Chapter 8
Odontocete Social Strategies and Tactics Along and Inshore

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Abstract Odontocetes are social animals, and long-term studies of nearshore species have documented high levels of social complexity, cultural innovation, cooperation, and social bonding within populations. While odontocete social lives may ultimately owe their existence to the predator protection benefits of grouping, it is becoming clear that there is great variability in the nature of social relationships and fitness consequences of social behavior for whales, dolphins, and porpoises. Although much of what we know still comes from limited longitudinal studies of identified individuals from a handful of species at multiple sites, information from new populations and species highlights the flexibility and vulnerability of odontocete societies in close proximity to humans and the need for robust conservation and management plans that account for social and cultural processes.

Keywords Social complexity · Culture · Social learning · Behavioral flexibility · Cooperation · Fission–fusion dynamics · Social vulnerability

8.1 Introduction

Sociality is one of the hallmarks of the odontocete suborder, with members displaying some of the most complex societies in the animal kingdom. Sociality likely has evolved because it confers survival and reproductive advantages within varied environments. However, the strengths and complexities of some social bonds among odontocetes appear remarkable—stories of apparently grieving mothers carrying dead infants for days (Bearzi et al. 2018), entire social groups stranding alongside the sick (Odell et al. 1980), menopausal grandmothers caring for extended

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Fig. 8.1 Resident common bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida, swim in shallow waters nearshore, where they frequently encounter human activities within their community range. Image credit: Sarasota Dolphin Research Program, taken under National Marine Fisheries Service Scientific Research Permit No. 15543

family members (Brent et al. 2015), and males forming complex lifetime alliances (Wells 2014; Connor and Krützen 2015) confound those seeking simple evolutionary explanations (see also Chap. 1).

Socioecological models link female grouping patterns to predictability and distribution of resources and potential threats from predators, with male strategies then built around distribution and availability of potentially receptive females (Gowans et al. 2008). This general mammalian "rule" of females focusing on food and fear and males monopolizing mates somewhat fits observed patterns among odontocetes, but we are still discovering the broad diversity and flexibility of social strategies among toothed whales and dolphins. Most of our understanding is based on research limited to a handful of species and almost entirely on those that live close to shore. A few long-term studies that document details of social relationships of identified individuals over multiple generations, and the potential fitness consequences of different social strategies, have shed light on richness of odontocete social lives (Wells et al. 1980; Connor et al. 1998; Mann and Karniski 2017).

Some odontocetes display a large capacity to adapt and survive in the face of rapid environmental change and increasing anthropogenic impacts. But, many odontocete populations and species are nevertheless at risk—especially those found in nearshore and inshore habitats where ranges overlap extensively with human activities (Fig. 8.1). While some nearshore populations are well documented, we may be too late in many cases to fully learn about newly acquired social patterns of which we are only starting to gain a glimpse.

My aim here is to introduce several themes emerging from growing knowledge about social lives of odontocetes living close to shore. This serves as an extension of Chap. 1 (by Gowans), which focused on grouping behaviors among odontocetes, and as a jumping off point for the more detailed accounts and examples presented in Part II. This chapter excludes discussions of social strategies of river dolphins (*Platanista*, *Inia*, or *Lipotes*) and porpoises (Phocoenidae) because detailed social information of these is generally lacking (summarized in chapters by Sutaria et al. and Teilmann and Sveegard, respectively).

8.2 Costs and Benefits of Grouping

For dolphins and whales in an aquatic environment with few places to hide, the primary benefit of group living appears to be predator protection from sharks and killer whales, along with perhaps some degree of protection from conspecific harassment or aggression (e.g., Wells et al. 1980; Connor 2000, 2002; Gowans et al. 2008; Möller 2012; Würsig and Pearson 2015). Cooperation in resource acquisition may also favor group formation. Major costs of group living are competition for limited and generally non-defensible food resources, mate competition, and the potential for disease transmission through social networks. Connor (2000, 2002) argued that low transport costs and large range sizes in aquatic environments help to reduce costs of grouping and philopatry for dolphins and whales, in comparison with terrestrial mammals. In addition, perhaps as a means to balance the competing costs and benefits of group formation, dynamic fission–fusion societies are a dominant social organization among nearshore odontocetes but with more stable groupings in several species and specific environments (Connor 2000; Gowans et al. 2008). Sexual segregation outside of breeding and female-biased social and/or geographic philopatry also appear repeatedly among odontocetes close to shore, again with exceptions for those where opposite sex kin are frequent associates and in a few bisexually bonded populations (Möller 2012).

