TOPP AS A MARINE LIFE OBSERVATORY: USING ELECTRONIC TAGS TO MONITOR THE MOVEMENTS, BEHAVIOUR AND HABITATS OF MARINE VERTEBRATES

Daniel P. Costa[(1)], Barbara E. Block[(2)] , Steven Bograd[(3)], Michael A. Fedak[(4)], John S. Gunn[(5)]

(1) Dept of Ecology & Evolutionary Biology, University of California at Santa Cruz, 100 Shaffer Rd, Santa Cruz, CA. USA 95060, E-mail: costa@biology.ucsc.edu
(2) Hopkins Marine Station, Stanford University, Pacific Grove, CA, USA, 93950, E-mail: bblock@stanford.edu,,
(3) NOAA/NMFS, Southwest Fisheries Science Center, Environmental Research Division, 1352 Lighthouse Avenue, Pacific Grove, CA, USA 93950, E-mail: steven.bograd@noaa.gov.
(4) NERC Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, East Sands, St Andrews KY15 5QJ UK, Email: maf3@st-andrews.ac.uk
(5)Australian Antarctic Division, Channel Highway, Kingston Tasmania 7050, AUSTRALIA E-mail: John.Gunn@aad.gov.au

Abstract
The Tagging of Pacific Pelagic (TOPP) a field program of the Census of Marine Life has proven the concept of using electronic tags to develop a Marine Life Observatory (MLO) to monitor the habitat utilization, movement patterns and behaviour of large marine predators. Given the difficulty of observing the behavior of highly pelagic marine species we know relatively little about their habitat requirements. This is especially true for tunas, sharks, turtles, seabirds, seals and whales that disperse over vast areas of the pelagic realm spending most of their time underwater and at great distances from shore. The new, miniaturized sensors provide oceanographic quality environmental data directly from wild animals living free and undisturbed in their natural habitats, in addition to detailed information about the behaviour of the animals themselves. The availability of this technology is leading to a partnership between physical oceanographers and organismal biologists. These studies are providing a unique avenue for animal acquired data to be incorporated into the operational oceanography community. The data derived from these advanced electronic tagging technologies and scientific methods will help us meet the challenges of the 21st century for marine resource management and ocean modeling. Biologging has been employed on a large scale and in an operational mode showing that it can play an important role in a Global Ocean Observing System.

1. INTRODUCTION.

The Tagging of Pacific Pelagics (TOPP), a field program of the Census of Marine Life, has proven the concept of using electronic tags to develop a Marine Life Observatory (MLO) to monitor the habitat utilization, movement patterns and behaviour of large marine predators. The technical capability and cost-effectiveness of this technology in addressing both physical and biological questions is leading to a partnership between physical oceanographers and organismal biologists. These studies are providing a unique avenue for animal acquired data to be incorporated into the operational oceanography community. The data derived from these advanced electronic tagging technologies and scientific methods will help us meet the challenges of the 21st century for marine resource management and ocean modeling. To date the TOPP program has deployed 4000 electronic tags and tracked mako, blue, thresher, salmon and white sharks, elephant seals, California sea lions, bluefin and yellowfin tuna, black-footed and Laysan albatross, sooty shearwaters humpback and blue whales, and loggerhead and leatherback sea turtles (Fig. 1). Animal tracks are mapped on remote satellite

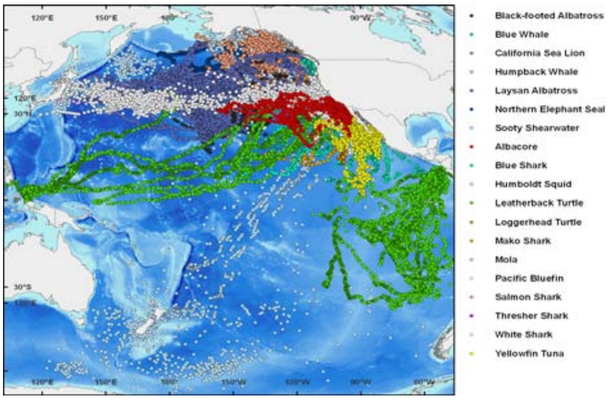

Figure 1. Tracks of 19 species of marine vertebrates tracked as part of the TOPP program.

imagery of oceanographic features, which define the attributes of biological hot spots and provide insight into areas of high biodiversity (Fig. 2). This approach is providing critical new insights into the behavior and habitat preferences of highly migratory pelagic marine species. This is especially true for tunas, sharks, turtles, seabirds, seals and whales that disperse over vast areas of the pelagic realm spending most of their time underwater and at great distances from shore. Prior to

