Chapter 11
Killer Whales: Behavior, Social Organization, and Ecology of the Oceans' Apex Predators

John K. B. Ford

Abstract The killer whale—the largest of the dolphins and the top marine predator—has a cosmopolitan distribution throughout the world's oceans. Although globally it could be considered a generalist predator with a diverse diet, it is deeply divided into ecotypes, many of which have distinct foraging strategies involving only a narrow range of prey species. These ecotypes, which often exist in sympatry, are believed to arise from culturally driven dietary specializations that develop within matrilineal social groups and are transmitted among matriline members and across generations by social learning. Specializations are maintained by behavioral conformity and social insularity of lineages, which result in reproductive isolation and, ultimately, genetic divergence of ecotypes. Ecotypes have distinct patterns of seasonal distribution, group size, social organization, foraging behavior, and acoustic activity that are related to the type of prey being sought. Sophisticated cooperative foraging tactics have evolved in some ecotypes, and prey sharing within matrilineal social groups is common. Remarkable behavioral and demographic attributes have been documented in one well-studied ecotype, including lifelong natal philopatry without dispersal of either sex from the social group, vocal dialects that encode genealogical relatedness within lineages, and multi-decade long post-reproductive periods of females. Cultural traditions of killer whales, including foraging specializations, can be deeply rooted and resistant to change, which may limit the ability of ecotypes to adapt to sudden environmental variability.

Keywords *Orcinus orca* · Orca · Ecological specialization · Cultural traditions · Matrilineal society · Foraging tactics · Dialects · Menopause

J. K. B. Ford (✉)
Department of Zoology, University of British Columbia, Vancouver, BC, Canada

Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC, Canada
e-mail: john.ford@ubc.ca

B. Würsig (ed.), *Ethology and Behavioral Ecology of Odontocetes*, Ethology and Behavioral Ecology of Marine Mammals,
https://doi.org/10.1007/978-3-030-16663-2_11

11.1 Introduction

The killer whale, or orca—with its striking black and white coloration, wide range in the world's oceans, and fame at oceanariums—is one of the most widely recognized and familiar marine mammals. But until quite recently, scientific understanding of *Orcinus orca* was minimal, and knowledge of the animal was based almost entirely on anecdotal and scattered opportunistic observations. From dramatic and fanciful accounts of early mariners witnessing the predatory nature of the species, it acquired a reputation of almost mythical proportion as a savage, bloodthirsty demon, malevolent to both marine animals and humans alike. In his tome *Naturalis Historiæ*, written almost 2000 years ago, Roman naturalist and philosopher Pliny the Elder described the orca as "a mightie masse and lumpe of flesh without all fashion, armed with the most terrible, sharpe, and cutting teeth" that showed no mercy in its vicious attacks on female baleen whales and their calves. More recently, nineteenth-century whaling captain and naturalist Charles Scammon concluded that "in whatever quarter of the world the Orcas are found, they seem always intent upon seeking something to destroy or devour" (Scammon 1874). It is only in recent decades that scientific field studies have shed much needed light on the true behavior and ecology of killer whales, and it has become clear that this is indeed a most remarkable and, in many respects, unique social predator.

11.2 Distribution and Population Structure

Killer whales—the largest of the dolphins (family Delphinidae)—are the most widely distributed marine mammals with a cosmopolitan range in all the world's oceans and most seas. Despite the widespread occurrence of killer whales, it is not an abundant species. They are rare in many regions, especially the tropics, and reach highest densities in cool, productive, high-latitude waters. They do not undertake long-range migrations between feeding and breeding areas, but distribution shifts associated with seasonal occurrence of prey aggregations are common (e.g., Similä et al. 1996; Ford et al. 2000). Killer whales have successfully exploited a diversity of marine habitats. They occur pelagically in deep oceanic waters but much more commonly in continental shelf and nearshore waters, where they can be found moving through confined passes and channels and up narrow inlets and fjords. Notable concentrations occur along the northwestern coast of North America, around Iceland, along the coast of northern Norway, and in the Southern Ocean around Antarctica. In the Antarctic, killer whales are commonly found up to the pack ice edge in many areas and may extend well into ice-covered waters.

