REVIEW SUMMARY

ECOLOGY

Aquatic animal telemetry: A panoramic window into the underwater world

Nigel E. Hussey, Steven T. Kessel, Kim Aarestrup, Steven J. Cooke, Paul D. Cowley, Aaron T. Fisk, Robert G. Harcourt, Kim N. Holland, Sara J. Iverson,* John F. Kocik, Joanna E. Mills Flemming, Fred G. Whoriskey

BACKGROUND: Global aquatic environments are changing profoundly as a result of human actions; consequently, so too are the ways in which organisms are distributing themselves through space and time. Our ability to predict organism and community responses to these alterations will be dependent on knowledge of animal movements, interactions, and how the physiological and environmental processes underlying them shape species distributions. These patterns and processes ultimately structure aquatic ecosystems and provide the wealth of ecosystem services upon which humans depend. Until recently, the vast size, opacity, and dynamic nature of the aquatic realm have impeded our efforts to understand these ecosystems. With rapid technological advancement over the past several decades, a suite of electronic tracking devices (e.g., acoustic and satellite transmitters) that can remotely monitor animals in these challenging environments are now available. Aquatic telemetry technology is rapidly accelerating our ability to observe animal behavior and distribution and, as a consequence, is fundamentally altering our understanding of the structure and function of global aquatic ecosystems. These advances provide the toolbox to define how future global aquatic management practices must evolve.

ADVANCES: Aquatic telemetry has emerged through technological advances in miniaturization, battery engineering, and software and hardware development, allowing the monitoring of organisms whose habitats range from the poles to the tropics and the photic zone to the abyssal depths. This is enabling the characterization of the horizontal and vertical movements of individuals, populations, and entire communities over scales of meters to tens of thousands of kilometers and over time frames of hours to years and even over the entire lifetimes of individuals. Electronic tags can now be equipped with sensors that measure ambient physical parameters (depth, temperature, conductivity, fluorescence), providing simultaneous monitoring of animals' environments. By linking telemetry with biologgers (e.g., jaw-motion sensors), it is possible to monitor individual feeding events. In addition, other devices on instrumented animals can communicate with one another, providing insights into predator-prey interactions and social behavior. Coupling telemetry with minute nonlethal biopsy allows understanding of how trophic dynamics, population connectivity, and gene-level basis for organismal health and condition relate to movement. These advances are revolutionizing the scope and scales of questions that can be addressed on the causes and consequences of animal distribution and movement.

OUTLOOK: Aquatic animal telemetry has advanced rapidly, yet new challenges present themselves in coordination of monitoring across large-spatial scales (ocean basins), data sharing, and data assimilation. The continued advancement of aquatic telemetry lies in establishing and maintaining accessible and cost-effective infrastructure and in promoting multidisciplinary tagging approaches to maximize cost benefits. A united global network and centralized database will provide the mechanism for global telemetry data and will promote a transparent environment for data sharing that will, in turn, increase global communication, scope for collaboration, intellectual advancement, and funding opportunities. An overarching global network will realize the potential of telemetry, which is essential for advancing scientific knowledge and effectively managing globally shared aquatic resources and their ecosystems in the face of mounting human pressures and environmental change. ■

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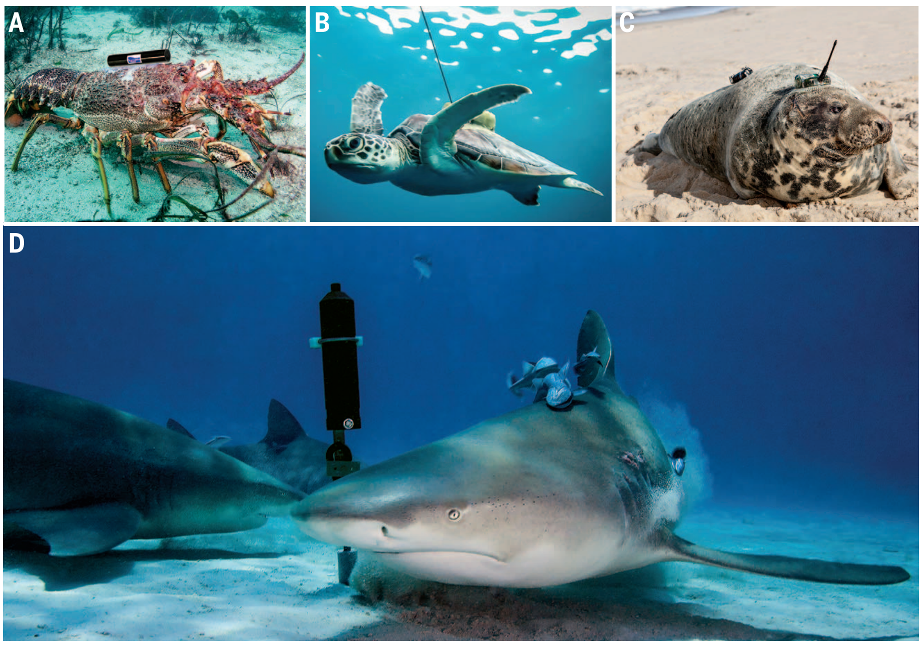

Aquatic telemetry in action. A southern rock lobster (*Jasus edwardsii*) (**A**) and a lemon shark (*Negaprion brevirostris*) (**D**) fitted with acoustic tags are detected and logged by moored receivers (D) or mobile receivers attached to opportunistic platforms or carried by large animals (C). A juvenile green turtle (*Chelonia mydas*) (**B**) fitted with a satellite tag is monitored in real time via orbiting satellites. A grey seal (*Halichoerus grypus*) "bioprobe" (**C**), fitted with intercommunicating acoustic and satellite transmitters, transmits and receives data on animal interactions and ocean conditions.

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Aquatic animal telemetry: A panoramic window into the underwater world

Nigel E. Hussey,[1] Steven T. Kessel,[1] Kim Aarestrup,[2] Steven J. Cooke,[3] Paul D. Cowley,[4] Aaron T. Fisk,[1] Robert G. Harcourt,[5] Kim N. Holland,[6] Sara J. Iverson,[7]* John F. Kocik,[8] Joanna E. Mills Flemming,[9] Fred G. Whoriskey[7]

The distribution and interactions of aquatic organisms across space and time structure our marine, freshwater, and estuarine ecosystems. Over the past decade, technological advances in telemetry have transformed our ability to observe aquatic animal behavior and movement. These advances are now providing unprecedented ecological insights by connecting animal movements with measures of their physiology and environment. These developments are revolutionizing the scope and scale of questions that can be asked about the causes and consequences of movement and are redefining how we view and manage individuals, populations, and entire ecosystems. The next advance in aquatic telemetry will be the development of a global collaborative effort to facilitate infrastructure and data sharing and management over scales not previously possible.

Most aquatic life forms—from microscopic bipolar bacteria (*Polaribacter* spp.) to the immense blue whale (*Balaenoptera musculus*)—move, which facilitates countless ecological processes. Animals move to acquire food, avoid predation or adverse conditions, seek out suitable mates, and locate spawning or nursery areas (*1*). Collectively, these movements transport nutrients, biomass, and dynamic energy across distinct ecosystems. Consequently, movements, influenced by environmental context and the physiological, endocrine, and energetic states of individuals, structure populations and ecosystems, maintain ecosystem function, and ultimately determine global aquatic productivity (*2*).

The vastness, complexity, and opacity of aquatic environments have historically impeded our efforts to acquire and process information on animal movements. However, recent advances in remote monitoring devices have revolutionized our capabilities for observation. These evolving and increasingly miniaturized electronic devices not only provide detailed information on the movements of free-ranging animals in space and time, but with the addition of sensors and/or biosampling, can document the ambient conditions surrounding an organism and measure its behavioral and physiological states (*3*). New generations of tracking devices even allow communication among instruments on different individuals, enabling novel insights into social behavior and predator-prey interactions. Aquatic telemetry now provides the tools to understand the causes and consequences of species' movements and their underlying patterns and processes over ecologically meaningful spatial and temporal scales.

Aquatic telemetry

Historically, the predictable occurrence of where and when valued aquatic animals could be caught (e.g., salmon returning to rivers to spawn, coastally migrating whales) provided the only measure of abundance and movements (*4*). This local or traditional knowledge transitioned to systematic marking of individuals for mark-recapture studies during the early phases of both whaling and fisheries management in the past century (*5*, *6*). These methods documented coarse-scale movement patterns and distributions but were typically limited in resolution (e.g., providing knowledge of only tagging location and recapture site). With the arrival of the technological era, these methods progressed to telemetry (*7*), which involves placing electronic devices ("transmitters" or "tags") on animals that autonomously transmit data to data-logging or relay-receiving stations. Because radio waves do not propagate in salt water, most aquatic telemetry is rooted in two principal approaches: acoustic (*8*) and satellite telemetry (*9*). Acoustically tagged animals are detected and logged by receivers moored at fixed locations that are retrieved periodically or by mobile receivers (e.g., on a pursuit vessel), whereas satellite observations are sent to land-based receivers via orbiting satellites. Electronic tags may be secured externally, inserted into the stomach, or surgically implanted in animals and programmed to record and/or transmit various data types, ranging from simple presence and location to extensive time series records of the animal's movements and environment (e.g., depth, temperature). Although other telemetric tools are available, such as short-range radio telemetry in freshwater environments and passive integrated transponders, we focus here on the two most widely used methods in aquatic ecosystems (acoustic and satellite telemetry). Biologging platforms (*10*) that do not have the capacity for data transmission are excluded from this Review.

Technological advances driving telemetry applications and growth

Telemetry is revolutionizing the discovery of aquatic animal movement, stemming from the groundbreaking acoustic tracks that revealed nightly excursions of scalloped hammerhead sharks (*Sphyrna lewini*) from seamounts into adjacent deep waters (*11*) and the first ARGOS (Advanced Research and Global Observation Satellite) satellite track of a basking shark (*Cetorhinus maximus*) off the west coast of Scotland (*12*). Miniaturization continues to be pivotal in the advancement of aquatic telemetry by expanding both the number of species and the life stages of animals that can be tracked. The smallest acoustic transmitters now weigh less than 1.4 g, enabling the tagging of tiny neonate fish. Similarly, advances in battery technology are allowing longer and more reliable deployments, while sophisticated software developments are providing more detailed movement information and greater data logging and transmitting flexibility. These hardware and software developments and cross-pollination of technologies are fuelling the animal movement ecology revolution.