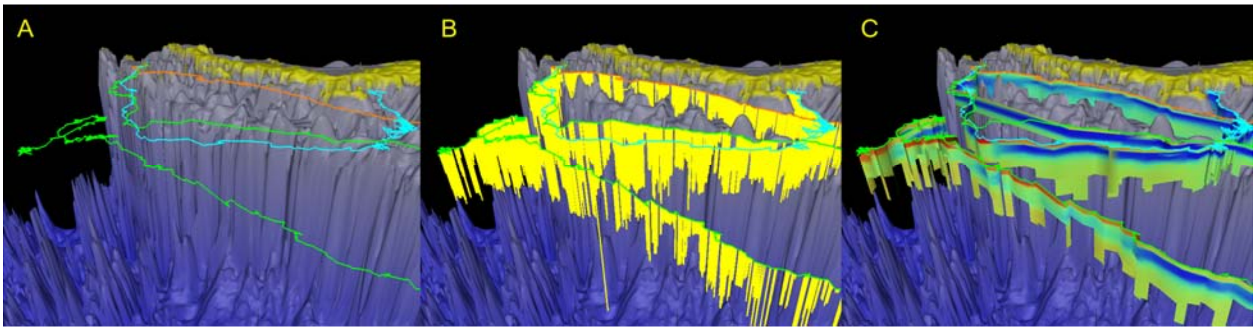

Figure 3. Track of southern elephant seals in the Western Antarctic Peninsula obtained using the SMRU CTD-SRDL 9000. 3A shows just the surface track, 3B shows the surface track along with diving behavior, and 3C shows the temperature and salinity profiles that can be obtained to provide data on the physical environment the animals are moving through. Costa, Crocker, Goebel and McDonald unpublished data.

GLOBEC (www.globec.org), CLIOTOP and TOPP programs our knowledge of the linkages between biology and physics of higher trophic levels was quite descriptive [1,2]. For example, we knew that apex predators occur in areas where oceanographic features such as currents, frontal systems, thermal layers, sea mounts and continental shelf breaks increase the availability of prey [3,4,5,6]. All of these oceanographic features and processes are thought to impact marine predator distributions by physically forcing prey aggregations and, thus, creating areas where foraging efficiency can be increased [7,8,9,10,11].

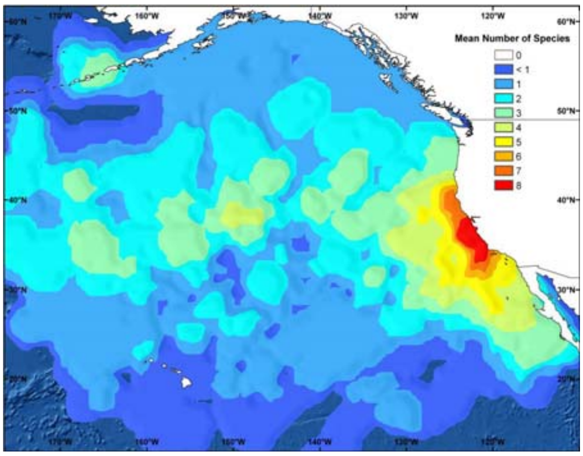

Figure 2 Patterns of marine biodiversity that can be identified using the methods developed by TOPP.

Indeed, for many marine predators, regions of highly localized productivity may be essential for reproduction and survival [12,13,14,15,16]. While the TOPP program has provided significant insights into the movements and distributional patterns of apex predators, a complete understanding of upper trophic level processes will require measurements over longer time frames and with integration across trophic levels and with ocean physics. The rationale for such work is increasingly apparent as we become aware of the importance of upper trophic levels in structuring marine communities due to their role as predators [17,18] and in their ability to transport nutrients across and within the water column [19]. Furthermore, many upper trophic level species are considered "charismatic megafauna" and are valuable to the public, both as a food resource (bluefin tuna, salmon) and for their emotional appeal (whales, dolphins, penguins etc). This is even more critical as many upper trophic level species are increasingly under threat of extinction along with a loss in marine biodiversity.

As a result of the TOPP program we have gained significant insights and developed new tools to study highly migratory upper trophic level species. However these studies have focused primarily on the movement patterns of these species and have not been integrated with studies of the lower trophic web and the biophysical forces that drive the food chain. Imagine what could be accomplished if this research was applied in an integrated manner, providing a seamless transition from an understanding of the biophysical processes at the bottom of the food chain to the movements and behavior patterns of upper trophic level apex predators. With measurements of the movement patterns of top predators, coupled with the abundance of zooplankton and biophysical process [20]. Such an integrated effort would need to be focused on a number of regions where existing infrastructure is in place or locations that are representative of critical marine habitats. Such an integrated effort would provide not just a onetime snapshot of the biodiversity of a marine habitat, but would provide a dynamic view into the processes that maintain biodiversity and a better understanding of how it can be protected. A critically important aspect of this is that we will be able to monitor how life in the ocean is changing in response to climate change [21,22,23,24,25]. Such information will be critical to policy makers to provide them with the information necessary to mitigate such impacts.

