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OCEANOGRAPHY AND CETACEANS OF THE COSTA RICA DOME REGION

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U.S. DEPARTMENT OF COMMERCE
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Abstract

A seasonally predictable, strong, and shallow thermocline makes the Costa Rica Dome a distinct biological habitat where phytoplankton and zooplankton biomass are higher than in surrounding waters in the eastern tropical North Pacific. We constructed seasonal climatologies of oceanographic variables (sea surface temperature and salinity, mixed layer depth, thermocline depth and strength, a stratification index, surface winds and currents, and upwelling) from a composite of ocean reanalysis data sets, plus two primary production variables (surface chlorophyll and net primary productivity). The results confirm a previous study of the annual cycle based on shipboard oceanographic observations. Based on ten SWFSC cetacean and ecosystem surveys of the eastern tropical Pacific during 1986-2006, we estimated spatial distributions of the encounter rate of commonly encountered cetaceans with generalized additive models that relate observed sightings to environmental variables. Among the 21 cetacean species and subspecies present in the Costa Rica Dome region, three show a clear association with the Dome and 14 have distributions that extend into the Dome. The Costa Rica Dome is a regional center of high productivity and likely supports high prey availability for cetacean predators both within the Dome and in surrounding waters. The eastern Pacific warm pool to the northwest of the Dome and the productive equatorial waters to the south are also important regional habitats for cetaceans.

Introduction

The Costa Rica Dome, located off the coast of Central America, is a shoaling of the generally strong and shallow thermocline of the eastern tropical Pacific Ocean. It is a site of enhanced productivity due to near-surface nutrient availability (Sasai et al., 2007) and is known as a biological hotspot (Palacios et al., 2006). The Costa Rica Dome is similar to other tropical thermocline domes in several respects: it is part of an east–west thermocline ridge associated with the equatorial circulation, surface currents flow cyclonically around it, and its seasonal evolution is affected by large-scale wind patterns. The Costa Rica Dome is unique because it is also forced by a coastal wind jet. It was first observed in 1948 (Wyrtki, 1964) and first described by Cromwell (1958). The Dome has been observed and studied several times since the late 1950s, when a productive tuna fishery began to develop in the region, but has been sampled intensively only a few times. Fiedler (2002) reviewed the structure and seasonal cycle of the Dome using historical shipboard observations. For the first part of this review, we use ocean reanalysis data to construct an updated and more complete picture of the spatial structure and temporal variability of the Dome and the surrounding region. For the second part, we use species distribution models to describe relationships between abundant cetacean species and the Costa Rica Dome.

The eastern tropical Pacific Ocean (ETP), including the Costa Rica Dome, supports a diverse assemblage of cetaceans. Cetaceans are ecologically important predators that feed at a range of trophic levels (Ballance et al, 2006). Many species are apex predators, meaning that they feed closer to the top of the food chain than the bottom. Cetaceans are also ‘‘K-selected’’ species: they are relatively long-lived, have delayed reproductive maturity, and low reproductive output. This suite of life history traits generally buffers species from environmental perturbation compared to those with shorter lives and higher reproductive output (‘‘r-selected species’’).

An important ecological feature of the ETP is the ‘‘tuna-dolphin-seabird assemblage’’, a multi-species feeding association between yellowfin tuna, spotted and spinner dolphins, and a relatively large number of seabird species (Ballance et al., 2006). The dolphins in this assemblage are often in mixed-species schools. The tunas and dolphins are accompanied by flocks of seabirds which feed on prey made available at the surface by the subsurface predators. The tunas, due to their large size, near-surface occurrence, and visibility through their association with air-breathing cetaceans and seabirds, form the basis for one of the world's largest yellowfin tuna fisheries (Perrin, 1969; Gosliner, 1999). Although these tuna, dolphins, and many of the seabirds are found throughout tropical oceans of the world, their association is rare in other regions. In general, the ETP supports a diverse and abundant community of seabirds and cetaceans relative to other tropical oceans.

The Marine Mammal and Turtle Division at NOAA Fisheries' Southwest Fisheries Science Center conducted 10 cetacean and ecosystem assessment surveys in the ETP, including the Costa Rica Dome region, between 1986 and 2006. The purpose of these surveys was to assess the status of dolphin stocks that are incidentally caught by the yellowfin tuna purse-seine fishery. These surveys were conducted during the months of August-November, corresponding to the season of the most intense development of Costa Rica Dome. Line-transect methods were used to collect cetacean data during daylight hours for a total of 302,381 km of search effort in the larger ETP study area (for details about the data collection methodology, see Kinzey et al., 2000). These data are collected systematically: transects are randomly placed (given the logistical constraints of ship travel) within strata defined by the geographic distribution of the dolphin populations of interest and observers record search effort, sighting conditions, and sightings. The ETP is one of the most intensively surveyed areas for marine mammals in the world, in large part because of the SWFSC surveys (Kaschner et al., 2012).

Basic ETP Oceanography

The Costa Rica Dome is an important oceanographic feature of the ETP, a tropical ocean region with distinctive oceanographic characteristics (Fiedler and Lavín, 2016). The ETP lies between the subtropical gyres of the North and South Pacific and encompasses both the eastern terminus of the equatorial current system of the Pacific and the eastern Pacific warm pool. Figure 1 summarizes the basic oceanographic patterns of the ETP. The structure and variability of water masses and circulation are determined by solar and atmospheric processes, both within and outside of the region. In a physical-biological or ecological sense, it is part of the low-latitude Trades Biome influenced by easterly trade winds and by east-west equatorial current systems (Longhurst, 2007).

The eastern Pacific warm pool (*1* in Figure 1a) forms half of the western hemisphere warm pool straddling Central America (Wang and Enfield, 2001). The warm pool is part of the warm, low-salinity Tropical Surface Water mass (*3* in Figure 1b). Surface salinity is lowest in the Gulf of Panama, due to high rainfall and river runoff (Amador et al., 2006). In contrast to higher latitudes, wind mixing is relatively weak and net heat flux is into the ocean or near zero year-round; surface waters never lose a significant amount of heat to the atmosphere. As a result, ETP surface waters are highly stratified, meaning that a strong vertical temperature gradient, the thermocline, is always present at shallow depths. The Tropical Surface Water mass in particular is highly stratified, with a shallow thermocline (Figure 1c), which results in a shallow oxygen minimum layer (Fiedler and Talley 2006).

The Costa Rica Dome is a regional high point in the ETP permanent thermocline, located at the end of a countercurrent thermocline ridge that extends to the central Pacific (Fiedler, 2002). The Dome is a site of moderate oceanic upwelling and enhanced productivity. The top of the thermocline is about 15m deep at the Dome, compared to 30–40m to the north and south. The North Equatorial Countercurrent flows eastward along the equatorward side of this ridge, the Costa Rica Coastal Current flows poleward during summer between the Dome and the coast, and the North Equatorial Current flows westward along the poleward side of the Dome and ridge. Surface winds and currents in the region change seasonally as the intertropical convergence zone (ITCZ) between the trade wind belts moves north and south with the sun. The relative strengths of the northeast and southeast trade winds vary considerably during the year. Winter high pressure systems over the Gulf of Mexico and Caribbean Sea force strong winds through low altitude passes in the mountainous backbone of southern Mexico and Central America. Intense and narrow wind jets blow offshore at the Gulfs of Tehuantepec, Papagayo, and Panama (Figure 2). In summer, the southeast trade winds (*9* in Figure 1e) blow strongly across the equator as far as 8°N.

Important features on the periphery of the Costa Rica Dome region include the equatorial cold tongue (*2* in Figure 1a), which is cool, moderate-salinity water overlying an equatorial thermocline ridge resulting from equatorial upwelling (the red band in Figure 1f). The equatorial front is the northern boundary of the equatorial cold tongue. Cold, low-salinity eastern boundary currents, the California and Peru Currents, flow into the ETP along the coasts of North and South

America. These currents are the eastern, equatorward segments of the North and South Pacific subtropical gyres. The subtropical gyres encompass warm, high-salinity Subtropical Surface Water masses (*4* in Figure 1b). Productivity is enhanced seasonally in the regions of coastal and oceanic upwelling: the eastern boundary currents, the equatorial cold tongue, and the Costa Rica Dome (Figure 1d).

