THE SECRET LIFE OF MARINE MAMMALS

NOVEL TOOLS FOR STUDYING THEIR BEHAVIOR AND BIOLOGY AT SEA

By Daniel P. Costa

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Given the interest by both the lay and scientific communities, it is surprising how little is known about the open ocean ecology of marine mammals. Their patchy distribution and low abundance leads to infrequent encounters at sea. Most of our information on marine mammals has been obtained from shipboard or aerial observations, which provide a very limited perspective on their life at or near the surface, with little insight into their behavior under the water where they spend up to 90% of their time. Recent advances in technology are providing an opportunity to gain new insights into the underwater lives of marine mammals. Preliminary information indicates that marine mammal distribution and abundance is highly correlated with oceanic features like frontal systems, thermocline depth, bathymetry, eddies, jets, and warm core rings. These features concentrate or aggregate prey, permitting effective predation. The technologies now available or under development will enable an examination of how oceanic features and processes affect marine mammal biology. This article summarizes some of the novel technologies that are currently available or under development. It is hoped that an increased awareness of the research potential of these approaches will stimulate interdisciplinary collaborations between marine mammal biologists, fisheries biologists, and physical and biological oceanographers.

Recoverable Data Loggers

Recoverable multichannel digital data loggers are available with variable sampling rates that record depth, light level, water temperature, swim velocity, and surface location. The first instruments to be deployed measured dive depth as a function of time and have provided a wealth of information on the diving performance of marine mammals (Kooyman 1989; Costa 1991a,b). Typically these devices are attached to the animal (using a harness or glue; Fig. 1), and the data are retrieved when the device is recovered after recapture of the animal. The need to recapture the animal limits this system, but it has been used quite successfully on studies of pinnipeds (sea lions, fur seals, and seals). An example of a time-depth record obtained for an Australian sea lion is shown in Figure 2.

A summary of the diving data obtained indicates that the "true" or earless seals (*Phocidae*) are capable of deeper longer dives than sea lions and fur seals (*Otariidae;* Fig. 3). These differences reflect optimization for exploitation of different habitats and resources (Costa, 1993). Sea lions and fur seals feed on vertically moving prey that approach the surface, whereas true seals feed on sedentary benthic or midwater prey. The considerable difference between mean dive depth/duration and maximum dive depth/duration suggests that seals and sea lions rarely reach their physiological limit with respect to dive depth or duration. Other factors such as prey type, depth, and availability determine the optimal diving pattern, and prey availability is directly related to oceanic features and processes.

Coordination of data on diving pattern with information on prey species indicates that prey size, behavior, and energy content influence the foraging pattern employed (Costa, 1991a,b). The most detailed study of foraging behavior carried out on Antarctic fur seals (Croxall *et al.*, 1985), showed that these seals made most (75%) of their dives at night, when dives were consistently shallower (<30 m) than dives during the daytime (mostly 40–75 m). This pattern closely followed the vertical distribution of krill, which during daylight hours was below a depth of 50 m and at night was present in substantial quantities above 50 m. Even though >40% of the krill was below 75 m depth at all times of the day, fur seal dives seldom (3%) exceeded this depth. The authors concluded that krill are captured only from shallow depths, since this is when they are most efficiently obtained.

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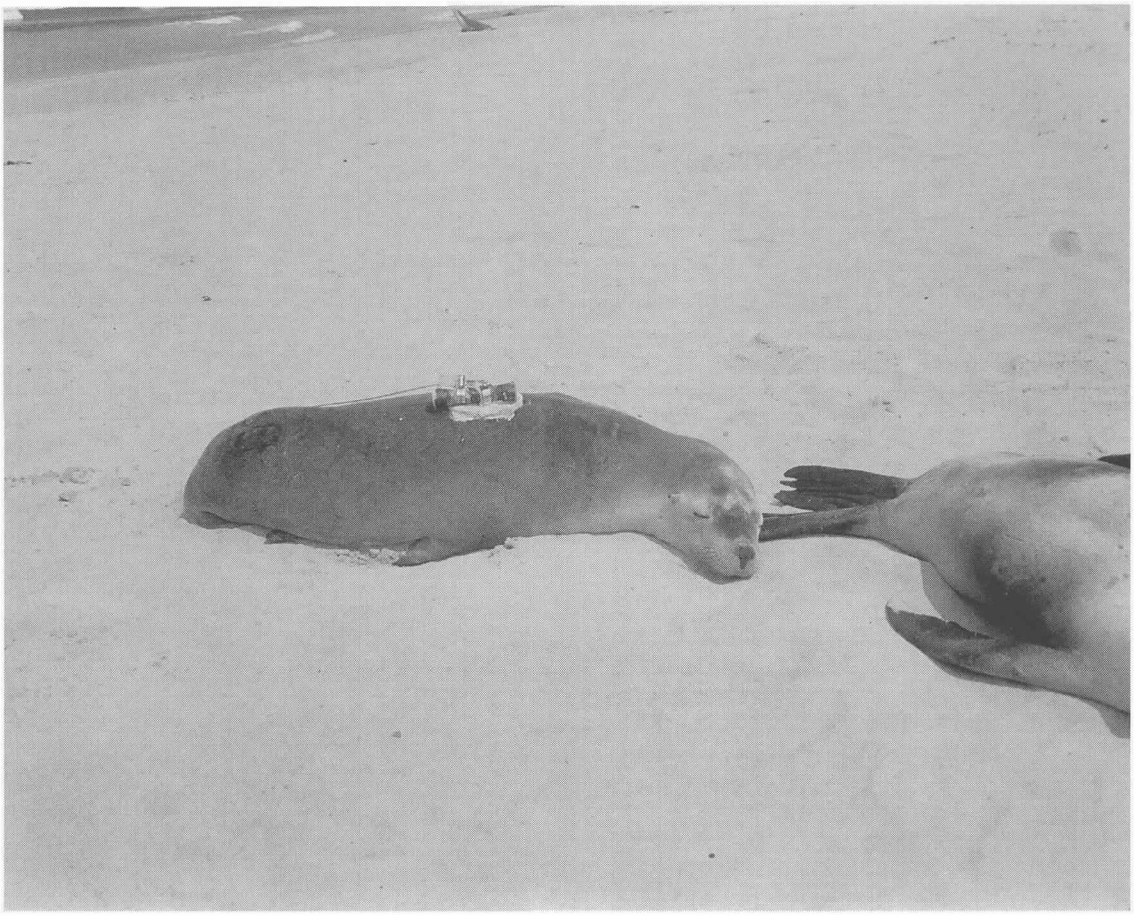

