

Bio-telemetry as an Essential Tool in Movement Ecology and Marine Conservation

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Abstract

Marine top predators represent an essential part of marine ecosystems. They are generally regarded as “sentinels of the sea” since their presence reflects high biological productivity. However, many populations are experiencing dramatic declines attributed to various human-induced threats (e.g., pollution, climate change, overfishing), highlighting the need for effective conservation. In this review, we show that bio-telemetry can be an essential tool, not only to improve knowledge about the animals’ ecology, but also for conservation purposes. As such, we will first discuss the most important state-of-the-art devices (e.g., time-depth recorders, accelerometers, satellite tags) and illustrate how they can improve our understanding of movement ecology. We will then examine the challenges and ethical issues related to bio-telemetry, and lastly, demonstrate its enormous value in resolving present and future conservation issues.

Introduction

Marine top predators are widely regarded as potential qualitative indicators of the health and status of marine ecosystems (Burger et al. 2004; Piatt et al. 2007; Boersma 2008; Campbell et al. 2012; Wikelski and Tertitski 2016). Their

responses to changes in the environment can be measured by examining different aspects of their ecology using corresponding methods, for example, foraging behavior (e.g., satellite-linked logging devices and time-depth recorders), energy expenditure (e.g., double-labelled water), stress levels (e.g., corticosteroid hormone concentrations), and diet trends (e.g., stable isotopes and fatty acid analyses) (Votier et al. 2010). The decline of top predators can result in trophic downgrading, which has far reaching consequences on the structure and dynamics of marine ecosystems (Heithaus et al. 2008; Estes et al. 2011; Boaden and Kingsford 2015). At the moment, marine top predators face unprecedented challenges and their future existence is threatened, due to the effects of rapid environmental changes, overfishing, pollution, and many other anthropogenic disturbances (Robinson et al. 2005). If we consider seabirds, for instance, their conservation status has deteriorated faster than any other bird group over recent decades (Croxall et al. 2012; Paleczny et al. 2015). There are also countless examples available for other marine top predators, such as cetaceans (Rosenbaum et al. 2014; McKenna et al. 2015), pinnipeds (Antonelis et al. 2006; Costa et al. 2010a), elasmobranchs (Baum et al. 2003; Graham et al. 2012), and large teleosts (Block et al. 2001; Boyce et al. 2008).

In this review, we focus on the knowledge that can be derived from bio-telemetry and its efficacy in movement ecology and conservation studies. Bio-telemetry can be defined as the remote recording of behavioral, physiological, and environmental data by means of electronic tags, attached to animals (Hays et al. 2016). Here, we use the term bio-telemetry synonymously with bio-logging; the latter includes loggers that must be recovered to download the data, which were stored on the device. We aim to give a general overview of existing devices, assess specifically how bio-telemetry can improve our understanding of movement ecology, while taking the negative impacts on the animals into account, and discuss how bio-telemetry can help in recommending conservation measures.

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Existing Bio-telemetry Devices

We are undoubtedly living in the golden age of bio-telemetry studies (McIntyre 2014; Hussey et al. 2015; Hays et al. 2016). The following section provides an overview of the most commonly used animal-borne bio-telemetry devices and their potential in the context of studying animal behaviors. We start with archival loggers, which can be defined as

Box 1: Quick Guide to Bio-telemetry Terminology

Acoustic telemetry:	tagged animals are detected and recorded by acoustic receivers at fixed moorings that are recovered periodically; this enables tracking of individual animals
Archival logger:	animal-borne instrument that records and stores data on-board; must be relocated for data download
Argos satellite tag:	animal-borne device that communicates with polar-orbiting Argos satellites to determine its location; typical location errors range between 500 m and 10 km
Bio-telemetry:	method of remote recording of behavioral, physiological and environmental data by electronic tags attached to animals
Fastloc® GPS:	takes a snapshot of relevant satellite information in a fraction of a second, when a diving animal surfaces; the calculation of a GPS position is performed on-board the tag, even when not in view of satellites
GPS tag:	device that determines an animal's position via the Global Positioning System (GPS); typical location errors range between 20 m and 50 m
GSM:	Global System for Mobile Communications; a cellular network that is the global standard for mobile communication, however, also frequently used to relay data from animal-borne instruments (e.g., GPS tags)

Hydrophone:	an underwater microphone
Jaw movement sensor:	device consisting of Hall sensor and magnet, which are attached to upper and lower mandible, respectively; detects mouth openings and hence feeding events
Pop-up archival transmitting tag (PAT):	satellite-linked data logger that is commonly deployed on sharks; logger records and stores temperature, depth and ambient light levels over pre-programmed period until it pops up to the surface and delivers data via the Argos satellite system
Satellite-linked data logger:	combination of a satellite tag (Argos and/or GPS) with an archival logger; records an animal's position as well as information on different behaviors and ambient conditions
Stomach temperature logger:	device that monitors internal body temperature; a sharp drop in temperature can be attributed to the ingestion of relatively cold prey, enabling the detection of feeding events
Time-depth recorder (TDR):	device that records a time-series of dive depths, resulting in time-depth profiles
Tri-axial accelerometer:	measures acceleration caused by earth's gravitational field as well as acceleration by the animal in all three space dimensions
Tri-axial magnetometer:	measures the orientation towards the earth's magnetic field in all three space dimensions

instruments that record and store data on-board. This holds true not only for standard time-depth recorders (TDRs), but also for cameras, accelerometers and magnetometers. As they only store the data on-board, one is usually required to recover the instrument and download the data. In the next section we introduce location-only satellite tags. Collecting animal locations is straightforward for Argos satellite tag users, as once they are deployed, the data is relayed and provided online to the user, which enables near real-time tracking. However, this fundamentally differs from global positioning system (GPS) devices, since the position determination works differently. With Argos, the satellite system determines the device's position, while with GPS, the device determines its own position. The latter has the disadvantage that one usually needs to recover the GPS tags, or couple them with satellite or mobile phone networks. Finally, there are tags, which consist of both an archival tag (e.g., TDR, accelerometer, magnetometer) and a satellite tag (e.g., Argos, GPS). These satellite-linked data loggers are the most sophisticated ones and also the ones most commonly used. A 'Quick guide to bio-telemetry terminology' can be found in Box 1.

Archival Loggers

Archival loggers are deployed on animals to record, in general, movements, specific behaviors, physiological processes or environmental conditions. It is necessary to retrieve these instruments to download data, which can be challenging in highly mobile marine predators. This disadvantage is offset by deploying archival loggers on species with high site fidelity that haul out or breed on land (e.g., elephant seals, seabirds during breeding season), or by combining them with a radio transmitter (Very High Frequency – VHF, or Ultra High Frequency – UHF) to relocate the tag when it falls off (Wilson et al. 2002; Dragon et al. 2012; Villegas-Amtmann et al. 2013). Since data transmission is not a constraint for archival loggers, these devices are able to collect data in high-resolution, which are otherwise impossible to obtain and extremely valuable to study fine-scale processes.

Per Scholander is generally regarded as the pioneer of bio-logging; he deployed the first archival loggers on marine animals in the 1940s (Ropert-Coudert and Wilson 2005; Kooyman 2007; McIntyre 2014). In his famous monograph on diving physiology, he recorded the maximum dive depths of whales, dolphins, and seals by using a capillary tube depth gauge attached to the animal (Scholander 1940; Ponganis 2013). Later, maximum dive depth recorders were used on Weddell seals *Leptonychotes weddellii* in Antarctica, to study their maximum diving and breath-holding capacities

(DeVries and Wohlschlag 1964). A major step in the history of bio-logging was the development of the first TDR by Gerald Kooyman, which was able to record full time-depth profiles of a dive (Kooyman 1965, 1966). This invention led to fascinating opportunities to study the diving behavior of marine top predators and the related physiological adaptations (Kooyman 1973). At the time, these devices were still quite heavy and, for instance, too large for most bird species. However, due to rapid technological advances, their dimensions have decreased quickly, which means that they can presently be used on a variety of animals (Ropert-Coudert and Wilson 2005; McIntyre 2014; Hussey et al. 2015).

At the same time, improved and additional sensors were included in the classic TDR deployment, enabling diving behavior to be studied in even greater detail. For instance, magnetometers were incorporated, which measure the orientation towards the earth's magnetic field in three axes (heading/yaw, pitch, and roll) and are especially sensitive to record angular rotations (Fig. 1b). Tri-axial magnetometry enables researchers to track three-dimensional movements of diving animals via dead-reckoning, and thus to reconstruct three-dimensional profiles of a dive (Davis et al. 1999; Mitani et al. 2003; Wilson et al. 2007; Williams et al. 2017). This was an important improvement, as marine animals inhabit a three-dimensional space and respond to environmental cues in all three dimensions. For diving predators both the horizontal and vertical distribution of prey patches is important. Foraging chinstrap penguins *Pygoscelis antarctica*, for instance, choose to pass by shallow and dense prey aggregations and reach for deeper and more homogeneously distributed prey fields with higher encounter probabilities (Zamon et al. 1996)—a finding which would be overlooked in a conventional, two-dimensional analysis of predator-prey distribution. Therefore, taking all three dimensions into consideration is essential to understand fine-scale habitat use or foraging behavior.

