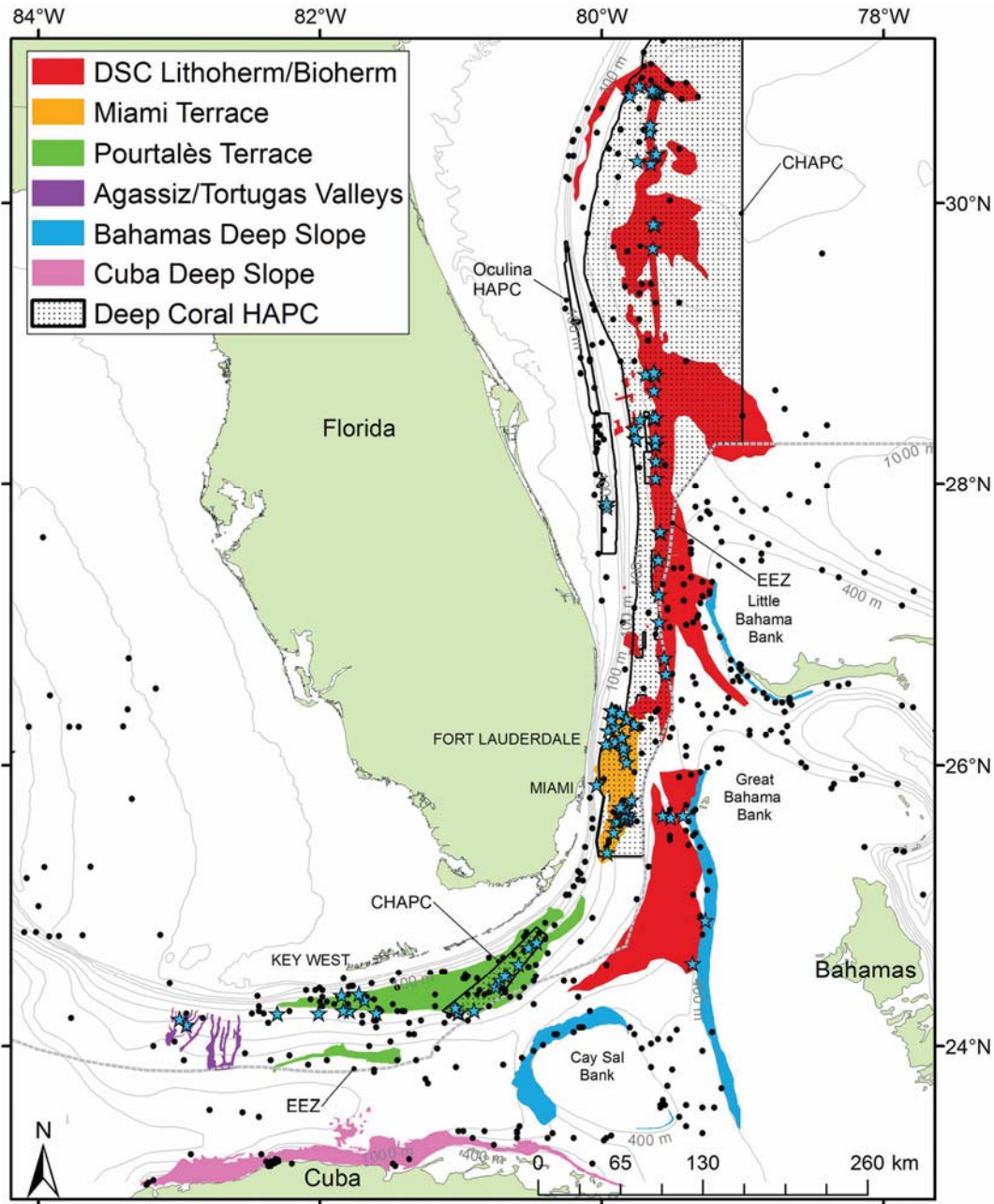
area include small colonies of *Lophelia pertusa*, *Madrepora oculata*, and *Enallopsammia profunda*; various stylasterids, black corals and gorgonians (Partyka et al. 2007).

At Stetson Banks on the Blake Plateau, Reed et al. (2006) identified of 11 coral taxa. The colonial Scleractinia were dominated by colonies of *L. pertusa* (30–60 cm tall), along with *E. profunda* and *Solenosmilia variabilis*. Small stylasterid corals were common and numerous species of solitary cup corals were abundant. They reported at least six taxa of octocorals, dominated by primnoids (Family Primnoidae), *Paramuricea* spp. (Family Plexauridae), bamboo corals (Family Isididae), as well as smaller stoloniferan and nephtheid soft corals.

The Savannah Banks off Georgia include numerous lithoherms at depths of 490 to 550 m along the western Blake Plateau. Corals and sponges occurred on exposed terrace pavements, with the greatest abundances along the rock outcrop edges and on pinnacle crests (Reed et al. 2006, Partyka et al. 2007). The estimated cover of sponges and gorgonians was 10% on exposed rock areas. Colonies of *L. pertusa* (15–30 cm diameter) were common but only accounted for ~1% of the benthic cover and were intermixed with small colonies of *M. oculata* and stylasterid hydrocorals. Primnoids, plexaurids and black corals were also observed. Diversity of octocorals, black corals and sponges increases from this point south on the

Blake Plateau, and the branching stony corals *Madrepora oculata* and *Enallopsammia profunda* become more abundant.

Lophelia pertusa and *E. profunda* coral mounds appear to reach their highest densities from the Jacksonville Lithoherms off southern Georgia and N. Florida, and stretching southwards through the Straits of Florida (Reed et al. 2013a; Fig. 5). New multibeam sonar mapping surveys conducted since 2007 have revealed the abundance of the mound-structures, particularly off eastern Florida. Reed et al. (2013a) estimated that this habitat off eastern Florida covers over 13,400 km². Live coral cover ranges from less than 5% to nearly 100% on the peaks and up-current slopes facing the Gulf Stream or Florida Current, a component of the Gulf Stream that flows through the Florida Straits separating Florida from Cuba and the Bahamas (Reed et al. 2013a). These mounds are predominately *L. pertusa* but some are apparently entirely *E. profunda*, and some are intermixed. *Madrepora oculata* is not a major component of these mounds and occurs only as isolated, small colonies with either *L. pertusa* or *E. profunda*. For reasons unknown, extensive areas of dead *E. profunda* rubble are also common throughout the region and often observed at the bases of the mounds and the foot of the Miami Terrace. The mounds also provide substrate for other structure-forming taxa, such as gorgonian, black and stylasterid corals and sponges.



*Figure 5. Coral regions of deep-sea coral habitats mapped from northeastern Florida (31°N) through the Straits of Florida. Dashed gray line = U.S. EEZ; polygons (heavy bold line) = boundaries of deepwater Coral Habitat Areas of Particular Concern (CHAPC) and deep-water Oculina Bank HAPC; colored polygons = deep-sea coral habitat regions and major geological/topography features (see legend). Stars = Deep-sea coral habitats mapped with ROV or submersible. Museum records from National Museum of Natural History, Smithsonian Institution: Dots = *Lophelia pertusa*, *Enallopsammia profunda*, *Madrepora oculata* or other deep-water coral species (> 50 m depth). See Reed et al. (2013c) for methodology used to identify the deep-sea coral habitat regions (Data from Reed et al. 2005, 2006, 2013c, 2014). Depth contours in meters.*

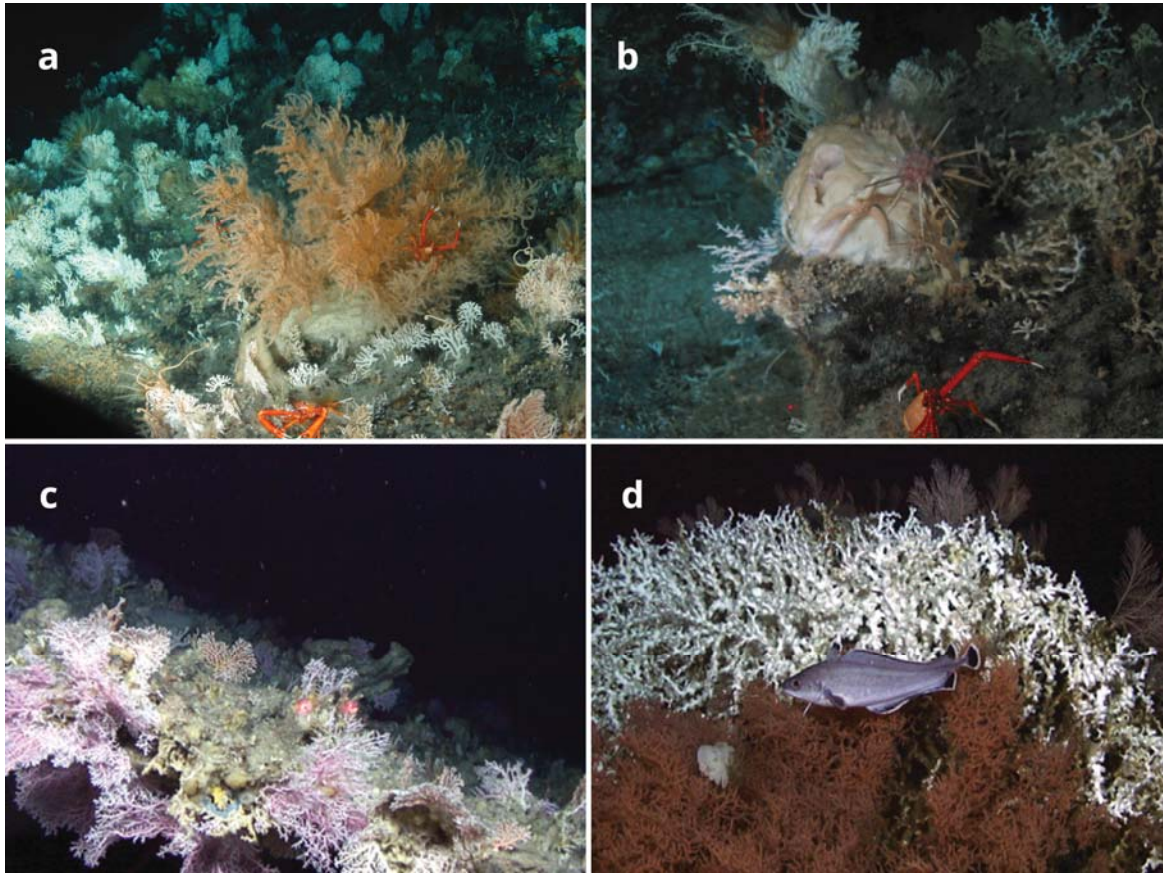


Figure 6. Miami Terrace: a) Rock pavement and ledges provide habitat for a variety of species including black corals, stylasterid corals, gorgonians, and sponges; b) diverse habitat of sponges, stylasterid corals, pencil urchins and squat lobsters; Pourtalès Terrace: c) Ledge with dense cover of stylasterid corals; d) Deepwater *Lophelia pertusa* coral mound; live coral colony (~1 m diameter), black coral (*Leiopathes* sp.), and mora codling (*Laemonema melanurum*).

Several relatively shallow bioherms have recently been identified from multibeam surveys off northeastern Florida. Habitat surveys in 2010 revealed a matrix of *L. pertusa*, including living colonies fused into thickets along with dead colonies and rubble at the crest of these bioherms at around 210 m (Ross et al. 2015a). This is significantly shallower than previous records of live *L. pertusa* in the region, which generally occurs from around 360-800 m (Ross and Nizinski 2007). These represent the

shallowest recorded bioherms with large living colonies from the western North Atlantic (Ross et al. 2015a). Other corals (e.g., *Leiopathes* sp.) and fishes commonly observed on deeper reefs were also observed in these sites.

Measurements of environmental parameters at these sites revealed colder, nutrient-rich waters, leading Ross et al. (2015a) to conclude that these sites were subject to persistent conditions of Gulf Stream-driven upwelling of deep, nutrient-rich water.



Miami and Pourtalès Terraces: The upper Miami Terrace extends for 145 km off southeast Florida at around 275 m depth (Brooke 2007, Grasmueck et al. 2007a,b, Messing et al. 2008, Vinick et al. 2012, Reed et al. 2006, 2013a). The bordering escarpment drops steeply to a lower terrace at depths of 500 – 700 m, with low discontinuous ridges perpendicular to the current and patchy colonies of *L. pertusa* and *E. profunda*, as well as gorgonians, stylasterids, and sponges (Fig. 6 a,b). The slope below the lower terrace (710-870 m) has a series of much longer ridges reaching 20 m in height and capped with sponges and various corals, *L. pertusa*, stylasterids, isidids and other octocorals (Correa et al. 2012). *Enallopsammia* coral mounds and coral rubble are the dominant habitat types near the foot of the escarpment.

Portalès Terrace stretches 213 km at depths of 200 – 450m along the southern edge of the Florida Keys reef track and provides extensive, high relief, hard-bottom habitat (Gomberg 1976, Reed et al. 2005, 2013c, 2014). Hard-bottom, topographic features consisting of numerous high-relief mounds and ridges on the mid-terrace and a chain of sinkholes extend for ~100 km along the southwest terrace margin. Stylasterids appear far more abundant on Pourtalès Terrace, compared to the nearby Miami Terrace. *Lophelia* and *Enallopsammia* mounds appear to be relatively rare, though surveys in 2011 revealed a *Lophelia* mound, the southernmost mound known from U.S. waters (Reed et al. 2014; Fig. 6 c,d). The reasons for these faunal differences between the Miami and Pourtalès terraces remain unclear. Cairns (1992) hypothesized that distributions of stylasterids

may be partially limited by their preference for oligotrophic waters and sensitivity to fluctuating salinity and sedimentation often associated with continental margins.

Broad-scale biogeographic distribution

patterns: Prior to 2007, most distributional studies focused on stony corals (e.g., Cairns and Chapman 2001), with particular interest in the framework-forming corals such as *L. pertusa*, and *O varicosa* (Ross and Nizinski 2007). While there was recognition that gorgonian and black corals were important components of habitat (Ross and Nizinski 2007), this report includes the first regional maps of gorgonian and black coral distributions (see appendix maps). A number of species of gorgonian and black corals are associated with the *Lophelia* coral mounds, but they are not limited to these habitats. For example, gorgonians (e.g., *Plumarella* sp., *Swiftia exserta*) can reach high densities in shelf-edge habitats. Black corals and hexactinellid sponges are relatively rare on the North Carolina coral banks (Ross and Quattrini 2009), but are common further south (Reed et al. 2006).

The distribution of stylasterid corals also suggests discontinuities within the Southeast U.S. region. These species are relatively small, but colonies can occur in dense aggregations in the Caribbean and the southern portion of the region, being especially important on Pourtalès Terrace (Reed et al. 2014). They are largely absent north of 32.5° N latitude.

