

# New Insights into Pelagic Migrations: Implications for Ecology and Conservation

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## Keywords

animal navigation, animal tracking, Argos, global positioning system (GPS), marine protected area, migration, satellite telemetry, transect survey

## Abstract

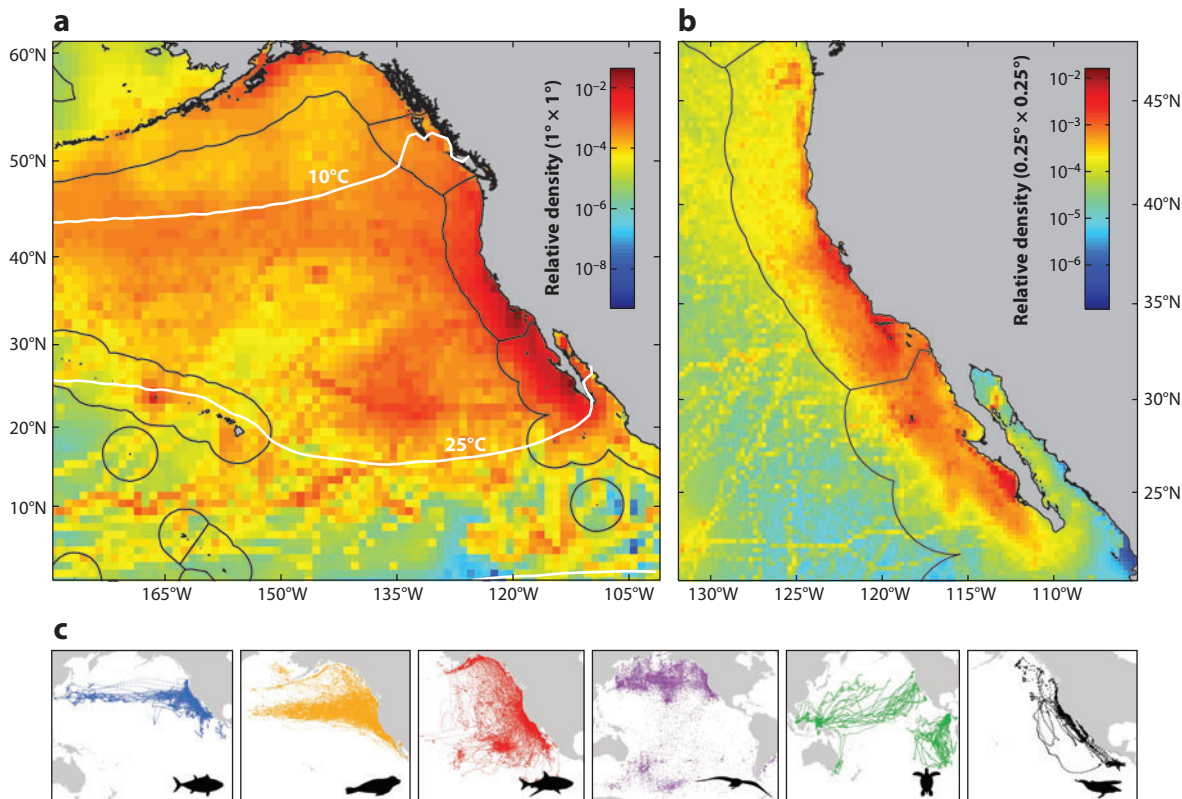
Highly pelagic large marine vertebrates have evolved the capability of moving across large expanses of the marine environment; some species routinely move across entire ocean basins. Our understanding of these movements has been enhanced by new technologies that now allow us to follow their movements over great distances and long time periods in great detail. This technology provides not only detailed information on the movements of a wide variety of marine species, but also detailed characteristics of the habitats they use and clues to their navigation abilities. Advances in electronic tracking technologies have been coupled with rapid development of statistical and analytical techniques. With these developments, conservation of highly migratory species has been aided by providing new information on where uncommon or endangered species go, what behaviors they perform and why, which habitats are critical, and where they range, as well as, in many cases, better estimates of their population size and the interconnectedness of subpopulations. Together these tools are providing critical insights into the ecology of highly pelagic marine vertebrates that are key for their conservation and management.

## 1. INTRODUCTION

Many pelagic vertebrates have evolved migratory life histories that allow them to adjust to dynamic marine environments by moving long distances to acquire needed resources that vary predictably in space and time. For many marine species, food resources and suitable breeding habitat are separated by hundreds or thousands of kilometers, necessitating seasonal migrations (Bost et al. 2009b, Boustany et al. 2010, Costa 1991, Le Boeuf et al. 2000, Mate et al. 1998, Rasmussen et al. 2007, Shillinger et al. 2008, Weng et al. 2005). These migrations may be repeated several times each year, as in the case of highly mobile species like albatross, but also annually or across multiple years as is the case for some tunas and sea turtles. Optimal habitat temperature, as much as food resources or breeding habitat, may also drive the migrations of both ectothermic and endothermic marine species (Block et al. 2011, Boustany et al. 2010, Durban & Pitman 2012, Rasmussen et al. 2007, Sleeman et al. 2010, Weng et al. 2005). In some species, the migratory cycle is associated with development; juveniles migrate to distant regions where prey resources are more available and later return to the breeding grounds as adults (Bestley et al. 2009, Boustany et al. 2010, Polovina et al. 2006). In colony-breeding species, the limited availability of predator-free regions, particularly islands, has resulted in many seabirds and pinnipeds evolving life histories that necessitate traveling hundreds or thousands of kilometers from breeding colonies to regions where suitable prey are abundant enough to profitably forage (Bost et al. 2009b, Costa 1991, Egevang et al. 2010, Le Boeuf et al. 2000, Shaffer et al. 2006, Weimerskirch et al. 2012).

The earliest studies of animal migration relied upon the seasonal presence or absence of animals on a breeding colony, region, or their seasonal availability in a fishery. Although this provided an understanding of population-level movement patterns, it was not until investigators applied unique identification tags to the legs, flippers, and bodies of animals, or took advantage of natural marks or scars, that it became possible to measure where, when, and how far individuals were actually migrating (Anderson et al. 2011, Rasmussen et al. 2007). More recently, stable isotopes have proven to be an excellent way to identify where animals forage during migrations because they can be used to track the large-scale displacements and also the geographic range of both extant and ancient animals (Newsome et al. 2010, Zbinden et al. 2011). Passive acoustic methods have also been used to track large-scale movements of vocal species such as whales (Sirovic et al. 2004).

Although conventional tagging and natural marks provide information on the general patterns of arrival and departure for many species, they do not provide information on migration corridors or individual movement patterns. Recent advancements in the size and power efficiency of electronic tracking tags ensures that tags are small enough not to affect natural behavior and robust enough to withstand the rigors of the marine environment; these factors have revolutionized our understanding of marine animal migration. A variety of electronic tagging technologies have been developed and deployed on large scales. Archival and satellite-linked data-logging tags have made possible the study of ocean basin-scale movements, oceanographic preferences, and the fine-scale behaviors of many pelagic species (Bailey et al. 2008; Bailleul et al. 2007; Block et al. 2005, 2011; Bost et al. 2009a; Boustany et al. 2010; Cotté et al. 2007; Dias et al. 2011; Guinet et al. 2001; Jorgensen et al. 2010; Le Boeuf et al. 2000; Shaffer et al. 2006; Shillinger et al. 2008). The most ambitious tagging effort to date has been the Tagging of Pacific Predators (TOPP) project, where 4,306 tags were deployed on 23 species in the North Pacific Ocean (Block et al. 2011) (**Figure 1**). Many of the TOPP animals exhibited clear periodicity in their movement patterns, which corresponded with changes in water temperature and primary production. Two regions stood out as important habitats, the highly productive California Current and the North Pacific Transition Zone. Leatherback sea turtles, Laysan and black-footed albatrosses, sooty shearwaters, bluefin

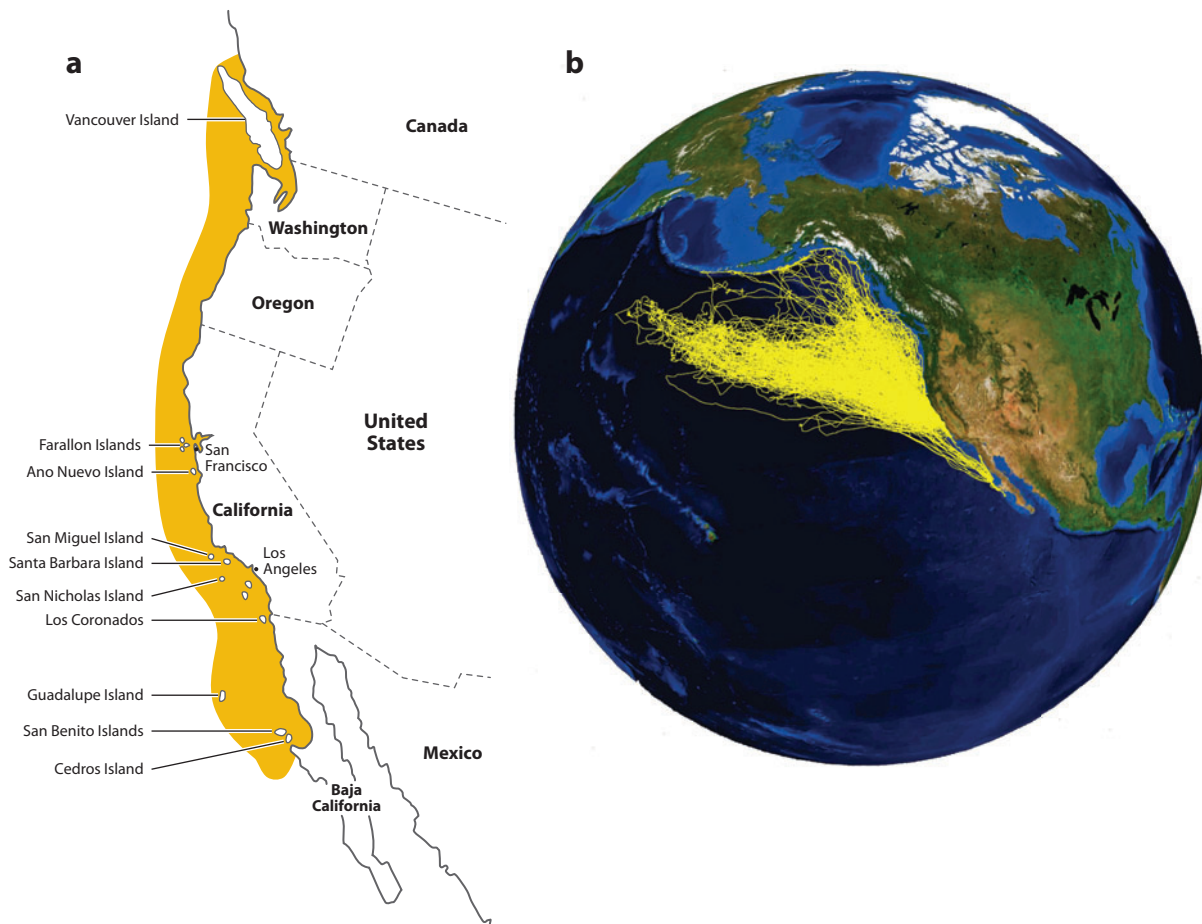


**Figure 1**

Predator density maps and residency patterns. (a) Density of large marine predators within the eastern North Pacific. Densities of the time-weighted and species-normalized position estimates of all tagged individuals were summed within  $1^\circ \times 1^\circ$  grid cells. (b) Density of large marine predators within the California Current Large Marine Ecosystem at a  $0.25^\circ \times 0.25^\circ$  resolution. Sea surface temperature contours in panel a are denoted by solid white lines. Exclusive economic zones are delineated by solid black lines. Bottom panels show the daily mean position estimates of the major Tagging of Pacific Predators (TOPP) guilds (from left): tunas (yellowfin, bluefin, and albacore), pinnipeds (northern elephant seals, California sea lions, and northern fur seals), sharks (salmon, white, blue, common thresher, and mako), seabirds (Laysan and black-footed albatrosses and sooty shearwaters), sea turtles (leatherback and loggerhead) and cetaceans (blue, fin, sperm, and humpback whales). Figure reproduced from Block et al. (2011).