Although only a single species is currently recognized, there is an increasingly compelling body of evidence that multiple species of killer whales likely exist (Morin et al. 2010). Discrete populations with distinctive genetic, morphological, ecological, and cultural attributes—variously described as types, forms, races, lineages, or, most commonly, ecotypes—have been identified in several regions. These ecotypes often exist in sympatry, sharing the same waters yet maintaining social and reproductive isolation from each other and specializing on different types of prey. Recent genetic studies of killer whales from multiple global regions suggest that ancestral killer whales diverged rapidly within the past 250,000–350,000 years through various processes of population expansion, dispersal, and colonization, with founder groups radiating into diverse ecological niches through dietary specialization and subsequent cultural and reproductive isolation followed by genetic drift or adaptation (Morin et al. 2015; Moura et al. 2015; Foote et al. 2016; Hoelzel and Moura 2016). Ecological and genetic divergence may have taken place both in allopatry and in sympatry (Hoelzel et al. 2007; Riesch et al. 2012; Hoelzel and Moura 2016).

11.3 Sympatric Ecotypes: Foraging Specializations as Cultural Traditions

Globally, the killer whale could be considered a generalist predator since an extremely diverse array of prey types has been documented, either through direct observation of predation or from identification of stomach contents of stranded animals. Overall, almost 200 species of marine vertebrates and invertebrates have been recorded as prey, including 37 species of cetaceans, 20 of pinnipeds, 44 of bony fishes, 29 of sharks and rays, 27 of seabirds, 29 of squid and octopus, 2 of sea turtles, and even 2 species of terrestrial mammals (Ford 2014, unpubl.). However, ecotypes of killer whales can have remarkably specialized diets and forage selectively for only a very small subset of the prey species that this versatile predator is capable of consuming. It seems that ecological specializations reflect cultural traditions that have evolved over millennia, passing from one generation to the next by social learning. The matrilineal social structure typical of killer whales, as described later, is well suited to the inter-generational cultural transmission of dietary habits and the specialized knowledge of when, where, and how to acquire their prey.

Sympatric ecotypes of killer whales are best known from long-term field studies in coastal waters of the eastern North Pacific, from California north to the Aleutian Islands, Alaska. Three ecotypes with largely distinct diets share these waters but do not mix—*Residents*, *Transients* (also known as *Bigg's killer whales*), and *Offshores* (Bigg 1982; Ford et al. 2000; Ford and Ellis 2014). Each ecotype is distinct genetically and differs subtly in appearance, but perhaps most striking are the numerous differences in patterns of movement and habitat use, social structure, and behavior that are related to their particular foraging specialization. The Resident ecotype in the northeastern Pacific feeds predominantly on fish, particularly Pacific salmon. Although all six species of salmon in northeastern Pacific waters are eaten by Resident killer whales, Chinook salmon (*Oncorhynchus tshawytscha*) is by far their preferred prey despite being one of the least abundant salmon species (Ford and

Ellis 2006). This is likely due to the Chinook's large size, high fat content, and year-round availability in the coastal range of Residents. Pink salmon (*O. gorbuscha*) and sockeye salmon (*O. nerka*), considerably smaller in size but vastly more abundant during their summer spawning migrations through coastal waters, are surprisingly not significant prey items. Chum salmon (*O. keta*), second in size to Chinook, is an important prey species during fall. Resident killer whales also feed occasionally on bottom-dwelling fishes and squid but have not been seen to prey on marine mammals in over 45 years of observation.

In striking contrast to the diet of Residents, the Transient ecotype feeds on small marine mammals and does not consume fish. They prey on pinnipeds (mostly harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*)) and small cetaceans (mostly harbor porpoises (*Phocoena phocoena*) and Dall's porpoises (*Phocoenoides dalli*)) (Ford et al. 1998; Saulitis et al. 2000). Common minke whales (*Balaenoptera acutorostrata*) are occasionally attacked by Transient killer whales, and gray whale (*Eschrichtius robustus*) calves and juveniles are hunted during their northward spring migration (Ternullo and Black, 2002; Barrett-Lennard et al. 2011). Transients rarely attack mature large baleen whales, likely because they are too energetically costly or risky to routinely pursue (Ford and Reeves 2008). Transients have not been observed to eat any species of fish, but they do feed on a variety of squids, including the Robust clubhook squid (*Onykia robusta*), with a mantle length of more than 1 m and a weight of more than 13 kg (Ford 2014). They also have been observed killing a variety of seabird species, but only a minority of these are actually consumed.

