



## Diving beneath the surface: long-term studies of dolphins and whales

JANET MANN\* AND CAITLIN KARNISKI

Department of Biology, Georgetown University, 3700 O Street NW, Washington, DC 20057, USA (JM, CK)

\* Correspondent: [Mannj2@georgetown.edu](mailto:Mannj2@georgetown.edu)

Although aquatic mammals are elusive subjects, long-term studies of cetaceans have revealed remarkable life-history traits, including long life spans, bisexual philopatry, prolonged maternal care, and even menopause. Long-term cetacean research, defined here as studies lasting  $\geq 10$  years, has also helped shape our understanding of large multilevel societies, fission–fusion dynamics, cultural processes, complex sociality, and cognition. Yet relative to their terrestrial counterparts, little is known about many cetacean societies, especially pelagic species; similarly, collection of biological samples (such as blood, feces, urine) from live subjects is rarely possible. Cetaceans have been severely impacted by human activities, from commercial whaling to fisheries bycatch, prey depletion, habitat loss, and chemical and noise pollution. Longitudinal research, defined as measuring the same individuals repeatedly over time, can provide vital information necessary for devising viable solutions for mitigating these impacts and promoting sustainable practices. This review evaluates key findings gleaned from continuous and systematic longitudinal studies of free-living cetaceans. We present examples for each topic, though our condensed review cannot be comprehensive. Given their adaptations to the marine environment, slow life histories, and complex societies, continued investment in long-term research is vital for both understanding and protecting this taxonomic group.

Key words: Cetacea, dolphins, life history, longitudinal research, marine mammals, whales

As cetaceans are 1 of only 2 mammalian orders that spend their entire lives at sea, long-term research (defined here as  $\geq 10$  years of field study) on cetaceans is challenging because they are deep-diving, fast-moving, and wide-ranging, sometimes migrating from polar to equatorial regions or further. Consequently, we know far less about their behavior, social systems, and life histories than we do for terrestrial mammals. Cetaceans, nested in the order Cetartiodactyla (Thewissen et al. 2007; Committee on Taxonomy 2016), have 2 major suborders, Odontoceti (toothed whales) and Mysticeti (baleen whales), which have markedly diverse feeding ecology, movement, social systems, and life histories.

Given our dependence on terra firma, most long-term studies have focused on coastal species (Mann et al. 2000a) such as bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*), killer whales (*Orcinus orca*), and species that migrate, breed, and feed along our coastlines such as humpback (*Megaptera novaeangliae*) and right whales (*Eubalaena* spp.—see Supplementary Data SD1). A much smaller subset of studies have tracked individuals from birth to old age and across generations (Weinrich

et al. 2006; Mann et al. 2012; Wells et al. 2014; Brent et al. 2015). Additionally, since cetaceans are cathemeral, that is, active day and night with variable rest periods, the nocturnal portion of their lives remains unseen for even the best-studied species.

Systematic behavioral observations (such as focal animal sampling) on individual cetaceans are inherently difficult to conduct unless the group sizes are relatively small and individuals are visually distinct enough to be quickly recognized during brief surfacings (Mann 1999). Additionally, repeated behavioral sampling of individuals over time is unlikely for many species. Animal-borne tags can be deployed, often at great expense, on a limited number of individuals in order to log detailed behavior and multi-sensor data (e.g., swimming speed, foraging tactics, energy use, prey consumption, and communication) and to track individuals over large spatial and temporal scales (migration and habitat use—Bailey et al. 2009; Nowacek et al. 2013). Most of these are single-effort sampling occasions and not amenable to long-term research, but they do provide considerable insights into the behavioral ecology of wide-ranging or deep-diving species.