tuna, and salmon sharks exhibited migrations greater than 5,000 km to regions throughout the Pacific Ocean with a strong affinity to the highly productive waters of the California Current. Those species that remained in the California Current (tunas, salmon, mako and blue sharks, and blue whales) showed an annual north-south migration, which was associated with changes in water temperature and primary productivity. Other species migrated between the California Current and pelagic waters: elephant seals, blue and mako sharks, and leatherback sea turtles traveled to the North Pacific Transition Zone. The subtropical gyre and north equatorial current was an important region for blue and mako sharks and leatherback sea turtles. Similarly, the “Café” region of the eastern Pacific and the Hawaiian Islands was routinely visited by white sharks, albacore tunas, and black-footed albatrosses (see Jorgensen et al. 2010).

Northern elephant seals are a classic example of how such technology has radically changed our understanding of their biology. Using ship and aerial surveys, their range was thought to be

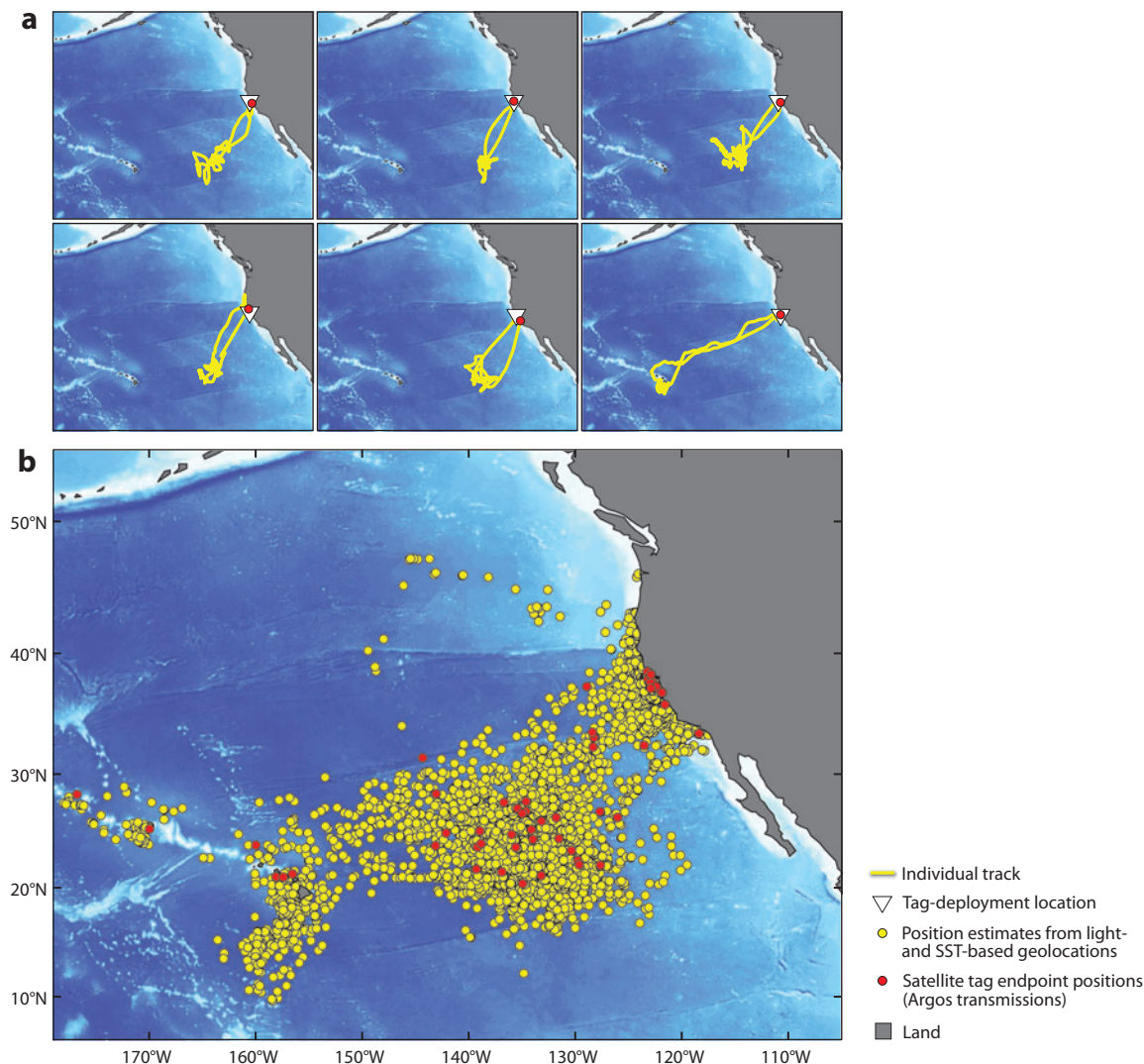


**Figure 2**

(a) Distribution of northern elephant seals (orange) as determined using boat- and plane-based surveys (redrawn from Riedman 1990; islands not shown to scale). (b) Distribution of female northern elephant seals determined from their migration tracks (yellow) observed using satellite telemetry (from Robinson et al. 2012).

restricted to offshore regions hugging the west coast of North America (**Figure 2a**). As electronic tracking data became available, it was discovered that these animals range throughout the Northeast Pacific Ocean (**Figure 2b**). Ship or plane surveys are limited to where we look, whereas tags carried by the animals provide information wherever the animal goes. Similarly, we knew white sharks periodically appeared along the coast of California, but it was impossible to know where they might be at other times or that they were congregating in a nondescript area between Hawaii and California (the so-called White Shark Café; see Jorgensen et al. 2010) for much of the year (**Figure 3**). Electronic tags have also provided unique insight into the fidelity of migratory paths of individual animals. For example, a female northern elephant seal was found to follow nearly identical migration paths 11 years apart (**Figure 4**). Electronic tracking data have also elucidated in great detail how the greatest migrations on Earth are timed and executed by Arctic terns and sooty shearwaters (Egevang et al. 2010, Shaffer et al. 2006) (**Figure 5**).



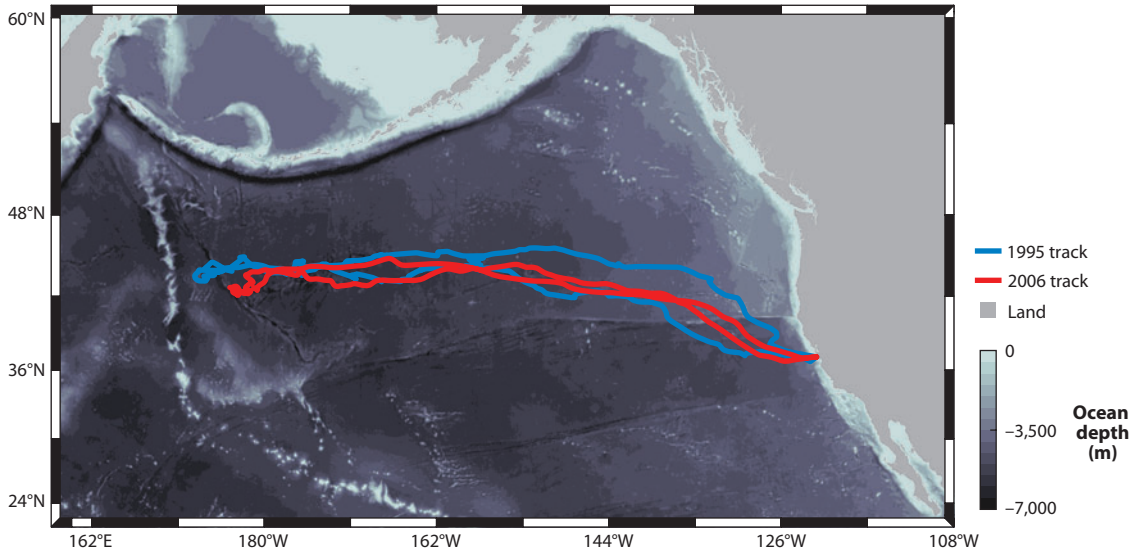


**Figure 3**

Site fidelity and homing of white sharks tagged along the Central California Coast during 2000–2007 revealed by pop-up archival tag records (PAT). (a) Site fidelity demonstrated by six individual tracks (yellow lines; based on five-point moving average of geolocations). Triangles indicate tag-deployment locations and red circles indicate the position where the PAT popped up and made an Argos satellite transmission. (b) Site fidelity of all satellite-tagged white sharks ( $n = 68$ ) to three core areas in the Northeast Pacific including the North American continental shelf waters, the waters surrounding the Hawaiian Island Archipelago, and the White Shark Café. Yellow circles represent position estimates from light-based and sea surface temperature (SST)-based geolocations. Ocean color indicates depth, from white (shallowest) to dark blue (deepest). Figure reproduced from Jorgensen et al. (2010).

### 1.1. New Technologies

The primary tools used today for tracking marine animals are global positioning system (GPS) and Argos satellite telemetry. Archival data logging tags that collect light-level data are also extremely popular, as light level can be used to reconstruct positions using day length and clock offset to calculate position. Acoustic tracking on an ocean basin scale is also becoming more widespread.