Details of the foraging habits of Offshore killer whales are not as well known, but evidence is now compelling that this is a shark-specialist ecotype. Offshores have been observed feeding on Pacific sleeper sharks (*Somniosus pacificus*) on numerous occasions, as well as on blue sharks (*Prionace glauca*), spiny dogfish (*Squalus suckleyi*), and salmon sharks (*Lamna ditropis*). It appears that these whales feed so extensively on sharks that their teeth become severely worn due to the abrasive quality of shark skin, which is roughened by embedded dermal denticles (Ford et al. 2011; Ford 2014). The teeth of all adult stranded Offshore killer whales observed to date have been worn flat to the gums, a pattern that has not been observed in even very old Residents or Transients. The Offshores appear to eat just the liver of sharks, which is rich in lipids, and likely wear their teeth while ripping the body open to access it. The diet of Offshores is not exclusively elasmobranchs, however, since predation on some teleost fishes has also been documented (Ford et al. 2011; Ford 2014).

Five distinctive ecotypes have been described in waters of the Southern Ocean surrounding Antarctica—these are referred to as types A, B1, B2, C, and D. Antarctic Type A killer whales are open-water marine mammal predators that may specialize on Antarctic minke whales (*Balaenoptera bonaerensis*), especially during austral summer (Pitman and Ensor 2003). Type B1, also known as pack ice killer whales, have a circumpolar distribution and feed on pinnipeds in loose pack ice. They forage selectively for Weddell seals (*Leptonychotes weddellii*), typically ignoring the much more abundant crabeater seals (*Lobodon carcinophaga*) and leopard seals (*Hydrurga leptonyx*) occupying the same waters (Pitman and Durban 2012). Type B2, also called Gerlache Strait killer whales, have a similar appearance to the sympatric pack ice killer whales but are almost one-quarter smaller in size (Durban et al. 2017). They are known only from the Antarctic Peninsula, where they appear to feed mostly on penguins. Type C are also known as Ross Sea killer whales, which is where they are mostly found. This ecotype, which is even smaller than Type B2 whales, appears to feed only on fish, including Antarctic toothfish (*Dissostichus mawsoni*) and potentially Antarctic silverfish (*Pleuragramma antarcticum*) and other smaller fish species (Pitman et al. 2018). Finally, Type D, also known as subantarctic killer whales, have a circumpolar distribution in deep, oceanic waters between 40°S and 60°S (Pitman et al. 2011). It is very distinctive in appearance and highly divergent genetically from other ecotypes (Foote et al. 2013). Little is yet known about its foraging ecology, but it has been observed depredating fisheries targeting Patagonian toothfish (*Dissostichus eleginoides*), suggesting it may naturally be a fish feeder.

In the eastern North Atlantic, there appear to be at least three ecotypes, although the picture is still unclear. Type 1 is primarily a fish-feeding ecotype, targeting herring and mackerel around Norway, Iceland, and Scotland, although some groups are reported to occasionally prey on seals as well (Foote et al. 2009; Jourdain et al. 2017). Type 2 is partly sympatric with Type 1 and is a marine mammal specialist ecotype, preying on both cetaceans and pinnipeds. A third unnamed ecotype is found in the Strait of Gibraltar, where the whales hunt migrating Atlantic bluefin tuna (*Thunnus thynnus*) (Esteban et al. 2016).

It is likely that specialized killer whale ecotypes exist wherever sufficiently abundant and predictable prey resources are available to sustain them year-round. Many aspects of the biology of ecotypes, such as seasonal distribution, group size, social organization, foraging tactics, and acoustic activity, are strongly influenced by their dietary specialization, as will be explored in greater detail in the following sections. It should be noted, however, that more generalist foraging strategies may be expected of killer whales in some regions, particularly in low-productivity tropical and oceanic waters such as around Hawaii (Baird et al. 2006).