The Florida Current appears to form a biogeographic barrier for a number of coral species. Numerous coral species that are



common in the Bahamas and the Caribbean appear to be rare or absent in U.S. waters off Florida. For example, the zoanthid gold coral, *Kulamanamana* sp. (formerly known as *Gerardia* sp.) occurs in dense aggregations along upcurrent crests of mounds at depths of 500 – 700 m in the Bahamas (Messing et al. 1990), but this taxon has not been recorded from the U.S. side of the Florida Straits (C. Messing, pers. comm.). There are several other examples of coral species that have not been reported from southeast Florida waters, but occur nearby across the Florida Straits. These include two black corals (*Distichopathes filix* and *Tanacetipathes tanacetum*) and a stony coral (*Balanophyllia* (*Balanophyllia*) *cyathoides*) both found in Cuba and the Bahamas, and two additional stony corals (*Caryophyllia* (*Caryophyllia*) *antillarum* and *Deltocyathus agassizii*) and a soft coral (*Chironophthya agassizii* = *Siphonogorgia agassizii*) known from the Bahamas. A single species of stony coral (*Thalamophyllia gombergi*) appears to be endemic to the Florida side of the straits and has not been reported from Cuba or the Bahamas (Cairns and Chapman 2001).

Morrison et al. (2011) used microsatellite DNA markers to examine population connectivity in *L. pertusa* in the North Atlantic, including samples from the Southeast U.S. They found distinct genetic groupings among corals collected in the Gulf of Mexico, Southeast U.S., New England Seamounts, and Northeast Atlantic, suggesting that these represent distinct populations. The corals from the Southeast U.S. were distinguishable from, but

most closely related to those from the Gulf of Mexico. The Gulf of Mexico Loop Current draws warm water from the Caribbean into the eastern Gulf, then loops south along the west Florida slope, feeding into the Florida Current through the Florida Straits, and then into the Gulf Stream. This current system likely transports pelagic larvae from the eastern Gulf of Mexico to the Southeast region (Morrison et al. 2011). Hare and Walsh (2007) used satellite-tracked drifters released from three MPAs (the Tortugas South Ecological Reserve, Oculina Bank HAPC and Gray's Reef National Marine Sanctuary) along with transport models to investigate larval transport in the region. The results predicted export of larvae by the Florida Current/Gulf Stream, but with some retention in the lower Florida Keys and off Georgia.

II.2.ii – Sponges

a. Sponge taxonomy

Unlike deep-sea corals, there has not been a systematic inventory of sponge taxa from deep waters of the Southeast Region. Van Soest et al. (2012) reported nearly 300 described species of shallow and deepwater sponges in the three ecoregions that are in or adjacent to the Southeast U.S. (Carolinean – 34, Floridian – 153, and Bahamian – 95) (Table 2). These are predominantly in the Class Demospongiae, however the authors acknowledge that deep-sea sponge species are under-reported. Most sampling in the region has focused on shallow-water, easily accessible species. The Class Hexactinellida (or glass sponges) is found at depths greater than 200m, and along with the

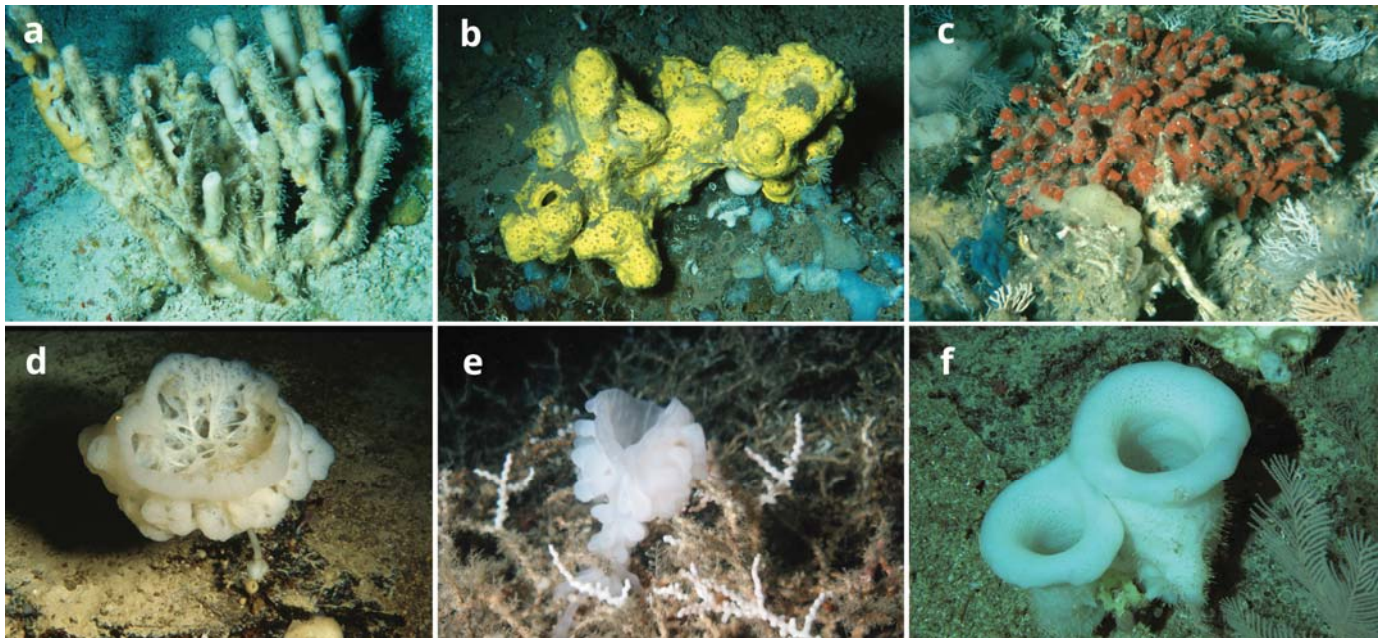


Figure 7. Important structure-forming deep-sea sponges of the Southeast U.S. Demosponges: a) *Discodermia* sp.; b) *Spongosorites* sp.; c) newly described species *Theonella wrightae* Pisera and Pomponi, 2015; Hexactinellid glass sponges: d) *Rhadopectella tintinnus*; e) *Aphrocallistes beatrix*; f) *Nodastrella asconemaoida* from Miami Terrace.

perception that this group is difficult to identify, the number of described species is low, relative to the Class Demospongiae (Table 2). Species within the Class Calcarea occur in both shallow and deep water, but also considered difficult to identify. Few experts have focused on these two groups. The Class Homoscleromorpha is likely under-reported because many of the deepwater species are thinly encrusting and difficult to collect.

An example of unexplored and largely undocumented deep-sea sponge fauna are the carnivorous sponges (Demospongiae: Poecilosclerida: Cladorhizidae). This unusual group of sponges differs significantly in body plan and cellular organization from the rest of

the Phylum Porifera, and was only recently discovered (Vacelet and Boury-Esnault 1995). Since that time, at least 41 new species of carnivorous sponges have been described, primarily in deep water (Cristobo et al. 2015). Nine species are found in the Caribbean region, four of which occur off the coast of Florida (Hestetun et al., 2016).

Several recent publications (e.g. Vacelet 2006, Vacelet et al. 2009, Kelly and Vacelet 2011, Lopes and Hajdu 2014, Hestetun et al. 2017) have demonstrated that identification of sponges from previously poorly known areas has resulted in a high diversity of carnivorous sponge species. It is likely that further examination of the sponge fauna from the



Table 2. Number of shallow and deepwater sponge species reported by van Soest et al. (2012) from the Carolinian, Floridian, and Bahamian ecoregions (which encompass the Southeast U.S. and neighboring areas) compared with the number of deepwater sponge taxa reported in this chapter (from Reed et al. 2005, 2006, 2013c, 2014, 2015). Note that deep-sea sponges are under-represented in the numbers reported by van Soest et al. (2012) and are only used for comparison with the numbers of deep-sea sponges reported in this chapter.

Taxon	Van Soest et al. (2012) (primarily shallow water)	This report (50 816 m)
Class Demospongiae	267	98
Class Hexactinellida	7	18
Class Homoscleromorpha	1	5
Class Calcarea	7	7
Total	282	121

Southeast U.S. will yield additional species, not only in the Cladorhizidae, but also in the Hexactinellida, Homoscleromorpha, and the Calcarea.

A number of sponges have been collected under an ongoing program of biomedical and biotechnology research at Harbor Branch Oceanographic Institute, Florida Atlantic University. This program has provided museum voucher specimens and information on taxonomy, morphology and chemistry of species and the habitats in which they are found. More recent expeditions by Harbor Branch and NOAA have focused on quantifying density and diversity of benthic invertebrates using photographic surveys. While some common taxa can be identified to genus or species, many can only be identified to a higher level such as class, order, or family. Sponges are especially difficult to identify without a sample that can be used for microscopic analyses of the skeleton.

b. Sponge distribution

Within the Class Demospongiae, the most common deep-sea taxon that occurs in the Southeast U.S. region is the Order Tetractinellida (formerly Astrophorida). In general, worldwide, this order includes massive sponges that dominate hard-bottom deep-sea ecosystems, both in biomass and abundance. Additionally, the Tetractinellida also includes the “lithistid” or rock sponges, members of a polyphyletic group, which occur worldwide, primarily in deep-water environments of temperate and tropical latitudes (Maldonado et al. 2016). Lithistid sponges are characterized by spicules that have become fused into a rigid silica framework. Recently, biological and chemical interest in lithistid sponges has increased, since these sponges are the source of more than 300 novel and diverse compounds, many of which have potential human health applications (for review, see Winder et al. 2011). Pomponi et al. (2001) described the diversity

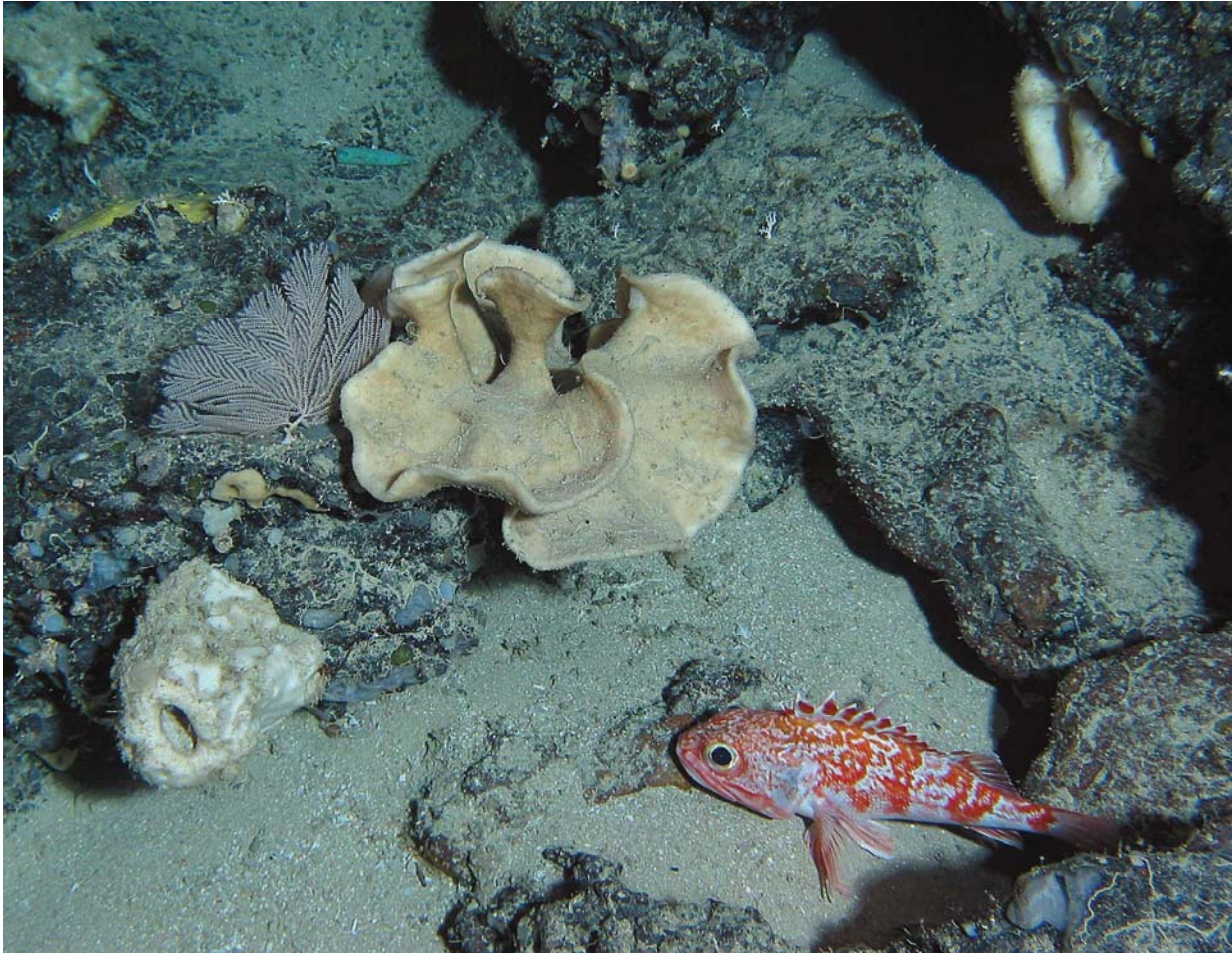


Figure 8. The lithistid demosponge, Leiodermatium sp. (foliose tan sponge in the middle), is an important structure-forming deep-sea sponge on the Miami Terrace. It is also the source of potent anticancer compounds.

and bathymetric distribution of lithistids collected during expeditions to the Southeast U.S. Thirty species of lithistid sponges have been reported from the tropical western Atlantic region (which includes the U.S. Southeast Region), but unpublished data suggest a much higher number of species present in this region (Pisera and Pomponi 2015).

Certain tetractinellid sponges form aggregations, known as “sponge grounds” which have been best documented further north in the Atlantic

(e.g., northeastern Atlantic, Klitgaard and Tendal 2004; northwestern Atlantic. Knudby et al. 2013). Aggregations have been observed in the Southeast U.S. and Caribbean (e.g., Maldonado and Young, 1996), but are much smaller in extent. These sponges, along with the glass sponges (Order Hexactinellida), reach the size and density to suggest that they have particular significance related to provision of habitat, benthic-pelagic coupling, and biogeochemical cycling (reviewed by Maldonado et al. 2016).



Sponges are important components of the sessile epifauna and occur in most of the same habitats that harbor deep-sea corals. The descriptions below summarize observations on sponge distributions in the same major habitat regions previously reviewed for corals.