Acoustic telemetry can now monitor the movements of tagged individuals for periods ranging from days to more than 10 years. Study durations are dictated by battery life, attachment method, and data resolution and/or complexity, allowing measurements of high-resolution continuous movements over small spatiotemporal scales or presence-absence data over vast spatial scales and multiple years (*8*). Acoustic telemetry traditionally depended on the recovery of submerged acoustic receivers or their interrogation by modems, but data can now be telemetered via satellite from remote locations, such as anchored or drifting buoys (*13*) or cabled underwater arrays. Most recently, acoustic receivers have been deployed on large animal carriers (e.g., seals) (*14*) and on ocean gliders, providing mobile platforms

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to detect tagged animals; autonomous underwater vehicles can even actively follow them (*15*).

Complementary to acoustic telemetry, satellite tags have evolved to suit the morphological and behavioral traits of the animal carrier, ranging from fish to marine mammals and reptiles. Pop-up archival tags log ambient variables and movements of ocean-roaming animals before popping off, whereupon they float to the surface and transmit data. Real-time satellite tags transmit logged dive behavior and location of tagged animals each time they surface. Satellite tags are bigger than acoustic tags and hence are restricted to larger animals, but they can record fine-scale time series data on the depth, temperature, and location of animals transiting thousands of kilometers. The recent addition of solar power cells and improved attachment designs now permit multiyear observations of individual animals (*16*).

The scale of aquatic telemetry monitoring

The application of aquatic animal telemetry has grown rapidly over the past 30 years, with thousands of studies having been conducted spanning all continents and biomes (Fig. 1). The sixfold increase in aquatic telemetry studies over the past decade (Fig. 1, A to C, and movies S1 and S2) has provided information across diverse taxa (Fig. 1D) that are crucial to ecosystem health, economically important, and/or imperilled (Fig. 1E).

Through the global coverage of the ARGOS satellite system, satellite telemetry can monitor animal movements over vast spatial scales encompassing the open ocean and even in politically unstable regions (Fig. 1B) (*17*). The dependence of acoustic telemetry on fixed receivers that detect transmissions over small distances (<1000 m) has focused the majority of research on coastal, estuarine, and freshwater ecosystems in the developed world (Fig. 1A). This has enabled the study of fine-scale movements of organisms that are too small to equip with satellite tags or where satellite location data are insufficiently precise. However, the rapid expansion of acoustic telemetry arrays in coastal regions and on offshore and mobile platforms now presents the opportunity for cost-effective and large-scale integrated monitoring of large numbers of individuals over the long term.

Movements of aquatic animals in four dimensions

The two-dimensional (2D) horizontal plane of the aquatic world consists of a diverse mosaic of polar to tropical habitats. Horizontal movements of species are subdivided into those that occur within well-defined home ranges and those that take place between two or more distinct habitats, typically referred to as migrations (*18*). Telemetry has allowed accurate estimation of the horizontal space use of a diverse range of organisms from Atlantic cod (*Gadus morhua*) (Fig. 2A) (*19*) to king prawns (*Penaeus plebejus*) (*20*). At localized scales, these data have defined home ranges and core habitat use, delineated species distributions, and identified spawning site fidelity. This has permitted estimation of complex population parameters required for stock assessments, such as both fisheries and natural mortality (*21*). At the

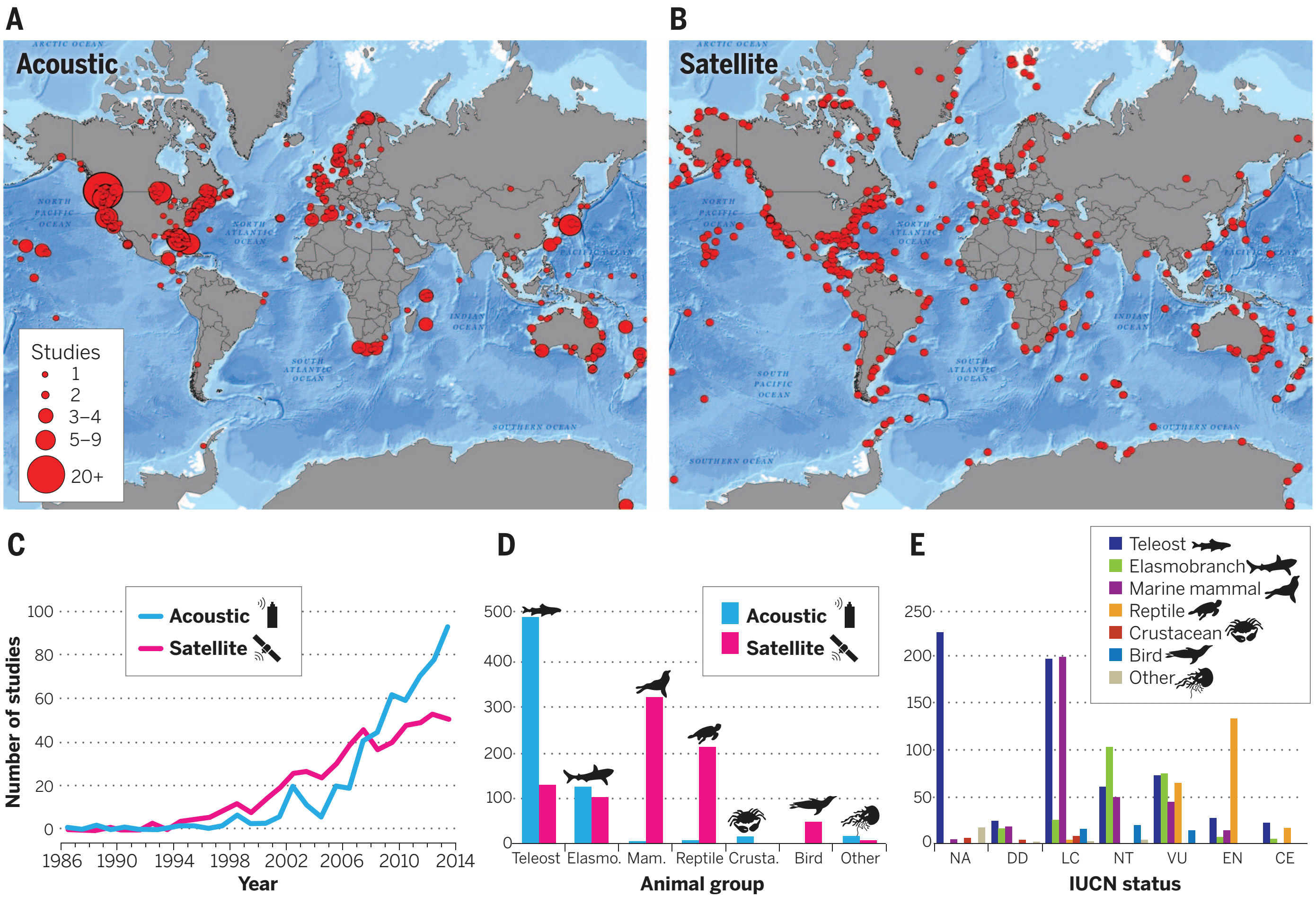


Fig. 1. Global distribution of aquatic telemetry studies. (**A**) Acoustic telemetry studies only. (**B**) Satellite telemetry studies only. (**C**) Increase in number of acoustic and satellite telemetry studies per year since 1986. (**D**) Number of acoustic and satellite telemetry studies by major aquatic animal groups [Elasmo., elasmobranch; Mam., marine mammals (including polar bears); Crusta., crustacean; Bird, flightless marine birds only]. (**E**) Number of acoustic and satellite telemetry studies per major animal group by International Union for Conservation of Nature (IUCN) threat categorization. NA, not assessed; DD, data deficient; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CE, critically endangered. See the associated data repository at DOI: 10.14286/20150203/KESSEL.