11.4 Social Organization

Like most delphinids, killer whales are highly social animals, typically living in groups of a few individuals to 20 or more. However, in contrast to the considerable social fluidity of many coastal dolphin species (Connor et al. 2000), killer whale groups are often highly stable and cohesive over time. In most areas where killer whales have been studied for long periods using individual photographic identification, their primary social units consist of strongly bonded kin related by matrilineal descent (Bigg et al. 1990; Ford and Ellis 1999; Similä and Ugarte 1999; Iñíguez et al. 2005; Tosh et al. 2008; Tixier et al. 2014). Temporal persistence of these bonds is a primary variable determining group sizes and structure in different ecotypes.

Fig. 11.1 A matrilineal group of Resident killer whales, *Orcinus orca*, with three generations. Shown is the ca. 63-year-old matriarch A30 at left in the image, in the back, her ca. 41-year-old son A38 to her left, and her 27-year-old daughter A50 to his left. A50's two young offspring, A84 (6 years old, at the rear) and A99 (newborn, surfacing), swim alongside their mother. Photo by Jared Towers

The best known society is that of Resident killer whales, which have been studied continuously for over 45 years in coastal British Columbia and Washington State (Bigg et al. 1990; Ford et al. 2000; Towers et al. 2015) and for over 30 years in southern Alaska (Matkin et al. 2014). Long-term studies have also been conducted on Resident-type killer whales off the east coast of Kamchatka (Ivkovich et al. 2010). Resident killer whales live in complex societies based on matrilineal genealogy, social association, and patterns of vocalizations. The basic social unit—the *matriline*—is a highly stable kin group that consists of a matriarch, her sons and daughters, and the daughters' offspring. Because the lifespan of females can reach 80 years and females have their first calf at 12–14 years (Olesiuk et al. 2005), matrilines may contain four and occasionally five generations of maternally related individuals. Remarkably, both males and females stay with their close kin for life—no individual whales have been observed to leave their matriline and join another on a long-term basis. Lifetime natal philopatry with the complete absence of dispersal is exceedingly rare in mammals (Wright et al. 2016). As a result, the matrilines of Resident killer whales are perhaps the most enduring social groupings of any mammal (Fig. 11.1).

Members of Resident matrilines travel together and seldom separate by more than a few kilometers or for more than a few hours. Contact is maintained among matriline members by the exchange of stereotyped underwater calls that form a dialect unique to the group (see Acoustic Behavior, below) (Ford 1991; Miller et al. 2004). Matrilines frequently travel in the company of certain other matrilines that are closely related, based on high degrees of dialect similarity, and these likely shared a common matrilineal ancestor in the recent past. Matrilines that spend the majority of their time together are designated as *pods* (Bigg et al. 1990). Pods are less stable than matrilines, and member matrilines may spend days or weeks apart. However, matrilines still spend more time with others from their pod than with those from different pods. In British Columbia, Resident pods are on average composed of three matrilines (range = 1–11), with a mean total size of 18 whales (range = 2–49; Ford et al. 2000). Residents may form large temporary aggregations involving multiple matrilines and pods, especially at times when salmon densities are high—these are often referred to as “superpods.”

Resident killer whale society is not just matrilineal in structure, but matrifocal, with old females playing a key role as matriarchs of the kin group. Resident killer whales are extremely unusual among mammals in that females undergo menopause at around 40 years of age, then live for another decade on average and sometimes for another 30–40 years (Olesiuk et al. 2005). By this time, post-reproductive females are grandmothers, great-grandmothers, or even great-great-grandmothers and are central to the social cohesion and day-to-day functioning of the group. They are the oldest members of the group and no doubt have the greatest experience and ecological knowledge of when and where to locate Chinook salmon, their preferred prey. The bond between matriarchs and their adult sons is particularly strong—sons spend more time near their mother than with others in the group (Bigg et al. 1990; Brent et al. 2015) and have a higher probability of dying compared to daughters, following the death of their post-reproductive mother (Foster et al. 2012). The death of a matriarch can also increase the probability of fission of the group along maternal lines—for example, two adult sisters together with their respective offspring may spend increasing time apart after their mother dies (Stredulinsky 2016).

A level of social structure above the Resident pod is the *clan*, which is defined solely by the vocal repertoire of pods. All pods within a clan have vocal dialects that include shared call types, indicating a common ancestral matrilineal heritage. The dialects of different clans have no calls in common. Pods from different clans often travel together and mix despite their completely distinct call repertoires. Finally, above the clan is the *community*, which consists of pods that regularly associate with one another. Thus, unlike matrilines and clans, the community is defined solely by association patterns. Even though the ranges of communities may overlap, pods from one community avoid contact with those from another.