Shelf and shelf break: Sponges are an important component of the benthic macrobiota in hard-bottom habitats along the continental shelf break. Harter et al. (2015) reported 52 taxa of sponges from surveys of the South Atlantic MPAs established under the Council's Snapper-Grouper Fishery Management Plan. Sponge cover ranged from < 1% to over 6%. The dominant sponges were demosponges in the Orders Agelasida (*Agelas* sp.), Axinellida (*Auleta* sp., *Scopalina* sp.), Biemnida (*Neofibularia nolitangere*), Chondrillida (*Chondrilla* sp.), Chondrosiida (*Chondrosia* sp.), Clionaida (Spirastrellidae, *Cliona* sp.); Dictyoceratida (*Ircinia campana*, *Ircinia strobilina*) Haplosclerida (*Callyspongia vaginalis*, *Niphates* sp., *Oceanapia* sp., *Siphonodictyon coralliphagum*, *Xestospongia muta*), Poecilosclerida (*Clathria* sp., *Desmapsamma anchorata*, *Zyzzya* sp.), Polymastiida (*Polymastia* sp.), Suberitida (*Spongosorites* sp.), Tetractinellida (*Cinachyra/Cinachyrella* sp., Corallistidae, *Erylus* sp., *Geodia* sp., *Leiodermatium* sp., *Theonella* sp.), and Verongiida (*Aiolochoiria crassa*, *Aplysina* sp.). Only one species (*Farrea* sp.) of Hexactinellida (glass sponge) was identified.

Oculina Coral Mounds: Eighteen species of sponges have been identified from the deep-water *Oculina* mounds. Several species of

Geodia, *Erylus*, *Ircinia*, and unidentified demosponges dominated the sponge assemblage (Reed et al. 2013b, Harter et al. 2015).

Continental slope and Blake Plateau: Occurring principally in areas of hard substrate (e.g., coral mounds, rocks and ledges, etc.), sponges are among the important and obvious components of epifaunal communities in the deeper water areas surveyed on the continental slope and Blake Plateau (Partyka et al. 2007, Reed 2002b, Reed et al. 2006, Ross 2010). The sponge fauna includes both demosponges (Class Demospongiae) and glass sponges (Class Hexactinellida), many of which can reach much larger sizes than generally found on the shallower *Oculina* mounds (Reed 2002a,b). As with corals, the diversity of sponges appears to increase south of Cape Fear (Partyka et al. 2007).

Reed et al. (2006) identified 18 sponge taxa on the Stetson Banks. The most abundant taxa were demosponges (*Geodia* spp., *Leiodermatium* spp., and sponges in the families Pachastrellidae and Corallistidae) and glass sponges. On the steeper, upper flanks of the mounds (625 to 671 m), the density, diversity, and size of sponges increased, with 15–50 cm sponges most abundant. Massive *Spongosorites* spp. and hexactinellids were common, and pachastrellid tube sponges were abundant. On the top of plateaus, the dominant sponges were fan sponges (*Phakellia* spp.) and numerous other demosponges.

On the Savannah Lithoherms, 12 sponge taxa were identified, occurring principally on exposed terrace pavements, with greatest



abundance observed along the edges of rock outcrops and on pinnacle crests. Dominant sponges included large fan sponges (*Phakellia ventilabrum*), plate sponges (pachastrellids and tetractinellids), and hexactinellid glass sponges. Some ridges and terraces at some sites had nearly 100% cover of sponges (*Phakellia* spp., *Geodia* spp., Pachastrellidae, and hexactinellids; Reed et al. 2006)

On the East Florida *Lophelia* mounds, Reed et al. (2006) identified 18 sponge taxa. Dominant sponges consisted of numerous demosponges and dominated by *Phakellia* spp., *Geodia* spp., *Spongosorites* spp., pachastrellids and petrosiids. Hexactinellids were also common, especially *Aphrocallistes beatrix* and species in the family Euretidae.

Miami and Pourtalès Terraces and

Escarpmets: The Miami Terrace and Escarpment host diverse and dense sponge assemblages (Reed et al. 2006), including hexactinellids (e.g., *Heterotella* sp.) and demosponges (including *Spongosorites* spp., *Geodia* spp., *Vetulina* spp., *Leiodermatium* spp., *Petrosia* spp., and sponges in the families Raspailiidae, Tetractinellida, Pachastrellidae, and Corallistidae). In separate studies on Pourtalès Terrace, Reed et al. (2005, 2014) identified 91 sponge taxa from the quantitative ROV and submersible photo-transects. Of these taxa, 48 were identified to genus or species level, and four are possible new species. Thirteen sponge taxa were found solely in the sinkholes and not on the rock mounds. A newly described species, *Phakellia wrightae* (Pisera and Pomponi 2015), and other sponges in the

Family Theonellidae were found exclusively on the mounds. Other dominant taxa included *Geodia* spp. (three species new to science [Paco Cardenas, Evolutionary Biology Center, Uppsala University, Sweden, personal communication]), *Pachastrella* sp., Corallistidae, *Theonella* spp., *Leiodermatium* sp.; encrusting Spirastrellidae; Poecilosclerida (Raspailiidae, encrusting *Hymedesmia* sp.); *Auletta* sp.; *Topsentia* sp.; and Homoscleromorpha (*Plakortis* spp.). Glass sponges included *Aphrocallistes beatrix beatrix*, *Hexactinella* sp., *Iphiteon* sp., and a recently described genus, *Nodastrella* (Dohrmann et al. 2012). More surveys were conducted on Pourtalès Terrace than in other regions, which may explain in part the higher number of sponges identified. Densities of sponges were very high, especially on the plateaus and terraces of the mounds on Pourtalès Terrace. Maximum densities of sponges (> 5 cm) on the plateaus ranged from 1 to 80 individuals m⁻². The walls of the sinkholes were also densely encrusted with sponges (1 to 50 individuals m⁻²).

Broad-scale biogeographic patterns:

Information on the distribution of sponges is currently too fragmentary to draw many conclusions about their geographic distribution patterns. There are distinct differences between the shelf-edge (< 150 m) sponge assemblages and those in deeper habitats. The former are dominated by demosponges (e.g., *Ircinia* spp., spirastrellids), while the latter are characterized by more demosponges of Order Tetractinellida (e.g., pachastrellids, corallistids, geodiids) and Axinellida (e.g., *Phakellia* spp.), along with significant numbers of glass sponges.



II.3. Species Associations with Deep-Sea Corals and Sponges

Ross and Nizinski (2007) summarized information on species associations with deep-sea coral habitats. Since then, there have been additional studies involving deep-coral and faunal associations within this region. In many cases, sponges are also an important contributor to 3-dimensional structure in the same habitats where corals are present, but this habitat component remains poorly documented.

Many deep-sea fishes and perhaps other fauna in the North Atlantic Ocean are closely associated with complex habitats, at least on the upper slope (200-1000 m). However, the specific roles of deep-sea corals in structuring or influencing communities remain unclear (Ross et al. 2015b). Although there are a few studies from other regions indicating that certain fishes or invertebrates may use corals for specific activities (spawning, nurseries, feeding; e.g., Buhl-Mortensen and Mortensen 2004, Mah et al. 2010, Baillon et al. 2012, Henry et al. 2013, Reed et al. 2014, Ross et al. 2015b), most studies have not demonstrated a statistically significant link in faunal occurrence to living corals or demonstrated a functional relationship for fishes (Auster 2007, Ross and Quattrini 2007, Harter et al. 2009, Biber 2014, Ross et al. 2015b). Often standing dead coral framework has proved to be as significant a habitat for associated fauna as living coral (Lessard-Pilon et al. 2010, Quattrini et al. 2012). It is important to stress that fauna may be mostly influenced by habitat structure (size, profile, rugosity, etc.) and not any one component of the habitat (e.g.,

corals). However, deep-sea corals are a major contributor to overall habitat complexity on the slope and in some areas are the dominant habitat component (as in coral-built bioherms). Quattrini et al. (2015) indicated that coral diversity was important in explaining variation in fish assemblages in the Northeast U.S. Canyons region. Thus, considering that corals are a major contributor to deep-sea habitat complexity and that fauna is often more diverse and abundant in such habitats (as suggested by Milligan et al. 2016), it seems most prudent to consider deep-sea corals as Essential Fish Habitat (EFH) for associated fishes.

Shelf and shelf break: Shelf-edge habitats are home to 167 different fish species, including 33 species from the snapper-grouper complex (Quattrini and Ross 2006, Schobernd and Sedberry 2009, Harter et al. 2015). The distribution of coral and live hard-bottom habitat in this region (to about 300 m) is considered a proxy for the distribution of the species within the snapper grouper complex (SEAMAP-SA 2001, SAFMC 2007a). Harter et al. (2015) and Quattrini and Ross (2006) found distinct differences in fish communities from shelf-edge habitats in different geographic areas. Surveys were not able to discriminate the extent to which the association of fishes might have been influenced by the 3-dimensional structure provided by corals or sponges, distinct from the topography of the rocky hard-bottoms themselves. Quattrini and Ross (2006) noted that species richness was greatest in the highest profile habitats. These shallower habitats do not include coral bioherms, and the relative role corals and sponges in providing



habitat structure for fishes compared with the underlying rocky outcrops has not been teased-out. Corals and sponges are also important habitat for numerous invertebrate species, however we are not aware of any studies of these associations for shelf and shelf break hard-bottom habitats in the Southeast U.S. region.

Oculina Coral Mounds: The *Oculina* biogenic refuge consists primarily of standing live and dead coral habitat (Reed et al. 2007). As long as the coral is standing, the living space within the colony branches supports dense and diverse communities of associated invertebrates (Reed et al. 1982, 2002a,b, Reed and Mikkelsen, 1987). However, once reduced to unconsolidated coral rubble, little living space is left except for the infauna (Reed, 1998). A hypothetical trophic model of the *Oculina varicosa* ecosystem indicates that a significant loss of habitat, in particular intact live and dead standing coral, could bring dramatic shifts in the ecosystem (George et al. 2007). Unfortunately, such a loss of habitat on the *Oculina* reefs has occurred, due to extensive mechanical damage from bottom trawling for rock shrimp (*Sicyonia brevirostris*) (Reed et al. 2007). Between 1977 and 2001, submersible surveys found nearly 100% loss of live-coral cover (range 98.4%–100%) outside of the protected *Oculina* Bank HAPC boundaries, whereas the only reefs that survived (e.g., – Jeff’s and Chapman’s Reefs) were within the protected area. Fish populations experienced dramatic declines (Koenig et al. 2000, 2005). Even within the *Oculina* Bank HAPC, several reefs were destroyed (e.g., Sebastian Pinnacles,

Steeples) between 1977 and 2001, apparently as a result of illegal fishing, highlighting the importance of effective enforcement.

The importance of the standing coral for biodiversity of the region is evident in the associated community of invertebrates found in the coral. Collections of 41 *O. varicosa* colonies (~15-20 cm diameter), which were broken up and sieved through 0.5 mm mesh, resulted in 20,000 invertebrate specimens. These collections, along with additional qualitative collections by manned submersibles and dredge samples of coral rubble, have documented the following biodiversity within the *Oculina* habitat: 230 species of mollusks, 50 decapods, 47 amphipods, 21 echinoderms, 15 pycnogonids, 100+ polychaetes, 42 bryozoans, 11 sipunculans, and numerous other taxa (references in Reed et al. 2006, Winston 2016; M. Rice, Curator emeritus, Smithsonian Natural History Museum, pers. comm.).

Harter et al. (2009) analyzed fish assemblages and benthic habitats inside and outside the *Oculina* Experimental Closed Area (OECA), in 2003 and 2005 using ROVs. The OECA was closed to all bottom fishing in 1994 in order to evaluate the effectiveness of the reserve for the management and conservation of managed fish populations. A total of 62 fish species were observed, including economically-important grouper species such as speckled hind (*Epinephelus drummondhayi*), red grouper (*E. morio*), snowy grouper (*Hyporthodus niveatus*), scamp (*Mycteroperca phenax*), gag (*M. microlepis*), and rock hind (*E. adscensionis*; not typically a target species but kept as bycatch). Even though fish assemblages were not



different among management areas, biodiversity and grouper densities were higher inside the OECA compared to outside. The study did not track coral restoration, however, the percentage of intact coral was also higher inside the OECA. These results provide initial evidence demonstrating effectiveness of the OECA for restoring reef fish populations, and add support to the value of intact *O. varicosa* habitat for these species. Additionally, gag and scamp were known to aggregate on and use *O. varicosa* for spawning habitat and juvenile speckled hind use the coral for shelter suggesting a nursery value of the coral (Gilmore and Jones 1992, Koenig et al. 2000, 2005).

New ROV surveys provided some indication of potential recovery by populations of certain fish species. In the 1980s, large, mature black sea bass (*Centropristis striata*) dominated the *O. varicosa* reefs, but had disappeared by the 1990s (Koenig et al., 2000). In 2005, black sea bass, mostly small juveniles, ranging in length from 10 to 20 cm, were observed, suggesting initial stages of recovery for this species. Subsequent ROV surveys in 2015 and 2016 observed black sea bass throughout the *Oculina* region, including Chapmans Reef inside the OECA, in the newly designated northern extension area of the *Oculina* Bank HAPC, as well as in the satellite areas of the *Oculina* Bank HAPC (Harter, personal communication). All of these findings combined present initial evidence demonstrating effectiveness of the OECA for restoring reef fish populations and their habitat.

Continental slope and Blake Plateau: Ross and Quattrini (2009) analyzed fish assemblages at

nine *Lophelia*-dominated sites at depths of 366-770 m along the Southeast U.S. slope between Cape Lookout, North Carolina to Cape Canaveral, Florida. They found regional differences in the deep-reef associated fauna, with sites off North Carolina differing from those off the central Blake Plateau and off Cape Canaveral. Depth and habitat structure seemed to be the drivers of these differences. Quattrini et al. (2012) in a smaller scale study noted that habitat structure, especially height off bottom, influenced faunal composition.

Because these deep reefs are difficult to sample and remain poorly studied, there continue to be discoveries of new species and new distributional records for the area resulting from new surveys. Since 2007, four new species of benthic fishes were described (McCosker and Ross 2007, Fernholm and Quattrini 2008, Nielsen et al. 2009). Caruso et al. (2007) and Pietsch (2009) reviewed the lophiform fishes from the Gulf of Mexico and Southeast U.S. deep reefs, noting many large range extensions. Similarly, Henry et al. (2008) reviewed the deepwater hydroids collected on *Lophelia* and rocky reefs and reported a number of species new to the southeast region.

Reed and Farrington (2010) and Reed et al. (2017) analyzed video from submersible and ROV surveys to document the occurrence and distribution of golden crab (*Chaceon fenneri*) in deep-water habitats (200-900 m deep), including coral habitats, off eastern and southern Florida. Golden crabs were observed at depths of 247–888 m, with most crabs found between 400-500m. While crabs were observed in habitats



ranging from dense live coral thickets to flat soft bottoms, Reed et al. (2017) found that densities were significantly higher on soft-bottom habitat (sand and mud) compared to hard-bottom habitat (rocky or coral-dominated habitats). Within the hard-bottom habitats, mean crab density appeared to be higher on rocky substrata (pavement, rock slabs, boulders, cobble and rubble) compared to coral substrata (standing live/dead coral, coral rubble). The authors noted that it may be easier to see crabs on open flat soft-bottom habitat compared to more complex habitats, however, they found no evidence that crabs were hiding or sleeping in crevices during the daytime surveys.