Coupling the behavior of upper trophic levels to biophysical processes will require development of new approaches that merge biological functions and behaviors of upper trophic levels, with flux rates that are typically used to define nutrient delivery with primary production. While Nutrient-Phytoplankton-Zooplankton (NPZ) models have proven quite informative for lower trophic levels, they do not scale up to higher trophic levels. IBMs can represent the movements of a single marine animal and can incorporate an energy budget that includes the costs of movement and acquiring prey. Such a model would be spatially explicit, and influenced by environmental and other relevant factors affecting animal behavior. A suite of these IBMs could be released into a model that represents a population of a given species. The movement patterns relative to oceanographic features and prey availability could then be modeled along with information on species interactions. The development of such models would require a mechanistic understanding of the habitat utilization patterns of higher trophic levels. Electronic tags can be used to help elucidate these patterns of habitat utilization and provide the data necessary to develop IBMs. Integration of oceanographic data with marine animal distribution and behavior can be used build models that describe the interrelationships of marine animal movements to their physical and ecological habitat. Such a modeling approach would provide an "experimental test bed" to examine the processes that determine animal distributions, local abundance and movement patterns.

2. TAGGING TECHNOLOGY.

Under the auspices of TOPP (see www.topp.org), the Pacific Ocean Shelf (POST) program (www.post.org), and more recently the Ocean Tracking Network (OTN) www.oceantrackingnetwork.org) a variety of electronic tagging technologies have been developed, and deployed on a large integrated scale that allows observations of the movements and behavior of large marine vertebrates [26]. These new tools, or electronic tags have provided field biologists with a new form of "biotechnology" that allows the study of complex behavior and physiology in freely ranging animals [27]. This technology has produced data-loggers small enough to be attached to animals while they freely go about their activities [28,29]. Information on the movement patterns, depth utilization and or diving behavior are obtained when the tags are recovered (archival tags) or when transmitted via satellite. Archival and satellite linked tags have made possible the study of ocean basin scale movements, oceanographic preferences and behaviors of many pelagic species [30,31,32,33,34,35,36,37,38,39,40]. Further advances in informed data compression have made it possible to get significantly more information through the limitations of the ARGOS system, including detailed oceanographic and behavioral information [41]. The primary methods for tracking marine organisms include: GPS, ARGOS satellite, acoustic and archival data storage tags. Tagging data provides a time series that can last from months to in some cases years and provides behavioral information that can be used to identify behaviors and associated habitats and depending on the type of tag deployed, data can acquired can range from a simple surface track (Fig. 3A), to a surface track with a dive profile (Fig. 3B) or a surface track and dive profile with associated environmental data (Fig. 3C; temperature, salinity and or light level). Such behavioral data are important to identify differences in the movement patterns and habitat utilization of different species. For example, some species may travel over considerable distances (southern elephant seals), while others may remain within a smaller home range (Weddell seals) (Fig. 4).

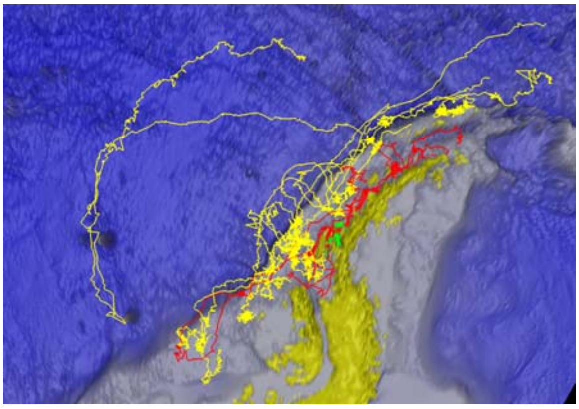

Figure 4. Differences in the movement patterns of southern elephant seals (yellow), crabeater seals (red) and Weddell seals in (green) are shown along the Antarctic Peninsula. The tracks cover the same time period during 2007. Costa, Crocker, Goebel and McDonald unpublished data.

2.1 Archival Tags

Archival tags are data logging tags that record data as a time series from sensors that measure depth (pressure), water temperature, body temperature, salinity, and light level. The major limitation of archival tags is that they must be recovered in order to obtain the data. However, judicious choice of animals, or use on exploited species where a reward is offered has provided a wealth of information on the foraging behavior and habitat utilization of a large group of marine organisms [28,29,42,43,44,45]. Archival tags have provided tracks covering at least 3.6 years [40].

Movement patterns can be derived with archival tags by examining changes in light level to determine local apparent noon to determine longitude and day length from precise determination of sunrise and sunset to determine latitude [33]. These locations can be further corrected using sea surface temperatures [46,47]. Salmon researchers have also been using depth and temperature archival tags to discern more about the behavior, and movement of salmonids in relationship to their environment (Walker *et al.* 2000). The data intensity of these devices allows determination of both fine and large-scale behavioral patterns, migratory routes and physiology, all in relation to the environment. Environmental data collected from these tags include water temperature, salinity and chlorophyll profiles

2.2 Argos Satellite Tags

Satellite tags provide at sea locations and have the advantage that the data can be recovered remotely without the need to recover the tag. Satellite-linked data recorders have expanded our understanding of the fine scale movements of marine birds [48,49,50], sea turtles [51,52], sharks [53,54] and marine mammals [29,38,55,56,57,58].