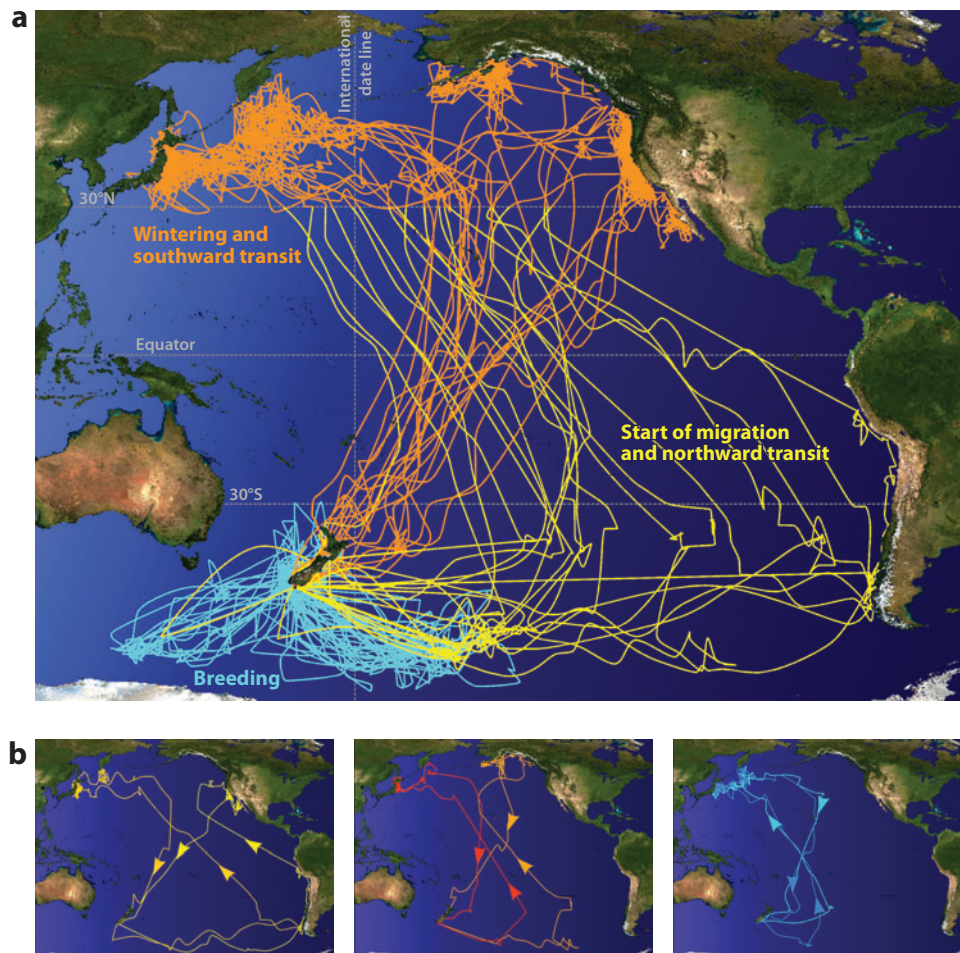
**Figure 4**

Argos transmission tracks of a female northern elephant seal recorded in 1995 when she was 6 years old (blue) and then again in 2006, 11 years later, when she was 17 years old (red) (D. P. Costa, P. W. Robinson, J. L. Hassrick, S. E. Simmons, unpublished data).

Finally, accelerometer/magnetometer data enable 3D dead-reckoning calculations to reconstruct true 3D tracks of diving animals through the ocean at incredibly fine resolution (Wilson et al. 2008). These tracks can last from weeks to years, and the tags can also collect ancillary behavioral information that can be used to identify behaviors and associated habitats and collect pressure data to measure the dive pattern (Figure 6b). This suite of associated data can be used to describe the environment a tracked animal experiences (Figure 6c) including temperature, salinity, and light level. Such behavioral and environmental data are often key in identifying differences in the movement patterns and habitat utilization of different species (Block et al. 2011, Costa et al. 2010a).

**1.1.1. Archival tags.** Archival tags record data as a time series from sensors that can record depth (pressure), water and/or body temperature, salinity, chlorophyll, three-axis acceleration, orientation, heart rate, stomach temperature, pO<sub>2</sub>, GPS positions, and light level. The major limitation of archival tags is that they must be recovered in order to obtain the data they collect. Judicious choice of animals or use on exploited species where a reward is offered for tags collected in commercial fisheries has nonetheless provided a wealth of information on the foraging behavior and habitat use of many marine animals (Block et al. 2005, Johnson et al. 2006, Miller et al. 2004, Shaffer & Costa 2006, Shaffer et al. 2006, Tinker et al. 2007). Movement patterns can be derived with archival tags using light level. Local noon can be used to calculate longitude and day length to calculate latitude. These locations often contain error but can be refined by correcting with sea surface temperature data (Shaffer et al. 2005). Archival tags have the advantage of being relatively inexpensive, and they do not incur fees for accessing the data via satellite networks.

**1.1.2. Argos satellite tags.** Argos satellite tags provide at-sea locations and have the advantage that the data can be recovered remotely. The Argos receivers fly on National Oceanic and Atmospheric Administration low-orbiting weather satellites; they receive transmissions from tags



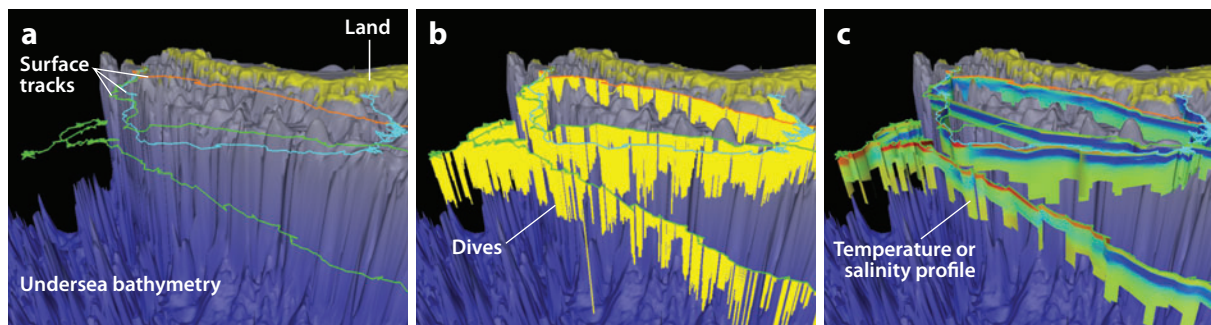
**Figure 5**

Shearwater migrations originating from breeding colonies in New Zealand. (a) Interpolated geolocation tracks of 19 sooty shearwaters during breeding (light blue) and subsequent migration pathways (yellow, start of migration and northward transit; orange, wintering grounds and southward transit). (b) Representative figure-eight movement patterns of individual shearwaters traveling to one of three “winter” destinations in the North Pacific. Each panel also represents a breeding pair and their subsequent migration after the breeding season. Figure reproduced from Shaffer et al. (2006).

and are capable of downloading data to Service Argos (Toulouse, France, or Landover, MD). Service Argos uses the Doppler shift of a tag’s radio frequency to calculate the geolocation in successive uplinks. Tags with onboard data processing and compression have made it possible to transmit ancillary data through the Argos system, including detailed oceanographic and behavioral information such as dive profiles and ocean salinity and temperature (Boehme et al. 2009).

Argos tracking systems have been available longer than all other satellite tracking technologies and have been used on a wide variety of marine vertebrates, providing insight into the movements of marine birds (Bost et al. 1997, Kappes et al. 2010, Pinaud & Weimerskirch 2007, Weimerskirch et al. 2012), sea turtles (e.g., James et al. 2005, Maxwell et al. 2011a, Polovina et al. 2000), sharks





**Figure 6**

Tracks of three southern elephant seals in the Western Antarctic Peninsula. Panels show (a) just the surface track, (b) the surface track along with diving behavior, and (c) the temperature and salinity profiles that can be obtained to provide data on the physical environment the animals are moving through. Figure reproduced from Costa et al. (2010a).

(Eckert et al. 2002, Hammerschlag et al. 2011, Weng et al. 2005), and marine mammals (Bailey et al. 2009, Costa et al. 2010a, Guinet et al. 2001, Le Boeuf et al. 2000, Mate et al. 1998, Shaffer & Costa 2006). Because the tag's antenna must be out of the water to communicate with the satellites, the technology has mainly been used on air breathers that surface regularly. For animals that remain submerged, pop-up archival tags (PATs) are favored (Block et al. 1998, 2005; Boustany et al. 2010; Campana et al. 2011; Carlson et al. 2010). PATs combine archival tags with satellite transmitters and then send their data to researchers via Argos satellites once the tag is released from the tracked animal and floats to the surface.

**1.1.3. Global positioning system tags.** Although standard GPS tags have been deployed on seabirds for some time, the long time and high battery demands required to calculate GPS satellite positions delayed their application to marine animals that are only at the surface periodically (Weimerskirch et al. 2005, 2007). However, tags are now available that take a snapshot of the GPS satellite data, which is either stored for later calculation after tag recovery or is used to calculate pseudoranges that can then be transmitted via Argos (Tomkiewicz et al. 2010). Researchers can now track marine animal movements to within 10 meters, a vast improvement over the 1–10-km error currently possible with Argos satellite tags (Costa et al. 2010b, Kuhn et al. 2009). However, communication bandwidth to the Argos satellites is still a barrier and often only a small fraction of collected GPS locations can be remotely recovered. In practice, complete GPS tracks are usually attainable only by recovering tracking tags and downloading the data from them. GPS tags have been developed that can link to cell phone networks, which have enormous bandwidth to upload archived GPS position and behavioral data (McConnell et al. 2004). These tags are, of course, limited to species that regularly enter the range of wireless telecommunication networks.

**1.1.4. Acoustic animal tracking.** A variety of marine organisms have been tagged with tiny acoustic pingers that can be tracked with fixed or mobile acoustic receiver arrays (Dagorn et al. 2007). Movements of animals ranging from tiny salmon smolt on their migration from rivers into the ocean (Welch et al. 2011) to large sturgeon and sharks have been tracked (Andrews et al. 2010, Lindley et al. 2011). Mobile acoustic transceivers (so-called business card tags) that both send and receive acoustic signals are now being developed and deployed. These tags can listen for signals sent by animals too small to have receivers, chronicling all of the acoustic tags that an animal



encounters (Hayes et al. 2012). In addition, both active and passive acoustic methods have been used to track large-scale movements of whales (Sirovic et al. 2004).