The most typical types of long-term monitoring of cetaceans are opportunistic or transect surveys with photo-identification (Eguchi 2014; Urian et al. 2015). Such data can provide rich information on demography and social structure, but can have little to offer in explaining why some patterns exist and their adaptive function. Critically, longitudinal study (the systematic study of individuals over time) is essential for understanding the natural variation within populations and how such variation impacts fitness. Longitudinal and focal-animal study of calf and juvenile bottlenose dolphins (*Tursiops aduncus*) demonstrated early sex differences in social strategies and that social position in the network predicts juvenile survival (Stanton et al. 2011; Stanton and Mann 2012). We would not know why male bottlenose dolphins associate closely without having observed them repeatedly for many years in focal groups as they cooperate in battles against other males, coerce cycling females to remain with them, and have higher mating success than males who are not in alliances (Connor and Krützen 2015).

As cetaceans are considerably wide-ranging, members of a population may move freely between local and intercontinental waters. Because of this, collaborative efforts are necessary. Teams from the United States and Canada study the same populations of killer whales in Pacific waters (Ford et al. 1998), and groups of Russian and American scientists joined together in 2010 to tag a gray whale (*Eschrichtius robustus*) with a subcutaneous satellite telemetry transmitter to study its movements in the western North Pacific (Mate et al. 2011). This ultimately led to a study of the movements of whales between the western and eastern North Pacific via combined comparisons of photo-ID catalogs (Weller et al. 2012). In the North Atlantic, an outstanding level of cooperation was demonstrated by scientists studying North Atlantic right whales (*Eubalaena glacialis*) and humpback whales across 7 countries (Smith et al. 1999; Hamilton et al. 2007). Maintenance of common identification catalogs and databases has been facilitated by technological advances for online storage and access but are difficult to support without considerable effort and financial investment of investigators. Employment of qualified personnel to update, curate, and facilitate access to such databases is an ongoing challenge and expense.

Much of the data acquired on cetaceans are opportunistic and cross-sectional, based on bycatch, strandings, fisheries, or whaling data (Marsh and Kasuya 1986), rather than from systematic or longitudinal studies of healthy individuals representative of the population. Although valuable in the context of a long-term effort, these data in isolation can confound accurate estimation of basic demographic information such as weaning age, reproductive age, mortality, and life span. For example, weaning age is documented as 1–2 years for most delphinids based on cross-sectional studies, but longitudinal study (long-term study that follows the same individuals over time) of Shark Bay bottlenose dolphins show that some calves wean as late as 8 years of age, and the average weaning age is 4 years (Mann et al. 2000b). Few studies have followed individual calves from birth to weaning (Gibson and Mann 2008a, 2008b; Stanton et al. 2011). A longitudinal study of Atlantic spotted

dolphins (*Stenella frontalis*) reports nursing until 3–5 years of age (Herzing 1997), whereas estimates using stomach contents from calves (killed in the tuna fishery in the eastern tropical Pacific) of the closely related Pantropical spotted dolphin (*Stenella attenuata*) indicate they are weaned much earlier, by 2 years of age (Archer and Robertson 2004). Probably all odontocete calves begin eating fish or squid well before weaning, and while otoliths (fish earbones) and squid beaks are readily identifiable in stomachs, milk is not so easy to detect (Oftedal 1997). Weaning ages are routinely underestimated based on bycatch, fisheries, and whaling data.

We reviewed the literature on 89 extant species of cetaceans (though 1 of these is listed as possibly extinct) and compiled the long-term studies, with emphasis on the continuous, longitudinal study of individuals. Of the 127 long-term studies of cetaceans, 68 of these have monitored individuals longitudinally (Supplementary Data SD1). Long-term study has helped us understand cetacean social structure and association (Wiszniewski et al. 2010; Elliser and Herzing 2014; Wells 2014; Gero et al. 2015), habitat use (Cañadas et al. 2005; MacLeod et al. 2008; Azzellino et al. 2012), anthropogenic impacts (Azevedo et al. 2009; Dungan et al. 2012; Fandel et al. 2015), life-history traits (Herzing 1997; Mann et al. 2000b; Brent et al. 2015; Gabriele et al. 2017), culture (Daura-Jorge et al. 2012; Mann et al. 2012; Riesch et al. 2012; Allen et al. 2013; Cantor et al. 2015), and communication and cognition (Sayigh et al. 1990; Connor and Mann 2005).