Since the antenna on the satellite transmitter must be out of the water to communicate with an orbiting satellite, the technology has mainly been used on air-breathing vertebrates that surface regularly. For large fish and other animals that remain continuously submerged, the ability to transmit to ARGOS at the surface is not possible. For these organisms, a pop-up satellite archival tag (PSAT) has been developed [31,36,59]. Pop-up satellite tags combine data storage tags with satellite transmitters. The pop-up satellite devices communicate with the ARGOS satellites that serve to both up-link data and calculate an end-point location. Importantly, the tags are fisheries independent in that they do not require recapture of the fish for data acquisition.

2.3 GPS Tags

The TOPP program was instrumental in the development of a GPS tag that has increased the precision of animal movement data to within 10 meters compared to the 1-10 kilometers currently possible with ARGOS satellite tags. Such precision is allowing measurements of animal movements relative to the mesoscale features and will provide higher resolution locations for the physical oceanographic data collected by the animals. However, standard navigational GPS units require many seconds or even minutes of exposure to GPS satellites to calculate positions and the onboard calculations require consume considerable power. A GPS system that can obtain GPS satellite information in less than a second and can transmit the location information within the narrow bandwidth confines of the ARGOS system has been developed by Wildtrack Telemetry Systems Ltd (Leeds, England). The *Fastloc* uses a novel intermediate solution that couples brief satellite reception with limited onboard processing to reduce the memory required to store or transmit the location. This system captures the GPS satellite signals, and identifies the observed satellites, calculates their pseudo-ranges without the ephemeris or satellite almanac and produces a location estimate that can be transmitted via ARGOS. Final locations are post processed from the pseudo-ranges after the data are received using archived GPS constellation orbitography data accessing through the Internet.

2.4 Future Technology Development

Over the last decade the capability of electronic tags has increased considerably. However, there are a number of technological advances that need further development, including novel ways of powering the tags, increased sensor capabilities (including oceanographic sensors and animal behavior and or physiology), better attachment methods, miniaturization of tags, and alternative methods of data recovery [57]. While new higher capacity batteries may be developed, an alternative would be to develop alternate methods of obtaining power. For example, these animals move through the water and some undergo considerable changes in pressure. Conceptually, this seems very straightforward, but the development of reliable power harvesting systems has not begun. Other sensors that could be added to the tags include such important oceanographic measure as O_2, pH, CO_2, and chlorophyll, as well as important measures of animal behavior as 3-axis acceleration, feeding and heart rate and possibly active sonar to measure prey fields in front of the animal [58].

Finally, novel methods of data recovery would greatly enhance the range of species that these tags could be deployed on. Currently, archival tags have to be recovered to obtain the data. This is done when the animal returns to a rookery (seals and birds), the tag is released and floats to the surface where it transmits a subset of the information (pop up tags), or the data are transmitted via ARGOS when the animals comes to the surface (air-breathing vertebrates and some sharks). A major advance would be achieved if the data obtained by electronic tags could be telemetered underwater via an acoustic modem. While there are issues with the power requirements and range it is possible to collect data when the animal swims past an acoustic receiver such as being deployed by the OTN program.

Archival tag technology has become sufficiently miniaturized so that juvenile fish less than 100g can be tagged without significant increases to their mortality.

However, for juvenile salmon which reliably return to a river of origin where they can be predictably captured, marine survival rates are only 2 to 5% making the cost of deploying archival tags prohibitive. As a result, acoustic technologies have moved to the forefront of marine fisheries movement research. In the North Pacific alone thousands of fish from over a dozen species are now being tagged with small, relatively inexpensive acoustic transmitters, and their movements are being monitored by a growing network of acoustic arrays led by the Ocean Tracking Network (OTN) and Pacific Ocean Shelf Tracking Project (POST). These networks are providing new insights into the movements of fish past fixed listening arrays in the ocean without the need for tag recovery. Unfortunately, these data have two limitations over the archival and satellite tag technologies. The first is a lack of oceanographic habitat sensors to collect data in the environment where the fish is found and second is array deployment limited to the continental shelf. These limitations could be overcome by deploying "business card tags" (BCTs) on larger marine animals. BCTs are capable of alternating between transferring and receiving data from other BCTs and regular acoustic pinger tags when they come within range [26]. As more tags are deployed there would be a high probability of regular encounters between a BCT tagged animal and other acoustically tagged species. While one might consider the ocean to be vast, marine organisms' are likely to converge on the same oceanographic features, dramatically increasing the probability of encounters. An added advantage is that larger marine organisms could not only carry the larger BCT tag, but could carry additional sensors that would provide information on the physical environment (e.g. CTD).