At present, it is also common to incorporate accelerometers into archival loggers. These devices measure acceleration, which is caused by earth's gravity (static component) and a change in the animal's speed (dynamic component). It usually records accelerations in three dimensions, the x-, y-, and z-axes or surge, sway, and heave (Fig. 1a). When positioned on the head and/or jaw of a marine predator, accelerometers can provide information about rapid head movements, indicating prey capture attempts (Naito et al. 2010; Kokubun et al. 2011; Gallon et al. 2013). However, accelerometers are often deployed close to the animal's center of gravity, i.e., in the center of the trunk, which is more useful to record overall movement patterns (e.g., swimming, resting, and flying). As such, tri-axial accelerometry can be used to identify and quantify different behaviors and activity patterns, and subsequently, put them in relation to energy

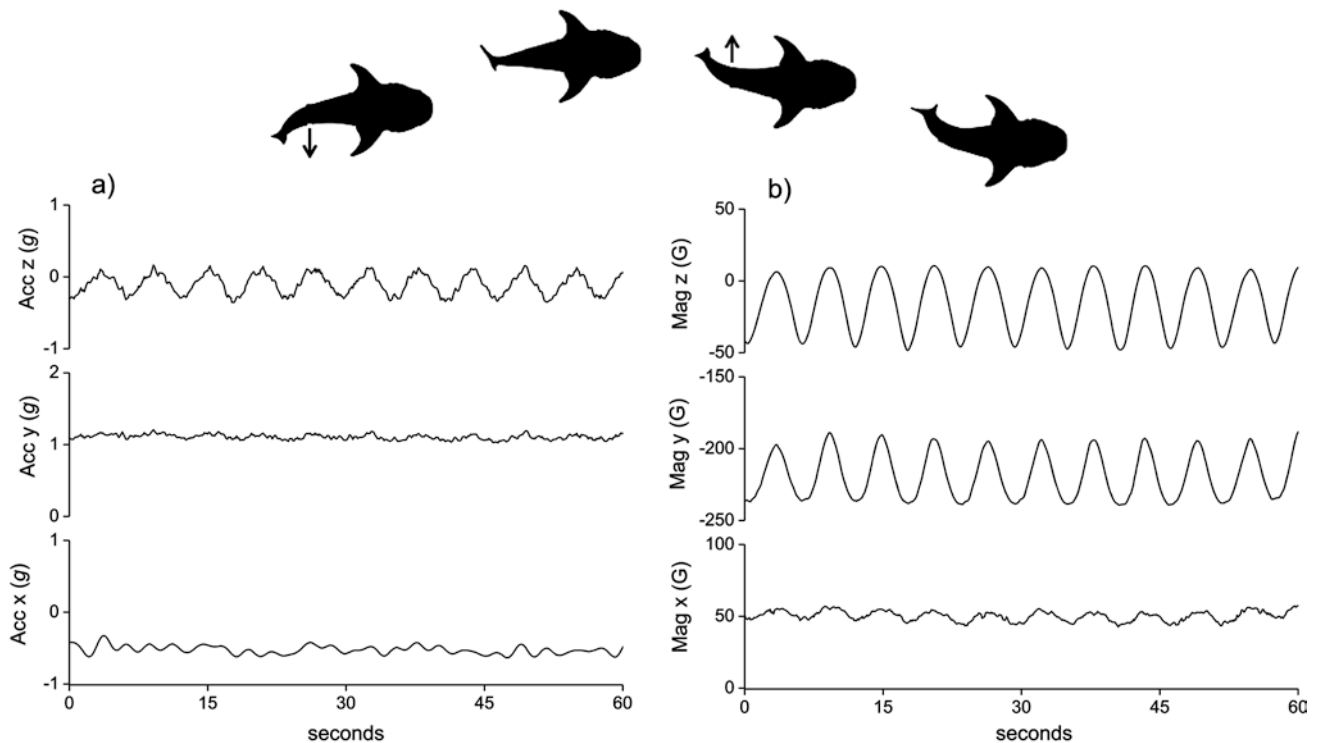


Fig. 1 Swimming behavior of a whale shark *Rhincodon typus* as indicated by tri-axial (a) accelerometry, and (b) magnetometry. One oscillation corresponds to one tail stroke. Note the weak signal and high degree of noise in the accelerometer data (due to the low stroke fre-

quency). The magnetometer is less susceptible to this noise and is, therefore, better to resolve the angular rotation of the tail strokes. (Reproduced from Williams et al. (2017) (CC-BY 4.0))

expenditure (Wilson et al. 2006, 2008; Shepard et al. 2008; Sakamoto et al. 2009a). For instance, different at-sea activities (i.e., diving, transiting, resting, and surfacing) during foraging trips of lactating northern fur seals *Callorhinus ursinus* and Antarctic fur seals *Arctocephalus gazella* were classified based on accelerometer and dive data. Using these classified behaviors, time-activity budgets were determined and activity-specific energy expenditures were accurately calculated from accelerometer data (Jeanniard-du-Dot et al. 2017). These various applications make accelerometers a powerful and promising tool for future employments.

Video and still-picture cameras are another example of archival loggers, commonly deployed on marine top predators (Fig. 2a) (Moll et al. 2007). These devices not only take photos at regular intervals or record video sequences, but additional incorporated sensors are also able to gather data on environmental conditions (e.g., dive depths and ambient temperature) (Ponganis et al. 2000; Moll et al. 2007; Naito et al. 2010). Over the years, the quality of video footage and photographs has increased substantially, with high-definition cameras being the current status quo (Chapple et al. 2015; Krause et al. 2015; Machovsky-Capuska et al. 2016). High quality recordings require enormous memory capacities; thus the recording time ranges between hours and a few

days, when a duty cycle is activated. Nevertheless, camera loggers can be extremely valuable tools to obtain direct observations of difficult to observe, and therefore rarely documented, animal behaviors (Takahashi et al. 2004; Sakamoto et al. 2009b; Handley and Pistorius 2016). For example, it could be demonstrated that black-browed albatrosses *Thalassarche melanophris* actively follow killer whales *Orcinus orca* and possibly feed on prey remains that were left over by them (Sakamoto et al. 2009b). Such observations are crucial to understand how far-ranging animals locate prey patches in the vast ocean. Camera loggers are also frequently deployed to investigate a predator's foraging behavior in greater detail. Animal-borne imaging can reveal foraging strategies and hunting behavior (Davis et al. 1999; Watanuki et al. 2008; Goldbogen et al. 2012; Krause et al. 2015), quantify prey intake (e.g., Ponganis et al. 2000; Watanabe et al. 2003), or validate prey capture events derived from accelerometers or dive characteristics (Watanabe and Takahashi 2013; Volpov et al. 2015, 2016). Furthermore, cameras attached to diving predators can serve as remote sensors to monitor the surrounding environment. They can, for instance, provide information on the behavior and occurrence of prey species (Fuiman et al. 2002), or detect hitherto unknown faunal communities (Watanabe et al. 2006).



Fig. 2 (a) Adult Weddell seal *Leptonychotes weddellii* equipped with an infrared camera logger. (b) Adélie penguin *Pygoscelis adeliae* with GPS and dive logger. (c) Young grey seal *Halichoerus grypus* with a GSM-relayed Fastloc® GPS data logger, tagged on Helgoland, Germany. (d) Male southern elephant seal *Mirounga leonina* instrumented with a CTD-Satellite Relay Data Logger on King George Island/Isla 25 de Mayo. (e) Lesser black-backed gull *Larus fuscus*

tagged with a solar-powered GPS logger and tri-axial accelerometer. (f) Harbor porpoise *Phocoena phocoena* with a Digital Sound Recording-Tag (DTAG), attached by suction cups. Photos used with permission from Dominik Nachtsheim (a), Nina Dehnhard (b), Abbo van Neer (c), Alfred-Wegener-Institut/Horst Bornemann (CC-BY 4.0) (d), Brigitte Heylen (e), and Jonas Teilmann (f)

Besides these commonly used archival loggers, there are a variety of alternative devices, which record very specific behaviors or physiological processes. Jaw movement sensors are able to detect mouth-opening-events, and can therefore provide a proxy for prey capture attempts (Wilson et al. 2002; Ropert-Coudert et al. 2004; Liebsch et al. 2007). Another measurement used to detect prey capture can be the drop in internal body temperature when relatively cold prey is ingested by marine endotherms. As such, esophagus or stomach temperature loggers have been regularly deployed in seabirds and marine mammals to record feeding activities (Wilson et al. 1992; Ropert-Coudert et al. 2001; Austin et al. 2006a; Ropert-Coudert and Kato 2006). Other sensors are able to record heart rate (Woakes et al. 1995; Hindell and Lea 1998; Froget et al. 2004; Chaise et al. 2017) or flipper strokes (Sato et al. 2003; Insley et al. 2008; Jeanniard-du-Dot et al. 2017) to study field metabolic rates and energy expenditures.

There are certainly many more archival loggers available for various applications and research questions, however, a discussion of those is beyond the scope of this review.

Argos Satellite Tags

The Argos satellite system was initiated in the late 1970s and represents a cooperative project between Centre National d'Études Spatiales (CNES) in France, and the National Oceanic and Atmospheric Administration (NOAA) and National Aeronautics and Space Administration (NASA) in the USA. Argos is operated and managed by Collecte Localisation Satellites (CLS) in Toulouse, France. Soon after its initiation, the high importance of Argos satellites for wildlife telemetry studies was recognized. Satellite telemetry was developed as a means of overcoming the logistical difficulties

and high costs of conventional VHF radio telemetry (Fancy et al. 1988). Animal locations are determined through Doppler shift via communication between an animal-borne satellite transmitter and polar-orbiting satellites. The estimated locations are provided online by CLS and allow quasi-live tracking of tagged individuals (Fancy et al. 1988; Costa et al. 2012).

Argos satellite tags represent the first reliable system to track horizontal movements of marine animals. This information is essential to analyze habitat use or migration patterns. The first successful deployment was conducted on a basking shark *Cetorhinus maximus* and only provided locations over the course of two weeks (Priede 1984). Nevertheless, this was sufficient to conclude that the shark was probably feeding on zooplankton along a frontal system (Priede 1984; Priede and Miller 2009). Since then, enormous improvements in both the Argos satellite system and satellite tags have been achieved (e.g., more polar-orbiting satellites, better sensitivity of satellite sensors, longer transmitter battery life, more streamlined tag shapes), ultimately leading to a larger quantity of collected data (Hays et al. 2007). Argos satellite tags have been deployed on a diverse assemblage of marine top predator species, including seabirds (Jouventin and Weimerskirch 1990; Spencer et al. 2014; Pistorius et al. 2017), sharks (Priede 1984; Eckert and Stewart 2001; Weng et al. 2005), pinnipeds (Costa et al. 2010a; Dietz et al. 2013; Arcalís-Planas et al. 2015) and cetaceans (Andrews et al. 2008; Edrén et al. 2010; Hauser et al. 2010; Reisinger et al. 2015).