However, evident from our review of long-term studies of cetaceans is that we have much to discover about their behavior, life history, and ecology. The extent and types of research coverage is highly variable across all studies (longitudinal and non-longitudinal). Many species have traits that make them difficult to find, identify, and follow (such as being pelagic, deep-diving, solitary, or scarce), but the most accessible species have been studied at multiple locations. For example, the common bottlenose dolphin, *T. truncatus*, is the subject of several long-term studies (Supplementary Data SD1) off the coasts of Brazil, the Bahamas, California, Florida, New Zealand, Scotland, and Italy. As this species is found in the shallow, coastal habitats of most continents and is often residential, they are relatively convenient for longitudinal study. This summary focuses on the contributions of long-term studies to our understanding of the ecophysiology, social systems, population and community ecology, and conservation of cetaceans.

## ECOPHYSIOLOGY

Cetaceans have specialized physiology to cope with aquatic environments, especially related to breeding, diving, and foraging. For example, lactating female humpback whales convert prodigious amounts of energy stores into milk with a high fat content (30–50%—Oftedal 1997) for fast-growing calves that must make the long migration from warm waters to high latitudes. Long-term research has been critical for documenting the migration routes and critical habitat for baleen whale populations, as well as physiological and life-history traits

that support these annual cycles (Clapham 2000; Craig et al. 2014). For example, photo-ID catalogs maintained on humpback whales that move between the warm waters of Hawaii to the cold waters off of Alaska enable scientists to document individual life histories and to know that virtually all breeding occurs in warm waters and all feeding occurs in cold waters (Gabriele et al. 2017).

However, to study how physiological parameters change in response to the environment, it is necessary to sample blood, urine, feces, respiratory vapor, or tissue from individuals across time, a problematic feat for cetacean research. Samples from captive bottlenose dolphins can be useful for developing and validating field methods or observations, e.g., monitoring changes in reproductive state. Similar constraints exist in other mammalian groups, where researchers have been able to use non-invasive sampling of feces and even hair of terrestrial or arboreal species (Chapman et al. this issue; Kappeler et al. this issue). A few long-term studies have opened new avenues of research by repeated sampling of, for example, killer whale feces (Ford et al. 2016), bottlenose dolphin blow (Frère et al. 2010a), and sloughed skin of sperm whales (*Physeter macrocephalus*—Marcoux et al. 2007). Recent developments in biological sampling have the potential to advance our understanding of cetacean ecophysiology, but are still in their infancy.

For example, a study of bacteria from biopsies and freshly sloughed skin of humpback whales revealed how bacterial communities differ based on geographic and metabolic state of the whales. The bacterial communities differed depending on whether the whales were fasting or feeding, and in some cases entangled and dead individuals harbored pathogenic bacteria not found in free-swimming animals (Apprill et al. 2014). Such analyses could be excellent indicators of metabolic state, immune function, and animal health, as well as population membership (Apprill et al. 2014).

Similarly, scientists recently demonstrated that dolphin blubber can be used to obtain a good indicator of circulating cortisol concentrations (Champagne et al. 2017). This opens up new uses for remote biopsy sampling, which collects skin and blubber tissue from dolphins and whales, to determine responses to both chronic and acute environmental stressors, whether natural or anthropogenic. Such techniques have yet to be applied in long-term research on cetaceans.