Yet, despite decades of research on group dynamics and social strategies, long-term data remain limited to several species with multiple sites or populations. While long-term studies were few early on (Wells et al. 1980, Connor et al. 1998; Chap. 16), by 2017, researchers had greatly expanded the breadth of species represented by intensive, long-term studies—with 30 of 75 odontocete species now having some long-term study of at least 10 years, 19 of which have longitudinal data tracking identified individuals over time (Mann and Karniski 2017). However, there still remain only six spp. (including the two *Tursiops*) for which there are long-term longitudinal studies at multiple locations to allow for understanding of intra-specific variation in social and grouping patterns (Table 8.1).

Table 8.1 Long-term, longitudinal studies (LTS) of odontocetes providing insight into social strategies

Family	No. of species[a]	No. of species with LTS[b]	No. of study locations[b]	IUCN status[c]
Offshore				
Physeteridae (sperm whale)	1	1	5	VU
Kogiidae (dwarf/ pygmy sperm whale)	2	–	–	DD
Ziphiidae (beaked whales)	22	3	1 (each spp.)	DD (20), LC (2)
Inshore/rivers				
Platanistidae (S. Asian river dolphin)	1	–	–	EN
Iniidae (Amazon river dolphin)	1	1	2	DD
Lipotidae (Yangtze river dolphin)	1	–	–	CR
Pontoporiidae (Franciscana)	1	–	–	VU
Arctic				
Monodontidae (narwhal, beluga)	2	1	1	LC
Cosmopolitan				
Delphinidae (dolphins)	37	13	1 (9 spp.) 2 (*S. guianensis*) 4 (*T. aduncus*) 9 (*T. truncatus*) 11 (*O. orca*)	DD (15), LC (14), NT (1), VU (3), EN (3), CR (1)
Phocoenidae (porpoises)	7	–	–	DD (2), LC (2), VU (1), EN (1), CR (1)
Total	75	19	46 (6 spp. *with multiple LTS sites*)	40 (DD), 8 (EN/CR), 7 (NT/VU), 20 (LC)

[a] Committee on taxonomy. 2017. List of marine mammal species and subspecies. Society for Marine Mammalogy, www.marinemammalscience.org, consulted on August 7, 2018

[b] Mann and Karniski 2017. LTS = includes only continuous, systematic long-term (≥10 years), longitudinal studies (tracking identified individuals). No. of study locations also only includes LTS

[c] IUCN Red List of Threatened Species, www.iucnredlist.org, consulted on August 8, 2018. *DD* Data Deficient, *LC* Least Concern, *NT* Near Threatened, *VU* Vulnerable, *EN* Endangered, *CR* Critically Endangered

8.3 Social Complexity

Nearshore odontocete societies vary in group size and stability of bonds. There are short-term associations thought to be characteristic of porpoises, stable matrilineal pods of resident killer whales (*Orcinus orca*), and multitiered alliance networks of

Fig. 8.2 Male common bottlenose dolphins, *Tursiops truncatus*, engage in highly active sociosexual behavior during the juvenile period as they build relationships that may become important alliances later in life. Image credit: Sarasota Dolphin Research Program, taken under National Marine Fisheries Service Scientific Research Permit No. 20455

bottlenose dolphin (*Tursiops* sp.) males operating within a fluid fission–fusion society (Connor 2000). There is even limited evidence for socially monogamous (or at least longer term) relationships between unrelated male and female franciscana dolphins (*Pontoporia blainvillei*; Wells et al. 2013).