4. ANIMALS AS OCEAN SENSORS

As these tools evolved, they reached a sophistication and reliability where the data collected were equivalent to the industry standards for oceanographic sampling tools, for example elephant seals can sample the water column 60 times a day reaching depths of 1000m under their own power across broad expanses of the ocean that are difficult to reach by ships or other conventional means [60]. The research subjects became research tools and can provide oceanographic data for a fraction of the costs and can provide coverage in regions where conventional methods do not work such as Polar Regions [57,58,61,62,63,64,65]. A significant advantage of tag-collected oceanographic data is that they are collected at a scale and resolution that matches the animals' behavior. As more environmental information is gathered and delivered from the tagged animals, new insights will be obtained about their individual behaviors, as well as how they respond to environmental variability on daily, seasonal, and inter-annual time scales. Animal-collected oceanic data can complement more traditional methodologies for assimilation into oceanographic models. At the same time technologies have been improving to study the movements of smaller fish species at sea. Instrument size currently limits satellite telemetry to the largest fish species such as sharks and tunas.

The feasibility of marine animals as autonomous ocean profilers has been proven by deployments of temperature and salinity tags on host of marine species, such as marine mammals [60,64,66,67,68,69,70], seabirds [71,72,73], turtles [74], and fish [53,75]. While the acquisition of such environmental data has been ongoing only recently have these data begun to be used to address specific oceanographic questions [64,68,72]. A more complete description of the use and potential of using animals as ocean sensors can be found in community white papers [57,58].

5. CONCLUSIONS.

The importance of tracking data to conservation and management of marine living resources is increasingly clear. Many TOPP species are harvested by human fishers (tuna and sharks) whiles others are caught indirectly as a byproduct of fishing activities (leatherback sea turtles, shearwaters and albatross). Tracking data clearly shows that TOPP species don't recognize political boundaries and travel through the EEZs of multiple countries making it clear that many TOPP species require multi-national protection. For example, Laysan albatrosses tagged at Guadalupe Island, Mexico are found within the CCS and within at least three different EEZ's. Pacific bluefin tuna that swam to the Eastern Pacific Ocean from Japan are so overexploited that few of the tagged fish live long-enough to make trans-Pacific migrations back to spawn. Leatherback sea turtles have been observed to use a corridor shaped by oceanographic features that are predictable [76,77]. This has led to an IUCN resolution to conserve leatherback sea turtles in the open seas. An important product of TOPP is an identification of key geographic areas where creation of MPAs might protect critically endangered species. A specific example of the success of the TOPP program in this respect is the creation of an MPA off the coast of Baja California to protect loggerhead sea turtles (Fig. 5) [78]. TOPP tracking data have been used in listing black-footed albatrosses as an endangered species by the USFWS and have been incorporated into BirdLife International and the USFWS for deliberations within the international Agreement for the Conservation of Albatrosses and Petrels (ACAP).

Marine Life Observatories employing electronic tags have been developed and are operational. The technology is proven and the community is ready to incorporate this capability into a Global Ocean Observing System.

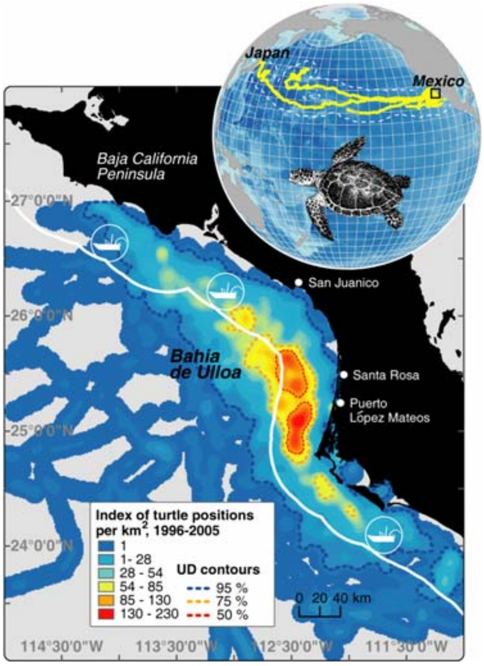

Figure 5. Kernel Density of Loggerhead Turtle Habitat Use in the North Pacific. Inset: Positions of tracked loggerheads (yellow) spanned the North Pacific Basin. The 50% utilization distribution for observed loggerheads consisted of an area of 4,115 km centered, 32 km from the Baja California South coast, well within the 55 km range of small-scale fisheries (white line). doi:10.1371/journal.pone.0001041.g001