Fig. 1: An Australian sea lion female with a Wildlife Computers time-depth recorder glued to the hair on her back.

In a similar study it was found that female northern fur seals exhibit distinct diving patterns specific to the type of prey consumed. During a foraging trip (typically lasting 7 days), an individual northern fur seal female exhibited one of the following dive patterns: those composed exclusively of deep dives with a mean depth of 185 m, those composed exclusively of shallow dives with a mean depth of 50–60 m, and those with a mixture of both deep and shallow dives (Gentry and Kooyman, 1986). Deep-diving northern fur seals did not exhibit diurnal fluctuations in diving depth, which implied that they were feeding on demersal or benthic species, whereas shallow divers exhibited a striking diurnal fluctuation in diving pattern quite similar to that observed for Antarctic fur seals eating krill. A subsequent study using a combination of time-depth recorder and VHF telemetry determined that deep-diving fur seals feed on demersal fish such as pollock on the Bering Sea shelf, whereas shallow-diving fur seals feed on vertically migrating squid over deep water beyond the Bering Sea shelf (Goebel *et al.*, 1991). Like krill, squid are available throughout the day, and like krill-consuming Antarctic fur seals, northern fur seals wait for squid to move into shallow water before preying on them.

The most impressive data obtained so far on pinniped diving behavior come from studies of northern and southern elephant seals (Le Boeuf and Laws, 1994). Northern elephant seals dive continuously, day and night, for the entire trip to sea, which lasts between 2 and 8 months (Fig. 4). Two-month trips are associated with females who have just completed lactation and are returning to molt, whereas the 8-month foraging trip follows the molting period and is when gestation occurs. While at sea, they spend 90% of their time underwater, with dives averaging 20 minutes (maximum dives in excess of ½ hr) followed by surface intervals of less than 3 minutes. Their diving patterns follow a diurnal cycle with the deepest dives occurring during the day and shallowest at night. Modal dive depths are 300–600 m with maximum dives exceeding 1,500 m!

Recently, the track of elephant seals during these foraging trips have been determined by measurements of light level and water temperature while they are at the surface. Location is calculated by extrapolation of light levels to provide time of

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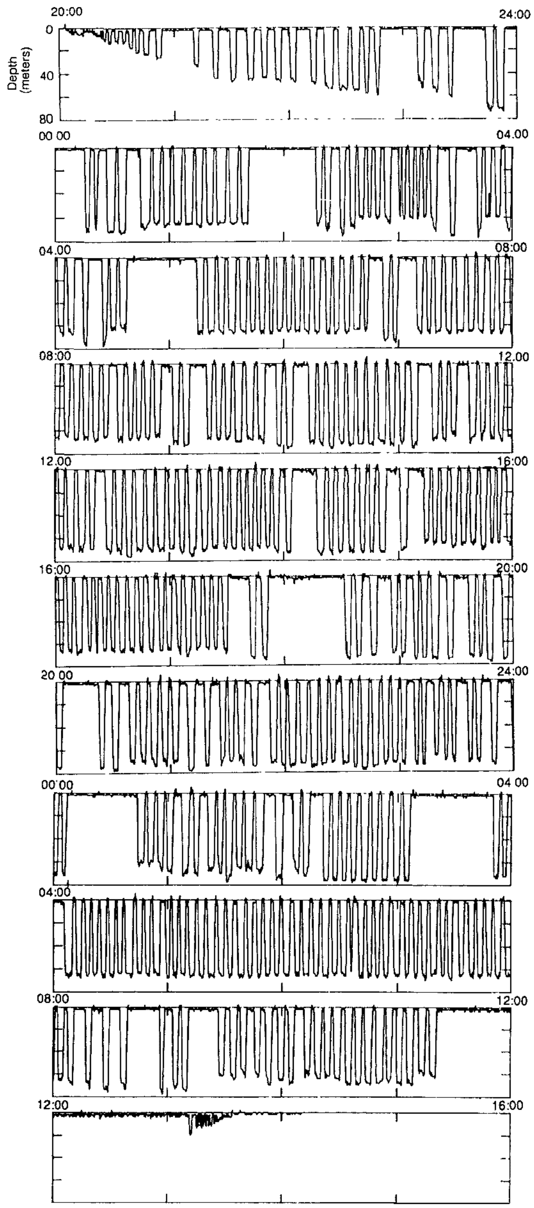

Fig. 2: The diving pattern (dive depth versus time) over a complete 42-h foraging trip obtained from an Australian sea lion female (from departure to return to shore). Time is divided into 4-h blocks and depth extends from 0 to 80 meters.

sunrise, sunset, and local apparent noon. Latitude is calculated from day length, and longitude from local apparent noon as referenced to Greenwich mean time (DeLong *et al.*, 1992). Previously, it had been assumed that northern elephant seals existed in offshore waters from California to British Columbia. However, geolocation time-depth recorders indicate that males travel from California to foraging areas along the continental slope from the state of Washington north to the upper reaches of the Gulf of Alaska and to the eastern Aleutian Islands, whereas females disperse more widely across the northeastern Pacific, as far as 150°W (about due north of the Hawaiian Islands), in the range 44–52°N (De Long *et al.,* 1992) (Fig. 5).