The majority of species live in fluid societies with a high degree of fission–fusion dynamics and complex interaction, communication, and cognitive requirements (Aureli et al. 2008). Dyadic relationships vary in strength and stability and may depend on behavioral context (e.g., Gero et al. 2005; Gazda et al. 2015). Most species display long-term bonds with kin and nonkin, often mediated by complex affiliative, aggressive, and sociosexual behaviors (Fig. 8.2). Dolphins and whales use vocal communication, touch, and synchrony to maintain affiliative bonds and display physical and acoustic aggression intra- and intersexually (Connor 2002). Cooperation between relatives and nonkin is frequent in odontocete social lives, from simple group hunting to complex cooperative foraging techniques requiring division of labor (Gazda et al. 2005), unrelated males forming lifetime cooperative alliances (Connor and Krützen 2015), and even species where menopausal grandmothers within stable matrilineal groups care for family past their own reproductive lives (e.g., Brent et al. 2015). Cooperative behaviors may provide direct or inclusive fitness benefits to those involved (or would result in fitness consequences to individuals who refused to participate).

Some larger-bodied odontocetes display stable matrilineal groups, such as sperm whales (*Physeter macrocephalus*; Whitehead 2003), killer whales (Bigg et al. 1990; Ford et al. 2000), long- and short-finned pilot whales (*Globicephala* spp., Amos et al. 1993; Kasuya and Marsh 1984), false killer whales (*Pseudorca crassidens*; Baird et al. 2008), and pygmy killer whales (*Feresa attenuata*; McSweeney et al. 2009). Strong lifetime associations are formed between family members, with daughters (and in some cases sons) staying with mothers through their own adulthood, and matriarchs likely serve pivotal leadership roles (Brent et al. 2015). Substantial allocare of young by other group members occurs (including allonursing, e.g., sperm whales, Gero et al. 2009), as does widespread food sharing (e.g., killer whales, Ford and Ellis 2006). Some matrilineal species also display an extremely rare feature among animals—extended postreproductive life spans of females who continue caring for family after ceasing their own reproduction. They are killer whales, short-finned pilot whales, false killer whales (Photopoulou et al. 2017), beluga whales (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*; Ellis et al. 2018).

Allocare, food-sharing, and postreproductive care are forms of cooperative behavior that may have energetic or fitness consequences to the provider but which appear to remain viable social strategies because potential consequences are overridden by affiliative and inclusive fitness benefits of cooperating with and caring for close family members within tightly bonded kin groups. Killer whales are the only nearshore species with stable matrilineal groups and also the only species for which bisexual social and geographic philopatry is common among resident pods. Postreproductive females are more likely to lead foraging groups (Brent et al. 2015), particularly when food is scarce and for their sons, thus serving as repositories of ecological knowledge while maximizing their own inclusive fitness. Intergenerational reproductive conflict and costs to older mothers co-breeding with daughters, coupled with increases in local group relatedness with age, may have favored evolution of early reproductive senescence among resident killer whales (Croft et al. 2017).

Strong cooperative male alliances among bottlenose dolphins (*Tursiops* spp.) are a striking feature of societies that otherwise exhibit high levels of fission–fusion dynamics, with frequent changes in group composition and membership. In Sarasota Bay, Florida, unrelated males form stable long-term alliances, coordinating with a single partner to obtain mating opportunities and fend off predators and rivals, and these paired males enjoy higher reproductive success than males without a partner (Wells 2014). Elsewhere, alliances are more flexible in size, with larger alliances conferring greater fitness benefits (e.g., Wiszniewski et al. 2012). Male Indo-Pacific bottlenose dolphins in a large and open social network in Shark Bay, Australia, form multitiered alliances seeking access to receptive females (Connor and Krützen 2015; Chap. 16), possibly a unique mammalian social structure (Randić et al. 2012). While these complex alliances are currently only well understood among bottlenose dolphins studied long term, it is possible that other species or populations may display strategies that would hold more clues to development of complex social organizations and associated cognitive and communicative abilities.