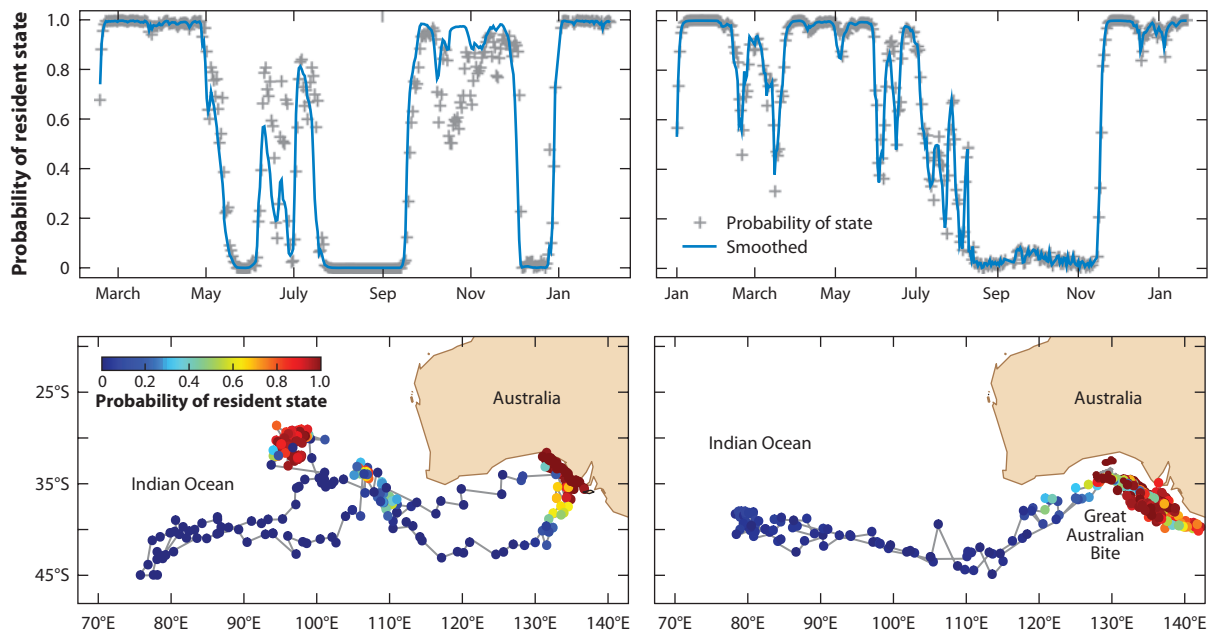
## 1.2. Analyses for Understanding Animal Migration

Animal tracking data are often of immediate qualitative value to identify previously unknown ecological patterns such as migratory pathways or home ranges. Developments in quantitative techniques to process raw tracking data are now helping to extract fine-scale information that was previously obscured by factors such as location error. Analyses of animal movement and migration have used diffusion and random walk processes (Dobzhansky & Wright 1947); Skellam (1951) was the most influential of early studies. Developments and extensions of diffusion models in biology are reviewed and updated by Okubo & Levin (2002). Analyses of movement to understand behavioral processes of individuals were developed in the 1970s and 1980s as the first tracking data became available (Siniff & Jessen 1969). Most analyses of individual tracking data are based upon correlated random walks (CRWs) (Turchin 1998), but fractals, first passage time (FPT) analysis, and Lévy flight methods have also been introduced. As Turchin (1998) provides an excellent guide for analyses of animal movement, we focus on analytical developments after 1998.

Computational power has been the single most important advance and has allowed ecologists to borrow, from the physics and engineering communities, sophisticated Bayesian model fitting methods (Markov chain Monte Carlo, particle filters, expectation maximization, etc.) to fit diffusion, CRW, mixed-effects, and generalized additive models with much more ecological and behavioral complexity. Large sample sizes and high data quality are an ideal combination for advanced methods and are allowing the detection of subtle behavioral signals to reveal deeply complex behavior and ecology in migrating animals.

**1.2.1. State-space models and hidden Markov models.** State-space models (SSMs) and hidden Markov models (HMMs) are by far the most powerful and sophisticated new tools for analyzing animal movement and migration from electronic tracking data. These models have been applied to a wide range of engineering, physics, geoscience, and economics problems, where the goal is to infer an unobservable “hidden” or “latent” system state. In animal movement and migration, the hidden condition is an animal’s behavioral state (**Figure 7**). That state affects how an animal moves, and both SSMs and HMMs fit CRW models that utilize movement properties such as turn angles, move lengths, and autocorrelation to infer latent behavioral state from telemetry data (Jonsen et al. 2005; Morales et al. 2004; Patterson et al. 2008, 2009). These models can also be structured to detect both the mechanisms and accuracy of animal navigation (Jonsen et al. 2006; Mills-Flemming et al. 2006, 2010).

Both SSMs and HMMs are fit to CRW models; the most powerful are so-called switching models or composite CRWs (Breed et al. 2009; Jonsen et al. 2005, 2006; Mills-Flemming et al. 2006). In these models, two, three, or sometimes more sets of parameters, each parameter set representing a behavioral state, are estimated for a CRW. These parameters control attributes such as move speed, turn angle, cardinal direction, and autocorrelation, as well as the degree of stochasticity. The parameter space can produce many different kinds of movement. Most switching models have a fixed number of discrete states to be inferred, and the model fits a track by inferring which of the two or three sets of parameters is most likely at any point in the track (**Figure 8**). Some are set up as mixing models, where the behavioral state is determined strictly from the movement pattern at a particular time in the track, whereas others have transition equations between states, so that both the current movement pattern and the movement leading up to it affect which state is inferred at any given time.

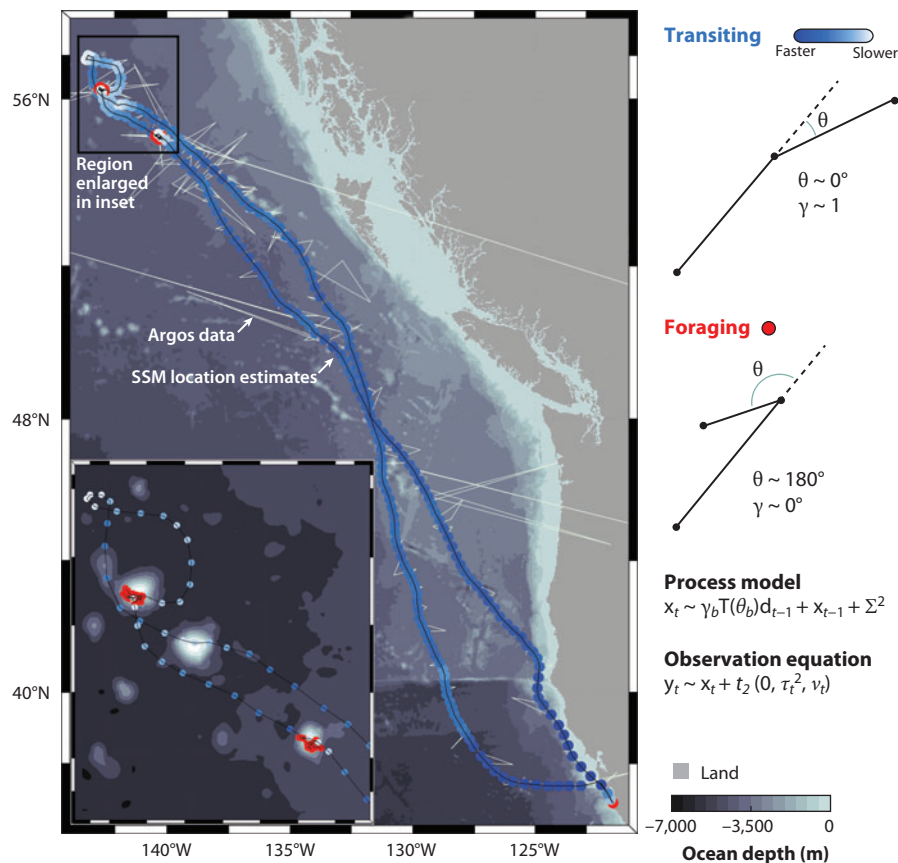


**Figure 7**

Hidden Markov model fits for two southern bluefin tuna tracks, estimating the probability of being in a “migratory” or “resident” behavioral state. Upper panels show the behavioral state time series; lower panels show those probabilities on a map. Modified from Patterson et al. (2009).

SSMs are a special case of HMMs. In an HMM, the hidden states are a set of discrete, categorical states that must be predefined before a model is fit. In an SSM, the hidden states are distributed on a continuum, or space, and are not discrete, thus the term state space. As implemented, the state-space aspect of SSMs is usually restricted to handling observation error in animal tracking data, particularly in Argos and light-level geolocation data, to estimate the most likely location. This improved location estimate more accurately reflects the movement pattern made by the animal. Thus, switching SSMs actually have an HMM for behavioral state linked to and embedded within an SSM for location. SSMs have two equations: one models behavior and accounts for behavioral stochasticity (the process equation), and the other models observation error (the observation equation). The two equations make SSMs much better for analyzing data with significant degrees of observation error (e.g., Argos, light-level geolocation), but this comes at the cost of being more difficult to implement than HMMs. Many researchers use SSMs solely for track correction (e.g., Tremblay et al. 2009). One practical solution is to implement a simple SSM using a Kalman filter to fit a random walk with no behavior to correct for observation error followed by an HMM to estimate the hidden behavioral state (Patterson et al. 2010). Otherwise HMMs are generally useful only for analyzing GPS quality tracking data; if observation error is not accounted for, it interferes with behavioral state discrimination.

SSMs can be fit in either continuous or discrete time. Discrete-time models estimate locations and behavioral state at regular time steps. These have many favorable properties, but are somewhat more complex to fit (Breed et al. 2009, 2011). Continuous-time SSMs estimate a location for every observation on irregular intervals, and some argue this is a more natural framework (Johnson et al. 2008, Kuhn et al. 2009).



**Figure 8**

Example of a switching state-space model (SSM) fit to an Argos satellite track collected from a northern elephant seal, in this case revealing intense use of a seamount chain (Maxwell et al. 2011b). The map shows the highly error-prone Argos data overlaid with the SSM best-location estimates; color indicates inferred behavioral state. The switching model fit is shown to the right of the map, with behavioral state inferred from the autocorrelation ( $\gamma$ ) to the previous displacement ( $d_{t-1}$ ) and turn angle  $\theta$ . The parameters are indexed into two states by the vector  $b$ . The Argos error is modeled with the observation equation and assumes  $t$ -distributed error, with variance  $\tau$  and degrees of freedom  $\nu$  (Jonsen et al. 2005). The nominally “foraging” state had low estimates for  $\gamma$  and estimates of  $\theta$  near  $180^\circ$ , whereas nominally “transiting” states had high values of  $\gamma$  and estimates of  $\theta$  near zero.

Finally, there are a few examples of models that fit behavior using a continuum of parameters within state-space or similar time-series frameworks (Breed et al. 2012, Gurarie et al. 2009). This is a promising new direction and should allow more flexible and natural frameworks for inferring a wide range of behavioral states from movement patterns.

**1.2.2. Heuristic approaches.** Several heuristic approaches have gained traction in recent years. These methods qualify track properties using sets of rules that describe turning angles, time spent in a region, or other movement metrics to infer search intensity or foraging activity. These approaches can be extremely useful and practical in many situations. However, because many are not well grounded in probability theory, objective interpretation can be difficult.

**1.2.2.1. Fractals.** Fractal analyses have been especially popular and useful in landscape ecology (Halley et al. 2004, Turcotte 1997) and were introduced as a method to quantify animal movement by Dicke & Burrough (1988). A series of influential papers (Johnson et al. 1992, Milne 1991, Wiens et al. 1995) built on the work of Dicke & Burrough (1988) lay out a simple method for calculating the fractal dimension ( $d$ ) of an animal's track. Some researchers also argued that because fractals are scale invariant,  $d$  could be used to compare directly the behavior of animals of very different sizes moving through landscapes (Wiens et al. 1995).

$d$  represents the 2D space that would be covered by various movement patterns and is calculated by log-log regressing "ruler length" against measured path length. Shorter ruler lengths measure more detail, and the measured path length is thus longer. The slope of this regression is the fractal dimension  $d$ , and it has been interpreted biologically as the intensity of search or foraging effort. However, Turchin (1996) clearly demonstrated that the log-log regression needed to calculate  $d$  turns into a curve as the ruler length goes to infinity; to be valid, the relationship must be linear. Since the critique by Turchin (1996), the popularity of fractals for analyzing animal movement has dropped considerably.