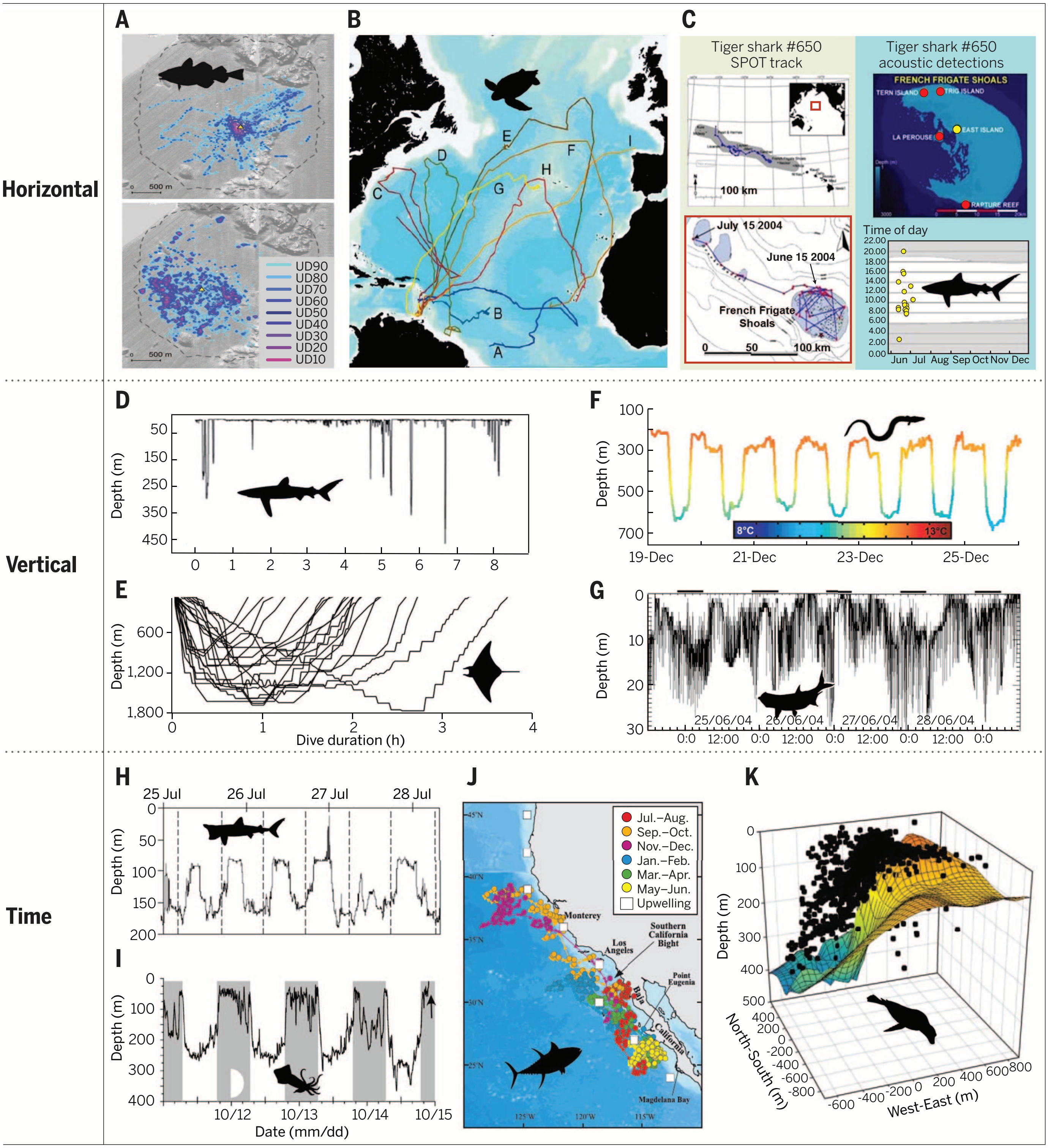


Fig. 2. Aquatic telemetry to understand the movements of animals in four dimensions: horizontal (2D), vertical (depth), and over time. (**A**) Fine-scale utilization distribution (UD) probabilities of Atlantic cod (*G. morhua*) at their spawning grounds, [altered from (*19*)]. (**B**) Transatlantic migrations of individual (A to I) leatherback turtles (*D. coriacea*) [taken from (*23*)]. (**C**) Small- and large-scale movements of tiger sharks (*G. cuvier*) revealed through a combination of satellite and acoustic telemetry [altered from (*29*)]. (**D**) Vertical movement behavior of a blue shark (*P. glauca*) [altered from (*35*)]. (**E**) Varying dive profile patterns of Chilean devil rays (*M. tarapacana*) [taken from (*32*)]. h, hours. (**F**) Oceanic diel migration of a European eel (*A. anguilla*), showing distinct temperature and vertical patterns [altered from (*27*)]. (**G**) Shallow-water dive profile of an Atlantic tarpon (*M. atlanticus*) [taken from (*34*)]. (**H**) Tidal-driven vertical movement patterns of a basking shark (*C. maximus*) [altered from (*40*)]. (**I**) Diel vertical movement patterns of a jumbo squid (*D. gigas*) [taken from (*41*)]. mm/dd, month/day. (**J**) Seasonal spatial utilization patterns by bluefin tuna (*T. orientalis*) [taken from (*43*)]. (**K**) Three-dimensional dive profile of female Weddell seals (*L. weddellii*) [taken from (*47*)] in relation to bathymetry and over two breeding seasons.

macroscale, telemetry has documented species migrations over tens of thousands of kilometers, confirming connectivity between populations at oceanic basin scales. This has revealed the intricacies and previously unanticipated complexity of migratory paths of bluefin tuna (*Thunnus thynnus*) (*22*), unsuspected transoceanic migrations of leatherback turtles (*Dermochelys coriacea*) (Fig. 2B) and white sharks (*Carcharodon carcharias*) (*23*, *24*), and transequatorial migrations of basking sharks (*25*). To date, much work has focused on simply describing these movement patterns, but due to their increasing size, such data sets, in the context of environmental variation, now lend themselves to an understanding of the mechanistic drivers of population structure and connectivity and metapopulation dynamics of species through quantifying emigration and immigration (*26*).

Unexpected horizontal movements of smaller animals are also challenging ideas that animal size dictates the scale of movement. For example, satellite telemetry revealed much of the long-suspected spawning migration of the critically endangered European eel (*Anguilla anguilla*) between Europe and the Sargasso Sea, with individuals measuring <1 m in length moving >1000 km in a few months (*27*). Through our capacity to examine horizontal movements of large numbers of individuals (>20,000 salmon smolts in one study alone in the Columbia River basin) (*28*), we can now begin to tease apart population processes built on individual-level behavior. Combining different telemetry techniques also provides opportunities to simultaneously elucidate movements over multiple scales. For example, fine-scale spatiotemporal movements of tiger sharks (*Galeocerdo cuvier*) seasonally feeding on fledgling albatrosses at a Hawaiian atoll were revealed through implanted acoustic tags, whereas the subsequent dispersal of these sharks over thousands of kilometers was revealed through satellite tags attached to the same individuals (Fig. 2C) (*29*).

Aquatic realms have a third dimension, depth, and a number of important environmental variables—including light level, pressure, temperature, and oxygen and salinity concentrations—vary predictably with depth. These parameters can divide species occurrence (e.g., by adaptive morphology and physiology), but other species can traverse these distinct vertical habitats. Some of the most notable telemetry results have revealed the extent and plasticity of these movements. These include highly dynamic vertical behaviors, from exclusively surface-orientated movements of salmon smolts (<5 m) (*30*) and obligate benthic movements of Greenland halibut (*Reinhardtius hippoglossoides*) (*31*) in the deep ocean (>1000 m) to species that undertake sporadic or prolonged deep diving, repetitive bounce dives, and/or consistent yo-yo movements (Fig. 2, D to G). Very deep dives to ~2000 m by Chilean devil rays (*Mobula tarapacana*) were characterized by two distinct dive profiles: one of rapid descent with slow stepwise ascent potentially related to prey searching and a second where rays rapidly descended and remained at depth (Fig. 2E) (*32*). By combining temperature and depth data derived from sensors integrated in transmitters, environmental profiles of the vertical habitats used by an animal can be compiled (Fig. 2F). These profiles provide explanatory power for the shape and duration of dive behavior observed related to the environment the animal encounters and have revealed behavioral and physiological thermoregulation in the world's largest fish, the whale shark (*Rhincodon typus*) (*33*). Even within shallow-water environments, diverse, highly structured shallow-water dive profiles have been recorded across numerous fish species, such as the Atlantic tarpon (*Megalops atlanticus*) (Fig. 2G) (*34*).

These vertical observations are providing insight into ecological linkages among depth zones and the foraging decisions of aquatic animals. Vertical movements of both pelagic and benthic predators such as blue sharks (*Prionace glauca*) (Fig. 2D) (*35*) and freshwater burbot (*Lota lota*) (*36*) show distinct profiles associated with bioenergetic gains, the vertical structuring of prey resources, predator avoidance, and social behavior. This has stimulated investigations into the occurrence of optimal foraging strategies such as Lévy walks, whereby animals undertake fractal vertical movement trajectories to optimize searching complex and sparsely distributed prey fields (*37*). Synthesizing horizontal and vertical movement data through state-space models to determine resident or directed movement states (*38*) will undoubtedly advance our understanding of foraging decisions, species interactions, and species redistributions under natural and anthropogenic change.

Time provides the fourth dimension within which 3D spatial utilization can be understood. The quality of habitat patches and their associated resources varies over time and is frequently in a state of disequilibrium. Examining how animals optimally synchronize their endogenous biological clocks with geophysical cycles is a critical step to resolving species' temporal distributions (*39*). Geophysical cycles produce predictable changes in the environment animals inhabit, from tidal changes in depth, temperature, and salinity to the contrasting dark and light periods of daily cycles. Tidally induced zooplankton aggregations, for example, are thought to cause the rhythmic dive patterns observed in basking sharks (Fig. 2H) (*40*), whereas many species, including jumbo squid (*Dosidicus gigas*), undertake diel vertical movement patterns related to prey distribution (Fig. 2I) (*41*). Telemetry has been instrumental in deciphering spawning aggregation dynamics of many reef fishes, where lunar cycles elicit spawning activity (*42*). Telemetry has also unveiled seasonal movements of endothermic Pacific bluefin tuna (*Thunnus orientalis*), driven by thermal fronts and strong downwellings that shape prey distributions (Fig. 2J) (*43*). For ectotherms that inhabit seasonally distinct temperate and subtropical zones, telemetry is showing how species use movements to compensate for localized environmental fluctuations. For example, estuarine yellow fin bream (*Acanthopagrus australis*) exhibit intricate behavioral switches, reversing depth distributions and diel activity patterns as a result of heavy rainfall and severe changes in turbidity and salinity (*44*).

The longevity of electronic tags now allows for measures of the consistency, repeatability, and interindividual variation in animal movements over time and, ultimately, during behavioral ontogeny. Through multiyear satellite telemetry of leatherback turtles, fidelity to a single migratory route was identified, providing clear conservation recommendations for a population that has declined by >90% over the past two decades (*45*). Conversely, highly complex and diverse movement patterns among tiger sharks tracked for several years around Hawaii could be explained by partial migrations, with some females moving for reproduction, whereas others undertook localized interisland movements driven by environmental conditions (*46*). Monitoring the spatiotemporal variability in territory use of Weddell seals (*Leptonychotes weddellii*) under ice and its influence on reproductive strategies over multiple consecutive breeding seasons (Fig. 2K) has also been possible (*47*). Coupling long-term telemetry tracking with biological data (e.g., maturity state) and environmental data (remote sensing imagery of sea surface temperature and productivity) will become central for quantifying temporal variation in the occurrence, timing, and destination of animal movements. These approaches will enable the first investigations of the role of memory and cognition in animal movement and navigation in aquatic ecosystems (*48*).

