ANNUAL REVIEWS

*Annual Review of Animal Biosciences*

# Biologging and Biotelemetry: Tools for Understanding the Lives and Environments of Marine Animals

Yuuki Y. Watanabe[1,2] and Yannis P. Papastamatiou[3]

[1]National Institute of Polar Research, Tachikawa, Tokyo, Japan;
email: watanabe.yuuki@nipr.ac.jp

[2]Department of Polar Science, The Graduate University for Advanced Studies, SOKENDAI, Tachikawa, Tokyo, Japan

[3]Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, Florida, USA

Annu. Rev. Anim. Biosci. 2023. 11:247–67

The *Annual Review of Animal Biosciences* is online at animal.annualreviews.org

https://doi.org/10.1146/annurev-animal-050322-073657



## Keywords

movement ecology, field physiology, predator–prey interaction, social interaction, anthropogenic stressor

## Abstract

Addressing important questions in animal ecology, physiology, and environmental science often requires in situ information from wild animals. This difficulty is being overcome by biologging and biotelemetry, or the use of miniaturized animal-borne sensors. Although early studies recorded only simple parameters of animal movement, advanced devices and analytical methods can now provide rich information on individual and group behavior, internal states, and the surrounding environment of free-ranging animals, especially those in marine systems. We summarize the history of technologies used to track marine animals. We then identify seven major research categories of marine biologging and biotelemetry and explain significant achievements, as well as future opportunities. Big data approaches via international collaborations will be key to tackling global environmental issues (e.g., climate change impacts), and curiosity about the secret lives of marine animals will also remain a major driver of biologging and biotelemetry studies.

# INTRODUCTION

> You know those ducks in that lagoon right near Central Park South? That little lake? By any chance, do you happen to know where they go, the ducks, when it gets all frozen over? Do you happen to know, by any chance?
>
> —J.D. Salinger, *The Catcher in the Rye*

Both children and adults wonder what animals do, where they go, and why they go there, when direct observations are difficult. This fundamental curiosity has been, and will continue to be, a major driver of the biological research on wild animals. Marine environments exemplify the difficulty of direct observations, as researchers can view only a small number of species over short time periods. For example, underwater observations of fishes are generally made on slow-moving species in clear water during the daytime. Air-breathing divers (e.g., penguins, seals) can be observed continuously only when they come on land. This issue had been a major barrier for understanding the lives of marine animals in their natural habitats before biologging and biotelemetry techniques emerged. With these techniques, miniaturized sensors are attached to free-living animals to acquire information on their behavior, internal states, and the environment (**Figure 1**). With

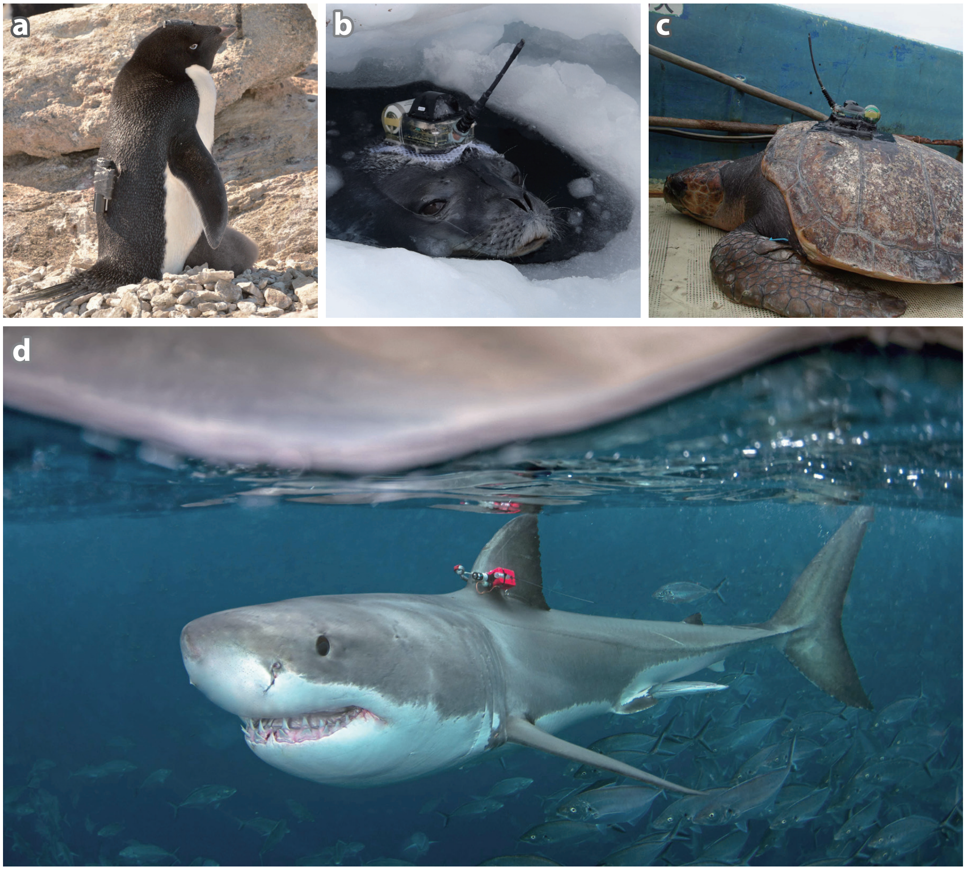



**Figure 1**

Biologging and biotelemetry tag attached to (*a*) Adélie penguin, (*b*) Weddell seal, (*c*) loggerhead turtle, and (*d*) white shark. Photos courtesy of (*a*) Yuuki Watanabe, (*b*) Nobuo Kokubun, (*c*) Tomoko Narazaki, and (*d*) Andrew Fox.

increasingly sophisticated sensors and electronics, these tools can now provide far more detailed information on wild marine animals than direct observation, allowing researchers to investigate how they behave, survive, function, and interact with other individuals (or species) in their given environments.

During the last few decades, the field of biologging and biotelemetry has expanded rapidly for both marine and terrestrial animals. The number of published studies has increased exponentially, with taxonomically and geographically broader ranges of species being covered (1, 2). Increasing types of sensors, data-collecting systems, and analytical tools are becoming readily available. Study topics have also broadened, ranging from individual movement (i.e., classic biologging studies) to group behavior, to interactions with other species, and even to cross-species analyses on the impact of changing environments. Not surprisingly, several authors have reviewed the concepts, methodologies, trends, and achievements of biologging and biotelemetry, with each study having a specific perspective (1–6). Yet, given the rapid expansion of the field, an updated, convenient, and accessible review on biologging and biotelemetry is warranted. In this article, we focus on marine systems, in which tracking animals is particularly difficult without the use of biologging and biotelemetry; however, we acknowledge that research technologies and directions are increasingly converging among studies of marine, freshwater, and terrestrial systems. We first provide a brief history of marine biologging and biotelemetry and then explain its major achievements and current trends. Finally, we discuss its future directions and opportunities.

## BRIEF HISTORY

Strictly speaking, biologging refers to a method using animal-borne devices that store data (called a data logger or archival tag) for later retrieval (i.e., devices must be physically recovered). Biotelemetry refers to a method using animal-borne devices that transmit data to receivers (i.e., data are acquired remotely). Biotelemetry can be further categorized into radio, acoustic, and satellite telemetry, depending on the types of signals and receivers used. In marine environments, radio telemetry is of limited use, and data loggers, acoustic telemetry, and satellite telemetry are the three major methods used for tracking animals. Below, we provide a brief history of each method (**Figure 2**). The distinction between biologging and biotelemetry is becoming increasingly murky, because there are hybrid devices (e.g., pop-up satellite archival tags) and because many researchers use both types of devices to tackle a specific question. In this article, we use the two terms interchangeably.

### Data Loggers

In the 1930s, a prominent physiologist, Per Scholander (7), attached capillary tube manometers to several seals and cetaceans with a long tow line and a float at the end and recorded their maximum dive depths. Although this experiment was undoubtedly pioneering work, it is our view that the first real biologging studies targeting free-living animals started decades later, in the early 1960s, when Gerald Kooyman (8) attached custom-made time-depth recorders to Weddell seals in Antarctica. In the early 1980s, Rory Wilson built inexpensive devices that recorded the cumulative time at depth of penguins using autoradiography (9). At the same time, Yasuhiko Naito built mechanical time-depth recorders that used tiny recording paper and styluses and attached them to elephant seals (10) and penguins (11). In the early 1990s, these analog data loggers started to be replaced by digital ones, allowing further miniaturization and the simultaneous recording of many parameters (12) (**Figure 2*b***). Since then, numerous types of data loggers have been built and used in the field. Several important parameters that are routinely recorded today, such as body acceleration (13), video images (14), echolocation (15), and GPS position (16), started to be measured

