

# Chapter 7

## Social Organization of Baleen Whales



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**Abstract** Baleen whales are specialized to find and exploit prey that form dense patches seasonally within broad ocean areas. Most populations have an annual reproductive cycle that separates their breeding season from their feeding season, often with long-distance migrations between feeding and breeding areas. The longest bond we know of for most baleen whale species is the mother-calf bond. Calves suckle for five to seven months in most species and wean by the next feeding season. The species whose social behavior has been most studied is the humpback whale, enabled by their distribution, which often is near shore, and their individually distinctive natural markings. Some humpback whales feeding on mobile prey form stable groups where each individual learns specific roles to perform coordinated group foraging. Aside from these groups, which may last for many years, most baleen whale groups are reported to be fluid with few strong associations between individuals other than mother and calf. However, most researchers define whale groups in terms of the number of whales that are close enough to be sighted within a certain distance of one another. Sound propagates so well underwater that whale sounds can be heard at distances of tens to hundreds of kilometers away. This means that whales may be able to maintain contact over much greater ranges than are usually assessed by human observers—they may form long-range “heards” in addition to shorter range “herds.” The social organization of whales during the breeding season is structured in part by songs—acoustic reproductive advertisement displays. The potential scale of “heards” is indicated by the ability of scientists to track one singing blue whale for 43 days as it swam > 1700 km. Scientists will start to develop a fuller understanding of the social organization of baleen whales when they apply methods that can make observations and test hypotheses over the temporal and spatial scales at which baleen whales move and communicate.

**Keywords** Baleen whale · Social organization · Annual cycle · Feeding · Migration · Breeding and calving · Song · Effective range of communication

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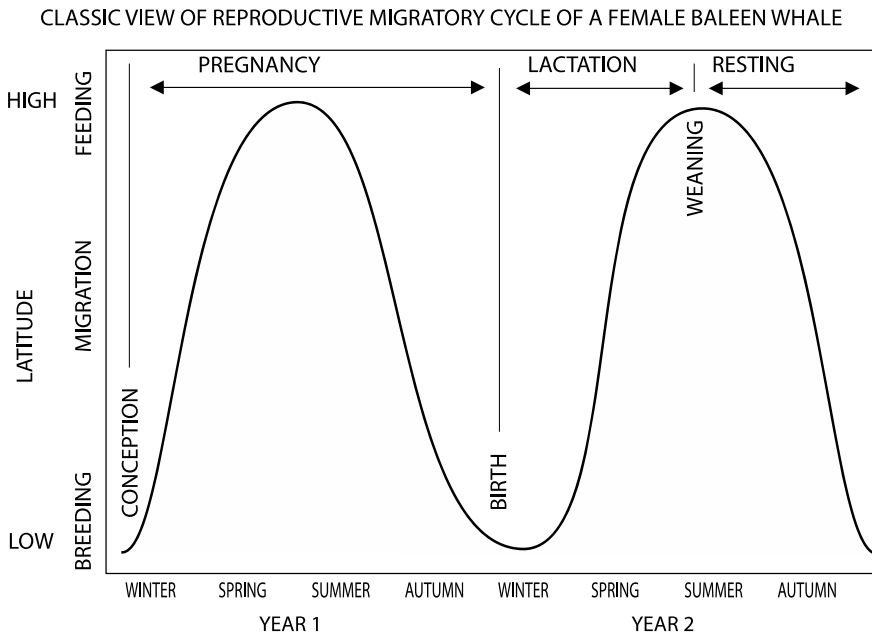
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## 7.1 Introduction

### 7.1.1 Annual Cycle of Baleen Whales

Most baleen whale species have an annual cycle of a winter breeding and calving season in low latitudes, migration to summer feeding areas in higher latitudes, and another migration back to the winter breeding and calving areas (Fig. 7.1). The selection pressures operating on social behavior likely differ during these different phases of the annual cycle, leading to the potential for differences in social organization in different seasons. Most baleen whales feed little if at all during the breeding and calving season, so selection focuses on maternal care of the young and on the mating system. The migration seasons select for efficient and safe movements over thousands of kilometers, but also may involve feeding, care of young, and behavior associated with the mating system. The primary feeding adaptation of baleen whales involves their ability to engulf large aggregations of prey in one mouthful, through ram filtration in balaenids (Simon et al. 2009), benthic and epi-benthic suction feeding in gray whales (Nerini 1984), or gulping in balaenopterids (Goldbogen et al. 2006). Baleen



**Fig. 7.1** Schematic timeline for the reproductive and migratory cycles of female baleen whales (adapted from Lockyer 1984). Some minke (*Balaenoptera acutorostrata*) and humpback whales (*Megaptera novaeangliae*) may conceive soon after birth, with no resting period, but balaenid whales have multi-year resting periods (adapted from Lockyer 1984). Some resident populations of baleen whale do not migrate.

whales have a variety of social adaptations to improve foraging efficiency, and social organization during the feeding season is driven primarily by foraging ecology. The abundance of dense patches of prey during summer in high latitudes is thought to represent the primary factor for migrating to summer feeding areas (Chap. 4).

The reasons for the migration of baleen whales to lower latitude breeding areas are less well understood (Corkeron and Connor 1999). Several hypotheses focus on energetics. Brodie (1975) argued for a metabolic advantage for whales swimming from high-latitude waters that are cold in winter to warmer lower latitude waters. However, most modeling studies suggest that baleen whales have a low energetic cost for maintaining body temperature in cold water. Payne (1995) argued that foraging opportunities might be better in lower latitudes than in higher latitudes during winter. Southern right whales (*Eubalaena australis*) feed on copepods during the breeding season on the Península Valdés, Argentina, calving ground (D'Agostino et al. 2016), and Norris et al. (1977) observed gray whales (*Eschrichtius robustus*) engaged in behavior that looked like foraging near their Baja California, Mexico, breeding grounds. However, the whaling literature conclusively shows for the most heavily whaled populations that foraging provides a minor contribution to energy reserves outside of the feeding season when fat reserves are laid down, as lipid stores decrease during the migration and breeding seasons (e.g., Chittleborough 1965 for humpback whales (*Megaptera novaeangliae*). Therefore, it seems unlikely that rare foraging opportunities drive selection for the fall migration to the breeding and calving grounds. The bowhead whale (*Balaena mysticetus*) has an unusual high-latitude range and may be an exception to this pattern. Many bowhead whales in the North Pacific spend the winter in the Bering Sea, which is a summer foraging habitat for gray whales. Stable isotope analyses suggest that they acquire much of their energy through foraging in fall and winter (Schell et al. 1989); foraging in spring is also important for bowheads in some regions of the North Atlantic (Heide-Jørgensen et al. 2013).