As telemetry data become more available, management strategies are incorporating geophysical cycles, variation in species' life histories, and environmental stochasticity to guide dynamic spatial planning efforts (*49*). For southern bluefin tuna (*Thunnus macoyii*), this approach integrated a habitat model conditioned with temperature-preference data from satellite tags on fish with an open-ocean model to enable near–real-time predictions of fish occurrence. These data were made available to fisheries managers, leading to the implementation of complex dynamic spatial zoning through which managers request data and repeatedly update spatial zoning plans. These advances make it feasible to consider creating spatially dynamic marine reserves that would vary in location annually as a function of predicted environmental conditions and associated animal movement patterns (*50*). Telemetry movement data are also allowing an assessment of the vulnerability of species to different fishing gears (*51*) to understand the post-release behavior and survival of released fishery bycatch (*52*) and to predict collisions between vessels and cetaceans (*53*). Such data will be imperative to inform fishery development and sustainability and to the conservation of vulnerable species.

Scaling from individual to multispecies movements

The movements of individuals of a species form only one component for understanding system-wide ecological organization in aquatic environments. Predators hunt for, locate, and consume their prey, driving direct behavioral responses (e.g., predation and competition and predator avoidance). Many species are social and can co-occur in aggregations. Monitoring interactions among species and communities and coordinated movements of social groupings mark the critical next steps. The ability of telemetry to capture movement data for almost all aquatic species is a major contribution toward disentangling these interactions and for facilitating spatially explicit ecosystem-based management (*54*).

Telemetry of co-occurring Antarctic and sub-Antarctic fur seals (*Arctocephalus gazella* and *A. tropicalis*), for example, recorded considerable temporal and spatial foraging overlap (*55*) and a lack of resource partitioning. Conversely, sympatric jellyfishes (*56*) and whales (*57*) (Fig. 3A), with known dietary overlap, exhibited contrasting movements to avoid direct resource competition. Simultaneous monitoring of predators and prey can reveal the timing of predation events, such as sperm whales (*Physeter macrocephalus*) feeding on jumbo squid (Fig. 3B) (*58*). Emerging telemetry technologies include animal-borne acoustic-receiver tags that have recorded intra- and interspecific interactions of Galapagos sharks (*Carcharhinus galapagensis*) (*59*), whereas satellite-linked units on seals have documented spatiotemporal patterns of encounters with conspecifics and prey species (*14*). Moreover, abdominally implanted satellite tags equipped with temperature sensors are enabling the first monitoring of aquatic animals over their entire lifetimes. For instance, these tags revealed that some Steller sea lion (*Eumetopias jubatus*) deaths are apparently due to predation by Pacific sleeper sharks (*Somniosus pacificus*) (*60*).

Monitoring of multispecies movement patterns also provides a tool to assess the effectiveness of spatial management practices. So far, telemetry has revealed both successes and failures. Eighteen species of acoustically tagged reef fishes in the Caribbean region showed fidelity to marine protected areas (MPAs). However, three-quarters of the species examined travelled outside their protective limits (*61*). In contrast, telemetry data for five historically overfished snapper and grouper species in the Dry Tortugas islands indicated that the fish stayed primarily in a no-take marine reserve, which should provide sufficient protection for species recovery (Fig. 3C) (*62*). By directly quantifying multispecies movements and home ranges relative to protective boundaries, improvements in the design (e.g., stepping stone MPAs encompassing habitat hotspots) (*63*) and approach (e.g., spatially and temporally flexible closures) (*64*) to MPAs can be made and their limitations fully understood.

The ability of telemetry to resolve multispecies movements over scales much larger than those used in the current spatial management practices, encompassing cross-national and political borders, is a great asset. A foremost example is the Tagging of Pacific Predators (TOPP) program. Coordinated satellite telemetry of 23 apex marine predators—including tunas, pinnipeds, sharks, sea turtles, and cetaceans—documented systematic migration pathways, congener niche separation, and the location of multispecies biodiversity hotspots (*65*). These data, and those from a similar effort in Antarctica (*66*), are unveiling the first oceanscale view of the movement dynamics of entire predator guilds (Fig. 3D). Through characterizing daily, seasonal, and multiyear scales of species movements and interactions, as well as of imperilled species distributions and biodiversity hotspots, these data will be foundational for macroscale marine ecosystem management. Recent predictive modeling of projected climate change scenarios on species-specific core habitat use and basin-scale biodiversity patterns provides one such management application (*67*).

Integrating telemetry with other biological measures

Huey's (*68*) seminal paper established the first framework on the physiological consequences of animal habitat selection, but only through the emergence of telemetry tools can those relationships be empirically tested. Increasingly, physiological approaches are being combined with telemetry to link animal behavior, physiology, movement, and habitat selection (*69*). This allows the prediction of how anthropogenic and climate changes will affect ecosystems, for example, by determining cause and effect relationships and identifying optimal habitats and stressor thresholds for species, populations, and communities. This is achievable with the use of nonlethal tissue sampling (e.g., blood sample, muscle biopsy) of telemetered animals and laboratory experiments linked with telemetry of free-ranging animals (often including sensors that measure acceleration or cardiac activity, for example) (*70*).

Satellite telemetry of salmon sharks (*Lamna ditropis*) documented a subarctic-to-subtropical migration, with animals occupying an extreme thermal range of 2° to 24°C. Subsequent tissue analysis revealed that enhanced expression of specific cardiac proteins enabled exploitation of this thermal range (Fig. 4A) (*71*). In the vertical dimension, tropical bigeye tuna (*Thunnus obesus*) were shown to use behavioral and physiological thermoregulation to allow pursuit of prey into cold and hypoxic deep water, by using warm surface waters to regain body heat (*72*). In salmonids, combining telemetry measurements with laboratory manipulation of their endocrine and neurophysiology revealed links between migration speed, timing, and testosterone concentrations and the mechanisms underlying migration timing and homing in these commercially and culturally important fish (*73*, *74*).

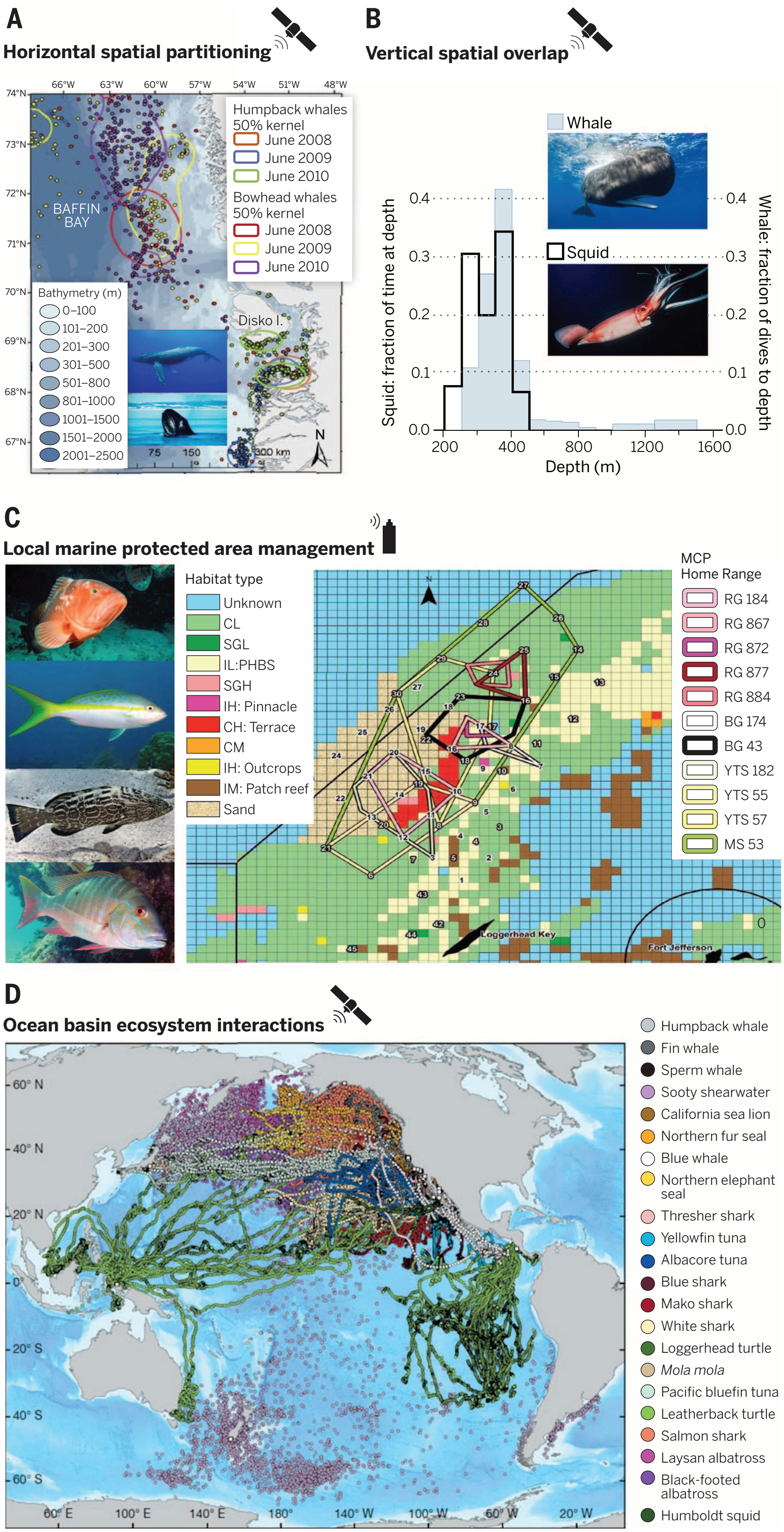
Feeding, energetic requirements, digestive physiology, and body condition are major factors that shape species' movements, distributions, and survival. By linking jaw-attached sensors with satellite telemetry, it was possible to remotely identify individual feeding attempts of free-swimming northern elephant seals (*Mirounga angustirostris*) (Fig. 4B) (*75*). Refined feeding estimates of the planet's largest predatory fish, the white shark, have only been possible by coupling swimming speeds derived from high-resolution movement data with experimental measurements of standard metabolic rate and respiration (Fig. 4C) (*76*). Similarly, the correlation between lipid stores measured using ultrasound and drift dives derived from satellite telemetry has led to reconstruction of a time series of elephant seal body condition over fine spatial and temporal scales (Fig. 4D) (*77*). The miniaturization of archival multi-instrumented biologger devices that incorporate triaxial accelerometers and video and audio capability, coupled with telemetric approaches, provides one of the most exciting avenues for directly relating behavior and physiology to stimuli in the environment (*78*). Remote streaming of these high-sampling–rate and high-resolution data-rich files through rapid data transmission is the next needed evolution in telemetry technology.

