SPECIAL ISSUE: CONSERVATION BEHAVIOUR

Animal Behaviour 120 (2016) 235–244

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Conservation Behaviour

Studying cetacean behaviour: new technological approaches and conservation applications

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ARTICLE INFO

Article history:
Received 16 September 2015
Initial acceptance 4 January 2016
Final acceptance 6 June 2016
Available online 13 August 2016
MS. number: SI-15-00799

Keywords:
behaviour
biologging
passive acoustics
population consequences
technology

Animal behaviour can provide valuable information for wildlife management and conservation. Studying the detailed behaviour of marine mammals involves challenges not faced by most animal behaviour researchers due to the size, mobility and lack of continuous visibility of these animals. We describe several methods developed by marine mammal scientists to study behaviour, primarily of cetaceans, focusing on technological advances: unmanned aerial systems (UAS), satellite-linked telemetry, passive acoustics and multisensor high-resolution acoustic recording tags. We then go on to explain how the data collected by these methods have contributed to and informed conservation actions. We focus on examples including: satellite data informing the interactions between cetaceans and offshore oil and gas development; passive acoustics used to track distributions of several species of cetaceans, including their movements near shipping lanes; and high-resolution acoustic recording tags used to document responses of cetaceans to anthropogenic activities. Finally, we discuss recent efforts to link animal behaviour to individual fitness and, particularly for behavioural disturbances, to population-level consequences, which can be helpful for informing conservation efforts. The infusion of technological advancements into studies of cetacean behaviour combined with emerging analytical techniques brings us to the next 20+ years of studying these animals. These developments will improve our capabilities in areas such as testing whether their behaviour adheres to traditional behavioural theory, and will certainly assist the guiding of conservation efforts.

Marine mammals are notoriously difficult to study, particularly with respect to detailed sampling of behaviour. Many of the techniques used by researchers studying terrestrial animal behaviour (Altmann, 1974) are simply not available to marine mammal scientists owing to the short periods that animals are observable at the surface and the lack of visibility when animals are below the surface for prolonged periods. Over the last 75 years though, engineers and marine mammal scientists have developed creative solutions for observing the behaviour of wild marine mammals, from modifying observational methods (Mann, 1999) to a host of technological innovations. From Scholander's (1940) use of manometric tubes to Pryor and Norris' (1991) 'seasickness machine', an underwater viewing pod attached to the hull of a small boat, and Kooyman's (1965) use of ordinary kitchen timers to measure and record depth, to researchers hanging cameras from small tethered aerostats (Nowacek, Wells, & Tyack, 2001), gaining observational windows into marine mammal behaviour has been a challenge. Some locations, where shallow, clear waters allow for nearly continuous observations to be conducted (Samuels & Tyack, 2000), have provided excellent sources of detailed behavioural observations, including for conservation-related issues (Bejder, Samuels, Whitehead, Gales N, 2006; Bejder, Samuels, Whitehead, Gales NJ et al., 2006), but for most locations observations of detailed behaviour have been limited.

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http://dx.doi.org/10.1016/j.anbehav.2016.07.019

We provide the following retrospective as well as prospective look at the study of marine mammal behaviour, specifically that of cetaceans, and how this research has been affected and improved by technological advances. ‘Behaviour’ can connote different levels of detail, from the very detailed postures (e.g. head turn, suckling events, affiliative and antagonistic body gestures) to larger-scale movements (e.g. migration and habitat use patterns), and we provide examples at several scales, which are largely determined by the technique being used. We do not offer an exhaustive review of these studies, rather examples that focus on four techniques that are relatively new or have come of age in recent years: unmanned aerial systems (UAS), passive acoustics, satellite-linked telemetry tags, and multisensor high-resolution acoustic recording tags (MHARTs). By utilizing novel combinations of technologies and analytical techniques, the field of marine mammal behaviour has made significant advances. For example, the remarkable data density resulting from the MHARTs has allowed the development of sophisticated analytical techniques that permit us to study, among other things, the kinematics of feeding and diving. In the subsections describing the four technological advances, we provide examples of the types of data now available via these techniques and some of the empirical results. Some of these results have immediate and direct conservation applications, and we indicate these ties within the context of these sections. Conservation applications for other products of these technologies (e.g. photogrammetry, feeding kinematics) are described in the penultimate section of the paper on ‘Linking behaviour changes to population viability’, and it is in this section that we provide the connections between the sampling of behaviour and one of the primary and heated conservation topics in marine mammal science: population-level impacts of disturbance. As we will describe, robust behavioural data are critical for investigating these links, and this discussion of population-level impacts cuts across many conservation issues (e.g. noise impacts, bycatch, vessel interactions, etc.). Overall, behavioural data from UAS, passive acoustics, satellite tags and high-resolution acoustic recording tags are providing us with unprecedented windows into the lives of marine mammals, and these data are playing an integral role in addressing many current conservation concerns.