Although these results are impressive, they have yet to be integrated into models that relate animal location and behavior with oceanographic phenomena such as frontal systems, eddies, upwelling zones, warm core rings, and thermoclines. However, one recent study on southern elephant seals used a time-depth recorder that incorporated data on water temperature (Boyd and Arnbom, 1991). An elephant seal was observed to descend rapidly to the discontinuity between cold surface water and warmer deep water. The animal spent a substantial amount of its time (57%) at or near the thermocline indicating the likelihood that it was foraging there. Further, the structure of the water mass indicated that the animal was foraging south of the Antarctic Polar Front. Ultimately marine mammal distribution, abundance, and behavior is related to the oceanographic factors that determine prey distribution. Our understanding of this relationship is limited and is thus a fertile area for investigation.

Significant insights have been gained from data on time and depth and additional sensors are being incorporated into the devices. For example, investigators are looking for ways to incorporate precise information on location derived from the Global Positioning System Satellite (GPS). Equipment is being designed and tested that would allow the data logger to be released from the animal upon command from a radio transmitter, or permit stored data to be recovered via short-range radio or acoustic telemetry. Data loggers currently available can record at-sea location (within 40 km), dive frequency and profile, swim velocity, heart rate, and water temperature. Other sensors that can measure and record information on ambient acoustic environment, ocean structure (salinity), and feeding behavior are being tested or are under development.

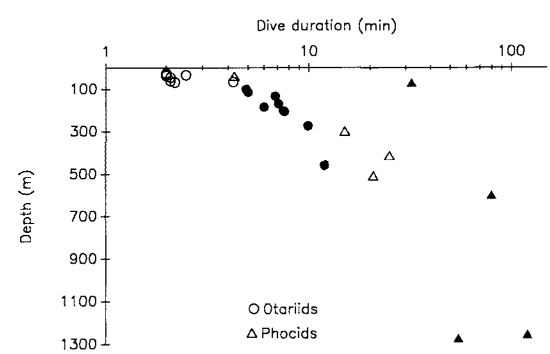

Fig. 3: Mean (○, △) and maximum (●, ▲) dive depth plotted as a function of dive duration for 4 seals (△, ▲) and 7 sea lions or fur seals (○, ●). (See Costa, 1993 for references).