Collectively, integration of the tools of telemetry and physiology provides real-world views of animal-environment interactions that directly feed into conservation and management (*79*). For example, biochemical measures of stress responses linked with telemetry can explain and predict mortality rates associated with fishing; examples include salmon bycaught and released from nets (*80*) or sharks released from drum lines (*81*). Telemetry data focused on thermally influenced behavior can be combined with laboratory-based studies on swimming energetics to estimate potential mortality in the face of climate change (*82*). Nonlethal biosampling of tagged barracuda (*Sphyraena barracuda*) revealed differences in habitat use among fish with different levels of ciguatera biotoxin, with implications for human consumption and health (*83*).

The integration of telemetry with molecular genetics will allow us to address questions on population structure and rates and patterns of organism dispersal that will be central for understanding metapopulations and ensuring population resilience. Long-term movements of lemon sharks (*Negaprion brevirostris*) off coastal Florida combined with molecular genetics confirmed connectivity between a seasonal aggregation of migratory adults and juveniles resident in genetically and geographically distinct nurseries (Fig. 4E) (*84*). In the first integrated framework of its kind, biogeographic, genetic, and telemetry data on global turtle populations were used to define regional management units at multiple biological and spatial scales (*85*). Incorporating telemetry with genetics will improve fisheries managers' confidence in stock delineation units. Scaling to ecological genomics provides the next generation of tools to study the genetic basis for organismal health and behavior related to movement. For instance, gene assays have identified key physiological processes that predicted the failure of sockeye salmon during migrations on the high seas (*86*).

Biosampling and the analysis of biochemical tracers—including stable isotopes of carbon and nitrogen, fatty acids, and trace elements in animal tissues—can link movement to an animal's diet and trophic ecology. This approach can elucidate food web dynamics, specifically rates of energy transfer through herbivores to carnivores and nutrient coupling among distinct

Fig. 3. Multispecies aquatic telemetry studies. (**A**) Spatial partitioning between humpback (*Megaptera novaeangliae*) and bowhead (*Balaena mysticetus*) whales limits resource competition [altered from (57)]. (**B**) Spatial overlap between sperm whales (*P. macrocephalus*) and jumbo squid (*D. gigas*) supports predation hypotheses [altered from (58)]. (**C**) Home ranges of four exploited teleost fish species (BG, black grouper; MS, mutton snapper; RG, red grouper; YTS, yellowtail snapper) fall within marine reserve boundaries (habitat types: C, contiguous; I, isolated; SG, spur-and-groove; H, high; M, medium; L, low relief; HB, hard bottom; PHBS, patchy HB in sand) [altered from (62)]. MCP, minimum convex polygon. (**D**) Long-term tracking of 23 apex predators across the Pacific Ocean [altered from (65)]. [Photo credits for (C), starting second from top: G. Carter; C. Estape; J. McEvoy]



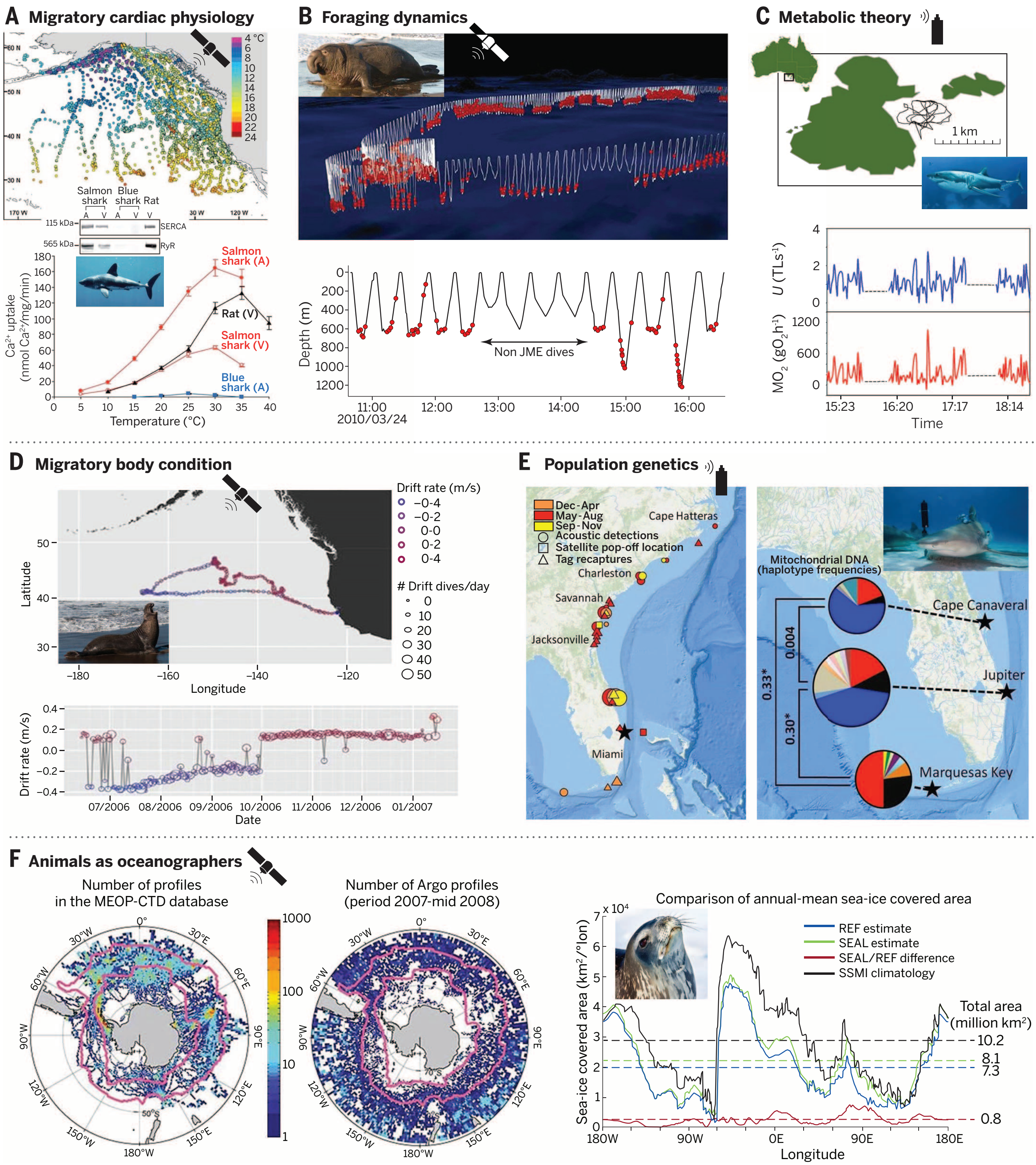


Fig. 4. Multidisciplinary aquatic telemetry approaches. (**A**) Satellite telemetry and tissue analysis reveal the physiological mechanism for spatial distribution of salmon sharks (*L. ditropis*) [altered from (71)]. (A) atrium; (V) ventricle. (**B**) Monitoring horizontal and vertical movements of seals and their jaw-motion events (JMEs) to quantify feeding events in northern elephant seals (*M. angustirostris*) [altered from (75)]. (**C**) High-resolution localized movements of white sharks (*C. carcharias*) using acoustic telemetry tied with metabolic theory to infer feeding rates [taken from (76)]. MO_2 (gO_2h^{-1}), routine metabolic rate; U (TLs^{-1}), swimming speed. (**D**) Blubber thickness and drift dive rates derived from satellite telemetry are used to estimate the rate of resource acquisition and the at-sea body condition of free-ranging northern elephant seals [taken from (77)]. (**E**) Population ecology of lemon sharks (*N. brevirostris*) on the east coast of the United States investigated using acoustic and satellite telemetry (left) and mitochondrial DNA analysis (right) [altered from (84)]. Stars represent tagging location (left) and genetic sampling location (right). (**F**) Improved estimates of the Southern Ocean general circulation using data from seals equipped with conductivity-temperature-depth sensors and satellite transmitters [altered from (91)]. MEOP-CTD, marine mammals exploring the oceans pole to pole–conductivity-temperature-depth database; REF, reference state estimate; SEAL, state estimate constrained with Argo and seal telemetry data; SSMI, Special Sensor Microwave Imager satellite observation data. [Photo credits: (A) B. Olsen; (B and D) M. Baird; (E) M. Potenski]

ecosystems. The analysis of these tracers in a large number of individuals, including telemetered animals, allows extrapolation of observations to the population level. Moreover, it can permit a retrospective view of a population's movement patterns and trophic dynamics to examine the effects of climate- and human-induced change. Biochemical tracers combined with telemetry have documented resource partitioning among eared seals (87), detected trophic linkages among alligators (88), and characterized the effects of tourism-related provisioning (i.e., baiting sharks into areas where divers can view them) on reef sharks (89). Telemetry coupled with genetics and/or genomics and biochemical tracers provides cutting-edge opportunities to examine the effects, roles, and evolutionary successes of invasive, commercial, and imperilled species.

Animal oceanographers

Telemetered animals undertaking their daily routines encounter environmental variation and compile data sets with a frequency and over a range of scales that humans could not feasibly collect using conventional tools. Satellite-linked transmitters attached to marine mammals can record time series data on temperature, salinity, fluorescence, light, and partial pressure of oxygen as a function of location and depth in the different water masses that animals encounter (90). This approach has proven extremely effective for sampling regions that are logistically challenging and costly to observe, for example, areas under sea ice during fall and winter (91).