UNMANNED AERIAL SYSTEMS

From surveys for population assessment (Torres, McLellan, Meagher, & Pabst, 2005) to the use of aerial systems to observe behaviour (Nowacek et al., 2001), the advantages of viewing marine mammals from aerial platforms have been appreciated for many years. A recent boom in the creation of small UAS by hobbyists, several commercial sectors and researchers alike holds substantial promise for the use of such systems in the study of animal behaviour; indeed entire research centres focused on the use of UAS in marine science have been established (http://marineuas.net). Fixed-wing UAS stand to be very useful for surveying nearshore areas for inter alia population assessments of pinnipeds, turtle nests, etc. Multirotor UAS (e.g. hexacopters) have an advantage from the perspective of studying animal behaviour, as they are capable of hovering over a target individual(s) (Fig. 1). Currently UAS are somewhat limited in flight time, although increasing battery power density and rapid advances in charging technology are likely to increase these flight times in the near future. The fixed-wing and multirotor platforms are beautifully complementary with respect to their strengths in conducting behavioural research. Some cetacean data collected by UAS have been published (Durban, Fearnbach, Barrett-Lennard, Perryman, & Leroi, 2015), and although this study was not focused on behaviour, the photogrammetry information collected will undoubtedly be useful in our efforts to link behavioural changes or disturbances to potential individual-level and then population-level impacts. As with any method, care will be needed to ensure that animals are treated ethically and that the platform itself has limited impact on the study subjects (Ditmer et al., 2015).

PASSIVE ACOUSTICS

Cetaceans use sound for various life functions, including communication, locating prey, avoiding predators and navigation. Occurrence of these sounds has been known for decades (Schevill & Lawrence, 1953; Schevill & McBride, 1956), and such sounds can be used to detect, classify and track cetaceans (e.g. Watkins & Schevill, 1974; and see review by Zimmer, 2011). Broadly described as passive acoustic monitoring (PAM), there are limitations to the use of this technique, primarily that it relies on the animals vocalizing and knowledge of vocal rates of particular species (Zimmer, 2011). Another notable limitation is in our ability to classify sounds to the species level in some cases. While some species are relatively straightforward to classify (e.g. sperm whales, *Physeter macrocephalus*: Zimmer, Johnson, D'Amico, & Tyack, 2003; some beaked whales: Johnson, Madsen, Zimmer, De Soto, & Tyack, 2006), other species are much more difficult to identify from the sounds they produce (e.g. echolocation clicks of closely related toothed whales). With good information on the vocal rates, the PAM data become more useful as we can better interpret the occurrence of sounds, the lack thereof, and the number of sounds recorded. For example, with good vocal rate information (Stimpert et al., 2015), our statistical capabilities using PAM data are enhanced to the point of being able to estimate population densities (Marques, Thomas, Ward, DiMarzio, & Tyack, 2009). PAM also has significant advantages over other observational techniques. Animals do not need to be tagged or even followed, which has the added benefit of minimizing the potential effect of the researcher on the behaviour of the studied animals. Sounds can, in the case of low-frequency signals (e.g. <1 kHz), travel hundreds or even thousands of kilometres through the ocean (Urick, 1983), allowing animals using these frequencies the ability to communicate over such distances. Short-range, high-frequency signals can also still be useful (Verfuß et al., 2007) as they permit the resolution of fine-scale detail.

Although PAM provides us ‘presence only’ information, the acoustic behaviour of individual animals that rely so heavily on sound does provide us with information about the behavioural state (e.g. foraging, socializing). These PAM data can then be used in conservation applications, which have blossomed in recent years, from assessment of stock structure (Delarue, Todd, Van Parijs, & Di Iorio, 2009) to assisting with mitigation of potential impacts of human activities. The Northeast Passive Acoustics Network (NEPAN, Van Parijs et al., 2015), for example, combines mobile and stationary passive acoustic platforms to form a network of sensors that provide long-term year-round information on the presence and spatial distribution of cetaceans, as well as fish. The data can be used to address critical conservation and management needs (e.g. seasonal use of areas by particular species including some real-time capabilities), as well as to reduce threats from anthropogenic activities (e.g. shipping, offshore energy activities). Part of NEPAN is a set of near real-time automated buoys (Spaulding et al., 2009) that report on the presence of North Atlantic right whales, *Eubalaena glacialis*, in the shipping channel approaching Boston, Massachusetts, U.S.A. Other parts of NEPAN are archival, so upon data processing, the hourly, daily, weekly, etc., utilization of particular areas by particular species can be explored. Although it may not seem novel, the ability to know year-round patterns of habitat use by

Figure 1. Quadcopter unmanned aerial systems (UAS) hovering in the foreground with a humpback whale in the background. Although it appears large, the copter is 500 mm in diameter and 230 mm in height, with landing gear. These platforms, multirotors and fixed-wings are being used to collect data of several types (e.g. photogrammetry, exhalent samples, thermal imagery). Given the rapid acceleration in the UAS technology, we expect the use of these systems to increase for behavioural as well as other research applications.

cetaceans is a significant step forward for answering questions of basic ecology as well as helping to address conservation concerns.