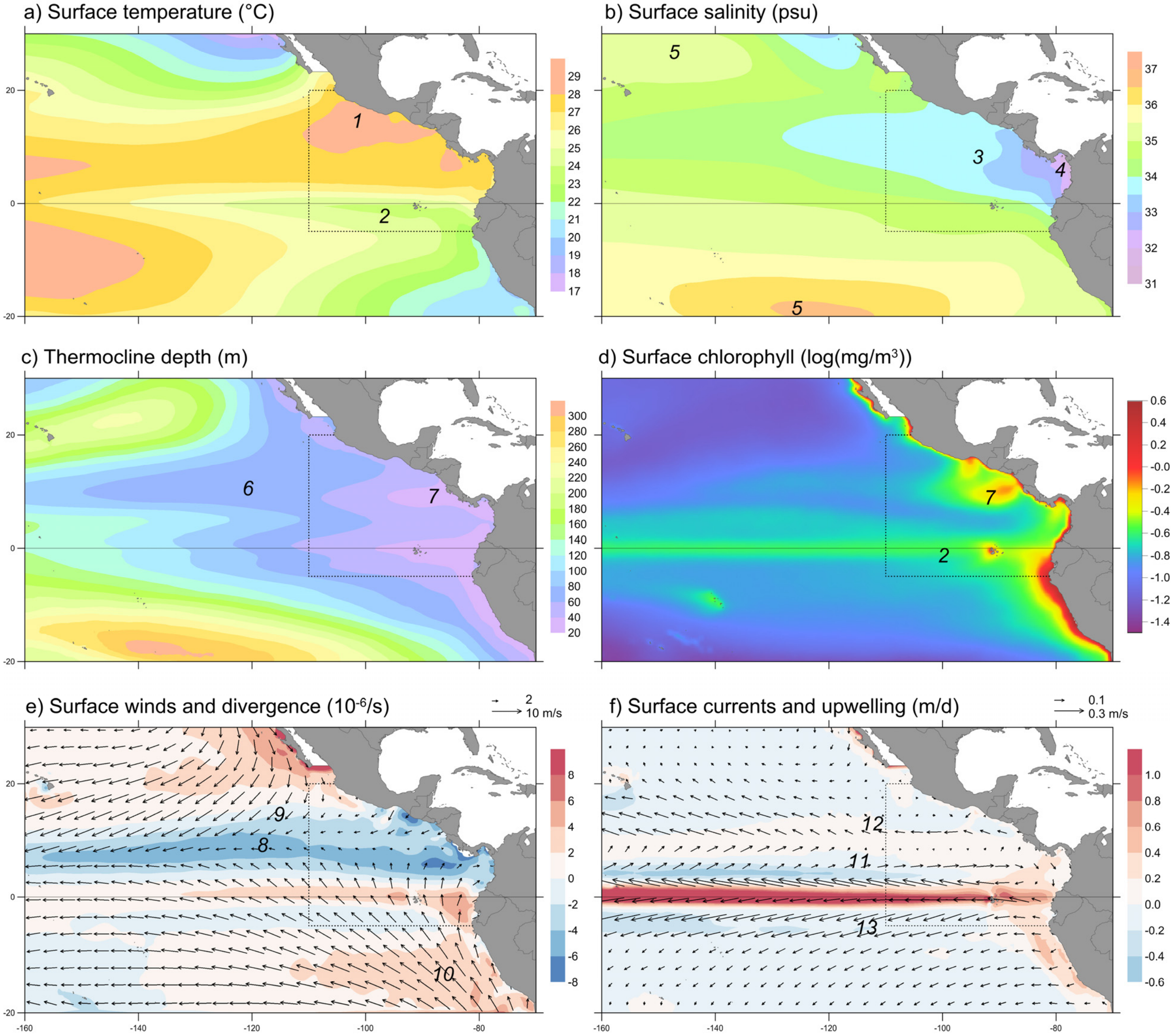


Figure 1. Mean climatological maps (1980-2015) of variables (ranges in parentheses) illustrating the basic oceanography of the eastern tropical Pacific. *1*) eastern Pacific warm pool, *2*) equatorial cold tongue, *3*) Tropical Surface Water mass, *4*) Gulf of Panama, *5*) Subtropical Surface Water masses, *6*) countercurrent thermocline ridge, *7*) Costa Rica Dome, *8*) Intertropical Convergence

Zone, *9*) northeast trade winds, *10*) southeast trade winds, *11*) North Equatorial Countercurrent, *12*) North Equatorial Current, *13*) South Equatorial Current. Dotted line indicates the Costa Rica Dome region covered in Figures 5-8. Data sources in Methods.

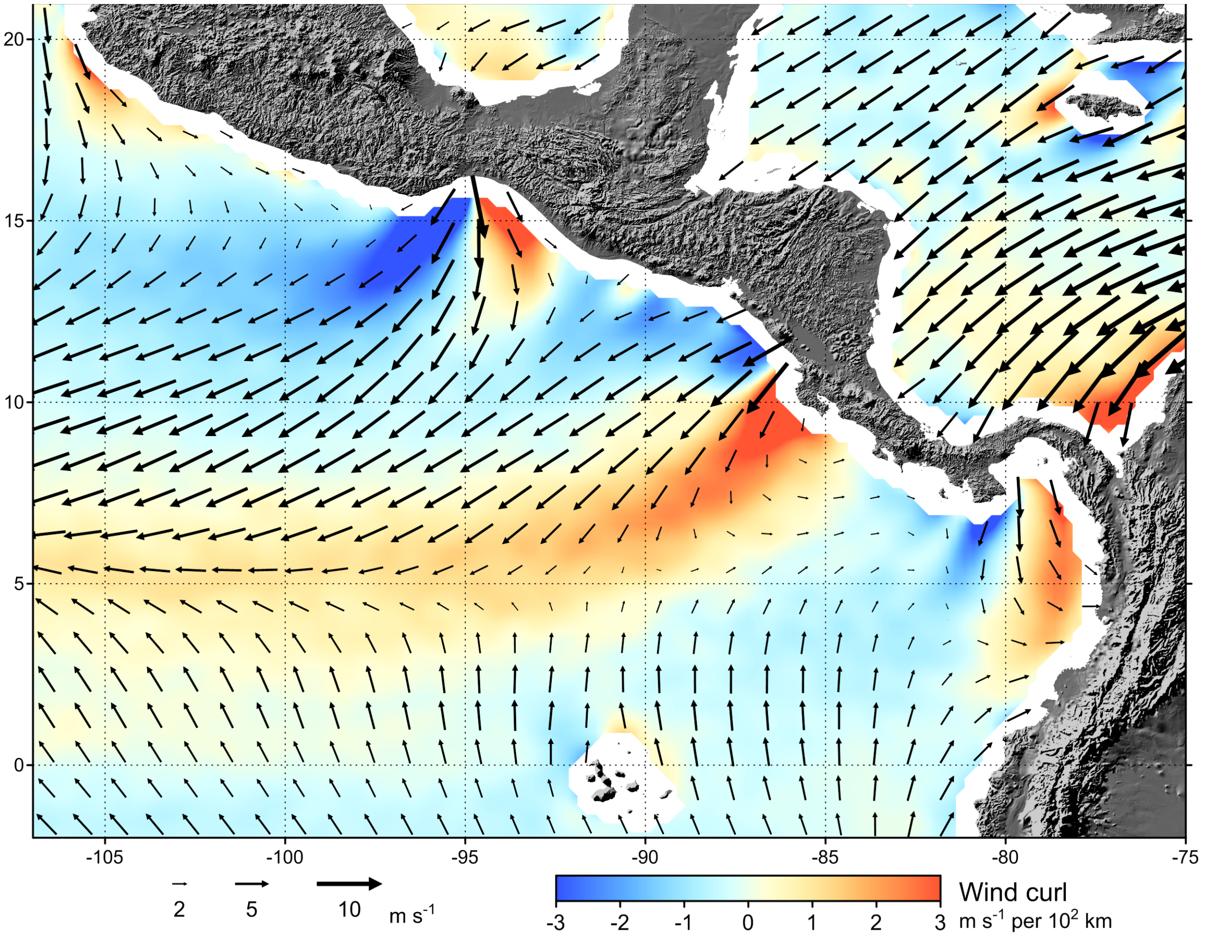


Figure 2. January climatology (1999–2009) of surface winds (vectors) and curl (vorticity or rotation of winds, colors). Three prominent wind jets at narrow, low points of Central America are Tehuantepec (~95°W), Papagayo (~11°N), and Panama (~79°W). Paired centers of anticyclonic (negative) and cyclonic (positive) wind curl are associated with each of these jets. Data from Risien and Chelton (2008; http://cioss.coas.oregonstate.edu/scow)

Fiedler (2002) used shipboard oceanographic observations to describe the annual cycle of the Costa Rica Dome (Table 1). This cycle of wind-forced development and maturation of the Dome, using the new data described below, is illustrated in Figure 3. Based on examination of monthly climatologies of regional oceanographic variables, we decided that two seasons would capture the basic character of seasonality of doming and related variables influencing the Costa Rica Dome Ecosystem: February-April and August-November. The August-November season corresponds to the period when SWFSC conducted ten cetacean and ecosystem surveys in the ETP between 1986 and 2006.

Table 1. Annual cycle of the Costa Rica Dome, summarized from Fiedler (2002).

January	Dome is weak under strong NE trade winds.
February - April	Thermocline shoals near the coast under the Papagayo wind jet.
May - June	Dome separates from the coast as wind jet weakens.
July - November	Dome intensifies as the countercurrent thermocline ridge shoals due to cyclonic wind stress curl in the ITCZ.
December	Dome weakens as ITCZ moves south and wind jet strengthens.

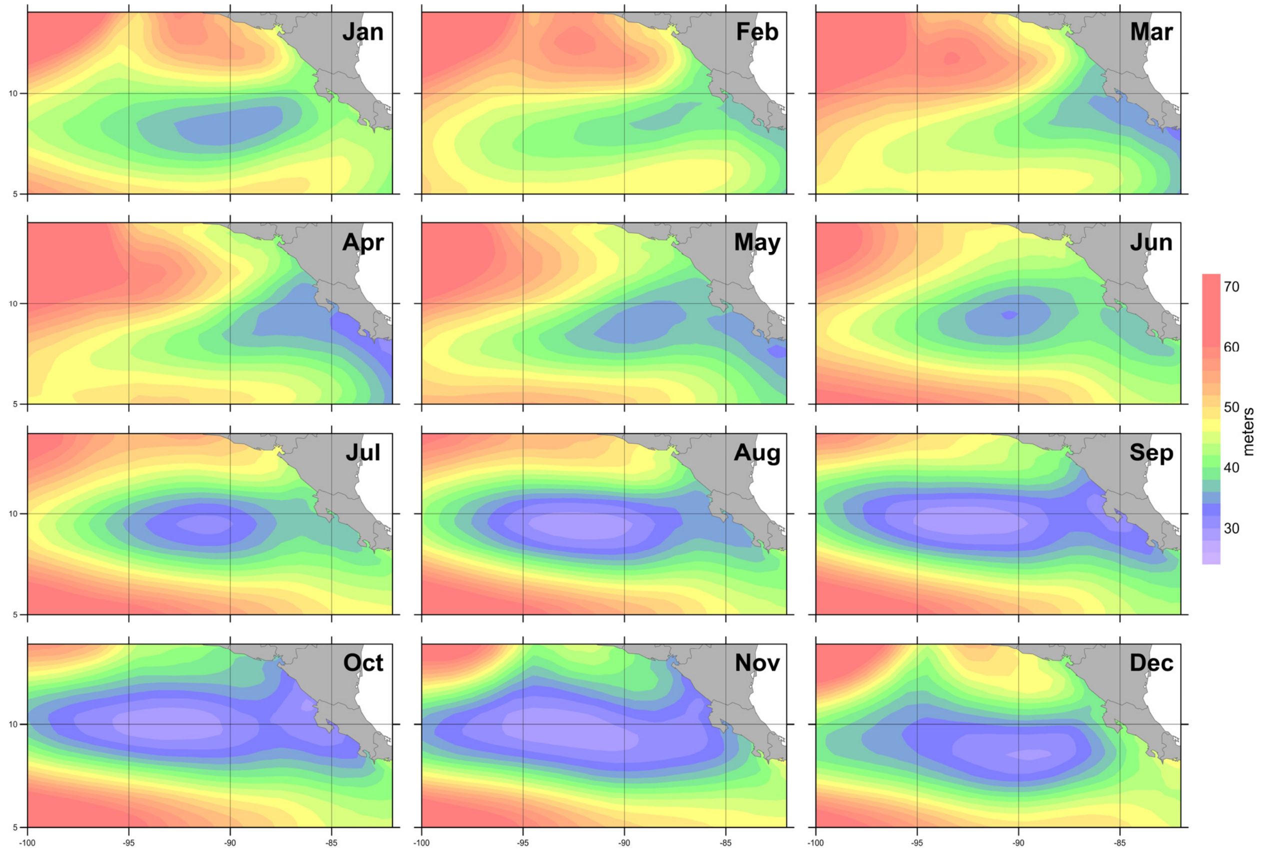


Figure 3. Monthly thermocline depth maps illustrating the seasonal cycle of the Costa Rica Dome. Cooler, nutrient-rich water is closer to the surface when the thermocline shoals during July-November.