Most of the other hypotheses suggested for migration to low-latitude breeding grounds focus on neonate calves. Dingle (1996) argued that calves may face difficulties thermoregulating in cold high-latitude waters, but Watts et al. (1993) and Kanwisher and Sundnes (1966:408) argue that baleen whale calves “are theoretically insulated sufficiently for the coldest seas.” Another hypothesis for migration to low latitudes focuses on safety for young calves. Whitehead and Moore (1982) point out that female humpback whales with calves prefer calm waters inshore of coral reefs off the Dominican Republic, an observation that is replicated in Madagascar by Ersts and Rosenbaum (2003) who report that humpback mothers with calves prefer shallow waters near shore. Parks (Chap. 13) summarizes evidence that right whale mothers with calves also prefer shallow coastal waters. This preference for shallow inshore waters may reduce the odds of detection by predators, such as a shark or killer whale (*Orcinus orca*), which are likely to come from offshore, and may reduce the predator’s abilities to maneuver and attack from below (Ford and Reeves 2008). However, some baleen whale species that migrate to lower latitudes during the breeding season do not congregate in inshore waters. For example, some blue (*Balaenoptera musculus*) and fin whale (*Balaenoptera physalus*) populations

are thought to disperse in offshore waters during the breeding season. Corkeron and Connor (1999) argue that reducing the risk of killer whale predation may be a prime driver for autumn migrations to lower latitudes for both inshore and offshore species. They cite data that the densities of killer whales are much lower in lower latitudes, and they suggest that pregnant female whales may migrate to the lower latitudes to reduce the risk of predation on their neonate calves.

Ford and Reeves (2008) agree with Corkeron and Connor (1999) that killer whale predation has been an important selection pressure for baleen whales. They propose that the inshore vs. offshore strategies for calving grounds may stem from two categories of baleen whale responses to killer whale attacks. They review evidence that five species of baleen whale, the southern and North Atlantic right whales (*Eubalaena glacialis*), bowhead whale (*Balaena mysticetus*), gray whale, and humpback whale, fight killer whales to protect themselves and their calves. By contrast, they argue that six balaenopterid species have a flight strategy. These flight species can sustain prolonged flight reactions at speeds of 20–40 km/h, but show little evidence of defense if overtaken. Ford and Reeves (2008) suggest that it is the flight species that seek shallow coastal refuges for their newborn calves. They argue that the flight species disperse into pelagic habitats where they can escape in all directions. They suggest that for this flight strategy to work in a calving area, young calves in the flight species must also be able to sustain prolonged rapid swimming.

The multi-year breeding cycle for most female baleen whales means that many adult females are not pregnant at the end of each feeding season. It is not known how many non-pregnant females of any baleen whale species migrate to the calving grounds for breeding. If they are not going to give birth to a calf, then the advantages of low-latitude calving grounds may not be relevant for deciding about migratory destinations. This raises the possibility that there might be breeding areas separate from the calving areas. In right whales, which tend to take several years after having a calf to conceive the next one, females tend not to be sighted on the calving grounds the year before they give birth, suggesting that they mate elsewhere (Chap. 13). If not enough years have passed for a female right whale to become pregnant again, she may choose winter habitats that are neither breeding nor calving areas. Here, the priority may be to continue feeding to reduce the time it takes to build up enough energy stores to reproduce again. In some other baleen whale species, the rate of post-partum ovulation is high enough (Lockyer 1984; Chittleborough 1958) to select for adult males to follow pregnant females for mating opportunities (Corkeron and Connor 1999). If males form a mating assemblage around the areas where females calve, non-pregnant females may have to migrate to the same area for mating. However, the reproductive advertisement displays of fin and humpback whales have been recorded during every month of the year on some feeding grounds (Vu et al. 2012; Morano et al. 2012), suggesting a broader distribution of mating opportunities for females, some of whom may not migrate for mating.

The classic view of the migratory cycle of baleen whales (Fig. 7.1) stems from observations from the whaling industry, which focused on finding times and places when whales were concentrated in areas where they could efficiently be hunted. However, there is much more variability in baleen whale annual movements than

suggested by this classic view. Most populations of humpback whales have an annual migratory cycle, but there is a population that resides all months of the year in the Arabian Sea (Mikhalev 1997). Similarly, genetically distinct populations of fin whales are mostly resident year-round in the Mediterranean and in other ocean regions, with seasonal movements to good feeding habitats (Geijer et al. 2016). As Geijer et al. (2016) emphasize, methods such as tagging, genetics, photo-id, and acoustic monitoring can identify the full range of migratory patterns in baleen whales. Understanding how these vary with varying ecological conditions can help sharpen our understanding of how and when baleen whales choose to reside or move, which will broaden our understanding of their social organization.

### 7.1.2 *Mother-Calf Bond*

The longest social bond known in most baleen whale species is the mother-calf bond. Mothers are thought to nurse their calf for five to seven months or more in most species (Oftedal 1997). This means that the calf will accompany its mother on the migration from the calving area to the feeding area (Fig. 7.1). The calf must be ready for migration after about three months on the calving ground. This requires an intense period of lactation during which a blue whale mother may produce 4000 MJ/d (Oftedal 1997) and a southern right whale calf may grow in volume by 0.08 m<sup>3</sup>/day, while the mother shrinks by 0.13 m<sup>3</sup>/day (Christiansen et al. 2018). In some species, the calf may be able to start feeding on prey during this first summer, and in most species, the calves appear to learn how to migrate to their feeding ground from their mother on this first migration (e.g., for humpbacks: Clapham and Mayo 1987; Barendse et al. 2013) and even specific regions within a feeding ground (Weinrich 1998). Studies of social learning define this kind of transmission of information from mother to offspring as vertical transmission, in contrast to horizontal transmission, which is defined as learning from peers (Chap. 8).

In some baleen whale species, calves may associate with the mother for up to a year. Valsecchi et al. (2002) analyzed genetic relationships of humpback whales migrating together and found mothers traveling with offspring estimated to be 11–12 months old, and Baker et al. (1987) sighted yearling humpback whales with their mothers on the Hawaiian breeding grounds. Taber and Thomas (1984) studied southern right whales on their calving ground and found that mothers returned in late winter with their yearling calves who remained with the mother for the first two to six weeks after return. Consistent with the idea that mothers put a high priority on protecting their offspring, Taber and Thomas (1984) found that young right whale calves spent nearly 90% of their time within ¼ body length of the mother, and the mothers were responsible for maintaining this proximity. By contrast, after a year of age, it is the yearlings who are primarily responsible for maintaining proximity. Even though mothers and calves spend most of their time close together, they do separate, with infants departing more often than approaching and mothers approaching more often than departing. This pattern reverses for yearlings (Taber and Thomas 1984).

When mother and calf are within  $\frac{1}{4}$  body length, they can probably sense one another's proximity by sight or touch. Visibility is so limited in seawater, however, that they may lose visual contact during separations of more than a body length. The ability to reliably regain contact is critical for the lactating mother and dependent calf. Acoustic communication plays an important role in maintaining contact when whales separate, and contact calls have been identified for right whales and humpback whales. While making acoustic recordings, Clark (1983) observed the behavior of southern right whales, and he reports that in about half of the cases when right whales made an upsweep identified as a contact call, another whale called back and both whales exchanged upcalls as they approached one another, stopping calling once they had joined. Videsen et al. (2017) and Nielsen et al. (2019) attached acoustic recording tags on lactating female humpback and southern right whales, respectively, and showed that mothers and calves are more likely to call during active dives which are likely to be associated with separations. Contact calls are used by both species in a variety of settings, including adult male right whales seeking contact with adult females (Parks and Tyack 2005) and including humpbacks on the feeding grounds (Wild and Gabriele 2014). However, killer whale predators can detect the presence of whales by eavesdropping on their calls. Videsen et al. (2017) and Nielsen et al. (2019) report that the source levels of calls between mothers and calves are quite low, yielding an effective range of communication of 200 m or less. They argue that while mothers and calves must call to maintain contact during separations, they adopt a strategy of acoustic crypsis to prevent detection by more distant threats.