SATELLITE TAGS

One of the most basic elements of an animal's behavioural ecology is its use of an area or habitat, referred to inter alia as ‘home’ or ‘home range’ or ‘core area.’ For migratory animals this area obviously changes with season or some other temporal schedule, in which case its use of alternating core areas remains of interest. For cetaceans, which are highly mobile and for which we have only relatively recently been able to track their movements (Watkins et al., 1996) and/or the use of core areas, home ranges have often been defined for groups or stocks of animals. One example is the seven breeding populations of humpback whales, *Megaptera novaeangliae*, defined by the International Whaling Commission (Gales, Bannister, Findlay, Zerbini, & Donovan, 2011). These populations have been known to make long migrations between summer feeding grounds in nutrient-rich, high-latitude waters and winter breeding grounds in nutrient-poor, low-latitude tropical waters (Mackintosh, 1942; Townsend, 1935). The impressive extent of these migrations (i.e. they do not necessarily just swim directly along a north–south route) has recently been confirmed (Robbins et al., 2011) and is important for conservation. The International Whaling Commission (IWC) divides the cetacean populations into regions for management purposes, and for whales in the Southern Ocean this has traditionally meant assuming that whales travel simply north to south on their migrations; that is, from the West Antarctic Peninsula (WAP) up and down the west coast of South America. Robbins et al. (2011), however, documented a humpback whale migrating between the West Antarctic Peninsula and American Samoa, a trip of ca. 10 000 km one way, and, importantly for conservation and management purposes, ca. 105 degrees of longitude. Next, among cetaceans we see several different patterns with respect to the size of home/core areas and the extent of their use. These same Southern Ocean humpback whales, for example, utilize relatively small areas during feeding seasons; note the term ‘relative’ is important in this context as, for example, Antarctic humpback whales use the entire northern two-thirds of the WAP as their ‘home range’ during the feeding season (Curtice et al., 2015). Knowing that these whales use most of the WAP during the feeding season is important for conservation, as this information informs, for example, the management of krill stocks in the WAP region. The impressive distances over which these animals range limit traditional behavioural sampling methods, but emerging tag technology (e.g. long-term tags with greater sampling capabilities) as well as analytical techniques will allow us greater insight in the future.

Satellite data and their derivatives (e.g. the use of cell phone technology for near-shore animals; Cronin & McConnell, 2008) are increasingly being used to address conservation-related questions. The ability to use positions of animals derived from satellite data to allow subsequent calculation of movement patterns has evolved significantly in recent years. Behavioural switching state-space model (SSM), for example, originally developed by Jonsen, Flemming, and Myers (2005) and refined by Breed, Jonsen, Myers, Bowen, and Leonard (2009), estimates model parameters by Markov-chain Monte Carlo methods (MCMC) to the locations of each humpback whale with the free software programs R (R Core Team) and Win-BUGS (Bayesian inference Using Gibbs Sampling). These models allow the researcher to make inferences about the behaviour in which the individual is engaged (e.g. travelling, foraging) at a particular point in the record based on, for example, turning angles or speed of travel.

A recent study effectively used such satellite data to explore the conservation issue of migrating humpback whales overlapping with areas of intense anthropogenic activity. Rosenbaum, Maxwell, Kershaw, and Mate (2014) characterized how humpback whales used areas in the exclusive economic zones (EEZs) and oceanic areas of several West African countries and how that use overlapped with human activities in these areas. They calculated the whale tracks' utilization distribution (UD), which is a type of home range calculation that represents the probability an animal will occur in a given location within a defined period (Kernohan, Gitzen, & Millspaugh, 2001). They then overlaid these UDs with human activity data for the area as reported in Halpern et al. (2008), specifically looking at the overlap of whale movements with location and density of offshore oil platforms, ocean-based toxicants from ports and commercial ship activity and density of vessel traffic in shipping lanes. In addition to observing, for the first time, the direct migration of whales from West Africa to their sub-Antarctic feeding areas, Rosenbaum et al. (2014) found the highest potential overlap of whale habitat with human activities in EEZs, close to shore, and particularly in areas used by the hydrocarbon industry. They discuss the fact that the platforms are likely to pose little threat to the whales, but that the vessel traffic associated with servicing those platforms does represent some increase in risk. Finally, Rosenbaum et al. (2014) found overlap between whale movements and different human activities during each stage of their migration, thus making traditional mitigation measures such as time–area closures less effective. We are only just beginning to effectively apply behavioural data at these large spatial scales to conservation issues, and there should be continued effort to develop these applications. Additionally, while these data represent movements and behavioural state information at relatively large temporal and spatial scales, they are at relatively low resolution with respect to individual behaviours (e.g. prey capture). We believe that there could be considerable strength in combining these types of large-scale data with high-resolution data collected at relatively short temporal and spatial scales, like those collected with multisensor acoustic tags.