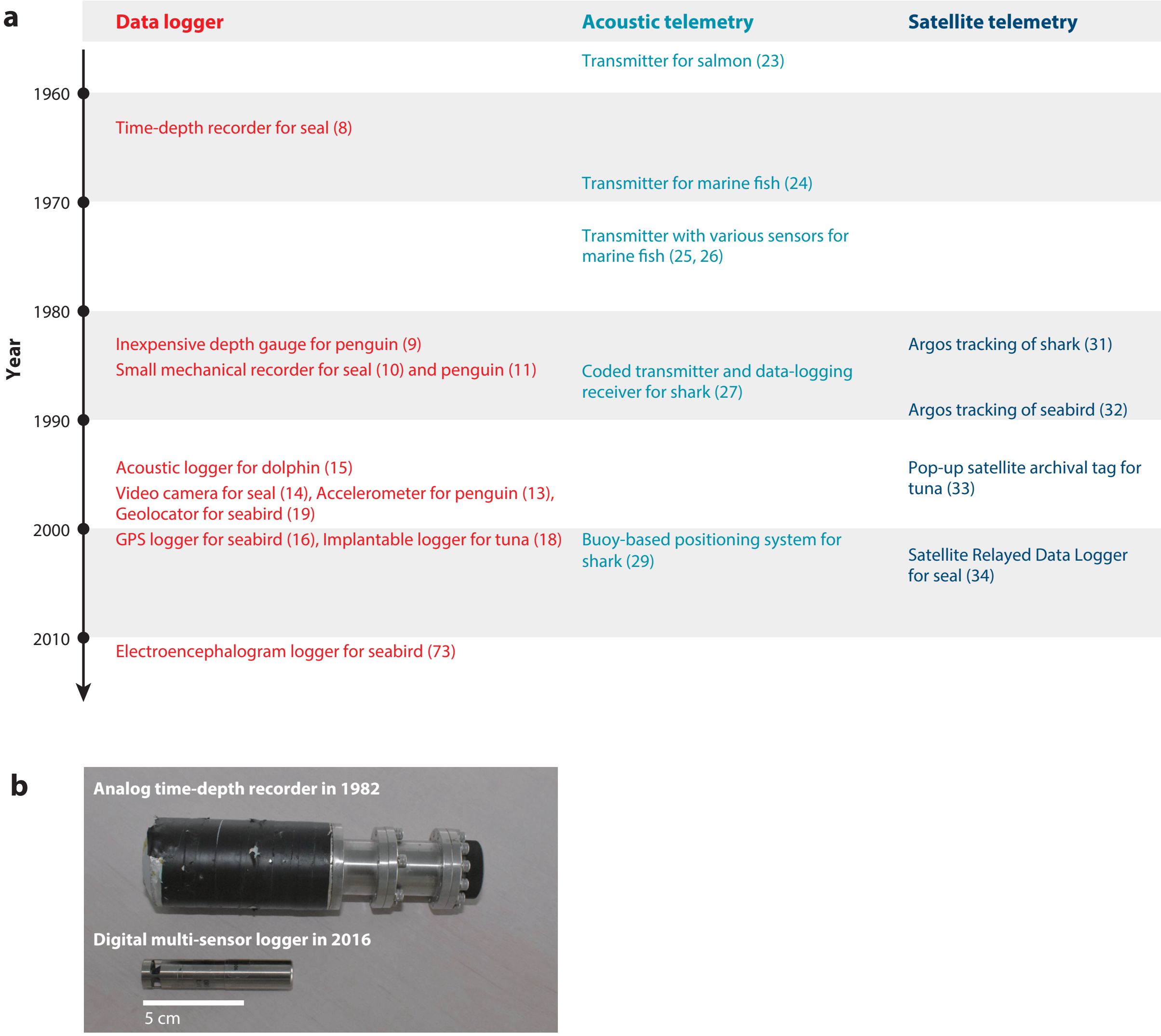



**Figure 2**

(*a*) Summarized history of data logger, acoustic telemetry, and satellite telemetry. Numbers in parentheses are references. (*b*) Rapid technological advances as exemplified by an analog time-depth recorder developed in 1982 (*top*) and a digital multi-sensor logger (measuring depth, temperature, speed, tri-axial acceleration, and tri-axial geomagnetism) developed in 2016 (*bottom*). Photo courtesy of Yuuki Watanabe.

in the late 1990s or early 2000s. A method for estimating geographical positions of migrating animals based on light level data (albeit with relatively large errors) was first demonstrated for elephant seals in the early 1990s (17). This method was soon replaced by satellite telemetry in the studies of marine mammals; however, it led to the development of implantable archival tags (for pelagic fishes, especially tuna) (18) and tiny geolocators (attached to a ring on the bird's leg) (19) in the 1990s, both of which are used routinely today. In early studies, the need for physical recovery limited the application of data loggers to animals that can be readily recaptured. Methods for detaching data loggers from animals [by using mechanical releasing devices (20) or suction cups for tag attachment in cetaceans (21)] and recovering them via radio telemetry were developed in the 1990s and early 2000s. These methods have expanded the taxa for which data loggers can be applied and are used routinely today.

### Acoustic Telemetry

The efforts to locate animals remotely by attaching radio or acoustic transmitters started in the 1950s (22). The earliest acoustic telemetry study, published in 1956, attached acoustic transmitters developed by the US Fish and Wildlife Service to salmon in a holding pond (23). Owing to commercial interests and limited transmission ranges, most acoustic telemetry studies conducted in the 1950s and 1960s targeted fishes in freshwater systems, especially salmon. Yuen (24) first applied this technology to a marine fish (skipjack tuna) in 1969. Subsequently, Nelson (25) and Carey & Lawson (26) independently developed acoustic tracking devices with various sensors (e.g., depth, temperature) and applied them to tunas and sharks. These early studies required the fish to be manually followed by the tracking vessel, and tracking durations were thus limited to days. In the 1980s, coded transmitters and automated data-logging receivers were developed (27). These technologies, which became widely available through the 1990s and 2000s, are arguably the greatest advancement in acoustic telemetry, with many individual fish now being tracked simultaneously over time periods of years (28). Additional innovations included combining an acoustic positioning system based on hyperbolic multi-lateration with a buoy-based positioning system (e.g., Vemco's VRAP system) (29) or fixed synchronizing acoustic transmitters (e.g., Vemco's VPS system) (30). These systems have enabled continuous tracking with high spatial resolution while the tagged fish are near the systems, over periods up to 10 years.

### Satellite Telemetry

A satellite-based, location- and data-collecting system called Argos, begun in 1978, has revolutionized the ways in which we observe marine animals and environments. Although Argos was developed originally for meteorological and oceanographical applications, the miniaturization of transmitters made it possible to track animals from the polar-orbiting satellites. In the earliest application to marine animals, a basking shark was tracked by an Argos transmitter attached to the animal via a 10-m towline in 1982 (31). Foraging trips of albatrosses covering thousands of kilometers over the sea were first recorded by attaching Argos transmitters to the birds in 1989 (32). Since then, transmitters have been further miniaturized and attached to a range of air-breathing diving animals, flying seabirds, and surface-oriented fishes. In the late 1990s, pop-up satellite archival tags were developed, which store data (depth, temperature, and light levels for geolocation), detach from the animals at a preprogramed time, float to the surface, and then transmit a summary of data to the Argos satellites. This innovation allowed researchers to track a range of pelagic fishes that do not surface frequently (33). In the early 2000s, integrated tags best suited for large, air-breathing, diving animals were developed, such as Satellite Relayed Data Loggers of the Sea Mammal Research Unit (34). These tags store data (e.g., depth, temperature) and transmit compressed data to the Argos satellites while animals are at the surface. With the addition of salinity sensors, these devices led to the unique approach of using marine animals as platforms for oceanographic measurements (see below).

## MAJOR ACHIEVEMENTS AND TRENDS

To provide an overview of the wide research areas covered by marine biologging and biotelemetry, we propose a diagram showing seven major research categories (**Figure 3**): (*a*) individual movement, (*b*) internal state, (*c*) predator–prey interactions, (*d*) social interactions, (*e*) oceanographic

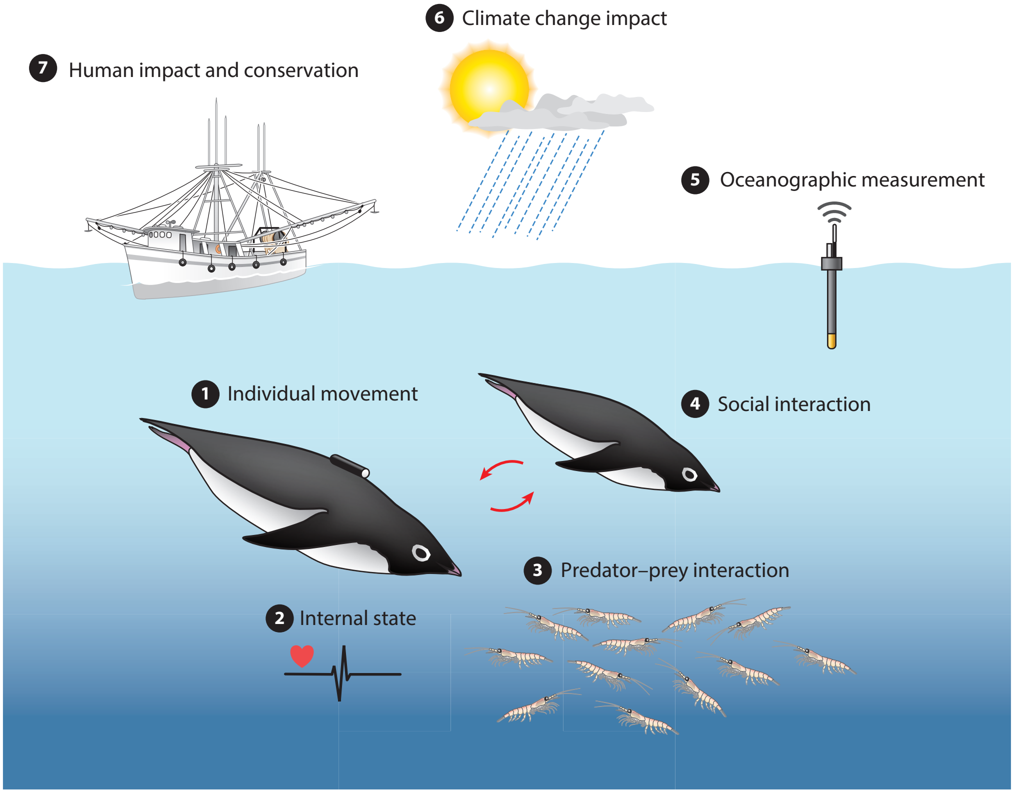



**Figure 3**

Biologging and biotelemetry diagram, showing seven major research categories.

measurements, (*f*) climate change impacts, and (*g*) human impacts and conservation. The order is arranged approximately chronologically, with *a* representing the classic type of biologging research and *f* and *g* representing the more recent types of research. Below, we discuss the significant achievements and trends for each research category.