## SOCIAL SYSTEMS

Cetacean social organization can be roughly characterized, following Kappeler and van Schaik (2002), as either solitary or group-living. No cetaceans are pair-living. Baleen whales are classified as solitary, including bowhead whales (*Balaena mysticetus*), sei whales (*Balaenoptera borealis*), fin whales (*Balaenoptera physalus*), blue whales (*Balaenoptera musculus*), Bryde's whales (*Balaenoptera edeni*), gray whales, humpback whales, right whales, and pygmy right whales (*Caperea marginata*—Dines et al. 2015). In contrast, all species of toothed whales live in groups, although adult males may be fairly solitary and roam between groups of females (e.g., sperm

whales—Christal and Whitehead 2001). On one extreme are several species that maintain close association for life in relatively stable pods or units, including killer whales (Baird 2000; Ford et al. 2000), sperm whales (Christal and Whitehead 2001; Gero et al. 2015), long-finned pilot whales (*Globicephala melas*) and short-finned pilot whales (*Globicephala macrorhynchus*—Amos et al. 1993; Kasuya and Tai 1993), false killer whales (*Pseudorca crassidens*—Baird et al. 2008), and pygmy killer whales (*Feresa attenuata*—McSweeney et al. 2009). These associations are based on the matriline, with daughters and sometimes sons remaining with their mothers into adulthood. Matrilineal units often split when they become large, but they may join up periodically depending on feeding or social contexts (e.g., mating occurs between killer whale pods during temporary encounters—Baird 2000; Ford et al. 2000). On the other extreme are bottlenose dolphins, with high fission–fusion dynamics whereby groups change membership many times daily (Tsai and Mann 2013). The spatial and temporal fluidity and complexity of many cetacean social systems discovered through long-term study has inspired innovative and influential approaches to the study of animal social systems, especially using social network analysis (Lusseau 2003; Whitehead 2008).

Social structure can be considered at multiple levels, from fleeting associations to stable groups embedded in a larger population. While populations may be delineated by geographic location or genetic sampling, determination of social units within a population depends on observation. Most researchers on cetaceans define social groups, i.e., who is associated with whom, based on spatial behavior and activity. For example, animals within 100-m radius might be considered members of the same group, or those moving in the same direction or engaged in the same activity also might be considered group members. Such assessments are especially difficult for some pelagic delphinids (such as common dolphins, *Delphinus delphis*, and Atlantic spotted dolphins—Jefferson et al. 2008) that often occur together in the hundreds or thousands. Furthermore, these definitions depend greatly on the human observer's ability to identify group members (spatial clustering) rather than on the cetacean's social experience. For example, if social communication were used to define social units or groups, unit boundaries would be difficult to determine for most odontocetes, whose calls can carry be heard for several kilometers, and impossible to determine for baleen whales, who use low frequency (< 100 Hz) communication that travels over hundreds of kilometers (e.g., fin whales—Clark and Gagnon 2002).

At a macro-level, genetics can help define population or community structure, especially when long-term data are absent. For lesser-known species, such as Gray's beaked whale (*Mesoplodon grayi*), genetics has been the only mechanism for understanding population structure across vast areas of ocean (Thompson et al. 2016). Long-term studies have contributed substantially to our understanding of cetacean social structure, but are best combined with genetic sampling, given the expansive spatial behavior common to so many cetacean species. Fidelity to natal or breeding sites is often used by scientists to define social structure (network or community composition),

but this can be hard to assess when an animal travels many thousands of kilometers (Stevick et al. 2011). Despite these challenges, there are 3 genera (bottlenose dolphins, killer whales, and sperm whales) which have been studied for decades and which illustrate strikingly complex social structures.