Reed and Farrington (2010) also reported on observations of three other economically important fisheries species, blueline tilefish (*Caulolatilus microps*), golden tilefish (*Lopholatilus chamaeleonticeps*), and royal red shrimp (*Pleoticus robustus*). Observations of tilefishes were limited, although five out of seven blueline tilefishes were observed associated with high-relief bioherms on the Pourtalès Terrace (186 to 285 m). Royal red shrimp are also an important species targeted by fishers at these depths, but were difficult to document using submersibles or ROVs.

Portalès Terrace: Reed et al. (2015) reported over 50 fish species, including 11 economically-important species observed in deepwater habitats of Pourtalès Terrace. Thirteen species observed on Pourtalès Terrace (Reed et al. 2005, 2006, 2015) are also found on deepwater *Lophelia* reefs from North Carolina to Cape

Canaveral (Ross and Quattrini 2007). Along the Pourtalès Terrace and escarpment, deepwater fish assemblages differed by depth (150-300 m and 450-850 m), habitat geomorphology and substrate (Reed et al. 2015). The fish assemblages associated with *Lophelia* coral habitat on Pourtalès Terrace appeared to differ from assemblages on other pavement and rock wall substrates, but the associations did not appear to be obligate. Additionally, Baumberger et al. (2010) reported a large spawning aggregation of beardfish (*Polymixia lowei*) associated with a sinkhole on the outer edge of the Pourtalès Terrace.

Sponge associations: Sponges are known to host significant communities of associated invertebrates (Hogg et al. 2010). Sedberry et al. (2004) analyzed five individual sponges of different genera collected off South Carolina and NE Florida at depths between 50-194m. They reported 947 invertebrates representing ten taxonomic groups living in the sponges. Polychaetes accounted for 69% of the faunal associates. Amphipods (14%), cirripeds (8%), and decapods (6%) were also important constituents of the associated fauna. The number and composition of faunal associates appeared to vary by sponge species. *Erylus* sp. hosted primarily annelids (96%); *Chondrilla* sp. hosted primarily arthropods (77%), including amphipods, decapods, and isopods; while annelids and arthropods were both abundant on *Aplysina archeri* and *Ircinia campana* (Sedberry et al. 2004). Unfortunately, there are no comparable studies on sponge communities from deeper waters in this region.



II.4. Predictive Habitat Modeling of Deep-Sea Corals

Only a very small portion of the deeper waters off the Southeast U.S. has been surveyed for deep-sea coral or sponge habitats. In the face of such limited sampling, predictive modeling of habitat suitable for these taxa can be a useful and cost-effective tool that can help guide research surveys and support conservation action (Guinotte et al., this volume).

Two sets of predictive habitat suitability models for deep-sea coral taxa have been developed for this region. Davies et al. (unpublished) developed a predictive model for framework-forming stony corals in the region. Kinlan et al. (2012) developed a set of models that included the four major framework-forming stony corals (*Oculina varicosa*, *Lophelia pertusa*, *Enallopsammia profunda*, and *Madrepora* spp.), as well as black corals, gorgonians, soft corals, sea pens, and stylasterid corals (Fig. 9). Both modeling teams used the Maximum Entropy (Maxent; Phillips et al. 2006) modeling approach relying on presence-only data.

Although a useful tool, these predictive habitat models have not yet been fully validated by in-situ observations in the field. Additionally, the model resolution (~ 370 – 1000 m) is generally not fine enough to depict the mound features that represent bioherms created by framework-forming stony corals. Maxent presence-only model results also tend to over-predict suitable deep-sea coral habitat, both because of the absence of high-quality substrate data and in cases where higher taxonomic levels (e.g.,

Order or Suborder) are modeled that contain disparate numerous species with different distributions. Nevertheless, the models closely approximate the coral habitat zones identified by Reed et al. (2013a, and Fig. 5) and suggest that the region of potential coral habitat is larger than was imagined a decade ago. The Kinlan et al. (2012) model also accurately predicted the occurrence of suitable *O. varicosa* habitat north of the Oculina Bank HAPC (Fig. 9b). Surveys in 2010 confirmed the presence of previously unknown *Oculina* mounds in this area, providing vital information that led to the expansion of the HAPC in 2015 (see below).

II.5. Other New Information from Published Studies Since 2007

Brooke et al. (2013) and Mienis et al. (2014) noted that deep-sea corals and associated fauna occur in very dynamic and sometimes harsh environments in this region, largely due to Gulf Stream influences. Extreme and rapid changes in bottom temperatures and other parameters occur around *Lophelia* bioherms off Cape Lookout, NC (Brooke et al. 2013, Mienis et al. 2014). Although temperatures can rise over the expected lethal limit for *Lophelia* and persist at those levels for almost a week, Brooke et al. (2013) noted that *L. pertusa* colonies survived these extremes. Mortality increased greatly after a week at higher temperatures. While they cautioned that the effects of temperature on survival of *L. pertusa* were complex, and they proposed that the species was unlikely to be found in habitats where temperatures were 15°C or higher for extended periods.

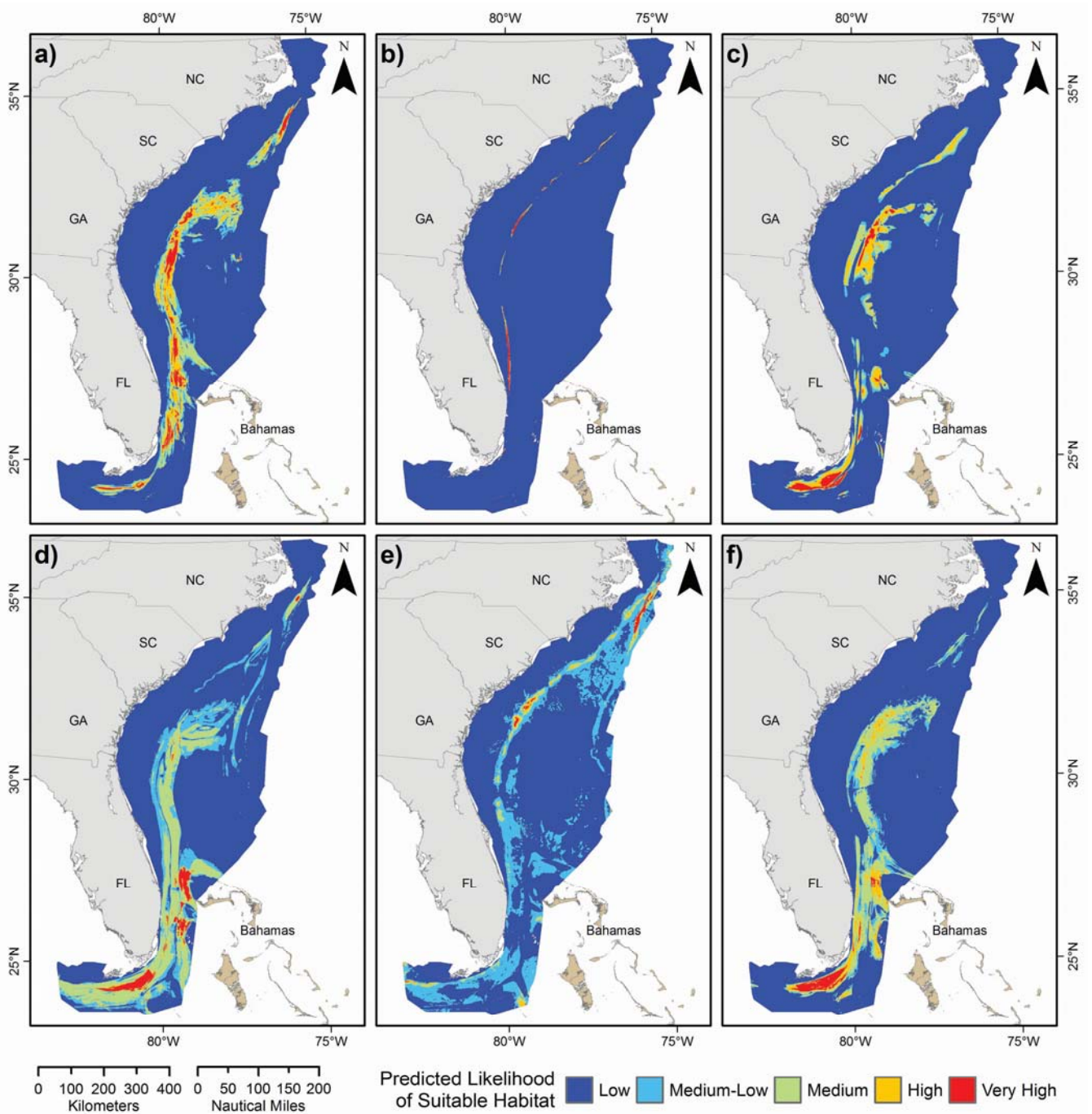


Figure 9. Maxent predictive habitat model for six different deepwater coral taxa in waters off the Southeast U.S.: a) *Lophelia pertusa*; b) *Oculina varicosa*; c) *Antipatharia* (black corals); d) *Gorgonian octocorals*; e) *Pennatulacea* (sea pens); f) *Stylasteridae* (lace corals). Warmer colors indicate greater likelihood of suitable habitat, determined by a cross-validation method that determined likelihood thresholds using the ratio of false positive to false negative classification results when the model was tested on data left out of the fitting process.



Gartner et al. (2008) noted the occurrence of large aggregations of mesopelagic fishes and macronekton invertebrates in areas of the upper continental slope off North Carolina. They observed persistent aggregations near or on the bottom that appeared to forego daily vertical migrations. Aggregations were especially dense in areas of steeply sloping ridges, canyons, or other sharp relief, including *Lophelia* coral mounds. Benthic fishes and invertebrates on the coral mounds fed on species in the near-bottom aggregations, indicating that they clearly contribute to energy flow around deep reefs. Since their contributions might be substantial, additional studies of midwater and benthic interactions are needed.

Long-lived deep-sea corals continue to be important proxies for understanding the historical environment relevant to deep reefs over the last 2000 years. Species of black corals examined in paleoecological studies in the Gulf of Mexico (e.g., Prouty et al. 2011, 2014) also occur in the Southeast U.S. region. Sinclair et al. (2011) estimated a bamboo coral (*Keratoisis* sp.) from the region to be between 330 and 580 years old. These authors noted that the skeleton of this species may provide a good record of certain signals, but that more research was needed to verify the utility of this coral.

II.6. Research Priorities

Ross and Nizinski (2007) identified a number of deep-sea coral research priorities for the region. Also in 2007, the South Atlantic Fishery Management Council (SAFMC) approved a Deepwater Research and Monitoring Plan

(SAFMC 2007b) to guide conservation and management of deep-sea coral ecosystems in the Southeast U.S. and to support mandates in the Magnuson-Stevens Fisheries Conservation and Management Act (MSA). The plan has two phases: 1) mapping and describing known and expected deepwater coral ecosystems in the region; and 2) determining the ecological role of these ecosystems, especially as essential fish habitat (EFH), and understanding the biology and ecology of structure-forming species. The Deep Sea Coral Research and Technology Program held research priority workshops in 2009 (NOAA 2010) and 2015 (Schull et al. 2016) that built on and expanded research priorities for the region (see below). Table 3 summarizes research priorities identified in these efforts.

New priorities: While a number of the priorities were addressed in the Deep Sea Coral Research and Technology Program's 2009-11 research initiative, there remain significant gaps in our understanding of these ecosystems, including the following priorities.

Mapping and habitat characterization:

Mapping the location of deep-sea coral and sponge habitats remains a high priority. High-resolution multibeam sonar maps, ideally with backscatter, are a foundation for most other research, modeling, and conservation (Correa 2012). This is especially true in this region, where *L. pertusa*, *E. profunda*, and *O. varicosa*, form coral mounds that can be identified in multibeam surveys. The recent discovery of hundreds of additional mound features off Florida and Georgia suggest a much richer deep-reef province than previously



Table 3. Summary of deep-sea coral research priorities developed for the U.S. Southeast. NOAA held workshops in 2009 (NOAA 2010) and 2015 (Schull et al. 2016). Specific recommendations have been paraphrased and reorganized to highlight commonalities among specific recommendations.

Ross and Nizinski 2007	SAFMC 2007b	NOAA 2010	Schull et al. 2016
Map: Detailed mapping of the southeastern U.S. shelf edge and slope (esp. multibeam in the depth range of 350-800 m).	Map: Map the distribution of deepwater coral ecosystems in the Southeastern U.S. EEZ; assess their condition	Map: Inventory existing data; complete multibeam sonar surveys for proposed deepwater Coral HAPCs, and explore and characterize sites of interest identified within the C-HAPCs	Map: What topographic features are associated with deep-sea coral ecosystems? Where are the hotspots and what is their spatial extent?
Biodiversity & Habitat Associations: Document species composition and distributions of deep corals within the region; document the whole living habitat matrix and associated fauna.	Biodiversity & Habitat Associations: Describe and inventory biota of deepwater coral ecosystems; Describe the population dynamics, movements and habitat associations of both economically and ecologically important associated species. Determine the nature, patterns, and processes of communities of microbial coral associates.	Biodiversity & Habitat Associations: Describe types, strengths, and patterns of habitat association of other species with deep-sea corals and sponges	Biodiversity & Habitat Associations: Which species of deep-sea corals and sponges are present in these ecosystems? What are the relationships between deep-sea corals and sponges and their epifauna? What drives community structure differences among sites?
Population connectivity: Genetic studies for the major coral species and dominant associated fauna to examine taxonomic status, dispersal, relationships among coral banks, and community genetics	Reproduction & Population Connectivity: Describe reproductive strategies (gametogenic cycles, sex ratio, fecundity, larval development modes) of priority structure-forming groups, including scleractinians (<i>L. pertusa</i> , <i>E. profunda</i> , <i>M. oculata</i>), octocorals, antipatharians and stylasterids. Describe the genetic characteristics of structure-forming coral populations.	Reproduction & Population Connectivity: Understand the biology and ecology of deep-sea corals and Sponges; including: demographics of deepwater coral and sponge species; recruitment, connectivity and reproduction. Conduct genetic analysis and determine population dynamics; understand the connectivity between shallow, mesophotic, and deep-sea corals.	Reproduction & Population Connectivity: What is reproductive biology and ecology of deep-sea corals and sponges (larval biology, colony size-frequency distribution, recruitment, environmental drivers, etc.)? How are populations connected and what factors shape the genetic connectivity of deep-sea coral ecosystems in the South Atlantic (e.g. stepping stones, dispersal barriers)?
Food webs: Trophodynamics studies of coral banks and surrounding areas (whole water column)	Food webs: Describe food web dynamics of DWCEs		Food webs: What is trophic ecology of deep-sea coral and sponge ecosystems? What are the food sources?