GPS Tags

Despite the many advantages of Argos satellite tags, one of the major drawbacks is the relatively low location accuracy, with errors generally ranging between 500 m and 10 km (Costa et al. 2010b). Qualitatively poor Argos locations are especially prevalent in studies involving diving top predators, since the time spent at the surface to enable successful uplinks to the satellite is limited (Vincent et al. 2002; Costa et al. 2010b; Patterson et al. 2010). GPS tags provide a much better accuracy, usually with errors less than 50 m (Costa et al. 2010b; Dujon et al. 2014). Despite this higher location accuracy, most researchers have, for quite some time, refrained from using GPS tags, mainly due to the length of time (10–30 min) and high energy demand required to fix a GPS position (Tomkiewicz et al. 2010; Costa et al. 2012). This meant that they were well suited for seabirds (Fig. 2e) (Ryan et al. 2004; Pinaud and Weimerskirch 2007; Votier et al. 2010), but less so for diving animals. This problem has more recently been overcome by the development of a Fastloc® GPS, for which GPS positions can be obtained within milliseconds, which enables a successful location fix even within a short surfacing event (Costa et al. 2010b). Thus, GPS tags are now also increasingly used on marine mammals (Heide-Jørgensen

et al. 2013; Villegas-Amtmann et al. 2013; McKenna et al. 2015). The GPS positions are either stored on-board the device and must be downloaded from a recovered tag, or can be transmitted via the Argos satellite system (Costa et al. 2010b; Patterson et al. 2010). GPS locations can also be relayed through communication with the Global Systems for Mobile Communication (GSM)—the mobile phone network (McConnell et al. 2004; Cronin and McConnell 2008). The locations are stored internally and transmitted as a text message, together with ancillary information, when the animal is within the coverage of the GSM network (Cronin and McConnell 2008). These devices represent a promising tool for the relatively inexpensive and accurate tracking of coastal top predator species (Fig. 2c) (Jessopp et al. 2013; Wilson et al. 2017), especially in the light of the rapidly expanding GSM network around the globe.

Satellite-linked Data Loggers

For many applications, simultaneous information on both horizontal movements and specific behaviors, for example, diving behavior, is required to better understand how marine animals respond to their environment and use their habitat. This is achieved by combining a satellite tag (Argos and/or GPS) with an archival logger (e.g., time-depth recorders, accelerometers), i.e., a satellite-linked data logger. These devices not only record an animal's position, but also log information on different behaviors and ambient conditions. Some instruments are able to transmit these data via Argos satellites, while others need to be recovered for data download. Remotely collected data via satellite only provide compressed and reduced information due to bandwidth limitations, whereas retrievable instruments offer data in high resolution. However, it is expected that the impact of this constraint will continue to lessen with the on-going rapid technological advance and further developments in the field of bio-telemetry (see, for example, Cox et al. 2017).

The first satellite-linked data logger was a combination of a satellite transmitter and a TDR (Merrick et al. 1994). This provided the opportunity to combine location data with concurrent behavioral data, and thus enabled the analysis of horizontal and vertical movements (Merrick et al. 1994; Ryan et al. 2004; Burns et al. 2008; Bestley et al. 2015; Heerah et al. 2016). The first satellite-linked dive recorders were effective to study habitat use in relation to diving behavior, but had restricted applicability, due to the limited information available about each dive (Merrick et al. 1994; Burns 1999; Davis et al. 2007; Nachtsheim et al. 2017). The development of the satellite relay data logger (SRDL) revolutionized the study of top predator movements, providing locations and compressed time-depth profiles for each dive via satellite communication (Fedak et al. 2002). These

devices can also incorporate high precision environmental sensors, which are able to record valuable CTD (Conductivity, Temperature, Depth) data. The collected temperature and salinity profiles have a relatively good quality and accuracy, compared to traditional oceanographic measurements, such as floats and moorings (Boehme et al. 2009). This development meant that studying foraging behavior in relation to actual environmental conditions, as experienced by the animals, became possible (Fig. 2d) (Biuw et al. 2007; McIntyre et al. 2011; Lowther et al. 2013; Blanchet et al. 2015; Labrousse et al. 2015).

Accelerometers and magnetometers can also be coupled with Argos or GPS devices, providing even more powerful tools to study animal behavior (Fig. 2e) (Wilson et al. 2008; Bouten et al. 2013; Cox et al. 2017). These instruments are able to give extremely detailed information about three-dimensional movements and behaviors. More sophisticated devices have also incorporated a hydrophone for sound recordings of diving predators, such as cetaceans, which enables researchers to relate their movements to acoustic behavior as well as to the surrounding soundscape (Fig. 2f) (Nowacek et al. 2001; Johnson and Tyack 2003; Aguilar Soto et al. 2008; Wisniewska et al. 2016). Such instruments usually have to be recovered for data retrieval, but recently other systems have been developed, which allow the remote downloading of concurrent GPS and accelerometer data at ground base stations (Bouten et al. 2013). Another exciting and promising approach is the recent launch of the ICARUS initiative (Icarus Initiative 2018). Specifically-designed ICARUS satellite tags will be

able to record GPS positions as well as tri-axial accelerometer data and transmit the data to the ICARUS antenna on-board the International Space Station. The data will then be made available to the users in near real time via the database Movebank (see Box 2 for an overview on databases for animal movement data). These remotely-operating systems enable the study of migration patterns and habitat use of migratory species over large spatial and temporal scales in great detail (Wikelski et al. 2007; Bouten et al. 2013; Stienen et al. 2016; Wikelski and Tertitski 2016).

For animals that do not regularly come to the surface, such as fish, pop-up archival transmitting tags (PATs) can be used (Carlson et al. 2010; Jorgensen et al. 2010; Campana et al. 2011; Hammerschlag et al. 2011). PATs usually constitute an archival logger and an Argos satellite transmitter, and, in the case of sharks and other elasmobranchs, are anchored in the dorsal fin or dorsal musculature (Hammerschlag et al. 2011). The logger records and stores temperature, depth, and ambient light levels over several months to years. After a pre-programmed period, the tag detaches from the animal and pops up to the ocean surface. While floating, it transmits the recorded data to Argos satellites (Hammerschlag et al. 2011). The animal's horizontal movements are reconstructed from the *in situ* measured sea surface temperature and light levels, resulting in a daily estimate of latitude and longitude. Since the location estimate is relatively imprecise, with mean errors ranging between 60 and 180 km, only large-scale movements and migrations patterns can be investigated (Block et al. 2011; Campana et al. 2011; Hammerschlag et al. 2011). A comparable technology is used to track large-scale and often multi-year movements of pinnipeds and flying seabirds, however, this system is not linked to satellites. Similar to PATs, light level geolocators record light levels from which locations can be derived. They are relatively inexpensive and the spatial resolution (ca. 100–200 km) is often sufficient for wide-ranging species, such as petrels, albatrosses, terns, or elephant seals (Afanasyev 2004; Bradshaw et al. 2004; Phillips et al. 2004; Egevang et al. 2010; Weimerskirch et al. 2014).

Box 2: Links to Online Databases Hosting Marine Animal Movement Data

Biodiversity.aq—Antarctic biodiversity data base: <http://www.biodiversity.aq>
 Lifewatch.be—A virtual laboratory for biodiversity research: <http://www.lifewatch.be/>
 OBIS-SEAMAP—Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Populations: <http://seamap.env.duke.edu/>
 Ocean Tracking network: <https://members.oceantrack.org/projects>
 OCEARCH's Global Shark Tracker: <http://www.ocearch.org>
 MEOP—Marine Mammals Exploring the Oceans from Pole to Pole: <http://www.meop.net>
 MMT—Marine Mammal Tracking: <https://www.pangaea.de/?q=project%3Alabel%3AMMT>
 Movebank: A Database for Animal Tracking Data: <https://www.movebank.org>

Acoustic Telemetry

Tracking animals by means of acoustic telemetry was specifically developed for use in marine and freshwater ecosystems. It is based on the idea that tagged animals, most often fish, are registered by submerged receiving stations (Donaldson et al. 2014; Hussey et al. 2015). The tag is usually a transmitter, which is either surgically implanted or attached externally to the animal and emits signals with a given pulse rate. The transmitters can be miniscule (<0.5 g in some cases), and can even be used to tag small or juvenile fish (McMichael et al. 2010). The presence of the animal is recorded when the trans-

missions are detected by a hydrophone in the receivers. However, the detection efficiency, i.e., the attenuation of sound, varies between different environments and water conditions, which represent a major limitation of acoustic telemetry (Donaldson et al. 2014). Often, multiple acoustic receivers are organized in a comprehensive array or network to cover the pre-defined study area, enabling the tracking of each individual's movements. The data are stored within the receiver station and can either be downloaded by recovering the device or via wireless technology (Dagorn et al. 2007; Donaldson et al. 2014; Hussey et al. 2015). Such acoustic receivers can also be installed on mobile platforms, such as predators, to detect encounters with tagged individuals. This means that interactions between a predator and its prey, as well as spatiotemporal patterns of predator and prey distribution can be studied (Lidgard et al. 2014).