HIGH-RESOLUTION MULTISENSOR TAGS

Studying the behavioural processes of cetaceans is especially problematic because they are fully aquatic and, in most cases, their large size precludes capture for direct measurement or instrumentation. For the past 75 years, scientists have sought novel ways to ‘see’ below the surface and gain an understanding of the behaviour, ecology and physiology of large aquatic animals using animal-borne tags and telemetry (Goldbogen & Meir, 2014; Hussey et al., 2015). The first attempts to study the diving capacity of marine mammals were performed by Per Scholander and employed harpoons outfitted with simple manometric tubes invented by Lord Kelvin (Scholander, 1940). These devices recorded only the maximum depth of the animal, and of an individual that was clearly injured, and so the data collected may not necessarily reflect natural behaviour. The next iteration of tags occurred several decades later and represented a revolutionary step in our ability to quantify behaviour. Specifically, researchers integrated a pressure sensor with an ordinary kitchen timer to quantify the dive profile (depth as a function of time) of tagged Weddell seals, *Leptonychotes weddellii* (Devries & Wohlschlag, 1964; Kooyman, 1965, 1966). This innovative technology, the time–depth recorder (TDR), continues to be one of the most common devices used to study the diving behaviour of many taxonomic groups of marine organisms in diverse ocean ecosystems (Hussey et al., 2015), and when combined with other sensors (e.g. accelerometers, magnetometers) produce rich data streams that are opening new areas of inquiry for marine mammal behaviourists and ecologists.

Although biologging devices, which include the high-resolution multisensor tags we discuss here, continue to simultaneously decrease in size and increase in capacity to include high-resolution movement sensors, they remain relatively large instruments that cannot be attached to many free-ranging animals without the potential to affect their behaviour (Vandenabeele, Shepard, Grogan, & Wilson, 2012). Because of the relatively large size of these tags, whales remain a robust system for biologging approaches to the study of animal behaviour, e.g. feeding energetics and diving behaviour, all of which have major implications for conservation efforts (see below).

Among cetaceans, there are two suborders: Odontocetes (toothed-whales) and Mysticetes (baleen whales). In general, toothed whales and dolphins use high-frequency acoustics for interanimal communication and feeding. In the marine environment, where sight is limited, sound propagates extremely well and all marine mammals communicate primarily through acoustic cues. Similar to bats, toothed whales and dolphins feed via high-frequency sound production known as echolocation, where acoustic signals reflect off of targets and the returning echoes can be translated into information on the environment or potential prey. For many years, independent passive acoustic recorders have been used to study the vocalizations of marine mammals. However, the incorporation of acoustic recorders (hydrophones) into animal-borne tags has only occurred in the past 20 years (Fletcher, Le Boeuf, Costa, Tyack, & Blackwell, 1996). The information that is recorded on the sensors in these tags (e.g. acoustic, movement) can be used to determine the frequency and acoustic structure of vocal behaviours that occur concomitant with motor behaviour, for example, echolocation signals during feeding events (Madsen, De Soto, Arranz, & Johnson, 2013) or contact calling while diving (Jensen, Marrero Perez, Johnson, Aguilar Soto, & Madsen, 2011). Echolocation ‘clicks’ and ‘buzzes’ have been used from animal-borne tags to study the foraging behaviour of a wide range of odontocetes, from the small harbour porpoise, *Phocoena phocoena*, to the largest, the sperm whale (Fais et al., 2015; Wisniewska et al., 2015). This information has provided critical data on the feeding depths, frequency, timing and prey types targeted by different species and the behaviours associated with foraging (Johnson, de Soto & Madsen, 2009). These insights into feeding behaviour have recently been used to help determine foraging performance and foraging ecology (Watwood, Miller, Johnson, Madsen, & Tyack, 2006), as well as the energetic consequences of disturbing this behaviour (Miller et al., 2009). These new data products are ripe for linking to conservation efforts such as the individual and population consequences of human activities disrupting these behaviours (e.g. the use of naval sonar and seismic surveys). We explore below the tools produced, as well as new ones in development, to forge these links.

In contrast to toothed whales, baleen whales are large-bodied filter feeders that generally produce low- to mid-frequency acoustic signals. Although these acoustic signals are sometimes recorded in the context of foraging (Oleson, Calambokidis, & Burgess, 2007; Stimpert, Wiley, Au, Johnson, & Arsenault, 2007), they are not a recognized mechanism that is required for successful foraging (Goldbogen et al., 2006; Ware, Friedlaender, & Nowacek, 2011). Baleen whales show different modes of filter feeding, ranging from intermittent engulfment (Goldbogen et al., 2006) to continuous ram filter feeding (Simon, Johnson, & Madsen, 2012). Despite the different hydrodynamic mechanisms that underlie these feeding behaviours (Potvin, Goldbogen, & Shadwick, 2009; Werth, 2004), they both function to process vast quantities of water to filter aggregations of small-bodied zooplankton. Researchers have integrated tag and morphological data in order to estimate the engulfment capacity of baleen whales in terms of the volumetric filtration rate (Goldbogen, Friedlaender et al., 2013; Simon, Johnson, & Madsen, 2012). Concurrent active hydroacoustic surveys surrounding tagged whales provide important information about the density and distribution of the prey field (Friedlaender et al., 2009; Hazen et al., 2009). The combination of feeding performance (Fig. 2), energy expenditure from activity and the quality of prey patches collectively inform the estimates of foraging energetics (Goldbogen et al., 2011) and consequently population fitness (Wiedenmann, Cresswell, Goldbogen, Potvin, & Mangel, 2011). Population consequences are important for marine mammals, as