Ross and Nizinski 2007	SAFMC 2007b	NOAA 2010	Schull et al. 2016
<i>Age and growth:</i> Understand the age and growth of the major structure forming corals (e.g., <i>Lophelia</i> , <i>Madrepora</i> , bamboo and black corals) and evaluate the age, history and present status (accreting, eroding) of the underlying coral mounds.	<i>Age and growth:</i> Describe patterns and processes of colony growth and mortality of important structure-forming species, and determine how they are affected by environmental factors and stressors		
<i>Anthropogenic impacts:</i> Long-term monitoring, research, education, and enforcement of deep-sea coral MPAs. Monitoring of bottom fisheries.	<i>Anthropogenic impacts:</i> Map human activities that may impact deepwater coral ecosystems; Identify and quantify natural and anthropogenic stressors	<i>Anthropogenic impacts:</i> Map fishing and non-fishing activities; Identify and assess impact to areas from fishing and non-fishing activities; monitor coral recovery; determine appropriate mitigation strategies.	<i>Anthropogenic impacts:</i> What interactions occur between fishing gear from the golden crab, royal red shrimp, and wreckfish fisheries and deep-sea coral and sponge ecosystems? How do deep-sea coral communities differ inside and outside of protected areas? How can we assess the health and resilience of deep-sea coral and sponge ecosystems? How much can deep-sea fish and benthic communities be impacted and still maintain sustainable fisheries? Are there signs of recruitment or recovery in areas that have been impacted in the past?
<i>Environmental archives:</i> paleoclimate or paleo-environmental studies of corals			<i>Environmental archives:</i> Can we reconstruct paleoclimates using deep-sea corals and sponges?
	<i>Physical factors and habitat modeling:</i> Describe the physiographic environment of deepwater coral ecosystems; Describe relationships of coral ecosystem composition, structure and distribution and abiotic and biotic factors; develop models to enable predictions of coral ecosystem status and trends.	<i>Habitat suitability modeling:</i> Develop and groundtruth modeling tools to predict where corals are likely to occur.	<i>Physical factors and habitat modeling:</i> What topographic features are associated with deep-sea coral ecosystems? How accurate are model predictions of deep-sea coral habitat, particularly for structure-forming taxa? What is the most useful level of spatial and taxonomic resolution for models to guide cruise planning and management?
			<i>Climate change impacts:</i> What are the environmental limitations (i.e., temperature, depth, dissolved oxygen, aragonite saturation, pH, etc.) of deep-sea coral and sponges, as well as their associated species, and what is the variability in these environmental parameters? How do deep-sea corals calcify under low aragonite saturation states and low oxygen levels?



imagined – perhaps among the world’s richest. Likewise, multibeam surveys of portions of the Stetson Banks (S.W. Ross, unpubl. data) revealed many more mounds and rocky hard-bottoms than previously known. Both these areas should be a high priority for new surveys. The key second phase is to better classify, map, and characterize the coral and sponge assemblages and their associated biological communities in relation to underlying geology and oceanography.

Modeling: Species and habitat distribution modeling is becoming a fundamental tool in every U.S. region. Needed steps in the region include ground-truthing existing coral models, developing new ensemble models for both corals and sponges, and developing approaches to model abundance and diversity (not merely presence) of these taxa. Improving the environmental and biological data inputs to these models is also a critical activity.

Population connectivity: New genetic techniques are providing tools to better understand the connectivity of populations at both fine and ocean basin scales (Morrison et al., this volume). Next generation sequencing is a promising new methodology to answer these questions. These genetic tools can complement and link to other studies and modeling of current dynamics (e.g., Hilário et al. 2015).

Climate and ocean acidification: Since 2007, the potential impacts of ocean acidification and climate change have been identified as a significant research need. The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) highlighted the limited

information available on the risks of climate change and ocean acidification to the deep-sea. The importance of improving this understanding given the size of the deep-sea region is imperative (Hoegh-Gulberg et al. 2014).

A number of recent laboratory studies have been conducted to determine responses of *L. pertusa* to decreased aragonite saturations levels associated with lower pH (e.g., Form and Riebesell 2012, Lunden et al. 2014). These studies have shown that this species is capable of continued calcification even under reduced aragonite saturation levels. However, the long-term consequences of ocean acidification for *L. pertusa* and other reef-forming species, as well as the underlying coral frameworks that they build, remain unclear. There is an extensive unanalyzed database of ocean carbonate chemistry for this region (Ross and Brooke, unpubl. data) that indicates that several deep-sea coral species occur in areas of low aragonite saturation, as reported in the Gulf of Mexico (Lunden et al. 2014). These extensive data on carbonate chemistry and nutrients would be valuable as model inputs as well as basic environmental descriptors. Given the important role that reef-forming deep-sea corals play in the region, understanding carbonate chemistry is especially important. A better understanding of the synergistic effects of changing temperatures, oxygen concentrations, and current regimes due to climate change is needed, as well as how these factors may interact with ocean acidification.

Sponges: This chapter is the first effort to summarize our knowledge of the deep-water



sponge fauna of the region. Understanding these species and the habitats they form lags far behind that of deep-sea corals. There are critical data gaps at every level, including basic taxonomy, life history, and ecology. In addition, sponges and their rich endosymbiotic microorganisms rank among the most important targets for bioprospecting (Hogg et al. 2010).

Two new international consortia ([Deep-sea Sponge Grounds Ecosystems of the North Atlantic](#) [SponGES] and [A Trans-Atlantic assessment and deep-water ecosystem-based spatial management plan for Europe](#) [ATLAS]) have begun research on sponge grounds in the northeastern Atlantic. They hope to quantify the ecosystem services these habitats provide, and to identify the threats they face from both commercial activities (e.g., fishing) and climate change. These projects were established with support from the European Commission's Horizon 2020 program. The U.S. will partner with these consortia to explore and identify sponge grounds in the Southeast U.S.

III. Update on Management of Deep-Sea Corals and Sponges

III.1. New Information on Impacts and Stressors

III.1.i – Fishing

Fishing continues to be among the most important stressors to deep-sea coral

ecosystems in the Southeast U.S. However, beginning in 2010, the potential of fishing to adversely impact these ecosystems was drastically constrained by historic management actions proposed by the South Atlantic Fishery Management Council and implemented by NMFS (see below). Trawl fisheries have the potential to damage both corals and sponges in the region (van Dolah et al. 1987). The principal fisheries of concern in deeper waters have been the localized royal red shrimp (*Pleoticus robustus*) trawl fishery and the golden crab (*Chaceon fenneri*) trap fishery. These are small fisheries operating in a limited geographic range, but both had the potential to severely damage deep-sea coral habitats. In shallower water on the shelf, the rock shrimp (*Sicyonia brevirostris*) fishery had been a significant concern off parts of Florida, particularly to *Oculina* reefs (Reed et al. 2007, 2008) prior to the implementation of vessel monitoring requirements for the fishery. Roth (2007) conducted interviews with stakeholders and concluded that inadequate surveillance and enforcement resulted in continuing illegal snapper-grouper fishing in the *Oculina* Bank Habitat Area of Particular Concern (HAPC). Although potentially illegal incursions by shrimp vessels into the *Oculina* Bank HAPC have been reported (SAFMC 2015), regulations and requirements for vessel monitoring systems (VMS) have reduced impacts of fishing gear on *O. varicosa* coral. Lesser impacts to shelf-edge coral and sponge habitats may also occur from limited bottom-set longline fishing (prohibited south of 27°10'N and elsewhere in depths less than 50 fathoms [91 m]).



Analyses of golden crab and royal red shrimp fisheries conducted in association with SAFMC fishery management plan amendments (SAFMC 2009, 2013) have provided a much better understanding of the geographic footprint of these fisheries. While neither of these fisheries specifically target areas with corals, geographic and bathymetric overlap between the fisheries and *Lophelia* habitat indicates that these bottom-contact fisheries are the most likely to interact with these habitats.

Golden crab occur on both soft-bottom and hard bottom-habitats, including *Lophelia* mounds, at depths between 205 - 1,007 m (Wenner and Barans 1990, Reed and Farrington 2010, Reed et al. 2017). The current golden crab fishery operates off eastern Florida, where fishers deploy strings of 20 to 50 traps that can stretch up to 8 km (SAFMC 2009). Fishers target soft sediment areas adjacent to deepwater coral habitat, but strong currents can carry the traps into coral habitats. It is likely that the greatest potential damage to deep-sea coral and sponge habitats would occur during retrieval of the trap lines, when the trap ground line is hooked with a grapple towed behind the fishing vessel. The sweep of the traps and lines as they are lifted off the bottom has the potential to damage areas of coral habitat and cause sediment re-suspension that can suffocate coral polyps. Lost traps and line have also been observed near coral habitat (S. Brooke, pers. comm). It is a small fishery, with approximately 5 to 6 vessels landing golden crab in recent years (SAFMC 2009) and 11 permits authorized in 2016 (NMFS South East Regional Office).

Royal red shrimp are found on the continental slope at depths from 180 – 730 m, with the largest concentrations of shrimp occurring primarily off northeast Florida at depths of between 250 – 550 m (Anderson and Lindner 1995, SAFMC 2013). Based on the analysis of VMS tracks, the primary royal red shrimp fishing areas are from around 26.4° N to 30° N off eastern Florida, between about 250 – 400 m depths. This range overlaps with the shallower end of the *Lophelia* reef distribution. Although the royal red shrimp is not a federally managed species in the South Atlantic, regulations for the Stetson-Miami Terrace deepwater Coral Habitat Area of Particular Concern (C-HAPC) were designed to prevent trawling impacts to *Lophelia* coral habitats from the fishery (see below).

In June 2008, NMFS implemented a mandatory Federal observer program to characterize the South Atlantic penaeid and rock shrimp fisheries (Scott-Denton et al. 2011). The commercial rock shrimp fishery is focused off eastern Florida, from approximately St. Augustine to Vero Beach – primarily at 25 – 65 m depths. Fishing at these depths potentially overlaps with *Oculina* reef habitat. Invertebrates other than crustaceans represented 6% of the rock shrimp fisheries catch (Scott-Denton et al. 2011), but these data were not reported in sufficient taxonomic specificity to determine the extent to which corals or sponges were represented in the bycatch.

III. 1. ii – Other stressors

Oil and gas development: A potential future stressor in the region may be oil and gas



development and associated risks of oil spills. Studies from the 1970s and 1980s indicated that certain areas off the Southeast U.S. may contain significant oil and especially gas resource potential (BOEM 2014). In 2015, the Bureau of Ocean Energy Management (BOEM) published a Draft Proposed Program (DPP) for 2017-2022 Outer Continental Shelf Oil and Gas Leasing. The DPP identified an option for a potential lease sale in an area located at least 50 miles offshore from the coasts of Virginia, North Carolina, South Carolina, or Georgia. However, in March 2016, the U.S. Department of the Interior removed the U.S. Atlantic region from oil and gas exploration from the current (2017-2022) five-year plan (BOEM 2016). Thus, risks from this activity in the near future are not expected unless this decision is overturned. In addition to potential threats from U.S. oil and gas development, Cuba is starting to develop capabilities to extract oil and gas resources in the Florida Straits within their EEZ. Any spills associated with such development could also threaten U.S. deep-sea coral and sponge habitats downstream. As described in the Gulf of Mexico chapter (Boland et al., this volume), the Deepwater Horizon disaster demonstrated the potential for an oil spill to damage deep-sea corals. Additional fossil fuel development projects proposed for Southeast Florida and that have included surveys for potential impacts on benthic habitats include a liquid natural gas (LNG) port facility (Messing et al. 2006a) and a natural gas pipeline between Florida and the Bahamas (Messing 2006b).

Renewable energy: In the Southeast U.S., as in other U.S. regions, there is increasing interest in

offshore ocean-based renewable energy. Offshore wind energy is the most mature technology, and it has been successfully implemented around the world, especially in Europe. There are currently no facilities under construction in the Southeast U.S., and when implemented these facilities will likely be sited predominantly nearshore in relatively shallow waters – with little impact to deep-sea coral and sponge habitats.

Various entities have expressed interest in the potential for developing marine current energy or ocean thermal energy conversion (OTEC) projects offshore of southeastern Florida (Vinick et al. 2012). The exceptionally strong currents associated with the Gulf Stream flowing through the Florida Straits off the southeastern Florida coast, represent the best ocean current resource for renewable energy development in the United States. While still in early planning stages, both facility siting and transmission lines to bring electricity onshore have a potential to damage vulnerable benthic habitats.

Submarine cable deployment: Southeast Florida is a major hub for communications cables to the Caribbean and Central and South America. Although the footprint of cables is much smaller than that of fisheries, their deployment can result in adverse impacts to sensitive habitats (Hourigan et al. 2007, Messing et al. 2012). The State of Florida has been a leader in developing incentives for companies to route cables away from environmentally-sensitive habitats, including deep-sea coral habitats.



Invasive species: There have been no systematic surveys for invasive species in deeper waters of the Southeast region. However, since 2007, observations of increasing numbers of the introduced Pacific lionfishes, *Pterois volitans* and *P. miles* have raised concerns (Morris and Whitfield 2009) in waters shallower than 150 m. Large numbers of lionfish have been observed down to 100 m in surveys throughout the region, (Meister et al. 2005), with some observations extending to 300 m (Grant Gilmore pers. comm. cited in: Muñoz et al. 2011). Harter et al. (2015) recently documented thousands of lionfish at depths of 50 to greater than 100 m in protected hard-bottom areas along the Southeast U.S. from Florida to North Carolina. While unlikely to damage corals and sponges directly, predatory lionfish have the potential to reduce forage fish biomass in the associated communities (Muñoz et al. 2011). In studies of mesophotic reefs in the Bahamas, lionfish predation on herbivorous fish caused a shift in benthic community structure, with an increase in algae relative to corals and sponges at depths to 61 m (Lesser and Slattery 2011).

Climate change and ocean acidification. Since 2007, significant new information has become available on the potential impacts of climate change and ocean acidification on deep-sea corals. The IPCC Fifth Assessment Report concluded that while most ocean warming has occurred in shallow waters, warming has also been observed in ocean depths between 700 and 2000 m from 1957 to 2010 and likely involves a significant anthropogenic signal (Hoegh-Guldberg et al. 2014). Rising atmospheric CO₂ poses a risk to deep-sea coral and sponge

communities through increasing temperature (e.g., Brooke et al. 2013), decreasing O₂ (Keeling et al., 2010, Stramma et al. 2010), decreased productivity of surface waters and export of food to the deep-sea (Jones et al. 2014), and ocean acidification with associated changes in carbonate chemistry that affect coral calcification (Guinotte et al., 2006). Based on laboratory and *in situ* experiments, Brooke et al. (2013) concluded that the upper lethal temperature limit for *L. pertusa* in the Southeast U.S. is near 15°C. A number of upper-slope areas within the region may already be facing temperatures in this range, at least for short periods (Brooke et al. 2013, Mienis et al. 2014). In a similar manner, climate-driven expansion of the oxygen minimum zone could adversely affect coral growth. Lunden et al. (2014) found in laboratory experiments that both high temperatures (> 14°C) and low oxygen concentrations (1.5 ml/l) resulted in mortality of *L. pertusa* collected from the Gulf of Mexico. There is also the potential for climate change to shift the periods of peak primary productivity, which provide food to the seafloor. Food delivery drives deep-sea species population dynamics, reproduction and species composition.

