Chapter 24
Cetacean Sociality, Reproduction, and Conservation

Sarah L. Mesnick, Randall R. Reeves, Paul R. Wade, Philippa Brakes, and Taylor A. Hersh

Abstract The world's cetaceans (like most of biodiversity) are in crisis, and the need for well-informed conservation action has never been greater. Scientific advancements over the last few decades have provided much insight on the reproductive anatomy, physiology, and behavior of whales, dolphins, and porpoises. Our goal in this chapter is to link scientific findings to practical actions that will improve resilience and conservation prospects of cetaceans. We provide an overview of human activities and their impacts on cetacean reproduction and review the progress (or lack thereof) toward conserving species, with a particular focus on those for which sociality and culture may be important to population recovery. For all cetaceans, it is important to preserve or, where necessary and feasible, reestablish the ecological, demographic, and social conditions that allow the animals to reproduce successfully in their natural environment. The better we understand and integrate knowledge concerning cetacean reproductive health into conservation strategies, the better the chances of achieving species recovery, protecting biodiversity, and preventing future extinctions.

S. L. Mesnick (✉)
Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, CA, USA
e-mail: sarah.mesnick@noaa.gov

R. R. Reeves
IUCN SSC Cetacean Specialist Group, Okapi Wildlife Associates, Hudson, QC, Canada

Committee of Scientific Advisers, Marine Mammal Commission, Bethesda, MD, USA

P. R. Wade
Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA

P. Brakes
Centre for Ecology and Conservation, University of Exeter, Cornwall, UK

Whale and Dolphin Conservation (WDC), Chippenham, Wiltshire, UK

T. A. Hersh
Comparative Bioacoustics Group, Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands

B. Würsig, D. N. Orbach (eds.), *Sex in Cetaceans*,
https://doi.org/10.1007/978-3-031-35651-3_24

Keywords Anthropogenic noise · Bycatch · Cetacean · Climate change · Conservation · Fecundity · Human impacts · Insemination · Mating · Recovery · Reproduction · Resilience

24.1 Introduction

Like most of biodiversity, the world's cetaceans are in crisis and the need for well-informed conservation action has never been greater. Scientific advancements over the last few decades have improved our knowledge of reproductive anatomy and physiology, mating behavior, and parental care of many species of whales, dolphins, and porpoises. Our goal in this chapter is to link these scientific findings to practical actions that will improve conservation prospects for cetaceans.

Human impacts on, attitudes toward, and relationships with cetaceans have changed over time (Notarbartolo di Sciara and Würsig 2022). Commercial whaling, essentially ended since the mid-1980s, killed millions of baleen whales (mysticetes) and sperm whales (*Physeter macrocephalus*, an odontocete) (Rocha et al. 2014) and sparked global conservation efforts (Fig. 24.1). Drive hunts of small- and medium-sized cetaceans continue in a few regions (e.g., Japan, Faroe Islands, Solomon Islands), but the most serious known obstacle to conserving small cetaceans is incidental mortality in fishing gear (i.e., bycatch) (Read et al. 2006; Brownell et al. 2019). Non-deliberate killing and injuring have also hindered or prevented the recovery of some species and populations of large whales (Johnson 2005; Knowlton et al. 2016). In addition to mortality in fishing gear, the energetic cost of nonfatal entanglement—due to drag from towing gear—can influence a pregnant or lactating whale's energy budget, increase the time needed for her to replenish her energy stores, and ultimately lengthen the birth interval by months or years (van der Hoop et al. 2017; Stewart et al. 2022). There are numerous other sublethal threats, that cetaceans face including habitat loss and degradation, depletion of prey, anthropogenic noise and disturbance, biotoxins, and pathogens. Climate change heightens the threats facing cetaceans through direct, indirect, and cascading effects on habitat, prey, predators, and human activityies in our oceans, rivers, and lakes (Gulland et al. 2022).

The reproductive health of some populations of mysticetes is apparently quite good as they are recovering from the impacts of commercial whaling (Thomas et al. 2016; Fig. 24.2). However, some species of toothed cetaceans (odontocetes) appear less capable than mysticetes of recovering from the severe depletion caused primarily by direct removals through whaling, hunting, and fishery bycatch (Wade et al. 2012; Whitehead and Shin 2022). Wade et al. (2012) suggested that this apparent difference in resilience is at least partly due to the effects of exploitation on highly social odontocetes, including, for example, social disruption, fragmentation of social units, and loss of key individuals. In this chapter, we revisit, update, and expand on these ideas. We do not assume that humans can improve upon what the cetaceans have evolved to do themselves with regard to reproduction. Rather, we consider an important role of conservation biologists is to find ways to preserve, or reestablish,

Fig. 24.1 A large male sperm whale socializing with a group of females and young in waters off the island of Dominica in the Caribbean Sea. Sperm whales are the most sexually dimorphic cetacean in body size. The male's gigantic nose, which is the largest sexually selected organ on the planet (Cranford 1999), contains the spermaceti organ complex, the world's most powerful natural sonar system. The valuable spermaceti oil was part of the impetus for two massive waves of commercial whaling that targeted sperm whales (along with large baleen whales). Post-whaling, population trajectories are varied. Sperm whale populations facing minimal human impact are recovering slowly, but the lingering impacts of whaling may be impeding recovery in some areas by affecting the sex ratio and/or the social cohesion of females. In populations currently experiencing anthropogenic impacts, calving rates are declining (Whitehead and Shin 2022). Photo: ©Flip Nicklin/Minden Pictures; 1994. All rights reserved

the environmental, demographic, and social conditions that would enable cetaceans to reproduce successfully.

As noted by van der Hoop et al. (2017, p 103), "Historically, whale conservation measures have focused on reducing mortality; a shift is required to also address morbidity and the sublethal impacts on individuals and their reproductive rates."

Fig. 24.2 A singing male humpback whale, Maui, Hawaii. Many humpback whale populations have recovered from commercial whaling and some populations are increasing at maximal rates of about 7% per year (Calambokidis et al. 2008; Calambokidis and Barlow 2020). Humpback whale songs are once again reverberating through the ocean soundscape on traditional mating grounds and migratory routes where males sing complex, evolving songs (Darling et al. 2019). While their function and relationship to other aspects of male reproductive behavior remain largely unknown, songs indicate some degree of association between individuals and are generally thought to play a role in breeding (Darling et al. 2019). As human activities in the oceans increase, ambient noise levels are rising too, with potential impacts on communication space for humpback whale song. Photo: ©Flip Nicklin/Minden Pictures (NOAA Fisheries permit #19225); 2020. All rights reserved

Many approaches to the management of human-caused mortality involve calculation of reference points, which are considered "best practice" for managing bycatch and other human-induced mortality (Wade et al. 2021). The "potential biological removal" (PBR) level is one specific reference point used in the United States to meet the objectives of the Marine Mammal Protection Act (Wade 1998). PBR input values are designed to account for population differences in reproduction (see Box 24.1), which theoretically allows for the PBR approach to accommodate cases where a population's reproductive rate has been decreased by sublethal human-caused factors.

Our specific objectives are to (1) define resilience in the context of cetacean reproductive health and conservation, (2) review progress on understanding the social conditions necessary for maximizing cetacean reproductive success, (3) summarize the accumulating evidence showing that aspects of cetacean "reproductive health" (fecundity, mating, survival of young) can be impacted by human activities, and (4) suggest ways of using knowledge about cetacean reproductive health to improve management models and strengthen conservation actions and outcomes.

24.2 Resilience

Wade et al. (2012) defined resilience as the ability of a cetacean population to recover from extreme depletion (very low numbers), the condition that some of the large baleen whales had reached by the time commercial whaling was either brought under strict control or otherwise banned. Such use of the term comports with that of psychologists, who regard resilience as a construct with two distinct dimensions, namely, significant adversity (e.g., whaling) and positive adaptation (e.g., ability to recover) (Fleming and Ledogar 2008; see also Hodgson et al. 2015).

Wade et al. (2012) evaluated species or population differences in resilience to extreme depletion. Moore and Reeves (2018) applied the concept of resilience to the ability of cetaceans to adapt to the effects of climate change. Here, we extend this thinking to examine the resilience of cetaceans to disruption of, or damage to, their reproductive health and how behavioral and physiological plasticity, and sociality, may play a role in aspects of reproductive success. Reproductive health can be impaired by some of the same factors that determine an organism's survival (e.g., bycatch, ship strike, acute disease, toxicity), but there are several additional forms of "significant adversity" that affect reproduction itself (e.g., decreased fertility due to high pollutant burden, sublethal injury, or chronic disease, inadequate nutrition, social disruption). Although survival has generally been viewed as the most pertinent parameter for long-lived animals, it is likely that reproduction is just as (or even more) important and relevant in some cases (Manlik 2019).

24.3 The Social Context of Reproduction

Social living can enhance resilience in an increasingly human-dominated ocean (Brakes and Rendell 2022). Here we briefly review our understanding of sociality and its importance to cetacean reproductive health but also how it can increase vulnerability to disruption by human activities. Perrin et al. (1984) and numerous chapters in this book provide examples of how cetaceans may adapt their reproductive strategies depending on body condition, age, and dominance status (Chivers and Danil 2023, this book; Manitzas Hill et al. 2023, this book). Much has also been written about density-dependent changes in female reproduction following commercial exploitation or high levels of incidental mortality in fisheries (reviewed in Hohn et al. 2007). Density-compensatory changes in reproductive parameters, such as decreased age at sexual maturation and increased rates of ovulation and calving following intense harvest or fisheries bycatch, are generally attributed to changes in prey resources (Fowler 1981, 1984; Hohn et al. 2007). Less focus has been given to the impacts of sublethal anthropogenic impacts on reproductive rates, which may result in delayed age of first reproduction, longer interbirth intervals, and/or extended lactation (e.g., Cramer et al. 2008; Ward et al. 2009; McGuire et al. 2020; Stewart et al. 2022).