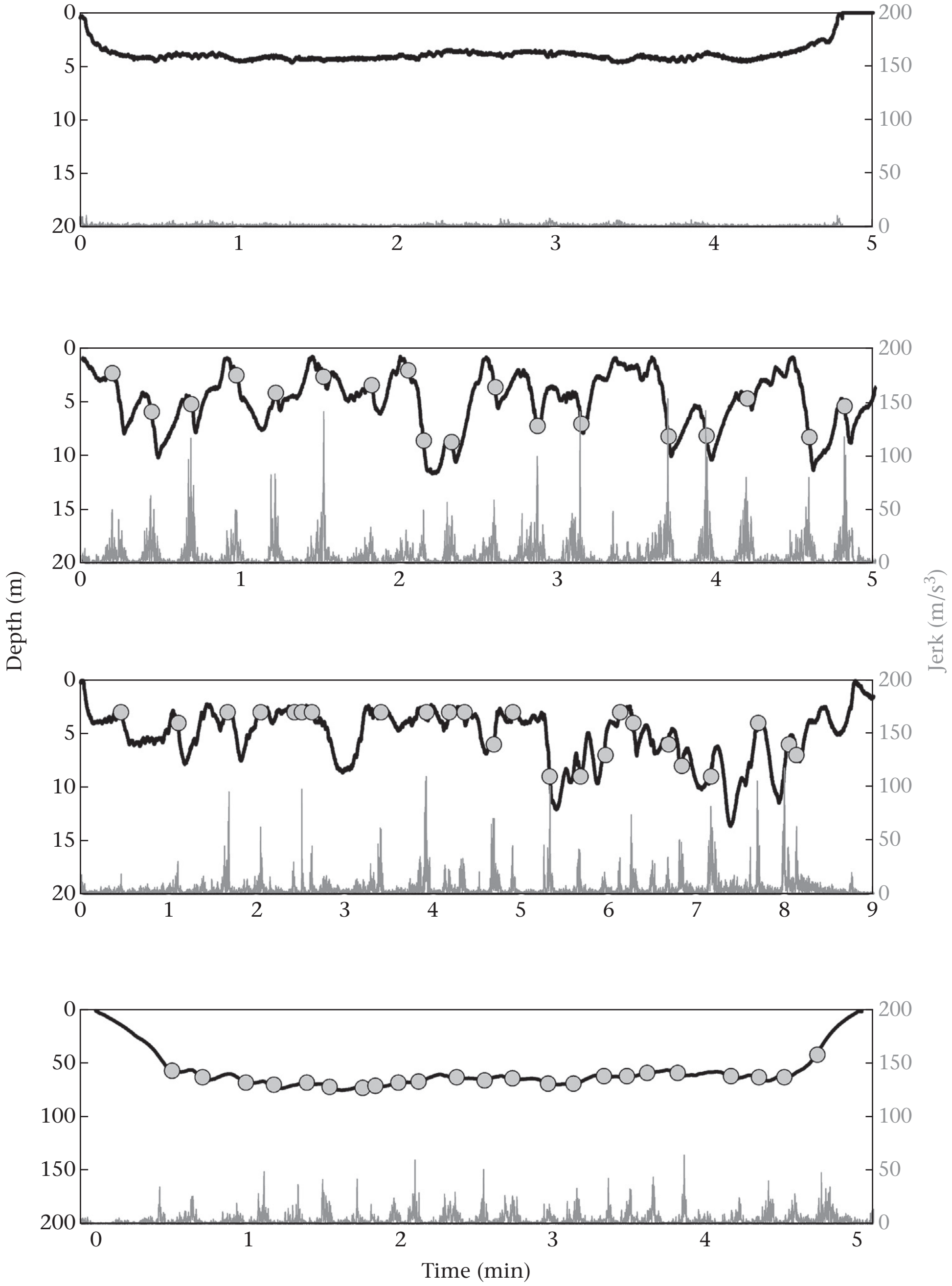

Figure 2. Time–depth records for a diving and foraging minke whale as recorded on a high-resolution tag. Depth (m) of dive is shown on the left *Y* axis and ‘jerk’ on the right *Y* axis. The jerk signal is derived from the accelerometers on the tag and indicates a rapid change. The grey dots indicate lunges performed by the whale as it engulfs water to feed.

management of stocks of each species is common (e.g. the IWC) as well as federally mandated in the U.S.A.