Odontocete social complexity likely requires significant cognitive capacity for individual recognition and communication while tracking relationships with (and perhaps between) other community members. Social demands are probably not the sole driver of large brain size and cognitive ability in dolphins and whales, but high encephalization is thought to have developed in humans, primates, and others due primarily to challenges associated with managing a dynamic social world, including cooperation and coordination, while also linked to breadth of cultural behaviors or ecological factors (Fox et al. 2017; also Chap. 18). Although odontocetes provide an important comparative group for considering selection pressures favoring large brains (Connor 2007), their social intelligence cannot (and should not) be understood apart from special factors of their ecology that separate them from other groups like primates (Barrett and Würsig 2014). For example, odontocetes are social predators that live in an underwater environment favoring sensory and communication systems built around sound, which differs greatly from the ecological context of terrestrial counterparts. Nevertheless, some species display cognitive and communicative features indicative of the critical importance of individual recognition and long-term tracking of social relationships, such as the development and referential use of individually distinctive signature whistles in bottlenose dolphins (Sayigh et al. 1998; King et al. 2013) coupled with long-term social memory for these signals (Bruck 2013). Recent efforts to understand proximate and ultimate links between social complexity and communicative complexity in birds and other animals (e.g., Freeberg et al. 2012; Freeberg and Krams 2015), and model broader connections between cooperation, acoustic communication, and cognition in predator species (e.g., Kershenbaum and Blumstein 2017), provide new directions for understanding odontocete social lives.

8.4 Behavioral Flexibility and Cultural Diversity

Odontocete societies close to shore exhibit intraspecific variation indicative of both a high degree of behavioral flexibility and cultural diversity within and among populations. For example, killer whale ecotypes display differing behavioral patterns in feeding specializations, seasonal habitat use, group size, social organization, long-term bonds, and acoustic communication patterns (Ford and Ellis 2014; see also Chap. 11). Resident killer whales, which specialize on salmon, have stable bisexually philopatric matrilineal pods (Bigg et al. 1990). Within these pods lie the core matrilines, where both sons and daughters remain in their natal group for life, with up to four generations of maternally related individuals forming strong and stable long-term bonds and sharing stereotyped vocal calls (Ford and Ellis 2014). In contrast, transient killer whales in the same waters feed on marine mammals and generally occur in smaller groups that maximize their foraging efficiency but do not share the same strict matriline structure of residents (Baird and Whitehead 2000). Female dispersal of transients is commonly observed at sexual maturity, with sons also dispersing occasionally, and strong long-term bonds form almost exclusively between mothers and sons. Associations between matrilines are much more dynamic, without consistent long-term groupings into hierarchical pods or vocal clans, as in residents (Ford and Ellis 2014). Additional culturally transmitted ecological specializations occur in killer whale populations offshore and in other geographic areas, making killer whale ecotypes one of the strongest examples of cultural evolution in the animal kingdom, providing a better understanding of dynamics and consequences of culturally driven specialization and reproductive isolation (Whitehead and Ford 2018).

Some odontocete populations exhibit differing patterns of social associations and bonding dependent upon local ecological characteristics and geographic isolation. While bottlenose dolphins in most locations usually exhibit fluid fission–fusion societies with some stronger sex-specific bonds, a population in the fjords of Doubtful Sound, New Zealand, instead forms large mixed-sex groups displaying close, long-term associations and stable community structure with no dispersal (Lusseau et al. 2003). This population lives in a harsh, low-productivity environment that may require higher cooperation and group stability, whereby population isolation and ecological constraints may drive social behavior differences from bottlenose dolphins elsewhere (Lusseau et al. 2003). Similarly, Indo-Pacific humpback dolphins (*Sousa chinensis*) also form fluid fission–fusion communities. However, the Taiwan Strait population exhibits stronger cohesion and long-term stability in social network structure, built primarily around presumed mom–calf pairs. This unique pattern may be a response to local conditions making long-term cooperative behavior, specifically calf care, more advantageous to buffer against effects of small population size, isolation, and other stressors (Dungan et al. 2015). Roughly similar scenarios may affect sociality in facultative freshwater dolphins, with differences in social patterns observed in different environments. For example, Irrawaddy dolphins (*Orcaella brevirostris*) live in coastal waters throughout Asia as well as in river systems and inland lakes, where many populations are in severe decline. In Indonesia, the open ocean coastal population is less social with interactions focused on feeding, whereas riverine dolphins display more long-term intensive associations across behavioral contexts (Kreb 2004). This intraspecific pattern is in contrast to the "true" river dolphins whose social behavior is less well known but who appear to display less sociability and lower group sizes than coastal species (Smith and Reeves 2012; Gomez-Salazar et al. 2012).