## Individual Movement

Recording the movement of individual animals and interpreting it in an ecological and physiological context is a classic—and still important—type of biologging study. Kooyman's original questions when attaching time-depth recorders to Weddell seals in the 1960s related to how deep and how long animals could dive within a single breath-hold. Half a century later, we now have a good understanding of the diving capabilities of a range of breath-hold divers, as well as how their dive durations scale with body mass due to metabolic constraints (35, 36). Extreme diving capabilities have been demonstrated for beaked whales (family Ziphiidae), which routinely dive to nearly 1,000 m depth for 47–58 min for foraging (37), with the maximum recorded dive depth and duration of 2,992 m and 137.5 min, respectively (38). Given the large amount of data collected to date, it is unlikely that any unstudied animal groups have better diving capabilities than beaked whales. Biologging and biotelemetry studies show that pelagic fishes (teleosts and elasmobranchs) also exhibit vertical oscillations in the water column, and many can dive to mesopelagic depths (200–1,000 m) (39). The recording of additional parameters (e.g., body temperature, video images) indicates that these occasional mesopelagic dives are often related to foraging but may have other functions, including behavioral thermoregulation, escape from predation, and navigation (39, 40). Extreme dives to nearly 2,000-m depths have been reported for whale sharks (41) and devil rays (42). Their extreme diving capabilities are apparently related to their high tolerance of deep cold water, due to either their gigantic body size and high thermal inertia (whale sharks) (43) or their regionally endothermic physiology (devil rays) (42).

Biologging and biotelemetry have also revealed the horizontal movement, especially seasonal migration, of many flying and swimming marine animals. As extreme cases, Arctic terns (44), sooty shearwaters (45), and south polar skuas (46) exhibit "endless summer" migrations by flying >60,000 km per year across both hemispheres. Trans-oceanic migrations have also been reported for a range of swimmers, including marine mammals, sea turtles, and pelagic fishes (47), although none of them exhibit endless summer migrations across both hemispheres. The migration patterns of marine animals recorded by biologging and biotelemetry are often distinct from simple, latitudinal movements pursuing milder climates. For example, albatrosses breeding in Antarctica exhibit longitudinal, circumpolar migrations, with some individuals showing round-the-world journeys (48). Leatherback sea turtles breeding in the Caribbean migrate throughout the North Atlantic with broad individual differences in travel routes (49). In many migratory species, only a proportion of individuals migrate, whereas others are residential (50, 51). This phenomenon, called partial migration, may relate to individual variability in reproductive state, body condition, and predation risk (51, 52). Rapid data accumulation of migratory tracks has offered opportunities for cross-species and -taxon comparisons of migration patterns. These analyses have revealed important regions for long migrators, common environmental triggers of seasonal migration, and the role of physiology in determining migration range (47, 53).

Besides the variability in movement patterns across species, interindividual variability within a population of a species can be extensive, as shown by biologging and biotelemetry studies that included tens or even hundreds of individuals. For example, in snappers in an estuary in The Bahamas, site use of individual animals often differs from that predicted from the population-level distribution, indicating that movement at the scale of the individual has important consequences for ecosystem functioning (54).

## Internal State

Biologging and biotelemetry can also record the internal state of marine animals, such as heart rate, body temperature, and electronic brain activity. This technique, recently termed physiologging (55), allows researchers to study the physiology of marine animals in unrestrained conditions (in the field or in the controlled captive conditions) and has produced many important insights. For example, a traditional approach for studying how air-breathing divers (e.g., seals) manage their limited oxygen store during diving was to experimentally force animals to be submerged in the laboratory (7). Biologging studies took this approach to the field, showing that heart rates decrease upon descending (bradycardia) and increase upon (or before) surfacing in a range of free-ranging diving animals (e.g., 56), including gigantic blue whales (57). However, bradycardia in the wild is often less intense than observed in forced submersion experiments. Bradycardia is a mechanism to balance central arterial blood pressure against the dramatic changes in peripheral vascular resistance during diving (58). Heart rates change according to the anticipated dive durations, indicating that blood redistribution during dives is under some degree of cognitive control (59). Some studies recorded the changes in oxygen partial pressure in the blood of seals (60) and penguins (61) during dives, demonstrating their extreme hypoxemic tolerance. At the end of long dives, these animals had blood oxygen partial pressures that were so low they would cause loss of consciousness in human divers. The need to surgically insert $O_2$ sensors into blood vessels and its invasive nature has been a major obstacle for the wider applications of this method. A recent test of noninvasive, near-infrared spectroscopy loggers with captive seals revealed this tool's potential to track blood volume and oxygenation patterns in different tissues of diving animals (62).

Thermal physiology in fishes and reptiles was traditionally studied in the laboratory with relatively small species amenable to captivity. Biologging and biotelemetry studies showed that tunas (26, 63), some lamnid sharks (64, 65), and leatherback sea turtles (66) maintain higher body temperatures than ambient water temperature under natural conditions, and that their body temperature can vary with ambient water temperature and activity. These animals have well-developed vascular countercurrent heat exchangers and can conserve the heat generated by locomotor muscles. Their thermal strategy, termed regional endothermy or mesothermy (67), represents an intermediate form between ectotherms and endotherms. Elevated stomach temperatures of some of these animals are thought to increase digestion rates (68). Further, due to their elevated red muscle temperatures, regionally endothermic fishes can cruise at faster speeds and conduct longer-range seasonal migrations compared to ectothermic counterparts, as shown by a comparative analysis of biologging and biotelemetry data (53). Biologging studies also showed that large-bodied ectothermic fish (40), including gigantic whale sharks (43), and sea turtles (69) maintain a narrow range of body temperatures during diving, primarily due to their large thermal inertia. This ability allows these animals to explore a wide depth range for foraging with reduced risks of overheating or overcooling. Thermal physiology and behavioral thermoregulation strategies are key for better understanding the geographical and vertical distributions of marine animals (70) and how they are affected by climate change.

Sleep physiology is normally studied with human and nonhuman model species (e.g., mice) in the laboratory. Recording body motion and posture by using animal-borne accelerometers provided insight into how seals (71) and whales (72) may sleep in the sea; however, direct evidence of sleep was lacking before electroencephalogram (EEG) loggers were developed. With this new technology, the male sandpiper, a polygynous Arctic-breeding shorebird, has been shown to greatly reduce sleep time during intense male–male competition periods (73). Frigate birds, which can stay aloft for months over the ocean, have been shown to sleep during soaring flight with either one hemisphere at a time or both hemispheres simultaneously (74). Yet, their total on-flight sleep duration was $<1$ h per day, indicating strong ecological demands for attention during flight. Fur seals have been shown to sleep at the water surface primarily with one hemisphere, allowing them to move flippers on one side of the body for maintaining body posture and to watch for predators with one eye (75). These studies highlight how animals balance physiological demands for sleep against ecological demands in their daily lives, opening new avenues in the field of animal sleep.

Recording heart rates of free-ranging marine animals by using biologging and biotelemetry allows their energy expenditure in the field to be estimated, given that relationships between heart rates and metabolic rates are validated in the laboratory (76). More recently, researchers began to use body acceleration, which can be readily measured by externally attached tags, as a proxy for energy expenditure (77, 78). This proxy, called overall dynamic body acceleration, is now used for a range of marine animals.

## Predator–Prey Interactions

The foraging ecology of marine animals has traditionally been studied via stomach content (or scat) analyses and more recently via chemical analyses (e.g., stable isotope ratio). Biologging and biotelemetry have provided a new method complementary to these approaches. A pioneering study showed, for both captive and wild animals, that feeding events of seabirds can be detected from the record of stomach temperature (79). Another landmark study used animal-borne video cameras and data loggers to record the fine-scale behavior of Weddell seals hunting fish in Antarctic waters (14). An advantage of the biologging approach is that, unlike stomach content and chemical analyses, time-stamped information on foraging events can be gained along with the animals' behavior and environment. Later studies used a range of sensors to record the signals of foraging events [e.g., head or jaw acceleration (80), changes in stomach temperature (81), echolocation clicks of toothed whales (82)], with some studies validating indirect signals by using simultaneously recorded video images (83). These approaches have greatly expanded our understanding of predator–prey interactions that occur underwater and their impacts on ecosystems. Examples include the spatial distribution of foraging success in migratory fishes (84), deep-diving seals (85), and seabirds (81); the extremely high foraging rates of diving mammals (82, 86) with specialized teeth (87); the evolutionary divers of gigantic body sizes (88); and region-scale prey consumption rates of baleen whales (89).