Methods - Oceanography

We have compiled a set of oceanographic data based on six ocean reanalysis datasets (1980-2015, Table 2). An ocean reanalysis combines oceanographic observations with a three-dimensional ocean model to produce estimates of variables describing the changing state of the ocean in time and space; the observations correct biases in the model, while the model fills in gaps between observations. Each of the monthly reanalysis data fields (temperature, salinity, current velocity) or surface grids (sea surface height, wind velocity) was spline-interpolated onto 0.25-degree longitude-latitude grids in order to accommodate the different horizontal resolutions and locations. Data fields were also interpolated at depths of 0, 5, 10, 20, 30,…500 m for a similar reason. The interpolations of the six reanalysis datasets were then averaged to produce a composite. Variables derived from the reanalysis data – mixed layer depth, thermocline depth and strength, stratification, wind divergence, wind stress curl, upwelling – were derived from the reanalysis composite field averages.

Table 2. Ocean reanalysis data sets used to derive monthly predictor variables. Resolution is longitude x latitude.

	Resolution	
ECDA v3.1	1° x 0.33°	Ensemble Coupled Data Assimilation www.gfdl.noaa.gov/ocean-data-assimilation/ (Chang et al., 2013)
ESTOC v02c	1° x 1°	Estimated Ocean State for Climate Research www.godac.jamstec.go.jp/estoc/e/ (Osafune et al., 2015)
GECCO2 v34_55	1° x 1°	German contribution of the Estimating the Circulation and Climate of the Ocean project icdc.zmaw.de/1/daten/reanalysis-ocean/gecco2 (Köhl 2015)
GODAS	1° x 0.33°	Global Ocean Data Assimilation System www.cpc.ncep.noaa.gov/products/GODAS (Saha et al., 2006)
ORAS4	1° x 1°	Ocean Reanalysis System 4 ecmwf.int/en/research/climate-reanalysis/ocean-reanalysis (Balmaseda et al., 2013)
SODA 3.3.1	0.5° x 0.5°	Simple Ocean Data Assimilation apdrc.soest.hawaii.edu/data/ (Carton and Giese, 2008)

The oceanographic variables derived from the composites of the ocean reanalyses are:

1) sea surface temperature (°C),
2) sea surface salinity (pss),
3) mixed layer depth (m),
4) thermocline depth (m),
5) thermocline strength (°C $10m^{-1}$),
6) stratification index (°C),
7) surface wind speed and surface wind vectors (m s^{-1}),
8) wind divergence (10^{-6}/s),
9) wind stress curl (10^{-7} N m^{-3}),
10) surface current vectors (m s^{-1}), and
11) upwelling at 40m depth (m d^{-1}).

Mixed layer depth is the depth at which temperature is 0.5°C less than sea surface temperature. The thermocline was defined as the depth interval that included the upper decile (10%) of 1m temperature gradients in the composite 0-300m depth profile of temperature. Thermocline strength is the mean of this set of 1m gradients. Thermocline depth is the weighted mean of the depths of this set, with each depth weighted by the value of the 1m temperature gradient. Stratification index is the standard deviation of temperature in the near-surface layer, 0 - 300m (Fiedler 2010).

For primary production variables, we used monthly ocean color satellite data from two sources: surface chlorophyll, an index of phytoplankton biomass (1998-2016, GlobColour data (http://globcolour.info) developed, validated, and distributed by ACRI-ST, France) and net primary productivity (2003-2015, standard VGPM product from http://www.science.oregonstate.edu/ocean.productivity/).

The primary production variables are:

(12) surface chlorophyll (mg m^{-3}), and
(13) net primary productivity (mg C m^{-2} d^{-1}).

Methods – Cetaceans

Most species distribution models relate observations of species presence or abundance to environmental variables corresponding to the observations. The model then uses environmental variables to predict species distributions in space or time. We built species distribution models using the entire SWFSC data set that covers the larger study area in the ETP, excluding the Gulf of California. The Costa Rica Dome region is part of the core area of these surveys, where survey effort was concentrated. There are a variety of methods used to construct maps of species distributions from environmental variables and observed species presences; some methods also use information about species absences. We used generalized additive models (GAM), a powerful alternative among regression techniques that are most commonly used for modeling cetacean-habitat relationships (Redfern et al., 2006), to relate the number of sightings in each of n=2087 survey days to the environmental variables.

We divided the cetacean line-transect data into continuous-effort segments of approximately 10 km as described by Becker et al. (2010). Our dependent variable was the number of sightings for each species; typically, a sighting represents a school comprised of multiple individuals, although large whales are often sighted as single individuals. For predictor variables, we used the ocean reanalysis estimates of four dynamic environmental variables: surface temperature, surface salinity, thermocline depth, and stratification. A fifth environmental variable, distance to coast (excluding islands $<10^4$ km^2) was included to account for fixed geographic effects that are not related to the dynamic oceanographic variables. We added latitude as a predictor variable because it improved predictions for north temperate species such as Baird's beaked whale and for seasonal migrants such as humpback whales. Segment sightings were summed and the segment environmental variables were averaged by day, so that the sampling unit was a full day of survey effort (mean = 141 km). This spatial resolution has been found to be relevant to cetaceans in the ETP (Reilly 1990, Fiedler and Reilly 1994, Reilly and Fiedler 1994).

We fit Poisson GAMs, in which overdispersion was corrected with a quasi-likelihood model, using the R (version 3.4.0; R Core Team, 2017) package mgcv (version 1.8-4; Wood, 2011). The distance traveled on effort was an offset in the models because daily effort ranges between 0.3 and 273.2 km. Smoothing parameter estimation by penalized regression splines was allowed to completely remove terms. We set the gamma parameter to 1.4 (Wood, 2006) and allowed a maximum of two degrees of freedom for each spline to capture non-linear relationships but limit over-fitting.

We used the models to predict the number of sightings, per 1000 km of survey effort, from the oceanographic data. This predicted value is an encounter rate of sightings, but we show below that it represents the density of individuals. Specifically, we made predictions for each year of survey data using the yearly oceanographic grids for the August-November survey season, in each cell of the 0.25 x 0.25 degree grid of the study area. We summarized the expected number of sightings for each species throughout the study area by calculating the average of the ten annual predictions (1986-1990, 1998-2000, 2003, 2006). The annual predictions do not account for within-year variation in species distributions; the averages represent expected long-term patterns in the number of sightings between August and November.

Model performance is summarized in Table 3; we consider that models with deviance explained <10% have insufficient explanatory power to give useful predictions of spatial distribution; predictions for these species and the seven species that were never sighted in the Dome regions, are not considered further. Successful models (deviance explained >10%) also had AUC values > 0.7 (except for short-finned pilot whale) and relatively high correlations with observed sightings (COR).

Table 3. Cetacean species in the SWFSC data set modeled to predict spatial distribution. N = total number of sightings; Prevalence = the fraction of survey days on which the species was sighted; % Dev. = deviance explained, a measure of the observed variability in the number of sightings accounted for by the model; AUC = area under the receiver operating characteristic curve, a measure of the overall ability of the model to discriminate observed presence/absence; COR = correlation between observed sightings and predicted number of sightings.

Species	N	Preva-lence	% Dev.	AUC	COR
Offshore spotted dolphin, *Stenella attenuata*	1368	0.655	22.2	0.790	0.494
Eastern spinner dolphin, *Stenella longirostris orientalis*	601	0.288	48.1	0.921	0.740
Striped dolphin, *Stenella coeruleoalba*	1626	0.779	11.2	0.704	0.326
Short-beaked common dolphin, *Delphinus delphis*	690	0.331	32.3	0.869	0.535
Bottlenose dolphin, *Tursiops truncatus*	986	0.472	30.0	0.865	0.570
Risso's dolphin, *Grampus griseus*	405	0.194	10.5	0.716	0.319
Coastal spotted dolphin, *Stenella attenuata graffmani*	227	0.109	72.4	0.991	0.719
Rough-toothed dolphin, *Steno bredanensis*	329	0.158	17.4	0.821	0.529
Pygmy killer whale, *Feresa attenuata*	51	0.024	15.3	0.833	0.169
Melon-headed whale, *Peponocephala electra*	19	0.009	16.7	0.766	0.093
Short-finned pilot whale, *Globicephala macrorhynchus*	461	0.221	12.3	0.586	0.124
Dwarf sperm whale, *Kogia sima*	177	0.085	11.8	0.831	0.498
Pygmy beaked whale, *Mesoplodon peruvianus*	39	0.019	22.1	0.899	0.331
Blaineville's beaked whale, *Mesoplodon densirostris*	18	0.009	19.2	0.785	0.105
Blue whale, *Balaenoptera musculus*	143	0.069	31.6	0.894	0.560
Humpback whale, *Megaptera novaeangliae*	44	0.021	52.7	0.967	0.666
Unsuccessful models:					
False killer whale, *Pseudorca crassidens*	75	0.036	5.9	0.592	0.072
Killer whale, *Orcinus orca*	131	0.063	1.6	0.537	0.030
Sperm whale, *Physeter macrocephalus*	220	0.105	7.1	0.629	0.171
Cuvier's beaked whale, *Ziphius cavirostris*	170	0.081	4.2	0.620	0.120
Bryde's whale, *Balaenoptera edeni*	355	0.170	9.0	0.536	0.015
Not sighted in Dome region:					
Long-beaked common dolphin, *Delphinus capensis*	67	0.032	82.8	0.995	0.613
Fraser's dolphin, *Lagenodelphis hosei*	32	0.015	34.0	0.829	0.169
Pacific white-sided dolphin, *Lagenorhynchus obliquidens*	27	0.013	80.4	0.999	0.853
Other spinner dolphins (whitebelly, southwestern, Gray's), *Stenella longirostris subsp.*	326	0.156	33.2	0.751	0.374
Pygmy sperm whale, *Kogia breviceps*	10	0.005	57.7	0.982	0.378
Baird's beaked whale, *Berardius bairdii*	12	0.006	100.0	0.998	0.053
Fin whale, *Balaenoptera physalus*	6	0.003	56.7	0.963	0.336