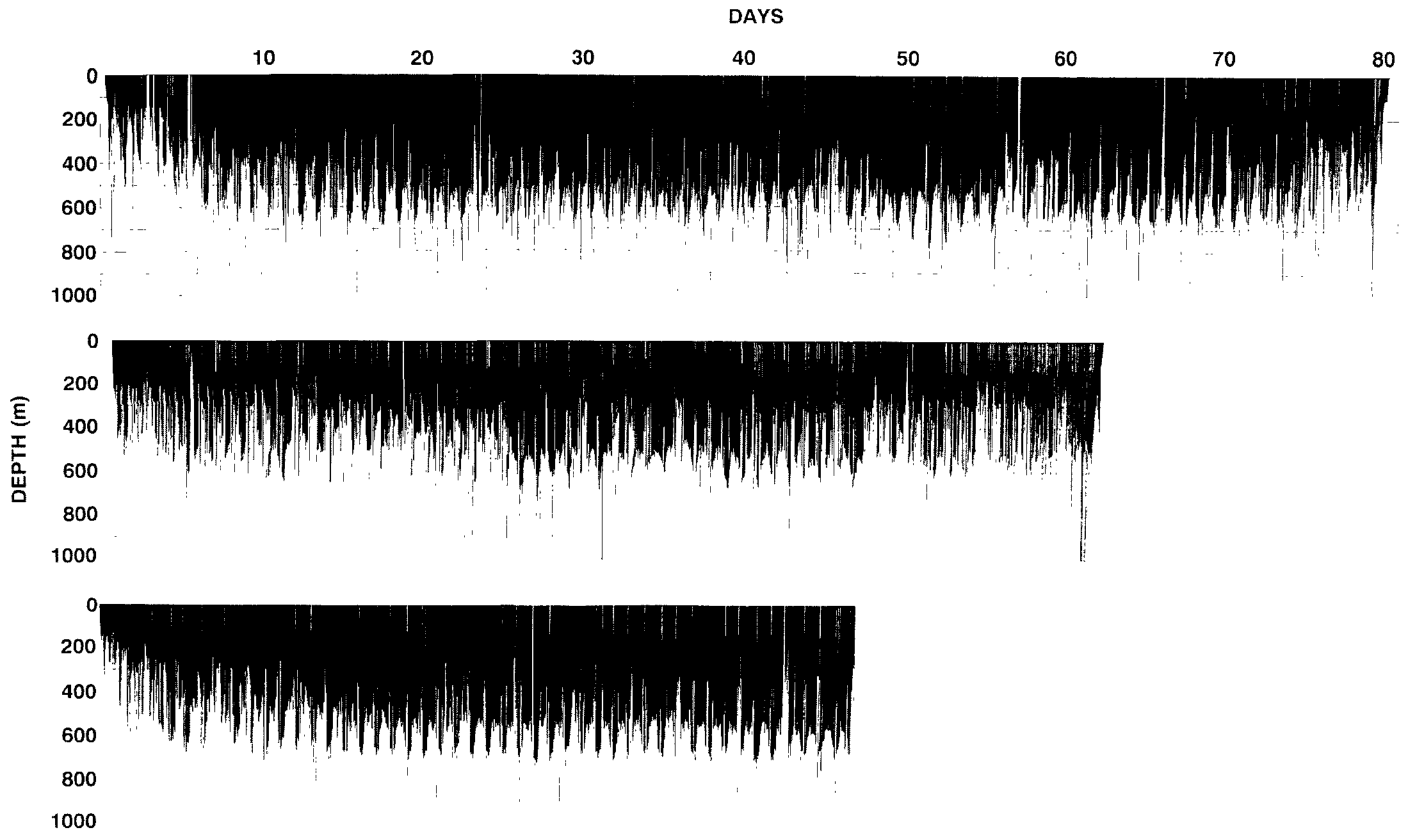

Fig. 4: Diving patterns typical of three adult female northern elephant seals over one complete foraging trip to sea (departure and return to Año Nuevo Island). Notice the diurnal pattern with regard to dive depth and that diving in continuous throughout the 80-day period. (From Le Boeuf et al., 1989).

Satellite Telemetry

Most marine mammals are difficult to approach once, let alone twice to recover a data logger. Furthermore, standard radio telemetry requires the investigator to be within 1–20 km of the animal. This is where satellite telemetry provides an excellent tool to track animals anywhere in the world. Although ARGOS satellite tracking systems have been operational since 1979, the tags used to be too big, expensive, or unreliable for systematic deployment on marine mammals. Recent reductions in size due to solid-state electronics and greater transmission efficiency has led to significant advances in our ability to track marine mammals with this system. The ARGOS system is a French instrument that flies aboard two National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites and is jointly operated by Service Argos Inc. (Landover, MD, USA) and CLS/Service ARGOS (Toulouse, France). ARGOS is a random access, one-way system that collects uplinked messages from platform transmitter terminals (PTTs) operating within view of the satellite. An ARGOS PTT uplink consists of a 1-sec, 401.65-MHz signal every minute, carrying a maximum message per transmission of 256 bits. However, the satellite is only overhead for a few minutes every few hours depending on the latitude of the PTT. For a PTT that is always on the surface (like a buoy) typically eight transmissions can be received every 2 hrs. Unfortunately, marine mammals are often underwater while the satellite is overhead, so this uplink rate is rarely achieved. Geographic position of a PTT is calculated by the ARGOS satellite from information on its orbit, speed, and the received doppler shift of the PTT signal. Location accuracy varies from class 3 (68% within 150 m of truth) to class 0 (unguaranteed) and is determined primarily by the number of uplinks per satellite pass. Because marine mammals spend most of their time underwater, most locations are class 0. However, filtering algorithms have been developed which exclude class 0 locations with large errors (McConnell *et al.*, 1992b). The two ARGOS satellites can provide up to 6 locations per day in equatorial regions, 8 in temperate regions, and up to 20 per day in the polar regions of the world. A variety of manufacturers produce ARGOS-certified PTTs, including Telonics Inc. (Mesa AZ), Microwave Telemetry (Columbia, MD), Southwest Research Institute (San Antonio, TX), and Toyocom (Tokyo, Japan). Other manufacturers have incorporated data loggers that

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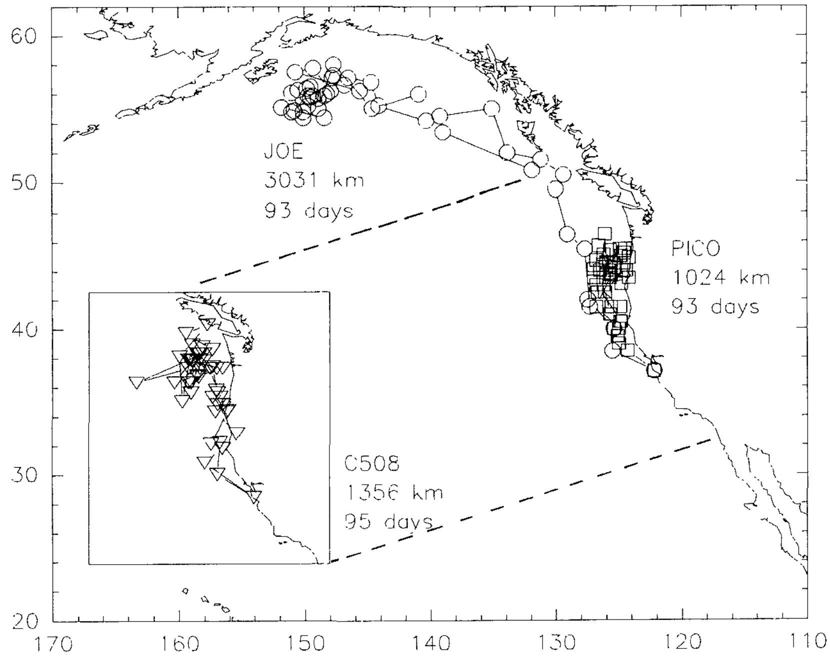

Fig. 5: Migratory path of an adult female (Pico) and adult male (Joe) northern elephant seal after the breeding season. The track starts at Año Nuevo, California. Positions were plotted from light levels and sea surface temperature every 2 days. (From Le Boeuf et al., 1993).

record data on the animal's diving pattern with PTTs to provide information on behavior at sea. These include Wildlife Computers (Woodinville, WA) and the Sea Mammal Research Unit (Cambridge, England).