Finally, we provide some specific examples in which the use of high-resolution tags has provided detailed behavioural data used to inform our understanding of particular conservation issues. North Atlantic right whales are critically endangered, and one of the ongoing threats to this species is mortality from vessel collisions. One of the solutions suggested to this problem was to equip ships with some sort of alerting device that would, in theory, cause whales to move out of the path of an oncoming ship. Nowacek, Johnson, and Tyack (2004) exposed right whales carrying high-resolution acoustic tags to a variety of sounds, including an ‘alarm’ signal, and they found that the whale's response was maladaptive for avoiding vessel collisions as the whales abandoned deep foraging dives and swam rapidly just below the surface (i.e. vulnerable but not visible). The ‘alarm’ signal was developed to pique the whale's attention by spanning the suspected auditory range and containing features that are known to stimulate the mammalian auditory system (e.g. disharmonic tones). Nowacek et al. (2004) concluded that the whale's response was consistent with an antipredator behaviour as the whales came to the surface (for oxygen) while cryptically (staying just below the surface as much as possible) swimming energetically away from the sound. To our knowledge, there has been no further discussion of using alarm signals; instead, vessel speed restrictions have been implemented along the east coast of the U.S.A. as relatively high vessel speeds have been linked to morbidity and mortality (Jensen & Silber, 2004; Laist, Knowlton, Mead, Collet, & Podesta, 2001). Next, the exposure of cetaceans to anthropogenic noise (e.g. military sonar, marine seismic surveys) has received increasing attention in light of known and potential impacts of noise on wildlife (Shannon et al., 2015). Data from high-resolution tags have provided significant insight into the responses of several species of cetacean exposed to sonar and seismic signals. Blue whales, *Balaenoptera musculus*, exposed to simulated sonar signals showed changes in behaviour varying from cessation of deep feeding to increased swimming speed and travel away from the sound source (Goldbogen, Southall, et al., 2013); the study documented considerable variability in responses, but consequences such as the cessation of feeding are cause for concern, as they can affect individual fitness. Similarly, tag data have been used to explore responses of Cuvier's beaked whales, *Ziphius cavirostris*, to military sonar (DeRuiter et al., 2013), with similar results to those seen in blue whales. Finally, again using acoustic recording tags, substantial changes in foraging rates with documented exposure to seismic airgun signals has been documented in sperm whales (Madsen et al., 2006; Miller et al., 2009; Tyack, 2009). The potential impacts on individual fitness documented in these latter studies, which are consistent with a recent review of the impacts of noise on wildlife (Shannon et al., 2015), are extremely important and useful in informing the conservation management of these sound sources as they provide a direct link between behavioural changes and potential population-level consequences (see NRC, 2005).

LINKING BEHAVIOUR CHANGES TO POPULATION VIABILITY

Evidence of the intricacies of wildlife responses to human activities has led to disapproval of traditional behavioural sampling approaches to evaluate effects of anthropogenic disturbance (Bejder, Samuels, Whitehead, Finn, & Allen, 2009; Gill, Norris, & Sutherland, 2001; Nisbet, 2000). Fortunately, some cetacean studies have used traditional behavioural sampling methods (sensu Altmann, 1974; Mann, 1999) successfully to inform and implement conservation measures (e.g. Tyne, Johnston, Rankin, Loneragan, & Bejder, 2015). However, we must continually strive to improve our ability to measure behaviour accurately. So far in this review, we have discussed existing and novel methods and technologies to measure behaviour of marine mammals on fine as well as relatively coarse temporal and spatial scales. From a conservation perspective, these tools have allowed researchers to measure behaviourally mediated impacts of various anthropogenic threats to marine mammals, including whale watching (Christiansen, Rasmussen MH, & Lusseau, 2013; Lusseau, 2003; Meissner et al., 2015; Williams, Lusseau, & Hammond, 2006), marine renewables (Brandt, Diederichs, Betke, & Nehls, 2011; Carstensen, Henriksen, & Teilmann, 2006), vessel traffic and shipping noise (Jensen et al., 2009; Lesage, Barrette, Kingsley, & Sjare, 1999), seismic activity (Pirotta, Brookes, Graham, & Thompson, 2014) and navy sonar (Goldbogen, Friedlaender et al., 2013, Goldbogen, Southall et al., 2013; Nowacek, Thorne, Johnston, & Tyack, 2007). While short-term behavioural response studies are a great way of linking the source of the disturbance to the behaviour of animals (Bejder, Samuels, Whitehead, Gales N, 2006; Carney & Sydeman, 1999; Lima & Dill, 1990; Sutherland, 1998), the ability to predict long-term, population-level consequences is very limited (Beale & Monaghan, 2004; Bejder & Samuels, 2003; Bejder et al., 2009; Bejder, Samuels, Whitehead, Gales NJ et al., 2006, Gill et al., 2001).

However, seemingly benign nonlethal, repeated behavioural effects can accumulate over time and can eventually affect an individual's fitness by decreasing vital rates, such as survival and reproduction (Christiansen & Lusseau, 2014; New et al., 2014). If a large enough proportion of a population is affected, this in turn can result in negative effects on population dynamics (McMahon, Hindell, Burton, & Bester, 2005). From a management perspective, disturbances that have the potential to affect population viability (via the survival and reproductive success of individuals), and hence a species conservation status, are of significant concern (Bejder, Samuels, Whitehead, Gales NJ et al., 2006; Christiansen & Lusseau, 2014; Gill et al., 2001; NRC, 2005). Therefore, we need to understand the mechanisms leading to the population consequences of disturbance (PCoD) (Christiansen & Lusseau, 2015; Duffus & Dearden, 1990; New et al., 2014; NRC, 2005).