We used number of sightings (per 1000 km of survey effort) as an index of the abundance or density of each species. The surveys also estimated group size for each sighting, but this variable must be modeled independently of the number of sightings for species with large group sizes. The model predictions of number of sightings represent the number of individuals very well for most species (Figure 4). Among the successful species models, between 50% and 100% of the number of individuals sighted (vertical axis) occur in the 20% of cells with the highest predicted number of sightings (0.2 on the horizontal axis). The only exceptions are striped dolphins (50% of sighted individuals in 23% of cells), which is the most common or prevalent species in our data set, and short-finned pilot whales (50% of sighted individuals in 27% of cells).

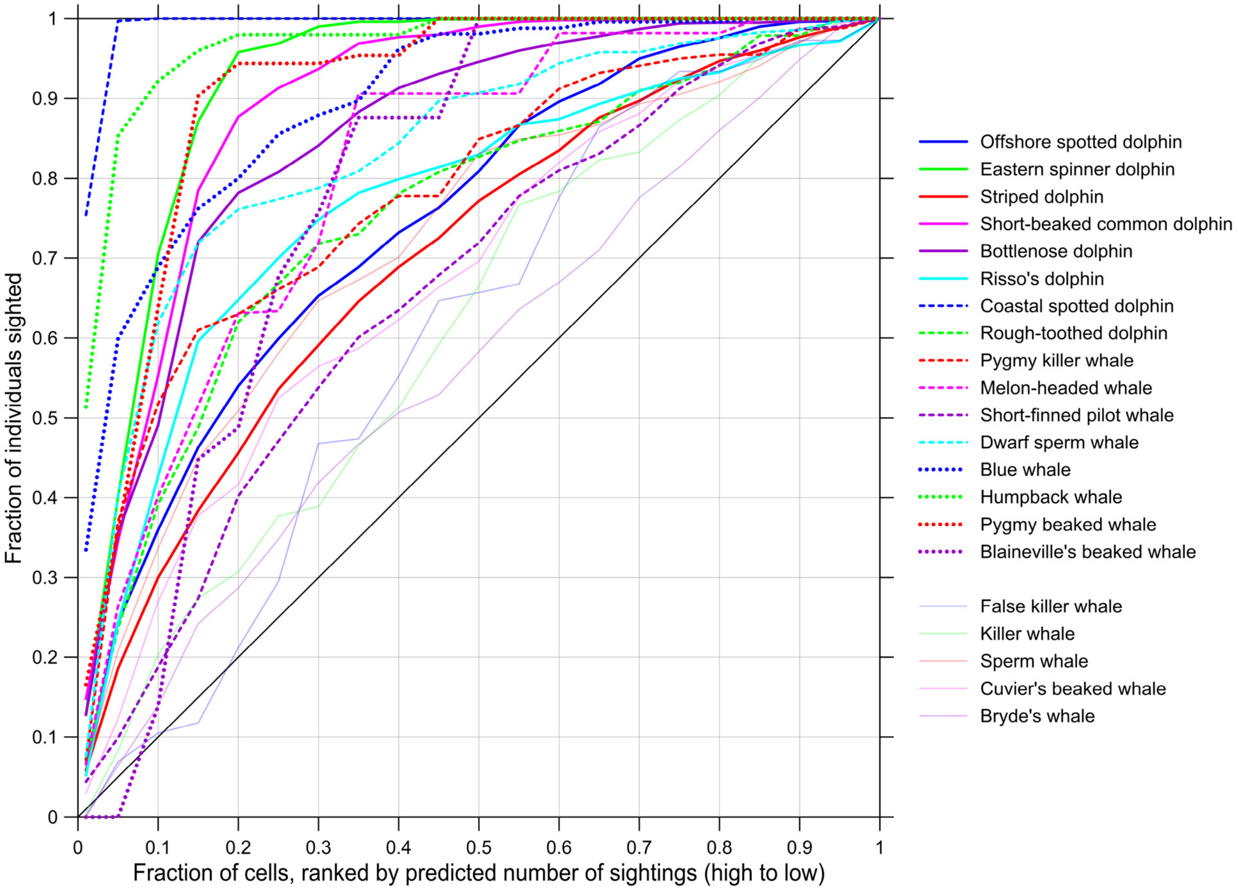


Figure 4. Relationships between predicted number of sightings and observed number of individuals, for 21 species that were sighted in the Costa Rica Dome region. The fraction of model cells, ranked by the predicted number of sightings, is plotted against the fraction of sighted individuals that were observed in those cells. Models for the last five listed species were unsuccessful (Table 3).

Results: Oceanography

Seasonal Winds and Currents

Wind variables, along with surface currents, are the primary factors determining seasonal changes in the region (Figure 5). The ITCZ is indicated by the blue bands of negative wind divergence; wind speed is reduced in the ITCZ. During winter-spring (Feb-Apr), the ITCZ is centered at ~4°N and the northeast trade winds are strong across Central America. During summer-fall (Aug-Nov), the ITCZ is centered at ~8°N, the southeast trade winds extend across the equator, and winds are weak at the latitude of the Dome. Wind jets at Tehuantepec, Papagayo, and Panama begin to strengthen in November as the ITCZ moves south. The jets are indicated in winter-spring by increased wind speed off the coast in these locations, and by lobes of wind stress curl extending off the coast: a negative (anticyclonic) lobe on the poleward side of the jet and a positive (cyclonic) lobe on the equatorward side of the jet. The Tehuantepec jet is the first of these three jets to strengthen, beginning in October, and can be seen in the Aug-Nov maps.

The North Equatorial Countercurrent (NECC), the eastward current at ~6°N, and the Costa Rica Coastal Current (CRCC) are very weak during Feb-Apr, as is equatorial upwelling. In Aug-Nov, the NECC extends all the way to the Central American coast, and the CRCC flows strongly along the coast from Costa Rica to southern Mexico. Equatorial upwelling is stronger in this season. The red bands of positive wind stress curl associated with the ITCZ in both seasons cause moderate oceanic upwelling north of the equator by a process called Ekman pumping. Coastal upwelling, forced by alongshore winds or by curl at the coastal wind jets, is not represented well in the ocean reanalysis data.

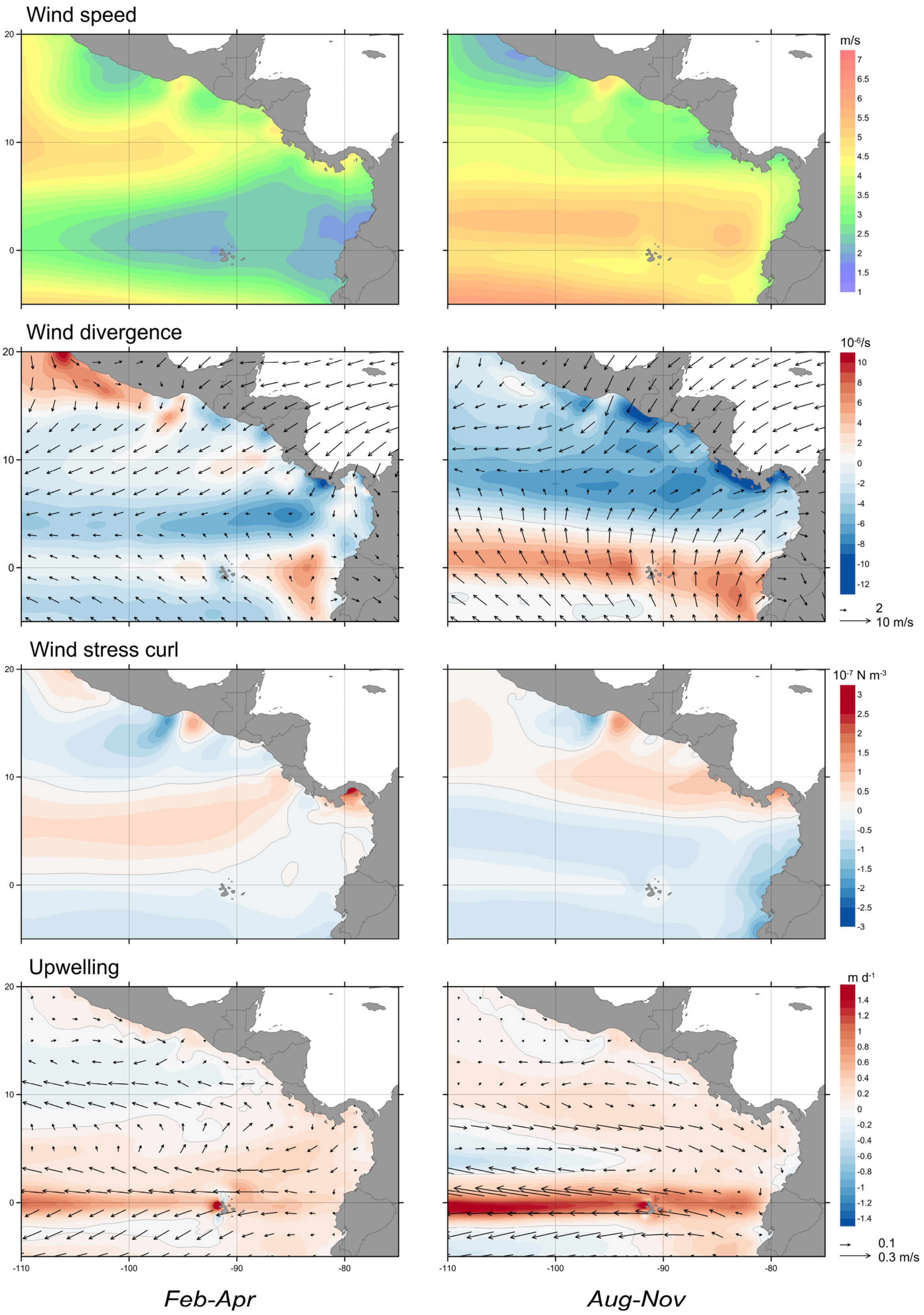


Figure 5. Seasonal maps of wind and current variables, as defined in Methods.