Despite the attention that social behavior garnered in the early years of conservation biology (Allee 1931; Ehrenfeld 1970) and recently renewed attention (Brakes et al. 2021; Brakes and Rendell 2022), consideration of animal sociality is complex and not easily integrated into conservation actions. Reduction of a local population to a very small size can exacerbate Allee effects ("undercrowding" or density-decompensation; reviewed in Stephens and Sutherland 1999) and even lead to population collapse (Gilpin and Soulé 1986). When population size is greatly reduced, individuals can have difficulty finding one another for mating (Gascoigne et al. 2009). Antoniou et al. (2018) suggested that a high observed incidence of introgressive hybridization in the Gulf of Corinth, Greece, between an extremely depleted, geographically isolated population of common dolphins (*Delphinus delphis*) and a less depleted and comparatively large local population of striped dolphins (*Stenella coeruleoalba*) was due to the scarcity of conspecific mates, a situation referred to as the Hubbs principle, also known as the "desperation hypothesis" (Hubbs 1955). For some species, returning regularly to a specific location could be a mechanism for ensuring that mates can be found. This may be the case for humpback whales (*Megaptera novaeangliae*), which congregate around tropical and sub-tropical islands in winter, although humpbacks may in fact mate during migration as well (Darling et al. 2019). Reductions to extremely low population sizes can also lead to inbreeding, which has been identified as a factor potentially impeding the recovery of one population of eastern North Pacific salmon-eating killer whales (*Orcinus orca*) (Lacy et al. 2017; Ford et al. 2018; Kardos et al. 2023).

Group living has numerous benefits (Gowans 2019). For mating and reproduction, these include the ease of finding and assessing a suitable mate, such as in dusky dolphins (*Lagenorhynchus obscurus*) that engage in scramble competition (Orbach et al. 2014) and in Amazon river dolphins (*Inia geoffrensis*) that gather in lek-like aggregations (Martin et al. 2008; da Silva and Spinelli 2023, this book). The formation of dominance hierarchies among males presumably confers preferential access to mates and enables females to mate with fit and dominant males (e.g., beaked whales, Alves et al. 2023, this book; narwhals (*Monodon monoceros*), Graham et al. 2020; Fig. 24.3). Alliance formation, such as in male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), provides advantages over rivals and facilitates control of females (Connor 2007), and male "squads" of offshore pantropical spotted dolphins (*Stenella attenuata attenuata*) may play a role in social ordering and reproduction (Pryor and Shallenberger 1991; Mesnick et al. 2019; Fig. 24.4). Communal calf care and defense against predators are some of the many benefits females may derive from group living; these groups may be temporary or long-lasting associations (Wells 2003; Whitehead 2003; Konrad 2019; Mesnick et al. 2019).

When sociality is disrupted, mating, fecundity, and the ability to raise young can be compromised. Populations of highly social species may take longer than expected to recover from depletion if individuals that enhance reproductive success, such as dominant males and female matriarchs, have been lost. Some populations of sperm whales, for example, have not recovered since the end of commercial whaling, perhaps due to the lingering demographic effects of the removal of large males on

Fig. 24.3 "Tusking" male narwhals, Baffin Island, Nunavut, Canada (1985). The tusk of the narwhal, which is actually a greatly enlarged left-spiraling upper left tooth, usually erupts only in males and can exceed 3 m in length. The tusk likely functions as a signal and a weapon during aggressive disputes between rivals (Graham et al. 2020). Narwhals are hunted for their tusks, which are in demand from distant markets, and for their skin which is valued by Inuit as a nutritious delicacy (Heide-Jørgensen 2018). Some populations are still overexploited even though quotas are now established for nearly all areas where narwhals are hunted. A host of other threats are increasing. Noise from vessel traffic, seismic surveys, ice-breaking, fishing, and other sound sources may disturb and stress the whales and decrease their fecundity (NAMMCO 2021). Photo:

reproduction, while other populations face present-day threats to female social cohesion and pregnancy rates (Whitehead et al. 1997; Gero and Whitehead 2016; Whitehead and Shin 2022). In the eastern tropical Pacific, repeated chase, encirclement, and release of dolphins in the tuna purse seine fishery can cause separation of mothers and calves and decrease weaning and pregnancy rates (Archer et al. 2004) and have negative effects on female reproductive rates (Cramer et al. 2008, Kellar et al. 2013). In one of the populations impacted by the fishery, eastern spinner dolphins (*Stenella longirostris orientalis*), only a tiny fraction of males examined reached fully active testes weights and were thus likely capable of successful mating, a situation that suggests a polygynous mating system that could be susceptible to perturbation by the fishery (Perrin and Mesnick 2003).

Although the degree to which mating and rearing strategies in cetaceans are socially learned is unknown, there are hints that some aspects are socially transmitted, such as the socio-sexual "dances" within the lek-like aggregations of Amazon river dolphins, where males wave objects in the air, possibly to attract or impress females (Martin et al. 2008; Fig. 24.5). Baleen whales are dispersed over vast areas, which could make locating a suitable mate challenging. Social learning of the timing

Fig. 24.4 Adult male subgroup of offshore pantropical spotted dolphins in the eastern tropical Pacific Ocean. An individual from another adult male subgroup rising from below gapes his jaws in an apparent threat gesture at the group passing over him. Dominant adult male "squads," all with prominent post-anal keels, heavily spotted bodies, and striking facial coloration, swim in precision while other individuals move aside. We know little about the function of these squads, but observations suggest they have a role in social ordering and reproduction (Pryor and Shallenberger 1991). Chase, encirclement, and release from tuna purse seines likely disrupts these and other subgroups in the (Wade et al. 2012; Mesnick et al. 2019). Photo: Karen Pryor; 1979

and routes of migration between feeding and breeding habitat (Carroll et al. 2015), as well as horizontally transmitted song patterns (Garland and Carroll 2022), may have evolved in part to ameliorate the problems associated with long-distance dispersal, although the role of song in male-male interactions, mate selection, and assortative grouping remains enigmatic (Darling et al. 2019; Garland and McGregor 2020; Fig. 24.2). Remarkably, male humpbacks in a population sing fundamentally the same song at any one time, and the song progressively evolves over the course of a season, and over years (Darling et al. 2019). How this is accomplished is not clear, but apparently it involves mutual melding or adoption, which are forms of cultural transmission (Noad 2011; Darling et al. 2019). Similar mechanisms of vocal learning may occur in blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) (McDonald et al. 2006; Archer et al. 2020), in which males typically sing the same song within a region, and in other baleen whale species that sing (Cerchio 2022; Risch 2022), although there is variation in the degree of social conformity and individual innovation among species (Stafford 2022). The importance of social learning is also evident in the evolution of post-reproductive lifespans in killer

Fig. 24.5 Displaying Amazon river dolphin or boto. Surrounded by other adult males and females, an adult male boto waves vegetation, or sometimes a lump of clay, above the surface of the water in a ritualized "dance", which has been interpreted as being part of a socio-sexual display within a lek-like mating system (Martin et al. 2008; da Silva and Spinella 2023, this book). In the folklore and culture of some Amazonian people, botos were feared and accorded supernatural powers and, as a result, were rarely hunted. Today, however, botos face many threats, including bycatch in fishing gear, directed hunts, and hydroelectric dams that fragment populations and increase the risk of local extirpations (da Silva et al. 2023). A reduction in the number of individuals in the population could impact the frequency and social context of display. Photo: Projeto Boto, Mamirauá Sustainable Development Reserve, Amazonas, Brazil

whales and short-finned pilot whales (*Globicephala macrorhynchus*) (Croft et al. 2015). The fitness benefits are revealed by higher offspring survival rates when post-reproductive mothers or grandmothers are still alive (Nattrass et al. 2019). In killer whales, socially inherited ecological niches and cultural traditions can influence mating patterns, which in turn can drive evolutionary divergence of ecotypes (Riesch et al. 2012; Foote et al. 2016; Ford 2019).

The costs of disrupting the transmission of socially learned behavior associated with reproduction can have both short-term and lasting consequences. For example, anthropogenic noise can decrease communication space and mask male song for baleen whales (Clark et al. 2009) or displace singers (Cerchio et al. 2014), while the loss of older individuals with knowledge of traditional feeding and breeding grounds and migratory routes could explain why some formerly important habitat of sperm whales and right whales remains deserted despite the cessation of commercial whaling (Kraus and Rolland 2009; Whitehead 2010).

As climate anomalies such as marine heatwaves become more common, our understanding of how such events affect cetacean reproductive health needs to keep pace. In some cases, social learning can provide opportunities for increased ecological resilience, by providing a behavioral buffer to ecological change (Brakes and Rendell 2022). This is evident when looking at socially transmitted foraging strategies, which ultimately translate to individual fitness and reproductive potential. For example, in Indo-Pacific bottlenose dolphins in Western Australia, diverse foraging strategies for some social groups appeared to buffer against the cascading effects of a marine heatwave on the food web (Wild et al. 2019).

24.4 Human Activities and Their Impact on Cetacean Sociality and Reproduction

It is difficult to identify and quantify all the ways by which human activities disrupt cetacean reproductive health. One major mechanism is by killing or otherwise removing animals from the population, which means that key individuals disappear suddenly; any social structure that exists, in terms of group size or composition, is changed abruptly (Williams and Lusseau 2006). Sublethal impacts are more difficult to identify and subtle in their effects on fecundity, behavior, and sociality. Human activities can cause, either directly or indirectly, the fragmentation of social groups, disruption of social behavior, and the loss of key individuals (Lusseau and Newman 2004; Williams and Lusseau 2006; Wade et al. 2012). The effects on reproductive health can be long-lasting, nonlinear, and unpredictable (Wade et al. 2012).

Table 24.1 summarizes some examples of how human activities disrupt aspects of cetacean reproductive health. Disruptive processes rarely take place in isolation. For example, in the eastern North Pacific, the multiplicity of anthropogenic impacts (e.g., Chinook salmon (*Oncorhynchus tshawytscha*) depletion, high levels of contaminants, vessel noise and disturbance, history of live-capture removals) and intrinsic processes (e.g., inbreeding, cultural isolation) confound efforts to understand the root causes of one salmon-eating killer whale population's failure to recover (Lacy et al. 2017; Murray et al. 2021; Kardos et al. 2023). The following case studies illustrate the cumulative impacts of multiple disruptive processes affecting two endangered cetacean populations.