The decreased size and greater capability of satellite tags has led to a significant increase in their use with marine mammals. Many studies are currently underway and the results have yet to be published. Nonetheless the following is a sampling of the exciting results satellite telemetry has yielded. During 1989 and 1990 seven North Atlantic right whales were tagged and tracked in the Bay of Fundy (Mate *et al.*, 1992). The study tracked right whales for 6 weeks and led to a revision of our belief that these animals are slow-moving, nearshore, surface-oriented creatures. They traveled long distances at high speeds, going more than 500 km offshore into waters >4,000 m deep, routinely diving to 200 m, with a male reaching a maximum depth of 272 m. A female and her calf traveled 3,800 km in 43 days between the Bay of Fundy and New Jersey, and a male right whale was observed to travel 3,000 km. These animals left the Bay of Fundy and then returned, indicating that they are not strictly resident in this area. Individual whales averaged 30–113 km/d (1.3–4.7 km/hr) with an overall mean of 3.7 km/hr. Speeds of 10 km/hr were recorded while animals were traveling in current

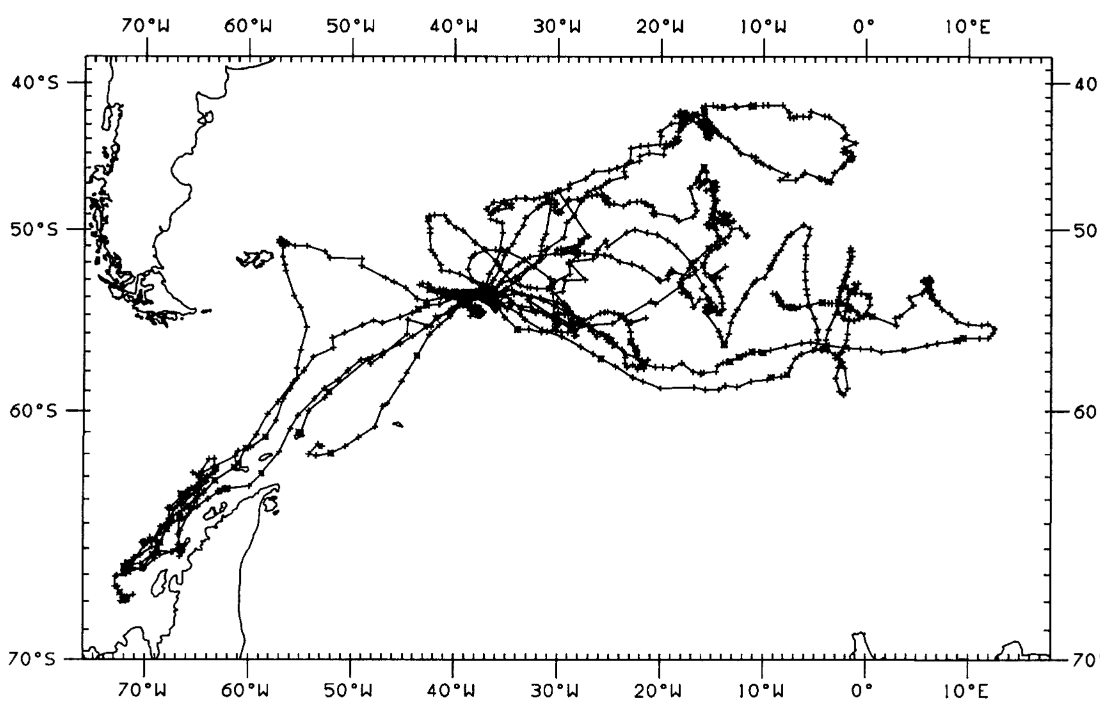

Fig. 6: Tracks of 10 southern elephant seals leaving South Georgia Island for foraging grounds in the southern ocean. Over 1,800 seal-days of location and dive data were obtained using ARGOS-linked satellite telemetry. The southern tip of South America can be seen in the top left and the Antarctic Peninsula in the bottom left. (B. McConnell and M. Fedak, personal communication).

systems. In several cases movements were associated with oceanographic features of the Gulf Stream including temperature gradients, warm core rings, and eddies. These areas are associated with increased local primary production or aggregation of prey.

Investigators at the Sea Mammal Research Unit (SMRU) have developed satellite tags that acquire information on animal location, dive depth, and swim velocity. The first application of these units was on grey seals off the coast of England, where an animal was observed for up to 111 days and routinely traveled between haul-out sites 265 km apart (McConnell *et al.,* 1992a). Similar tags have now been deployed on over 30 beluga whales in the Canadian Arctic. Previously thought to be a coastal species, beluga whales were found to spend considerable amounts of time offshore in deep water. They dive to at least 440 m and remain submerged for up to 18 minutes (Martin and Smith 1992; Martin, *et al.,* 1993). The dive depth and swim velocity profiles were indicative of feeding on bottom-dwelling fish like halibut or on benthic invertebrates. During the fall migration average sustained speeds of 4 km/hr are common, illustrated by one whale that swam from Franklin Strait off southeast Prince of Wales Island to southern Ellesmere Island, a distance of 1,400 km in 15 days .