Seasonal Surface Water Properties

The Dome does not have a surface expression in the composite sea surface temperature maps (Figure 6). In Feb-Apr, the equatorial cold tongue is weak and the warmest surface waters are off Costa Rica, north of the equatorial front. Surface cooling beneath the three winter wind jets is seen along the coast. Cooling at Tehuantepec is also seen in Aug-Nov because this wind jet is strengthening as the ITCZ moves south. The low salinity water west of Colombia and SW of Panama at this time is not related to the Dome. In Aug-Nov, the equatorial cold tongue is much colder and the warm pool off southern Mexico has warmed. Surface salinity has decreased due to summer rains in the ITCZ (Amador et al., 2006), with the lowest salinity in the Gulf of Panama enhanced by seasonal river runoff.

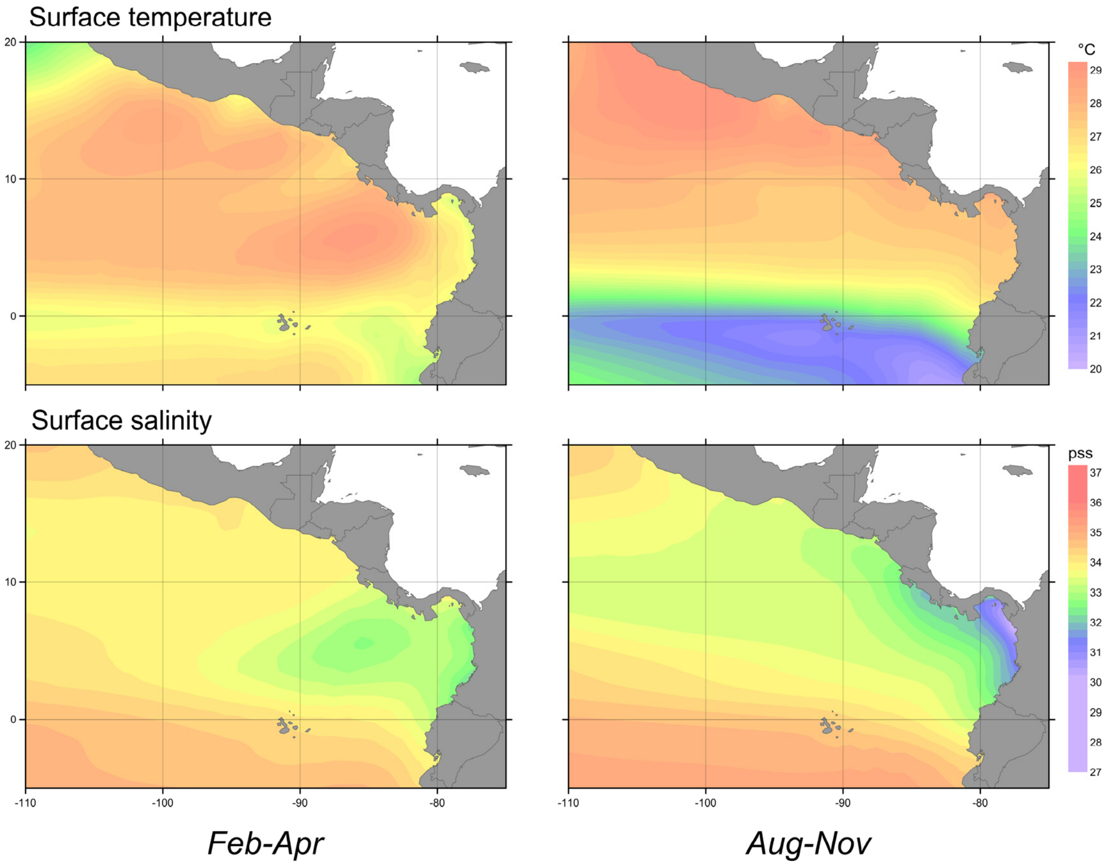


Figure 6. Seasonal maps of surface water variables, as defined in Methods.

Seasonal Thermocline Structure

The vertical structure of the water column (Figure 7), or mixed layer and thermocline, is affected by seasonal buoyancy forcing (heating/cooling, evaporation/precipitation) and wind forcing at the surface and by other processes related to advection, including currents and upwelling (Figure 5). Mixed layer depth is primarily determined by the strength of wind mixing, which is proportional to wind speed squared, as well as by solar radiation and precipitation. The most shallow mixed layer depths are beneath the seasonal ITCZ where surface winds are weak. The thermocline responds more to the geostrophic balance of surface and subsurface circulation or currents, producing the equatorial and countercurrent thermocline ridges. The deepening of the mixed layer and thermocline towards the subtropical gyres reflects the geostrophic balance of the large-scale basin circulation in the Pacific Ocean (Fiedler and Talley, 2006). Stratification, measured by the standard deviation or variability of temperature between the surface and 300m depth, reflects both wind mixing and advective processes.

In Feb-Apr, the mixed layer is deep north of the equator due to mixing by strong NE trade winds, but is shallow along the equator because the SE trades are weak. The countercurrent thermocline ridge is deep and the equatorial thermocline ridge is shallow. The tongue of shallow thermocline and low stratification extending from the coast of Costa Rica represents the coastal development phase of the Costa Rica Dome. The coastal wind jets influence surface waters by wind mixing beneath the jet (Figure 5). However, the jets also cause upwelling by Ekman pumping on the cyclonic curl side of the jets (left-hand side looking downwind, as seen in Figure 2), where both the mixed layer and thermocline are slightly more shallow than on the poleward anticyclonic side.

In Aug-Nov, the mixed layer is shallow north of the equator and deeper along the equator in response to seasonal changes in wind mixing. The countercurrent thermocline ridge is more shallow and the equatorial thermocline ridge is deeper. The dome of shallow thermocline and low stratification centered at 9°N, 90°W represents the mature phase of the Costa Rica Dome annual cycle.

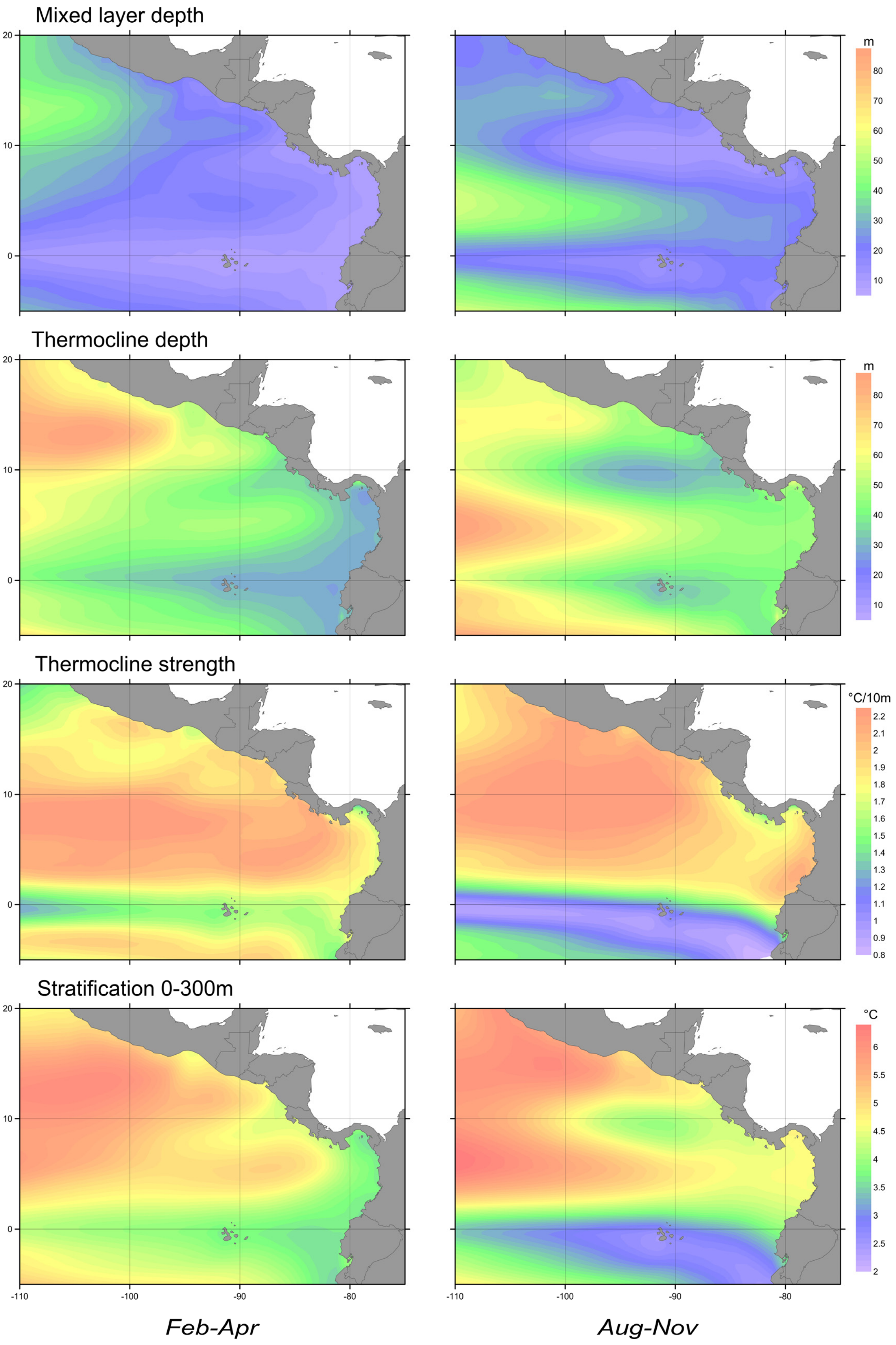


Figure 7. Seasonal maps of thermocline structure variables, as defined in Methods.