Data derived from these "animal oceanographers" are now enhancing regional oceanographic models. Transmitters carried by narwhals (*Monodon monoceros*) and beluga whales (*Delphinapterus leucas*) have provided more than 200,000 temperature and salinity profiles of the Arctic Ocean (92), whereas transmitters carried by seals and sea lions have provided almost circumpolar oceanographic sampling of the Southern Ocean (Fig. 4F) (91). Approximately 70% of all animal oceanographer profiles from this region are from south of 60°S (93), with considerable data from south of the Antarctic Circumpolar Current where Argo buoy data are effectively absent due to ice. These data produce hydrographic profiles with high spatial and temporal resolution (2.5 profiles per day, on average). These profiles are improving estimates of Southern Ocean circulation (91), revealing upper ocean and coastal processes that affect the basal melting of ice shelves (94), and elucidating previously unknown physical properties of upwelling off the southern coast of Australia (95).

These successes are encouraging the further development and testing of oceanography-capable telemetry tags on nonmammalian species such as tuna and sharks. Satellite tag measurements of the depth at which blue marlins (*Makaira nigricans*) limit their dives (requiring oxygen concentrations >3.5 ml·liter^{-1}) now allow inferences over the 3D extent of the oxygen minimum zone in the tropical northeast Atlantic (96). Animals monitoring their environments have the potential to record these oceanographic data across all biomes, from the poles to the tropics and the photic zone to the abyssal depths. These data will continue to enhance existing ocean-atmosphere observation platforms but will also provide opportunities to improve ocean forecasting.

The future of aquatic telemetry, obstacles to traverse, and relevance for aquatic management and conservation

Aquatic telemetry has revealed distinctive insights into our blue planet, in a range of organisms and over previously unimaginable spatiotemporal scales. It has led to paradigm shifts in our understanding of animal-environment interactions and how aquatic ecosystems are structured. Most importantly, telemetry now provides the opportunity for the development of next-generation aquatic governance frameworks. Traditionally, management of aquatic resources has lagged behind that of the terrestrial realm, where landscape ecology principles are well founded, broadly accepted, and incorporated into management regimes. The terrestrial approach is built on understanding the causes, changes, and ecological functions associated with spatial animal-environment patterns under a nonequilibrium view. Aquatic resource management requires a similar approach, but its adoption has been hindered by a lack of data over relevant spatiotemporal scales. Telemetry can now provide these data, facilitating aquatic-scape approaches for conservation and management, while also bridging the gap between terrestrial and aquatic ecosystems (97), inspiring a unified approach to global resource management.

However, addressing global scientific and management questions will require expanded telemetry infrastructure and animal-tagging efforts

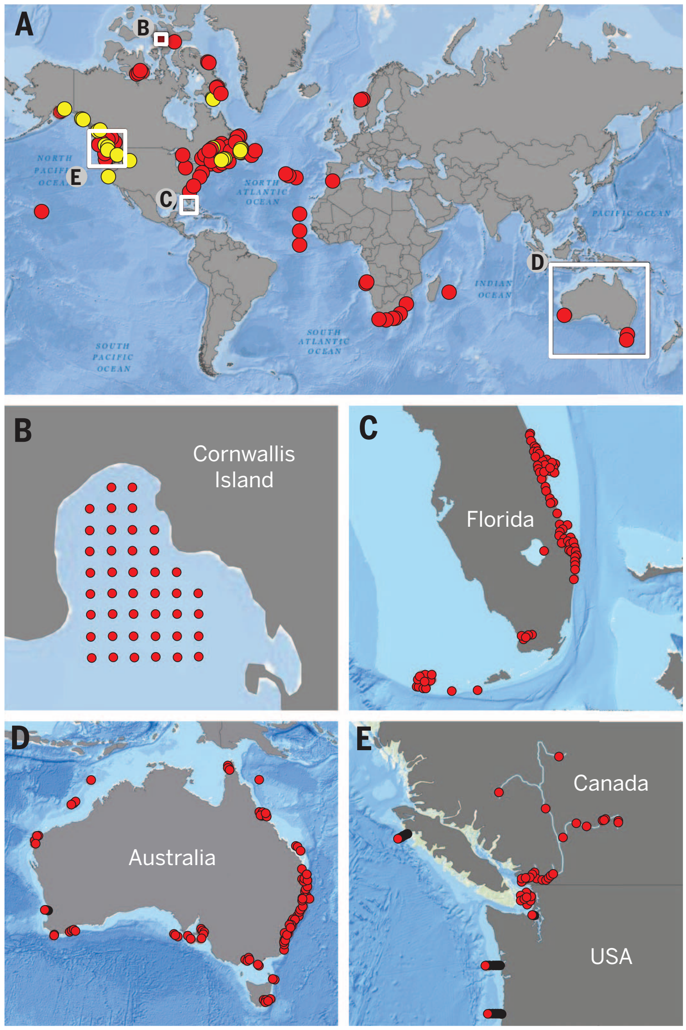


Fig. 5. The network model (or approach) of acoustic telemetry to facilitate monitoring of aquatic species over required ecological and biological scales. (**A**) Global monitoring (OTN global). Red points indicate current receiver stations; yellow points denote proposed receiver stations. Monitoring (**B**) within a 2 km by 3 km high Arctic embayment, (**C**) along the coast of an entire state [Florida Atlantic Coast Telemetry (FACT) array], (**D**) across an entire country coastline [Australian Animal Tagging and Monitoring System (AATAMS) array], and (**E**) trans-boundary between Canada and the United States [Pacific Ocean Shelf Tracking (POST)/OTN array]. In most instances, these network models integrate both acoustic and satellite telemetry approaches.

over scales larger than those previously considered. Industry commitment to advance technologies and ensure compatibility will be imperative. Collaborative research groups are emerging to facilitate sharing of equipment, facilities, and expertise and to foster coordinated data sharing. This "network model" integrates acoustic and satellite telemetry and covers scales from individual bays to coastal shelves that cross national boundaries and, in the case of Australia, an entire continent (Fig. 5). This recognition that aquatic animal movements and the dynamic nature of the physical environment they inhabit transcend geopolitical, economic, and management boundaries is driving the formation of global consortia such as the Ocean Tracking Network (OTN) (*98*) (Fig. 5A) and the Global Tagging of Pelagic Predators (*99*).

The establishment of these global networks raises new challenges over data sharing and will require strategies to address data management, ownership, and public release. Successful models exist in the physical oceanography, ocean chemistry, and molecular genetic domains (e.g., the GenBank archive) (*100*). Varying levels of data sharing are already apparent in current telemetry networks: The early success of animal oceanographers provides one such example (*91*), and centralized telemetry databases are available, such as the Ocean Biogeographic Information System–Spatial Ecological Analysis of Megavertebrate Populations (*101*). Aquatic telemetry may benefit from a single centralized governing body for data archiving and management, similar to the GenBank model that is funded across organizations and continents. This would promote data standardization and would benefit the global research community through increased communication, scope for collaboration, intellectual exposure, and funding opportunities. Recognizing that large spatial gaps in aquatic monitoring currently exist, a concerted effort is needed. This is particularly true in developing countries, where the status of aquatic resources is poorly known and only fragmented management exists yet resources are often exploited by developed nations. An integrated global telemetry approach would substantially improve equitable decision-making at local and international scales and would generate considerable dividends with regard to resource management, commerce, and food security.

Conclusions

Telemetry has profoundly altered and, at times, revolutionized our understanding of the complexities of animal movements and interactions and how these structure aquatic ecosystems. Technological advancements in telemetry and multidisciplinary approaches will continue to promote new avenues of enquiry, growing the knowledge base. Challenges remain in building a unified global network approach that will enable us to meet the upcoming needs in ocean management and to achieve telemetry's potential for deriving and disseminating knowledge on the spatial and temporal scales over which aquatic resources are structured and must be sustainably managed. It is certain that the ocean will continue to change. The global network approach will realize and facilitate an environment for knowledge and the sharing of resources and data. Additionally, through centralized data archiving and the promotion of collaboration across disciplines, this approach will provide great potential for the development and implementation of global aquatic-scape management, as well as for reaction to future changes in aquatic populations and ecosystems dominated by mobile animals.