Ocean acidification may be of particular concern in the Southeast U.S. given that this region holds the most extensive deepwater coral bioherms in U.S. waters. Recent studies suggest that living *L. pertusa* may be able to continue calcification even in the face of projected shoaling of the aragonite and calcite saturation horizons (e.g., Form and Riebesell 2012). However, the three-dimensional dead coral framework that composes the mounds



may weaken and become more susceptible to bioerosion in under-saturated waters (Maier et al., 2013, Hennige et al. 2015). Projections based on IPCC emission scenarios indicate that most living *L. pertusa* in the Southeast U.S. region is likely to remain above the aragonite saturation horizon for the remainder of this century (Jiang et al. 2010).

III.2. New or Planned Management Actions

III.2.i – Fisheries management

As described by Ross and Nizinski (2007), the South Atlantic Fishery Management Council (SAFMC) was an early leader in deep-sea coral habitat protection. The 1984 Oculina Bank Habitat Area of Particular Concern was the world's first deep-sea coral protected area. Helies et al. (2011) recently conducted the first survey of socioeconomic impacts of the Oculina Bank HAPC based on surveys primarily targeted at the recreational, charter and commercial fisher communities in nearby Fort Pierce, Florida. They reported different perceptions of outcomes among the commercial bottom-fish long-liners (overwhelmingly negative), rock-shrimpers (short-term negative, but long-term positive) of the regulations implemented between 1984 and 2000.

In 2010, NMFS approved the SAFMC's Comprehensive Ecosystem-Based Amendment 1 (SAFMC 2009). This management action, under development since 2001, established five deepwater Coral Habitat Areas of Particular Concern (C-HAPCs). The C-HAPCs protect a

total area of 62,717 km² (24,215 mi²), off the coasts of the Carolinas, Georgia, and eastern and southern Florida, containing complex deepwater coral habitats (Fig. 6). The Cape Lookout and Cape Fear C-HAPCs protect known *Lophelia* habitats off North Carolina. The Stetson Reefs, Savannah and East Florida lithoherms, and Miami Terrace (Stetson-Miami Terrace) C-HAPC stretches from South Carolina to the Miami Terrace and until 2016 represented the largest marine protected area (MPA) in the U.S. Atlantic. It includes the vast majority of *Lophelia* and *Enallopsammia* habitats identified by Reed et al. (2013a) as well as habitat predicted to include these framework-forming corals (see above). The Pourtales Terrace C-HAPC protects a significant portion of this the Terrace and its unique coral habitats. Within most areas of the C-HAPCs, all fishing vessels are prohibited from using all bottom-damaging gear, including bottom longlines, trawls (bottom and mid-water), dredges, pots or traps, or the use of an anchor, anchor and chain, or grapple and chain. "Allowable Golden Crab Fishing Areas" and four "Shrimp Fishery Access Areas" were included in the Stetson-Miami Terrace and Pourtales Terrace C-HAPCs in order to accommodate these small-scale traditional fisheries in historic fishing grounds. Within C-HAPCs, possession of corals (with the exception of octocorals off Florida) is also prohibited. Reed et al. (2017) reported that at least eight documented or potential *Lophelia* coral mound habitat areas overlap with the Allowable Golden Crab Fishing Areas, and recommended that managers should adjust the boundaries to protect vulnerable habitat while



allowing benthic fisheries to continue operating in areas of soft-bottom habitat.

In 2013, the SAFMC proposed further adjustments to the Oculina Bank HAPC and the Stetson-Miami Terrace C-HAPC (SAFMC 2013, Martin 2014) based on new findings from research by NOAA's Deep Sea Coral Research and Technology Program as described above. In addition, examination of museum records of *L. pertusa* from off Cape Lookout, NC provided a target location for additional multibeam sonar mapping and the discovery of numerous low profile mounds north of the Cape Lookout C-HAPC (Ross et al. 2012). A northward expansion of the boundaries of this C-HAPC to include these mounds was also included in Coral Amendment 8. Coral Amendment 8 was approved by NMFS in 2015.

In addition to the C-HAPCs, the SAFMC's Snapper-Grouper Amendment 14 established a series of deepwater marine protected areas (MPAs) along the shelf edge (Fig. 6). NMFS approved the amendment in 2009. The MPAs are designed to protect seven long-lived "deepwater" grouper and tilefish species (speckled hind, snowy, yellowedge, Warsaw and misty groupers; and golden and blueline tilefish), but also serve to protect corals and sponges from fishing impacts. The MPAs range in size from 27 km² to 514 km². Fishing with potentially-damaging bottom-contact gear, including bottom longlines, bottom-trawls, gill nets, golden crab trap or other traps is prohibited, as well as fishing for or possession of any snapper-grouper species. Although much smaller, the SAFMC has also approved a number

of Spawning Special Management Zones and submitted these for approval by NMFS.

Together these actions have significantly decreased the potential for damage from fisheries to deepwater coral and sponge habitats in the region.

III.2.ii – Other resource management

Oil and Gas: The Southeast U.S. Region encompasses the Bureau of Ocean Energy Management (BOEM) Planning Areas for the Straits of Florida, South Atlantic, and portions of the Mid-Atlantic Outer Continental Shelf (OCS). There has been renewed interest in oil and gas exploration in the South Atlantic and Mid-Atlantic Planning Areas. At present, there are no active oil and gas leases in any of these areas, and no oil and gas lease sales are proposed under the current Five Year Leasing Program 2017-2022.

Renewable Energy: BOEM is also responsible for development of the Atlantic OCS wind, wave, and other renewable energy resources. As in other regions, there is increasing interest in ocean-based renewable energy development. While wind energy utilization is expected to be predominantly nearshore in relatively shallow waters, the exceptional currents associated with the Gulf Stream that flow through the Florida Straits has catalyzed interest in hydrokinetic energy development. The Florida Current is close to the major metropolitan area of Miami, and represents the best ocean current resource for renewable energy development in the United States. The proximity to relatively deep

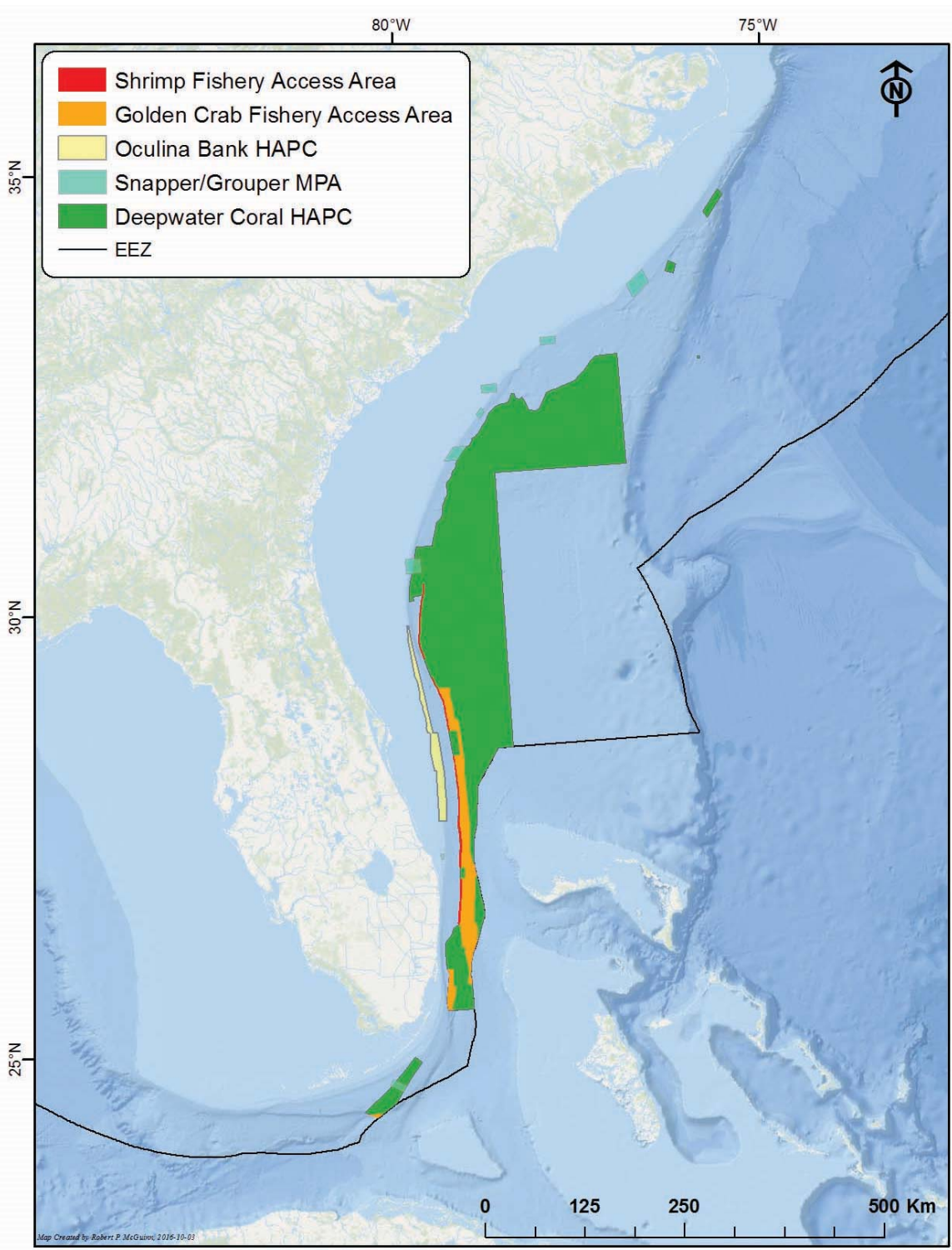


Figure 10. Major area-based fishery management measures that protect deep-sea coral and sponge habitats in the South Atlantic Fishery Management Council region. These areas include Oculina Bank Habitat Area of Particular Concern (HAPC) including the 2015 expansion; deepwater Coral HAPCs (2010 and expanded in 2015); and shelf-edge Marine Protected Areas (MPAs).



water also holds promise for potential ocean thermal energy conversion (OTEC) projects. While still in early planning stages, both facility siting and transmission lines to bring electricity onshore have a potential to damage vulnerable benthic habitats, including deep-sea coral and sponge habitats on the Miami Terrace. Vinick et al. (2012) assembled a seafloor survey methodology and siting framework that developers of marine and hydrokinetic projects in this region could use. The authors identified two major areas offshore southeastern Florida that appear suitable for installing commercial scale marine and hydrokinetic energy facilities, including subsea electrical transmissions cables to shore.

IV. Conclusions

New compilations and analysis of past research, along with new benthic mapping and research since 2006 have significantly improved our understanding of the distribution of the region's deep-sea corals and their associated fauna.

- New mapping and surveys have confirmed that the Southeast U.S. has by far the nation's highest concentration of scleractinian deep-sea coral mounds, and probably ranks among the top such provinces globally. Despite research progress, much of this region remains unexplored.
- Genetic studies of the important framework-forming species, *Lophelia pertusa* and *Oculina varicosa*, have begun to reveal information on population structure and connectivity, while oceanographic studies are elucidating factors that lead to coral mound formation.
- In addition to branching stony corals, gorgonians and black corals are important contributors to habitat structure in areas of hard bottoms. A more thorough cataloging of these taxa has more than doubled the number of species reported in the 2007 report.
- The first deep-sea coral habitat suitability models have been developed for the region, but need to be validated using visual surveys.
- Deep-sea coral habitats are home to a large number of associated species and act to enhance local biodiversity.

The sponge fauna of the Southeast U.S. region has not been systematically cataloged and remains poorly known. Like corals, a number of species form structurally complex habitats in deeper waters, primarily on hard-bottoms, and likely contribute to habitat for numerous species. There is a clear need for additional research on the region's sponges, including their life histories and ecological roles.

The last decade has also seen the realization of regional-scale efforts to protect from fishing impacts both deep-sea coral reef provinces and shelf-edge coral and sponge habitats through a series of deepwater Coral Habitat Areas of Particular Concern (C-HAPCs) and a network of shallower MPAs, respectively. These new fishing measures, developed by the South Atlantic Fishery Management Council and



implemented by NOAA, have significantly reduced the scope for fishing damage to deep-sea coral and sponge habitats.

V. Acknowledgements

We would like to thank Brian Kinlan and Matt Poti for assistance on the predictive modeling section. Stephen Cairns kindly reviewed the taxonomy and coral distribution sections and co-authored the online annex. The chapter was strengthened by reviews from Sandra Brooke, Chip Collier, Martha Nizinski and Andrea Quattrini. Robert McGuinn developed the coral and sponge distribution and other maps for this chapter, and Heather Coleman provided editing assistance.

Online Annex – Comprehensive list of deep-sea corals in the U.S. Southeast region link: <https://deepseacoraldata.noaa.gov/library/2017-state-of-deep-sea-corals-report>

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[Online Annex 1. Deep-sea Coral Taxa in the U.S. Southeast Region: Depth and Geographic Distribution](#)



Appendix

Table A. Sites of major research expeditions (2007 – 2015) referenced in the chapter that included deep-sea coral and sponge research. (DSCRTP = NOAA Deep Sea Coral Research and Technology Program; OER = NOAA Ocean Exploration and Research; HBOI = Harbor Branch Oceanographic Institution; NIOZ = Royal Netherlands Institute for Sea Research; SEFSC = NMFS Southeast Fisheries Science Center; USF = University of South Florida).