In order to understand how human-induced behavioural changes can lead to population-level effects on cetaceans, the U.S. National Research Council (NRC) developed a conceptual framework to investigate the PCoDs on marine mammals (NRC, 2005). The initial framework, developed by the NRC in 2005, focused mainly on the population consequences of acoustic disturbance (PCAD) model, but was later changed to the more general framework, the PCoD model (King et al., 2015; Schick et al., 2013). The PCoD framework has subsequently been developed into a more formal model structure, which defines the mechanistic links between disturbances and their consequences (Fig. 3). The concept of the PCoD framework is that a *source* of disturbance (e.g. anthropogenic noise) will lead to *behavioural changes* (e.g. activity state change) of the targeted animal, which then affects the animals' *life functions* (e.g. energy acquisition), which are inherently linked to *vital rates* (e.g. survival and reproduction rates), which can ultimately lead to *population effects* (population dynamics) through a series of transfer functions (NRC, 2005).

Since being introduced nearly a decade ago, considerable advances have been made to further improve our understanding of PCoD, both theoretically and empirically (Christiansen & Lusseau, 2015; Nabe-Nielsen, Sibly, Tougaard, Teilmann, & Sveegaard, 2014; New et al., 2013, 2014; Pirotta, New, Harwood, & Lusseau, 2014; Schick et al., 2013). From a modelling perspective, advanced mechanistic models have been developed to link behaviour to changes in body condition, vital rates and population dynamics. New et al. (2013) developed a mathematical model for bottlenose dolphins, *Tursiops truncatus*, to investigate the effect of vessel traffic; this model was extended by Pirotta, New et al. (2014). In both models, the behavioural state of individual bottlenose dolphins was affected by their motivational state, which in turn was influenced by previous behavioural states as well as the health (body condition) of the animal. The model incorporated a feedback loop from health to behaviour, representing the dolphin's ability to compensate for a decrease in health resulting from behavioural disruption. The model was developed further in another study, in which the health of the animals was linked to adult survival and reproductive success (New et al., 2013). In another species, New et al. (2014) developed a mechanistic model for southern elephant seals, *Mirounga leonina*, in which the foraging success during trips to sea was linked to maternal lipid mass (a proxy for health and measured by calculating the animal's buoyancy with tag data). Maternal lipid mass was in turn linked to pup survival, and then a Leslie matrix approach was finally used to connect changes in pup survival to population dynamics. Schick et al. (2013) developed a hierarchical Bayesian model to link movement to health (body condition) to survival in North Atlantic right whales. The model captured both normal variations in health status as well as how anthropogenic stressors can affect health and ultimately survival of individuals. Assessing the health of individual cetaceans at sea is challenging, although noninvasive methodologies to assess body condition are improving, including ultrasound measurements of blubber thickness (Miller et al., 2011) and aerial photogrammetry techniques (Durban et al., 2015; Miller, Best, Perryman, Baumgartner, & Moore, 2012). Christiansen and Lusseau (2015)