## 7.2 Feeding

During the feeding season, the social organization of baleen whales has been studied directly for species where individuals have distinctive natural markings and forage near shorelines accessible to field workers. Field workers typically describe whales as being in the same group if they are sighted within a few body lengths of one another with coordinated behavior. During the feeding season, most humpback whales are reported as alone or in pairs, with fluid fission/fusion groups seldom lasting for more than hours to days (e.g., Whitehead 1983; Clapham 1993; Ramp et al. 2010). One of the reasons suggested for the fluidity of groupings on a feeding ground is the high variability in the size of prey patches that may lead to variability in the number of whales that can be supported by each patch. The size of humpback groups feeding off Newfoundland is proportional to the size of the prey patch (Whitehead 1983). However, there is some evidence for social bonds in foraging baleen whales that are stable over several years. Some of the best evidence stems from humpback whales during the feeding season. Ramp et al. (2010) studied association patterns of humpback whales feeding in the Gulf of St Lawrence over nine years and report that some pairs of non-lactating females had stable associations that lasted for up to six feeding seasons. They hypothesized that whales that learn how to forage cooperatively may maintain stable associations of individuals who have learned to coordinate

their social foraging. More detail on coordinated behavior in social foraging groups is available for humpback whales that feed on mobile euphausiid and herring prey in Southeast Alaska. D'Vincent et al. (1985) provide detailed observations of this social foraging specialization. They observed a group of eight humpback whales vertical lunge feeding in Southeast Alaska that not only was stable over three days, but “always surfaced simultaneously in an identical formation” and “each whale maintained a constant physical orientation and spatial relationship within the group” [p. 42]. Some of the vertical lunge feeding involved whales exhaling underwater to form bubble nets that are thought to constrain and/or concentrate prey (Sharpe and Dill 1997). Stereotyped vocalizations appeared to initiate this cooperative foraging and to synchronize simultaneous surfacing in the lunge-feeding group (D'Vincent et al. 1985). Sharpe (2001) studied patterns of association of humpbacks foraging in Southeast Alaska for five feeding seasons. Most of these whales had weak associations, but 25 of the 257 whales formed a stable association with one or more of the other 24 whales, which he called a core community. The sex of 19 of these 25 whales was determined genetically: 11 were male and eight were female. Sharpe (2001) found no relationship between the coefficient of association and genetic relatedness of these whales. Pierszalowski (2014) tested the genetic relationships of humpback whales in large groups on these foraging grounds and found “that feeding in large stable groups did not typically occur among closely related individuals” [p. 105]. Calves born to mothers in the core community were not found to feed preferentially with their mothers in following years. When members of this core community were foraging in large groups, these groups usually included at least one whale that was not part of the community. In such cases, non-community whales associated with a core group for an average of 1.9 days, but most of these visitors were only observed feeding with a community group on one day.

When the core group of humpback whales studied by Sharpe (2001) was lunge feeding, specific whales produced the vocalizations used to coordinate foraging, individual whales dove in the same order, and individuals maintained a specific position within the group. These observations led Sharpe (2001) to suggest that this form of group foraging may require individuals to learn the timing and path they must swim to maintain the spatial configuration of the group during lunging, as well as roles such as bubble blower, vocalizer, and herder. The structure of these groups suggests that social learning of these roles involves horizontal transmission of information. The actual dynamics of learning have not been documented in this case, but they were observed for a novel feeding behavior in the Gulf of Maine. One whale was observed in 1980 lobtailing just before bubble net feeding. The high numbers of researchers observing whales in the Gulf of Maine made it possible to track the spread of this lobtail feeding behavior over 27 years. Allen et al. (2013) analyzed when individual whales started lobtail feeding coupled with data on the amount of time different individuals associated with one another to test different models of social transmission of the behavior. These models showed that whales who associated with lobtail feeders were more likely to start lobtail feeding, providing strong evidence for social transmission. Having a mother who engaged in lobtail feeding did not increase the chances of the calf lobtail feeding. These results show that horizontal

transmission, not vertical transmission, is most likely responsible for the acquisition of lobtailing. As in the case of social foraging in Southeast Alaska, horizontal social transmission may speed the ability of whales to learn behaviors that are tuned to local conditions (Chap. 8).

Outside of these cooperative groups, baleen whales often congregate as they feed on patches of prey, but the groupings are fluid with few strong associations between individuals other than mother and calf. It is not well understood how baleen whales find dynamic patches of concentrated prey as they search over large distances. It is possible that individual whales each find good prey patches on their own, with congregations resulting from several animals independently finding the same patch. Alternatively, Payne and Webb (1971) hypothesized that if a whale finds a patch of food that is too large for it to consume alone, it could call to broadcast the location to other whales nearby. If nearby whales reciprocated, Payne and Webb hypothesized that this could improve the foraging efficiency of the local population. Several species of whale do in fact call when feeding on a large patch (e.g., fin whales; Croll et al. 1992) or when feeding in groups (e.g., blue whales; Oleson et al. 2007). Watkins and Schevill (1979) used an airplane to observe fin whales approaching a large group of feeding whales, making a beeline from distances as far as 10 km away, and starting to feed immediately as soon as they joined the group. This hypothesis that whales broadcast the location of prey would change our understanding of social organization of baleen whales on the feeding grounds, but it has not been tested systematically.

### 7.3 Migration

The migrations of many baleen whales cover thousands of kilometers and may take considerable energy and a significant proportion of the annual cycle. Migratory behavior has been best studied for species that migrate along a populated coast where whales can be visually observed, such as the migration of gray whales off the west coast of North America or of humpback whales along the east coast of Australia (Chap. 4). It has long been observed that different age/sex classes may migrate at different times. For example, in most species, pregnant females are the first to arrive at the summer feeding ground and the last to leave, probably because of the high energetic demand of pregnancy and lactation, while lactating females with calves are late to arrive, perhaps, slowed down by the calves (Lockyer 1984). Many species tend to migrate in small groups rather than alone, but Valsecchi et al. (2002) found no indication that whales swimming in the same group tend to be more related, except for groups containing a mother-calf or mother-yearling pair. This suggests that most groups on migration are transitory and not based on kinship. Migrating bowhead whales have been recorded exchanging calls as they navigate around ice, with whales closer to the obstacle potentially signaling the route to those behind (Würsig and Clark 1993). This indicates acoustic coordination among whales that would not be judged to be in the same group by most field workers based on visual observation.



At the end of the breeding season, when whales start to migrate to their feeding grounds, there is not a sudden complete stop to breeding behavior. An example comes from humpback whales that have been observed closely during their migration off the east coast of Australia. Humpback song has commonly been recorded during this migration as well as during the breeding season, and many of the interactions observed between migrating singers and other migrating humpback whales were the same as those observed between singers and other animals on a breeding ground (Smith et al. 2008). Data from whaling off the east coast of Australia showed a peak of ovulation during the winter breeding season in August, but some females ovulated up to three times in one year, which may extend some ovulation into the migration season (Chittleborough 1965). Male humpbacks have a broad reproductive season with spermatozoa present from June to October in the Southern Hemisphere (Chittleborough 1965), and song has been recorded outside of the classical breeding season (Vu et al. 2012; Garland et al. 2013). These observations suggest that at least for some baleen whale species, mating may take place outside of the classic breeding season.