*Bottlenose dolphins.*—Two longitudinal studies, 1 in Florida (Wells 2014) and 1 in Shark Bay, Australia (Mann et al. 2012), highlight extreme fission–fusion dynamics. For example, sizes of dolphin groups in Shark Bay average 4–5 animals (Gibson and Mann 2008b), and group composition can change 4–10 times per hour, even while maintaining long-term same-sex bonds of variable strength within subcommunities embedded in a large network (Mann et al. 2012). This population also has multilevel male alliances (pairs or triplets of males in alliances that cooperate with other alliances) lasting from a few years to decades (Connor and Krützen 2015). Females form more fluid bonds that are embedded in strong female networks based on kinship, spatial proximity, and other factors. Remarkably, females form bonds based on shared practices, such as tool-use with marine sponges, a pattern that appears to be distinctly cultural (Mann et al. 2012). Tool-use with sponges has been well documented in Shark Bay and represents the best known case of tool-use in any wild cetacean. About 5% of the female dolphins in the Shark Bay population regularly forage by wearing basket sponges on their beaks, which they use as protection and to assist in finding bottom-dwelling prey. The behavior is restricted to deep-water channels and is vertically transmitted from mother to offspring, particularly daughters (Mann and Patterson 2013). In addition to showing social preferences based on behavioral traits, demographic factors such as sex, age, genetic relatedness, and reproductive status also play an important role in social relationships and structure (Gibson and Mann 2008a, 2008b; Frère et al. 2010b; Mann et al. 2012).

Unlike most mammals, bottlenose dolphins are 1 of several species of cetaceans that are bisexually philopatric, where females show social philopatry (continued association with the mother) and both sexes show locational philopatry (remaining in their natal area—Tsai and Mann 2013). Genetic methods are often used to determine dispersal patterns, but they must also account for mating patterns (Prugnolle and De Meeûs 2002). For example, although Shark Bay dolphins are clearly residential (Tsai and Mann 2013), genetic data suggest that males disperse (Krützen et al. 2004). Longitudinal research shows that males range widely in search of females (Connor and Krützen 2015), often taking females far from their core home ranges during consortships (Wallen et al. 2016). During consortships, male alliances escort and guard an individual female for days and occasionally weeks, during which they attempt mating. The consortships are often marked by aggression directed at the female, particularly if she tries to escape (Connor et al. 1996). The fact that females are escorted away from their core home ranges (but males are typically within their core home ranges) helps explain conflicting results, i.e., that males disperse based on genetics, but are philopatric based on behavior. Put simply, males will temporarily move into areas outside of their typical range to find females and escort them back to their core

area. Combined genetic and behavioral methods are preferable to using only 1 strategy for determining social and mating patterns. The dolphins in Shark Bay represent 1 of the best-studied cetacean mating systems, where males form alliances to compete with other male alliances for access to females (Connor et al. 1996; Connor and Krützen 2015). Allied sexual coercion is evident based on longitudinal study. Scars seen on females were noted as evidence of aggression by males (since aggression by females is virtually absent). Cycling females had many more fresh scars from aggression by males than non-cycling females (Scott et al. 2005), and direct attacks on cycling females have been observed (Connor et al. 1996). Long-term alliances in bottlenose dolphins have been documented at a number of other research sites (Owen et al. 2002; Parsons et al. 2003; Wiszniewski et al. 2012) and may function similarly in mating systems of other cetaceans such as spotted dolphins (Elliser and Herzing 2014).

*Killer whales.*—Long-term study of killer whales in the northeast Pacific has revealed not only distinct ecotypes, but ecotype-specific dispersal patterns. Fish-eating killer whales maintain stable matrilineal groups in which sons and daughters remain with their mothers for life, in contrast to sympatric mammal-eating killer whales in which all daughters disperse, but some male offspring remain with the mother (Baird 2000). That is, the fish-eating ecotype has social and locational bisexual philopatry, whereas the mammal-eating ecotype has female-biased social dispersal, but locational bisexual philopatry. Another rare feature revealed through longitudinal study is that killer whales exhibit menopause (Brent et al. 2015). Killer whales, which can survive into their 90s, typically become sexually mature around the age of 12 years but females cease reproduction in their 40s (Olesiuk et al. 1990). Recent studies relying on long-term data sets explore the possible roles of these post-reproductive females: Foster et al. (2012a) found that post-reproductive females have considerable impact on survival of adult offspring; Brent et al. (2015) suggest that post-reproductive females confer such benefits through social transmission of ecological knowledge. Further research on age-specific behavior of females is needed to understand the adaptive significance of an extended post-reproductive life span.