Movement Ecology

Movement is a fundamental characteristic of many species, and as such, plays an important role in the survival and reproduction of individuals. This, in turn, affects the structure and dynamics of populations and ecosystems. Therefore, to manage marine ecosystems properly, it is imperative to understand the causes, patterns, mechanisms, and consequences of individual movement. Data derived from bio-telemetry can provide insight into animals' movement ecology and show interactions within the ecosystem they inhabit (Cagnacci et al. 2010). This enables a mechanistic understanding of movement ecology, including foraging behavior and seasonal migration. However, interpreting bio-telemetry data remains a challenge in certain applications, (e.g., habitat modelling), due to the inherent features of telemetry data. These features include spatial and temporal auto-correlation, uneven sampling intervals, uneven sampling effort across individuals and uneven detectability across different habitats (Aarts et al. 2008). Choosing an appropriate analytical approach for the respective research questions is, therefore, crucial. An overview of the currently available methods is described in Carter et al. (2016).

Foraging Behavior

Optimal foraging theory predicts that every individual strives to minimize its foraging effort, while maximizing its foraging success to assure its survival and reproduction—the drivers for natural selection (MacArthur and Pianka 1966; Schoener 1971; Pyke 1984). For instance, Antarctic fur seals have distinct foraging strategies, with associated trade-offs related to habitat availability, travel costs, prey accessibility and prey quality (Arthur et al. 2016). We can differentiate

between top predators that are central place foragers (CPFs), which regularly return to a specific location between foraging trips to feed young, store food, or rest, and thus face spatial constraints on foraging (Orians and Pearson 1979), and roaming foragers, a term we use for all non-CPFs. CPFs prefer foraging habitat near their central place, because, when travel time between the central site and the prey resource increases, their net energy gain decreases (Andersson 1978). For both CPFs and roaming foragers, efficiency is determined by the trade-offs between energy expenditures and gains (Shoji et al. 2016). Individuals may further optimize their foraging efficiency by concentrating on a specific prey type or the exploitation of a specific habitat. In stable environments, specialization in foraging strategies can be highly advantageous as individuals decrease search and handling costs, and reduce their niche overlap with other individuals, thus minimizing competition (Bolnick et al. 2003). A potential cost of specialization is that individuals may lack the flexibility to respond to environmental change (Bolnick et al. 2003; McIntyre et al. 2017). Within the light of rapid environmental change as a result of anthropogenic activities, behavioral plasticity in foraging behavior becomes particularly important. Climate change may affect top predators' geographic ranges and energy balance by altering the distribution and abundance of prey populations (MacLeod 2009; Hazen et al. 2013). Additionally, food resources may change at the local scale due to other anthropogenic influences. Local depletion and competition with fisheries can be regarded as general examples of the latter (Lidgard et al. 2014; Cronin et al. 2016). A topical issue is the future European Union ban on fisheries discards, currently providing a major resource for a wide range of seabird species (Garthe et al. 1996; Furness 2003; Votier et al. 2010, 2013; Bicknell et al. 2013; Krüger et al. 2017).

Specialization may require specific foraging behaviors (Patrick and Weimerskirch 2014). Single individuals may apply multiple foraging strategies or only a single one, or they may temporarily switch between strategies. When individuals use different foraging strategies, their choice may depend on a range of intrinsic and extrinsic factors (Patrick et al. 2013; Camphuysen et al. 2015). These factors are not mutually exclusive, as the underlying processes influence each other notably. As such, it is difficult to identify the causal effects of each of these factors separately. Therefore, a multifactorial approach is required to investigate their influence on foraging ecology. Integrating multiple types of data at different scales enhances our understanding of a predator's foraging behavior as well as the circumstances that lead to foraging success, as these can differ not only between and within species, but even within individuals depending on the conditions (Austin et al. 2006b; Watanabe and Takahashi 2013; McIntyre et al. 2017).

Intrinsic factors can strongly influence foraging efficiency. One of these factors is age or experience. It is generally

assumed that older individuals have learned to improve their energy gain and lower their effort per feeding attempt, as illustrated in the Caspian Gull *Larus cachinnans* (Skórka and Wójcik 2008). Another, more frequently observed defining intrinsic factor of foraging efficiency is sex, which can be observed in many taxa as a possible mechanism to reduce intra-specific competition. Sexually distinct foraging strategies were observed, amongst others, in lesser black-backed gulls *Larus fuscus* and harbor seals *Phoca vitulina* (Camphuysen et al. 2015; Wilson et al. 2015b). A healthy body condition is also vital for efficient foraging. African penguins in low body condition after an energy-demanding breeding season may have difficulties in gaining enough fat reserves to molt, and consequently forage less efficiently as feather quality deteriorates, eventually leading to starvation (Crawford et al. 2011). Lastly, brood demand is also an important factor. In general, when offspring is present, net energy demand is higher, which will affect parental feeding strategies (Pinaud et al. 2005; O'Dwyer et al. 2007; Rishworth et al. 2014; Shoji et al. 2015). Additionally, the increasing energetic demands of developing progeny may make it even harder to deliver sufficient food as the breeding season progresses.

Movement, hence foraging ecology, is also significantly determined by extrinsic factors, such as prey distribution and availability, environmental features, intra- and interspecific competition, and the presence of anthropogenic food sources (Lewis et al. 2001; Grémillet et al. 2004; Biuw et al. 2007; Dragon et al. 2010; Labrousse et al. 2015). For the latter, fisheries discards are one of the most important drivers of seabird distributions (Garthe et al. 1996; Bartumeus et al. 2010; Patrick et al. 2015; Krüger et al. 2017), while recreational fisheries, offshore wind farms, and terrestrial refuse tips can play a role too (Griffiths et al. 2004). Environmental factors, such as sea surface temperature (SST), oceanographic features, sea ice conditions, and atmospheric conditions, are also highly important, since they are the main drivers for prey distribution and availability (Tremblay et al. 2009; Labrousse et al. 2015; Cox et al. 2016). For instance, a study using satellite-linked dive recorders revealed that the distance to the continental shelf break and sea ice concentration were the most important drivers of crabeater seal's *Lobodon carcinophaga* distribution in the Weddell Sea in the summer of 1998 (Fig. 3) (Nachtsheim et al. 2017). Both their distribution and foraging behavior aligned well with the life

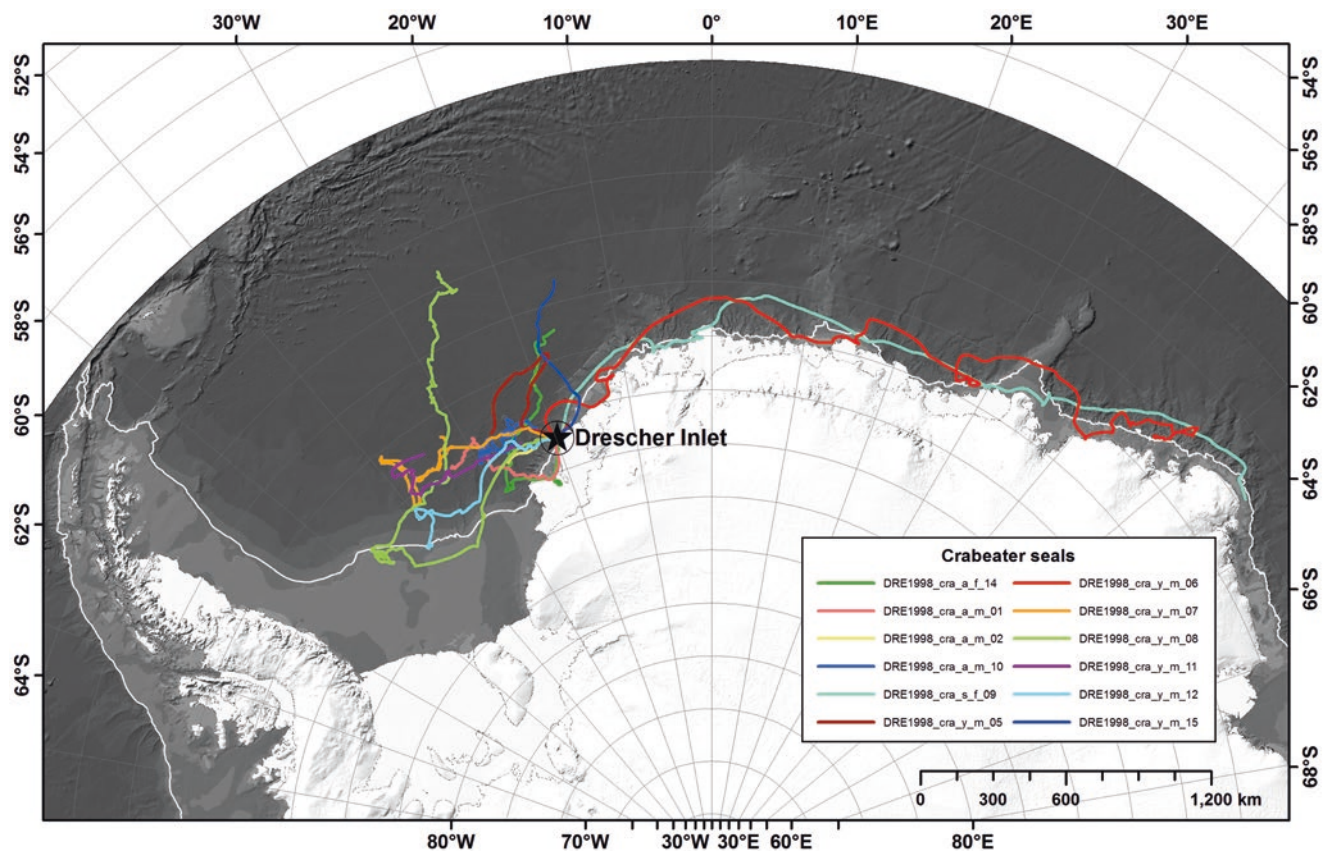


Fig. 3 Tracks of 12 crabeater seals *Lobodon carcinophaga* in the Weddell Sea dispersing from the tagging location in the Drescher Inlet (star). Each colored line represents an individual track. Bathymetry is indicated by various shades of grey (light = shallow, dark = deep). The

white line shows the 1000 m isobath defined as continental shelf break. Ten seals explored the eastern and central Weddell Sea, while two animals moved far eastwards up to 45°E along the coast. (Reproduced from Nachtsheim et al. (2017) (CC-BY 4.0))