Similarly, as whales migrate from the breeding grounds to the foraging grounds, they may take advantage of foraging opportunities on the way. For example, a bloom of phytoplankton starts at around 35° North latitude in the North Atlantic in December and January and spreads northward through the spring (Visser et al. 2011). The timing of this bloom and its northward spread varies from year to year. Visser et al. (2011) studied blue, fin, humpback, and sei (*Balaenoptera borealis*) whales sighted off the Azores at 38° N over a four-year period. The whales were observed feeding on krill in the area, and the timing of whales sighted off the Azores tracked the onset of the spring bloom with time lags of 13–16 weeks. These observations suggest that whales time their migration to take advantage of opportunities to forage on zooplankton prey species whose density is linked to the timing of the phytoplankton bloom. Silva et al. (2013) tagged fin and blue whales off the Azores and documented traveling behavior consistent with migration as well as whales remaining in a restricted area, a behavior consistent with foraging.

## 7.4 Breeding and Calving

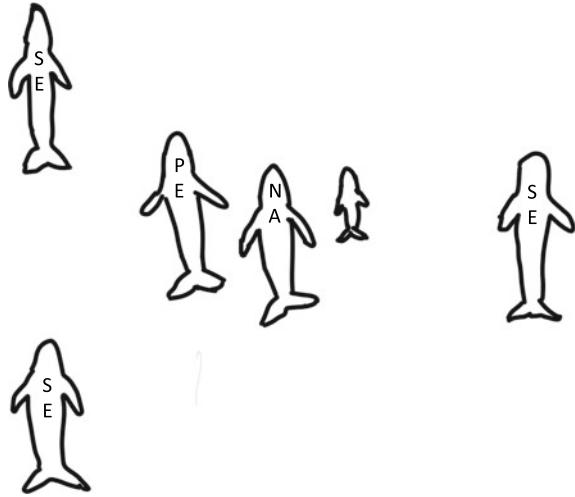
The duration of pregnancy in most baleen whales is about 12 months, so the breeding season is also the season when calves are born. As discussed above, one of the primary hypotheses for the baleen whale migration to lower latitudes during the breeding season is to provide a safer place for adult females to give birth and to care for their neonates without disturbance. Ford and Reeves (2008) distinguish two baleen whale anti-predator strategies. They review evidence that several baleen whale species, including balaenid whales, as well as the gray whale and the humpback whale, physically defend calves against killer whales. In most of these “fight” species, females with neonates seek out calm inshore waters at lower latitudes than the foraging grounds. For example, gray whale mothers and calves tend to stay far inshore in

lagoons on the Mexican breeding ground, with mating behavior concentrated near lagoon mouths (Norris et al. 1977). South Atlantic right whale females with calves concentrate in shallow inshore waters (Best 1990). The bowhead whale forages in high-latitude Arctic waters and spends the winter breeding season in the lower latitudes of the shallow Bering Sea (Braham et al. 1980) and about 65° N in the Davis Strait (Reeves et al. 1983). Rather than seeking shelter inshore, they appear to use pack ice as a refuge. Several studies of the habitat frequented by different humpback groups during the breeding season found that mothers with calves preferred shallow inshore waters compared to habitats preferred by other groups (Martins et al. 2001; Ersts and Rosenbaum 2003; Félix and Botero-Acosta 2011). Other balaenopterid whale species show a flight strategy involving rapid swimming away from killer whales. These other balaenopterid whale species, such as blue, fin, minke (*Balaenoptera acutorostrata*), and sei whales, appear to disperse in temperate pelagic waters, while Bryde's whales (*Balaenoptera edeni*) rarely venture outside of tropical pelagic waters.

Balaenopterid species that depend upon flight reactions are not known to rely on social defense against predation, while species that defend themselves against predators will group tightly if under attack (Ford and Reeves 2008). However, even for flight species, mothers with calves do not appear to form large groups to provide a social defense when not under attack from predators. For example, very few humpback groups are sighted with more than one neonate calf in the group (e.g., Martins et al. 2001; Félix and Botero-Acosta 2011), and between-group distances are greater for humpback groups with a calf than those without (Smultea 1994). Females with young calves may only spend a few months in the calm protected waters, a relatively short time for the calves to grow enough for efficient migration. Humpback whale calves were observed to spend about 20% of the time in a suckling position, while females are often resting (Videsen et al. 2017). Their vocalizations are so faint as to be detectable only out to a range of ~ 100 m. These observations are consistent with the hypothesis that mothers with calves are moving to a refuge location where threats are less likely and relying on a strategy of crypsis to maximize undisturbed time for resting and suckling.

Predators can pose a lethal threat for neonates, but adult males also may disrupt normal behavior of mother-calf groups. Elwen and Best (2004) report that neonate southern right whales were less likely to strand in areas dominated by mother-calf pairs than in those where adults without calves are more common. The segregation of mother-calf groups inshore of other humpback groups on the breeding ground may represent a strategy on the part of mothers to avoid disturbance by males as well as to avoid predators. A mother and calf humpback are seldom sighted with another female on the breeding ground, but may be sighted with one or more males. An increase in activity is often observed when a mother and calf are in a group with more than one adult humpback male, suggesting that the mother and calf expend more energy in these groups (Sullivan and Cartwright 2009). The group is usually less active when a single adult male escorts a mother and calf, suggesting that females may also have a strategy of selecting or accepting one male as an escort to reduce harassment from other males (Mesnick 1997). This is not a long-term association, however, as females are seen associated with different males throughout the breeding season, and males

**Fig. 7.2** Structure of surface-active groups (adapted from Tyack and Whitehead 1983). NA = nuclear animal, PE = principal escort, SE = secondary escort



associate with different females (Baker and Herman 1984). Clapham and Palsbøll (1997) used genetic analyses to demonstrate that females mate with different males to father their sequence of calves across different years.

Groups of more than two adult humpback whales on the breeding ground often have a clear structure in which one whale, the principal escort (PE), swims close to a nuclear animal (NA) who is the focal point of the group (Fig. 7.2). Secondary escorts may challenge the principal escort by trying to swim between the NA and PE; these challenges often involve agonistic displays and physical contact between the escorts (Tyack and Whitehead 1983; Baker and Herman 1984). Clapham et al. (1992) determined the sex of whales in 21 competitive groups. None of the groups contained more than one adult female, but 7/21 contained only males. All of the whales that challenged the PE were male, 23/24 PEs were male, and of the 22 whales identified as the NA, 17 were female, and five were male. Clapham et al. (1992) argue that these results suggest that some of these groups likely involve males competing for dominance, but that most of the groups involved a PE guarding a NA female to limit other males gaining access to the female. Clapham et al. (1992) also observed pairs of males joining or leaving competitive groups together with no aggression toward one another. They and Darling et al. (2006) argue that some male humpbacks may form coalitions to improve their ability to compete in these competitive groups. We do not know how much choice the female has in choosing either a single male escort, or principal escort in a competitive group, but the groups of males competing for access to the female represent male-male competition that may reduce the ability of the female to choose a mate over the short term.