*Sperm whales.*—Similar to elephants, sperm whales have a multilevel hierarchical organization based on matrilineal units that are closely associated; these units have been studied for decades (Gero et al. 2015). The most basic unit is several females and their offspring (calves and juveniles), considered a maternal or family group or unit. These family units have common associations with other units from their matriline that can last from a few hours to several days. At a higher level, a large number of family units constitute vocal clans that can include hundreds of units and thousands of individuals. Clans might spatially overlap with other vocal clans, but they do not associate with one another (Gero et al. 2016). Males leave their group before reaching sexual maturity and associate in temporary “bachelor” groups or remain alone. In a comparison of populations of Atlantic and Pacific sperm whales, Whitehead and colleagues (2012) argue that differences in social patterning and

behavior are driven by 3 factors: cultural differences, predation, and whaling practices. The cultural differences refer to shared practices that were socially inherited for generations. An 18-year empirical study of sperm whales shows that the multilevel complexity of sperm whale societies is driven primarily by cultural transmission (Cantor et al. 2015). In the Pacific, sperm whales experience higher predation pressure from killer whales than in the Atlantic and this is related to differences in group size. Finally, although historical whaling practices decimated populations worldwide, recovery rates have been particularly slow and even declining in the Atlantic compared to the Pacific for reasons that are not completely understood (Gero and Whitehead 2016).

### POPULATION AND COMMUNITY ECOLOGY

Studies of cetacean community ecology have been somewhat limited, in part because oceans are not amenable to the same kinds of experiments that are standard for research in terrestrial and coastal ecosystems. Predator–prey interactions between tiger sharks (*Galeocerdo cuvier*) and bottlenose dolphins have been well documented and illustrate the impact of apex predators on dolphin foraging and habitat use (Heithaus and Dill 2002). A number of long-term studies have examined population dynamics and community ecology but have not tracked individual life histories (Supplementary Data SD1). For example, a 19-year study of 4 baleen species (blue, fin, humpback, and minke—*Balaenoptera acutorostrata*—whales) showed trophic partitioning among these populations in that each species consumed different proportions of common prey in the NW Atlantic (Gavrilechuk et al. 2014). Because cetaceans live for decades, even centuries (George and Bockstoe 2008), longitudinal studies on population ecology and dynamics are limited, with some exceptions.

Killer whales in the NE Pacific show marked shifts in population dynamics and network structure in response to salmon abundance (Foster et al. 2012b). In this study, scientists examined long-term data on abundance of chinook salmon (*Oncorhynchus tshawytscha*) relative to social network dynamics of killer whales from 1984 to 2007. In years of high salmon abundance, network connectivity was high, meaning that killer whales aggregated more. Despite these fluctuations, the Southern Resident populations of killer whales in the NE Pacific have been declining and were listed as endangered since 2005, largely due to nutritional and other stresses (Lundin et al. 2016).

Perhaps the best-known study of the impact of cetaceans on biotic communities also comes from the NE Pacific, in the Aleutian archipelago, where killer whale predation on sea otters (*Enhydra lutris*) created a trophic cascade that allowed for dramatic growth in sea urchin populations, which decimated the kelp forests upon which many organisms depend (Estes et al. 1998). In the early 1990s, killer whales dramatically increased their predation rate on sea otters. Although the exact cause of this dietary shift is not known, it was linked to severe population declines of the killer whale's main prey—Stellar sea lions

(*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*). Not surprisingly, when killer whales began to prey regularly on sea otters, the sea otter population sharply declined. Because sea otters are key predators on sea urchins, the sea urchin populations exploded, which in turn caused kelp forests, upon which sea urchins graze, to collapse.