Biologging and biotelemetry also have the potential to track the fates of marine animals targeted by their natural predators. A notable previous approach was to attach acoustic receivers and GPS tags to seals (predators) and acoustic transmitters to several fish species (prey) in an area (90). This study successfully recorded a few events where tagged seals predated on tagged fish, providing a proof of concept for studying the spatiotemporal patterns of predator–prey interactions in open waters. In another example, specialized tags that transmit data after animals die were developed and tested in free-ranging sea lions (91). The tags provided information on the location, rate, and potential causes of natural mortality, including predation. More recently, acoustic predation tags have been developed, which are internally implanted into prey to track their movements, similar to conventional acoustic telemetry. When a predator ingests the prey, stomach acids induce a change in tag transmission, providing evidence for the predation event (92). These tags have revealed very high predation rates of native sea lamprey by introduced European catfish during their spawning migrations (93). Understanding the rates and causes of natural mortality is important in population ecology and conservation, and biologging and biotelemetry offer unique information that cannot be obtained by other methods.

## Social Interactions

Biologging and biotelemetry were originally developed to track individual animals. However, technological advances have made it possible to track multiple individuals simultaneously, providing insights into the group behavior, sociality, space partitioning, and other intraspecific interaction of marine animals under natural conditions. The development of acoustic trans-receivers allowed the recording of encounters of the tagged individuals with other individuals equipped with the same trans-receivers or simple transmitters, as first demonstrated for free-swimming sharks (94). Equipping grey seals with acoustic trans-receivers and satellite transmitters revealed that they are associated with other individual seals while area-restricted searching, suggesting some degree of social foraging (95). By combining trans-receivers with additional sensors (e.g., accelerometers, video cameras), associations can be measured in conjunction with the potential nature of the interactions (e.g., reactions), as demonstrated for some sharks (96, 97). To overcome the limitation that trans-receivers must normally be physically recovered, a new system composed of a trans-receiver and a satellite transmitter was developed and tested with gray seals (98). In the system, encounter data recorded by a trans-receiver are transmitted to a satellite transmitter on the same animal via Bluetooth and then sent to the Argos satellites when seals are on land or breathing at the surface (98). However, most previous studies that used trans-receivers had relatively small sample sizes, primarily due to the costs of trans-receivers.

Where applicable, simpler devices, such as GPS loggers, satellite transmitters, and acoustic transmitters, are advantageous in collecting large sample sizes for a population of marine species and thus providing statistically robust results for intraspecific associations. GPS tracking and direct visual observations showed that Guanay cormorants, colonial-breeding seabirds, join congeners aggregated at the sea surface near the colony before leaving for foraging trips (99). They apparently make a decision on the heading to be taken at the aggregation, indicating that information transfer about the locations of unpredictable food patches occurs among individuals. Tracking of northern gannets, colonial-breeding seabirds, across many neighboring colonies showed that foraging areas are well segregated among colonies despite the lack of territoriality in this species (100). Subsequent modeling showed that the observed segregation patterns stem from density-dependent competition, presumably enhanced by individual-level public information transfer at each colony. Constructing social networks of a group of animals based on biologging and biotelemetry data is an emerging approach toward better understanding sociality in marine animals (101). A network analysis of Australasian gannets, colonial-breeding seabirds, tracked during a breeding season showed that individuals actively associate during colony departure, foraging, commuting, and colony return (102). Papastamatiou et al. (103) used acoustic tracking via automated receivers to generate dynamic social networks of reef sharks at a Pacific atoll, highlighting that sharks form spatially assorted social groups, with associations lasting years in some cases. Recent development of high-resolution acoustic telemetry technology allows the movements of hundreds of individuals to be measured simultaneously at a temporal resolution of a few seconds and a spatial resolution of <1 m (104). This technology showed that razorfish in a temperate embayment form permanent harems, whereby males form territories within which they interact with multiple females while negatively interacting with other males at the edge of their territories (105). From individuals to groups, there is large potential for future research in applying biologging and biotelemetry to socially interacting marine species.

## Oceanographic Measurements

Biologging and biotelemetry provide data on the environment surrounding tagged animals. These data can complement oceanographic and atmospheric data obtained by satellite-based remote sensing, autonomous floats, moorings, and ship-based measurement, leading to the concept of "animals as oceanographers" (106). Deep-diving marine mammals equipped with Satellite Relayed Data Loggers (SRDL) with salinity sensor are analogous to ship-based CTD (conductivity-temperature-depth) casts in that they provide temperature and salinity profiles of the water column. Animal-derived data are especially useful in polar regions, where the presence of sea ice poses challenges in obtaining oceanographic data, as first demonstrated with white whales in Svalbard, Norway (107). The application of this method to southern elephant seals in the Southern Ocean provided important oceanographic insights, including the location of major fronts south of 60°S and the rate of sea ice formation (108). Animal-derived data were incorporated into the Southern Ocean general circulation models and improved the estimate of surface mixed-water properties and circulation patterns (109). The integration of animal-derived data with conventional oceanographic data led to the discovery of a source of Antarctic Bottom Water (i.e., cold, dense water contributing to the global overturning circulation) associated with intense sea ice formation in the Cape Darnley polynya (110). Along with water temperature and salinity, chlorophyl *a* and dissolved oxygen concentrations are fundamentally important in biological oceanography. SRDL with a fluorometer (a proxy for chlorophyl *a* concentration and primary production) (111) and a dissolved oxygen sensor (112) were recently developed and initially deployed on elephant seals. The concept of animals as oceanographers led to large international networks for observing global oceans, such as the Animal Borne Ocean Sensors (AniBOS) network (113).

Another successful example of animals as oceanographers is the use of flying seabirds as platforms for observing ocean surfaces. Seabirds equipped with GPS loggers are analogous to drifting buoys when they are resting at the surface, providing information on currents (114) and waves (115). Shearwaters and albatrosses exhibit dynamic soaring flight, during which flight speed relative to ground is maximized in tailwind and minimized in headwind. This simple principle allows the estimate of wind speed and direction at the ocean surface based on the GPS tracks of these birds (116). An obvious weakness of these approaches is that sampling locations and timing cannot be precisely selected. Nevertheless, animal-derived data have higher spatial and temporal resolution than satellite-based remote sensing and oceanographic buoys. These data can thus complement conventional meteorological monitoring and improve ocean nowcast/forecast models, as demonstrated for the currents in the north-eastern sea of Japan (117). Moreover, the spatial and temporal scales of animal-derived environmental data are most relevant to the animals themselves, helping us to better understand the responses of marine animals to changes in their environment.

## Climate Change Impacts

Understanding the effect of changing climate on wildlife and ecosystems is a major challenge in biological and environmental sciences. Biologging and biotelemetry offer a unique opportunity to study how climate variables affect the natural behavior of marine animals, and consequently their population sizes. In the Southern Ocean, winds have increased in intensity and shifted poleward during the past few decades. A long-term biologging study showed that wandering albatrosses, large dynamic soaring birds, increased travel speeds during chick-rearing periods due to this favorable meteorological change, and consequently increased breeding success (118). A multiyear biologging study on Adélie penguins in Antarctica showed that, in an unusual breeding season when sea ice was absent, penguins had favorable foraging conditions (119). They traveled faster by swimming (rather than walking on the sea ice), were freed from the need to find cracks for diving, and had enhanced prey availability. Consequently, their breeding success increased in the ice-free season, suggesting that the penguin population in that area would increase in the coming decades due to the projected rapid decline of Antarctic sea ice. By contrast, polar bears, ice-dependent Arctic predators, have been shown by a biologging study to have high energy demands and lose weight quickly when hunting on energy-rich prey (seals) is unsuccessful (120). This result suggests that the decreased prey availability associated with the ongoing decline of Arctic sea ice negatively impacts polar bear populations.

Biologging and biotelemetry also provide information on how changing climate could alter the distribution of marine species. The habitat use and diving behavior of crabeater seals, abundant Antarctic seals with a specialized diet (Antarctic krill), were recorded by satellite telemetry (121). The data were combined with projected atmospheric and oceanographic conditions to predict future changes in their foraging habitat. A satellite tracking study of tiger sharks over nine years in the Atlantic showed that sharks were extending their movements northward as ocean temperatures increased (122). In a different approach, the temperature dependence of animal activity, normally examined in laboratory experiments, was measured via biologging and biotelemetry data for free-swimming fishes (70), including tiger sharks that are too big for captive experiments (123). The results were largely consistent with the current geographical distribution of each species, suggesting that the approach can be used to predict the changes in the distribution of ectothermic species associated with ocean warming.