Groups with competitive behavior similar to that observed in humpbacks have been observed in other baleen whale species. Norris et al. (1977) report observing mother-calf pairs of gray whales in groups in the Mexican breeding lagoons that were involved in high-speed chases in which animals thought to be males were engaged



**Fig. 7.3** Surface-active group of right whales (from Roman et al. 2016)

in violent competition. During one such chase, Norris et al. observed a young calf struggling to keep up with three adults. The next day a calf was found partially stranded, suggesting that these chases may involve greater risks than just energy loss. Detailed observations of competitive groups are not extensive for right whales during the breeding season, but groups with surface-active behavior (surface-active groups or SAGs) that appear similar to those observed in humpbacks have been observed in right whales during the feeding season in the Bay of Fundy (Fig. 7.3; Kraus and Hatch 2001; Chap. 1, Fig. 1.6). While some SAGs are all-male or all-female, most involve a central female or multiple females surrounded by males (Parks and Tyack 2005). Parks and Tyack (2005) used an array of hydrophones to identify which individual whale produced some of the calls in SAGs. This evidence suggests that one type of call, referred to as a scream, is produced in extended sequences by a female in the group. Right whales produce an intense impulsive sound called the gunshot; when produced in stereotyped sequences by males, it may function as an advertisement to attract females and/or a threat to other males (Parks et al. 2005). Playback of gunshot sounds recorded from a lone North Atlantic right whale male elicited no approaches from North Atlantic right whales, but males did approach playbacks of calls recorded from SAGs (Parks 2003). Similar responses were observed from Southern right whales during playbacks of Southern right whale sounds recorded from active groups (Clark and Clark, 1980). The upcalls that are thought to function as contact calls are also heard in SAGs. Data from an array of hydrophones show that some males produce gunshots when entering a group or when searching for a female, perhaps, to announce their presence to the female or other members of the group.

Brownell and Ralls (1986) argue that sperm competition may play an important role in the mating system of right, bowhead, and gray whales. Right whales have the largest testes as a proportion of body mass of any baleen whale, a trait that has been

linked to sperm competition in mammals. Right whale males are less aggressive in right whale SAGs compared to males in humpback or gray whale SAGs, and multiple right whale males have been observed to mate with a female in surface-active groups. Kraus and Hatch (2001) observed right whale males joining SAGs from distances as far as 8 km. The observations that females produce screams and that males approach playback of calls from SAGs are consistent with the hypothesis that female right whales may call to attract males and incite male-male competition expressed in part as competition for access to the female and in part as sperm competition.

The most detailed observations of right whale SAGs come from the feeding season. Mating has been observed in these SAGs, but Kraus and Hatch (2001) point out that in the Northern Hemisphere most conceptions should occur from October through December, a period with few observations of northern right whales. Therefore, many of the females calling to males in SAGs are probably not receptive during the feeding season. If mating does not lead to conception in the feeding season SAGs, what is their function? Kraus and Hatch (2001) suggest two possibilities:

1. Females may keep track of the performance of different males, make a choice, and mate with the selected male at a later time.
2. Females may require repeated practice to learn how to assess and select males in SAGs, and it may be lower risk to assess them during the feeding season before the stakes become high during ovulation.

The presence of calves and juveniles in these SAGs also suggests that SAGs may provide opportunities for play or practice, and that they may function to reinforce social bonds (Parks et al. 2007).

A glaring knowledge gap in understanding the mating system of baleen whales stems from our lack of direct data on mating. In spite of extensive observer effort on the breeding grounds, observation of copulation has not been reported for humpback whales. Sexual activity has been observed in surface-active groups of right whales, but females involved in mating in these groups are very rarely seen with calves the next year, and the timing of births suggests that most mating occurs outside of the summer season in which most observations of right whale SAGs have taken place. For species that disperse into pelagic seas, we know even less about where mating takes place. The problems described above suggest that better observations of mating behavior are unlikely for many species, and even where they are available, they may not correctly identify the mating event that led to pregnancy. Genetic methods such as those used by Clapham and Palsbøll (1997) are more likely to provide the necessary data, especially when linked to observational data (e.g., Cerchio 2003).

## 7.5 Reproductive Advertisement Displays and Song

In many species of baleen whale, the mating strategies of males include producing reproductive advertisement displays that are often referred to as songs. The functions of reproductive advertisements in animals have been discussed for more than

150 years, with Darwin (1859, 1871) arguing that they evolve by sexual selection. Songs can advertise a challenge to other males within earshot, with intra-sexual selection operating between males. Females may also use song to select a male for mating, with inter-sexual selection operating between the sexes. Males may sing for either or both of these functions. The acoustic features of many animal songs include complex sequences of notes that are repeated. We all have experiences listening to the songs of birds, and scientists have written about bird song for more than 300 years, but it was just 50 years ago that Payne and McVay (1971) published a scientific paper describing that whales sing as well. Perhaps, the best-known whale song is the song of the humpback whale. The frequency range and tempo of humpback song are similar to those of human music, as is its complex repeated phrase structure. It is so accessible to our ears that in 1970, a vinyl recording of humpback song sold more than 100,000 copies. See Chap. 11 for more information on the acoustic structure of humpback song and Chaps. 9–15 for detailed species-specific song or call repertoire information.

Evidence that whale songs are associated with reproduction comes from studies discussed in Chaps. 9–15 showing that songs tend to be produced during the breeding season and that singing whales whose sex has been determined have been male. The humpback is the whale species for which we have the most detailed observations of interactions between singing whales and other whales, as is discussed in Chap. 11. These observations provide evidence that song functions in male-male competition and also for female choice of a mate. Darling et al. (2006) used visual observations along with listening underwater to report that 80% of singers on the Hawaiian breeding grounds were lone whales, 12% were escorting a mother and calf, and 8% accompanied an adult without a calf. The most common interactions observed by Darling et al. (2006) involved singers joining lone males; the other 11% involved singers stopping singing and approaching and joining groups of males competing directly for access to a female. Smith et al. (2008) studied interactions of humpbacks singing during the migration along the east coast of Australia and were able to distinguish whether a singer joined other whales or whether the other whales joined the singer. They report that singers were more likely to join mother-calf groups than any other kind of group, and they sang for a longer time when with mother-calf groups than with other groups. By contrast, the whales that joined with singers tended to be lone whales (those whose sex could be determined were males); the singer usually responded by stopping, and the interactions were briefer than when a singer joined with a mother-calf pair. There are rarer reports of female humpbacks approaching and joining a singer. Medrano et al. (1994) report two cases when a mother and calf or a female with one other adult joined a singer with no signs of aggressive behavior, and Tyack (1981) reports a case of a mother and calf approaching a singer who stopped singing and also approached the mother and calf. After they joined, behaviors were observed that have been associated with courtship and mating in baleen whales. The observations of Smith et al. (2008) are that 27 of 63 observed associations were with lone adults (10 of which were males), 20 of 63 observed associations of singing whales were with mother-calf pairs, and the observations of females approaching

singers all suggest that both males and females are audiences for the song and that song mediates both intra-sexual and inter-sexual interactions.

Research on interactions between songbirds during the breeding season is much more detailed and more extensive than that on whales, which can provide a useful comparative perspective. Females of some songbird species prefer mates with a familiar local dialect, and males may have difficulties establishing a territory if they have a foreign dialect. The idea that song dialects play a role in reproductive isolation of different populations led to studies (reviewed in Slabbekoorn and Smith 2002) of how well variation in song dialects corresponded with genetic boundaries. Some of these studies report a match between acoustic and genetic variation, but many others report that song dialects do not match well-defined genetic differences. One important reason for so much variation is that many species of songbird learn their song. If a male can disperse to a new dialect zone and learn the new dialect, this will break the connection between any natal genotype and his new local song phenotype. Learning takes place over much shorter time scales than genetic differentiation of a population, so dialects may be established through social learning well before there is any genetic differentiation.