Some of the most exciting work to come out of the SMRU is that on southern elephant seals. Although their diving pattern has been well described using recoverable time-depth recorders (Hindell *et al.,* 1991), there was little information on specific locations where the dives took place. Diving and traveling patterns of 10 elephant seal females tagged at South Georgia Island in the South Atlantic were recorded using ARGOS-linked satellite tags (McConnell *et al.,* 1992b) (Fig. 6). Regardless of the direction of travel, all animals traversed deep water before the initiation of "foraging" dives, apparently in an effort to feed in areas associated with hydrographic features where prey might be concentrated. One female swam 1,845 km in 23 days to Livingston Island, where she hauled out for 18 hrs and then traveled 805 km to the southwest following the continental shelf margin of the Antarctic Peninsula to the location of an underwater canyon 110 km west of Adelaide Island (Fig. 7). Once there she initiated a series of dives to the bottom (300–400 m), which were consistent with feeding. Prolonged transits to important foraging areas (associated with the Antarctic Polar front, continental shelf, or ice edge) are consistent with estimates inferred from sea-surface temperature measurements for elephant seals tagged on Macquarie Island (Hindell *et al.,* 1991).

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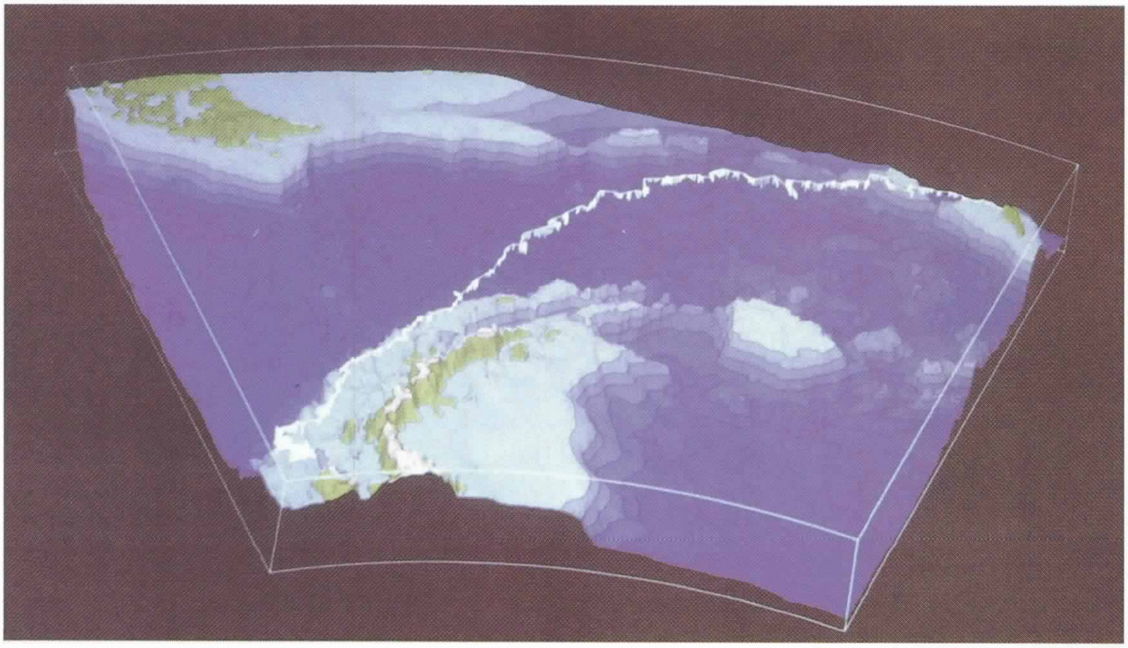

Fig. 7: Three-dimensional visualization of the track of a southern elephant seal that traveled from South Georgia Island to foraging grounds off Adelaide Island near the Antarctic Peninsula. The animal's dive depth and location have been merged with data on Southern Ocean bathymetry to help elucidate the role of oceanic features in the diving and foraging behavior of elephant seals (B. McConnell and M. Fedak, personal communication).

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Elephant seal physiology and reproductive biology are ideally suited for utilization of distant prey resources (Costa, 1993). These satellite data suggest that utilization of distant resources associated with relocatable hydrographic features, such as the Antarctic Polar Front and the continental shelf where prey is reliably concentrated is a more optimal foraging pattern than looking for prey patches nearer the breeding site (McConnell *et al.*, 1992b). However, recent data on southern elephant seals foraging from Patagonia, Argentina suggest that animals from this population do not forage near, in, or south of the Antarctic Polar Front (Campagna *et al.*, unpublished data). Obviously there is much to be learned about the role of oceanographic features in the foraging ecology of marine mammals.

Marine Mammals as Oceanographic Sensor Platforms or AUVs

Marine mammal biologists are interested in the physical environment utilized by marine mammals, but marine mammals can also be used to provide information on the oceanic environment. Data loggers that incorporate measurements of temperature and salinity or other parameters can be placed on marine mammals, which can thus be used as inexpensive autonomous vehicles. Each species of marine mammal occupies a unique range of oceanographic habitats and therefore could be used to sample different oceanographic regimes. For example, northern elephant seals could be used to acquire data from the Central and North Pacific down to 1,200 m. Coastal species such as California sea lions or bottlenose dolphins could acquire oceanographic profiles on nearshore systems, such as the California Current down to 300 m.