Seasonal Primary Production

Primary production is energy at the base of the food chain. In oceanic marine systems like the ETP, most of this energy is in phytoplankton biomass, measured as chlorophyll. The rate of primary production, or the fixation of carbon and nutrients into phytoplankton cells that will be available to consumers, is net primary productivity. In Feb-Apr, primary production is high in coastal waters beneath the seasonal wind jets (Figure 8). These winds begin blowing in November at Tehuantepec as the ITCZ moves south, as described above. Primary production in these waters is basically a response to nutrient input caused by wind mixing and Ekman pumping of deeper waters into the surface layer. In Aug-Nov, primary production is high along the equator and at the Costa Rica Dome due to upwelling. Production at the end of this season is beginning to respond to the Tehuantepec wind jet.

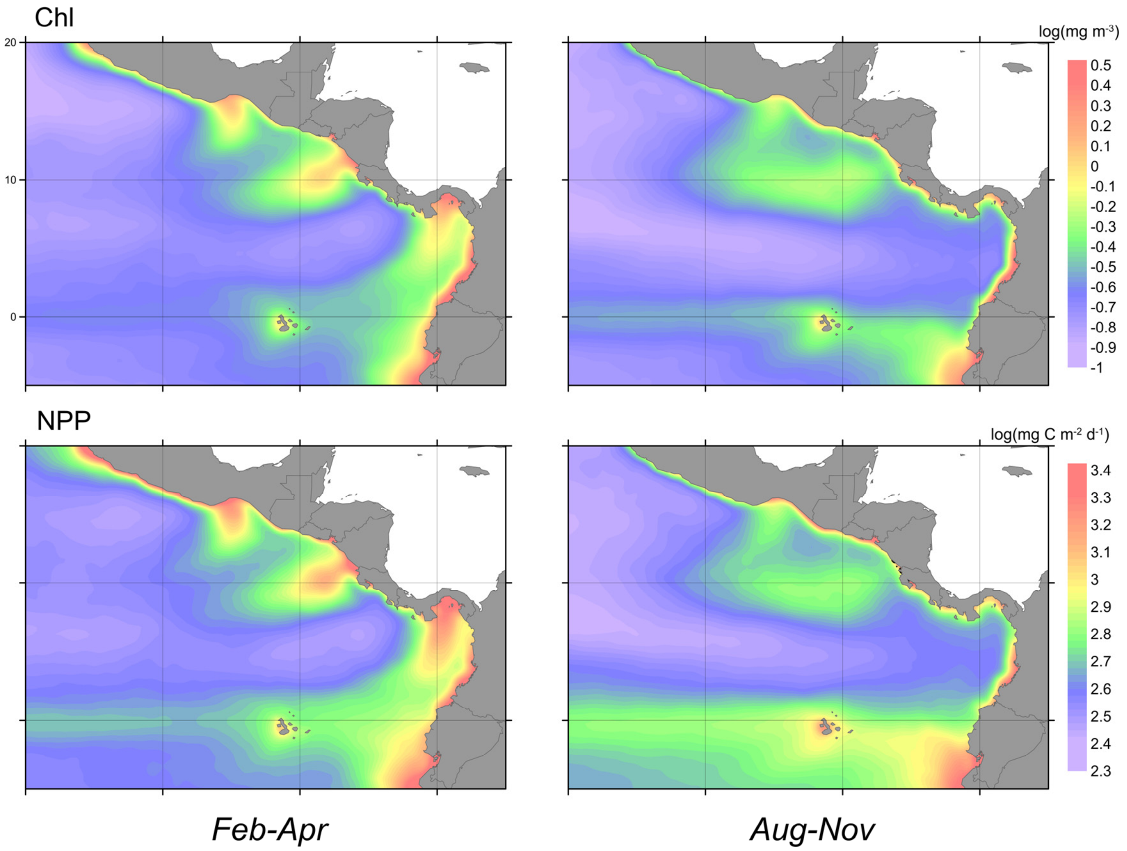


Figure 8. Seasonal maps of primary production variables, as described in Methods.

Results: Cetacean Distributions

As described in Methods, we estimated spatial distributions of the number of sightings for 28 cetacean species or recognized subspecies with species distribution models that relate observed sightings to the environmental variables described above (Table 3). Seven of these species were never sighted in the Costa Rica Dome region and are not considered further. Models were successful for 16 of the remaining 21 species, with a deviance explained of at least 10%. Here we map the predicted number of sightings (per 1000 km surveyed) with the sightings observed during all ten SWFSC cetacean surveys. The range of predicted number of sightings is different for each species, but the color scale is set from 0 (light purple) to the 99th percentile value for the entire ETP study area (red). Each map also shows the climatological boundaries of the Costa Rica Dome for each of the months of August through November (1980-2015), defined by the 35-m isoline of thermocline depth.

Distributions of the more abundant delphinids are illustrated in Figure 9. Spotted and spinner dolphins are often found in mixed schools, associated with tunas and seabirds (Ballance et al., 2006). Pantropical spotted dolphins (*Stenella attenuata*) are found worldwide in tropical and some subtropical waters (Perrin, 2009a). Eastern spinner dolphins (*Stenella longirostris orientalis*) are endemic to the ETP (Perrin, 2009b). Both of these species prefer the eastern Pacific warm pool, which is northwest of the Dome.

Striped dolphins (*Stenella coeruleoalba*) are common in warm-temperate and tropical waters around the world (Archer, 2009). Short-beaked common dolphins (*Delphinus delphis*) are the most abundant dolphin in offshore warm-temperate waters throughout the Atlantic and Pacific (Perrin, 2009c). Both show centers of abundance in the Costa Rica Dome and in the equatorial cold tongue, although the association with these relatively cold and productive upwelling regions is stronger for common dolphins than for striped dolphins.

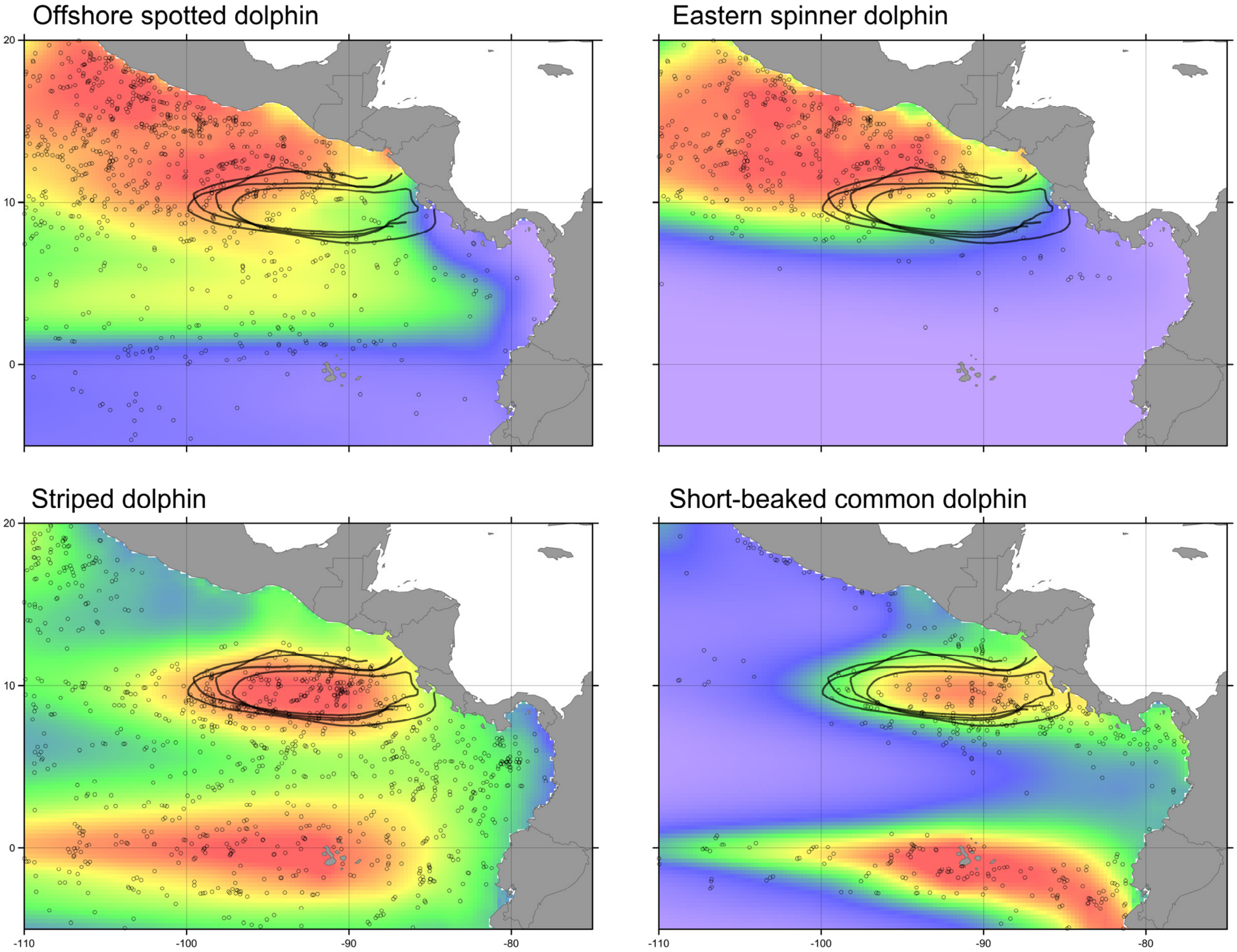
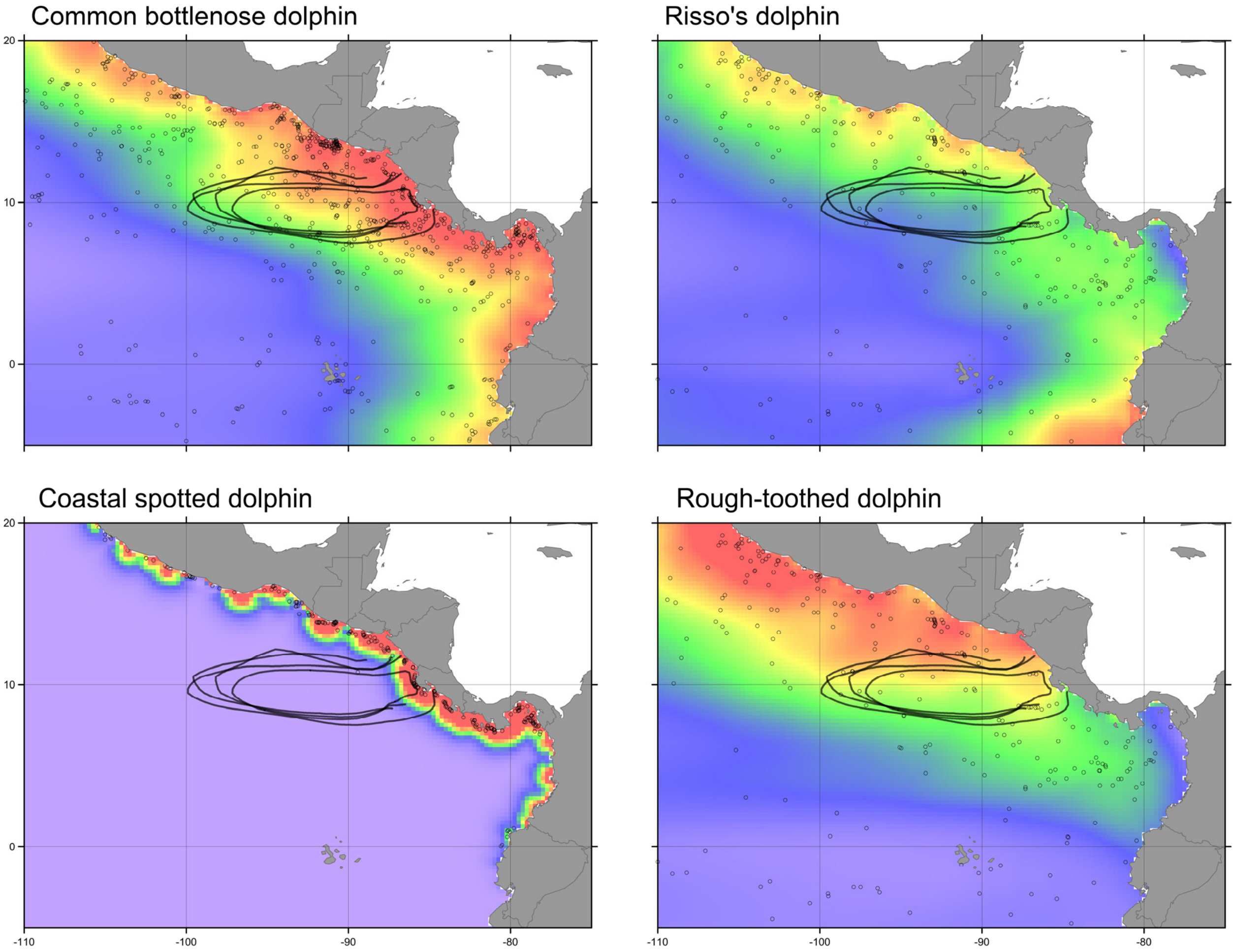