#	Locations	Year	Vessel	Description	Program
1	Cape Lookout <i>Lophelia</i> Banks - off North Carolina	2009 2010	NOAA Ships <i>Nancy Foster</i> and <i>Cape Hatteras</i> ; R/V <i>Pelagia</i>	6 month deployment of benthic Lander in <i>Lophelia</i> habitats. PI: S.W. Ross Oceanographic and geological studies, including box and piston core samples	U. North Carolina-Wilmington; NIOZ
2	Off South Carolina	2007	NOAA Ship <i>Nancy Foster</i>	Multibeam and side-scan sonar surveys to map bottom-topography on shelf edge and upper slope coral mounds and other suspected areas of EFH on the outer continental shelf and upper slope of the South Atlantic Bight. PI: G. Sedberry	NOAA Ocean Exploration
3	Shelf-edge MPAs N. Carolina to Florida	2009	NOAA Ship <i>Pisces</i>	ROV survey. PI: A. David	NOAA NMFS and CIOERT
		2010	M/V <i>Spree</i>	ROV survey. PI: A. David	
		2012	NOAA Ship <i>Pisces</i>	ROV survey and multibeam mapping (261.0 km ²). PI: S. Harter	
		2013	NOAA Ship <i>Pisces</i>	ROV survey and multibeam mapping (686.9 km ²). PI: S. Harter	
		2014	NOAA Ship <i>Nancy Foster</i>	ROV survey and multibeam mapping (542.6 km ²). PI: S. Harter	
		2015	NOAA Ship <i>Pisces</i>	ROV survey. PI: S. Harter	
4	Off Georgia and NE Florida	2010	NOAA Ship <i>Pisces</i>	ROV Surveys PI: G. Sedberry	DSCRTP
		2014	NOAA Ship <i>Okeanos Explorer</i>	Multibeam mapping of priority deepwater habitats	OER
5	Jacksonville Lithoherms, Daytona	2011	NOAA Ship <i>Pisces</i>	ROV survey and multibeam mapping (112 km ²). PI: J. Reed	DSCRTP
		2010	NOAA Ship <i>Ronald H. Brown</i>	ROV and multibeam surveys. 1575 km ² mapped. . PIs SW Ross, S Brooke	DSCRTP
6	Off SE Florida	2009	NOAA Ship <i>Nancy Foster</i>	Multibeam mapping of priority deepwater habitats within the Deepwater Coral HAPC. 580 km ² mapped. PI: B. Costa	DSCRTP
		2014	NOAA Ship <i>Okeanos Explorer</i>	Multibeam mapping of priority deepwater habitats	OER

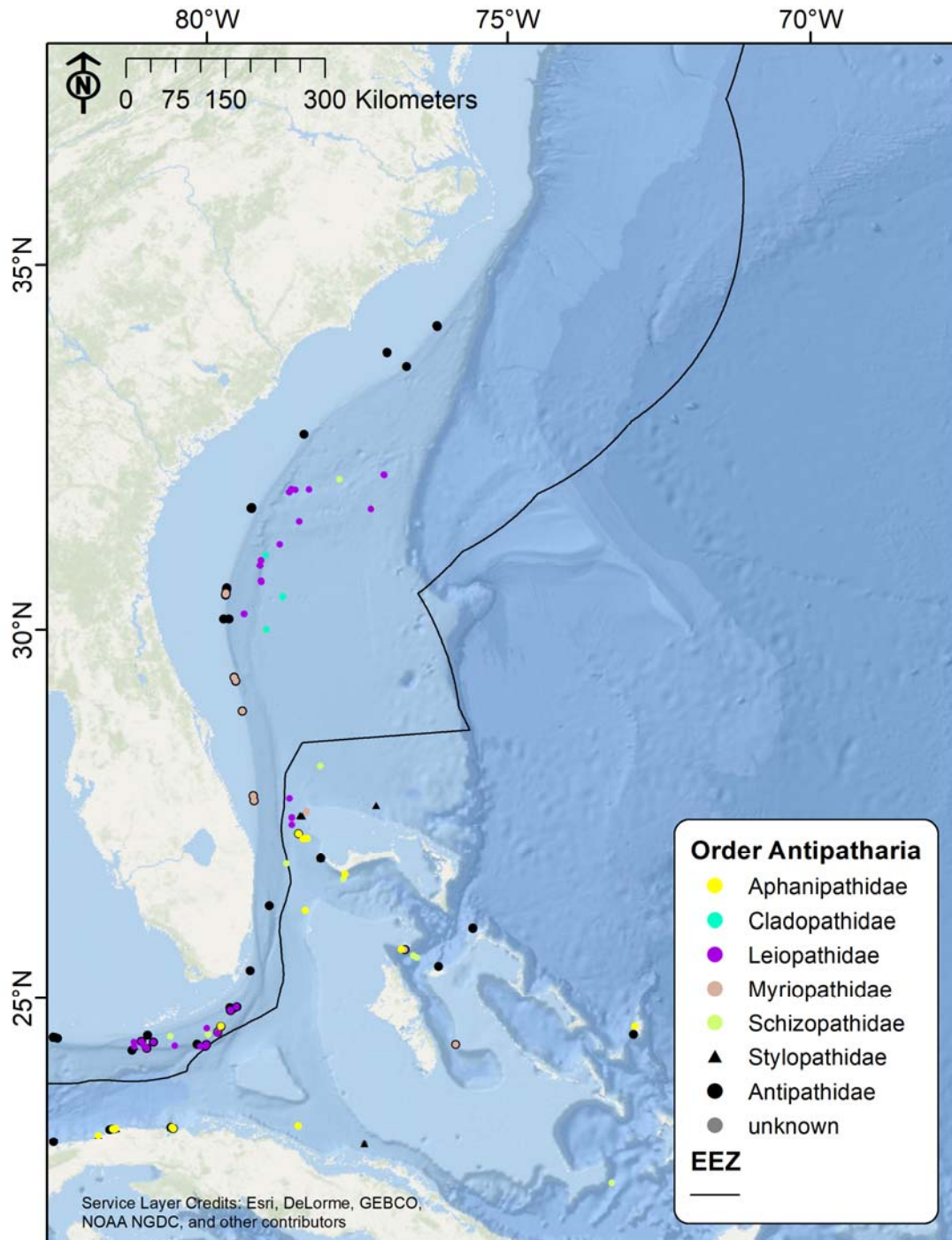
STATE OF THE DEEP-SEA CORAL AND SPONGE ECOSYSTEMS OF THE SOUTHEAST UNITED STATES



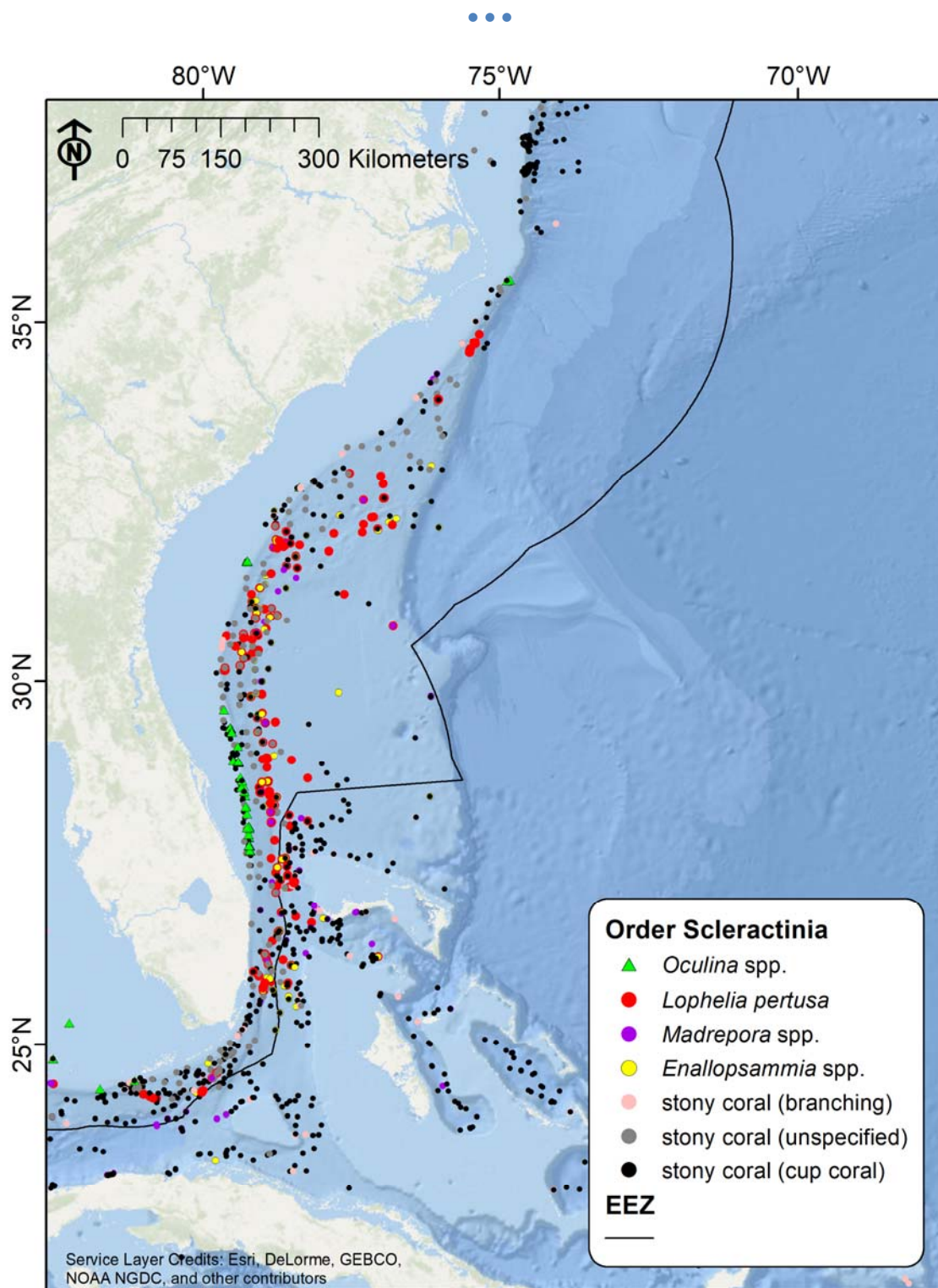
#	Locations	Year	Vessel	Description	Program
7	Off SE Florida, Canaveral Bioherms	2007	R/V Seward Johnson	Fort Pierce and St. Lucie Pinnacles Submersible dives. PI: J. Reed	HBOI
		2009	R/V Seward Johnson	<i>Life on the Edge Expedition</i> . 22 Submersible dives. PI: S.W. Ross http://fl.biology.usgs.gov/DISCOVRE/discovre_2009_index.html	DSCRTP, CIOERT, USGS
		2010	NOAA Ship Ron Brown	ROV and multibeam surveys. 1575 km ² mapped. PI: S.W. Ross, S. Brooke http://cioert.org/	DSCRTP
		2011	NOAA Ship Pisces	ROV surveys and some multibeam mapping (112 km ²)	DSCRTP
8	Oculina Mounds, Oculina HAPC	2010	R/V Lost Coast Explorer	Multibeam surveys – 7460 km ² mapped. PI: D. Naar	DSCRTP, USF
9	Off SE Florida Miami Terrace and Florida Straits,	2007	R/V Seward Johnson	Submersible dives. PIs: C Messing, J. Reed, S Brooke	HBOI/OER
10	Florida Straits, Pourtales Terrace	2007	R/V Seward Johnson	Submersible dives. PI: J. Reed	HBOI/OER
		2010	NOAA Ship Ron Brown	ROV and multibeam surveys. PIs: S.W. Ross, S. Brooke	DSCRTP
		2011	NOAA Ship Nancy Foster	ROV and multibeam surveys. 373 km ² mapped. PI John Reed	DSCRTP



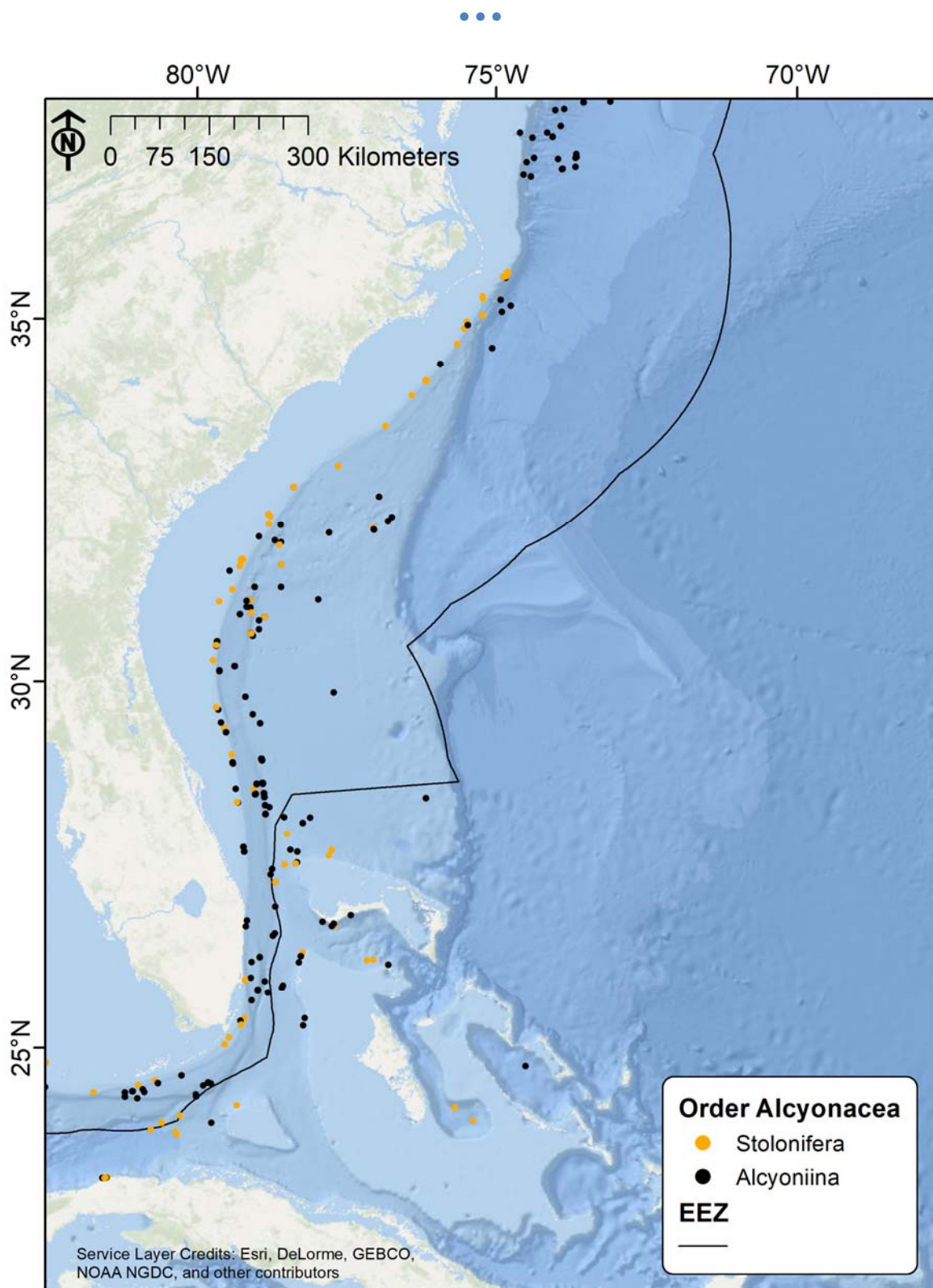
Appendix – Deep-Sea Coral and Sponge Distribution Maps