A variation of the fractal method has recently been implemented to identify area-restricted search (ARS) behavior in wide-ranging marine animals. Known as the fractal landscape method, tracks are objectively segmented as a moving window of a given size passes over the track, and  $d$  is calculated for the data subset in the window at any given time (Tremblay et al. 2007). Windows with higher  $d$  could be considered to have higher search or foraging intensity and represent more important habitat. The caveat from Turchin (1996) notwithstanding, the fractal landscape method is easy to implement and represents a simpler alternative for identifying pelagic ARS and foraging areas than behavior-discriminating SSMs or HMMs.

**1.2.2.2. First passage time analysis.** Another method similar to fractal analysis, but perhaps more flexible and less prone to bias, is FPT analysis. This method was first suggested for analyzing tracking data by Johnson et al. (1992), but it was not formalized until Fauchald & Tveraa (2003).

The analysis proceeds by linearly interpolating tracking locations so that they are evenly spaced in time, and circles with a radius  $r$  are placed around each point. The amount of time a tagged animal spends within each circle is calculated: If the animal moves slowly or turns frequently, the amount of time will be greater; if it moves straight or quickly, it will be smaller. The time it takes for the animal to leave the circle of a given  $r$  is the FPT for the point at the circle's center. It is then possible to see how the FPT index changes along the track. Large FPT values are associated with ARS and small values with directed or migratory movements (Fauchald & Tveraa 2003). The FPT index is very similar to the fractal dimension  $d$ , with high FPT values corresponding to high  $d$ .

This process is repeated for a range of  $r$ 's. For each  $r$ , an FPT value is generated for each point in the track, and it is possible to calculate a mean and variance of FPT for the entire track. Fauchald & Tveraa (2003) argued that this variance could be log transformed and plotted against  $r$ , and if a peak in  $\text{var}[\log(\text{FPT})]$  was clear at a particular  $r$  value, this value of  $r$  could be interpreted as the "characteristic scale" at which an individual animal's search movements are concentrated.

The FPT method is easy to apply and interpret, and it has been a popular choice since its introduction by Fauchald & Tveraa (2003), especially for marine birds (e.g., Fauchald & Tveraa 2006, Pinaud 2008, Weimerskirch et al. 2007). The method has also been extended to include a vertical dimension for diving animals (Bailleul et al. 2008). As an index of track sinuosity, it is at least as good as fractal analysis, and unlike fractals no mathematical problems associated with the calculation of FPT indices have been discovered. However, the method does require high-resolution data, and many of the published studies to date use GPS data with interpolation to get extremely fine temporal resolution.



**1.2.2.3. Lévy flight models.** Lévy flights are a particular variant of a random walk model. The random draws of step length come from a long-tailed probability distribution, most often a Pareto distribution with infinite variance,  $P(l_j) \sim l_j^{-\mu}$ , where  $P(l_j)$  describes the probability density of step lengths. To be considered a Lévy flight, the exponent  $\mu$  must be between 1 and 3 (Viswanathan et al. 1999). When  $\mu \leq 1$ , motion is ballistic, and when  $\mu \geq 3$  it is Brownian.

Lévy flight models have a very simple mathematical form, produce tracks very similar to real animals, and are easily fit using regression and maximum-likelihood methods. Their ease and intuitiveness have made them tractable to many biologists, and they have been fit to movement data collected from a wide range of migratory marine species (e.g., Humphries et al. 2010, Sims et al. 2008, Viswanathan et al. 1999). In addition, it has been suggested that a Lévy flight with  $\mu = 2$  is the most efficient search strategy possible (Viswanathan et al. 1999), and thus foragers entering unfamiliar environments should employ this strategy to find food (Reynolds & Rhodes 2009).

These findings, and the use of Lévy flight models for movement data, however, are highly controversial. Numerous papers have pointed out flaws in both the mathematical and logical underpinnings of Lévy flight analyses. Among other factors, these studies have found that Lévy searches are the most efficient only under very special, even peculiar circumstances (James et al. 2008); that Lévy flights have been misidentified in many of the foundational papers (Edwards 2008, 2011; Edwards et al. 2007); and that alternative models, especially composite CRWs, cannot be distinguished from Lévy flights in real data (Auger-Méthé et al. 2011, Benhamou 2007, Plank & Codling 2009). Given the multitude of potential issues, we cannot recommend the use of Lévy flight methods or theory in analysis or understanding of marine animal migration or movement.

### 1.3. Advances in Animal Navigation

Many species routinely migrate across vast expanses of oceanic habitats, regions seemingly devoid of the cues necessary for accurate navigation (Lohmann et al. 2008). Albatrosses, sea turtles, whales, seals, sharks, and many other taxa rely on well-developed navigation abilities to move between distant foraging and reproduction regions (Mueller & Fagan 2008). Thus, there is a strong selective pressure to maintain and refine navigation ability. Although considerable progress has been made in revealing the underlying mechanisms of animal navigation, particularly in the terrestrial realm (Able 1995), a holistic understanding remains elusive. This is in large part due to the use of multiple redundant or condition-dependent cues by navigating animals (Muheim et al. 2006a).

Pelagic migrants may use one or more of a diverse suite of environmental cues to navigate. Stable visual or bathymetric cues, such as shallow coastal areas or seamounts, may be used during part of a migration, but would not be available in deep pelagic habitats. Oceanographic features, including temperature fields, salinity, and associated fronts, vary reliably on a coarse scale; however, these features are dynamic and would require remarkable detection sensitivity (Bost et al. 2009a, Hays et al. 2001). Olfactory cues, such as aerosolized di-methyl sulfide, may be useful to direct predators toward prey patches (Nevitt & Bonadonna 2005, Nevitt et al. 2008), but again are likely not used for long-distance navigation (Lohmann et al. 1999).

Celestial and geomagnetic cues, however, are appealing candidates for pelagic migrants because they are ubiquitous and potentially very accurate. Diurnal celestial cues, including sunlight polarization and Sun position, are used by migrants (Gould 1998). Similarly, nocturnal celestial cues, including stellar orientation and moon position, are used to navigate by some species (Able & Able 1996, Muheim et al. 2006a). Geomagnetic cues have also been shown to be very important for many species (Lohmann et al. 2007). Geomagnetic inclination and field intensity show significant variation over the surface of Earth and, in many places, are orthogonally aligned (Akesson & Alerstam 1998). If animals can detect these features, the variation may provide enough information

to form a cognitive map sufficient for long-distance pelagic navigation (Lohmann & Lohmann 1996).

A priori, it is unlikely that visual, oceanographic, or olfactory cues are the dominant source of navigation information for ocean basin-scale movements. Although identifying the particular cues used during oceanic migration is logistically challenging, recent advances and miniaturization of tracking technologies enable detailed measurement of migratory pathways. These data can be used to test navigation performance (i.e., accuracy in following a particular route) and may give insight into the mechanisms at play. A recent study of migrating humpback whales demonstrated that individuals maintain straight paths by correcting for fine-scale current patterns, implying the use of cues that are both accurate and stable (Horton et al. 2011). In elephant seals, outbound migrations are oriented toward vague dynamic targets, whereas inbound migrations are oriented toward a discrete fixed target (the home colony). Seals swim nearly continuously during these transit phases, as evident by a constant forward trajectory and characteristic “transit” dives (Le Boeuf et al. 2000). The path of the animal during these transit phases is often direct with a stable orientation, although this has yet to be adequately characterized (Le Boeuf et al. 2000).

Despite the logistical difficulty of studying oceanic migrants, they are actually excellent models for the study of navigation because their environment lacks many cues available to terrestrial organisms. Existing studies focus largely on albatrosses and turtles. The remarkable navigation ability of turtles has long been known from conventional tagging studies (Carr 1967), but the precision of island homing was more recently demonstrated with satellite tracking (Papi et al. 1995). Subsequent studies utilizing translocated free-ranging turtles attempt to identify the importance of particular cues but met limited success. For example, experimentally displaced turtles with attached magnets (to disrupt a hypothesized magnetic sense) retained their navigation ability (Papi et al. 2000). Such studies are unable to implicate particular cues, but suggest redundancy. Complementary laboratory-based experiments have shown the importance of several cues including at least two components of the geomagnetic field: intensity and inclination angle (Lohmann et al. 1999).

Investigations into albatross navigation have found similar results. Satellite tracking clearly demonstrates a keen navigation ability (Weimerskirch et al. 2012), but experimental attachment of magnets was inconclusive; like turtles, albatrosses retained their navigation ability (Bonadonna et al. 2003). Controlled studies of other bird species demonstrate detection and potential use of many cues: olfactory, sky polarization or Sun position, and star patterns (Able & Able 1996, Muheim et al. 2006b, Nevitt & Bonadonna 2005). However, detection ability does not necessarily imply use in free-ranging conditions, and demonstration of reliance on particular cues remains elusive for most species. For example, albatross dynamic soaring (Alerstam 1996) or the impact of ocean currents on sea turtles (Gaspar et al. 2006) may mask important trends that would otherwise be apparent in movement patterns. Much additional experimental work is necessary to understand which cues pelagic animals use to navigate and how these are integrated into a cognitive map.

#### 1.4. Animals as Oceanographers

Electronic tags deployed on animals are also providing oceanographic data in areas where conventional methods are limited or absent (Boehme et al. 2009, Charrassin et al. 2008, Costa et al. 2010a) (**Figure 9**). Different water masses have unique temperature and salinity signatures and can be used to describe the hydrographic characteristics of habitat used by tracked animals. Tags are available that measure temperature, salinity, light, fluorescence, and  $pO_2$  while the animal moves through the water column. These hydrographic data are collected at a scale and resolution that is perfectly coincident with the animal’s behavior, allowing far better measures of habitat



**Figure 9**

A Weddell seal is shown wearing a Sea Mammal Research Unit conductivity-temperature-depth tag in McMurdo Sound, Antarctica. Photo by Dan Costa.

than remotely sensed satellite data. Such an approach has been used to define the foraging habitat of elephant and crabeater seals in the Southern Ocean by physical oceanographic characteristics (Biuw et al. 2007, 2010; Costa et al. 2010a). For elephant seals, changes in drift rate measured during periods when the seal was not swimming provide an index of body condition (fatter seals tend to be more buoyant, whereas leaner seals tend to sink). Changes in body condition were then correlated with temperature and salinity data collected by the tag and allowed identification of the specific water masses where elephant seals had the greatest foraging success. These areas were linked with warm, deep water known as circumpolar deep water. This warm and nutrient-rich water is associated with the Antarctic Circumpolar Current and upwells along the continental shelf. The data available from existing oceanographic sampling techniques and/or oceanographic models are too coarse or imprecise to identify the habitat characteristics of individual dives.

An added benefit is that hydrographic tags carried by animals provide highly cost-effective platforms from which detailed oceanographic data can be collected on a scale not possible with conventional methods. Such data are particularly lacking in the polar oceans where ship time is limited (especially in the winter), where cloud cover or sea ice limits the capability of satellite remote sensing, and where current patterns wash oceanographic floats away from the Antarctic continent. An international effort deployed conductivity-temperature-depth (CTD) tags on 85 elephant seals simultaneously at Kerguelen, South Georgia, Macquarie and the South Shetland Islands in the Southern Ocean between January 2004 and April 2006 (Biuw et al. 2007) and increased by ninefold the number of CTD profiles collected by traditional methods (Charrassin et al. 2008). Similar data sets can complement even well-studied regions by adding measurements from mesopelagic depths (Robinson et al. 2012). Animal-derived data are being made available to the general oceanographic community through databases historically reserved for ship-based data [e.g., Autonomous Pinniped Bathythermographs (APBs) in the World Ocean Database].