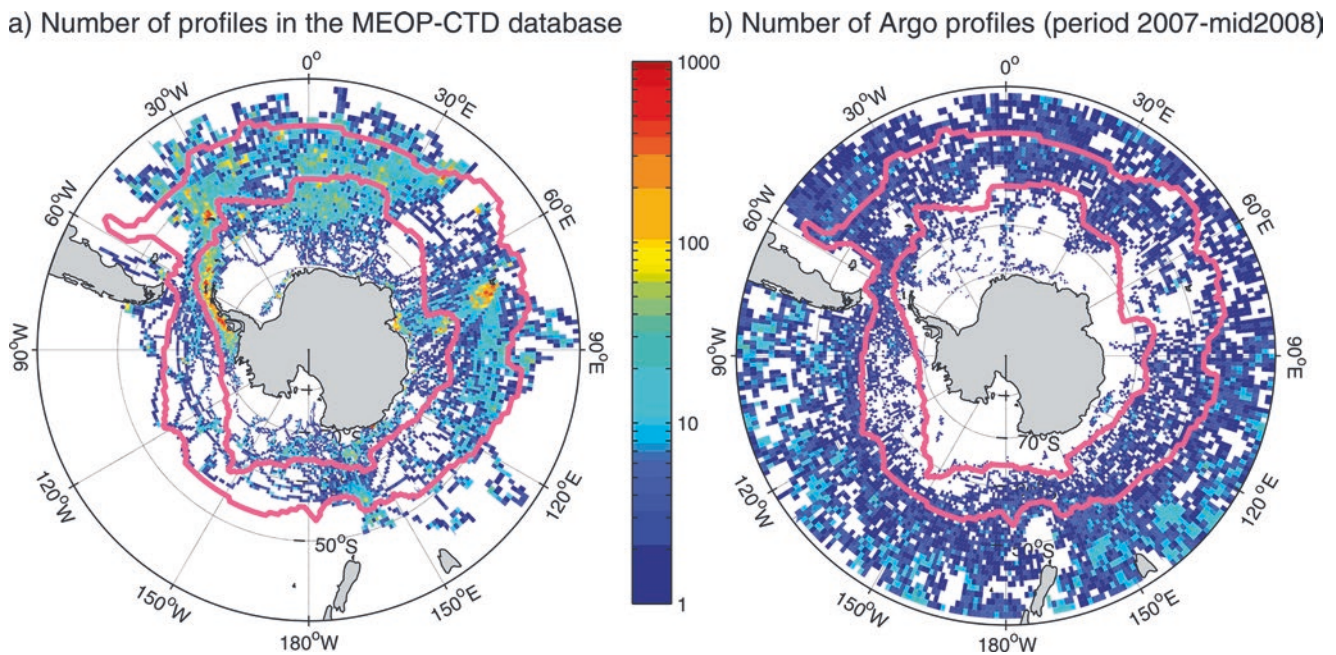


Fig. 4 Number of temperature-salinity profiles of (a) seal-derived data from the Marine mammal Exploring the Oceans Pole to Pole (MEOP) program, and (b) Argo float profiles (see Gould et al. (2004) for more details). Superimposed in pink are the Antarctic Circumpolar Current

borders. This figure shows clearly how animal-borne devices can complement traditional observations, particularly at places where access is limited (e.g., due to sea ice). (Reproduced from Roquet et al. (2013) (CC-BY 4.0))

history of Antarctic krill *Euphausia superba*, their preferred prey (Nachtsheim et al. 2017).

Oceanographic and environmental data are readily available online, with the NOAA and the Copernicus program being the largest providers (Copernicus 2017; NOAA 2017), or from the animal-borne devices themselves. The latter sometimes provide physical oceanographic data from areas that cannot be sampled using other conventional approaches (Fig. 4) (Årthun et al. 2012; Roquet et al. 2013). Following this further, detailed oceanographic data could provide information about how marine top predators will probably respond to climatic change (Costa et al. 2010a; McIntyre et al. 2011). For instance, CTD satellite tags deployed on southern elephant seals *Mirounga leonina*, crabeater seals, and Weddell seals in the Western Antarctic Peninsula have shown that these three species occupy very different habitat types, hence trophic niches, within this region, and will therefore be affected differently by climate change (Costa et al. 2010a). Additionally, many marine top predators feed at depth and several studies have demonstrated the association between oceanographic features of the water column and predator's diving behavior (Fig. 5) (Biuw et al. 2010; Heerah et al. 2013; Guinet et al. 2014). Quantifying foraging effort at depth, based on the detection of changes in diving behavior, can relate the actual behavior of the predator in three dimensions to the heterogeneous environment they

respond to (Heerah et al. 2016). For southern elephant seals, the switch from transit to hunting mode was associated with colder water temperatures, relatively short dive bottom time and rapid descent rates (Bestley et al. 2013). As mentioned before, foraging efficiency should be investigated by looking at both horizontal and vertical movements, as this can reveal interesting inter-specific behavioral differences, for example, resource partitioning through different dive behavior in closely related predator species (Wilson 2010; Villegas-Amtmann et al. 2013; Bestley et al. 2015). Information on foraging effort, which is, among others and depending on the species, determined by the number of dives, dive duration, vertical and horizontal travel distance, and the time a foraging trip takes, can be readily derived from conventional tracking data (Boyd et al. 2014). However, the study of movement ecology is lifted to another level by using tri-axial accelerometers combined with GPS loggers, which are able to provide high-resolution behavioral data on the level of decision-making (Wilson et al. 2008; Watanabe and Takahashi 2013; Bidder et al. 2014). For example, by linking GPS and accelerometer data of lesser black-backed gulls, a recent study was able to provide insight into how a flight generalist (i.e., a bird who has the ability to radically alter its flight mode in response to external conditions) can reduce the energetic cost of movement (Shamoun-Baranes et al. 2016).

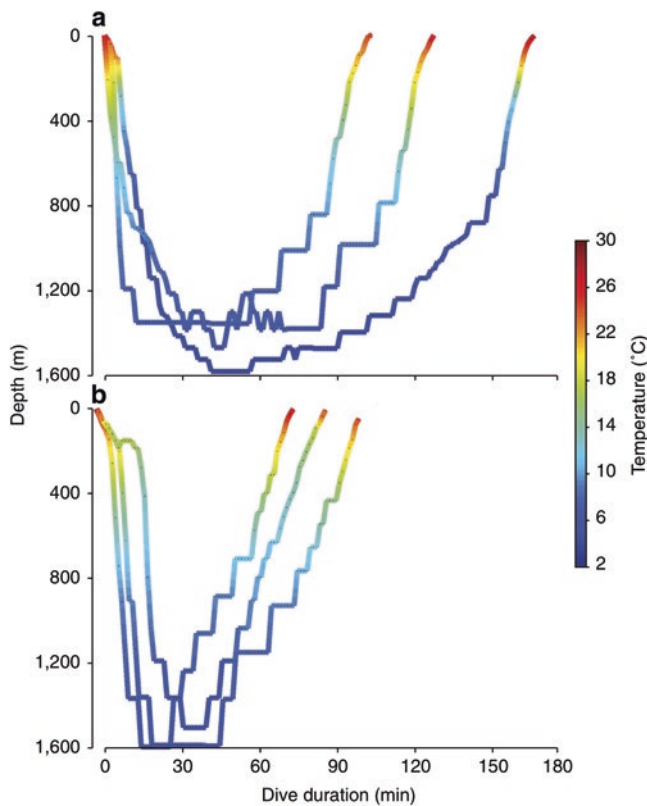


Fig. 5 Depth and temperature profiles from Chilean devil rays *Mobula tarapacana*, tagged with pop-up satellite archival transmitters during (a) daylight hours (6 a.m. – 6 p.m.), and (b) night-time hours (6 p.m. – 6 a.m.). These profiles show that devil rays are among the deepest-diving animals, especially at night, albeit shorter in time. (Reproduced from Thorrold et al. (2014) (CC-BY 4.0))

Hydroacoustic surveys can reveal the link between foraging habitat and the distribution of prey, and provide more insight into different aspects of foraging behavior. Although one might assume that predictable prey abundance determines foraging habitats, accessibility is an important factor too, especially for surface foragers, as is the case for Peruvian booby *Sula variegata* and guanay cormorant *Phalacrocorax bougainvilliorum* (Boyd et al. 2015). A specific foraging strategy may be influenced by several factors. Foraging range may be determined by the overall distribution of prey, the predators' ability to detect prey may be influenced by the distance between prey patches, and prey capture efficiency may be affected by individual patch characteristics (Carroll et al. 2017). Little penguins *Eudyptula minor* caught more prey where aggregations were relatively dense, compact and shallow (Carroll et al. 2017). Another study revealed that masked boobies *Sula dactylatra* from Phillip Island, Australia, showed a trade-off between strong foraging site fidelity around their colony where less prey is available, and more distant foraging trips with less predictable but larger prey patches (Sommerfeld et al. 2015). Temporal differences in foraging behavior can also be observed. For instance, dive

depths of most northern elephant seal *Mirounga angustirostris* showed a clear diel pattern, consistent with targeting vertically migrating prey species (Fig. 5) (Robinson et al. 2012). Pursuing this further by deploying the hydroacoustic devices directly on large marine mammals, a recently developed sonar tag is able to record acoustic backscatter in front of a diving predator, and as such, quantify their prey field (Lawson et al. 2015).