Figure 9. Observed sightings and predicted number of sightings (increasing from light purple to red) for more abundant delphinids. The outlines are the August-November monthly climatological (1980-2015) locations of the Costa Rica Dome.

Distributions of four moderately abundant delphinids are illustrated in Figure 10. These are more common in coastal waters, especially the coastal spotted dolphin (*Stenella attenuata graffmani*), which is endemic to the ETP. Common bottlenose dolphins (*Tursiops truncatus*) are found in temperate and tropical waters throughout the world; they are arguably the best known of all cetaceans because they are so common in coastal waters. Risso's dolphins (*Grampus griseus*) are distributed worldwide in temperate and tropical oceans with a strong preference for continental shelf and slope waters (Jefferson et al., 2014). Rough-toothed dolphins (*Steno bredanensis*) are a warm temperate species that is known to prefer shallow coastal waters in parts of its range (Jefferson, 2009). These four delphinids are common in Central America coastal waters, so that the edges of their preferred habitats overlap the Costa Rica Dome, but they do not show a preference for the Dome itself.



Common bottlenose dolphin

Risso's dolphin

Coastal spotted dolphin

Rough-toothed dolphin

Figure 10. Observed sightings and predicted number of sightings (increasing from light purple to red) for moderately abundant delphinids. The outlines are the August-November monthly climatological (1980-2015) locations of the Costa Rica Dome.

Distributions of less common delphinids are illustrated in Figure 11. All of these are found in tropical and warm temperate waters worldwide. The pygmy killer whale (*Feresa attenuata*) prefers the warmest waters of the eastern Pacific warm pool to the northwest of the Dome, but is also found to the southeast of the Dome and (not shown) in warm subtropical water at the western extreme of the ETP study area. The melon-headed whale (*Peponocephala electra*) shows a preference for the Gulf of Panama. Short-finned pilot whales (*Globicephala macrorhynchus*) show an association with equatorial waters; the Dome is on the edge of their distribution in this region. Dwarf sperm whales (*Kogia sima*) are another species, like those in Figure 3, with a coastal range that overlaps with the Costa Rica Dome. Pygmy beaked whales (*Mesoplodon peruvianus*) show an association with the Dome, but are also found in the eastern Pacific warm pool along the coast to the north of the Dome. Blaineville's beaked whale (*Mesoplodon densirostris*) is not associated with the Dome, but appears to prefer the North Equatorial Countercurrent to the south of the Dome.

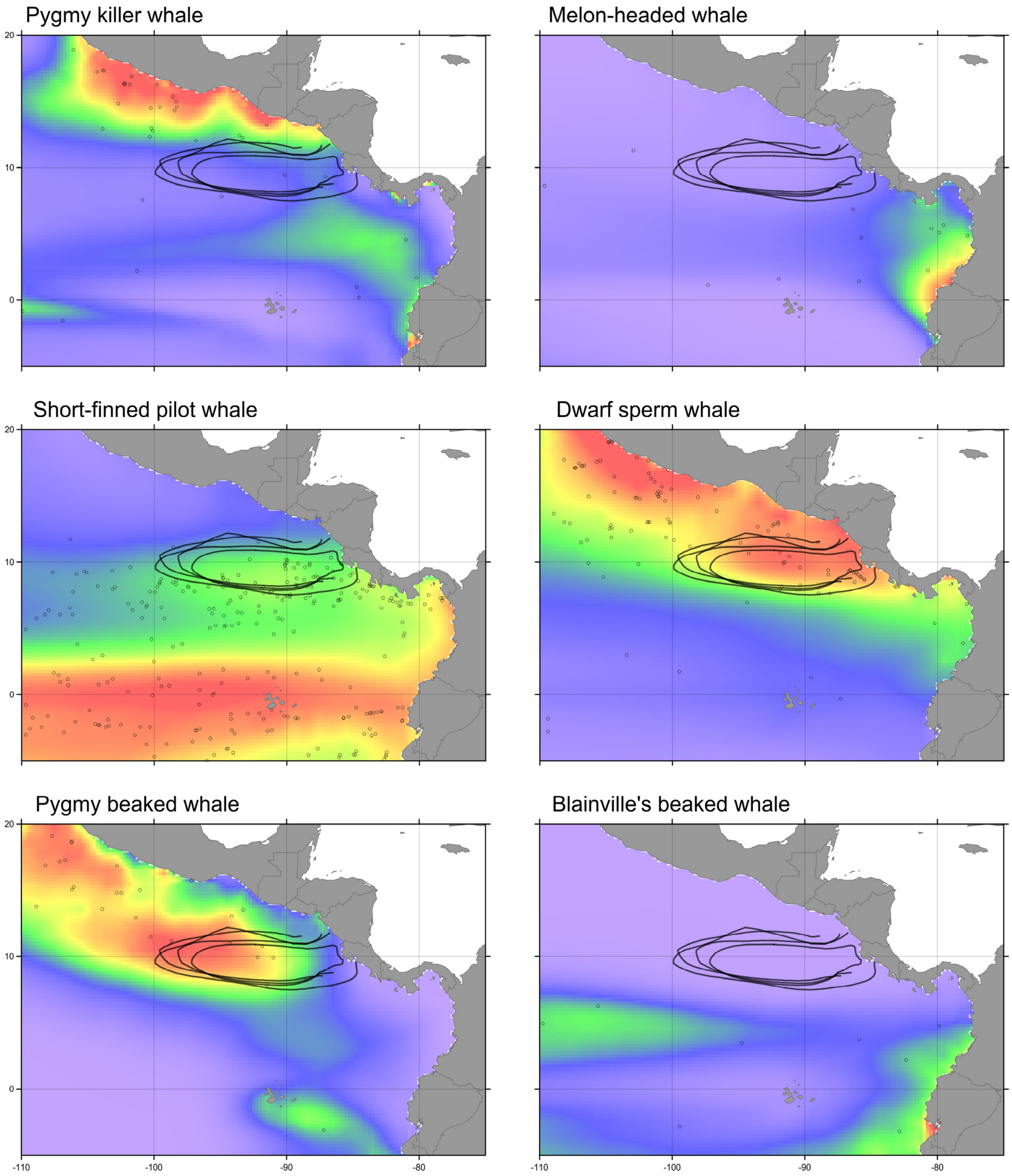


Figure 11. Observed sightings and predicted number of sightings (increasing from light purple to red) for less abundant delphinid species. The outlines are the August-November monthly climatological (1980-2015) locations of the Costa Rica Dome.