REFERENCES

1. Hofmann E.E., Wiebe P.H., Costa D.P. & Torres J. J. (2004) An overview of the Southern Ocean Global Ocean Ecosystems Dynamics program. *Deep Sea Research Part II: Topical Studies in Oceanography* 51: 1921-1924.
2. Hofmann E.E., Wiebe P.H., Costa D.P. & Torres J.J. (2008) Introduction to dynamics of plankton, krill, and predators in relation to environmental features of the western Antarctic Peninsula and related areas: SO GLOBEC Part II. *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 269-270.
3. Ainley D.G.& MeMaster D.P. (1990) The upper trophic levels in polar marine ecosystem. In: Dayton PK, editor. *Polar Oceanography, Part B: Chemistry, Biology, and Geology*. LaJolla: Academic Press, Inc. pp. 599-629.
4. Hunt G.L.J. (1991) Marine Ecology of Seabirds in Polar Oceans. *Amer Zool* 31: 131-142.
5. Tynan C.T. (1998) Ecological importance of the Southern Boundary of the Antarctic Circumpolar current. *Nature* 392: 708-710.
6. Ainley D.G., Spear L.B., Tynan C.T., Barth J.A., Pierce S.D., et al. (2005) Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep Sea Research Part II: Topical Studies in Oceanography* 52: 123-143.
7. Ainley, D.G. & Jacobs, S.S. (1981) Sea Bird Affinities for Ocean and Ice Boundaries in the Antarctic. *Deep-Sea Research Part I-Oceanographic Research Papers* 28: 1173-1186.
8. Croxall, J.P., Everson, I., Kooyman, G.L., Ricketts, C. & Davis R.W. (1985) Fur seal, *Arctocephalus gazella*, diving behavior in relation to vertical distribution of krill, *Euphausia superba*. *Journal of Animal Ecology* 54: 1-8.
9. Boyd, I. l. (1996) Temporal Scales of Foraging in a Marine Predator. *Ecology* 77: 426-434.
10. Bestley, S., Patterson, T.A., Hindell, M.A. & Gunn, J.S. (2008) Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming. *Journal of Animal Ecology* 77: 1223-1233.
11. Bestley S, Gunn, J.S. & Hindell, M.A. (2009) Plasticity in vertical behaviour of migrating juvenile southern bluefin tuna (*Thunnus maccoyii)* in relation to oceanography of the south Indian *Ocean. Fisheries Oceanography* 18: 237-254.
12. Haney J.C. (1986) Seabird patchiness in tropical oceanic waters: the influence of Sargassum "Reefs". *Auk* 103: 141-151.
13. Costa D.P., Croxall J.P. & Duck C.D. (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* 70: 596-606.
14. Veit R.R., Silverman E.D. & Everson I. (1993) Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *J Animal Ecology* 62: 551-564.
15. Croll D.A., Tershy, B.R. (1998) Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. *Polar Biol* 19: 365-374.
16. Fraser, W.R., Pitman, R.L, & Ainley, D.G. (1989) Seabird and Fur Seal Responses to Vertically Migrating Winter Krill Swarms in Antarctica. *Polar Biology* 10: 37-42.
17. Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473-476.
18. Myers, R.A. & Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283.
19. Smetacek, V., & Cloern, J.E. (2008) Oceans. On phytoplankton trends. *Science* 319: 1346-1348.
20. Croll D.A., Marinovic, B., Benson, S., Chavez, F.P., Black, N., et al. (2005) From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology-Progress Series* 289: 117-130.
21. Benson, S.R., Croll, D.A., Marinovic, B.B., Chavez, F.P., & Harvey, J.T. (2002) Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Nino 1997-98 and La Nina 1999. *Progress in Oceanography* 54: 279-291.
22. Costa, D.P. (2008) A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17: S44-S52.