24.4.1 Beluga Whales

Beluga whales in Cook Inlet, Alaska, USA, comprise a small, genetically distinct (O'Corry-Crowe et al. 1997) and geographically isolated population with year-round site fidelity to the inlet (Laidre et al. 2000; Fig. 24.6). The population declined dramatically in the 1990s, primarily due to overhunting (Mahoney and Shelden

Table 24.1 Evidence demonstrating or suggesting human impacts on cetacean reproductive health, some examples

Aspect of reproductive health affected	Species/population and location	Human activity	Evidence	Reference(s)
Whaling				
Insemination	Sperm whales, eastern tropical Pacific	Whaling (selective removal of large males)	Whalers almost eliminated large breeding males from the entire region, reducing pregnancy rates for many years; population decline, together with low calf counts and few large males off the Galapagos Islands, Ecuador, in the years following the end of whaling indicate the scale—around 5% per year—and duration—perhaps 15 years—of such effects	Whitehead et al. (1997); Whitehead and Shin (2022)
Pregnancy rate, calf production	Narwhals, East Greenland, Scoresby Sound region population(s)	Hunting (selective removal of young females)	Decline in observations of fetuses reported by hunters; decline in calves observed in aerial surveys; disproportionate hunt of young females has led to fewer and older females in the population (older females that may tend to have a lower average pregnancy rate)	NAMMCO (2021)
Fishing				
Pregnancy rate	Offshore pantropical spotted dolphins, eastern tropical Pacific	Tuna purse seining ("setting on" dolphins)	Pregnant females were exposed to significantly less fishery activity than non-pregnant ones, suggesting that the fishery may have an inhibitive effect on pregnancy	Kellar et al. (2013)

(continued)

Table 24.1 (continued)

Aspect of reproductive health affected	Species/population and location	Human activity	Evidence	Reference(s)
Calf production, age of weaning	Eastern spinner and offshore pantropical spotted dolphins, eastern tropical Pacific	Tuna purse seining ("setting on" dolphins)	Decline in proportion of adult females with calves; for offshore pantropical spotted dolphins, number of sets on dolphins was a predictor of both proportion with calves and length of disassociation (proxy for age at weaning); decline in reproductive output may be the proximate cause, or one of the proximate causes, of the failure of dolphin populations to recover at rates expected after reduction of high bycatch levels	Cramer et al. (2008)
Mother-calf bond	Offshore pantropical spotted dolphins, eastern tropical Pacific	Tuna purse seining ("setting on" dolphins)	Physical separation of cow/calf pairs caused by chase and encirclement, leading to calf mortality	Archer et al. (2004)
Prey availability				
Fecundity (birth rate)	Killer whales, eastern north Pacific fish-eating populations	Combination of habitat alteration, fishing, and natural variability (likely influenced by climate change) affecting prey populations (particularly of Chinook salmon)	The probability of a female calving differed by 50% between years of low and high salmon abundance. In times of low prey abundance, increased search time and less social cohesion may also affect reproduction. Nutritional stress on females associated with poor body condition and unsuccessful pregnancies	Ward et al. (2009); Wasser et al. (2017); Fearnbach et al. (2018)

Pollutants				
Fetus or neonate survival	Harbor porpoises, U.K.	Release of chemical compounds (organochlorines, mainly PCBs) into the environment	Resting mature females had significantly higher mean ∑PCBs than both lactating and pregnant females. Where data were available, these non-offloading [of PCBs] females were previously gravid, which suggests fetal or newborn mortality. Results suggest that reproductive failure could have occurred in up to 39% or more of mature females sampled	Murphy et al. (2015)
Neonate survival	Common bottlenose dolphins, southeastern U.S.	*Release of chemical compounds (organochlorines, mainly PCBs) into the environment*	Significantly higher mortality of calves born to primiparous females	Wells et al. (2005); Schwacke et al. (2002)
Testes weight	Harbor porpoise, U.K.	*Release of chemical compounds (organochlorines, mainly PCBs) into the environment*	Testes of adults in good nutritional condition were negatively associated with PCB concentrations; testes weight is a strong indicator of male fertility in seasonally breeding mammals	Williams et al. (2021)
Pregnancy rate	Common bottlenose dolphins, Gulf of Mexico	Petroleum exposure after *Deepwater Horizon* drilling rig explosion	Pregnant females were tracked for one year after the oil spill; the resulting estimated pregnancy rate was less than a third of those previously reported in unaffected areas (19.4% vs 64.7% respectively)	Kellar et al. (2017)

(continued)

Table 24.1 (continued)

Aspect of reproductive health affected	Species/population and location	Human activity	Evidence	Reference(s)
Live-capture				
Reproductive potential	Killer whales, eastern North Pacific fish-eating populations	Selective removal ("cropping") of young females	Temporary skew in sex ratio and deficit of reproductively capable females	Olesiuk et al. (1990)
Noise				
Number of singers	Humpback whales, Angola	Noise from seismic survey activity	Number of singers significantly decreased with increasing received level of seismic survey pulses	Cerchio et al. (2014)
Climate anomalies/change				
Number of calves born	Indo-Pacific bottlenose dolphins, Shark Bay, Western Australia	Marine heatwave	Number of calves detected was significantly higher before the marine heatwave. Survival of "spongers" declined less (5.9%) compared with non-spongers (12.2%)	Wild et al. (2019)
Reproductive rates	Humpback whales, Hawaii	Marine heatwave	Reproductive rates declined by 76.5%, coincident with marine heatwave	Cartwright et al. (2019)

Fig. 24.6 Cook Inlet beluga whaless. Beluga whales are highly social animals. Shown here are an adult whale (white; front-most whale), two young adults or subadults (light gray), and a young calf (small, dark gray). Beluga whales are facultative induced ovulators and while mating is difficult to observe in the wild, courtship in captive settings apparently follows ritualized sequences and it is possible that male mating displays help to induce ovulation (Steinman et al. 2012; Richard et al. 2021). Disturbance and disruption of beluga whale behavior and social structure may be a contributing factor to the lack of recovery by this and other beluga whale populations. Photo: NOAA Fisheries / Paul Wade (NOAA Fisheries permit #20465); August 2017

2000), and is classified as Critically Endangered on the IUCN (International Union for Conservation of Nature) Red List and as Endangered under the US Endangered Species Act (ESA). The population continued declining until about 2005 (when hunting stopped), increased somewhat until about 2010, began declining again, and reached its lowest point in 2018 (Wade et al. 2019).

Overhunting apparently caused all or most of the initial declines, but why has the population declined since 2010? Recent studies have shed light on what appear to be the proximal causes of the lack of recovery. First, age of first parturition (birth) appears to be substantially delayed in the Cook Inlet beluga whale population. In other beluga whale populations, age of sexual maturation in females occurs by age seven, with the age of first parturition occurring by age eight (e.g., Burns and Seaman 1986; Heide-Jørgensen and Teilmann 1994; Suydam 2009). In contrast, McGuire et al. (2020) found that the recent age of first parturition in Cook Inlet is considerably greater (at least 10 and probably as old as 13). Second, the birth rate also appears to be reduced. Suydam (2009) reported a birth rate of 0.41 in the eastern Chukchi Sea, where the calving interval was between two and three years. In contrast, mean fecundity in the Cook Inlet population for the period 2005–2017 was estimated to be 0.27, which suggests a calving interval of about 4.6 years (Himes Boor et al. 2022; Warlick et al. 2022). Warlick et al. (2022) concluded that survival of breeding females and young calves is relatively high, but survival of nonbreeders (which includes juveniles) and fecundity may be depressed in the Cook Inlet beluga whale population.

Warlick et al. (2022) extended their analysis to examine annual changes in life history parameters. Fecundity had the strongest correlation with annual population rate of change, followed by adult survival. Among a wide range of environmental covariates, an index of prey biomass (including several species of salmon as well as eulachon (*Thaleichthys pacificus*)) was positively correlated with fecundity and older calf survival. Fecundity and older calf survival were also positively correlated with the returning run size of Chinook salmon in the Susitna River, an important foraging habitat for the Cook Inlet whales (Castellote et al. 2021). Most of the life history parameters were at their lowest value in 2011, at the start of the recent decline in beluga whale abundance, with 2011 and 2012 representing the two lowest years for fecundity.

In the Gulf of Alaska, salmon and forage fish production has been severely impacted by climate change. In Cook Inlet, adult returns of Chinook salmon were low from 2008 to 2012, with one study concluding that this was caused by adverse freshwater conditions the previous five years, including above-optimal spawning and rearing temperatures in the rivers (Jones et al. 2020). Following that, from 2014 to 2016, the eastern North Pacific experienced an extreme marine heat wave that caused declines in forage fish species in the northern Gulf of Alaska, restricting energy transfer to upper-trophic-level species and leading to large-scale mortality events and declines in abundance and breeding success of forage-fish-dependent salmon, groundfish, birds, and mammals (Arimitsu et al. 2021; Suryan et al. 2021). While more research is needed, it is possible that climate effects have contributed to the lack of recovery of the Cook Inlet beluga whale population, by decreasing their food supply and consequently causing declines in birth rates and other life history parameters.