The way in which the songs of some baleen whale species change provides evidence that they are also learned. The strongest evidence comes from the way most of the humpback whales within a region sing similar songs at one time, with the song evolving over time (Payne et al. 1983; Payne and Payne 1985), and the way whales in one area can rapidly adopt song elements from another area (Noad et al. 2000; Garland et al. 2011). Chapter 12 describes how bowhead whales also sing complex songs that change over time, but with much more variability than humpbacks in song from different whales within an area at any one time. Chapter 9 describes that along with a basic pattern of stability in song units of blue whales within a region, and of stability in how these units are sequenced, there also have been long-term changes in the frequency of some tonal units and also of timing of units in some areas. All of these observations are hard to explain unless these whales learn acoustic features of their song from hearing the song of other whales within earshot.

The great interest in conservation of baleen whale populations that were decimated by commercial whaling led many marine bioacousticians to explore the potential for using song dialects in whales as a proxy for biological population structure, as defined by genetic differences. As with the earlier work on bird song, the data do not suggest a strong match between genetic definitions of populations and song dialect boundaries. Multiple song dialects have been recorded in one population of Southeast Pacific blue whales (Buchan et al. 2015). As described in Chap. 9, multiple populations sing one song type among Antarctic blue whales and another song type is shared among North Atlantic blue whale populations. As with songbirds that learn their song, the pace of change of learned song is so much faster than changes in the genetic structure of populations that there are many reasons to expect that song dialects may not map perfectly onto the genetic structure of populations. The sounds of blue and fin whale song may carry hundreds of kilometers, so whales may hear one another's song over distances well beyond what we normally think of as sympatric. Song features that are audible across long ranges may be learned across ocean basins that contain

several populations. Some higher frequency acoustic features of humpback song are not audible across ranges of more than tens of kilometers, but migratory patterns may also support cultural diffusion across greater ranges than genetic diffusion. For example, if humpback whales in the South Pacific hear songs when populations overlap on the feeding ground and then return to breed on their natal breeding ground, then song may be shared across populations if one singer picks up song from another population (Garland et al. 2013).

This review suggests that song dialects cannot be used as a reliable indicator of population structure in whales, just as they cannot in most songbird populations. It would, therefore, be problematic to manage protection of biological populations of whales based upon song dialects. Modern genetic methods enable measuring actual biological population structure using tissue that can be collected by non-invasive or minimally invasive methods. Song dialects may play a role in establishing geographical strategies for sampling whale genetics, even if they are not sufficient to define populations. Brakes et al. (2019) argue that animal cultures are worthy of conservation as well. This is the setting in which learned song dialects may prove most useful for conservation biology.

As described above, many studies of birdsong have focused on the role song might play as a reproductive isolating mechanism, testing whether song dialect boundaries matched population boundaries. Another hypothesis has focused on the ways sound propagation and ambient noise may provide selective pressures on the acoustic structure of songs, with different acoustic features propagating better in different habitats. Date and Lemon (1993) proposed that the acoustic features of habitats may select for the formation of song dialects, and Slabbekoorn and Smith (2002) proposed that if different habitats select for different traits within a species, that song can act as a marker for females to select a male best suited for that habitat. Boncoraglio and Saino (2007) performed a meta-analysis of 26 birdsong studies and found weak support for this acoustic adaptation hypothesis, but other factors such as energetic costs of singing and risk of eavesdropping by predators and parasites are likely also important. In the next section, we consider how the acoustic structure of whale songs may be affected by the ecological and acoustic setting in which they are produced.

## **7.6 The Ecological Setting in Which Songs of Different Whale Species Are Produced Has Selected for Their Acoustic Structure**

Propagation of sound in the ocean is driven by different factors than the terrestrial habitat features, such as dense vegetation, that are thought to affect bird song, but there is a clear pattern where the acoustic features of songs of different baleen whale species appear to be selected to propagate well over the ranges required for effective communication (Clark and Ellison 2004). As discussed in the introduction, Ford and Reeves (2008) review evidence that species such as humpback and bowhead whales,



that fight to protect their young, tend to congregate during the breeding season in high density in areas where they can find refuge from predators. By contrast, many populations of flight species, such as blue and fin whales, disperse into temperate and subtropical pelagic waters during the winter breeding season. The difference in expected range from singer to potential receivers between these two settings may have influenced the evolution of acoustic properties of the songs of these species.

Sound can propagate very efficiently in the deep ocean environment where blue and fin whales tend to sing during the breeding season. Their songs are relatively intense, with source levels of about 180 dB re 1  $\mu\text{Pa m}$  and have most of their energy well below 100 Hz. At frequencies this low, there is very little absorption of sound energy as it passes through seawater. The fundamental frequencies of finback and blue whale song also tend to center in a 10–30 Hz band at which Curtis et al. (1999) report particularly low levels of ambient noise deep in the North Pacific. The combination of high source level, low propagation loss, and low ambient noise means that fin and blue whale songs can be detected at long ranges. The effective range for detecting fin whale song in the deep ocean has been estimated using acoustic propagation models to be 400–1000 km (Spiesberger and Frstrup 1990). Using the US Navy Integrated Undersea Surveillance System (SOSUS), which is optimized for long-range detection of low-frequency sounds in open ocean, Clark and Gagnon (2002) report being able to detect, localize, and track a singing fin or blue whale at ranges of nearly 3000 km. Blue whale songs have been localized in the Antarctic at ranges of 200 km using recorders placed at depths that are less well suited for long-range detection than those of the SOSUS (Širović et al. 2007).

Humpback whales tend to select shallow coastal waters for their breeding grounds, and the Bering Sea breeding grounds of bowhead whales are quite shallow with an average depth of about 100 m. In shallow waters, whales cannot increase their range of communication simply by lowering the frequency of song (Mercado and Frazer 1999). In shallow water, there is a cutoff frequency below which sound will not propagate well; Mercado and Frazer (1999) estimate this frequency to range between 1–100 Hz for the water depths where humpbacks usually sing, suggesting selection for higher frequencies. Clark and Ellison (2004) suggest that in these shallow waters, the frequencies from 100–400 Hz offer a low noise window for communication. Cholewiak et al. (2018) modeled the effective range of communication for songs of fin and humpback whales in the relatively shallow waters of Stellwagen Bank in Cape Cod Bay. Even though the average source level of finback whales was 180 dB re 1  $\mu\text{Pa m}$  and that of humpback song was 170 dB re 1  $\mu\text{Pa m}$ , the higher frequency humpback song had a modeled effective range of 23 km versus 15 km for fin whale song under normal ambient noise in Cape Cod Bay.

Tervo et al. (2012) studied the songs of bowhead whales recorded in March in Disko Bay on the west coast of Greenland, which has an average depth of 200 m. The mean source level of bowhead song was 185 dB re 1  $\mu\text{Pa m}$ , which is within the range reported for fin and blue whales (Širović et al. 2007). Thus, the main difference for estimating the effective range of bowhead songs stems from the higher frequencies (mean frequency of 444 Hz) and broader bandwidth (284 Hz) of the bowhead song compared to fin whale song, whose main element ranges from 17 to 25 Hz. During

the March recording period, ice cover in Disko Bay reduced ambient noise levels to 65 dB re 1  $\mu$ Pa over the frequency band of bowhead song and 51 dB re 1  $\mu$ Pa over the much smaller frequency band of finback song.