23. Weise, M.J., Costa, D.P., Kudela, R.M. (2006) Movement and diving behavior of male California sea lion *(Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. *Geophys Res Lett* 33: L22S10.
24. Trathan, P.N., Forcada, J., Murphy, E.J. (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philosophical Transactions of the Royal Society B-Biological Sciences* 362: 2351-2365.
25. McMahon, C.R., Hays, G.C. (2006) Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biology* 12: 1330-1338.
26. O'Dor R, Yarincik K (2010) Bringing life to ocean observation. In these proceedings (Vol. 1).
27. Costa D. P.& Sinervo B. (2004) Field physiology: physiological insights from animals in nature. *Annu Rev Physiol* 66: 209-238.
28. Block, B.A. (2005) Physiological Ecology in the 21st Century: Advancements in Biologging Science. Integr Comp Biol 45: 305-320.
29. Shaffer, S.A. & Costa, D.P. (2006) A database for the study of marine mammal behavior: gap analysis, data standardization, and future directions. *Oceanic Engineering, IEEE Journal of Ocean Engineering* 31: 82-86.
30. Boustany, A. (2006) *Migratory movements, population structure and environmental preferences of northern bluefin tuna revealed through electronic tagging and population genetics* [Dissertation]. Palo Alto: Stanford University.
31. Boustany, A.M., Davis, S.F., Pyle, P., Anderson, S.D., Le Boeuf BJ, et al. (2002) Satellite tagging: Expanded niche for white sharks. *Nature* 415: 35-36.
32. Klimley, A.P., Voegeli, F., Beavers, S.C. & LeBoeuf, B.J. (1998) Automated listening stations for tagged marine fishes. Marine Technology Society Journal 32: 94-101.
33. Delong, R.L., Stewart, B.S. & Hill, R.D. (1992) Documenting Migrations of Northern Elephant Seals Using Day Length. *Marine Mammal Science* 8: 155-159.
34. Metcalfe JD (2006) Fish population structuring in the North Sea: understanding processes and mechanisms from studies of the movements of adults. *Journal of Fish Biology* 69: 48-65.
35. Block, B.A., Dewar, H., Williams, T., Prince, E.D., Farwell, C., et al. (1998) Archival tagging of Atlantic bluefin tuna (Thunnus thynnus thynnus). *Marine Technology Society Journal* 32: 37-46.
36. Block, B.A., Dewar, H., Farwell, C. & Prince, E.D. (1998) A new satellite technology for tracking the movements of atlantic bluefin tuna. *Proc Natl Acad Sci U S A* 95: 9384-9389.
37. Lutcavage, M.E., Brill, R.W., Skomal, G.B., Chase, B.C. & Howey, P.W. (1999) Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Sciences* 56: 173-177.
38. McConnell, B.J., Chambers, C., Nicholas, K.S. & Fedak, M.A. (1992) Satellite Tracking of Grey Seals (*Halichoerus grypus*). *Journal of Zoology* 226: 271-282.
39. McConnell, B.J., Fedak, M.A., Lovell, P. & Hammond, P.S. (1999) Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology* 36: 573-590.
40. Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., et al. (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293: 1310-1314.
41. Fedak M, Lovell P, McConnell B. & Hunter, C. (2002) Overcoming the constraints of long range radio telemetry from animals: Getting more useful data from smaller packages. *Integ Comp Biol* 42: 3-10.
42. Shaffer S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R., et al. (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc Natl Acad Sci U S A* 103: 12799-12802.
43. Block, B.A., Teo, S.L., Walli, A, Boustany A, Stokesbury MJ, et al. (2005) Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434: 1121-1127.
44. Johnson, M., Madsen, P.T., Zimmer, W.M., de Soto, N.A. & Tyack, P.L. (2004) Beaked whales echolocate on prey. *Proc Biol Sci* 271 Suppl 6: S383-386.
45. Tinker, M.T., Costa, D.P., Estes, J.A. & Wieringa, N. (2007) Individual dietary specialization and dive behaviour in the California sea otter: Using archival time-depth data to detect alternative foraging strategies. *Deep Sea Research Part II: Topical Studies in Oceanography* 54: 330-342.
46. Teo S.L.H., Boustany A., Blackwell, S.B., Walli A, Weng K.C., et al. (2004) Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Mar Ecol Prog Ser* 283: 81–98.
47. Shaffer S.A., Tremblay Y, Awkerman J.A., Henry R.W., Teo S.L.H., et al. (2005) Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* V147: 833-843.
48. Weimerskirch, H, Salamolard, M, Sarrazin, F., & Jouventin P. (1993) Foraging strategy of Wandering albatrosses through the breeding season: A study using satellite telemetry. *The Auk* 110: 325-342.
49. Weimerskirch, H., Guionnet, T., Martin, J., Shaffer S.A. & Costa, D.P. (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London Series B-Biological Sciences* 267: 1869-1874.
50. Burns, J.M.& Kooyman, G.L. (2001) Habitat use by Weddell seals and emperor penguins foraging in the Ross Sea, Antarctica. *American Zoologist* 41: 90-98.
51. Renaud, M.L., Carpenter, J.A. (1994) Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bulletin of Marine Science* 55: 1-15.
52. Polovina J.J., Kobayashi D.R., Parker D.M., Seki M.P., Balazs G.H. (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997-1998. *Fisheries Oceanography* 9:. 71-82.