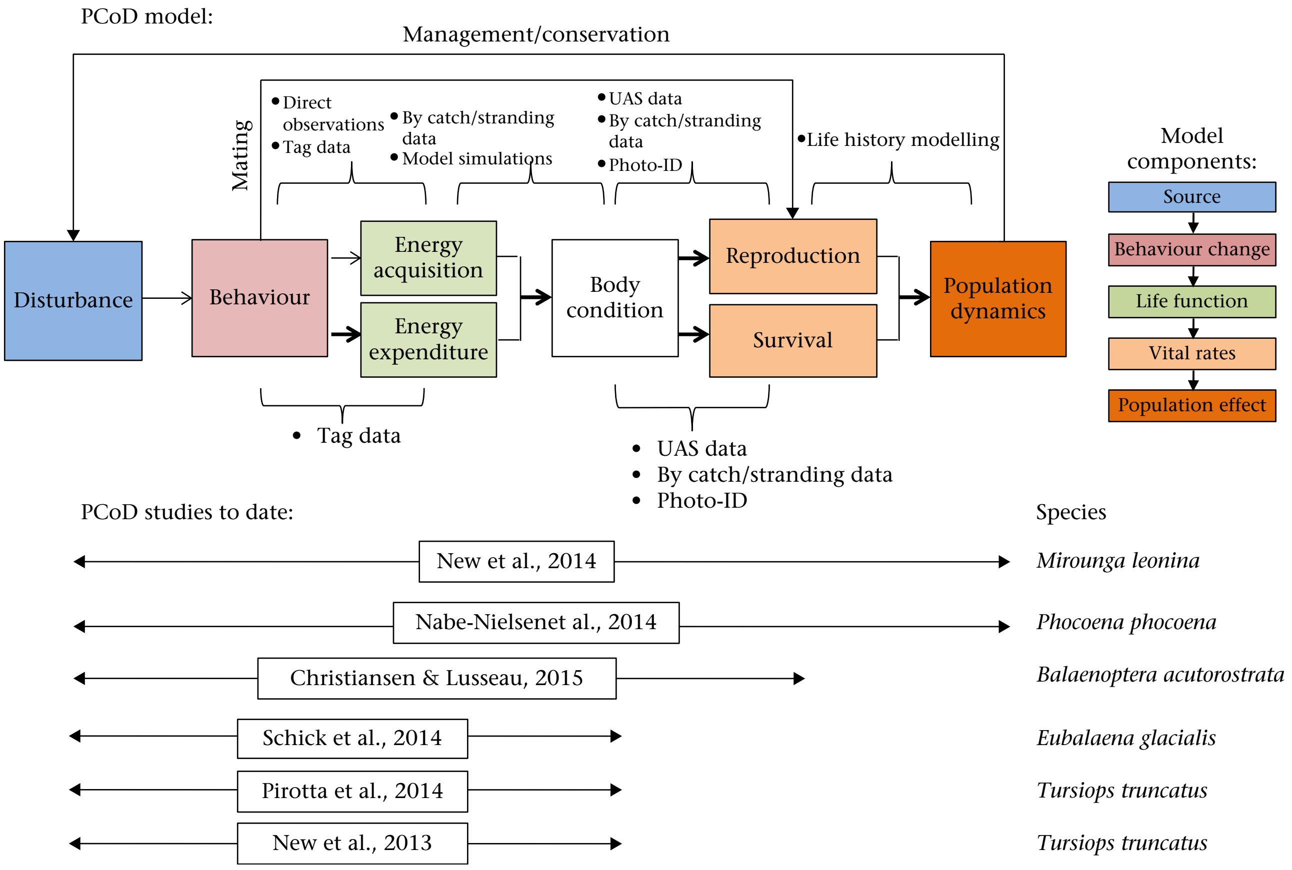

Figure 3. The population consequences of disturbances (PCoDs) model framework with methods useful for obtaining particular data types and studies to date that have employed the model. The arrows coming out from each study indicate which model components and transfer links were informed in each study. A fully implemented PCoD model can predict the population-level effects of a particular disturbance, which in turn can be used to inform management decisions (represented by the feedback arrow from Population dynamics to Disturbance) in a precautionary way. UAS: unmanned aerial systems.

developed a mechanistic framework for minke whales, *Balaenoptera acutorostrata*, to link behaviour to bioenergetics (energy expenditure and acquisition) and ultimately to vital rates to assess whale watching impacts (Christiansen, Rasmussen, & Lusseau, 2014; Christiansen, Rasmussen M, & Lusseau, 2013). An important aspect of the model was that it took into account the exposure level of individual minke whales to whale-watching boats (Christiansen, Bertulli, Rasmussen, & Lusseau, 2015), so that the effect of repeated interactions could be measured and also placed into a larger context of human–cetacean interaction (Higham, Bejder, Allen, Corkeron, & Lusseau, 2015). Perhaps the most comprehensive model linking behaviour to population dynamics is the one developed by Nabe-Nielsen et al. (2014), who built an individual-based model to investigate the effects of wind turbines and ships on harbour porpoises in Danish waters. The model linked the movement and foraging behaviour of harbour porpoises to a measure of body condition (e.g. energy levels), which in turn was linked to survival and reproductive success. By simultaneously simulating the behaviour of individuals of an entire population, the model could predict behaviourally mediated effects on population dynamics.

These studies have all helped to advance our understanding of the mechanisms of PCoD; attempts have also been made to implement these models using empirical data. New et al. (2013) implemented their model using empirical data on dolphin group activity states, recorded visually, while Pirotta, New et al. (2014) complemented this with data on respiration rates to inform body condition. New et al. (2014) used long-term telemetry devices to link elephant seal behaviour to body condition, while Schick et al. (2013) used >30 years of sighting and photographic data to inform the movement and body condition components of their model. Finally, Nabe-Nielsen et al. (2014) employed a movement model based on tag data from wild harbour porpoises.

As we have tried to convey, marine mammal behaviourists are working diligently and creatively to incorporate data from many different platforms and technologies into empirical as well as model-based, conservation-focused studies. There appears to be no lack of conservation applications for behavioural data, and the marriage of robust behavioural sampling with technologically advanced sampling platforms is yielding breakthrough data.

NEXT AND MISSING STEPS IN DEVELOPING TOOLS AND MODELS TO INFORM CONSERVATION MANAGEMENT

Despite recent advances in developing and empirically informing the PCoD model, it still requires development before being a ready tool to use for management. Perhaps the biggest hurdle is the difficulty in making long-term measurements of the different components (variables) for use as parameters in the PCoD model. Although existing tags are capable of recording very detailed movement data, which are used to infer behaviour as well as relative energy expenditure in marine mammals (Goldbogen et al., 2006, 2011), few if any tags are able to record such data over periods long enough to cover an animal's reproductive cycle, feeding season, breeding season, and so forth. The same conundrum applies to body condition. While movement data from tags can be used to infer body conditions in some pinniped species (from the rate of drift, which is determined largely by lipid-to-lean mass ratio; Schick et al., 2013), this technique has to be developed for cetaceans before long-term monitoring of body condition can be achieved. Finally, devices capable of measuring behavioural data and exposure to disturbance (e.g. noise) over extended periods need to be developed so that disturbance can be linked to behaviour and body condition. Once those links are well developed, linking body condition to vital rates can be done using, for example, time series of reproductive events across individuals and photogrammetry of offspring. Despite these hurdles, the management benefits of one day developing and fully implementing the PCoD model will be well worthwhile for conservation and management of marine mammals as well as other taxon, and rigorous behavioural sampling provides key data for these models.

Acknowledgments

We would like to acknowledge our colleagues who conducted this work, especially the memory of Dr Amy Samuels, who inspired us to really watch these animals and to meticulously study their behaviour.

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