Other factors could also be contributing to the lack of recovery. McGuire et al. (2020) noted that contamination by persistent organic pollutants or other contaminants might be affecting beluga whale reproduction. Another concern is congenital defects observed in some dead neonates (Burek-Huntington et al. 2022); although the cause is unknown, this could be reducing successful reproduction. Cumulative effects from disturbance by noise, vessel traffic, and other factors may also be playing a role (Castellote et al. 2018; McHuron et al. 2023). One possible mechanism is that human disturbance disrupts social behaviors that improve mating success, because beluga whales are facultative induced ovulators (Steinman et al. 2012). A recent aquarium study monitoring hormone levels and behavior showed that hormone levels in a captive female rose only after two males had initiated reproductive displays for three weeks, with ovulation following several weeks later (Richard et al. 2021). Breeding beluga whales in most North American aquaria has

Fig. 24.7 Snow Cone with her newborn calf near Cumberland Island, Georgia. The energy deficit caused by sublethal entanglements in fishing gear, as seen in this photo, and likely other factors are stunting the growth of North Atlantic right whales (Stewart et al. 2021). Smaller mothers have longer inter-birth intervals and produce fewer calves per potential reproductive year, which contributes to the low birth rate of these endangered whales (Stewart et al. 2022; Moore 2023). Photo: Florida Fish and Wildlife Conservation Commission (NOAA Fisheries permit #20556); December 2021

been difficult (Steinman et al. 2012); an exception is a facility that had 54 beluga whales in in two pools,[1] which may have allowed for more social interactions. Given that beluga whale courtship appears relatively complex (Hill et al. 2021), these whales may need relatively undisturbed areas for successful mating to occur.

24.4.2 North Atlantic Right Whales

Physical injury to and mortality of North Atlantic right whales (*Eubalaena glacialis*), caused almost entirely by entanglements in fishing gear and ship strikes, have been the focus of conservation efforts in recent decades, but the potentially related problem of poor reproduction is also of great concern (Corkeron et al. 2018; Moore 2023; Fig. 24.7). As noted by Moore (2023), a management strategy focused solely on minimizing right whale mortality, with inadequate attention paid to

[1] https://media.fisheries.noaa.gov/dam-migration/appendix_16_marineland_assurance.pdf.

reproductive health, is unlikely to be successful in the long term. The reproductive health challenges and other obstacles to recovery faced by North Atlantic right whales are in stark contrast to the situation of southern right whales (*Eubalaena australis*) in the Southern Hemisphere.

Even without the well-documented, recent changes in their phenology and distribution, North Atlantic right whales have for many decades shown signs of being less robust and less healthy than southern right whales (Christiansen et al. 2020). This includes their generally slimmer body profile that rarely exhibits the “fat roll” behind the blowholes—a striking feature of southern right whale morphology (Pettis et al. 2004). Reproduction rates and outcomes (e.g., ovulation, spermatogenesis, fetal development, calf survival) are heavily influenced by anthropogenic and natural environmental factors that control the quality and availability of food (Li Chen et al. 2009; Rolland et al. 2016; Corkeron et al. 2018). Those factors, in particular the availability of very dense aggregations of late-stage calanoid copepods, are increasingly affected by climate change (Fortune et al. 2013; Meyer-Gutbrod et al. 2021). Mother body condition has been linked to calf growth rate, and North Atlantic right whale calving rates are less than half those of southern right whales (Kraus and Hatch 2001; Christiansen et al. 2018, 2020). There is thus a large body of research showing that North Atlantic right whale reproduction has declined due to direct female mortality (Pace et al. 2017), gear entanglements (van der Hoop et al. 2017), and nutritional deficits from climate-related changes in prey quality and availability (Meyer-Gutbrod et al. 2015), but whether and how reproduction has also been impaired by factors related to sociality is uncertain.

Further compounding the factors affecting reproduction is the mating system itself. Right whales are renowned for phenomenally large testes relative to body size, and their mating system is one of the most compelling examples of sperm competition in mammals (Brownell and Ralls 1986). Parentage analysis, however, has found that older males have disproportionally more calves, with males not obtaining their first paternity until about 15 years of age —almost twice the average age of first fertilizations in females (Frasier et al. 2007). Male-male competition may be preventing young males from reproducing. The uneven distribution of paternities results in a lower effective population size in a species that already has one of the lowest reported levels of genetic diversity, which may further inhibit reproductive success (Frasier et al. 2007). The fact that females are declining at a faster rate than the overall population is further diminishing the effective population size (Reed et al. 2022).

It is unknown whether “surface active groups” of right whales (Kraus and Hatch 2001; Brown and Sironi 2023, this book) vary in size, composition, and/or male “quality” between North Atlantic and southern right whales. However, given the drastically different population sizes, plus the fact that participating in surface active groups must be energetically costly, it is possible that certain behavioral or social aspects conducive to successful copulation have been compromised or lost along the way in North Atlantic right whales. This could make them less capable of recovering when compared to some other baleen whales, including southern right whales. Even if a North Atlantic right whale conceives and gives birth to a calf, the inadequacy of socially transmitted knowledge could be hindering long-term calf survival. As explained by Brown and Sironi (2023, this book), southern right whale calves (and almost certainly calves of other right whale species) learn from their mothers where and when good food can be found. This culturally transmitted knowledge may serve a calf well in its first migration but could limit the extent to which young whales are inclined (or able) to search for new feeding areas and opportunities in the face of declining prey. For North Atlantic right whales, loss of knowledge may explain the fact that large expanses of their historical range (including southern Greenland, Iceland, and much of Western Europe) have not been reoccupied after more than a century of nearly complete protection from whaling (Kraus and Rolland 2009; Mellinger et al. 2011).

24.5 Integrating Cetacean Reproductive Health into Conservation Actions

As threats to cetaceans change, so must our conservation and management approaches (Jefferson 2019). Population dynamics models, such as population viability analysis (PVA), are being used to investigate cumulative human impacts on cetacean population growth, stability, and resilience (Lacy et al. 2017; Murray et al. 2021). More attention is being paid to understanding, linking, and tracking the consequences of short- and long-term behavioral disturbances from noise and other human activities to changes in cetacean health (body condition), reproductive rates, and population dynamics by evaluating mechanistic transfer functions (National Research Council 2005; Pirotta et al. 2018; Pirotta et al. 2019; McHuron et al. 2021, 2023). Knowledge gaps in understanding the reproductive biology and behavior of endangered species are being addressed by leveraging insights grained from more abundant species in managed care facilities (e.g., Integrated Conservation Planning for Cetaceans[2]). New efforts are being made to determine how sociality and culture structure populations. For example, clan-level differences in foraging strategies of eastern tropical Pacific sperm whales have resulted in signatories to the Convention on the Conservation of Migratory Species of Wild Animals committing to a “concerted action” to seek improved understanding of how social learning creates cultural structuring relevant to conservation (Brakes et al. 2019). A variety of tools and lines of evidence are being applied to identify population units in need of conservation (“units to conserve”) and specify the threats they face (e.g., IUCN Red List, US Endangered Species Act, US Marine Mammal Protection Act). Geographical differences in behavior conducive to constrictions in gene flow (female site fidelity, mating system, acoustics, dietary specializations) may be used as possible “lines of evidence” for delimiting cetacean subspecies (Taylor et al. 2017) and male song in blue whales and fin whales is being used to characterize population

[2] https://iucn-csg.org/integrated-conservation-planning-for-cetaceans-icpc/.

differences (McDonald et al. 2006; Delarue et al. 2009; Archer et al. 2020). In addition to these important approaches, we highlight four specific ways to improve conservation outcomes by explicit consideration of cetacean reproductive health: monitoring, modeling, mapping, and data sharing.

24.5.1 Programs and Tools to Monitor Reproductive Health

Foundational to all conservation efforts are effective population assessment and monitoring programs. Most rely on abundance estimation at frequent intervals. Augmenting this, when possible, by tracking calf numbers—temporally (within an impacted population over time) or geographically (comparing impacted populations vs. non-impacted populations)—can give an early indication of whether and how reproduction is being compromised. Today, innovative field technologies and laboratory approaches provide unparalleled access to information on reproductive health (Nowacek et al. 2016; Ramos et al. 2023, this book). Non-invasive techniques, such as aerial photogrammetry, have been used to track body condition of known individuals, which is linked with reproductive output in eastern North Pacific killer whales and North Atlantic right whales (Fearnbach et al. 2018; Stewart et al. 2022). Fecal steroid hormone assays from samples collected with the assistance of feces-sniffing dogs have been used to determine occurrence, stage and health of pregnancy in females, and the onset of sexual maturation and reproductive seasonality in males (Rolland et al. 2007; Wasser et al. 2017). Endocrine evaluations of biopsies from free- ranging cetaceans have been used to show high pregnancy rates consistent with population recovery in Australian humpback whales (Pallin et al. 2018) and to assess reproductive health in bottlenose dolphin stocks in the Gulf of Mexico following the Deepwater Horizon oil spill (Kellar et al. 2017). In addition to monitoring live animals, studying dead ones via stranding and carcass collection programs can provide critical information on sexual maturity and fertility.

24.5.2 Approaches for Explicitly Incorporating Reproductive Health into Conservation Reference Points

Box 24.1: Assessing Human Impacts: The PBR Example

The "potential biological removal" (PBR) level is a specific reference point developed and applied in the United States to meet the objectives of the US Marine Mammal Protection Act (US MMPA) (Wade 1998). PBR is calculated as the product of three values: (1) N_{min} (an estimate of population size that

(continued)

Box 24.1 (continued)
provides reasonable assurance that the population size is greater than that level), (2) 1/2 R_{max} (where R_{max} is the maximum annual per capita rate of increase in a population resulting from additions due to reproduction, less losses due to natural mortality), and (3) F_r, a recovery factor set between a value of 0.1 and 1.0; thus, PBR = N_{min} * $0.5R_{max}$ * F_r. The concept of R_{max} implicitly includes values of quantifiable population parameters, such as birth rates, survival rates, and the age of sexual maturity. In other words, it is designed to account, at least implicitly, for species and even population differences in reproductive potential and also outcomes. Where data are limited, the United States relies on default values for R_{max} according to taxonomic group (e.g., cetaceans vs. pinnipeds, NMFS 2023), but case-specific adjustments are allowed for populations for which R_{max} is known or suspected to be higher or lower than the default value. This allows, at least theoretically, for the PBR approach to accommodate cases where a population's reproductive rate has been suppressed by human-caused factors, by lowering the value of R_{max}.