## Human Impacts and Conservation

Lastly, understanding the impacts of human activity on marine animals and enacting conservation measures, if necessary, are increasingly important in the Anthropocene era. Fishing is a major human activity that affects the abundance of marine species directly (through targeted catches and untargeted bycatch) and indirectly (through changes in predator–prey interactions). Place-based conservation measures, such as Marine Protected Areas (MPAs) that restrict fishing to aid conservation of marine species, are being increasingly implemented in many countries. However, the efficacy of an MPA for conserving highly mobile species is often uncertain. Animal-tracking data recorded by biologging and biotelemetry offer opportunities for evaluating the efficacy of existing MPAs (124, 125), determining effective MPA sizes (126), and optimizing MPA design (127). Fine-scale GPS tracking of seabirds combined with anonymized fishery data allowed estimates of the distance over which bird behavior is influenced by fishing vessels (128). Overlaying the tracks of multiple marine species on the map of anthropogenic stressors (e.g., fishing activity) can reveal where important habits and high-risk areas are likely to coincide, as demonstrated for the California Current Ecosystem (129). A few recent studies organized large international teams and compiled thousands of animal tracks for large flying seabirds (130) and pelagic sharks (131) on a global scale and seabirds and marine mammals in the Southern Ocean (132). These analyses identified areas where protection measures will be most effective and provided insight into current conservation measures.

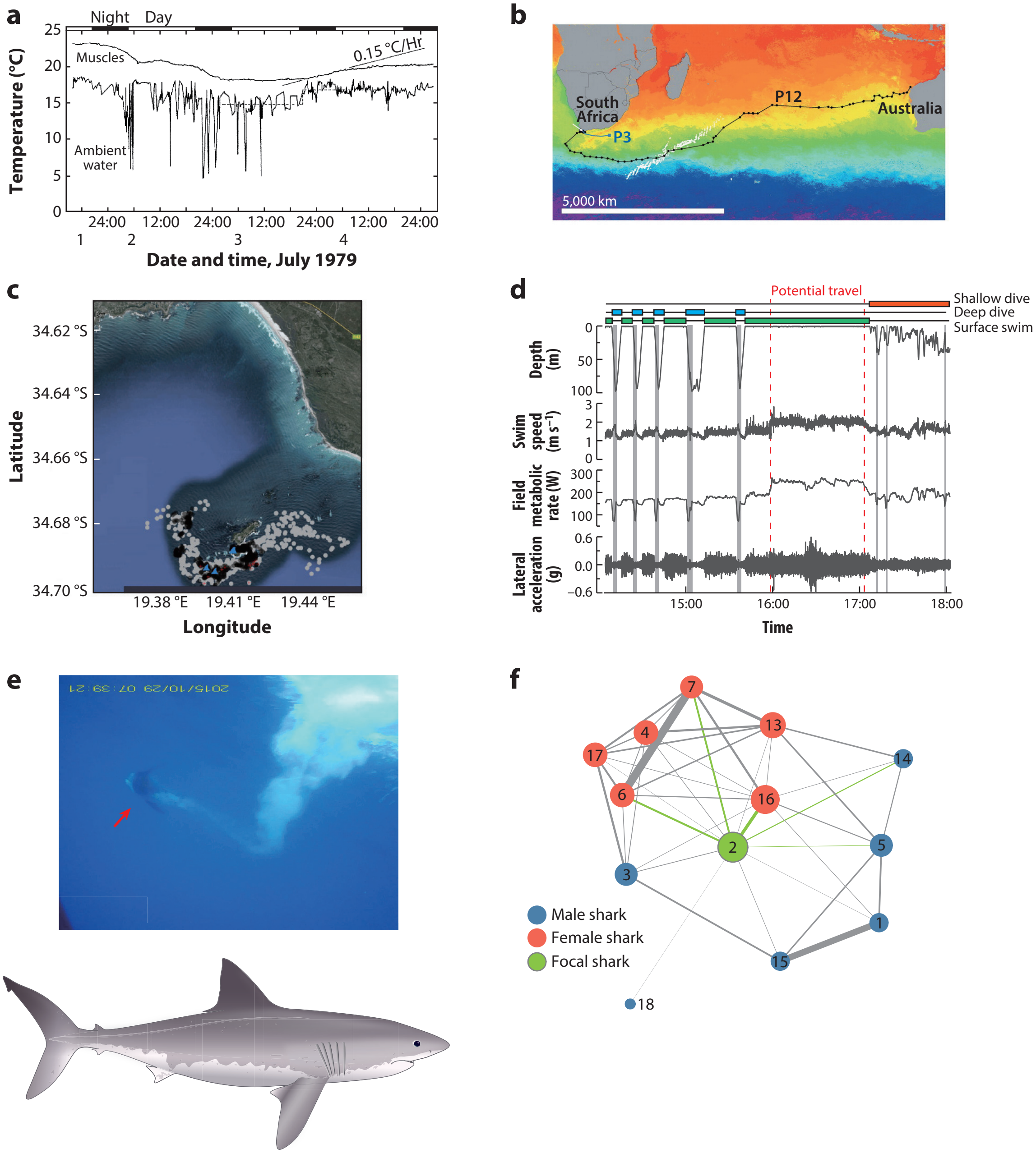
A novel biologging device was developed recently that records animal GPS positions and radar emission from nearby vessels and then transmits the data to Argos satellites (133). This tag was applied to albatrosses in the Southern Ocean, which often follow fishing vessels and thus are at high risk of being fishery bycatch. By combining the biologging data obtained from albatrosses with near-real-time information on the locations of declared fishing vessels, the study revealed the spatial distribution of bycatch risk in albatrosses and detected nondeclared and illegal fishing vessels. This example highlights that technological advancements in biologging and biotelemetry can open new avenues for animal conservation.

Importantly, large gaps exist between presenting animal-tracking data with proposals for conservation measures in scientific papers and using the data to address real-world conservation issues. A recent review revealed many examples of biologging and biotelemetry data on marine animals affecting the decision making of governmental and international bodies regarding conservation policies and management (134). As recommended in that review, marine biologists who use biologging and biotelemetry are encouraged to share data via public depositories (e.g., MoveBank) and communicate directly with stakeholders involved in policy development and implementation.

## FUTURE DIRECTION AND OPPORTUNITIES

Our discussion highlights that biologging and biotelemetry have already altered our understanding of the ecology and physiology of marine animals (**Figure 4**). Yet, with ever-expanding research communities (e.g., the International Bio-logging Society, with more than 1,000 members from more than 20 countries), continuing advancements in hardware and software, and increasing attention to the impacts of climate change and human activity on wildlife, we expect that the importance of biologging and biotelemetry in biological and environmental science will continue to increase. Below, we briefly discuss future directions and opportunities.

New technologies are always key components of biologging and biotelemetry. In addition to several already-mentioned novel devices, many new devices have large potential for future use. Examples include sonar tags that provide echoic information on the prey approached by tagged animals (135), small mark-report satellite tags that can reveal the large-scale horizontal movement of deep-sea fishes (136), and satellite transmitters with acceleration sensors that remotely transmit an activity metric of animals over several months (137). Improvements in satellite tracking bandwidth limitations and on-board data processing in the tags (before data transmission or storage) are key for obtaining more useful information for a range of species over long periods. In addition to the sensors and transmitters, new advances in tag attachment methods and data acquisition are important. For example, heart rate is now a classic parameter in biologging (e.g., 56), but the need to place electrodes externally or internally has long limited the application of heart rate loggers to animals that can be recaptured. Recently, suction cup–attached tags that record cetacean heart




(*Caption appears on following page*)

**Figure 4** (*Figure appears on preceding page*)

Examples of measurements made from free-swimming white sharks (a well-studied species) using biologging and biotelemetry. (*a*) Simultaneous measurements of muscle temperature (*upper line*) and ambient water temperature (*lower line*), showing regional endothermy (reproduced with permission from 65, with labels modified for better visibility). (*b*) Trans-oceanic migration from South Africa to Australia revealed by satellite telemetry, with sea surface temperature shown by color (*orange*, high; *blue*, low) (reproduced with permission from 143, with labels modified for better visibility). (*c*) Fine-scale habitat use off South Africa determined by acoustic telemetry, showing location of area-restricted searching (*black dots*) and patrolling (*gray dots*) behavior (144). (*d*) Fine-scale swimming behavior, showing depth, swim speed, estimated field metabolic rate, and lateral acceleration (tail beat activity) (145). Grey vertical bars represent passive gliding periods. (*e*) A predation attempt on a fur seal (*red arrow*) filmed by shark-borne camera off Australia (146). (*f*) Short-term social networks created using inter-animal telemetry off Mexico, with the green node representing the focal individual (97). Other nodes represent females (*red*) and males (*blue*), showing evidence of sexual assortment in the network.

rates and foraging behavior (138) demonstrated their great potential for better understanding how diving animals balance the needs of oxygen conservation and physical activities during foraging dives. To record the heart rate of non-cetacean marine animals that cannot be recaptured, methods for mechanically detaching electrodes from the animals at preprogrammed times are warranted.