Oceanographic data collected by elephant seals in the Western Antarctic Peninsula provided insight into the unexpected breakup of the Wilkins Ice Shelf (WIS) in 2008. Two sets of data were collected; the first relied on observations that elephant seals were diving deeper than the known bathymetry and, thus, provided a basis to improve the bathymetry in this region. This refined bathymetry led to the discovery of a series of deep troughs that extend from the outer to the inner continental shelf near the WIS (Padman et al. 2010). These troughs acted as conduits for on-shelf

movement of relatively warm ( $>1^{\circ}\text{C}$ ) upper circumpolar deep water across the continental shelf and under the WIS. The second data set—temperature records recorded from the seals' tags—confirmed the flow of this warm deep water underneath the WIS. The added heat contributed to the breakup of the ice shelf (Padman et al. 2012).

### 1.5. Including Migration in Marine Conservation

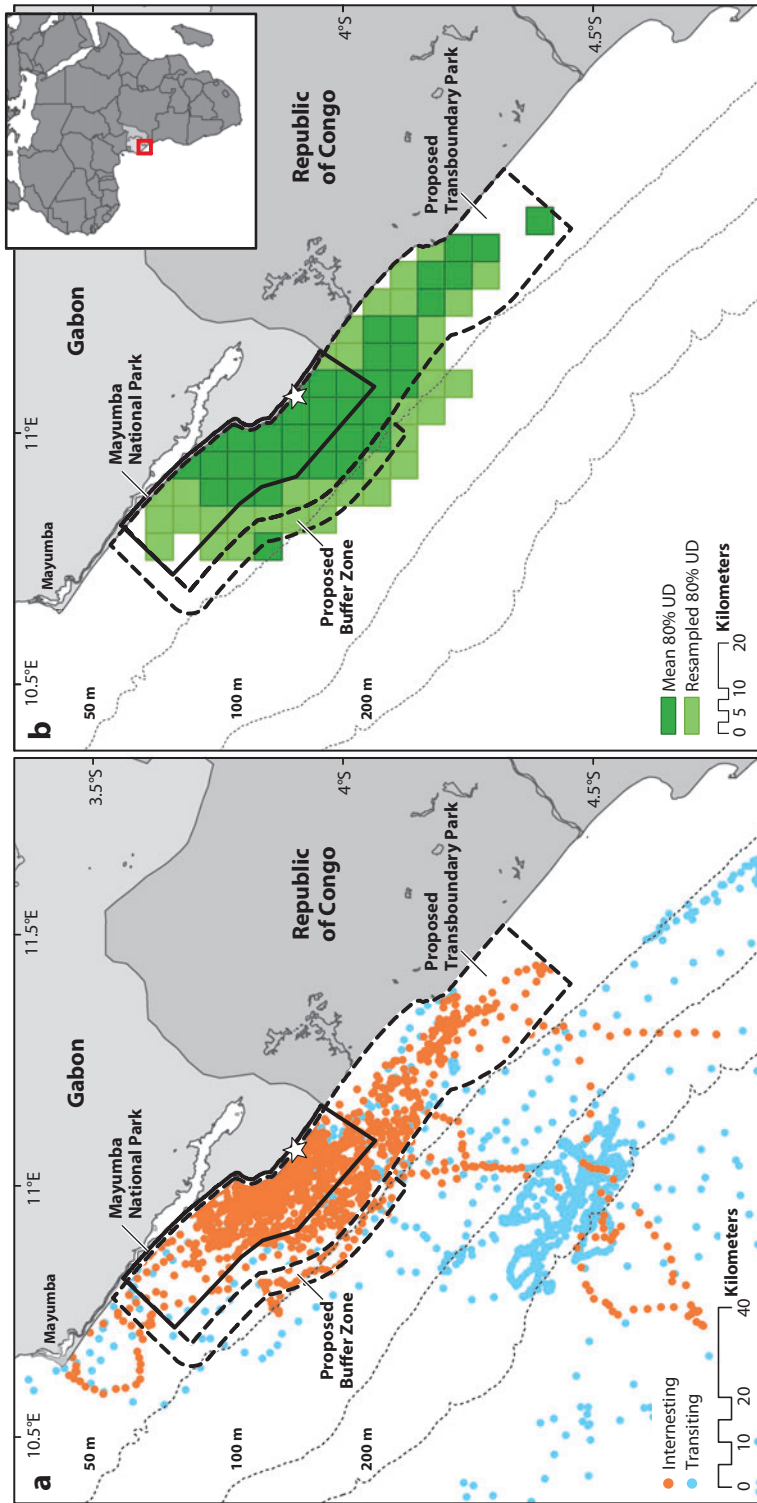
For centuries, fishers and hunters have relied on knowledge of the movement patterns of exploited species such as tuna, whales, seals, sea turtles, and seabirds to predict when and where to harvest them. Today, management and conservation of highly migratory species is a more pressing need and requires detailed information on movements of threatened species. This information is also fundamental to understanding how diseases might be spread and how disease networks might change as animals change their migration patterns (Altizer et al. 2011). Satellite and acoustic tagging of white sharks, combined with a Bayesian model, has been used to provide estimates of white shark populations (Jorgensen et al. 2010). Electronic tags are being used to reveal patterns of habitat utilization and to identify and/or help avoid or mitigate conflicts with oil and gas development, military activities, fisheries interactions, and shipping and research activities (Chilvers 2008, Costa et al. 2003, Goldsworthy & Page 2007, Peckham et al. 2007, Tyack et al. 2011, Żydelis et al. 2011). Tracking data were important in listing black-footed albatrosses as an endangered species by the US Fish and Wildlife Service and by BirdLife International for deliberations within the international Agreement for the Conservation of Albatrosses and Petrels, and tracking data have been crucial in the development of a management plan for the endangered Australian and New Zealand sea lions (Campbell et al. 2006, Chilvers 2008, Goldsworthy & Page 2007). Finally, tracking data are providing insights into the potential impact of climate change on pelagic species (Costa et al. 2010a, Weimerskirch et al. 2012).

Marine animals do not recognize political boundaries, so knowledge of their movement patterns and where they perform vital activities such as foraging and breeding can provide the basis for regional management plans. Such information is critical for identifying key habitat for both implementation of marine protected areas (MPAs) (Maxwell et al. 2011a, Peckham et al. 2007, Schofield et al. 2007, Wallace et al. 2011, Witt et al. 2011, Żydelis et al. 2011) and determination of the spatial and temporal extent of such management measures. For example, Laysan albatrosses tagged at Guadalupe Island, Mexico, are found within the California Current System and within exclusive economic zones of at least three other countries. Pacific bluefin tuna that swam to the Eastern Pacific Ocean from Japan are so overexploited that few tagged fish live long enough to make the return trans-Pacific migration to spawn (Block et al. 2011). Leatherback sea turtles have been observed to use corridors shaped by persistent oceanographic features such as the southern edge of the Costa Rica Dome and the highly energetic currents of the equatorial Pacific (Shillinger et al. 2008). These findings have led to an International Union for Conservation of Nature resolution to conserve leatherback sea turtles in the open seas. Similarly, tracking data were used to develop an MPA off the coast of Baja California to protect loggerhead sea turtles (Peckham et al. 2007) and to assess the efficacy of an implemented MPA to protect olive ridley sea turtles off the coast of Gabon (Maxwell et al. 2011a) (**Figure 10**).

## 2. FUTURE DIRECTIONS

In recent years, 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 tags, increased sensor capabilities (including oceanographic sensors and animal behavior and/or physiology), better attachment methods, miniaturization of tags, and alternative methods





**Figure 10**

(a) State-space modeled (SSM) tracks ( $n = 18$ ) of olive ridley sea turtles tagged from Mayumba National Park. Orange points represent interesting behavioral mode; blue points represent transiting behavioral mode. The star indicates the tagging location. (b) Confidence intervals of movements for olive ridley sea turtles derived from the data in panel a. Outer error bounds for 80% utilization distribution (UD) for mean SSM estimates (*light green*) and resampled SSM (*dark green*). Reproduced from Maxwell et al. (2011a).

of data recovery. Although new higher capacity batteries may be developed, an alternative is to develop technologies that collect energy from an animal's movement. Conceptually, this seems very straightforward, but the development of reliable power-harvesting systems has so far proven elusive. Other sensors that could be added to the tags include such important oceanographic measures as pH, CO<sub>2</sub>, and chlorophyll, as well as measures of animal behavior that include reliable measures of feeding behavior and even active sonar to measure prey fields in front of the animal. Novel methods of data recovery would greatly enhance the range of species that these tags could be deployed on. A major advance would be achieved if the data obtained by electronic tags could be transmitted underwater via an acoustic modem.

Electronic tags have provided a hitherto unprecedented view of the movement patterns and habitat preferences of highly migratory upper trophic-level species. Effective management and conservation requires a better understanding of both how migrants navigate to essential habitat and the processes that make these habitats desirable. Although there has been a significant move toward development of MPAs, the efficacy of such protected areas has yet to be considered. Protection of a species on their foraging or breeding grounds may not enhance population viability if the animals are caught along their migration corridor. Modeling efforts could examine the relative value of developing MPAs around species' movement patterns elucidated using electronic tagging.

Mysteries of long-distance navigation will be solved only by efforts targeting long-distance continuous migrants for controlled field-based manipulations, where navigational cues such as magnetic or visual senses are manipulated. The resulting change in the animal's navigational ability could then be monitored using high-resolution tracking. Such field experiments would be complemented by lab-based experiments (e.g., psychophysical) that allow a greater examination of mechanisms.

Further study of habitat association is also needed to integrate large-scale movement patterns with the lower trophic levels and the biophysical forces that structure ecosystems. Future discoveries will be made when these tools are applied in an integrated manner, providing a seamless understanding of the biophysical processes driving primary production at lower trophic levels to the movements and behavior patterns of apex predators. 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. This would provide not just a onetime snapshot of the biodiversity of a marine habitat, but a dynamic view into the processes that maintain biodiversity with 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 adjusting in response to climate change (Costa et al. 2010a, Weimerskirch et al. 2012). On a warming planet, that insight will be essential if we wish to mitigate the impacts of climate change on pelagic migrants and save those species for future generations.