Centuries of commercial whaling decimated cetacean populations worldwide (Baker and Clapham 2004). To estimate their recovery and determine how to sustainably manage existing species, population modeling has been crucial. This involves reconstructing historical population sizes based on whaling records, establishing intrinsic rates of increase, molecular sampling, and determining current abundance. Each method is subject to some error or bias. For example, Soviet and Japanese whalers routinely falsified catch records. Intrinsic rates of increase are based on limited demographic data where variation within and between populations is largely unknown. Improved estimates of life-history parameters from longitudinal research will greatly enhance population modeling. For example, individual variation in female reproductive rate and calf survival is critical for understanding population growth and viability (Manlik et al. 2016).

### CONSERVATION

The precipitous deterioration of oceans, estuaries, and rivers throughout the world is an urgent matter for both humans and cetaceans. Climate change has brought us warmer oceans, particularly in the last few decades, with the oceans absorbing 93% of the extra heat trapped in our atmosphere since 1970 (Wijffels et al. 2016). Critically, this warming is linked to the collapse of phytoplankton and zooplankton, upon which all marine species ultimately depend (Boyd et al. 2015). Cetaceans, as apex predators, have considerable influence on the ecological and evolutionary dynamics of prey populations and have been called “ecosystem engineers” because of their disproportionate impact (Roman et al. 2014). These impacts include physical engineering of ocean environments, such as when gray whales plow the seafloor during benthic feeding on crustaceans. Nutrient transfer occurs through release of fecal matter, urine, placental tissue, and carcasses, which in turn impacts productivity in marine environments. Whale falls (when carcasses sink and deposit on the seafloor) provide habitat structure and organic material. Cetaceans can have a disproportionate influence on food web interactions, as indicated by the killer whale–sea otter example described. Given the extensive movements of many cetacean species, these impacts are global, reaching from the Arctic to Antarctica.

Recently, networks of Marine Protected Areas have become the primary approach in marine conservation by the International Union for Conservation of Nature (IUCN—Laffoley et al. 2008), due to the urgent need for large-scale holistic approaches rather than studies of 1 area or 1 species at a time. Marine Protected Areas are coastal or offshore areas designated for management and protection due to their significant conservation, ecosystem services, or cultural values. These

areas are critical for protecting important breeding habitats, biological diversity, and a range of other services including nature-based tourism and recreation.

The IUCN Cetacean Specialist Group has assessed 87 of 89 cetacean species, but more than half are deemed “data deficient” (International Union for Conservation of Nature 2014). Seven species are endangered, including the Ganges river dolphin (*Platanista gangetica*), Hector’s dolphin (*Cephalorhynchus hectori*), and the sei, blue, fin, North Atlantic right, and North Pacific right whale (*E. japonica*). In addition to anthropogenic decline in marine habitats, cetaceans are directly targeted and exploited by fisheries, the entertainment industry (aquaria displays and shows), and are incidentally harmed by chemical and sound pollution (Laist et al. 2001), bycatch, or other fishery activities (Lewison et al. 2014). For example, pollution and harmful fishing practices caused the functional extinction of the Yangtze River dolphin (*Lipotes vexillifer*) in 2006 (Turvey et al. 2007). Chemical pollution such as organochlorine compounds accumulate in their blubber, which females depurate in milk to their 1st offspring, which in turn suffer high mortality than later-born offspring (Wells et al. 2005), a result only known through longitudinal study.

Long-term studies and data on stranding events have been critical in identifying major mortality events and their causes. For example, chemical pollution caused an unusual (mass) mortality event among common bottlenose dolphins in the Gulf of Mexico following the Deepwater Horizon oil spill. The Deepwater Horizon oil spill was a catastrophic event that stemmed from an explosion of an oil rig in 2010, resulting in the largest recorded marine oil spill in history with over 210 million U.S. gallons of oil leaking into the Gulf of Mexico. Dolphins impacted by the spill were more likely to have reproductive failure (Kellar et al. 2017), bacterial pneumonia, and thinner adrenal cortices than dolphins in areas not impacted (Venn-Watson et al. 2015).