Mammal-hunting Transient killer whales in coastal waters of the northeastern Pacific have a less structured and not so strictly matrilineal society than Residents. They usually travel in groups of about 3–6 individuals, much smaller than the typical size of Resident matrilines and pods. Although the core members of the social unit are a mother and her descendants, offspring may disperse from the natal matriline for extended periods or permanently (Ford and Ellis 1999; Baird and Whitehead 2000). Female offspring usually leave their natal group around the time of sexual maturity and travel with other Transient matrilines. These young females usually give birth to their first calf shortly after dispersing. Once dispersed, females may rejoin their natal matriline occasionally, but generally only for brief periods after they have calves of their own. Male dispersal also takes place, but less predictably. Adult males that have lost their mothers through mortality often travel alone or associate with a variety of different Transient matrilines, but rarely with other lone males. The associations of Transient matrilines are very dynamic, and they do not form consistent groupings equivalent to Resident pods. Also, in contrast to Residents, Transient populations do not seem to be acoustically subdivided into clans. Instead, all transients in a population share a distinctive set of calls, although some additional calls or variants of shared calls may be specific to subregions or portions of the population (Deecke et al. 2005).

The typically small size of Transient groups is likely a result of the foraging strategy of this ecotype. Transients generally hunt other marine mammals with stealth: they swim quietly to avoid detection by their acoustically sensitive prey and attack using the element of surprise (Barrett-Lennard et al. 1996; Deecke et al. 2005). This strategy no doubt constrains group size, as larger groups such as those of Residents would increase the probability of the predators being detected by their prey. Small groups may also be most energetically efficient for Transients when hunting smaller marine mammals such as harbor seals (Baird and Dill 1996).

Most killer whale societies studied in other ocean regions are matrilineal in structure, but none has yet been found to have the lifelong natal philopatry seen in Residents. Killer whales that feed on migrating bluefin tuna in the Strait of Gibraltar form highly stable matrilineal groups (Esteban et al. 2016), although it is not clear if some dispersal may take place. Associations within a group of seal-feeding killer whales in Norway have persisted for at least 30 years (Jourdain et al. 2017). Killer whales in the subantarctic Crozet Islands (Guinet 1991) and Prince Edward Islands (Tosh et al. 2008), which prey mostly on seals and penguins, live in small groups that appear similar in structure to those of Transients with strong maternal bonds but some fluidity in group composition. A possible exception to the pattern of structured societies with enduring kinship bonds occurs in a population of herring-eating killer whales in Iceland. These animals form large groups, but association analyses have so far failed to identify any clear matrilineally based hierarchical structure, perhaps beyond a mother and her immature offspring. Instead, many associations in social clusters appear weak and temporary, resulting in a complex, dynamic sociality (Tavares et al. 2017).

11.5 Acoustic Behavior and Dialects

As with most delphinids, killer whales have a well-developed acoustic system, producing pulsed signals and whistles for social communication and echolocation clicks for orientation and discrimination of objects in their surroundings. The most characteristic signals of killer whales globally are strident burst-pulsed calls about 1–2 s long. These loud, structurally complex calls are audible at ranges of over 15 km in quiet conditions. Individual whales have stable repertoires of several to ten or more stereotyped calls that are unique at various levels of social structure. Call repertoires appear to be learned by individuals and thus are passed across generations by cultural transmission (Ford 1991; Filatova et al. 2015). In coastal waters of the northeastern Pacific, the three sympatric ecotypes—Residents, Transients, and Offshores—produce repertoires of call types that are entirely distinct from each other. Distinctive variants of call repertoires exist within each ecotype as well. Dialects at the level of the social group are very rare in vertebrates (Ford 1991; Filatova et al. 2015).