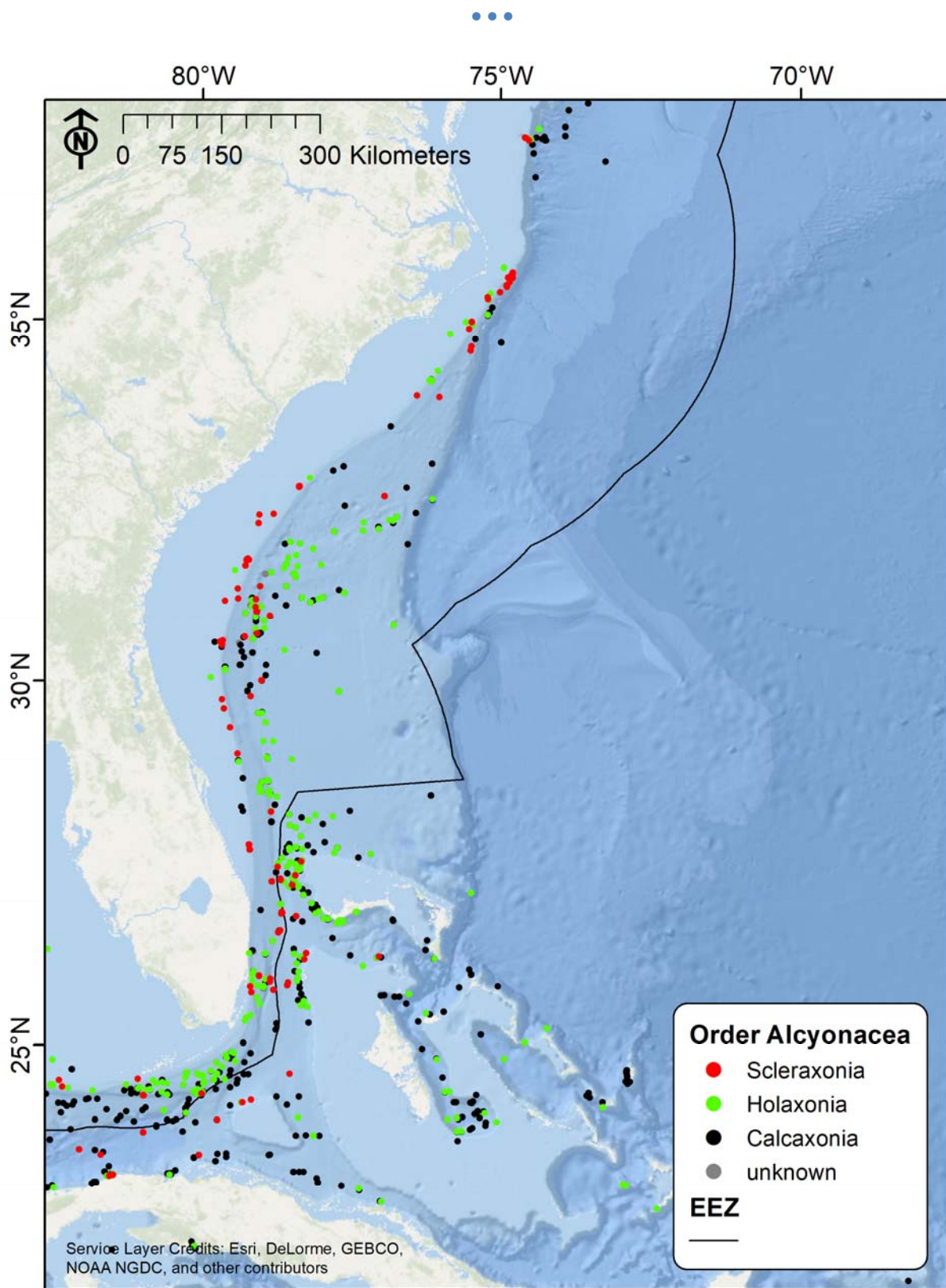
Map 1. Locations of deepwater (> 50 m deep) black corals (Order Antipatharia) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



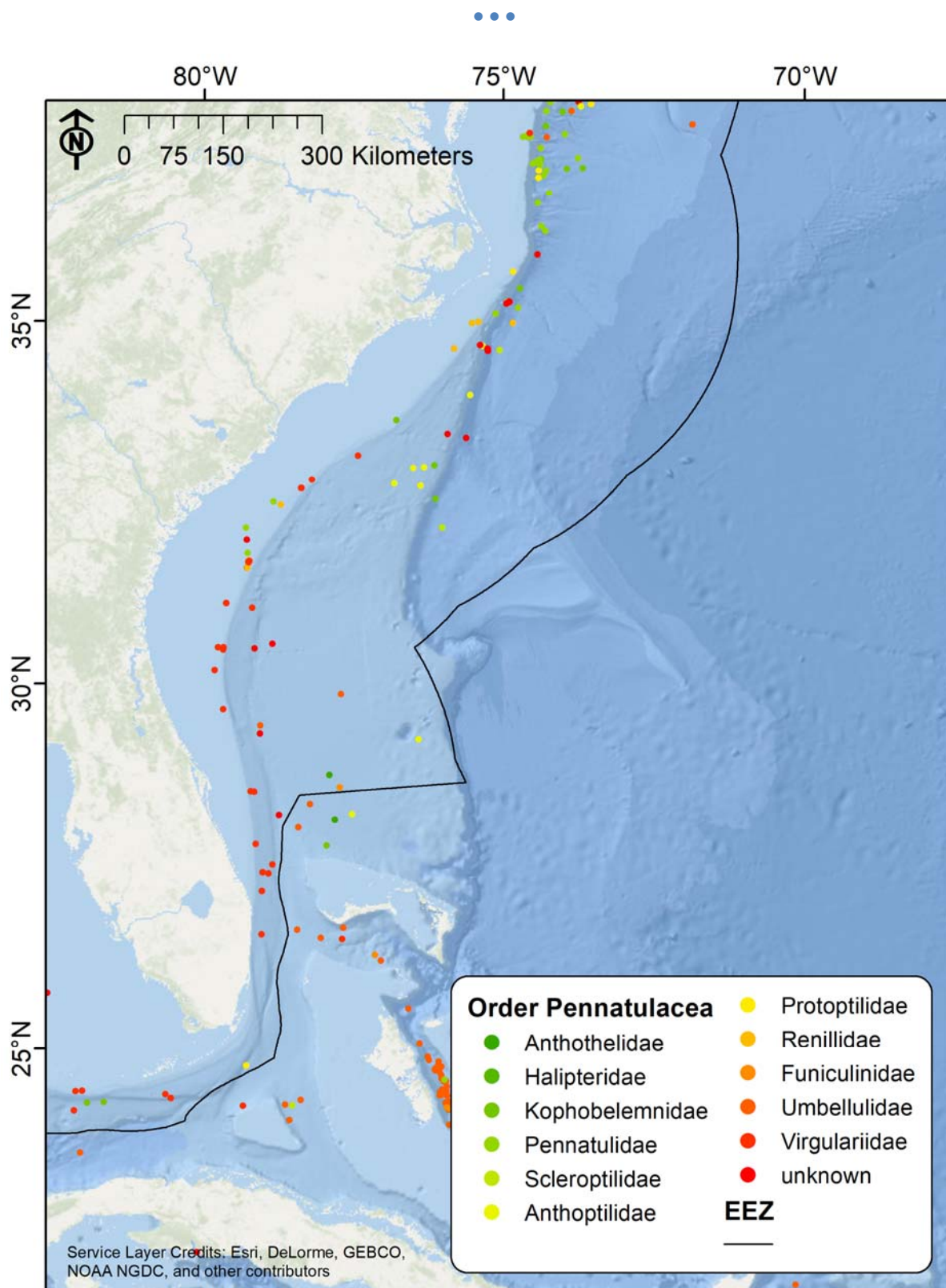
Map 2. Locations of deepwater azooxanthellate stony corals (Order Scleractinia) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017). Lophelia pertusa, Oculina varicosa, and Enallopsammia spp. are the major framework forming species, with contributions from Madrepora spp.



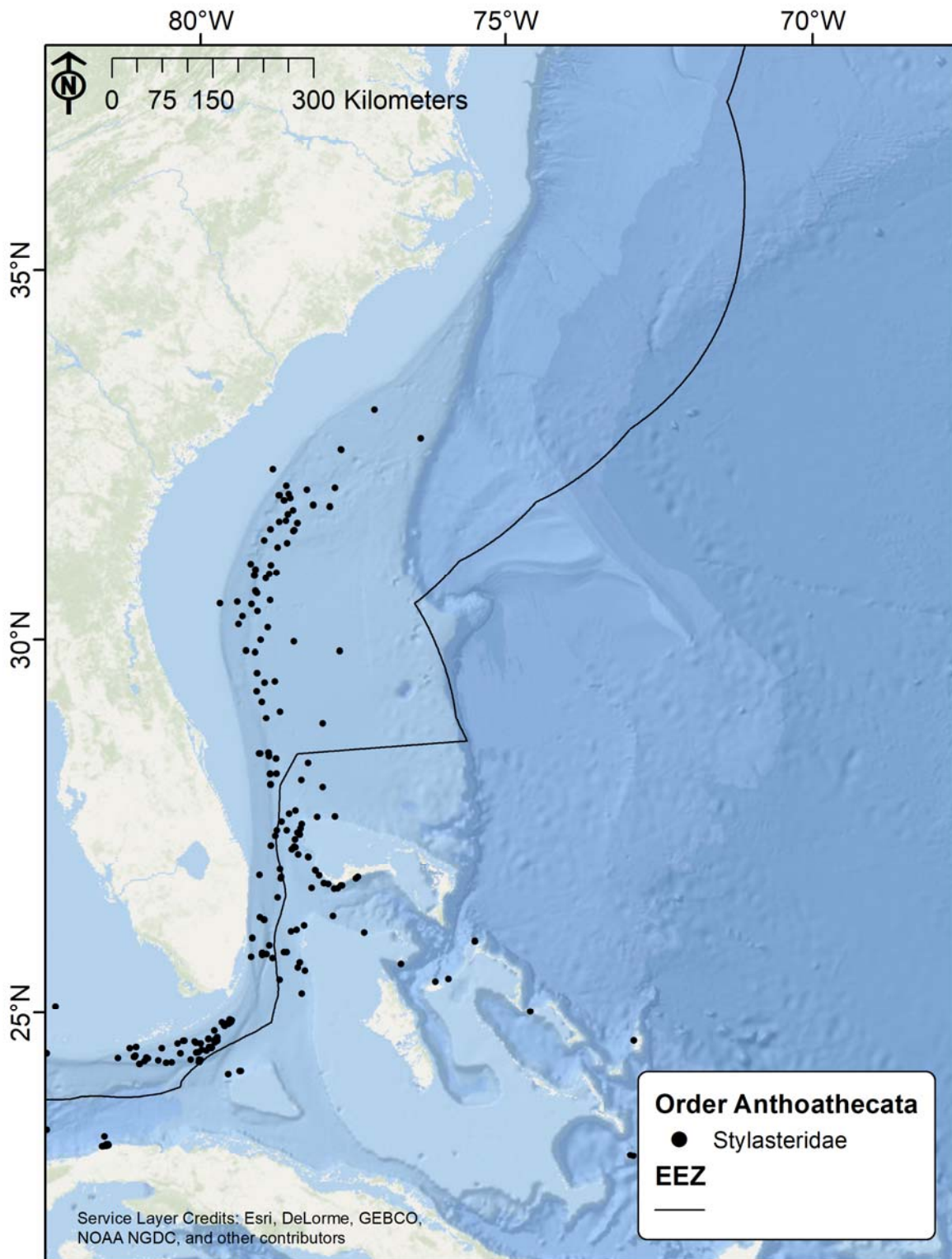
Map 3. Locations of deepwater non-gorgonian alcyonacean corals (Order Alcyonacea) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



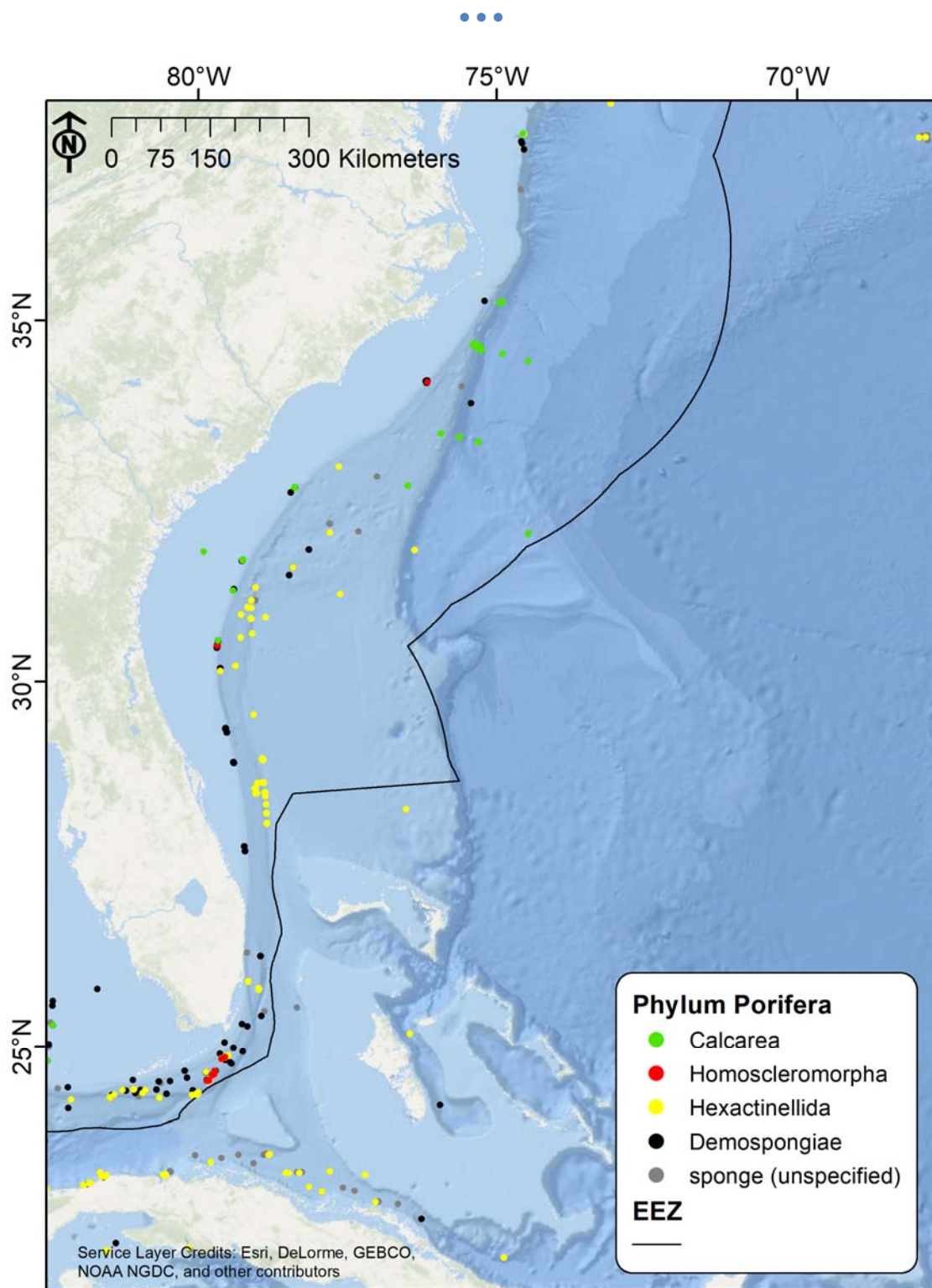
Map 4. Locations of deepwater gorgonians (Order Alcyonacea in part [formerly Gorgonacea]) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



Map 5. Locations of deepwater sea pens (Order Pennatulacea) recorded in the National Deep-Sea Coral and Sponge (as of November 2017).



Map 6. Locations of deepwater lace corals (Family Stylasteridae) recorded in the National Deep-Sea Coral and Sponge Database (as of November 2017).



Map 7. Locations of deepwater sponges recorded in the National Deep-Sea Coral and Sponge Database (as of June 2016). Although sponges are widespread throughout the region, observations have not been systematically recorded and organized, so records in the database are currently limited.