Long-term studies have documented unsustainable demographic and behavioral shifts as a consequence of human activity. For example, a 17-year study of Amazon river dolphins (*Inia geoffrensis*) revealed that the harvesting of river dolphins for catfish bait, occurring since 2000, is not sustainable due to decreasing survival of river dolphins compared to pre-harvest years (Mintzer et al. 2013). A 13-year study of short-beaked common dolphins, one of the most common species of cetaceans in the Mediterranean, analyzed the impact of various fisheries techniques on removal of biomass in the Ionian Sea. Bearzi et al. (2008) found that purse seiners had the greatest impact on the prey of common dolphins, with only 10 individual purse seiners contributing to 33% of the removal of biomass. This prey depletion resulting from overfishing has caused significant population declines of short-beaked common dolphins and the IUCN listing the species as endangered in 2003. Habitat destruction is linked to changes in social dynamics and ranging patterns among Indo-Pacific humpback dolphins (*Sousa chinensis*—Dungan et al. 2012). This 10-year study examined the distinct social structures of 2 overlapping communities of Indo-Pacific humpback dolphins in the Pearl River Estuary bordering Hong Kong, and found that the habitat loss from the

construction of an international airport may be responsible for the changing ranges of individuals, especially breeding females, from the north to the west of the estuary. This habitat degradation and the blocking of access to alternative habitats threaten the viability of this population. Esteban et al. (2016) compared the survival, calving rate, calving interval, and population growth rate between killer whales in the Strait of Gibraltar with different foraging tactics from a 13-year data set. This study found differences in these demographic parameters between killer whales that actively hunt and those that depredate (remove prey from long lines) from bluefin fisheries. Although all killer whales actively hunted, those that also depredated tuna from long lines had higher adult survival and calving rates than those that did not. Furthermore, killer whales that did not depredate from long lines were in sharp decline. These disparities suggest an effect of the fisheries on the vital rates of this population. Finally, when a 14-year longitudinal study in Shark Bay found a decline in dolphin abundance attributable to increasing dolphin-watching tourism (Bejder et al. 2006), the Australian Department of Parks and Wildlife took direct action to mitigate impacts by restricting the activities of local tour operators. A study on the effectiveness of this approach is ongoing. Longitudinal research offers essential guidance for development of sustainable practices, especially concerning fisheries and tourism.

## FUTURE DIRECTIONS

Clearly there is a need for detailed longitudinal study of cetaceans as they represent an important mammalian group given their extreme adaptations to marine environments, impact on ecosystems (such as sperm whales, which consume more squid biomass worldwide than all human fisheries combined—Santos et al. 2001), complex societies, large brains, and prolonged life histories. Longitudinal research is critical to understanding unusual phenomena such as why menopause occurs in killer whales and short-finned pilot whales, but not in other closely related species. Similarly, brain size of 2 sympatric species of Amazonian dolphins (Dos Santos et al. 2012) is approximately the same (634–688 g), even though the Amazon river dolphin, at a body mass of 92 kg is more than twice the size of the tucuxi (*Sotalia fluviatilis*) at 42 kg (Hof et al. 2005). Surely, in addition to phylogenetic analysis, long-term socio-ecological studies help identify selection pressures that favor variation in morphological traits. Given the depth and complexity of the knowledge we have of cetaceans revealed by systematic long-term study, the continuation of these types of continuous and longitudinal field studies will provide the most complete picture of their lives. Although advanced technologies are critical for accessing pelagic and deep-diving species, investments in long-term research and data sets are fundamental to revealing what lies beneath the surface of these beguiling mammals.

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### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Table of all extant cetacean populations with continuous and systematic long-term ( $\geq 10$  years) studies.

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