Using information on sound propagation in ice-covered Arctic seas, Tervo et al. (2012) estimate an effective range in this quiet environment of 130 km for bowhead song and about 3500 km for finback song. These are likely overestimates because of the very low noise levels used and because the local sound propagation conditions would not hold for 3500 km, which is greater than any distance in the Arctic Ocean, but the main point is that the songs of bowhead whales have about 4% the range of that of fin whales. High-frequency (> 1 kHz) components of bowhead song, which are likely important features of the complex song repertoire, would have effective ranges well below 40 km, similar to that estimated for humpback song by Cholewiak et al. (2018).

Fin and blue whales are thought to disperse into low-latitude seas during the breeding season and must rely upon the long effective ranges of their songs to structure mating interactions, while humpback and bowhead whales congregate in breeding grounds where effective ranges of several tens of km are likely sufficient to reach intended receivers. Whale researchers sometimes use the words “breeding grounds” because this was the term whalers used for areas where whales were concentrated enough for whaling to be effective. Whale researchers have continued to return to many of these areas as they are good for studying whales as well, but we must remember that we do not know where many whale species breed, especially for species that do not congregate inshore.

If fin and blue whale songs were selected for long-range propagation, this may have affected other features of the song such as their more stable, simple repeated elements of the song, which may make it easier to detect at low signal-to-noise ratios. By contrast, whales listening to singing humpback and bowhead whales are often close enough to hear song well above the noise, and this may enable selection for more variable and complex songs.

## 7.7 Future Directions

### 7.7.1 *Do Whales Form Herds or “Heards” (Payne and Webb 1971)?*

The discussion about effective range of communication raises questions about how to define a group of whales and interactions between whales. Most of the studies on associations between individual whales define groups in terms of distance between animals and/or animals coordinating their activities (Mann 2000). The appropriate distance to define whether animals are interacting depends upon the activity. For a male and female to mate or for a calf to suckle from its mother, they must be touching one another. The coordinated foraging described for humpback groups above requires

animals being within a body length or so of one another. This focus on close contact led Taber and Thomas (1984) to compare the amount of time mother and calf right whales spent more than  $\frac{1}{4}$  body length away (16%) versus two body lengths away (1.5%). One would reach different conclusions about the association patterns of mother and calf depending upon which of these close distance measures one used to define a mother-calf group. As discussed above, calves may temporarily leave their mother, swimming tens to hundreds of meters away. But, the calf is dependent on the mother, and when separated beyond visible range, the mother and/or calf can use calls to reunite. In keeping with their cryptic strategy, right and humpback whale mothers and calves vocalize little outside of separations, and they tend to produce faint calls only audible at ranges of  $< 200$  m (Nielsen et al. 2019; Videsen et al. 2017). These calls are so faint that they would seldom be audible to biologists recording them from a boat nearby; recording these whispered vocalizations reliably requires use of acoustic recording tags attached to the mother or calf. The distances between group members maintaining contact using whispered calls should be close enough that observers following whales visually from a vessel should be able to see all members of the group. By contrast, non-lactating adult female right whales on the calving grounds tend to produce higher amplitude calls such as upcalls (Parks et al. 2019). Munger et al. (2011) suggest that upcalls of North Pacific right whales are detectable at ranges of up to 100 km in the Bering Sea, appropriate for allowing widely dispersed whales to maintain contact. Payne (1995) used aerial surveys to find that right whales in the calving grounds of Peninsula Valdés, Argentina, formed loose herds about 37 km in diameter. These loose aggregations, which are within the effective range calculated for right whale high-amplitude calls, seem to define a higher level and larger scale of grouping than is typically used for baleen whales. Perhaps another important definition of being associated is being within range of such a contact call. The discussion of effective range of song also shows that whales may monitor one another at distances of tens to hundreds of kilometers. Tyack and Whitehead (1983) present an interaction in which a humpback whale singing in Hawaiian waters, stopped singing, accelerated, and made a beeline to a surface-active group of whales that was 9 km away. It took 40 min for the ex-singer swimming at high speed to join the surface-active group and understanding the interaction required following this individual whale for over four hours. This ability to notice that the singer was swimming toward a distant group and to pinpoint the location of whales was possible for boat-based observers following individual whale groups working with shore-based observers on a hill using a theodolite to pinpoint the locations of all of the whale surfacings, but 9 km is on the outer limits of the observation range of this method, which is limited to daylight hours, so it cannot track interactions for more than a day. The interaction took so long over such a large spatial scale that researchers only could understand it after it was mapped out after the fact. Field researchers need to be aware that methods are not available to study the range at which a female fin whale, for example, may assess the songs of male fin whales tens or even hundreds of km away. When I first heard of such long-range communication in whales, I recalled a quote from Henry David Thoreau “We are in great haste to construct a magnetic telegraph from Maine to Texas; but Maine and Texas, it may

be, have nothing important to communicate” (Thoreau 1854, p. 58). But tag data and acoustic tracks show that fin and blue whales can swim > 100 km in a day (Ray et al. 1978; Clark et al. 2019), so a female might assess dispersed males over these ranges when selecting a mate and then swim to the selected whale. We cannot fully understand the social organization of baleen whales until we can follow such interactions, which may take days to unfold over hundreds of kilometers. Analyzing such social communication interactions will require methods specifically designed to observe interactions that most likely operate over scales of time and space that are much larger than our terrestrial intuitions. Developing these methods will be an important challenge for the next generation of researchers studying the outer limits of social organization in baleen whales.

We have similar limitations for studying social coordination of foraging behavior in baleen whales. Some baleen whales vocalize frequently on the foraging grounds, and these sounds are detectable at ranges of 5 km or more (Cholewiak et al. 2018). These ranges may not be as large as those for songs in the deep ocean, but they are well beyond the typical sighting range of vessel-based observers. As discussed in the foraging section, Watkins and Schevill (1979) used a small airplane to observe whales foraging over two days on large schools of small fish associated with a dense patch of plankton about 5 km long. More than 20 finback whales and one humpback whale were observed feeding on the fish, while two right whales and a sei whale foraged on the plankton. No other whales were sighted after a search within 20 km on the first day, but two groups of three and six fin whales were sighted on the second day about 7 and 10 km away from the large group of foraging whales. These two groups were swimming rapidly, headed directly toward the foraging whales. The group of three whales began feeding as soon as they arrived at the fish schools. These observations suggest that the groups of three and six whales were alerted by calls of the feeding finbacks as to the foraging opportunity 10 km away. Is it possible that whales over hundreds of km<sup>2</sup> might be able to monitor when whales find large patches of prey as one dispersed feeding group (as suggested by Payne and Webb 1971)?