Both intraspecific and intrapopulation differences in social behavior occur in semipelagic delphinids that switch from pelagic to nearshore waters on diurnal or seasonal bases. Two "habitat switching" species with flexibility in social behavior based on environment are (1) island-associated versus atoll-living spinner dolphins (*Stenella longirostris*) off Hawaii and the Northwestern Hawaiian Islands (Karczmarski et al. 2005) and (2) dusky dolphins (*Lagenorhynchus obscurus*) off New Zealand that show both diel and seasonal habitat shifts (Würsig and Pearson 2015). While spinner dolphins also occur offshore, the focus here is on populations that generally stay close to shore during the day and shift to deeper waters to forage at night. Off Kona in the Main Hawaiian Islands, spinner dolphins are a diel fission–fusion society, resting in small bays during the day in groups of 20–100 with flexible membership that then coalesce at night in groups of hundreds to forage and socialize in deep waters—where large numbers are likely important both for predator protection and mating (Norris et al. 1994). However, off the more isolated Midway Atoll, spinner dolphins lack this diel fission–fusion pattern, instead forming stable, bisexually bonded groups that use the same atoll each day for resting and move offshore together each night to forage (Karczmarski et al. 2005). Occasional "macro fission–fusion" events bring groups of animals from one atoll to another, where they gradually integrate into the existing social group, but otherwise atoll spinner dolphins exhibit little fluidity in social associations (Karczmarski et al. 2005).

In New Zealand, dusky dolphins display behavioral flexibility in disparate habitats. They occur seasonally in coastal shallows in the Marlborough Sounds and year-round in waters off Kaikoura, where a deep canyon comes close to shore. Near Kaikoura, dusky dolphins spend days resting and socializing in shallows within a large school or smaller nursery groups and then move offshore to feed on fish and squid from the deep scattering layer at night (Würsig and Pearson 2015). They exhibit low fission–fusion dynamics, splitting up mostly during foraging, and their grouping patterns are indicative of fairly high predation risk from killer whales (Chap. 7). In contrast, a subset of the population changes foraging and social strategies as they travel to a seasonal habitat in Admiralty Bay. This winter habitat is a smaller extensive shallow area with relatively low predation risk, where dusky dolphins cooperatively herd schooling fishes in small groups during the day and rest in the same shallow nearshore waters at night (Würsig and Pearson 2015). Group size is variable, but generally smaller than the large school observed in Kaikoura, and duskies display high social fluidity with some behaviorally specific and longer-term preferential associations (Pearson et al. 2017). Although the driver of this unique seasonal "mode-switching" behavior is unknown, some bonds observed in Admiralty Bay persist across years, suggesting that seasonal migratory behavior could be a cultural tradition in dusky dolphins (Whitehead et al. 2004; Pearson et al. 2017; Chap. 18).

Arctic odontocetes—narwhals and beluga whales—have poorly understood social strategies but also display intrapopulation changes in social behavior along with seasonal habitat shifts related to ice cover. Narwhals are deep divers that congregate nearshore in bays and fjords in summer. Fidelity to nearshore summering areas appears matrilineally driven, and subpopulation structure is based on these predictable and likely culturally inherited migration patterns (Heide-Jorgensen et al. 2015). Narwhals in summer tend to travel in large groups containing many smaller, typically sexually segregated, clusters (Marcoux et al. 2009). Despite hypotheses of a matrilineal social structure and recent evidence indicating that narwhal females may exhibit postreproductivity (Ellis et al. 2018), genetic and fatty acid analysis of ice-entrapped groups suggests that relatives may not forage together, perhaps indicating instead that narwhals could display a fission–fusion social structure (Watt et al. 2015). Winter observations in the offshore pack ice are limited, but in Baffin Bay they form large aggregations of thousands of animals at remarkably high densities (on average 77 animals per km; Laidre and Heide-Jorgensen 2011), indicating a shift in sociality with season.