Several recent papers published by large international teams (130–132, 139) indicate that we are entering the big data era of biologging and biotelemetry. To better understand the space use of marine animals in the face of anthropogenic stressors and climate change on a global or regional scale, collaborations with other biologging researchers, statisticians, modelers, oceanographers, and stakeholders involved in policy decision making are increasingly important. To date, big data approaches in biologging and biotelemetry for marine animals have been mostly limited to horizontal tracking data (47, 130–132). However, biologging and biotelemetry provide a variety of information on animal ecology and physiology, as summarized in this article. Big data approaches using information other than horizontal tracking data, including within- or among-species interactions, three-dimensional space use, and behavioral and physiological responses to changing environments, thus have great potential. Such analyses would not only provide insight into the conservation and management of marine species but also reveal how their behavior and physiology have diversified and converged over evolutionary time. A critical component for future advancements is greater accessibility and standardization of biologging data sets collected by different research groups (140). This will lead to many discoveries by ensuring that research groups are aware of existing data sets in a format in which they can be combined easily with other data sets.

One key area of concern is the impact of biologging and biotelemetry tags on the behavior, physiology, and welfare of the animals being studied. No one should want to put tags on animals that will decrease their fitness or want data from an animal artificially stressed by the tagging process. The traditional rule of thumb was to keep tag mass below 3% or 5% of the animal mass. However, it is increasingly recognized that this rule is too simplistic, neglecting many complex factors, such as tag types, attachment methods, animal lifestyles, and traits that could be affected (141). In flying and swimming animals, drag caused by tags could have larger effects than tag mass, meaning that careful design of tags and floats, rather than just miniaturization, is important (142). As the available technology continuously changes, our knowledge of the potential ethical impacts of biologging and biotelemetry tags on animals should be updated.

Lastly, we emphasize that curiosity regarding the secret lives of animals will remain a major driver of biologging and biotelemetry studies. Many past studies that used state-of-the-art devices at that time produced truly surprising and insightful results. Examples include the near-3,000-m dives of beaked whales (38), polar-to-polar migration of Arctic terns (44), in-flight sleep of frigate birds (74), and physiological thermoregulation in tunas (63). Frontiers still remain. Many species or biological phenomena that we know little about can be studied with biologging and biotelemetry. Examples include filter-feeding behavior of megamouth sharks, foraging tactics of deep-diving visual hunters (e.g., emperor penguins) in complete darkness, and habitat use and possible migration of coelacanths and giant squids. Decreasing the size of animal-borne devices will make it possible to study small, enigmatic species, such as cookie-cutter sharks. Organizing teams and studying enigmatic species or biological phenomena of personal interest will remain the main avenue for discoveries in biologging and biotelemetry. Thus, a fundamental question for a researcher might be the same as for a child: What are they doing in the sea?

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

We thank Andrew Fox, Nobuo Kokubun, and Tomoko Narazaki for providing photos and Akinori Takahashi for providing comments on the draft. This is contribution #1466 from the Institute of Environment at Florida International University.

## LITERATURE CITED

1. Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, et al. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348(6240):1255642
2. Kays R, Crofoot MC, Jetz W, Wikelski M. 2015. Terrestrial animal tracking as an eye on life and planet. *Science* 348(6240):aaa2478
3. Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, et al. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* 19:334–43
4. Ropert-Coudert Y, Wilson RP. 2005. Trends and perspectives in animal-attached remote sensing. *Front. Ecol. Environ.* 3:437–44
5. Williams HJ, Taylor LA, Benhamou S, Bijleveld AI, Clay TA, et al. 2020. Optimizing the use of biologgers for movement ecology research. *J. Anim. Ecol.* 89:186–206
6. Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* 96:1741–53
7. Scholander PF. 1940. *Experimental Investigations on the Respiratory Function in Diving Mammals and Birds*. Oslo: Hvalråd. Skr.
8. Kooyman GL. 1965. Techniques used in measuring diving capacities of Weddell seals. *Polar Rec.* 12:391–94
9. Wilson RP, Bain CA. 1984. An inexpensive depth gauge for penguins. *J. Wildl. Manag.* 48:1077–84
10. Naito Y, Le Boeuf BJ, Asaga T, Huntley AC. 1989. Long-term diving records of an adult female northern elephant seal. *Antarct. Rec.* 33:1–9
11. Naito Y, Asaga T, Ohyama Y. 1990. Diving behavior of Adélie penguins determined by time-depth recorder. *Condor* 92:582–86
12. Naito Y. 2004. New steps in bio-logging science. *Mem. Natl. Inst. Polar Res.* 58(Spec. Issue):50–57
13. Yoda K, Sato K, Niizuma Y, Kurita M, Bost C, et al. 1999. Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *J. Exp. Biol.* 202:3121–26
14. Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, et al. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283:993–96
15. Nowacek DP, Tyack PL, Wells RS, Johnson MP. 1998. An onboard acoustic data logger to record biosonar of free-ranging bottlenose dolphins. *J. Acoust. Soc. Am.* 103:2908
16. Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G, Lipp H-P. 2002. GPS tracking of foraging albatrosses. *Science* 295:1259
17. Delong RL, Stewart BS, Hill RD. 1992. Documenting migrations of northern elephant seals using day length. *Mar. Mamm. Sci.* 8:155–59

18. Block BA, Dewar H, Blackwell SB, Williams TD, Prince ED, et al. 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293:1310–14
19. Weimerskirch H, Wilson RP. 2000. Oceanic respite for wandering albatrosses. *Nature* 406:955–56
20. Watanabe Y, Baranov EA, Sato K, Naito Y, Miyazaki N. 2004. Foraging tactics of Baikal seals differ between day and night. *Mar. Ecol. Prog. Ser.* 279:283–89
21. Baird R. 1997. Studying diving behavior of whales and dolphins using suction-cup attached tags. *Whalewatcher* 31:3–7
22. Hockersmith EE, Beeman JW. 2012. A history of telemetry in fishery research. In *Telemetry Techniques: A User Guide for Fisheries Research*, ed. NS Adams, JW Beeman, JH Eiler, pp. 7–20. Bethesda, MD: Am. Fish. Soc.
23. Trefethen PS. 1956. *Sonic equipment for tracking individual fish*. Spec. Sci. Rep. Fish. 179, Fish Wildl. Serv., US Dep. Inter., Washington, DC
24. Yuen HS. 1970. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. *J. Fish. Board Can.* 27:2071–79
25. Nelson DR. 1976. Ultrasonic telemetry of shark behavior. *J. Acoust. Soc. Am.* 59:1004–7
26. Carey FG, Lawson KD. 1973. Temperature regulation in free-swimming bluefin tuna. *Comp. Biochem. Physiol. A* 44:375–92
27. Klimley A, Butler S, Nelson D, Stull A. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *J. Fish Biol.* 33:751–61
28. Heupel M, Semmens JM, Hobday A. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar. Freshw. Res.* 57:1–13
29. Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, et al. 2001. The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar. Biol.* 138:617–36
30. Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG. 2011. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fish. Res.* 108:364–71
31. Priede IG. 1984. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing. *Fish. Res.* 2:201–16
32. Jouventin P, Weimerskirch H. 1990. Satellite tracking of wandering albatrosses. *Nature* 343:746–48
33. Block BA, Dewar H, Farwell C, Prince ED. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *PNAS* 95:9384–89
34. Fedak M, Lovell P, McConnell B, Hunter C. 2002. Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. *Integr. Comp. Biol.* 42:3–10
35. Halsey LG, Butler PJ, Blackburn TM. 2006. A phylogenetic analysis of the allometry of diving. *Am. Nat.* 167:276–87
36. Verberk WC, Calosi P, Brischoux F, Spicer JI, Garland T Jr., Bilton DT. 2020. Universal metabolic constraints shape the evolutionary ecology of diving in animals. *Proc. R. Soc. B* 287:20200488
37. Tyack PL, Johnson M, Soto NA, Sturlese A, Madsen PT. 2006. Extreme diving of beaked whales. *J. Exp. Biol.* 209:4238–53
38. Schorr GS, Falcone EA, Moretti DJ, Andrews RD. 2014. First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLOS ONE* 9:e92633
39. Braun CD, Arostegui MC, Thorrold SR, Papastamatiou YP, Gaube P, et al. 2022. The functional and ecological significance of deep diving by large marine predators. *Annu. Rev. Mar. Sci.* 14:129–59
40. Nakamura I, Goto Y, Sato K. 2015. Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. *J. Anim. Ecol.* 84:590–603
41. Tyminski JP, de la Parra-Venegas R, González Cano J, Hueter RE. 2015. Vertical movements and patterns in diving behavior of whale sharks as revealed by pop-up satellite tags in the eastern Gulf of Mexico. *PLOS ONE* 10:e0142156
42. Thorrold SR, Afonso P, Fontes J, Braun CD, Santos RS, et al. 2014. Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nat. Commun.* 5:4274
43. Nakamura I, Matsumoto R, Sato K. 2020. Body temperature stability in the whale shark, the world's largest fish. *J. Exp. Biol.* 223:jeb210286
44. Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *PNAS* 107:2078–81