By combining bio-telemetry data with other fine-scale measurements, such as vessel monitoring systems (VMS), we further enhance our multifactorial approach. These VMS are used globally, and since 2005, all fishing vessels in the European Union longer than 15 m are required to transmit their position through VMS. By looking at the fine-scale overlap between seabirds and fisheries, the ecological effect of foraging in association with fishing vessels can be determined, including carry-over effects, as not all species respond in the same way. For instance, foraging royal albatrosses *Diomedea sanfordi* showed low rates of overlap with fisheries and it provided them with no ecological advantage (Sugishita et al. 2015). Conversely, fisheries discards are an important part of lesser black-backed gulls' diet in the North Sea (Garthe et al. 1996; Sommerfeld et al. 2016). This is also the case for southern giant petrels *Macronectes giganteus*, whose non-breeding distribution largely overlap with zones of high fishing intensity off the coast of South America (Krüger et al. 2017). Northern gannets *Morus bassanus*, on the other hand, showed clear individual differences in discard consumption and foraging behavior (Votier et al. 2010).

To date, as a result of this multifactorial approach, marine scientists encounter new challenges in coordinating and analyzing high resolution datasets gathered across large spatial scales, (e.g., ocean basins). These challenges can only be overcome by means of multidisciplinary collaborations between biologists, oceanographers, statisticians and engineers (Hussey et al. 2015; Hays et al. 2016). Such collaborations can foster the development of new, innovative and cost-effective bio-telemetry approaches and promote cutting-edge analytical techniques.

Migration

Migration is defined as long-distance movement of individuals, with a temporal recurrence. Some marine top predators move across vast expanses of the marine environment to acquire spatiotemporal variable resources several times a year, annually or across multiple years. One of the most important uses of bio-telemetry is to identify migration routes and their overlap with anthropogenic features. This application is extremely useful for conservation purposes, and will, therefore, be discussed in more detail in section “Conservation”.

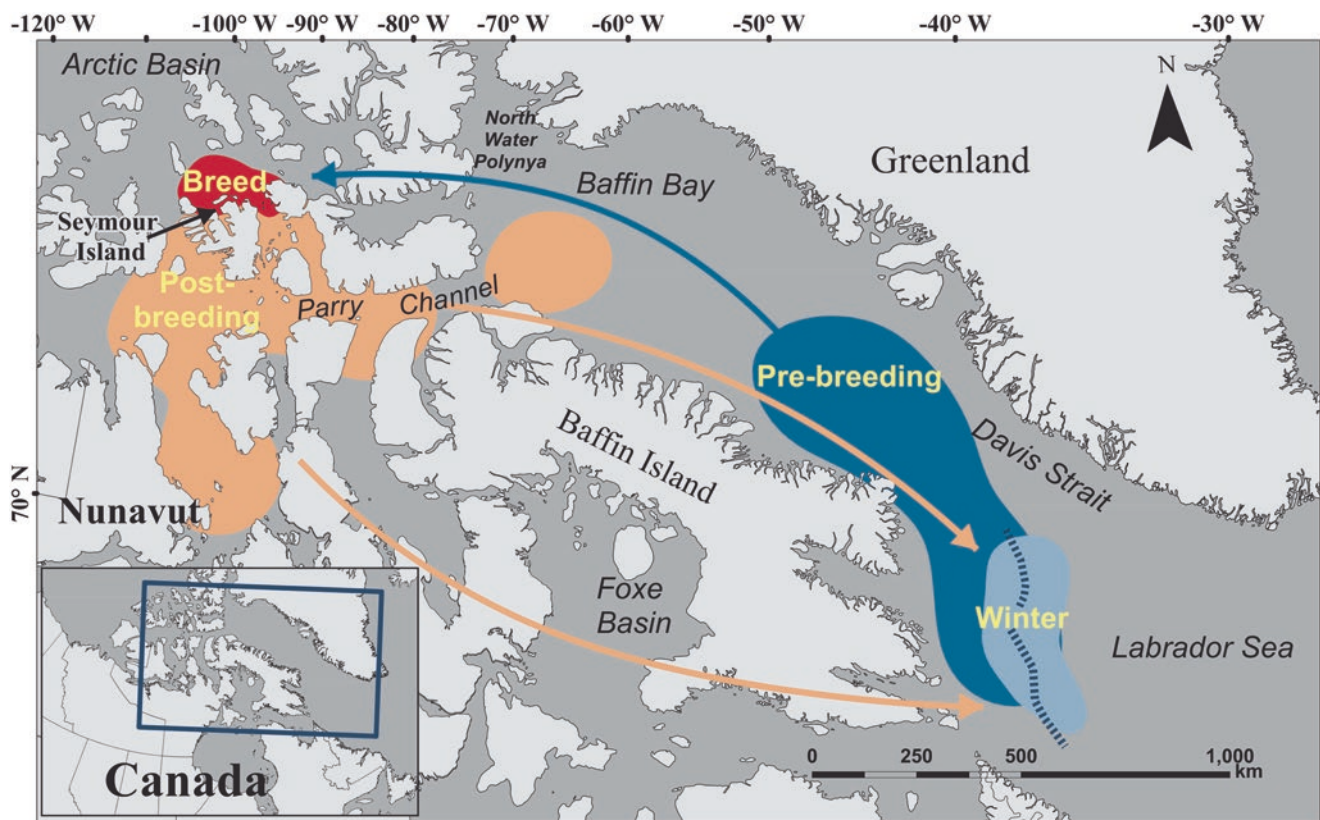


Fig. 6 Annual distribution and migration routes of the ivory gull *Pagophila eburnea* in the Canadian Arctic. The 50% kernels represent the general distribution during breeding (red), post-breeding (orange), winter (light blue) and pre-breeding seasons (dark blue). General direction of post-breeding migration is indicated by the orange arrows and

direction of pre-breeding migration is indicated by the blue arrow. The dashed line through the winter kernel represents a composite of the typical edge of the pack ice, 2010–2013 (December through April). (Reproduced from Spencer et al. (2014) (CC-BY 4.0))

Various spatiotemporal scales of movement are tied to different life-history functions (Bestley et al. 2009; Block et al. 2011; Putman et al. 2014). Many top predators have evolved life histories that involve travelling large distances between predator-free breeding colonies and areas with large prey abundance (Corkeron and Connor 1999; Costa et al. 2012; Weimerskirch et al. 2012). For example, chinook salmon *Oncorhynchus tshawytscha* hatch in freshwater, then migrate to the sea where they spend most of their adult life, to ultimately migrate back to freshwater where they spawn and die (Quinn 2005). Long-term observations of these predators' movements provide not only information on the spatial extent of their populations and potential rates of exchange among them, but also expose detailed characteristics of the habitats they use and clues to their navigation abilities (Block et al. 2011; Costa et al. 2012). Bio-telemetry represents a crucial approach to gain this valuable knowledge on migration routes and patterns.

Environmental features undoubtedly influence migration. Analysis of migratory behavior of ivory gulls *Pagophila eburnea* revealed considerable individual variation of post-breeding migratory route selection, and suggested that the

timing of formation/recession and extent of sea ice could play an important role in this (Fig. 6) (Spencer et al. 2014). González-Solís et al. (2009) showed that winds are a major determinant of the migratory routes of three shearwater species, the Manx *Puffinus puffinus*, the Cory's *Calonectris borealis*, and the Cape Verde *Calonectris edwardsii*.

For some species, migration appears to evolve through social learning, for instance in humpback whales *Megaptera novaeangliae* (Weinrich 1998). However, for many groups, the processes that shape migration routes remain enigmatic, despite the fact that satellite tracking can detail many migratory facets (Block et al. 2011). A particular challenge lies in explaining how juvenile animals, with no prior migratory experience, are able to locate specific oceanic feeding habitats (Lohmann et al. 2008; Gould and Gould 2012). One study showed that juvenile chinook salmon respond to magnetic fields at the latitudinal extremes of their ocean range, which lead towards their marine feeding grounds (Putman et al. 2014). The authors concluded that fish may use a combination of magnetic intensity and inclination angle to assess their geographic location (Putman et al. 2014). Whether this is the case for all migratory species remains to be deter-

mined. Studies on navigational ability in migratory seabirds showed that there can be many potential cues, for instance, olfactory, hydrodynamic, sky polarization, sun and star positions (Muheim et al. 2006; Lohmann et al. 2008; Gagliardo et al. 2013). However, detecting the geomagnetic field was, for example, in black-browed albatross *Diomedea melanophrys* not one of them (Bonadonna et al. 2003). As such, we need to remind ourselves that experimental studies are never able to look at the full spectrum of natural conditions that occur during migration and, therefore, cannot eliminate particular cues completely.

Bio-telemetry already enables scientists to study the migratory routes of marine top predators in detail. However, at present, many questions remain, especially concerning the drivers and the processes that shape migration. This opens up interesting opportunities for future research and invites scientists to think outside the box to tackle current practical problems. Again, inter- and multidisciplinary collaborations could provide solutions.

Challenges and Ethics of Bio-telemetry

Attaching a device to an animal necessarily raises ethical questions (Wilson and McMahon 2006), which still remain largely understudied (Vandenabeele et al. 2011). Is it appropriate to equip an animal with an instrument that may impact its natural behavior or may even affect its breeding success and survival? What is regarded as acceptable practice? Does the acquisition of knowledge outweigh the potential adverse effects of a tag? In this section we will first highlight, separately for each top predator group, the difficulties of attaching a tag to an animal, and then list the known tag effects for each group. Finally, we mention approaches for improvements in the field of bio-telemetry and give recommendations from the perspective of animal welfare.