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## LITERATURE CITED

- Able KP. 1995. Orientation and navigation: a perspective on 50 years of research. *Condor* 97:592–604
- Able KP, Able MA. 1996. The flexible migratory orientation system of the Savannah sparrow (*Passerculus sandwichensis*). *J. Exp. Biol.* 199:3–8
- Akesson S, Alerstam T. 1998. Oceanic navigation: Are there any feasible geomagnetic bi-coordinate combinations for albatrosses? *J. Avian Biol.* 29:618–25
- Alerstam T. 1996. The geographical scale factor in orientation of migrating birds. *J. Exp. Biol.* 199:9–19
- Altizer S, Bartel R, Han BA. 2011. Animal migration and infectious disease risk. *Science* 331:296–302
- Anderson SD, Chapple TK, Jorgensen SJ, Klimley AP, Block BA. 2011. Long-term individual identification and site fidelity of white sharks, *Carcharodon carcharias*, off California using dorsal fins. *Mar. Biol.* 158:1233–37
- Andrews KS, Williams GD, Levin PS. 2010. Seasonal and ontogenetic changes in movement patterns of sixgill sharks. *PLoS ONE* 5:e12549
- Auger-Méthé M, St. Clair C, Lewis M, Derocher A. 2011. Sampling rate and misidentification of Lévy and non-Lévy movement paths: comment. *Ecology* 92:8, 1699–1701
- Bailey H, Mate BR, Palacios DM, Irvine L, Bograd SJ, Costa DP. 2009. Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endanger. Species Res.* 10:93–106
- Bailey HR, Shillinger GL, Palacios DM, Bograd SJ, Spotila JR, et al. 2008. Identifying and comparing phases of movement by leatherback turtles using state-space models. *J. Exp. Mar. Biol. Ecol.* 356:128–35
- Bailleul F, Charrassin J-B, Ezratty R, Girard-Ardhuin F, McMahon CR, et al. 2007. Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice. Changes in movements and in diving behaviour. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* 54:343–55
- Bailleul F, Pinaud D, Hindell M, Charrassin J-B, Guinet C. 2008. Assessment of scale-dependent foraging behaviour in southern elephant seals incorporating the vertical dimension: a development of the First Passage Time method. *J. Anim. Ecol.* 77:948–57
- Benhamou S. 2007. How many animals really do the Lévy walk? *Ecology* 88:1962–69
- Bestley S, Gunn JS, Hindell MA. 2009. Plasticity in vertical behaviour of migrating juvenile southern bluefin tuna (*Thunnus maccoyii*) in relation to oceanography of the south Indian Ocean. *Fish. Oceanogr.* 18:237–54
- 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. *Proc. Natl. Acad. Sci. USA* 104:13705–10
- Biuw M, Nost OA, Stien A, Zhou Q, Lydersen C, Kovacs KM. 2010. Effects of hydrographic variability on the spatial, seasonal and diel diving patterns of southern elephant seals in the eastern Weddell Sea. *PLoS ONE* 5(11):e13816
- Block BA, Dewar H, Farwell C, Prince ED. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proc. Natl. Acad. Sci. USA* 95:9384–89
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, et al. 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- Block BA, Teo SL, Walli A, Boustany A, Stokesbury MJ, et al. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434:1121–27
- Boehme L, Lovell P, Biuw M, Roquet F, Nicholson J, et al. 2009. Technical note: animal-borne CTD-satellite relay data loggers for real-time oceanographic data collection. *Ocean Sci.* 5:685–95
- Bonadonna F, Chammille-Jammes S, Pinaud D, Weimerskirch H. 2003. Magnetic cues: Are they important in Black-browed Albatross *Diomedea melanophris* orientation? *Ibis* 145:152–55
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, et al. 2009a. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J. Mar. Syst.* 78:363–76
- Bost CA, Georges JY, Guinet C, Cherel Y, Puetz K, et al. 1997. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar. Ecol. Progr. Ser.* 150:21–33
- Bost CA, Thiebot JB, Pinaud D, Cherel Y, Trathan PN. 2009b. Where do penguins go during the interbreeding period? Using geolocation to track the winter dispersion of the macaroni penguin. *Biol. Lett.* 5:473–76

- Boustany AM, Matteson R, Castleton M, Farwell C, Block BA. 2010. Movements of Pacific bluefin tuna (*Thunnus orientalis*) in the Eastern North Pacific revealed with archival tags. *Progr. Oceanogr.* 86:94–104
- Breed GA, Costa DP, Goebel ME, Robinson PW. 2011. Electronic tracking tag programming is critical to data collection for behavioral time-series analysis. *Ecosphere* 2:art. 10
- Breed GA, Costa DP, Jonsen ID, Robinson PW, Mills-Flemming J. 2012. State-space methods for more completely capturing behavioral dynamics from animal tracks. *Ecol. Model.* 235–236:49–58
- Breed GA, Jonsen ID, Myers RA, Bowen WD, Leonard ML. 2009. Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. *Ecology* 90:3209–21
- Campana SE, Dorey A, Fowler M, Joyce W, Wang Z, et al. 2011. Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic. *PLoS ONE* 6(2):e16854
- Campbell RA, Chilvers BL, Childerhouse S, Gales NJ. 2006. Conservation management issues and status of the New Zealand (*Phocarcos bookeri*) and Australian (*Neophoca cinerea*) sea lion. In *Sea Lions of the World*, ed. AW Trites, SK Atkinson, DP DeMaster, LW Fritz, TS Gelatt, LD Rea, KM Wynne, pp. 455–71. Fairbanks, AK: Alsk. Sea Grant
- Carlson JK, Ribera MM, Conrath CL, Heupel MR, Burgess GH. 2010. Habitat use and movement patterns of bull sharks *Carcharhinus leucas* determined using pop-up satellite archival tags. *J. Fish Biol.* 77:661–75
- Carr A. 1967. Adaptive aspects of the scheduled travel of *Chelonia*. In *Animal Orientation and Navigation*, ed. RM Storm, pp. 35. Corvallis, OR: Or. State Univ. Press
- Charrassin J-B, Hindell M, Rintoul SR, Roquet F, Sokolov S, et al. 2008. Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. *Proc. Natl. Acad. Sci. USA* 105:11634–39
- Chilvers BL. 2008. New Zealand sea lions (*Phocarcos bookeri*) and squid trawl fisheries: bycatch problems and management options. *Endanger. Species Res.* 5:193–204
- Costa DP. 1991. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *Am. Zool.* 31:111–30
- Costa DP, Crocker DE, Gedamke J, Webb PM, Houser DS, et al. 2003. The effect of a low-frequency sound source (acoustic thermometry of the ocean climate) on the diving behavior of juvenile northern elephant seals, *Mirounga angustirostris*. *J. Acoust. Soc. Am.* 113:1155–65
- Costa DP, Huckstadt LA, Crocker DE, McDonald BI, Goebel ME, Fedak MA. 2010a. Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. *Integr. Comp. Biol.* 50:1018–30
- Costa DP, Robinson PW, Arnould JP, Harrison AL, Simmons SE, et al. 2010b. Accuracy of ARGOS locations of Pinnipeds at-sea estimated using Fastloc GPS. *PLoS ONE* 5:e8677
- Cotté C, Park Y-H, Guinet C, Bost C-A. 2007. Movements of foraging king penguins through marine mesoscale eddies. *Proc. R. Soc. B* 274:2385–91
- Dagorn L, Pincock D, Girard C, Holland K, Taquet M, et al. 2007. Satellite-linked acoustic receivers to observe behavior of fish in remote areas. *Aquat. Living Resour.* 20:307–12
- Dias MP, Granadeiro JP, Phillips RA, Alonso H, Catry P. 2011. Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proc. R. Soc. B: Biol. Sci.* 278:1786–93
- Dicke M, Burrough P. 1988. Using fractal dimensions for characterizing tortuosity of animal trails. *Physiol. Entomol.* 13:393–98
- Dobzhansky T, Wright S. 1947. Genetics of natural populations. XV. Rate of diffusion of a mutant gene through a population of *Drosophila pseudoobscura*. *Genetics* 32:303–24
- Durban JW, Pitman RL. 2012. Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations? *Biol. Lett.* 8(2):274–77
- Eckert SA, Dolar LL, Kooyman GL, Perrin W, Rahman RA. 2002. Movements of whale sharks (*Rhincodon typus*) in South-east Asian waters as determined by satellite telemetry. *J. Zool. (Lond.)* 257:111–15
- Edwards AM. 2008. Using likelihood to test for Lévy flight search patterns and for general power-law distributions in nature. *J. Anim. Ecol.* 77:1212–22
- Edwards AM. 2011. Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. *Ecology* 92:1247–57
- Edwards AM, Phillips RA, Watkins NW, Freeman MP, Murphy EJ, et al. 2007. Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature* 449:1044–48



- Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl. Acad. Sci. USA* 107:2078–81
- Fauchald P, Tveraa T. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–88
- Fauchald P, Tveraa T. 2006. Hierarchical patch dynamics and animal movement pattern. *Oecologia* 149:383–95
- Gaspar P, Georges JY, Fossette S, Lenoble A, Ferraroli S, Le Maho Y. 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc. R. Soc. B: Biol. Sci.* 273:2697–702
- Goldsworthy SD, Page B. 2007. A risk-assessment approach to evaluating the significance of seal bycatch in two Australian fisheries. *Biol. Conserv.* 139:269–85
- Gould JL. 1998. Sensory bases of navigation. *Curr. Biol.* 8:R731–38
- Guinet C, Dubroca L, Lea MA, Goldsworthy S, Cherel Y, et al. 2001. Spatial distribution of foraging in female Antarctic fur seals (*Arctocephalus gazella*) in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Mar. Ecol. Progr. Ser.* 219:251–64
- Gurarie E, Andrews RD, Laidre KL. 2009. A novel method for identifying behavioural changes in animal movement data. *Ecol. Lett.* 12:395–408
- Halley JM, Hartley S, Kallimanis AS, Kunin WE, Lennon JJ, Sgardelis SP. 2004. Uses and abuses of fractal methodology in ecology. *Ecol. Lett.* 7:254–71
- Hammerschlag N, Gallagher AJ, Lazarre DM. 2011. A review of shark satellite tagging studies. *J. Exp. Mar. Biol. Ecol.* 398:1–8
- Hayes SA, Teutschel N, Michel C, Champagne C, Robinson P, et al. 2012. Mobile receivers: releasing the mooring to ‘see’ where fish go. *Environ. Biol. Fishes*. In press (doi: 10.1007/s10641-011-9940-x)
- Hays GC, Dray M, Quaife T, Smyth TJ, Mironnet NC, et al. 2001. Movements of migrating green turtles in relation to AVHRR derived sea surface temperature. *Int. J. Remote Sens.* 22:1403–11
- Horton TW, Holdaway RN, Zerbini AN, Hauser N, Garrigue C, et al. 2011. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. *Biol. Lett.* 7:674–79
- Humphries NE, Queiroz N, Dyer JRM, Pade NG, Musyl MK, et al. 2010. Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* 465:1066–69
- James A, Plank MJ, Brown R. 2008. Optimizing the encounter rate in biological interactions: ballistic versus Lévy versus Brownian strategies. *Phys. Rev. E* 78:051128
- James MC, Myers RA, Ottensmeyer CA. 2005. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proc. R. Soc. B* 272:1547–55
- Johnson AR, Wiens JA, Milne BT, Crist TO. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landsc. Ecol.* 7:63–75
- Johnson DS, London JM, Lea MA, Durban JW. 2008. Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89:1208–15
- Johnson M, Madsen PT, Zimmer WM, de Soto NA, Tyack PL. 2006. Foraging Blainville’s beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. *J. Exp. Biol.* 209:5038–50
- Jonsen ID, Mills Flemming J, Myers RA. 2005. Robust state-space modeling of animal movement data. *Ecology* 86:2874–80
- Jonsen ID, Myers RA, James MC. 2006. Robust hierarchical state-space models reveal diel variation in movement rates of migrating leatherback turtles. *J. Anim. Ecol.* 75:1046–57
- Jorgensen SJ, Reeb CA, Chapple TK, Anderson S, Perle C, et al. 2010. Philopatry and migration of Pacific white sharks. *Proc. R. Soc. B* 277:679–88
- Kappes MA, Shaffer SA, Tremblay Y, Foley DG, Palacios DM, et al. 2010. Hawaiian albatrosses track inter-annual variability of marine habitats in the North Pacific. *Progr. Oceanogr.* 86:246–60
- Kuhn CE, Johnson DS, Ream RR, Gelatt TS. 2009. Advances in the tracking of marine species: using GPS locations to evaluate satellite track data and a continuous-time movement model. *Mar. Ecol. Progr. Ser.* 393:97–109
- Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PM, Houser DS. 2000. Foraging ecology of northern elephant seals. *Ecol. Monogr.* 70:353–82
- Lindley ST, Erickson DL, Moser ML, Williams G, Langness OP, et al. 2011. Electronic tagging of green sturgeon reveals population structure and movement among estuaries. *Trans. Am. Fish. Soc.* 140:108–22