45. 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. *PNAS* 103:12799–802
46. Kopp M, Peter H-U, Mustafa O, Lisovski S, Ritz MS, et al. 2011. South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Mar. Ecol. Prog. Ser.* 435:263–67
47. 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
48. Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR. 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* 307:249–50
49. Hays GC, Houghton JD, Myers AE. 2004. Pan-Atlantic leatherback turtle movements. *Nature* 429:522
50. Weng KC, Castilho PC, Morrissette JM, Landeira-Fernandez AM, Holts DB, et al. 2005. Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* 310:104–6
51. Papastamatiou YP, Meyer CG, Carvalho F, Dale JJ, Hutchinson MR, Holland KN. 2013. Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology* 94:2595–606
52. Reid JM, Travis JM, Daunt F, Burthe SJ, Wanless S, Dytham C. 2018. Population and evolutionary dynamics in spatially structured seasonally varying environments. *Biol. Rev.* 93:1578–603
53. Watanabe YY, Goldman KJ, Caselle JE, Chapman DD, Papastamatiou YP. 2015. Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. *PNAS* 112:6104–9
54. Allgeier JE, Cline TJ, Walsworth TE, Wathen G, Layman CA, Schindler DE. 2020. Individual behavior drives ecosystem function and the impacts of harvest. *Sci. Adv.* 6:eaax8329
55. Hawkes L, Fahlman A, Sato K. 2021. What is physiologging? Introduction to the theme issue, part 2. *Philos. Trans. R. Soc. B* 376:20210028
56. Hill RD, Schneider RC, Liggins GC, Schuette AH, Elliott RL, et al. 1987. Heart rate and body temperature during free diving of Weddell seals. *Am. J. Physiol. Regulatory Integr. Comp. Physiol.* 253:R344–R51
57. Goldbogen J, Cade D, Calambokidis J, Czapanskiy M, Fahlbusch J, et al. 2019. Extreme bradycardia and tachycardia in the world's largest animal. *PNAS* 116:25329–32
58. Blix AS. 2018. Adaptations to deep and prolonged diving in phocid seals. *J. Exp. Biol.* 221:jeb182972
59. Elmegaard SL, Johnson M, Madsen PT, McDonald BI. 2016. Cognitive control of heart rate in diving harbor porpoises. *Curr. Biol.* 26:R1175–R76
60. Meir JU, Champagne CD, Costa DP, Williams CL, Ponganis PJ. 2009. Extreme hypoxemic tolerance and blood oxygen depletion in diving elephant seals. *Am. J. Physiol.-Regul. Integr. Comp. Physiol.* 297:R927–39
61. Ponganis P, Stockard T, Meir J, Williams C, Ponganis K, et al. 2007. Returning on empty: extreme blood $O_2$ depletion underlies dive capacity of emperor penguins. *J. Exp. Biol.* 210:4279–85
62. McKnight JC, Bennett KA, Bronkhorst M, Russell DJ, Balfour S, et al. 2019. Shining new light on mammalian diving physiology using wearable near-infrared spectroscopy. *PLOS Biol.* 17:e3000306
63. Holland KN, Brill RW, Chang RK, Sibert JR, Fournier DA. 1992. Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* 358:410–12
64. Goldman KJ, Anderson SD, Latour RJ, Musick JA. 2004. Homeothermy in adult salmon sharks, *Lamna ditropis*. *Environ. Biol. Fishes* 71:403–11
65. Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt HL Jr. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* 1982:254–60
66. Casey JP, James MC, Williard AS. 2014. Behavioral and metabolic contributions to thermoregulation in freely swimming leatherback turtles at high latitudes. *J. Exp. Biol.* 217:2331–37
67. Grady JM, Enquist BJ, Dettweiler-Robinson E, Wright NA, Smith FA. 2014. Evidence for mesothermy in dinosaurs. *Science* 344:1268–72
68. McCosker JE. 1987. The white shark, *Carcharodon carcharias*, has a warm stomach. *Copeia* 1987:195–97
69. Sato K, Sakamoto W, Matsuzawa Y, Tanaka H, Naito Y. 1994. Correlation between stomach temperatures and ambient water temperatures in free-ranging loggerhead turtles, *Caretta caretta*. *Mar. Biol.* 118:343–51

70. Payne NL, Smith JA, van der Meulen DE, Taylor MD, Watanabe YY, et al. 2016. Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. *Funct. Ecol.* 30:903–12
71. Mitani Y, Andrews RD, Sato K, Kato A, Naito Y, Costa DP. 2010. Three-dimensional resting behaviour of northern elephant seals: drifting like a falling leaf. *Biol. Lett.* 6:163–66
72. Miller PJ, Aoki K, Rendell LE, Amano M. 2008. Stereotypical resting behavior of the sperm whale. *Curr. Biol.* 18:R21–R23
73. Lesku JA, Rattenborg NC, Valcu M, Vyssotski AL, Kuhn S, et al. 2012. Adaptive sleep loss in polygynous pectoral sandpipers. *Science* 337:1654–58
74. Rattenborg NC, Voirin B, Cruz SM, Tisdale R, Dell'Omo G, et al. 2016. Evidence that birds sleep in mid-flight. *Nat. Commun.* 7:12468
75. Lyamin OI, Kosenko PO, Korneva SM, Vyssotski AL, Mukhametov LM, Siegel JM. 2018. Fur seals suppress REM sleep for very long periods without subsequent rebound. *Curr. Biol.* 28:2000–5
76. Green JA. 2011. The heart rate method for estimating metabolic rate: review and recommendations. *Comp. Biochem. Physiol. A* 158:287–304
77. Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, et al. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* 75:1081–90
78. Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, et al. 2020. Estimates for energy expenditure in free-living animals using acceleration proxies: a reappraisal. *J. Anim. Ecol.* 89:161–72
79. Wilson RP, Cooper J, Plötz J. 1992. Can we determine when marine endotherms feed—a case-study with seabirds. *J. Exp. Biol.* 167:267–75
80. Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, Takahashi A. 2013. Unravelling the mysteries of a mesopelagic diet: A large apex predator specializes on small prey. *Funct. Ecol.* 27:710–17
81. Weimerskirch H, Gault A, Cherel Y. 2005. Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* 86:2611–22
82. Wisniewska DM, Johnson M, Teilmann J, Rojano-Doñate L, Shearer J, et al. 2016. Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Curr. Biol.* 26:1441–46
83. Watanabe YY, Takahashi A. 2013. Linking animal-borne video to accelerometers reveals prey capture variability. *PNAS* 110:2199–204
84. Bestley S, Patterson TA, Hindell MA, Gunn JS. 2008. Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming. *J. Anim. Ecol.* 77:1223–33
85. 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. *PNAS* 104:13705–10
86. Adachi T, Takahashi A, Costa DP, Robinson PW, Hückstädt LA, et al. 2021. Forced into an ecological corner: round-the-clock deep foraging on small prey by elephant seals. *Sci. Adv.* 7:eabg3628
87. Watanabe YY, Baranov EA, Miyazaki N. 2020. Ultrahigh foraging rates of Baikal seals make tiny endemic amphipods profitable in Lake Baikal. *PNAS* 117:31242–48
88. Goldbogen J, Cade D, Wisniewska D, Potvin J, Segre P, et al. 2019. Why whales are big but not bigger: physiological drivers and ecological limits in the age of ocean giants. *Science* 366:1367–72
89. Savoca MS, Czapanskiy MF, Kahane-Rapport SR, Gough WT, Fahlbusch JA, et al. 2021. Baleen whale prey consumption based on high-resolution foraging measurements. *Nature* 599:85–90
90. Lidgard D, Bowen W, Jonsen I, Iverson S. 2014. Predator-borne acoustic transceivers and GPS tracking reveal spatiotemporal patterns of encounters with acoustically tagged fish in the open ocean. *Mar. Ecol. Prog. Ser.* 501:157–68
91. Horning M, Mellish J-AE. 2009. Spatially explicit detection of predation on individual pinnipeds from implanted post-mortem satellite data transmitters. *Endanger. Species Res.* 10:135–43
92. Halfyard EA, Webber D, Del Papa J, Leadley T, Kessel S, et al. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods Ecol. Evol.* 8:1063–71
93. Boulêtreau S, Carry L, Meyer E, Filloux D, Menchi O, et al. 2020. High predation of native sea lamprey during spawning migration. *Sci. Rep.* 10:6122
94. Holland KN, Meyer CG, Dagorn LC. 2009. Inter-animal telemetry: results from first deployment of acoustic "business card" tags. *Endanger. Species Res.* 10:287–93