First of all, it is far from easy to equip an animal with a tag. It usually involves capturing and physically restraining the animal for a certain period of time. Sometimes even chemical immobilization is necessary, particularly in large pinnipeds (Gales and Mattlin 1998; Bornemann et al. 2013). The capture itself causes short-term stress for the animal, but does not usually have long-term consequences (Baker and Johanos 2002; McMahon et al. 2005; Blanchet et al. 2014). The tag attachment techniques vary considerably between, and even within, the different taxa, but can generally be divided into invasive and non-invasive attachments.

Most bio-telemetry devices for pinnipeds are non-invasive and commonly glued to the fur by using epoxy resin (Fedak et al. 1983; Lowther et al. 2013; Nachtsheim et al. 2017), or more recently, superglue (Cronin et al. 2016). The devices are either actively recovered or remain on the animal for up to one year until they fall off during the next annual molt.

The attachment procedure itself, i.e., gluing the device to the fur, can cause small superficial abrasions or even lesions in a few cases, however, these injuries heal completely soon after the tag has been shed (Field et al. 2012). There is evidence that the placement of particularly large and bulky tags increases the hydrodynamic drag, potentially causing elevated metabolic costs and leading to behavioral changes in the short term (Walker and Boveng 1995; Hazekamp et al. 2010; Blanchet et al. 2014; Maresh et al. 2015; Rosen et al. 2017). However, long-term studies on the mass gain and survival of seals could not find adverse effects of bio-telemetry devices (Baker and Johanos 2002; McMahon et al. 2008; Mazzaro and Dunn 2010).

The attachment of non-invasive telemetry devices on cetaceans has proven to be challenging. The smooth and rapidly regenerating skin of whales, dolphins and porpoises hampers the attachment of external tags. A commonly used non-invasive method is deploying tags, such as DTAGs, with suction cups (Fig. 2f). These devices usually stay on the animal for a few hours or days (Aguilar Soto et al. 2008; Wisniewska et al. 2016). This method is obviously not sufficient to study large-scale migration patterns and hence, invasive tags are frequently used on cetaceans. The tag is either anchored in the blubber or muscle tissue, especially on large whales and dolphins (Weller 2008; Hauser et al. 2010; Reisinger et al. 2014; Gendron et al. 2015), or pinned through the dorsal fin of small dolphins and porpoises (Irvine et al. 1982; Teilmann et al. 2007; Balmer et al. 2014). While the former can be remotely deployed (e.g., using a crossbow), the latter requires physically capturing the animals. The wound-healing and long-term effects of invasive tagging have rarely been studied, particularly due to the elusive nature of most cetaceans. Although swellings, cavities, and scars are frequently observed at the tag site in large whales, even over a period of multiple years, these injuries, however, had no impact on the body condition, overall health or reproductive success of the animals (Best and Mate 2007; Mate et al. 2007; Weller 2008; Gendron et al. 2015; Norman et al. 2017). In small cetaceans, dorsal fin-mounted tags can fall off due to corrosion of the pins. In some cases, mild inflammatory responses have been reported around the pin holes, but they usually heal without complication, resulting in the formation of scar tissue (Sonne et al. 2012; Heide-Jørgensen et al. 2017). More severe is the migration of dorsal fin tags through the tissue over time due to the constant hydrodynamic drag, ultimately leading to tag loss and fin damage (Irvine et al. 1982; Martin et al. 2006; Balmer et al. 2014). This raises the concern of whether or not such tags negatively affect the natural behavior of small cetaceans (van der Hoop et al. 2014). However, on the long term, body condition, survival rates and reproductive success of tagged small cetaceans were not affected (Martin et al. 2006; Heide-Jørgensen et al. 2017).



Fig. 7 Different steps of deploying a video camera logger on a Magellanic penguin *Spheniscus magellanicus*. (a) First, a template is placed on the back of the penguin and Tesa® tape is placed in layers between the feathers. (b) The logger is placed on the back and the tape

is wrapped tightly around the device before releasing the penguin back to the nest. (c) After the foraging trip, the tape is removed. (Photos used with permission from William Kay)

Similar problems occur when tagging sharks or other elasmobranchs. Due to their placoid scale epidermis, a non-invasive attachment procedure is almost impossible (Hammerschlag et al. 2011). Most PATs are forcefully implanted into the well-developed dorsal musculature, which reduces the probability of premature release (Carlson et al. 2010; Campana et al. 2011; Hammerschlag et al. 2011). As with dolphins, satellite transmitters are often attached to the shark's dorsal fin using bolts and pins, which can be a source of infection or lead to fin damage (Meyer et al. 2010; Hammerschlag et al. 2011; Jewell et al. 2011). Therefore, new non-invasive attachment methods are currently being tested and further developed. For example, a clamp system was successfully used to attach a combined accelerometer and magnetometer to the second dorsal fin of a whale shark (Fig. 1) (Gleiss et al. 2009; Williams et al. 2017).

Most deployments on seabirds involve the attachment of non-invasive bio-telemetry devices. Most commonly the tags are taped or glued to the back or tail feathers (Fig. 7), carried in a harness or attached to the leg in the form of a band ring (Wilson 1997; Phillips et al. 2003; Shaffer et al. 2005). Depending on the target species, certain attachment methods and locations are discouraged due to known adverse effects. For instance, the use of harnesses may have detrimental effects on petrels and albatrosses, which is why taping to the back feathers is the preferred method (Phillips et al. 2003; Weimerskirch et al. 2007; Mallory and Gilbert 2008). In contrast to other top predators, the effect of tagging has been relatively well studied in seabirds—possibly due to their small size and alarmingly large tags in the past (Wilson et al. 1986). Adult mass, breeding productivity and success, as well as foraging behavior are seemingly not altered and do not differ between tagged and untagged individuals (Phillips et al. 2003; Votier et al. 2004; Chivers et al. 2015; Thaxter et al. 2016). However, for the great skua *Stercorarius skua*, the over-winter return rate as a measure of survival were substantially lower for tagged than for untagged birds, whereas for the sympatric lesser black-backed gull neither short nor

long term effects were reported (Thaxter et al. 2016). Thus, even morphologically similar species can react quite differently to the same animal-borne device. Most of the problems which occur can be attributed to the size of the device, which is traditionally aimed to be below 5% of the body weight of the bird (Cochran 1980; Phillips et al. 2003), but also to the shape, position and attachment method (Bannasch et al. 1994; Vandenabeele et al. 2014). This extra weight means an increase in energy expenditure during flight of approximately 5%, without taking into account the increase in drag (Vandenabeele et al. 2012). Thus, large tags can have an influence on the activity budget of seabirds, leading to a reduction of time spent flying (Chivers et al. 2015). Even though humans' movement ecology is somewhat different from that of other animals, we can use the following example to illustrate the possible influence of a tags' weight. If an average sized human with a body weight of 80 kg was equipped with a device that makes up 5% of his body weight, he would carry an extra 4 kg—this is equal the weight of two six packs of canned drinks. If the device was only 1% of the body weight, the extra weight would constitute 800 g, which is comparable to a small laptop. Since most studies define 3–5% of the individual's body weight as acceptable practice, but do not take into account the substantial extra energetic costs, we recommend reducing the tag weight load to well below these values, as suggested by Phillips et al. (2003) and Vandenabeele et al. (2012), optimally below 1% of the body weight.

The tagging of charismatic marine top predators still remains a controversial topic, also within the scientific community (Hazekamp et al. 2010; van der Hoop et al. 2014). However, no adverse long-term effects of bio-telemetry devices were reported for the vast majority of study species. Both the quality and quantity of bio-telemetry data are otherwise impossible to obtain, and tagging studies can immensely enhance our understanding of movements and behavior of marine predators, leading to informed management decisions. These facts advocate the right of bio-telemetry exis-

tence (McMahon et al. 2012). Nevertheless, there are various valid points in the light of animal welfare that are of concern and must be addressed appropriately. In addition to the increase of drag caused by the attachment of an external device, the extra weight load still represents a major issue for many marine predators.

We believe that, as a further improvement, the scientific community should foster the development of new technologies and the on-going miniaturization of tags. To reduce hydrodynamic drag, Computational Fluid Dynamics (CFD) has proven to be a crucial tool to assess and improve the design of bio-telemetry devices (Pavlov et al. 2007; Balmer et al. 2014). In addition, CFD minimizes the risk of injury and other potentially adverse effects. Furthermore, potential capture and attachment methods for different animal groups should be reviewed and discussed among researchers. It is evident that tag effects must be more thoroughly investigated, and in particular the focus should be directed towards metabolic costs and fitness consequences (McIntyre 2015). It must not be forgotten that we, as scientists, have the responsibility to ensure the wellbeing of the animal. This is not only relevant from an animal welfare viewpoint, but also from a scientific position, as we aim to record and understand the natural behavior of animals in their environment.

Conservation

The marine environment is predicted to face marked changes by the year 2040 (Brierley and Kingsford 2009), so there is no time to lose. The current challenges require multidisciplinary collaboration to develop effective strategies that rely on an improved understanding of the threat that climate change imposes on species, and the way that it interacts with their natural coping mechanisms (Dawson et al. 2011). Telemetry-derived data have a tremendous potential to inform resource management and conservation, but unfortunately, relatively few examples of their application exist (Wilson et al. 2015a). The financial cost of collecting telemetry data is relatively high, which makes it essential to critically evaluate the conservation benefit of the currently used strategies (McGowan et al. 2017).

One of these strategies, is to combine high resolution bio-telemetry data with environmental data and data on anthropogenic activities to build individual-based models, with the aim of predicting habitat use in the (near) future (Grimm et al. 1999; Stillman et al. 2003; Bestley et al. 2013; Stillman et al. 2015; van der Vaart et al. 2016). In these models, different scenarios of anticipated anthropogenically-driven environmental change can be simulated. Once predictive models have been implemented, the outcome can be used for conservation purposes. One extensive study found that modelled physical changes under the Intergovernmental Panel on

Climate Change A2 scenario predict increased species overlap and a potential for niche compression across the North Pacific (Hazen et al. 2013). For species that are already under threat, such changes could exacerbate population declines or inhibit recovery. These models can undoubtedly be used, among other applications, to design marine protected areas (MPAs), which can be a powerful tool for attenuating anthropogenic threats. Several studies have already conducted extensive tracking programs on seabirds to identify foraging hotspots, and used those spatial patterns to inform MPA design (Le Corre et al. 2012; Thaxter et al. 2012; Lascelles et al. 2016).