Exploring fecundity and birth rates across species and populations may highlight ongoing changes and impacts that require adjustments to the way conservation management reference points are designed or applied. Not only are threats to cetaceans changing, but such changes may also affect individuals of different sex, age, or stage classes differently. So as threats change, so too must management models. Where a decrease in a population's birth rate can be measured, this can be relatively easily accounted for in the PBR equation (see Box 24.1). However, it is often the case that human-caused reductions in birth rate are suspected but not known or known but not quantified. To investigate this (and other considerations), Punt et al. (2021) evaluated how robust the PBR framework is to the sublethal effects of entanglements in fishing gear and the mainly sublethal (but sometimes lethal) effects of noise from human activities. Modeled sublethal effects had relatively small impacts on recovery probability as long as the recovery factor (F_r) was set to 0.5; if F_r was set to 1.0, sublethal effects could prevent a population from recovering. This emphasizes the need for conservative (i.e., precautionary or risk-averse) management approaches when sublethal effects are known or suspected.

Another consideration is that of age or sex selectivity of human-caused mortality. This follows from the concept of reproductive value in population dynamics, where reproductive value is defined as a female's expected reproductive output over her remaining lifetime. The reproductive value changes substantially with age, with newborn females having a low reproductive value (because they have to survive until the age of first reproduction) and females that have just reached the age of first reproduction having the highest reproductive value. Brandon et al. (2017) tested whether the PBR framework was robust to age- and sex-selective mortality. They found that if human-caused mortality consists predominantly of young animals or of males, PBR is likely more precautionary than necessary to achieve the conservation goal. Conversely, PBR may not be sufficiently precautionary if human-caused mortality consists predominantly of mature females. The same might occur if human-caused mortality consists largely of dominant males or males with high reproductive output, but this has not been examined.

The US guidelines allow for adjustment of the PBR calculation if human-caused mortality consists primarily of females (National Marine Fisheries Service 2023). This issue becomes more important for species with more extreme life histories, with a long delay until age of first reproduction. Curtis and Moore (2013) provided a framework for calculating reference points for mortality of sea turtles, where age selectivity can be extremely important. A similar approach might be necessary for long-lived cetaceans, if their human-caused mortality is particularly sex- or age-skewed.

Population models generally assume that individuals are interchangeable (i.e., one individual is equivalent to any other) even if age and sex are explicitly modeled in some manner. In highly social species, the removal of certain key individuals such as matriarchs in elephant (*Loxodonta africana*) herds and dominant males in Soay (*Ovis aries*) and bighorn (*Ovis canadensis*) sheep and African elephants can affect reproduction and survival well beyond the expected effect of the removal of a single individual (Wade et al. 2012). This has not been addressed adequately in management models, such as PBR, but could be addressed through individual-based models that recognize the effects of removing matriarchs or other particularly important individuals.

24.5.3 Identifying and Mapping Geographic Areas Important to Cetacean Reproductive Health

Protecting habitat essential for cetacean reproduction is challenging, as these locations may be unknown or span wide areas of ocean. Among the available mechanisms for identifying and describing areas that are important for mating, birthing, and nurturing young are Important Marine Mammal Areas (IMMAs)[3] (Tetley et al. 2022) and Biologically Important Areas (BIA's)[4] (Ferguson et al. 2015). Spatially explicit tools are a promising way of implementing successful marine mammal conservation with substantial benefit to associated biodiversity conservation (Hoyt 2022). In addition, there are benefits to incorporating social dyanamics in spatial management (Smith et al. 2016) and to clearly mapping relationships between prey and cetacean fecundity, as evidence has shown that nutrition affects all aspects of

[3] https://www.marinemammalhabitat.org/.

[4] https://www.dcceew.gov.au/environment/marine/marine-species/bias.

reproduction (e.g., Meyer-Gutbrod et al. 2015; IJsseldijk et al. 2021). When prey preferences are tied to social or cultural group membership, nutritional issues can be exacerbated. Eastern North Pacific salmon-eating killer whales are an exemplar: their culturally inherited and rigid preference for endangered Chinook salmon has been linked to an extremely high failed pregnancy rate (almost 70%) in one population (Wasser et al. 2017). In eastern tropical Pacific sperm whales, clan-specific foraging variation results in clans faring differently during times of environmental change, such as El Niño Southern Oscillation events (Whitehead and Rendell 2004). Whether variation in foraging success during such events is due to the availability of preferred prey or to some other factor remains unknown, but clans with more foraging success may also experience greater reproductive success (Cantor and Whitehead 2015).

24.5.4 Crosstalk, Data Sharing, and Collaboration Across Geographic Boundaries

Many cetacean species are highly mobile and frequently move across arbitrary national or other jurisdictional boundaries. Even within a single species, we find variation in residency and ranging patterns (e.g., sperm whales, Vachon et al. 2022; killer whales, Ford 2019; common bottlenose dolphins (*Tursiops truncatus*), Oudejans et al. 2015). Yet, researchers in different regions of the world often have vastly different levels of access to resources (financial, technical, etc.), which can result in a patchy understanding of a species throughout its full range. As a first step toward ameliorating this inequity, researchers can make processed data, analytical tools, and pipelines open access (e.g., GitHub). There is ample evidence to demonstrate that open-access data and resources (such as this book) improve science (Munafò et al. 2017; Popkin 2019; Gomes et al. 2022), as well as obvious benefits such as encouraging comparability, trust, collaboration, and transparency among researchers. The wide sharing of data, tools, and knowledge will afford us a more complete understanding of behavior, including reproductive behavior, throughout a species' range.

24.6 Summary

Cetacean conservation will benefit from efforts to preserve, or reestablish, the environmental, demographic, and social conditions that enable animals to reproduce successfully in their natural environment. The better we understand and integrate knowledge concerning cetacean reproductive health into conservation strategies, the better our chances of achieving species recovery, protecting biodiversity, and preventing future extinctions. As summarized whimsically by Marah Hardt (2016), but with much relevance and as a fitting end for this book, to conserve cetacean sex and reproductive strategies, we need to:

- Give them privacy so they can court without disturbance.
- Give them enough food so they have time for sex and are in good condition.
- Keep it quiet so they can hear each other's songs.
- Keep it clean so that pollutants do not impact their sex drive.
- Stop killing them, directly or incidentally, so key individuals are present and groups remain intact.
- Keep it safe—without hunting, chasing or otherwise stressing them—so they can pursue each other.
- Maintain the climate for sex so that we can slow, stop, or reverse the dire warming scenarios and give the oceans, and the biodiversity they support, a chance.

Acknowledgments We thank Bernd Würsig and Dara Orbach for the invitation to explore ideas at the intersection of cetacean sex and conservation. Bernd Würsig, Dara Orbach, Frank Cipriano, Mark Simmonds, and an anonymous reviewer provided thoughtful comments that improved the manuscript.

References

Allee WC (1931) Co-operation among animals. Am J Sociol 37(3):386–398

Alves F, Badenas A, Mesnick S, Pitman R, Rosso M (2023) Feeding, fighting, and social structure among mesoplodont beaked whales. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Antoniou A, Frantzis A, Alexiadou P, Paschou N, Poulakakis N (2018) Evidence of introgressive hybridization between *Stenella coeruleoalba* and *Delphinus delphis* in the Greek Seas. Mol Phylo Evol 129:325–337

Archer F, Gerrodette T, Chivers S, Jackson A (2004) Annual estimates of the unobserved incidental kill of pantropical spotted dolphin (*Stenella attenuata attenuata*) calves in the tuna purse-seine fishery of the eastern tropical Pacific. Fish Bull 102:233–244

Archer FI, Rankin S, Stafford KM, Castellote M, Delarue J (2020) Quantifying spatial and temporal variation of North Pacific fin whale (*Balaenoptera physalus*) acoustic behavior. Mar Mamm Sci 36(1):224–245

Arimitsu ML, Piatt JF, Hatch S, Suryan RM, Batten S, Bishop MA, Campbell RW, Coletti H, Cushing D, Gorman K, Hopcroft RR, Kuletz KJ, Marsteller C, McKinstry C, McGowan D, Moran J, Pegau S, Schaefer A, Schoen S, Straley J, von Biela VR (2021) Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. Glob Chang Biol 27:1859–1878

Brakes P, Rendell L (2022) Conservation relevance of individuals and societies. In: Notarbartolo di Sciara G, Würsig B (eds) Marine mammals: the evolving human factor. Springer Nature, Cham, pp 83–111

Brakes P, Dall SR, Aplin LM, Bearhop S, Carroll EL, Ciucci P, Fishlock V, Ford JK, Garland EC, Keith SA, McGregor PK (2019) Animal cultures matter for conservation. Science 363:1032–1034

Brakes P, Carroll EL, Dall SR, Keith SA, McGregor PK, Mesnick SL, Noad MJ, Rendell L, Robbins MM, Rutz C, Thornton A (2021) A deepening understanding of animal culture suggests lessons for conservation. Proc R Soc Lond B 288(1949):20202718

Brandon JR, Punt AE, Moreno P, Reeves RR (2017) Towards a tier system approach for calculating limits on human-caused mortality of marine mammals. ICES J Mar Sci 74:877–887

Brown RW, Sironi M (2023) Right whale sexual strategies and behavior. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Brownell RL Jr, Reeves RR, Read AJ, Smith BD, Thomas PO, Ralls K, Amano M, Berggren P, Chit AM, Collins T, Currey R (2019) Bycatch in gillnet fisheries threatens critically endangered small cetaceans and other aquatic megafauna. Endang Spec Res 5(40):285–296

Brownell RL, Ralls K (1986) Potential for sperm competition in baleen whales. Rep Int Whal Commn Spec Iss 8:97–112

Burek-Huntington KA, Shelden KEW, Guilfoyle C, Thewissen JGM, Migura M, Armien AG, Romero CH (2022) Congenital defects and herpesvirus infection in beluga whale *Delphinapterus leucas* calves from the critically endangered cook inlet population. Dis Aqua Org 151:29–35