Fish-eating Resident killer whales have call repertoires that are based on matrilineal genealogy—within a community, different acoustic clans can be found, each composed of a number of pods that share a portion of their call repertoires. Structural variants of shared calls that are pod-specific or matriline-specific are typical, forming a system of related dialects within each clan. These related dialects likely reflect a common matrilineal heritage of clan members, having evolved from the common call repertoire of an ancestral group that diverged acoustically when the matriline went through a process of growth and fission. Those pods with many shared features in their dialects are probably more closely related, and have split more recently, than those with more divergent features. Newborn whales presumably learn their natal group's dialect by mimicking their mother and other close kin, and dialects are retained within the matriline. Dialects are maintained even though groups from different clans regularly travel together, each using their own distinctive calls. Dialects that encode the matrilineal identity of individuals are no doubt very effective at maintaining group contact, cohesion, and stability. They also appear to serve an important role in inbreeding prevention. Because there is no dispersal of individuals from the natal group, Resident killer whales would seemingly have a high risk of mating with immediate kin. Genetic studies in the Northern Resident community in British Columbia have revealed that Resident males tend to mate outside their pod or clan with females that have unrelated or distantly related dialects (Barrett-Lennard 2000). Multiple clans with associated group-specific dialects have been documented within Resident killer whale populations off the coasts of eastern Kamchatka (Filatova et al. 2015) and southern Alaska (Yurk et al. 2002), as well as British Columbia (Ford 1991). A variety of stereotyped calls have been described from herring-feeding populations of killer whales in Norway and Iceland, at least some of which appear to be group-specific (Moore et al. 1988; Strager 1995; Filatova et al. 2015).

While fish-eating ecotypes of killer whales tend to be highly vocal while foraging, mammal-eating ecotypes typically hunt in near silence (Guinet 1992; Barrett-Lennard et al. 1996; Deecke et al. 2005, 2011; Jourdain et al. 2017). They rarely exchange stereotyped calls and use of echolocation clicks is much reduced. This appears to be a foraging tactic—pinnipeds and cetaceans have excellent underwater hearing and would be more difficult to catch if they heard the approaching predators. Mammal-hunting whales seem to rely on passive listening and vision rather than active echolocation to detect potential prey. However, once prey is detected and captured, the whales can become quite vocal. As with fish-eating killer whales, mammal-hunting killer whales have repertoires of distinctive stereotyped call types which may vary regionally but do not appear to have dialect variation at the level of the social group, at least within the Transient killer whale ecotype off the North American west coast. As there is dispersal from the natal matriline in this ecotype and more fluid associations, group-specific calls would not be expected. Also, dispersal reduces the risk of inbreeding, so the requirement for an acoustic outbreeding mechanism may be reduced in Transients.

11.6 Foraging Specializations and Tactics

Killer whales are highly versatile social predators that forage cooperatively for their preferred prey using a variety of predatory behaviors. Across the world's oceans, there are broad similarities in social structure, group size, and acoustic activity of ecotypes that feed primarily on fish versus those that mostly hunt marine mammals. The often highly specialized tactics used to catch their prey, however, can vary from place to place and across prey species. These local specializations likely result from the innovation of novel foraging methods that, when successful, are passed on by cultural transmission within lineages.

11.6.1 Predation on Fish

Killer whales that specialize on fish tend to have relatively large group sizes, generally 10–30 or more. This is the case with salmon-eating Residents and shark-eating Offshores in the northeastern Pacific (Ford and Ellis 2014), herring-eating populations in Norway and Iceland, (Similä and Ugarte 1999; Tavares et al. 2017), and fish-eating Ross Sea (Type C) killer whales in Antarctica (Pitman and Ensor 2003). Groups of fish-eating killer whales forage in a coordinated manner, sometimes with close cooperation among individuals, especially immediate kin. Resident killer whale pods disperse widely when foraging for Chinook salmon, often spread over areas of 10 km^2 or more. Resident pods do not herd or corral fish cooperatively—rather, individuals and small maternal groups (e.g., a mother and her youngest offspring) search for and catch fish independently. The great majority of salmon captured by adult females and subadults are brought to the surface where they are broken up and shared with others in the matriline (Fig. 11.2; Wright et al. 2016). The widespread prevalence of prey sharing is remarkable given that even large Chinook salmon could be easily consumed by an individual alone. All age–sex classes share their prey with their matrilineal kin but rarely with individuals outside the matriline, even when multiple matrilines forage together. This would be expected if prey sharing is driven primarily by kin selection, whereby individuals receive the greatest inclusive fitness gains by provisioning close relatives. Prey sharing also serves to reduce competition among kin and promotes the maintenance of matrilineal cohesion. Reproductive females share mostly with their offspring but also occasionally with their siblings, mother, or other more distant kin. Post-reproductive females