Integrated Undersea Surveillance System

A benefit of the greater access to military hardware resulting from the end of the cold war has been access to the Navy's Integrated Undersea Surveillance System (IUSS), which consists of both bottom-mounted and mobile hydrophone sensors that are used to localize low-frequency sound sources in the Atlantic and Pacific Oceans. Low-frequency sounds travel tremendous distances in the ocean, and, therefore, any animal that produces a low-frequency signal can be heard at comparable distances. The range over which a typical low-frequency blue whale vocalization can ensonify the environment and thus "communicate" to another whale, or receive information about the environment, can be seen in Figure 8. IUSS analysts visually identify such a whale signal on a time-versus-frequency display. If the signal is detected on more than one sensor, it is possible to determine the location of the animal. Results of a pilot effort in the

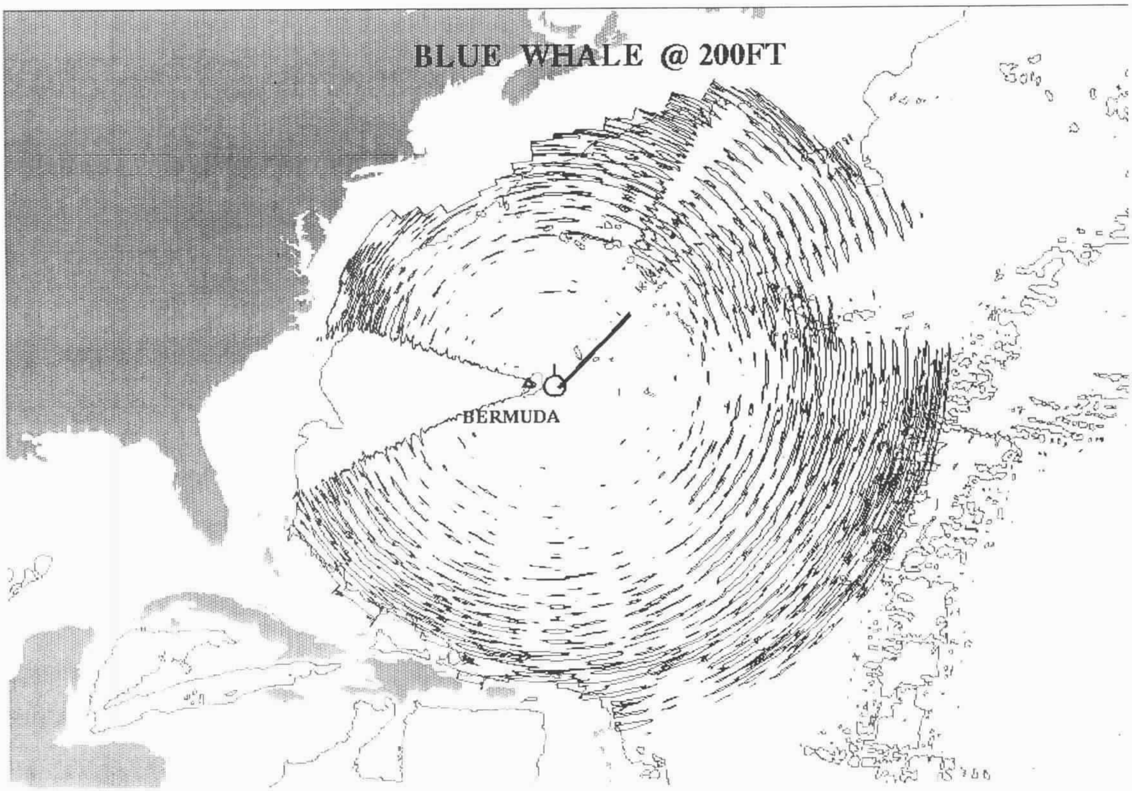

Fig. 8: The theoretical range (from sound propagation models) that a fin whale calling with an intensity of 185 dB re 1 μP at 15 Hz in 200 ft of water could be heard by another whale. The whale is located at the circle near Bermuda Island.

Atlantic IUSS are quite exciting (C. Clark, personal communication). Calls of minke, fin, blue and humpback whales have been tentatively identified and localized. Possibly the most exciting results come from observations of what appear to be blue whale vocalizations. Previously, the entire literature on blue whale vocalizations came from observations reported by Cummings and Thompson (1971) and from Edds (1982)! The low-frequency characteristics and duration make the call of blue whales ideal for tracking with the IUSS. The potential of this new tool was apparent on the first day of the program when more calls that fit the pattern for blue whales were recorded on one sensor's beam than had ever been previously reported (Clark, personal communication). Because individual animals may have unique characteristics or signatures to their calls, we should be able to follow the acoustic behavior of individuals. For example the movements of a single blue whale around Bermuda Island were tracked for 43 days covering >1,700 km (C. Gagnon, personal communication). If the details can be worked out and the appropriate validation experiments completed, this system will provide unequalled information on ocean-scale movements of whales and insights into how marine mammals use low-frequency signals and how they respond to acoustic disturbances in their environment. IUSS may allow us to define migration corridors, identify seasonal variations in vocalizations, and track individual animals. This system is capable of providing ocean-basin-scale synoptic observations of concentrations of vocalizing whales, crucial to understanding the distribution and abundance of large cetaceans. IUSS opens a new window on the ocean basin acoustic behavior of marine mammals. Not only are we finding calls that have been recorded before, but also numerous calls that are different from those previously reported. Just confirming which species are producing these sounds will be a challenging and rewarding endeavor.