Burns JJ, Seaman GA (1986) Investigations of belukha whales in coastal waters of western and northern Alaska. II. Biology and ecology. Final report. U.S. Department of Commerce, NOAA, Outer Continental Shelf Assessment Program NA 81 RAC 00049. Alaska Department of Fish and Game, Fairbanks, AK

Calambokidis J, Barlow J (2020) Updated abundance estimates for blue and humpback whales along the U.S. West Coast using data through 2018, U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-634

Calambokidis J, Falcone EA, Quinn TJ, Burdin AM, Clapham PJ, Ford JKB, Gabriele CM, LeDuc R, Mattila D, Rojas-Bracho L, Straley JM, Taylor BL, Urban J, Weller D, Witteveen BH, Yamaguchi M, Bendlin A, Camacho D, Flynn K, Havron A, Huggins J, Maloney N (2008) SPLASH: structure of populations, levels of abundance and status of humpback whales in the North Pacific. Final report for contract AB133F-03-RP-00078. 58 p. Available from Cascadia Research

Cantor M, Whitehead H (2015) How does social behavior differ among sperm whale clans? Mar Mamm Sci 31:1275–1290

Carroll EL, Baker CS, Watson M, Alderman R, Bannister J, Gaggiotti OE, Gröcke DR, Patenaude N, Harcourt R (2015) Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. Sci Rep 5:16182

Cartwright R, Venema A, Hernandez V, Wyels C, Cesere J, Cesere D (2019) Fluctuating reproductive rates in Hawaii's humpback whales, *Megaptera novaeangliae*, reflect recent climate anomalies in the North Pacific. R Soc Open Sci 6:181463

Castellote M, Thayre B, Mahoney M, Mondragon J, Lammers MO, Small RJ (2018) Anthropogenic noise and the endangered cook inlet beluga whale, *Delphinapterus leucas*: acoustic considerations for management. Mar Fish Rev 80:63–88

Castellote M, Mooney A, Andrews R, Deruiter S, Lee W-J, Ferguson M, Wade P (2021) Beluga whale (*Delphinapterus leucas*) acoustic foraging behavior and applications for long term monitoring. PLoS One 16(11):e0260485

Cerchio S (2022) The Omura's whale: exploring the enigma. In: Clark CW, Garland EC (eds) Ethology and behavioral ecology of mysticetes. Springer Nature, Cham, pp 349–374

Cerchio S, Strindberg S, Collins T, Bennett C, Rosenbaum H (2014) Seismic surveys negatively affect humpback whale singing activity off northern Angola. PLoS One 9(3):e86464

Chivers S, Danil K (2023) Interspecific comparison of reproductive systems. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Christiansen F, Vivier F, Charlton C, Ward R, Amerson A, Burnell S, Bejder L (2018) Maternal body size and condition determine calf growth rates in southern right whales. Mar Ecol Prog Ser 592:267–281

Christiansen F, Dawson SM, Durban JW, Fearnbach H, Miller CA, Bejder L, Uhart M, Sironi M, Corkeron P, Rayment W, Leunissen E (2020) Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. Mar Ecol Prog Ser 640:1–6

Clark CW, Ellison WT, Southall BL, Hatch L, Van Parijs SM, Frankel A, Ponirakis D (2009) Acoustic masking in marine ecosystems: intuitions, analysis, and implication. Mar Ecol Prog Ser 395:201–222

Connor RC (2007) Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. Phil Trans R Soc B 362(1480):587–602

Corkeron P, Hamilton P, Bannister J, Best P, Charlton C, Groch KR, Findlay K, Rowntree V, Vermeulen E, Pace RM III (2018) The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. R Soc Open Sci 5(11):180892

Cramer KL, Perryman WL, Gerrodette T (2008) Declines in reproductive output in two dolphin populations depleted by the yellowfin tuna purse-seine fishery. Mar Ecol Prog Ser 369:273–285

Cranford TW (1999) The sperm whale's nose: sexual selection on a grand scale? Mar Mamm Sci 15:1133–1157

Croft DP, Brent LJN, Franks DW, Cant MA (2015) The evolution of prolonged life after reproduction. Trends Ecol Evol 30:407–416. 608

Curtis KA, Moore JE (2013) Calculating reference points for anthropogenic mortality of marine turtles. Aqua Conserv Mar Freshw Ecosys 23(3):441–459

da Silva VMF, Spinelli LG (2023) Play, sexual display or just boredom relief? In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

da Silva VM, Brum SM, de Mello DM, de Souza AR, Gravena W, Campbell E, Gonçalves RD, Mintzer V (2023) The Amazon river dolphin, *Inia geoffrensis*: what have we learned in the last two decades of research? Lat Am J Aqua Mamm 18(1):139–157

Darling JD, Acebes JM, Frey O, Jorge Urbán R, Yamaguchi M (2019) Convergence and divergence of songs suggests ongoing, but annually variable, mixing of humpback whale populations throughout the North Pacific. Sci Rep 9(1):7002

Delarue J, Todd SK, Van Parijs SM, Di Iorio L (2009) Geographic variation in Northwest Atlantic fin whale (*Balaenoptera physalus*) song: implications for stock structure assessment. J Acoust Soc Am 25(3):1774–1782

Ehrenfeld DW (1970) Biological conservation. Holt, Rinehard, and Winston, New York, NY

Fearnbach H, Durban JW, Ellifrit DK, Balcomb KC (2018) Using aerial photogrammetry to detect changes in body condition of endangered southern resident killer whales. Endang Spec Res 35:175–180

Ferguson MC, Curtice C, Harrison J, Van Parijs SM (2015) Biologically important areas for cetaceans within US waters-overview and rationale. Aqua Mamm 41(1):2

Fleming J, Ledogar RJ (2008) Resilience, an evolving concept: a review of literature relevant to aboriginal research. Pimatisiwin 6(2):7–23

Foote AD, Vijay N, Ávila-Arcos MC, Baird RW, Durban JW, Fumagalli M, Gibbs RA, Hanson MB, Korneliussen TS, Martin MD, Robertson KM (2016) Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. Nat Comm 7:11693

Ford JKB (2019) Killer whales: behavior, social organization, and ecology of the oceans' apex predators. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer Nature, Cham, pp 239–260

Ford MJ, Parsons KM, Ward EJ, Hempelmann JA, Emmons CK, Hanson MB, Balcomb KC, Park LK (2018) Inbreeding in an endangered killer whale population. Anim Conserv 21(5):423–432

Fortune SME, Trites AW, Mayo CA, Rosen DAS, Hamilton PK (2013) Energetic requirements of North Atlantic right whales and the implications for species recovery. Mar Ecol Prog Ser 478: 253–272

Fowler CW (1981) Density dependence as related to life history strategy. Ecology 62:602–610

Fowler CW (1984) Density dependence in cetacean populations. Rep Int Whal Commn 6:373–379

Frasier TR, Hamilton PK, Brown MW, Conger LA, Knowlton AR, Marx MK, Slay CK, Kraus SD, White BN (2007) Patterns of male reproductive success in a highly promiscuous whale species: the endangered North Atlantic right whale. Mol Ecol 16(24):5277–5293

Garland EC, Carroll EL (2022) Culture and social learning in Baleen Whales. In: Clarke CW, Garland EC (eds) Ethology and behavioral ecology of mysticetes. Springer, Cham, pp 177–191
Garland EC, McGregor PK (2020) Cultural transmission, evolution, and revolution in vocal displays: insights from bird and whale song. Front Psych 11:544929
Gascoigne J, Berec L, Gregory S, Courchamp F (2009) Dangerously few liaisons: a review of mate-finding Allee effects. Popul Ecol 51:355–372
Gero S, Whitehead H (2016) Critical decline of the eastern Caribbean sperm whale population. PLoS One 11(10):e0162019
Gilpin ME, Soulé ME (1986) Minimum viable populations: processes of species extinction. In: Soulé ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, pp 19–34
Gomes DG, Pottier P, Crystal-Ornelas R, Hudgins EJ, Foroughirad V, Sánchez-Reyes LL, Turba R, Martinez PA, Moreau D, Bertram MG, Smout CA (2022) Why don't we share data and code? Perceived barriers and benefits to public archiving practices. Proc R Soc Lond B 289:20221113
Gowans S (2019) Grouping behaviors of dolphins and other toothed whales. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer Nature, Cham, pp 3–24
Graham ZA, Garde E, Heide-Jørgensen MP, Palaoro AV (2020) The longer the better: evidence that narwhal tusks are sexually selected. Biol Lett 16(3):20190950
Gulland FM, Baker J, Howe M, LaBrecque E, Leach L, Moore SE, Reeves RR, Thomas PO (2022) A review of climate change effects on marine mammals in United States waters: past predictions, observed impacts, current research and conservation imperatives. Clim Change Ecol 19:100054
Hardt MJ (2016) Sex in the sea: our intimate connection with sex-changing fish, romantic lobsters, kinky squid, and other salty erotica of the deep. St. Martin's Press, New York, NY
Heide-Jørgensen MP (2018) Narwhal. In: Würsig B, Thewissen JGM, Kovacs KM (eds) Encyclopedia of marine mammals, 3rd edn. Academic Press, London, pp 627–631
Heide-Jørgensen MP, Teilmann J (1994) Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. Meddr Grønland Biosci 39: 195–212
Hill HMM, Yeater DB, Noonan M (2021) Synergy between behavioural research on beluga whales (*Delphinapterus leucas*) conducted in zoological and wild settings. Polar Res 40(S1)
Himes Boor GK, McGuire TL, Warlick AJ, Taylor RL, Converse SJ, McClung JR, Stephens AD (2022) Estimating reproductive and juvenile survival rates when offspring ages are uncertain: a novel multievent mark-resight model with beluga whale case study. Meth Ecol Evol 14(2):631–642
Hodgson D, McDonald JL, Hosken DJ (2015) What do you mean, 'resilient'? Trends Ecol Evol 30(9):503–506
Hohn AA, Ewing RY, Zaias J (2007) Reproduction in relation to conservation and commercial exploitation. In: Miller DL (ed) Reproductive biology and phylogeny of cetacea: whales, porpoises and dolphins. Science Publishers, Enfield, NH, pp 371–389
Hoyt E (2022) Conserving marine mammal spaces and habitats. In: Notarbartolo di Sciara G, Würsig B (eds) Marine mammals: the evolving human factor. Springer Nature, Cham, pp 31–82
Hubbs CL (1955) Hybridization between fish species in nature. Syst Zool 4(1):1–20
IJsseldijk LL, Hessing S, Mairo A, Ten Doeschate MT, Treep J, van den Broek J, Keijl GO, Siebert U, Heesterbeek H, Gröne A, Leopold MF (2021) Nutritional status and prey energy density govern reproductive success in a small cetacean. Sci Rep 11(1):19201
Jefferson TA (2019) Endangered odontocetes and the social connection: selected examples of species at risk. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer Nature, Cham, pp 465–481
Johnson T (2005) Entanglements: the intertwined fates of whales and fishermen. University of Florida Press, Gainsville, FL