- Lohmann KJ, Hester JT, Lohmann CMF. 1999. Long-distance navigation in sea turtles. *Ethol. Ecol. Evol.* 11:1–23
- Lohmann KJ, Lohmann CMF. 1996. Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* 199:73–81
- Lohmann KJ, Lohmann CMF, Endres CS. 2008. The sensory ecology of ocean navigation. *J. Exp. Biol.* 211:1719–28
- Lohmann KJ, Lohmann CMF, Putman NF. 2007. Magnetic maps in animals: nature’s GPS. *J. Exp. Biol.* 210:3697–705
- Mate BR, Gisiner R, Mobley J. 1998. Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. *Can. J. Zool.* 76:863–68
- Maxwell SM, Breed GA, Nickel BA, Makanga-Bahouna J, Pemo-Makaya E, et al. 2011a. Using satellite tracking to optimize protection of long-lived marine species: olive ridley sea turtle conservation in Central Africa. *PLoS ONE* 6:e19905
- Maxwell SM, Frank JJ, Breed GA, Robinson PW, Simmons SE, et al. 2011b. Benthic foraging on seamounts: a specialized foraging behavior in a deep-diving pinniped. *Mar. Mammal Sci.: Early View* 28:E333–44
- McConnell B, Bryant E, Hunter C, Lovell P, Hall A. 2004. Phoning home: a new GSM mobile phone telemetry system to collect mark-recapture data. *Mar. Mammal Sci.* 20:274–83
- Miller PJ, Johnson MP, Tyack PL. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes “creaks” in prey capture. *Proc. R. Soc. Lond. Ser. B* 271:2239–47
- Mills-Flemming JE, Field CA, James MC, Jonsen ID, Myers RA. 2006. How well can animals navigate? Estimating the circle of confusion from tracking data. *Environmetrics* 17:351–62
- Mills-Flemming JE, Jonsen ID, Myers RA, Field CA. 2010. Hierarchical state-space estimation of leatherback turtle navigation ability. *PLoS ONE* 5:e14245
- Milne BT. 1991. Lessons from applying fractal models to landscape patterns. In *Quantitative Methods in Landscape Ecology*, ed. MG Turner, RH Gardner, pp. 199–235. New York: Springer-Verlag
- Morales JM, Haydon DT, Frair J, Hosinger KE, Fryxell JM. 2004. Extracting more from relocation data: building movement models as mixtures of random walks. *Ecology* 85:2436–45
- Mueller T, Fagan WF. 2008. Search and navigation in dynamic environments—from individual behaviors to population distributions. *Oikos* 117:654–64
- Muheim R, Moore FR, Phillips JB. 2006a. Calibration of magnetic and celestial compass cues in migratory birds: a review of cue-conflict experiments. *J. Exp. Biol.* 209:2–17
- Muheim R, Phillips JB, Akesson S. 2006b. Polarized light cues underlie compass calibration in migratory songbirds. *Science* 313:837–39
- Nevitt GA, Bonadonna F. 2005. Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biol. Lett.* 1:303–5
- Nevitt GA, Losekoot M, Weimerskirch H. 2008. Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proc. Natl. Acad. Sci. USA* 105:4576–81
- Newsome SD, Clementz MT, Koch PL. 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Mar. Mammal Sci.* 26:509–72
- Okubo A, Levin SA. 2002. *Diffusion and Ecological Problems*. New York: Springer-Verlag
- Padman L, Costa DP, Bolmer ST, Goebel ME, Huckstadt LA, et al. 2010. Seals map bathymetry of the Antarctic continental shelf. *Geophys. Res. Lett.* 37:L21601
- Padman L, Costa DP, Dinniman MS, Fricker HA, Goebel ME, et al. 2012. Oceanic controls on the mass balance of Wilkins Ice Shelf, Antarctica. *J. Geophys. Res. Oceans* 117:C01010
- Papi F, Liew HC, Luschi P, Chan EH. 1995. Long-range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open sea. *Mar. Biol.* 122:171–75
- Papi F, Luschi P, Akesson S, Capogrossi S, Hays GC. 2000. Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* 203:3435–43
- Patterson TA, Basson M, Bravington MV, Gunn JS. 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *J. Anim. Ecol.* 78:1113–23
- Patterson TA, McConnell BJ, Fedak MA, Bravington MV, Hindell MA. 2010. Using GPS data to evaluate the accuracy of state-space methods for correction of Argos satellite telemetry error. *Ecology* 91:273–85
- Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J. 2008. State-space models of individual animal movement. *Trends Ecol. Evol.* 23:87–94

- Peckham SH, Diaz DM, Walli A, Ruiz G, Crowder LB, Nichols WJ. 2007. Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS ONE* 2:e1041
- Pinaud D. 2008. Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems. *J. Appl. Ecol.* 45:91–99
- Pinaud D, Weimerskirch H. 2007. At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J. Anim. Ecol.* 76:9–19
- Plank MJ, Codling EA. 2009. Sampling rate and misidentification of Lévy and non-Lévy movement paths. *Ecology* 90:3546–53
- Polovina J, Uchida I, Balazs G, Howell EA, Parker D, Dutton P. 2006. The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep Sea Res. Part II* 53:326–39
- Polovina JJ, Kobayashi DR, Parker DM, Seki MP, Balazs GH. 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. *Fish. Oceanogr.* 9:71–82
- Rasmussen K, Palacios DM, Calambokidis J, Saborío MT, Dalla Rosa L, et al. 2007. Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biol. Lett.* 3:302–5
- Riedman M. 1990. *The Pinnipeds: Seals, Sea Lions, and Walruses*. Berkeley: Univ. Calif. Press. 439 pp.
- Robinson PW, Costa DP, Crocker DE, Gallo-Reynoso JP, Champagne CD, et al. 2012. Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PLoS ONE* 7(5):e36728
- Reynolds AM, Rhodes CJ. 2009. The Lévy flight paradigm: random search patterns and mechanisms. *Ecology* 90:877–87
- Schofield G, Bishop CM, MacLean G, Brown P, Baker M, et al. 2007. Novel GPS tracking of sea turtles as a tool for conservation management. *J. Exp. Mar. Biol. Ecol.* 347:58–68
- Shaffer SA, Costa DP. 2006. A database for the study of marine mammal behavior: gap analysis, data standardization, and future directions. *IEEE J. Ocean Eng.* 31:82–86
- Shaffer SA, Tremblay Y, Awkerman JA, Henry RW, Teo SLH, et al. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Mar. Biol.* 147:833–43
- Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, et al. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc. Natl. Acad. Sci. USA* 103:12799–802
- Shillinger GL, Palacios DM, Bailey H, Bograd SJ, Swithenbank AM, et al. 2008. Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol.* 6:e171
- Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJA, et al. 2008. Scaling laws of marine predator search behaviour. *Nature* 451:1098–102
- Siniff DB, Jensen CR. 1969. A simulation model of animal movement patterns. *Adv. Ecol. Res.* 6:185–217
- Sirovic A, Hildebrand JA, Wiggins SM, McDonald MA, Moore SE, Thiele D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep Sea Res. Part II* 51:2327–44
- Skellam JG. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196
- Sleeman JC, Meekan MG, Wilson SG, Polovina JJ, Stevens JD, et al. 2010. To go or not to go with the flow: environmental influences on whale shark movement patterns. *J. Exp. Mar. Biol. Ecol.* 390:84–98
- Tinker MT, Costa DP, Estes JA, 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 Res. Part II* 54:330–42
- Tomkiewicz SM, Fuller MR, Kie JG, Bates KK. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. *Philos. Trans. R. Soc. B* 365:2163–76
- Tremblay Y, Roberts AJ, Costa DP. 2007. Fractal landscape method: an alternative approach to measuring area-restricted searching behavior. *J. Exp. Biol.* 210:935–45
- Tremblay Y, Robinson PW, Costa DP. 2009. A parsimonious approach to modeling animal movement data. *PLoS ONE* 4:e4711
- Turchin P. 1996. Fractal analyses of animal movement: a critique. *Ecology* 77:2086–90

- Turchin P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Plants and Animals*. Sunderland, MA: Sinauer Assoc.
- Turcotte DL. 1997. *Fractals and Chaos in Geology and Geophysics*. Cambridge, UK: Cambridge Univ. Press
- Tyack PL, Zimmer WMX, Moretti D, Southall BL, Claridge DE, et al. 2011. Beaked whales respond to simulated and actual navy sonar. *PLoS ONE* 6:e17009
- Viswanathan G, Buldyrev S, Havlin S, da Luz M, Raposo E, Stanley H. 1999. Optimizing the success of random searches. *Nature* 401:911–14
- Wallace BP, DiMatteo AD, Bolten AB, Chaloupka MY, Hutchinson BJ, et al. 2011. Global conservation priorities for marine turtles. *PLoS ONE* 6:e24510
- Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proc. R. Soc. Lond. Ser. B* 272:53–61
- Weimerskirch H, Louzao M, de Grissac S, Delord K. 2012. Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335:211–14
- Weimerskirch H, Pinaud D, Pawlowski F, Bost CA. 2007. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *Am. Nat.* 170:734–43
- Welch DW, Melnychuk MC, Payne JC, Rechisky EL, Porter AD, et al. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc. Natl. Acad. Sci. USA* 108:8708–13
- Weng KC, Castilho PC, Morrisette JM, Landeira-Fernandez AM, Holts DB, et al. 2005. Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* 310:104–6
- Wiens JA, Crist TO, With KA, Milne BT. 1995. Fractal patterns of insect movement in microlandscape mosaics. *Ecology* 76:663–66
- Wilson RP, Shepard ELC, Liebsch N. 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. *Endanger. Species Res.* 4:123–37
- Witt MJ, Bonguno EA, Broderick AC, Coyne MS, Formia A, et al. 2011. Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic. *Proc. R. Soc. Lond. Ser. B* 278:2338–47
- Zbinden JA, Bearhop S, Bradshaw P, Gill B, Margaritoulis D, et al. 2011. Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. *Mar. Ecol. Progr. Ser.* 421:291–302
- Žydelis R, Lewison RL, Shaffer SA, Moore JE, Boustany AM, et al. 2011. Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proc. R. Soc. B* 278:3191–200





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