However, to ensure that these MPAs are highly efficient, adaptive and dynamic management is necessary (Agardy et al. 2003; Maxwell et al. 2015). At present, the majority of marine management approaches (e.g., quota setting, total allowable catches, and MPAs) are relatively static in contrast to the ocean itself and the majority of ocean uses (Agardy 1994; Hyrenbach et al. 2000; Crowder and Norse 2008). Some marine predators are highly mobile and travel great distances over different temporal scales, as is the case, for example, for Arctic terns *Sterna paradisaea* (Egevang et al. 2010), and gray whales *Eschrichtius robustus* (Mate et al. 2015). Others, like Atlantic bluefin tuna *Thunnus thynnus* show complex spatial dynamics, (e.g., homing) and population structure (e.g., several subpopulations of different sizes) (Fromentin and Lopuszanski 2014). To effectively manage this highly dynamic marine system, conservation measures must become more flexible in space and time in the same way as both the environment and the resource users have (Hyrenbach et al. 2000).

A robust understanding of the spatiotemporal distribution and ecology of migratory species is necessary for successful conservation. Conditions experienced during the non-breeding period may have carry-over effects on breeding performance, which in turn may affect population dynamics (Harrison et al. 2011). Consequently, the anthropogenic impact outside the breeding season also needs to be taken into consideration when making management decisions. Conservation efforts can be targeted at areas where the majority of the population congregate, as is the case for little auks *Alle alle* at two key areas located in the Greenland Sea and off Newfoundland (Fort et al. 2013).

Fast-acquisition satellite telemetry can provide evidence-based information on individual animal movements to delineate interspecific relationships, and can be used to increase the efficacy of conservation planning (Gredzens et al. 2014). Complimentary co-management, customized for each location, would be advisable when different species use similar habitats (Gredzens et al. 2014). By including data from different species, we obtain more information about commensal foraging associations or multispecies feeding flocks and intra- and interspecific interactions (Barlow et al. 2002; Elliott

et al. 2010; Lidgard et al. 2012). Areas of predator overlap often occur in regions with high ecological importance, and are therefore useful in designing MPA boundaries. Raymond et al. (2015) used combined tracking data of six species (Adélie *Pygoscelis adeliae* and emperor *Aptenodytes forsteri* penguins, light-mantled albatross *Phoebastria palpebrata*, Antarctic fur seals, southern elephant seals, and Weddell seals) to identify areas of particular ecological significance. These areas were characterized by their proximity to breeding colonies and by sea-ice dynamics, and were therefore considered in the MPA proposal for East Antarctica (Raymond et al. 2015). A similar study used tracking data from 14 different predator species to identify their foraging habitats around the Prince Edward Islands (Reisinger et al. 2018). Amongst others, the results of this study can support the conservation and management of Subantarctic ecosystems and the marine predators they sustain (Reisinger et al. 2018).

Another effective aspect of protective measures can be to establish corridors that link the breeding and foraging grounds of migratory species. One study used a geospatial approach to design a corridor along the north-west coast of Australia that incorporates 11 existing MPAs and overlaps with humpback whale migratory tracks (Pendoley et al. 2014). The study concluded that the proposed network would be beneficial for at least 20 other marine vertebrates, although not all at the same temporal scale (Pendoley et al. 2014).

Establishing pelagic MPAs for oceanic species is another possible measure in adaptive and dynamic management. Bio-telemetry can be a useful tool to acknowledge their necessity and to determine their flexible boundaries (Game et al. 2009). For instance, tiger sharks *Galeocerdo cuvier* were considered to be a reef-associated coastal species, but bio-telemetry actually showed that they display directional movements across ocean basins (Holland et al. 1999; Lowe et al. 2006; Heithaus et al. 2007). Another study determined the primary migratory corridor of gray whales, and concluded that they face a wider range of industrial activities and developments than previously thought (Ford et al. 2012). Protecting far-ranging species can present a major challenge for spatial management, but they are not always equally vulnerable over their entire range (Game et al. 2009). These species often exhibit increased vulnerability in a small number of demographically critical areas, as is the case in wandering albatrosses *Diomedea exulans* (Weimerskirch et al. 2006). Other species potentially overlap with different human activities during each stage of their migration (e.g., humpback whales) (Rosenbaum et al. 2014). This example highlights the need for adaptive and dynamic management once more, for it would be economically advisable to move the pelagic MPA in space and time synchronously with the whales' migration.

Tracking data can also identify high-use areas and coordinate policy actions that mitigate anthropogenic risks such as those associated with ship strikes, offshore wind farms, oil

spills, or bycatch. For instance, manta ray *Manta birostris* aggregations coincide with some of the busiest shipping lanes (Halpern et al. 2008). This, together with the expansion of megafauna tourism industry, could have an impact on their population numbers (Berman-Kowalewski et al. 2010). However, despite the fact that manta rays forage over large spatial scales (~100 km) far offshore, they also show high site fidelity and associate with frontal zones (Graham et al. 2012). This knowledge could be used to establish new dynamically protected areas overlaying the frontal region (Graham et al. 2012). Bio-telemetry can also be used to estimate seabirds' vulnerability to offshore wind farms by determining activity-specific and spatially explicit flight heights and collision risks (Cleasby et al. 2015). Another example revealed that 25% of the North American northern gannet populations migrate annually to the Gulf of Mexico and suffered from severe oiling in the aftermath of the Deepwater Horizon explosion (Montevecchi et al. 2012a, b). These findings contrasted discernibly with available mark-recapture data, and showed that tracking research can be extremely useful when little information on animal distribution in pollution zones is available (Montevecchi et al. 2012a). Tracking data combined with survival and reproduction measurements from their colonies can reveal many possible repercussions of marine pollution, and inform management about conservation concerns (Montevecchi et al. 2012a). Another widespread anthropogenic problem is air-breathing megafauna bycatch. This bycatch intensity varies substantially within and between catch gear and regions (Lewison et al. 2014). Tracking data of marine predators can be overlapped with fisheries data for a dynamic management approach, which could minimize bycatch. For example, an improved understanding of the horizontal and vertical spatiotemporal distribution of North Pacific albatrosses in relation to pelagic fisheries could improve management protocols (e.g., time-area closures and gear mitigation), to reduce the bycatch of these endangered and threatened species (Costa et al. 2012). Lastly, one of the most interesting applications to date is the automated, near-real-time density prediction tool for Eastern North Pacific blue whales *Balaenoptera musculus*, which enables a more accurate examination of the year-round spatiotemporal overlap of the whales with potentially harmful human activities, such as shipping (Hazen et al. 2016). This study identified high interannual variability in occurrence, emphasizing again the benefit of a dynamic approach (Hazen et al. 2016). Tools like this allow a finer-scale management, which is more economically feasible and socially acceptable (Hazen et al. 2016).

Undoubtedly, there is a necessity for innovative and interdisciplinary approaches, monitoring programs and research initiatives to inform decision makers (Cooke 2008), but it is not only those people who need to be informed. In light of current rapid environmental changes, it is also imperative to engage the general public, and to

gain their support for conservation. One of the biggest advantages of telemetry is its usefulness in outreach, as this data can be presented in a highly attractive way. However, it is not only their support that is vital. Web-based citizen science projects are a prime example of how volunteers can help process the enormous amount of telemetry-derived data (e.g., through the Zooniverse portal with links to Seabirdwatch, Weddell Seal Count, Snapshots at Sea, Penguin Watch, etc.) (Zooniverse 2017). In general, results from bio-telemetry studies on marine top predators can inform local, regional, and international conservation management, and the general public, which in turn, could trigger actions to mitigate potential anthropogenic threats. To be effective, these management measures should be highly flexible according to the very dynamic nature of marine ecosystems.

Conclusion

It is evident that tagging marine top predators with bio-telemetry devices has an enormous value – not only for studying their movement ecology but also for resolving marine conservation issues. Data from these devices have already answered numerous fundamental questions, and will continue to do so in the future (Hays et al. 2016). The current rapid technological advances will certainly lead to an ever growing variety of new devices and methodological approaches. Nevertheless, animal welfare may not be overlooked. Although no negative long-term effects of bio-telemetry devices were reported for most species, there is still potential for improvements. Tag effects must be thoroughly assessed and the miniaturization of bio-telemetry devices must continue to ensure the wellbeing of tagged animals.

In conclusion, adaptive and dynamic management is necessary to guarantee healthy marine ecosystems and this can benefit substantially from monitoring top predators with bio-telemetry devices (Maxwell et al. 2015). However, regardless of the management approach, it is clear that multidisciplinary collaboration is key and sharing data is imperative, if conservation is to be successful (Cvitanovic et al. 2015). Additionally, scientists need new tools and frameworks to link animal telemetry-derived data to conservation and management, while maximizing the outcome of the global investment in bio-telemetry devices (McGowan et al. 2017). This will enable us to address the relevant key questions in top predator movement ecology—in conjunction with governments and society—and ultimately lead to effective conservation and management of marine ecosystems.

Appendix

This article is related to the YOUMARES 8 conference session no. 1: “Sentinels of the Sea: Ecology and Conservation of Marine Top Predators”. The original Call for Abstracts and the abstracts of the presentations within this session can be found in the appendix “Conference sessions and Abstracts”, chapter “6 Sentinels of the Sea: Ecology and Conservation of Marine Top Predators”, of this book.

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