Distributions of two baleen whale species are illustrated in Figure 12. Both are seasonal migrants that are present in the warm ETP during their breeding seasons. The humpback whales (*Megaptera novaeangliae*) sighted along the coast of tropical Central and South America during August-November were observed on known calving grounds and were most likely southern-hemisphere whales (Rasmussen et al., 2007). Blue whales (*Balaenoptera musculus*) are found in productive waters of the Costa Rica Dome and the equatorial cold tongue, like short-beaked common dolphins (Figure 9), although their equatorial distribution is closer to the Galapagos. The blue whales could be migrants from the eastern North Pacific or Southern Ocean, or residents (Sears and Perrin, 2009).

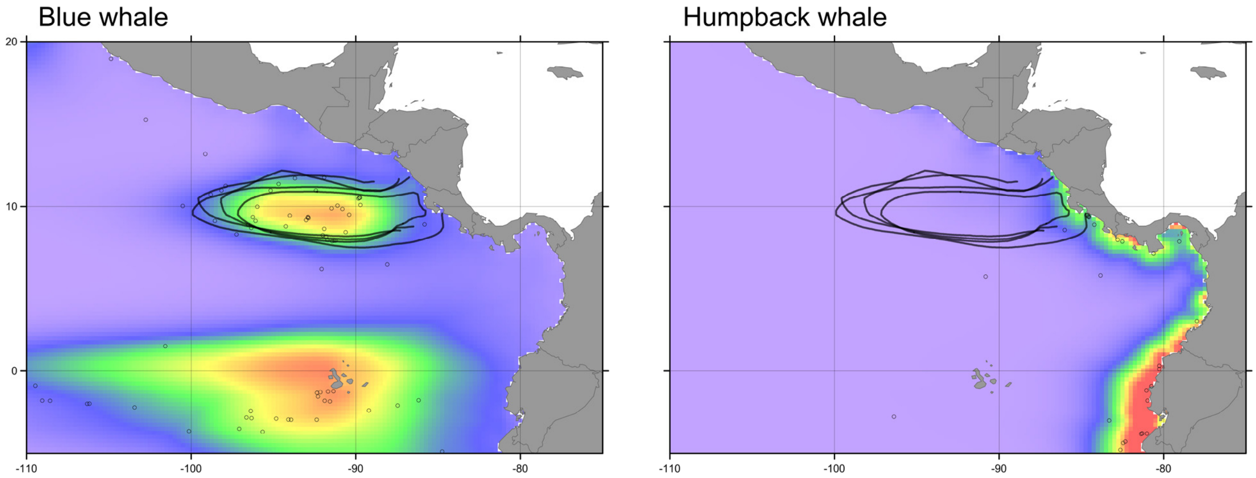
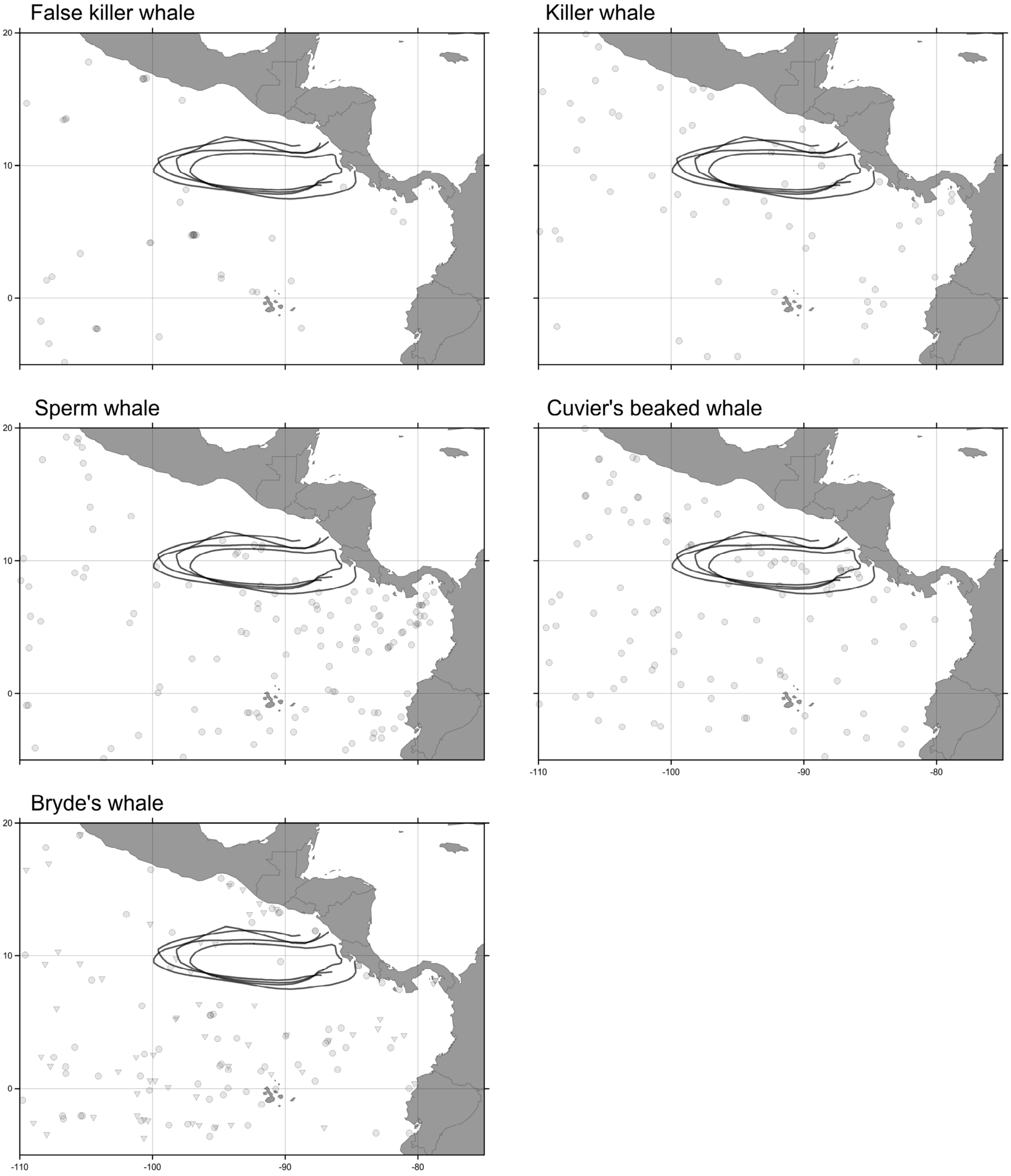


Figure 12. Observed sightings and predicted number of sightings (increasing from light purple to red) for two large baleen whale species. The outlines are the August-November monthly climatological (1980-2015) locations of the Costa Rica Dome.

Distributions of sightings of five other cetaceans, for which effective species distribution models could not be produced (Table 3), are illustrated in Figure 13. The false killer whale (*Pseudorca crassidens*) is one of the larger delphinids, distributed in tropical and warm temperate open-ocean waters worldwide (Baird, 2009). Killer whales (*Orcinus orca*) are the ultimate apex predator in marine ecosystems. They have a cosmopolitan distribution in all of the world's oceans and many marginal seas, but are most common in coastal, temperate waters of high productivity (Ford, 2009). Sperm whales (*Physeter microcephalus*) are another cosmopolitan cetacean species. Females and young males are found in tropical and subtropical waters. They are deep-diving predators with a broad diet of squids and other deep-sea animals (Whitehead, 2009). Cuvier's beaked whale (*Ziphius cavirostris*) is thought to be the most abundant and cosmopolitan of several rare beaked whales present in the ETP (Heyning and Mead, 2009). Beaked whales are large, deep-diving predators feeding on squids and other deep-living prey. The Bryde's whale (*Balaenoptera edeni*) is present in tropical and warm temperate waters worldwide (Kato and Perrin, 2009). Although all five of these species have been seen in or near the Costa Rica Dome, their sightings do not appear to be concentrated in the Dome.


False killer whale

Killer whale

Sperm whale

Cuvier's beaked whale

Bryde's whale

Figure 13. Sighting locations for five cetacean species that could not be effectively modeled (see Methods for details). The outlines are the August-November monthly climatological (1980-2015) locations of the Costa Rica Dome.

Conclusion

A seasonally predictable, strong, and shallow thermocline makes the Costa Rica Dome a distinct biological habitat where phytoplankton and zooplankton biomass are higher than in surrounding tropical waters (Fiedler, 2002). This production supports populations of mid-trophic level fishes (Blackburn et al., 1970; Chen et al. 2014) that likely support the tropical tuna fisheries in the region. The physical structure and biological productivity of the Dome also affect the distribution and feeding of whales and dolphins, probably through forage availability.

Among the 21 cetacean species and subspecies present in the Costa Rica Dome region, three show a clear association with the Dome and 14 have distributions that extend into the Dome. The three species with centers of abundance in the Dome are also abundant in the productive waters along the equator: striped dolphin, short-beaked common dolphin, and blue whale. Two abundant subspecies prefer the eastern Pacific warm pool to the northwest of the Dome, but their ranges extend into the Dome: offshore pantropical spotted dolphin and eastern spinner dolphin. One species is most abundant in equatorial waters, although the edge of its range reaches the Dome: short-finned pilot whale. Six species/subspecies are most abundant in coastal waters and their ranges extend at least partially into the Dome: common bottlenose dolphin, Risso’s dolphin, coastal spotted dolphin, rough-toothed dolphin, dwarf sperm whale and pygmy beaked whale. Four relatively rare species are most abundant in restricted areas near the coast, but not in the Dome: pygmy killer whale, melon-headed whale, humpback whale, and Blaineville's beaked whale (also found in near-equatorial waters to the west). Five species are found near and occasionally in the Dome, but show no preference for the Dome: false killer whale, killer whale, sperm whale, Cuvier’s beaked whale, Bryde’s whale, and Blainville’s beaked whale.

The Costa Rica Dome is a regional center of high productivity and likely supports high prey availability for cetacean predators both within the Dome and in surrounding waters. The coastal warm pool to the northwest of the Dome and the productive equatorial waters to the south are also important regional habitats for cetaceans.

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