Fig. 11.2 An adult female Resident killer whale, *Orcinus orca*, sharing a salmon with her 1-year-old calf. Taken from video recording made by Cetacean Research Program, Pacific Biological Station, Canada

share their prey more often with their adult sons than adult daughters, perhaps because their older sons have far greater reproductive potential, and enhancing their survival through provisioning would increase her inclusive fitness. Females only have about five surviving offspring in their lifetime (Olesiuk et al. 2005), while adult males can potentially have many offspring by mating with multiple females outside the matriline. Genetic studies in one Resident community have revealed that just two adult males jointly sired at least 36 progeny, or roughly half of all sampled offspring born in the population over a 25-year period (Ford et al. 2018).

In coastal fjords of Norway, killer whales feed on herring that congregate in high densities during fall and winter. To do so, the whales employ a cooperative foraging tactic known as "carousel feeding" to capture these small schooling fishes: this involves a group of whales encircling and herding a school of herring into a tight ball close to the surface (Fig. 11.3). Once the school is concentrated, individuals dive under the school and strike it with their tail flukes, stunning herring in the process. They then pick up and eat the debilitated herring floating in the water column (Similä and Ugarte 1993). Herring-feeding killer whales in Iceland also use tail slaps to debilitate the fish, but they first appear to manipulate the herring into a dense school by emitting a particular kind of pulsed call rich in energy at low frequencies to which herring are most sensitive (Simon et al. 2006). It is interesting that fish-eating Resident killer whales in the northeast Pacific do not target herring, which are extremely abundant in their range during spring spawning—perhaps the whales in this area lack any effective tactic for exploiting these small, schooling fish.

Fish-eating killer whales in New Zealand target several species of large rays that live on or in muddy seabeds. They sometimes dig into the soft substrate to dislodge the fish, surfacing with mud on their rostrum. The captured rays, which can reach many 10s of kg, are generally shared among group members (Visser 2000). Feeding

Fig. 11.3 Aerial view of killer whales, *Orcinus orca*, cooperatively encircling and foraging on a school of herring, northern Norway. Photo courtesy of Norwegian Orca Survey

on rays can be risky since they have sharp venomous spines that can cause injury or mortality to the whales (Duignan et al. 2000), but it appears to be a successful foraging strategy in New Zealand waters.

In the Strait of Gibraltar, a small population of killer whales specializes on predation of bluefin tuna as the fish enter and exit the Mediterranean Sea during their breeding migration (Esteban et al. 2016). To catch these swift tuna, the whales employ an endurance-exhaustion technique involving chases of individual fish that may last 30–40 min at swimming speeds of 12–14 km/h (Guinet et al. 2007). Killer whales can sustain sufficient swimming speeds necessary to catch small to medium (0.8–1.5 m) tuna using this technique but appear unable to match the swimming ability of larger fish.

A foraging technique that has developed among numerous fish-eating killer whale populations is depredation of human fisheries. In many different locations around the world, including the Pacific, Atlantic, and Southern Oceans and the Mediterranean and Bering Seas, killer whales have learned to remove fish caught on longline fishing gear as it is being hauled in. In most cases, depredation involves fish species that are naturally targeted by the whales, but in others the whales have learned to take and consume fish that may not be part of their regular diet. The whales can be highly selective in the fish they remove from the longlines—they typically take the largest individuals of species that are rich in oil, such as Patagonian toothfish and sablefish

(*Anoplopoma fimbria*), while ignoring small individuals or less desirable species with low oil content (Yano and Dahlheim 1995; Guinet et al. 2014). Killer whales can learn to depredate soon after a fishery begins within their range (Guinet et al. 2014), or the behavior can begin abruptly in fisheries that have existed for years, with the innovation of the technique by a single group, which can then spread to others in the population (Matkin and Saulitis 1994). Once the behavior is established, the whales can be extremely difficult to dissuade from the practice, and depredations may persist despite defensive actions such as shootings and underwater detonations. See Chap. 10 for a description of killer whale interactions with humans.