Belugas also display a seasonal shift in social behavior, where animals that use discrete coastal summering areas converge on common wintering grounds (O'Corry-Crowe et al. 2018). Belugas group based on relatedness during migration, indicating that relatives, especially females, maintain a migratory social structure that likely facilitates learning of different routes (Colbeck et al. 2013). Outside of migration, summer groups appear segregated by age, sex, and reproductive status (Loseto et al. 2006). Recent genetic analyses confirm natal philopatry to summer aggregation sites and migratory routes, with large numbers of closely related belugas together at these coastal sites, providing evidence that migratory culture and kinship have promoted the formation of demographically distinct subunits that nevertheless overlap spatially and temporally (O'Corry-Crowe et al. 2018). The most basic social units in belugas may be immediate matrilines, which could explain multiple observations of allonursing and allocare for individuals in human care (e.g., Leung et al. 2010; Hill and Campbell 2014) and the potential existence of menopause and postreproductive periods (Ellis et al. 2018). Older beluga females presumably could play similar roles to killer whale matriarchs serving as repositories of ecological knowledge, in this case perhaps how to avoid ice entrapment during migration. If they play a leadership role in migratory groups, as appears likely, this role may improve survival of kin during vulnerable periods.

Intrapopulation differences in social patterns in response to environmental disturbance and anthropogenic interactions also occur. Resident bottlenose dolphins in Sarasota Bay, Florida, have temporary but substantial changes in grouping and social network dynamics in response to severe harmful algal blooms, whereby dolphins associate in larger groups and with more individuals during red tide events, and the community network becomes significantly more connected and compacted (McHugh et al. 2011). It is uncertain whether these social shifts reflect an adaptive response facilitating information transfer or capitalization of different prey resources or are simply a consequence of individuals aggregating in relatively less impacted areas, but they have potential consequences in terms of heightened disease transfer during ecologically stressful times (McHugh et al. 2011). On a longer time scale, larger social restructuring occurred in response to two major hurricanes in the Bahamas, when about one-third of resident bottlenose and spotted dolphins (*Stenella frontalis*) disappeared. Here, bottlenose dolphins that initially interacted in one larger fluid fission–fusion community received an influx of immigrants and then split into two distinct units that rarely interacted though both new social clusters contained previous residents and immigrants (Elliser and Herzing 2011). In contrast, spotted dolphins showed no increase in immigration post-hurricane, but their social patterns also shifted, displaying increases in social differentiation and cohesion within previously established clusters and a change in male alliance structure, where adult alliances simplified but juveniles began to make alliance-level associations not seen previously (Elliser and Herzing 2014). Lastly, interspecific association between these two sympatric species also changed; while bottlenose and spotted dolphins still regularly interacted post-hurricane, there was a reduction in sexual-aggressive behavior and aggressive encounters (Elliser and Herzing 2016). Again, the specific reasons for these shifts are unclear, but they show a level of social flexibility in odontocetes that allows for adjustments in the face of environmental challenges.

An increasing number of studies have also documented examples of within-population differences in social patterns or social segregation based on anthropogenic interactions, especially human-centered foraging specializations utilized by only a subset of animals. For example, some bottlenose dolphins in Laguna, Brazil, participate in a cooperative foraging interaction with local beach-casting fishermen (Pryor and Lindbergh 1990), and these cooperative dolphins have stronger within-class associations and are divided into separate social clusters from noncooperative dolphins in the overall community network (Daura-Jorge et al. 2012). This social partitioning is not based solely on differences in space-use patterns but is focused around use of this specific foraging tactic, which is likely transmitted via social learning. Similar patterns occur in bottlenose dolphin populations where a subset of individuals interacts with commercial trawlers. Social differentiation and clustering within the shared community range of resident bottlenose dolphins in Savannah, Georgia, are based on human-related foraging associated with trawlers (a socially learned behavior) but not foraging via begging for food (possibly individually learned) that is distributed among clusters (Kovacs et al. 2017). In Moreton Bay, Australia, another bottlenose dolphin society changed due to interactions with fishermen, with humans driving social segregation (Chilvers and Corkeron 2001). Initially, there were two distinct social communities based on trawler-associated foraging rather than ranging differences, whereby community core areas overlapped, but individuals differed in feeding modes, habitat preferences, and group size, with trawler dolphins associating in larger groups than those that did not feed in association with humans. These social patterns nearly vanished after a reduction in commercial trawling, with the community now displaying less differentiation and more compaction in their social network, with more and stronger associations between individuals and a loss of prior partitioning, indicating that social structure can adapt quickly and may be resilient to disturbance (Ansmann et al. 2012). Lastly, killer whale social structure in the Strait of Gibraltar is being shaped by fishery interactions in a location where a subset of pods interact with a local tuna fishery (Esteban et al. 2016). Originally only one pod interacted, which then fissioned into two, with stronger within-pod interactions than seen in others, and this emerging situation may be an active example where social spreading of a novel foraging behavior begins to drive population fragmentation (Esteban et al. 2016). Thus, odontocete sociality and foraging behavior are both flexible and intertwined within local communities, with social learning of foraging specializations possibly driving social segregation.