REFERENCES AND NOTES

1. D. E. Bowler, T. G. Benton, Causes and consequences of animal dispersal strategies: relating individual behavior to spatial dynamics. *Biol. Rev.* **80**, 205–225 (2005).
2. T. R. Parsons, M. Takahashi, B. Hargrave, *Biological Oceanographic Processes* (Elsevier, Amsterdam, 2013).
3. D. P. Costa, G. A. Breed, P. W. Robinson, New insights into pelagic migrations: Implications for ecology and conservation. *Annu. Rev. Ecol. Evol. Syst.* **43**, 73–96 (2012). doi: 10.1146/annurev-ecolsys-102710-145045
4. R. L. Kelly, *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways* (Smithsonian Institution Press, Washington, DC, 1995).
5. K. Dahl, *Studier og Forsøk Over Ørret og Ørretvann* (Centraltrykkeriet, Kristiania, Norway, 1917).
6. E. D. Le Cren, A note on the history of mark-recapture population estimates. *J. Anim. Ecol.* **34**, 453–454 (1965). doi: 10.2307/2661
7. G. Arnold, H. Dewar, in *Electronic Tagging and Tracking in Marine Fisheries* (Springer, Dordrecht, 2001), pp. 7–64.
8. M. R. Donaldson *et al*., Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Front. Ecol. Environ* **12**, 565–573 (2014). doi: 10.1890/130283
9. E. L. Hazen *et al*., Ontogeny in marine tagging and tracking science: Technologies and data gaps. *Mar. Ecol. Prog. Ser.* **457**, 221–240 (2012). doi: 10.3354/meps09857
10. C. Rutz, G. C. Hays, New frontiers in biologging science. *Biol. Lett.* **5**, 289–292 (2009). doi: 10.1098/rsbl.2009.0089; pmid: 19324624
11. A. P. Klimley, S. B. Butler, D. R. Nelson, A. T. Stull, Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* griffith and smith, to and from a seamount in the Gulf of California. *J. Fish Biol.* **33**, 751–761 (1988). doi: 10.1111/j.1095-8649.1988.tb05520.x
12. I. Priede, A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing. *Fish. Res.* **2**, 201–216 (1984). doi: 10.1016/0165-7836(84)90003-1
13. L. Dagorn *et al*., Satellite-linked acoustic receivers to observe behavior of fish in remote areas. *Aquat. Living Resour.* **20**, 307–312 (2007). doi: 10.1051/alr:2008001
14. D. C. Lidgard, W. D. Bowen, I. D. Jonsen, S. J. Iverson, Predator-borne acoustic transceivers and GPS tracking reveal spatiotemporal patterns of encounters with acoustically tagged fish in the open ocean. *Mar. Ecol. Prog. Ser.* **501**, 157–168 (2014). doi: 10.3354/meps10670
15. C. M. Clark *et al*., Tracking and following a tagged leopard shark with an autonomous underwater vehicle. *J. Field Robot.* **30**, 309–322 (2013). doi: 10.1002/rob.21450
16. M. Domeier, N. Nasby-Lucas, Two-year migration of adult female white sharks (*Carcharodon carcharias*) reveals widely separated nursery areas and conservation concerns. *Anim. Biotelem.* **1**, 2 (2013).
17. S. M. Maxwell *et al*., Using satellite tracking to optimize protection of long-lived marine species: Olive ridley sea turtle conservation in Central Africa. *PLOS ONE* **6**, e19905 (2011). doi: 10.1371/journal.pone.0019905; pmid: 21589942
18. H. Dingle, V. A. Drake, What is migration? *Bioscience* **57**, 113–121 (2007). doi: 10.1641/B570206
19. M. J. Dean, W. S. Hoffman, D. R. Zemeckis, M. P. Armstrong, Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine. *ICES J. Mar. Sci.* **71**, 1474–1489 (2014). doi: 10.1093/icesjms/fsu040
20. M. Taylor, A. Ko, Monitoring acoustically tagged king prawns *Penaeus* (*Melicertus*) *plebejus* in an estuarine lagoon. *Mar. Biol.* **158**, 835–844 (2011). doi: 10.1007/s00227-010-1610-6
21. K. H. Pollock, H. Jiang, J. E. Hightower, Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Trans. Am. Fish. Soc.* **133**, 639–648 (2004). doi: 10.1577/T03-029.1
22. B. A. Block *et al*., Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434**, 1121–1127 (2005). doi: 10.1038/nature03463; pmid: 15858572
23. G. C. Hays, V. J. Hobson, J. D. Metcalfe, D. Righton, D. W. Sims, Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* **87**, 2647–2656 (2006). doi: 10.1890/0012-9658(2006)87[2647:FFMOLT]2.0.CO;2; pmid: 17089672
24. R. Bonfil *et al*., Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* **310**, 100–103 (2005). doi: 10.1126/science.1114898; pmid: 16210537
25. G. B. Skomal *et al*., Transequatorial migrations by basking sharks in the western Atlantic Ocean. *Curr. Biol.* **19**, 1019–1022 (2009). doi: 10.1016/j.cub.2009.04.019 pmid: 19427211
26. R. A. Cheke, J. A. Tratalos, Migration, patchiness, and population processes illustrated by two migrant pests. *Bioscience* **57**, 145–154 (2007). doi: 10.1641/B570209
27. K. Aarestrup *et al*., Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science* **325**, 1660 (2009). doi: 10.1126/science.1178120; pmid: 19779192
28. E. L. Rechisky, D. W. Welch, A. D. Porter, M. C. Jacobs-Scott, P. M. Winchell, Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia River estuary and coastal ocean. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 6883–6888 (2013). doi: 10.1073/pnas.1219910110; pmid: 23576733
29. C. G. Meyer, Y. P. Papastamatiou, K. N. Holland, A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Mar. Biol.* **157**, 1857–1868 (2010). doi: 10.1007/s00227-010-1457-x
30. M. D. Renkawitz, T. F. Sheehan, G. S. Goulette, Swimming depth, behavior, and survival of Atlantic salmon postsmolts in Penobscot Bay, Maine. *Trans. Am. Fish. Soc.* **141**, 1219–1229 (2012). doi: 10.1080/00028487.2012.688916
31. I. Peklova, N. E. Hussey, K. J. Hedges, M. A. Treble, A. T. Fisk, Depth and temperature preferences of the deep-water flatfish Greenland halibut *Reinhardtius hippoglossoides* in an Arctic marine ecosystem. *Mar. Ecol. Prog. Ser.* **467**, 193–205 (2012). doi: 10.3354/meps09899
32. S. R. Thorrold *et al*., Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nat. Commun.* **5**, 4274 (2014). doi: 10.1038/ncomms5274; pmid: 24983949
33. M. Thums, M. Meekan, J. Stevens, S. Wilson, J. Polovina, Evidence for behavioural thermoregulation by the world's largest fish. *J. R. Soc. Interface* **10**, 20120477 (2012). doi: 10.1098/rsif.2012.0477; pmid: 23075547
34. J. Luo, J. S. Ault, Vertical movement rates and habitat use of Atlantic tarpon. *Mar. Ecol. Prog. Ser.* **467**, 167–180 (2012). doi: 10.3354/meps09957
35. N. E. Humphries *et al*., Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* **465**, 1066–1069 (2010).pmid: 20531470
36. P. Harrison *et al*., Diel vertical migration of adult burbot: A dynamic trade-off among feeding opportunity, predation avoidance, and bioenergetic gain. *Can. J. Fish. Aquat. Sci.* **70**, 1765–1774 (2013). doi: 10.1139/cjfas-2013-0183
37. D. W. Sims *et al*., Scaling laws of marine predator search behaviour. *Nature* **451**, 1098–1102 (2008). doi: 10.1038/nature06518; pmid: 18305542
38. S. Bestley, I. D. Jonsen, M. A. Hindell, R. G. Harcourt, N. J. Gales, Taking animal tracking to new depths: Synthesizing horizontal-vertical movement relationships for four marine predators. *Ecology* **96**, 417–427 (2015). doi: 10.1890/14-0469.1
39. E. Naylor, Chronobiology: Implications for marine resource exploitation and management. *Sci. Mar.* **69**, 157–167 (2005).
40. E. L. C. Shepard *et al*., Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Mar. Ecol. Prog. Ser.* **328**, 205–213 (2006). doi: 10.3354/meps328205
41. W. Gilly *et al*., Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Mar. Ecol. Prog. Ser.* **324**, 1–17 (2006). doi: 10.3354/meps324001
42. Y. Sadovy, Y. S. de Mitcheson, P. L. Colin, *Reef Fish Spawning Aggregations: Biology, Research and Management* (Springer Science and Business Media, Dordrecht, 2011), vol. 35.