95. Lidgard DC, Bowen WD, Jonsen ID, Iverson SJ. 2012. Animal-borne acoustic transceivers reveal patterns of at-sea associations in an upper-trophic level predator. *PLOS ONE* 7:e48962
96. Barkley AN, Broell F, Pettitt-Wade H, Watanabe YY, Marcoux M, Hussey NE. 2020. A framework to estimate the likelihood of species interactions and behavioural responses using animal-borne acoustic telemetry transceivers and accelerometers. *J. Anim. Ecol.* 89:146–60
97. Papastamatiou YP, Mourier J, TinHan T, Luongo S, Hosoki S, et al. 2022. Social dynamics and individual hunting tactics of white sharks revealed by biologging. *Biol. Lett.* 18:20210599
98. Lidgard DC, Bowen WD, Jonsen ID, McConnell BJ, Lovell P, et al. 2014. Transmitting species-interaction data from animal-borne transceivers through Service Argos using Bluetooth communication. *Methods Ecol. Evol.* 5:864–71
99. Weimerskirch H, Bertrand S, Silva J, Marques JC, Goya E. 2010. Use of social information in seabirds: Compass rafts indicate the heading of food patches. *PLOS ONE* 5:e9928
100. Wakefield ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, et al. 2013. Space partitioning without territoriality in gannets. *Science* 341:68–70
101. Jacoby DM, Papastamatiou YP, Freeman R. 2016. Inferring animal social networks and leadership: applications for passive monitoring arrays. *J. R. Soc. Interface* 13:20160676
102. Jones TB, Green JA, Patrick SC, Evans JC, Wells MR, et al. 2020. Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. *Ecol. Lett.* 23:1085–96
103. Papastamatiou YP, Bodey TW, Caselle JE, Bradley D, Freeman R, et al. 2020. Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics. *Proc. R. Soc. B* 287:20201063
104. Aspillaga E, Arlinghaus R, Martorell-Barceló M, Follana-Berná G, Lana A, et al. 2021. Performance of a novel system for high-resolution tracking of marine fish societies. *Anim. Biotelemetry* 9:1
105. Aspillaga E, Arlinghaus R, Martorell-Barceló M, Barcelo-Serra M, Alós J. 2021. High-throughput tracking of social networks in marine fish populations. *Front. Mar. Sci.* 8:688010
106. Fedak M. 2004. Marine animals as platforms for oceanographic sampling: a "win/win" situation for biology and operational oceanography. *Mem. Natl. Inst. Polar Res.* 58:133–47
107. Lydersen C, Nøst OA, Lovell P, McConnell BJ, Gammelsrød T, et al. 2002. Salinity and temperature structure of a freezing Arctic fjord—monitored by white whales (*Delphinapterus leucas*). *Geophys. Res. Lett.* 29:2119
108. 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. *PNAS* 105:11634–39
109. Roquet F, Wunsch C, Forget G, Heimbach P, Guinet C, et al. 2013. Estimates of the Southern Ocean general circulation improved by animal-borne instruments. *Geophys. Res. Lett.* 40:6176–80
110. Ohshima KI, Fukamachi Y, Williams GD, Nihashi S, Roquet F, et al. 2013. Antarctic Bottom Water production by intense sea-ice formation in the Cape Darnley polynya. *Nat. Geosci.* 6:235–40
111. Guinet C, Xing X, Walker E, Monestiez P, Marchand S, et al. 2013. Calibration procedures and first dataset of Southern Ocean chlorophyll *a* profiles collected by elephant seals equipped with a newly developed CTD-fluorescence tags. *Earth Syst. Sci. Data* 5:15–29
112. Bailleul F, Vacquie-Garcia J, Guinet C. 2015. Dissolved oxygen sensor in animal-borne instruments: an innovation for monitoring the health of oceans and investigating the functioning of marine ecosystems. *PLOS ONE* 10:e0132681
113. McMahon CR, Roquet F, Baudel S, Belbeoch M, Bestley S, et al. 2021. Animal Borne Ocean Sensors–AniBOS–an essential component of the Global Ocean Observing System (GOOS). *Front. Mar. Sci.* 8:1625
114. Yoda K, Shiomi K, Sato K. 2014. Foraging spots of streaked shearwaters in relation to ocean surface currents as identified using their drift movements. *Prog. Oceanogr.* 122:54–64
115. Uesaka L, Goto Y, Yonehara Y, Komatsu K, Naruoka M, et al. 2022. Ocean wave observation utilizing motion records of seabirds. *Prog. Oceanogr.* 200:102713
116. Yonehara Y, Goto Y, Yoda K, Watanuki Y, Young LC, et al. 2016. Flight paths of seabirds soaring over the ocean surface enable measurement of fine-scale wind speed and direction. *PNAS* 113:9039–44
117. Miyazawa Y, Guo X, Varlamov SM, Miyama T, Yoda K, et al. 2015. Assimilation of the seabird and ship drift data in the north-eastern sea of Japan into an operational ocean nowcast/forecast system. *Sci. Rep.* 5:17672

118. 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
119. Watanabe YY, Ito K, Kokubun N, Takahashi A. 2020. Foraging behavior links sea ice to breeding success in Antarctic penguins. *Sci. Adv.* 6:eaba4828
120. Pagano A, Durner G, Rode K, Atwood T, Atkinson S, et al. 2018. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science* 359:568–72
121. Hückstädt LA, Piñones A, Palacios DM, McDonald BI, Dinniman MS, et al. 2020. Projected shifts in the foraging habitat of crabeater seals along the Antarctic Peninsula. *Nat. Clim. Change* 10:472–77
122. Hammerschlag N, McDonnell LH, Rider MJ, Street GM, Hazen EL, et al. 2022. Ocean warming alters the distributional range, migratory timing, and spatial protections of an apex predator, the tiger shark (*Galeocerdo cuvier*). *Glob. Change Biol.* 28:1990–2005
123. Payne NL, Meyer CG, Smith JA, Houghton JD, Barnett A, et al. 2018. Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator. *Glob. Change Biol.* 24:1884–93
124. Young HS, Maxwell SM, Conners MG, Shaffer SA. 2015. Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. *Biol. Conserv.* 181:226–35
125. White TD, Carlisle AB, Kroodsma DA, Block BA, Casagrandi R, et al. 2017. Assessing the effectiveness of a large marine protected area for reef shark conservation. *Biol. Conserv.* 207:64–71
126. Dwyer RG, Krueck NC, Udyawer V, Heupel MR, Chapman D, et al. 2020. Individual and population benefits of marine reserves for reef sharks. *Curr. Biol.* 30:480–89.e5
127. van Zinnicq Bergmann MP, Guttridge TL, Smukall MJ, Adams VM, Bond ME, et al. 2022. Using movement models and systematic conservation planning to inform marine protected area design for a multi-species predator community. *Biol. Conserv.* 266:109469
128. Bodey TW, Jessopp MJ, Votier SC, Gerritsen HD, Cleasby IR, et al. 2014. Seabird movement reveals the ecological footprint of fishing vessels. *Curr. Biol.* 24:R514–R15
129. Maxwell SM, Hazen EL, Bograd SJ, Halpern BS, Breed GA, et al. 2013. Cumulative human impacts on marine predators. *Nat. Commun.* 4:2688
130. Beal M, Dias MP, Phillips RA, Oppel S, Hazin C, et al. 2021. Global political responsibility for the conservation of albatrosses and large petrels. *Sci. Adv.* 7:eabd7225
131. Queiroz N, Humphries NE, Couto A, Vedor M, Da Costa I, et al. 2019. Global spatial risk assessment of sharks under the footprint of fisheries. *Nature* 572:461–66
132. Hindell MA, Reisinger RR, Ropert-Coudert Y, Hückstädt LA, Trathan PN, et al. 2020. Tracking of marine predators to protect Southern Ocean ecosystems. *Nature* 580:87–92
133. Weimerskirch H, Collet J, Corbeau A, Pajot A, Hoarau F, et al. 2020. Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of nondeclared fishing. *PNAS* 117:3006–14
134. Hays GC, Bailey H, Bograd SJ, Bowen WD, Campagna C, et al. 2019. Translating marine animal tracking data into conservation policy and management. *Trends Ecol. Evol.* 34:459–73
135. Goulet P, Guinet C, Swift R, Madsen PT, Johnson M. 2019. A miniature biomimetic sonar and movement tag to study the biotic environment and predator-prey interactions in aquatic animals. *Deep Sea Res. I* 148:1–11
136. Hussey NE, Orr J, Fisk AT, Hedges KJ, Ferguson SH, Barkley AN. 2018. Mark report satellite tags (mrPATs) to detail large-scale horizontal movements of deep water species: first results for the Greenland shark (*Somniosus microcephalus*). *Deep Sea Res. I* 134:32–40
137. Skubel RA, Wilson K, Papastamatiou YP, Verkamp HJ, Sulikowski JA, et al. 2020. A scalable, satellite-transmitted data product for monitoring high-activity events in mobile aquatic animals. *Anim. Biotelemetry* 8:34
138. McDonald BI, Elmegaard SL, Johnson M, Wisniewska DM, Rojano-Doñate L, et al. 2021. High heart rates in hunting harbour porpoises. *Proc. R. Soc. B* 288:20211596
139. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, et al. 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science* 375:eabg1780
140. Sequeira AM, O'Toole M, Keates TR, McDonnell LH, Braun CD, et al. 2021. A standardisation framework for bio-logging data to advance ecological research and conservation. *Methods Ecol. Evol.* 12:996–1007

141. Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, et al. 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. *Methods Ecol. Evol.* 9:946–55
142. Kay WP, Naumann DS, Bowen HJ, Withers SJ, Evans BJ, et al. 2019. Minimizing the impact of biologging devices: using computational fluid dynamics for optimizing tag design and positioning. *Methods Ecol. Evol.* 10:1222–33
143. Bonfil R, Meÿer M, Scholl MC, Johnson R, O'Brien S, et al. 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310:100–3
144. Towner AV, Leos-Barajas V, Langrock R, Schick RS, Smale MJ, et al. 2016. Sex-specific and individual preferences for hunting strategies in white sharks. *Funct. Ecol.* 30:1397–407
145. Watanabe YY, Payne NL, Semmens JM, Fox A, Huveneers C. 2019. Swimming strategies and energetics of endothermic white sharks during foraging. *J. Exp. Biol.* 222:jeb185603
146. Watanabe YY, Payne NL, Semmens JM, Fox A, Huveneers C. 2019. Hunting behaviour of white sharks recorded by animal-borne accelerometers and cameras. *Mar. Ecol. Prog. Ser.* 621:221–27