Observed variation in foraging traditions or specializations provides some of the best examples of cultural diversity in odontocetes. Cultural processes, with social learning as a key driver, have resulted in an impressive variety of vocal and behavioral “cultures” observed among the few whales and dolphins that have been studied extensively (Whitehead and Rendell 2015). While attributions of culture to whales and dolphins have been somewhat contentious (e.g., Rendell and Whitehead 2001; Laland and Janik 2006; McGrew 2015), remarkably diverse foraging strategies and differing patterns of foraging traditions observed among and within multiple bottlenose dolphin communities most likely result from cultural transmission (see Chap. 15; Wells 2003; Whitehead and Rendell 2015). Foraging specializations are passed on via social learning among associates, and many tactics either involve social coordination (such as cooperative mud ring and driver–barrier feeding styles) or social consequences for the individuals or communities where they are practiced [such as the human-centered foraging behaviors discussed above and the difficult and time-consuming sponge tool-use of Indo-Pacific bottlenose dolphins (Krützen et al. 2005, 2014; Mann et al. 2012)]. Thus, cultural diversity and social strategies in odontocetes may be highly interdependent, with culturally transmitted ecological specializations potentially driving social patterns in more species than currently documented.

8.5 Vulnerability

Odontocete societies alongshore cannot escape the persistent influences of human activities on their health, behavior, and critical habitats. Nearshore and inshore odontocete species' ranges overlap substantially with humans, and local populations often face severe impacts from anthropogenic noise, fishing pressure, industrial and recreational activity, directed and incidental takes, coastal pollution, and habitat loss and degradation. Although many odontocete species are still relatively unknown (over half are "data deficient," IUCN 2018), 13 of the 14 species listed as Vulnerable to Endangered on the IUCN Red List are found inshore or nearshore (Table 8.1), as are all three species listed as Critically Endangered. In addition, all 11 Critically Endangered odontocete subpopulations or subspecies come from inshore or nearshore habitats, which may be isolated from other suitable areas or members of their species.

While human impacts are clearly the major cause of declines, odontocetes appear perhaps less resilient in the face of conservation challenges than their mysticete cousins, many of which have demonstrated clear signs of population recovery after depletion from past hunting (e.g., Wade et al. 2012). Although life history traits constraining rapid population growth, such as late ages of first reproduction and low calving rates, explain some of this difference, social and behavioral factors are also likely at play, whereby the obligate sociality of many odontocetes means that their survival and reproductive success depends on maintaining connections to others (Wade et al. 2012). Certain aspects of odontocete societies, including high levels of mutual dependence, social cohesion, and reliance on social groups for predator defense and care of young, as well as intergenerational transfer of knowledge and leadership of older individuals, may be especially important during times of scarce prey or in avoiding high-risk circumstances (Wade et al. 2012). Species for which these factors are relevant are especially vulnerable to impacts from lost individuals, which may result in disruption or fragmentation of social bonds/units such that removal of only a few individuals can have disproportionate impacts on survival or birth rates. The endangered southern resident killer whales are an example of this phenomenon, with shifts in social cohesion resulting from recent population declines (Parsons et al. 2009), and the potential that removal of very few key individuals could be devastating (Williams and Lusseau 2006). Disproportionate impacts occur with losses of any matriarchal repositories of information whose removal leads to reduced survival of daughters and sons (Foster et al. 2012) or of juvenile females who may act as social brokers maintaining cohesion between groups within a larger pod (Williams and Lusseau 2006).