An important adaptation of baleen whales involves their ability to cover large areas of ocean to find dense patches of evanescent prey (Goldbogen et al. 2019). We do not know how whales find these patches. Payne and Webb (1971) suggested that when whales do find a patch larger than could be consumed by their group during the period when the patch is dense enough for filter feeding, there may be relatively low cost for advertising the location of a difficult-to-find patch in settings that would select for reciprocity. The group size of feeding humpback whales has been shown to be proportional to the size of the prey patch (Whitehead 1983), but how with their fluid fission/fusion groupings do whales aggregate into appropriately sized groups at a patch? The methods marine mammalogists have used to study foraging in the past are not well suited to studying these scales, but passive acoustic monitoring of calling behavior coupled with observations of the prey field and of foraging and traveling whales could address the hypothesis that baleen whales may broadcast the location of foraging opportunities and other whales may use these signals to find large evanescent patches of prey.

Baleen whales do not have the specialized high-frequency echolocation systems that evolved in toothed whales. However, it has been suggested that they might use lower frequency sound to listen for echoes from their own sounds to locate landmarks during migration as discussed by Clark and Ellison (2004) or dense patches of some kinds of prey during the foraging season. There have also been suggestions that two or more whales might use sound together to locate prey schools. Weston (1967) and Diachok (2000) report that when sound of about 1 kHz in frequency propagates underwater through schools of fish with air-filled swim bladders, sound is attenuated much more than when it passes through seawater. Tyack (1997) reviews evidence that whales separated by one to tens of km might be able to detect schools of fish with air-filled swim bladders by detecting attenuation of vocalizations when a fish school comes between caller and receiver. Gong et al. (2010) show how a receiver at some distance from a ~ 1 kHz sound source can detect echoes from fish schools to a range of 100 km. This suggests that a whale might be able to detect fish schools by listening for echoes from the sounds of other whales. If whales in groups use sounds in these ways to find prey patches, future testing of these hypotheses would change our understanding of whale sociality and foraging ecology on the feeding grounds.

### ***7.7.2 Do Baleen Whales Have Long-Term Individual-Specific Social Relationships Beyond Mother-Calf?***

In my 1986 review of social behavior in cetaceans, I argued that, except for the mother-calf bond, individual-specific relationships appeared to be the exception to the norm in baleen whales (Tyack 1986). Certainly, if groupings of whales are defined by being sighted together on a feeding ground, during migration, or on a breeding ground, then groups appear to be very transient, with few stable associations between individuals outside of special cases such as the humpbacks in Alaska and the Gulf of St Lawrence that feed in coordinated groups. However, animals such as bottlenose dolphins (*Tursiops truncatus*; Quintana-Rizzo 2006) and chimpanzees (*Pan troglodytes*; Lehmann and Boesch 2004) that maintain stable and strong individual-specific social relationships lasting many years may live in a fission–fusion society in which groupings are fluid and do not last long. There is strong evidence that individuals of these species can recognize one another using several sensory modalities, and individual recognition is common among mammals. Therefore, observation of fluid groups by itself does not demonstrate lack of individual-specific social relationships. Furthermore, the discussion above on range of communication raises the possibility that our definitions of groups, often defined as sightings of individuals within a few body lengths, may not match the ranges over which whales are able to maintain their social bonds.

Since 1986, a series of papers has suggested the potential for longer term, individual-specific social relationships in baleen whales. Considering that adult female right whales call males into competitive mating groups during the feeding

season when females are not ovulating, Kraus and Hatch (2001) suggested that females may keep track of the performance of different males, make a choice, and mate with the selected male at a later time. This would require the ability of the female to identify the same male during the feeding and breeding seasons. Clapham (1993) studied associations of humpback whales on the Gulf of Maine feeding ground. He found that adult male–female pairs were more common among groups than expected by chance, and he also surmised that perhaps “males establish bonds with many females in the summer with a possible payoff on the breeding grounds during the winter” [p. 142]. Clapham et al. (1992) and Brown and Corkeron (1995) determined the sex of humpback whales competing in groups during the breeding season or migration, respectively. Most of these groups fit the pattern described by Tyack and Whitehead (1983) of males competing for access to a female, but some of these groups of competing males did not include a female. Clapham et al. (1992) and Brown and Corkeron (1995) suggest that these all-male competitive groups may represent interactions in which males are sorting out their dominance status. Brown and Corkeron (1995) point out that this kind of dominance sorting requires whales to recognize one another as individuals and to remember the outcome of previous encounters with each individual. Darling and Bèrubè (2001) and Smith et al. (2008) determined that many of the lone whales which join singers are males. Darling and Bèrubè (2001) argue that these male-male interactions are also involved in dominance sorting and “that these animals know each other and continually reestablish their relationships, with some facilitation by the song” [p. 581]. Brown and Corkeron (1995) conclude: “If male humpback whales are establishing dominance hierarchies, associations between males may not be as ephemeral as described previously” [p. 175]. If they use song to track known individuals and if song can be detected to ranges of tens of km in humpbacks and farther in other species, then we would need studies designed to track associations over many tens of kilometers, much greater ranges than have previously been conducted. Carefully designed playback studies would be required to test whether a whale can identify other known individuals by their song.

The evidence for these individual-specific relationships is not very strong for baleen whales, nor do we know whether baleen whales can identify individuals acoustically using distinctive call features, visually based on natural markings, and/or by sensing distinctive combinations of odorants. However, as with most mammals, it is clear that mothers can keep in reliable contact with their young, and baleen whale mothers maintain a stable association with their young calf through migrations over thousands of kilometers and for periods of a year or more in some cases. We know right whales use a variety of calls including upcalls to maintain contact during short separations. McCordic et al. (2016) analyzed upcalls of 14 right whales of known age and sex and showed that these contact calls carry information about the identity and age/sex class of the caller. Classification based on simple acoustic features of the calls was correct 73% of the time for individual identification and 86% of the time for age/sex class. Given this demonstration, it does not seem far-fetched to hypothesize that adult whales might similarly recognize other adults. The complexity, stereotypy, and stability of bowhead song (Stafford et al. 2018) suggests the potential that a whale could recognize individuals by their songs. The way in which the songs of humpback

whales change over time seems to make individual identification difficult, but some acoustic features of the song may carry individual-specific cues. The key missing test is playback experiments to test for individual recognition. Once a vocalization is identified as potentially used for individual identification, a paired playback design such as used by Sayigh et al. (1999) for common bottlenose dolphins would suffice. The key is to find two pairs of animals where A has a stronger bond with B than to D and C has a stronger bond with D than to B. Upon playback of the calls of B and D to whales A and C, the prediction would be that A would respond to B, and that C would respond to D with responses appropriate to the bond. Clark et al. (2006) used a similar design to show that Magellanic penguin (*Spheniscus magellanicus*) females respond more strongly to calls of their mate than to those of a neighbor or a stranger, but they show no difference in response to neighbors and strangers. A common playback design for songbirds tests whether a subject responds less strongly to the song of a neighbor that is played from the neighbor's location than when it is played from a territory far from the neighbor's usual location. Birds that pass this test demonstrate that they recognize the neighbor's song and associate it with a particular location (Falls and Brooks 1975).

### 7.7.3 Conclusions

Since the days of whaling under sail, humans have learned that some baleen whale populations live on the scale of ocean basins. Most have an annual migratory cycle where they feed in areas thousands of km away from where they breed, and they can communicate acoustically over ranges of tens to hundreds of kilometers. However, it is only in the past few decades that human researchers are starting to appreciate that the methods we use to understand their behavior and social organization must match the temporal and spatial scales on which these whales operate rather than the scales that we as terrestrial primates apply to our own communication and social behavior.

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