43. T. Kitagawa et al., Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus orientalis*) in relation to seasons and oceanographic conditions in the eastern Pacific Ocean. *Fish. Oceanogr.* **16**, 409–421 (2007). doi: 10.1111/j.1365-2419.2007.00441.x
44. N. L. Payne et al., Rain reverses diel activity rhythms in an estuarine teleost. *Proc. Biol. Sci.* **280**, 20122363 (2013). doi: 10.1098/rspb.2012.2363; pmid: 23173211
45. G. L. Shillinger et al., Persistent leatherback turtle migrations present opportunities for conservation. *PLOS Biol.* **6**, e171 (2008). doi: 10.1371/journal.pbio.0060171; pmid: 18630987
46. Y. P. Papastamatiou et al., Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology* **94**, 2595–2606 (2013). doi: 10.1890/12-2014.1; pmid: 24400511
47. M. A. Hindell, R. Harcourt, J. R. Waas, D. Thompson, Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Mar. Ecol. Prog. Ser.* **242**, 275–284 (2002). doi: 10.3354/meps242275
48. W. F. Fagan et al., Spatial memory and animal movement. *Ecol. Lett.* **16**, 1316–1329 (2013). doi: 10.1111/ele.12165; pmid: 23953128
49. A. J. Hobday, J. R. Hartog, T. Timmiss, J. Fielding, Dynamic spatial zoning to manage southern bluefin tuna (*Thunnus maccoyii*) capture in a multi-species longline fishery. *Fish. Oceanogr.* **19**, 243–253 (2010). doi: 10.1111/j.1365-2419.2010.00540.x
50. S. D. Gaines, S. E. Lester, K. Grorud-Colvert, C. Costello, R. Pollnac, Evolving science of marine reserves: New developments and emerging research frontiers. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 18251–18255 (2010). doi: 10.1073/pnas.1002098107; pmid: 20978212
51. E. Cortés et al., Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. *Aquat. Living Resour.* **23**, 25–34 (2010). doi: 10.1051/alr/2009044
52. C. D. Moyes, N. Fragoso, M. K. Musyl, R. W. Brill, Predicting postrelease survival in large pelagic fish. *Trans. Am. Fish. Soc.* **135**, 1389–1397 (2006). doi: 10.1577/T05-224.1
53. H. M. Guzman, C. G. Gomez, C. A. Guevara, L. Kleivane, Potential vessel collisions with Southern Hemisphere humpback whales wintering off Pacific Panama. *Mar. Mamm. Sci.* **29**, 629–642 (2013).
54. J. D. Metcalfe, W. J. Le Quesne, W. W. Cheung, D. A. Righton, Conservation physiology for applied management of marine fish: An overview with perspectives on the role and value of telemetry. *Philos. Trans. R. Soc. London Ser. B* **367**, 1746–1756 (2012). doi: 10.1098/rstb.2012.0017; pmid: 22566680
55. S. A. Robinson, S. G. Goldsworthy, J. Van den Hoff, M. A. Hindell, The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Mar. Freshw. Res.* **53**, 1071–1082 (2003). doi: 10.1071/MF01218
56. P. E. Moriarty, K. S. Andrews, C. J. Harvey, M. Kawase, Vertical and horizontal movement patterns of scyphozoan jellyfish in a fjord-like estuary. *Mar. Ecol. Prog. Ser.* **455**, 1–12 (2012). doi: 10.3354/meps09783
57. K. L. Laidre, M. P. Heide-Jørgensen, Spring partitioning of Disko Bay, West Greenland, by Arctic and subarctic baleen whales. *ICES J. Mar. Sci.* **69**, 1226–1233 (2012). doi: 10.1093/icesjms/fss095
58. R. Davis et al., Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. *Mar. Ecol. Prog. Ser.* **333**, 291–302 (2007). doi: 10.3354/meps333291
59. K. N. Holland, C. G. Meyer, L. C. Dagorn, Inter-animal telemetry: Results from first deployment of acoustic "business card" tags. *Endanger. Species Res.* **10**, 287–293 (2009). doi: 10.3354/esr00226
60. M. Horning, J.-A. E. Mellish, In cold blood: Evidence of Pacific sleeper shark (*Somniosus pacificus*) predation on Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska. *Fish Bull.* **112**, 297–310 (2014). doi: 10.7755/FB.112.4.6
61. S. J. Pittman et al., Fish with chips: Tracking reef fish movements to evaluate size and connectivity of Caribbean marine protected areas. *PLOS ONE* **9**, e96028 (2014). doi: 10.1371/journal.pone.0096028; pmid: 24797815
62. N. A. Farmer, J. S. Ault, Grouper and snapper movements and habitat use in Dry Tortugas, Florida. *Mar. Ecol. Prog. Ser.* **433**, 169–184 (2011). doi: 10.3354/meps09198
63. S. K. Hooker et al., Making protected area networks effective for marine top predators. *Endanger. Species Res.* **13**, 203–218 (2011). doi: 10.3354/esr00322
64. A. Grüss, D. M. Kaplan, S. Guénette, C. M. Roberts, L. W. Botsford, Consequences of adult and juvenile movement for marine protected areas. *Biol. Conserv.* **144**, 692–702 (2011). doi: 10.1016/j.biocon.2010.12.015
65. B. A. Block et al., Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90 (2011). doi: 10.1038/nature10082; pmid: 21697831
66. B. Raymond et al., Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* **38**, 121–129 (2015). doi: 10.1111/ecog.01021
67. E. L. Hazen et al., Predicted habitat shifts of Pacific top predators in a changing climate. *Nat. Clim. Change* **3**, 234–238 (2013).
68. R. B. Huey, Physiological consequences of habitat selection. *Am. Nat.* **137** (suppl.), S91–S115 (1991). doi: 10.1086/285141
69. S. J. Cooke et al., Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental biology: An interdisciplinary case study on adult fraser river sockeys salmon. *Fisheries* **33**, 321–338 (2008). doi: 10.1577/1548-8446-33.7.321
70. S. J. Cooke et al., Biotelemetry: A mechanistic approach to ecology. *Trends Ecol. Evol.* **19**, 334–343 (2004). doi: 10.1016/j.tree.2004.04.003; pmid: 16701280
71. K. C. Weng et al., Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* **310**, 104–106 (2005). doi: 10.1126/science.1114616; pmid: 16210538
72. K. N. Holland, R. W. Brill, R. K. Chang, J. R. Sibert, D. A. Fournier, Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358**, 410–412 (1992). doi: 10.1038/358410a0; pmid: 1641023
73. G. Crossin et al., Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. *Mar. Biol.* **152**, 905–918 (2007). doi: 10.1007/s00227-007-0741-x
74. H. Ueda, Homing ability and migration success in Pacific salmon: Mechanistic insights from biotelemetry, endocrinology, and neurophysiology. *Mar. Ecol. Prog. Ser.* **496**, 219–232 (2014). doi: 10.3354/meps10636
75. Y. Naito et al., Unravelling the mysteries of a mesopelagic diet: A large apex predator specializes on small prey. *Funct. Ecol.* **27**, 710–717 (2013). doi: 10.1111/1365-2435.12083
76. J. M. Semmens, N. L. Payne, C. Huveneers, D. W. Sims, B. D. Bruce, Feeding requirements of white sharks may be higher than originally thought. *Sci. Rep.* **3**, 1471 (2013). doi: 10.1038/srep01471; pmid: 23503585
77. R. S. Schick et al., Estimating resource acquisition and at-sea body condition of a marine predator. *J. Anim. Ecol.* **82**, 1300–1315 (2013). doi: 10.1111/1365-2656.12102; pmid: 23869551
78. K. Evans, M.-A. Lea, T. Patterson, Recent advances in bio-logging science: Technologies and methods for understanding animal behaviour and physiology and their environments. *Deep Sea Res. Part II* **88–89**, 1–6 (2013). doi: 10.1016/j.dsr2.2012.10.005
79. G. T. Crossin, S. J. Cooke, J. A. Goldbogen, R. A. Phillips, Tracking fitness in marine vertebrates: Current knowledge and opportunities for future research. *Mar. Ecol. Prog. Ser.* **496**, 1–17 (2014). doi: 10.3354/meps10691
80. S. M. Wilson, G. D. Raby, N. J. Burnett, S. G. Hinch, S. J. Cooke, Looking beyond the mortality of bycatch: Sublethal effects of incidental capture on marine animals. *Biol. Conserv.* **171**, 61–72 (2014). doi: 10.1016/j.biocon.2014.01.020
81. A. Gallagher, J. Serafy, S. Cooke, N. Hammerschlag, Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Mar. Ecol. Prog. Ser.* **496**, 207–218 (2014). doi: 10.3354/meps10490
82. A. P. Farrell et al., Pacific salmon in hot water: Applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiol. Biochem. Zool.* **81**, 697–709 (2008). doi: 10.1086/592057; pmid: 18922081
83. A. C. O'Toole, M.-Y. Dechraoui Bottein, A. J. Danylchuk, J. S. Ramsdell, S. J. Cooke, Linking ciguatera poisoning to spatial ecology of fish: A novel approach to examining the distribution of biotoxin levels in the great barracuda by combining non-lethal blood sampling and biotelemetry. *Sci. Total Environ.* **427-428**, 98–105 (2012). doi: 10.1016/j.scitotenv.2011.11.053; pmid: 22560748
84. S. T. Kessel et al., Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). *Mar. Ecol. Prog. Ser.* **514**, 175–190 (2014). doi: 10.3354/meps10966
85. B. P. Wallace et al., Regional management units for marine turtles: A novel framework for prioritizing conservation and research across multiple scales. *PLOS ONE* **5**, e15465 (2010). doi: 10.1371/journal.pone.0015465; pmid: 21253007
86. K. M. Miller et al., Genomic signatures predict migration and spawning failure in wild Canadian salmon. *Science* **331**, 214–217 (2011). doi: 10.1126/science.1196901; pmid: 21233388
87. J. N. Waite, S. J. Trumble, V. N. Burkanov, R. D. Andrews, Resource partitioning by sympatric Steller sea lions and northern fur seals as revealed by biochemical dietary analyses and satellite telemetry. *J. Exp. Mar. Biol. Ecol.* **416–417**, 41–54 (2012). doi: 10.1016/j.jembe.2012.02.009
88. A. E. Rosenblatt, M. R. Heithaus, Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *J. Anim. Ecol.* **80**, 786–798 (2011). doi: 10.1111/j.1365-2656.2011.01830.x; pmid: 21418209
89. A. Maljković, I. M. Cote, Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. *Biol. Conserv.* **144**, 859–865 (2011). doi: 10.1016/j.biocon.2010.11.019
90. C. Lydersen et al., Salinity and temperature structure of a freezing Arctic fjord—monitored by white whales (*Delphinapterus leucas*). *Geophys. Res. Lett.* **29**, 2119 (2002). doi: 10.1029/2002GL015462
91. F. Roquet et al., Estimates of the Southern Ocean general circulation improved by animal-borne instruments. *Geophys. Res. Lett.* **40**, 6176–6180 (2013). doi: 10.1002/2013GL058304
92. J. P. Grist et al., Temperature signature of high latitude Atlantic boundary currents revealed by marine mammal-borne sensor and Argo data. *Geophys. Res. Lett.* **38**, L15601 (2011). doi: 10.1029/2011GL048204
93. M. Fedak, The impact of animal platforms on polar ocean observation. *Deep Sea Res. Part II* **88–89**, 7–13 (2013). doi: 10.1016/j.dsr2.2012.07.007
94. L. Padman et al., Oceanic controls on the mass balance of Wilkins Ice Shelf, Antarctica. *J. Geophys. Res.* **117**, C01010 (2012). doi: 10.1029/2011JC007301
95. A. D. Lowther, R. G. Harcourt, B. Page, S. D. Goldsworthy, Steady as he goes: At-sea movement of adult male Australian sea lions in a dynamic marine environment. *PLOS ONE* **8**, e74348 (2013). doi: 10.1371/journal.pone.0074348; pmid: 24086338
96. L. Stramma et al., Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* **2**, 33–37 (2012). doi: 10.1038/nclimate1304
97. M. Beger et al., Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biol. Conserv.* **143**, 565–575 (2010). doi: 10.1016/j.biocon.2009.11.006
98. S. J. Cooke et al., Ocean Tracking Network Canada: A network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. *Fisheries* **36**, 583–592 (2011). doi: 10.1080/03632415.2011.633464
99. B. A. Block, D. P. Costa, G. W. Boehlert, R. E. Kochevar, Revealing pelagic habitat use: The tagging of Pacific pelagics program. *Oceanol. Acta* **25**, 255–266 (2002). doi: 10.1016/S0399-1784(02)01212-4
100. D. A. Benson et al., GenBank. *Nucleic Acids Res.* **41**, D36–D42 (2013). doi: 10.1093/nar/gks1195; pmid: 23193287
101. P. Halpin et al., OBIS-SEAMAP: Developing a biogeographic research data commons for the ecological studies of marine mammals, seabirds, and sea turtles. *Mar. Ecol. Prog. Ser.* **316**, 239–246 (2006). doi: 10.3354/meps316239

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SUPPLEMENTARY MATERIALS

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Movies S1 and S2

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