Geographically isolated inshore odontocete populations also appear particularly vulnerable. There are now multiple examples where critically endangered subpopulations display different social dynamics—especially stronger/longer-term bonding and cooperative behavior—than observed elsewhere due in part to their isolation from others but likely also because remaining social bonds have become especially important to survival in these settings [e.g., Fiordland bottlenose dolphins (Lusseau et al. 2003), Taiwanese humpback dolphin (Dungan et al. 2015), Irrawaddy dolphins in rivers (Kreb 2004)]. Dungan et al. (2015) suggest that small populations subject to ecological stress from anthropogenic disturbance and other factors may develop these more stable social patterns to dampen impacts to survivorship and reproductive success, regardless of their isolation from others. However, Smith and Reeves (2012) stress the particular vulnerability of riverine cetaceans to effects of habitat degradation and population fragmentation due to human activities including dam construction, whereby further isolation continues to drive declines of small populations (see also Chap. 19). While the particular challenges in each situation may differ, the likelihood of heightened social reliance within struggling populations necessitates a focus on minimizing impacts that disrupt social dynamics in conservation planning, because—again—the loss of very few individuals may exert much larger population-level impacts than their numbers would otherwise suggest.

Strong, long-term bonds among odontocetes can lead to heartbreaking, and perhaps dangerous, responses to dead companions. Nurturant responses to dead conspecifics are much more commonly observed in odontocetes than mysticetes, and primarily among the Delphinidae, with probable mothers typically attending to calves or juveniles (Bearzi et al. 2018; Reggente et al. 2016). While these behaviors may begin as initial attempts to revive or protect, in many cases what could be adaptive caring behavior turns maladaptive, with long-term carrying of or standing by the dead (Bearzi et al. 2018). These behaviors may represent the strong attachment of mother–calf bonds or grief and mourning of lost long-term companions but either way likely result in at least short-term energetic consequences to attending animals and possibly longer-term fitness consequences in cases where individuals actually strand alongside others (e.g., Odell et al. 1980). In populations facing increasing stressors due to anthropogenic and environmental impacts, it is possible that what are now infrequent instances of potentially maladaptive caring for dead may become more common and pose greater risks within small, strongly bonded populations.

In some cases, social strategies that benefit individuals in other contexts may also become maladaptive in the face of anthropogenic impacts or when some individuals adopt risky behaviors. Cultural processes can both aid and constrain potential responses to environmental change (Keith and Bull 2017; Whitehead 2010; Whitehead et al. 2004), and so understanding aspects of behavioral ecology, including extent of behavioral plasticity and specialization, capacity for social learning, and patterns of individual behavioral variation, become increasingly important in conservation efforts for odontocetes the world over (Brakes and Dall 2016; Chap. 10).

While complex social interactions allow opportunities for social learning and cultural transmission that could provide resilience in the face of anthropogenic stressors and environmental change, these dynamic and widespread social connections can also leave individuals vulnerable to disease transmission or spread of maladaptive behaviors. Although potentially helpful in adapting quickly to changing environments, behavioral flexibility itself—especially in a foraging context—can be maladaptive. Foraging tactics connected to human activities, including commercial and recreational fisheries, are becoming more common among odontocete populations, and behaviors such as depredation and begging from or being provisioned by humans may pose risks to participating individuals, including entanglement in or ingestion of fishing gear or vessel strikes. While typically only a few individuals begin utilizing these strategies, they then can spread to others via social learning, potentially endangering larger proportions of vulnerable local communities (e.g., Donaldson et al. 2012a, b; Christiansen et al. 2016; see also Chap. 10).

8.6 Conclusion

While this chapter only scratches the surface of nearshore and inshore odontocete social lives, it sheds light on a few key features of toothed whale societies: social complexity, behavioral flexibility, cultural diversity, and vulnerability to anthropogenic impacts. Despite difficulties of observing social interactions underwater, long-term research is unraveling aspects of odontocete sociality that contribute to survival and reproductive success within complex societies and varied ways in which nearshore odontocetes depend upon each other. More work is needed on understudied species and geographic areas to develop a comprehensive understanding of social strategies and variability within and among taxa and provide behavioral and social integrity information that is critical for effective conservation of declining populations.

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