Integration with Oceanography

Recoverable data loggers, satellite tags, and IUSS are providing an unprecedented insight into the open ocean ecology of marine mammals. However, proper interpretation of these data will require incorporation of information on ocean structure and prey distribution. Although marine mammals have been observed in association with oceanographic features such as bottom topography, frontal systems, and the thermocline (Hui, 1985; Winn *et al.*, 1986; Reilly, 1990; Boyd and Arnbom, 1991; Mate *et al.*, 1992; Whitehead *et al.*, 1992), this association is not well understood. A better understanding would be achieved if we knew what aspects of ocean structure are correlated with specific behaviors and whether marine mammals rely on oceanographic features to concentrate prey. One approach would be to use satellite tags and/or recoverable data loggers to collect data on the physical environment (e.g., ambient acoustic environment, water temperature and salinity profiles) with simultaneous collection of data on behavior (diving pattern, swim speed, and physiological status). The data could then be integrated with satellite remote sensing observations of large scale oceanographic features such as squirts, jets, warm core rings, and eddies. Simultaneous measurements of marine mammal diving behavior and prey distribution using active acoustic methods (Greene and Wiebe, 1990) would provide information on prey abundance and distribution, which would give considerable insight into the foraging strategies employed by marine mammals. A variety of new tools are providing an unprecedented opportunity to understand the open ocean ecology of marine mammals for which a multidisciplinary approach will be essential.

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References

Boyd, I.L. and T. Arnbom, 1991: Diving behavior in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biology, 11,* 259–266.

Costa, D.P., 1991a: Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *Am. Zool., 31,* 111–130.

Costa, D.P., 1991b: Reproductive and foraging energetics of pinnipeds: implications for life history patterns. In: *Pinniped Behavior,* D. Renouf, ed., Chapman Hill.

Costa, D.P., 1993: The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. In: *Recent Advances in Marine Mammal Science,* I. Boyd, ed., Zoological Society of London, Oxford University Press. *66,* 293–314.

Croxall, J.P., I. Everson, G.L. Kooyman, C. Ricketts and R.W. Davis, 1985: Fur seal diving behavior in relation to vertical distribution of krill. *J. Anim. Ecol., 54,* 1–8.

Cummings, E.E. and P.O. Thompson, 1971: Underwater sounds from the blue whale, *Balaenoptera musculus. J. Acoust. Soc. Am., 50,* 1193–1198.

DeLong, R.L., B.S. Stewart and R.D. Hill, 1992: Documenting migrations of northern elephant seals using day length. *Marine Mammal Sci., 8,* 155–159.

Edds, P., 1982: Vocalizations of the blue whale, *Balaenoptera musculus* in the St. Lawrence River. *J. Mammalogy, 62,* 345–347.

Gentry, R.L. and G.L. Kooyman, 1986: *Fur Seals: Maternal Strategies on Land and at Sea.* Princeton University Press, Princeton, NJ.

Goebel, M.E., J.L. Bengston, R.L. DeLong, R.L. Gentry and T.R.

Recoverable data loggers, satellite tags, and IUSS are providing an unprecedented insight into the open ocean ecology of marine mammals.

Loughlin, 1991: Diving patterns and foraging locations of female northern fur seals. *Fishery Bull.*, *89*, 171–179.

Greene, C. and P.H. Wiebe, 1990: Bioacoustical oceanography: new tools for zooplankton and micronekton research in the 1990s. *Oceanography*, *3*, 12–17.

Hindell, M.A., D.J. Slip and H.R. Burton, 1991: The diving behavior of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Aust. J. Zool.*, *39*, 595–619.

Hui, C.A., 1985: Undersea topography and the comparative distributions of two pelagic cetaceans. *Fisheries Bull.*, *83*, 472–475.

Kooyman, G.L., 1989: *Diverse Divers: Physiology and Behavior*, Springer-Verlag, New York, 200 pp.

Le Boeuf, B.J., Y. Naito, A.C. Huntley and T. Asaga, 1989: Prolonged, continuous, deep diving by northern elephant seals. *Can. J. Zool.*, *67*, 2514.

Le Boeuf, B.J. and R.M. Laws, eds., 1994: *Elephant Seals: Population Ecology, Behavior and Physiology*, University of California Press, Los Angeles.

Martin, A.R. and T.G. Smith, 1992: Deep diving in wild, free-ranging beluga whales, *Delphinapteras leucas*. *Can. J. Fish. Aquat. Sci.*, *49*, 462–466.

Martin, A.R., T.G. Smith and D.P. Cox, 1993: Studying the behaviour and movements of high Arctic belugas with satellite telemetry. *Symp. Zool. Soc. Lond.*, *66*, 195–210.

Mate, B.R., S. Nieukirk, R. Mesecar and T. Martin, 1992: Application of remote sensing methods for tracking large cetaceans: North Atlantic Right Whales. Final Report OCS Study MMS 91-0069, U.S. Dept of Interior MMS, Alaska and Atlantic OCS Regional Offices.

McConnell, B.J., C. Chambers, K.S. Nichols and M.A. Fedak, 1992a: Satellite tracking of grey seals (*Halichoerus grypus*). *J. Zool. Lond.*, *226*, 271–282.

McConnell, B.J., C. Chambers and M.A. Fedak, 1992b: Foraging ecology of southern elephant seals in relation to the oceanography of the Southern Ocean. *Antarctic Sci.*, *4*, 393–398.

Reilly, S.B., 1990: Seasonal changes in the distribution and habitat differences among dolphins in the eastern tropical Pacific. *Marine Ecol. Prog. Ser.*, *66*, 1–11.

Thompson, D. P.S. Hammond, K.S. Nicholas and M.A. Fedak, 1991: Movements and foraging behaviour of grey seals (*Halichoerus grypus*). *J. Zool. Lond.*, *224*, 223–232.

Whitehead, H., S. Brennan and D. Grover, 1992: Distribution and behavior of male sperm whales on the Scotian Shelf, Canada. *Can. J. Zool.*, *70*, 912–918.

Winn, H.E., C.A. Price and P.W. Sorenson, 1986: The distributional biology of the right whale (*Eubalaena glacialis*) in the Western North Atlantic. *Rep. Intl. Whal. Commn. Special Issue 10*. ❑