53. Weng, K.C, Castilho, P.C., Morrissette, J.M., Landeira-Fernandez, A.M., Holts, D.B., et al. (2005) Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* 310: 104-106.
54. Eckert, S.A., Dolar, L.L., Kooyman, G.L., Perrin, W. & Rahman, R.A. (2002) Movements of whale sharks (Rhincodon typus) in South-east Asian waters as determined by satellite telemetry. *Journal of Zoology* 257: 111-115.
55. McConnell, B.J., Chambers, C., Fedak, M.A. (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* 4: 393-398.
56. Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., et al. (2000) Foraging ecology of northern elephant seals. *Ecological Monographs* 70: 353-382.
57. Boehme L, K. Kovacs K, C. Lydersen, O. A., Nøst, O.A., M., Biuw, M., et al. (2010) Biologging in the global ocean observing system. In these proceedings (Vol 2).
58. Charrassin, J.A., Roquet, F., Park, Y.H., Bailleul, F., Guinet, C., et al. (2010) New insights into Southern Ocean physical and biological processes revealed by instrumented elephant seals. In these proceedings (Vol 2).
59. Lutcavage, M.E., Bushnell, P.G. & Jones, D.R. (1990) Oxygen transport in the Leatherback Sea Turtle *Dermochelys coriacea*. *Physiological Zoology* 63: 1012-1024.
60. Boehlert GW, Costa DP, Crocker DE, Green P, O'Brien T, et al. (2001) Autonomous pinniped environmental samplers: Using instrumented animals as oceanographic data collectors. *Journal of Atmospheric and Oceanic Technology* **18:** 1882-1893.
61. Boehme, L, Meredith M.P., Thorpe, S.E., Biuw, M. & Fedak M (2008) Antarctic Circumpolar Current frontal system in the South Atlantic: Monitoring using merged Argo and animal-borne sensor data. Journal Geophysical Research 113.
62. Boehme, L, Thorpe, S.E., Biuw, M., Fedak, M., & Meredith, M.P. (2008) Monitoring Drake Passage with elephant seals: Frontal structures and snapshots of transport. *Limnol Oceanogr* **53**: 2350-2360.
63. Charrassin, J.B., Hindell ,M., Rintoul, S.R., Roquet, F., Sokolov, S., et al. (2008) Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. *Proceedings of the National Academy of Sciences of the United States of America* **105:** 11634-11639.
64. Costa, D.P., Klinck, J.M., Hofmann, E.E., Dinniman, M.S., Burns, J.M. (2008) Upper ocean variability in West Antarctic Peninsula continental shelf waters as measured using instrumented seals. *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 323-337.
65. Nicholls, K.W., Boehme, L, Biuw, M. & Fedak, M.A. (2008) Wintertime ocean conditions over the southern Weddell Sea continental shelf, Antarctica. *Geophys Res Lett* 35.
66. Hooker, S.K. & Boyd, I.L (2003) Salinity sensors on seals: use of marine predators to carry CTD data loggers. *Deep-Sea Research Part I-Oceanographic Research Papers* 50: 927-939.
67. Campagna, C, Piola A.R., Marin M.R., Lewis, M. & Fernandez T (2006) Southern elephant seal trajectories, fronts and eddies in the Brazil/Malvinas Confluence. *Deep-Sea Research Part I-Oceanographic Research Papers* 53: 1907-1924.
68. Lydersen, C., Nost, O.A., Lovell, P., McConnell, B.J., Gammelsrod, T., et al. (2002) Salinity and temperature structure of a freezing Arctic fjord - monitored by white whales (Delphinapterus leucas) - art. no. 2119. *Geophysical Research Letters* 29: 2119.
69. Charrassin, J-B., Hindell, M, Rintoul, S.R., Roquet, F., Sokolov, S., et al. (2008) Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. *Proceedings of the National Academy of Sciences* 105: 11634-11639.
70. Biuw M, Boehme L, Guinet C, Hindell M, Costa D, et al. (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proceedings of the National Academy of Sciences* 104: 13705-13710.
71. Weimerskirch H, Wilson, R.P., Guinet, C. & Koudil, M. (1995) Use of seabirds to monitor sea-surface temperatures and to validate satellite remote-sensing measurements in the Southern Ocean. *Marine Ecology Progress Series* 126: 299-303.
72. Charrassin, J-B, Park, Y-H, Le Maho,.Y. & Bost, C.A. (2002) Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecology Letters* 5: 317-466.
73. Charrassin, J.B., Park, Y.H., Le Maho, Y. & Bost, C.A. (2004) Fine resolution 3D temperature fields off Kerguelen from instrumented penguins. *Deep-Sea Research Part I-Oceanographic Research Papers* 51: 2091-2103.
74. McMahon, C.R., Autret, E, Houghton, J.D.R., Lovell, P., Myers, A.E., et al. (2005) Animal-borne sensors successfully capture the real-time thermal properties of ocean basins. *Limnology and Oceanography-Methods* 3: 392-398.
75. Block, B.A., Keen, J.E., Castillo, B., Dewar, H., Freund, E.V., et al. (1997) Environmental preferences of yellowfin tuna (Thunnus albacares) at the northern extent of its range. *Marine Biology* 130: 119-132.
76. Shillinger, G,L, Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., et al. (2008) Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol* 6: e171.
77. Bailey, H.R., Shillinger, G.L., Palacios, D.M., Bograd, S.J., Spotila, J.R., et al. (2008) Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology* 356: 128-135.
78. Peckham, S.H., Maldonado, D., Walli, A., Ruiz, G., Nichols, W.J., et al. (2007) Small-scale fisheries bycatch of Pacific loggerheads can rival that in large-scale oceanic fisheries. *PLoS Biology ONE* 2: 1-6.