Jones LA, Schoen ER, Shaftel R, Cunningham CJ, Mauger S, Rinella DJ, St. Saviour A (2020) Watershed-scale climate influences productivity of Chinook salmon populations across Southcentral Alaska. Glob Chang Biol 26:4919–4936
Kardos M, Zhang Y, Parsons KM, Kang H, Xu X, Liu X, Matkin CO, Zhang P, Ward EJ, Hanson MB, Emmons C (2023) Inbreeding depression explains killer whale population dynamics. Nat Ecol Evol 7:675–686
Kellar NM, Trego ML, Chivers SJ, Archer FI (2013) Pregnancy patterns of pantropical spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific determined from hormonal analysis of blubber biopsies and correlations with the purse-seine tuna fishery. Mar Biol 160:3113–3124
Kellar NM, Speakman TR, Smith CR, Lane SM, Balmer BC, Trego ML, Catelani KN, Robbins MN, Allen CD, Wells RS, Zolman ES (2017) Low reproductive success rates of common bottlenose dolphins Tursiops truncatus in the northern Gulf of Mexico following the Deepwater Horizon disaster (2010-2015). Endang Spec Res 33:143–158
Knowlton AR, Robbins J, Landry S, McKenna HA, Kraus SD, Werner TB (2016) Effects of fishing rope strength on the severity of large whale entanglements. Conserv Biol 30(2):318–328
Konrad CM, Frasier TR, Whitehead H, Gero S (2019) Kin selection and allocare in sperm whales. Behav Ecol 1:194–201
Kraus SD, Hatch JJ (2001) Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). J Cetacean Res Manag Spec Iss 2:237–244
Kraus SD, Rolland RM (eds) (2009) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA
Lacy RC, Williams R, Ashe E, Balcomb III KC, Brent LJ, Clark CW, Croft DP, Giles DA, MacDuffee M, Paquet PC (2017) Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Sci Rep 7:14119
Laidre KL, Shelden KEW, Rugh DJ, Mahoney BA (2000) Beluga, *Delphinapterus leucas*, distribution and survey effort in the Gulf of Alaska. Mar Fish Rev 62(3):27–36
Li Chen T, Wise SS, Kraus S, Shaffiey F, Levine KM, Thompson WD, Romano T, O'Hara T, Pierce Wise J Sr (2009) Particulate hexavalent chromium is cytotoxic and genotoxic to the North Atlantic right whale (*Eubalaena glacialis*) lung and skin fibroblasts. Envir Mol Mutagen 50(5):387–393
Lusseau D, Newman MEJ (2004) Identifying the role that animals play in their social networks. Proc R Soc Lond B 271:S477–S481
Mahoney BA, Shelden KEW (2000) Harvest history of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska. Mar Fish Rev 62(3):124–133
Manitzas Hill H, Dudzinski K, Lilley M, Ham J (2023) Sexual behaviors of odontocetes in managed care. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham
Manlik O (2019) The importance of reproduction for the conservation of slow-growing animal populations. In: Comizzoli P, Brown JL, Holt WV (eds) Reproductive sciences in animal conservation. Springer, Cham, pp 13–39
Martin AR, Da Silva VM, Rothery P (2008) Object carrying as socio-sexual display in an aquatic mammal. Biol Lett 4(3):243–245
McDonald MA, Mesnick SL, Hildebrand JA (2006) Biogeographic characterization of blue whale song worldwide: using song to identify populations. J Cetacean Res Manag 8:55–65
McGuire TL, Stephens AD, McClung JR, Garner CD, Shelden KE, Boor GK, Wright B (2020) Reproductive natural history of endangered cook inlet beluga whales: insights from a long-term photo-identification study. Polar Biol 43:1851–1871
McHuron EA, Aerts L, Gailey G, Sychenko O, Costa DP, Mangel M, Schwarz LK (2021) Predicting the population consequences of acoustic disturbance, with application to an endangered gray whale population. Ecol Appl 8:e02440
McHuron EA, Castellote M, Himes Boor GK, Shelden KEW, Warlick AJ, McGuire TL, Wade PR, Goetz KT (2023) Modeling the impacts of a changing and disturbed environment on an endangered cetacean population. Ecol Model 483:110417

Mellinger DK, Nieukirk SL, Klinck K, Klinck H, Dziak RP, Clapham PJ, Brandsdóttir B (2011) Confirmation of right whales near a nineteenth-century whaling ground east of Southern Greenland. Biol Lett 7(3):411–413
Mesnick SL, Ballance LT, Wade PR, Pryor K, Reeves RR (2019) Oceanic dolphin societies: diversity, complexity, and conservation. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer Nature, Cham, pp 183–209
Meyer-Gutbrod EL, Greene CH, Sullivan PJ, Pershing AJ (2015) Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. Mar Ecol Prog Ser 15(535):243–258
Meyer-Gutbrod EL, Greene CH, Davies KTA, Johns DJ (2021) Ocean regime shift is driving collapse of the North Atlantic right whale population. Oceanography 34:22–31
Moore MJ (2023) Policy enabling North Atlantic right whale reproductive health could save the species. ICES J Mar Sci:fsac239
Moore SE, Reeves RR (2018) Tracking arctic marine mammal resilience in an era of rapid ecosystem alteration. PLoS Biol 16(10):e2006708
Munafò MR, Nosek BA, Bishop DV, Button KS, Chambers CD, Percie du Sert N, Simonsohn U, Wagenmakers EJ, Ware JJ, Ioannidis J (2017) A manifesto for reproducible science. Nat Hum Behav 1(1):1–9
Murphy S, Barber JL, Learmonth JA, Read FL, Deaville R, Perkins MW, Brownlow A, Davison N, Penrose R, Pierce GJ, Law RJ (2015) Reproductive failure in UK harbour porpoises *Phocoena phocoena*: legacy of pollutant exposure? PLoS One 10(7):e0131085
Murray CC, Hannah LC, Doniol-Valcroze T, Wright BM, Stredulinsky EH, Nelson JC, Locke A, Lacy RC (2021) A cumulative effects model for population trajectories of resident killer whales in the Northeast Pacific. Biol Conserv 257:109124
NAMMCO-North Atlantic Marine Mammal Commission (2021) Report of the ad hoc working group on narwhal in East Greenland. October 2021, Copenhagen, Denmark. Available at https://nammco.no/topics/narwhal_beluga_reports/
National Marine Fisheries Service (2023) NOAA fisheries policy directive 02–204-01: guidelines for preparing stock assessment reports pursuant to the Marine Mammal Protection Act. Available Online at: https://www.fisheries.noaa.gov/s3/2023-02/02-204-01-Final%20GAMMS%20IV%20Revisions%20clean_kdr.pdf
National Research Council (2005) Marine mammal populations and ocean noise. National Academies Press, Washington, DC
Nattrass S, Croft DP, Ellis S, Cant MA, Weiss MN, Wright BM, Stredulinsky E, Doniol-Valcroze T, Ford JK, Balcomb KC, Franks DW (2019) Postreproductive killer whale grandmothers improve the survival of their grandoffspring. Proc Natl Acad Sci 116:26669–26673
Noad MJ (2011) Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Curr Biol 21:687–691
Notarbartolo di Sciara G, Würsig B (eds) (2022) Marine mammals: the evolving human factor. Springer Nature, Cham
Nowacek DP, Christiansen F, Bejder L, Goldbogen JA, Friedlaender AS (2016) Studying cetacean behaviour: new technological approaches and conservation applications. Anim Behav 120:235–244
O'Corry-Crowe GM, Suydam RS, Rosenberg A, Frost KJ, Dizon AE (1997) Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. Mol Ecol 6(10):955–970
Olesiuk PF, Bigg MA, Ellis GM (1990) Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. Rep Int Whal Commn Spec Iss 12:209–243
Orbach DN, Packard JM, Würsig B (2014) Mating group size in dusky dolphins (*Lagenorhynchus obscurus*): costs and benefits of scramble competition. Ethology 120(8):804–815

Oudejans MG, Visser F, Englund A, Rogan E, Ingram SN (2015) Evidence for distinct coastal and offshore communities of bottlenose dolphins in the north East Atlantic. PLoS One 10(4): e0122668

Pace RM III, Corkeron PJ, Kraus SD (2017) State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. Ecol Evol 7:8730–8741

Pallin LJ, Baker CS, Steel D, Kellar NM, Robbins J, Johnston DW, Nowacek DP, Read AJ, Friedlaender AS (2018) High pregnancy rates in humpback whales (*Megaptera novaeangliae*) around the Western Antarctic Peninsula, evidence of a rapidly growing population. R Soc Open Sci 5(5):180017

Perrin WF, Mesnick SL (2003) Sexual ecology of the spinner dolphin, *Stenella longirostris*: geographic variation in mating system. Mar Mamm Sci 19(3):462–483

Perrin WF, Brownell RL, De Master DP (1984) Reproduction in whales, dolphins and porpoises Rep Int Whal Commn, Spec Iss 6, Cambridge

Pettis HM, Rolland RM, Hamilton PK, Brault S, Knowlton AR, Kraus SD (2004) Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. Can J Zool 82(1):8–19

Pirotta E, Booth CG, Costa DP, Fleishman E, Kraus SD, Lusseau D, Moretti D, New LF, Schick RS, Schwarz LK, Simmons SE (2018) Understanding the population consequences of disturbance. Ecol Evol 8(19):9934–9946

Pirotta E, Mangel M, Costa DP, Goldbogen J, Harwood J, Hin V, Irvine LM, Mate BR, McHuron EA, Palacios DM, Schwarz LK (2019) Anthropogenic disturbance in a changing environment: modelling lifetime reproductive success to predict the consequences of multiple stressors on a migratory population. Oikos 128(9):1340–1357

Popkin G (2019) Data sharing and how it can benefit your scientific career. Nature 569(7756): 445–447

Pryor K, Shallenberger IK (1991) Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the eastern tropical Pacific. In: Pryor K, Norris KS (eds) Dolphin societies: discoveries and puzzles. University of California, Berkeley, CA

Punt AE, Siple MC, Francis TB, Hammond PS, Heinemann D, Long KJ, Moore J, Sepúlveda M, Reeves RR, Sigurðsson GM, Víkingsson G (2021) Can we manage marine mammal bycatch effectively in low-data environments? J Appl Ecol 58(3):596–607

Ramos EA, Hartman KL, Baird RW, Lerma JK, Rodríguez-González FM, Orbach DN (2023) Drone perspectives on cetacean mating and sex. In: Würsig B, Orbach DN (eds) Sex in cetaceans. Springer Nature, Cham

Read AJ, Drinker P, Northridge S (2006) Bycatch of marine mammals in U.S. and global fisheries. Conserv Biol 20(1):163–169

Reed J, New L, Corkeron P, Harcourt R (2022) Multi-event modeling of true reproductive states of individual female right whales provides new insights into their decline. Front Mar Sci 9:1–2

Richard JT, Levine R, Romano TA, Sartini BL (2021) Minimally invasive physiological correlates of social behaviour in belugas (*Delphinapterus leucas*) under human care. Polar Res 40(S1)

Riesch R, Barrett-Lennard LG, Ellis GM, Ford JKB, Deecke VB (2012) Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? Biol J Linn Soc 106: 1–17

Rocha RC, Clapham PJ, Ivashchenko YV (2014) Emptying the oceans: a summary of industrial whaling catches in the 20th century. Mar Fish Rev 76(4):37–48

Rolland RM, Hamilton PK, Kraus SD, Davenport BA, Gillett RM, Wasser SK (2007) Faecal sampling using detection dogs to study reproduction and health in North Atlantic right whales (*Eubalaena glacialis*). J Cetacean Res Manag 8(2):121

Rolland RM, Schick RS, Pettis HM, Knowlton AR, Hamilton PK, Clark JS, Kraus SD (2016) Health of North Atlantic right whales *Eubalaena glacialis* over three decades: from individual health to demographic and population health trends. Mar Ecol Prog Ser 542:265–282

Risch D (2022) Mysterious minke whales: acoustic diversity and variability. In: Clark CW, Garland EC (eds) Ethology and behavioral ecology of mysticetes. Springer Nature, Cham, pp 329–348

Schwacke LH, Voit EO, Hansen LJ, Wells RS, Mitchum GB, Hohn AA, Fair PA (2002) Probabilistic risk assessment of reproductive effects of polychlorinated biphenyls on bottlenose dolphins (*Tursiops truncatus*) from the Southeast United States coast. Envir Toxicol Chem 21:2752–2764

Smith H, Frere C, Kobryn H, Bejder L (2016) Dolphin sociality, distribution and calving as important behavioural patterns informing management. Anim Conserv 19(5):462–471

Stafford KM (2022) Singing behavior in the bowhead whale. In: Clark CW, Garland EC (eds) Ethology and behavioral ecology of mysticetes. Springer Nature, Cham, pp 277–296

Steinman KJ, O'Brien JK, Monfort SL, Robeck TR (2012) Characterization of the estrous cycle in female beluga (*Delphinapterus leucas*) using urinary endocrine monitoring and transabdominal ultrasound: evidence of facultative induced ovulation. Gen Comp Endocrin 175(3):389–397

Stephens PA, Sutherland WJ (1999) Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol Evol 14(10):401–405

Stewart JD, Durban JW, Knowlton AR, Lynn MS, Fearnbach H, Barbaro J, Perryman WL, Miller CA, Moore MJ (2021) Decreasing body lengths in North Atlantic right whales. Curr Biol 31(14):3174–3179

Stewart JD, Durban JW, Fearnbach H, Hamilton PK, Knowlton AR, Lynn MS, Miller CA, Perryman WL, Tao BW, Moore MJ (2022) Larger females have more calves: influence of maternal body length on fecundity in North Atlantic right whales. Mar Ecol Prog Ser 689:179–189

Suryan RM, Arimitsu ML, Coletti HA, Hopcroft RR, Lindeberg MR, Barbeaux SJ, Batten SD, Burt WJ, Bishop MA, Bodkin JL, Brenner R (2021) Ecosystem response persists after a prolonged marine heatwave. Sci Rep 11(1):6235

Suydam RS (2009) Age, growth, reproduction, and movements of beluga whales (*Delphinapterus leucas*) from the eastern Chukchi Sea. PhD thesis, University of Washington

Taylor BL, Archer FI, Martien KK, Rosel PE, Hancock-Hanser BL, Lang AR, Leslie MS, Mesnick SL, Morin PA, Pease VL, Perrin WF (2017) Guidelines and quantitative standards to improve consistency in cetacean subspecies and species delimitation relying on molecular genetic data. Mar Mamm Sci 33(S1):132–155

Tetley MJ, Braulik GT, Lanfredi C, Minton G, Panigada S, Politi E, Zanardelli M, Notarbartolo di Sciara G, Hoyt E (2022) The important marine mammal area network: a tool for systematic spatial planning in response to the marine mammal habitat conservation crisis. Front Mar Sci 2022:321

Thomas PO, Reeves RR, Brownell RL Jr (2016) Status of the world's baleen whales. Mar Mamm Sci 32(2):682–734

Vachon F, Eguiguren A, Rendell L, Gero S, Whitehead H (2022) Distinctive, fine-scale distribution of eastern Caribbean sperm whale vocal clans reflects island fidelity rather than environmental variables. Ecol Evol 12(11):e9449

van der Hoop J, Corkeron P, Moore M (2017) Entanglement is a costly life-history stage in large whales. Ecol Evol 7:92–106

Wade PR (1998) Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar Mamm Sci 14(1):1–37

Wade PR, Reeves RR, Mesnick SL (2012) Social and behavioural factors in cetacean responses to overexploitation: are odontocetes less "resilient" than mysticetes? J Mar Biol 2012:567276

Wade PR, Boyd C, Shelden KEW, Sims CL (2019) Group size estimates and revised abundance estimates and trend for the Cook Inlet beluga population. In: Shelden KEW, Wade PR (eds) Chapter 2: Aerial surveys, distribution, abundance, and trend of belugas (*Delphinapterus leucas*) JAFSC Proc Rep 2019-09. 93 pp

Wade PR, Long KJ, Francis TB, Punt AE, Hammond PS, Heinemann D, Moore JE, Reeves RR, Sepúlveda M, Sullaway G, Sigurgsson GM, Siple MC, Víkingsson GA, Williams R, Zerbini AN (2021) Best practices for assessing and managing bycatch of marine mammals. Front Mar Sci 8:757330

Ward EJ, Holmes EE, Balcomb KC (2009) Quantifying the effects of prey abundance on killer whale reproduction. Appl Ecol 46(3):632

Warlick AJ, Himes Boor GK, McGuire TL, Shelden KEW, Jacobson EK, Boyd C, Wade PR, Punt AE, Converse SJ (2022) Demographic and environmental drivers of population dynamics and viability in an endangered top predator using an integrated model. Anim Cons 123

Wasser SK, Lundin JI, Ayres K, Seely E, Giles D, Balcomb K, Hempelmann J, Parsons K, Booth R (2017) Population growth is limited by nutritional impacts on pregnancy success in endangered southern resident killer whales (*Orcinus orca*). PLoS One 12(6):e0179824

Wells RS (2003) Dolphin social complexity: lessons from long-term study and life history. In: de Waal FBM, Tyack PL (eds) Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA, pp 32–56

Wells RS, Tornero V, Borrell A, Aguilar A, Rowles TK, Rhinehart HL, Hofmann S, Jarman WM, Hohn AA, Sweeney JC (2005) Integrating life-history and reproductive success data to examine potential relationships with organochlorine compounds for bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Sci Tot Envir 349:106–119

Whitehead H (2003) Sperm whales: social evolution in the ocean. University of Chicago Press, Chicago, IL

Whitehead H (2010) Conserving and managing animals that learn socially and share culture. Learn Behav 38:329

Whitehead H, Rendell L (2004) Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. J Anim Ecol 1:190–196

Whitehead H, Shin M (2022) Current global population size, post-whaling trend and historical trajectory of sperm whales. Sci Rep 12(1):19468

Whitehead H, Christal J, Dufault S (1997) Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. Conserv Biol 11(6):1387–1396

Wild S, Krützen M, Rankin RW, Hoppitt WJE, Gerber L, Allen SJ (2019) Long-term decline in survival and reproduction of dolphins following a marine heatwave. Curr Biol 29:R239–R240

Williams R, Lusseau D (2006) A killer whale social network is vulnerable to targeted removals. Biol Lett 4:497–500

Williams RS, Curnick DJ, Brownlow A, Barber JL, Barnett J, Davison NJ, Deaville R, Ten Doeschate M, Perkins M, Jepson PD, Jobling S (2021) Polychlorinated biphenyls are associated with reduced testes weights in harbour porpoises (*Phocoena phocoena*). Envir Int 150:106303