11.6.2 Predation on Marine Mammals

Killer whales that specialize on marine mammal prey tend to have two behavioral traits in common—they have small group sizes (typically <10 individuals) and they forage in silence to avoid alerting their acoustically sensitive prey and to facilitate passive listening to detect potential prey. These features have been noted in the northeastern Pacific Transient ecotype (Deecke et al. 2005), Norway (Jourdain et al. 2017), Shetland (Deecke et al. 2011), Argentina (Iñíguez et al. 2005; J. Ford, unpubl. obs.), and the Crozet Islands (Guinet 1992). Small group sizes likely allow the stealthy hunting of the whales' vigilant prey by reducing the need to exchange vocalizations for coordination and by making the whales less conspicuous visually. In coastal British Columbia and southern Alaska, Transient killer whales forage in small groups averaging 3–4 whales for harbor seals, the most abundant marine mammal in the region and most common prey (Ford et al. 1998). Harbor seals are easy prey for these whales, and the great majority are captured and consumed quickly following detection. Other prey species of Transients are more difficult quarry. Fast-swimming Dall's porpoise require prolonged high-speed pursuits and escape in about half of observed chases (Ford et al. 1998). If their attempt to flee is unsuccessful, the porpoises are dispatched by ramming from below (Fig. 11.4). Steller sea lions, which may weigh in excess of 1000 kg, are a challenging and dangerous prey species as they can mount an aggressive defense. The whales attack by circling a sea lion in open water and taking turns ramming the animal or striking it with tail flukes while avoiding being bitten. By repeatedly pummeling the sea lion in this manner, which may go on for 1.5–2 h, it is finally debilitated enough to safely grasp and drown underwater, whereupon it is broken up and shared by the group.

Killer whales in Argentine Patagonia and the subantarctic Crozet Islands employ a novel and risky behavior to hunt young southern elephant seals (*Mirounga leonina*) and, in Patagonia, South American sea lions (*Otaria flavescens*). This hunting method involves intentional stranding on shallow, sloping beaches to catch naïve pups as they make their first forays into the water (Lopez and Lopez 1985; Guinet 1992). Considerable skill and agility are needed to successfully execute this tactic without becoming permanently stranded, and it is most commonly undertaken by adults. Young whales are provisioned by their mothers until they learn the technique

Fig. 11.4 A Dall's porpoise, *Phocoenoides dalli*, rammed at high speed by a mammal-hunting Transient (or Bigg's) killer whale, *Orcinus orca*. Photo by Jared Towers

and begin to attempt intentional strandings on their own at 5–6 years of age (Hoelzel 1991; Guinet and Bouvier 1995). During observations at the Crozet Islands, juvenile whales became temporarily stranded on two occasions and likely would have been unable to get off the beach without assistance from their mother on one occasion and human observers on the other (Guinet and Bouvier 1995).

Perhaps the most sophisticated cooperative hunting technique of mammal-eating killer whales is that of pack ice (Type B1) killer whales in Antarctica. Groups of these whales visually seek out a seal hauled out on a small ice floe by spy-hopping and then attempt to wash the targeted seal off the ice with a wave created by rushing toward the floe in a tightly coordinated manner just beneath the surface (Fig. 11.5; Visser et al. 2008; Pitman and Durban 2012). This wave-wash procedure may be repeated multiple times over periods of 30 min or more before the seal is dislodged or the attack is abandoned (Pitman and Durban 2012).

11.7 Conclusions

Killer whales are multifaceted social predators that have evolved to successfully occupy a variety of ecological niches in the world's oceans. They live in matrilineal groups of close kin with enduring bonds that may persist for many years or, in some

Fig. 11.5 Pack ice (Type B1) killer whales, *Orcinus orca*, creating a wave to wash a Weddell seal, *Leptonychotes weddellii*, off an ice floe, Antarctic Peninsula. Photo by John Durban

populations, for life. They have patterns of seasonal movements, group size, social organization, foraging behavior, and acoustic activity that are finely tuned to each ecotype's particular dietary habits. These adaptations appear to be acquired by social learning and are maintained by cultural transmission across generations in the matriline. Killer whales can be highly unconventional in their life history and behavior. The well-studied salmon-eating Resident killer whales of coastal northeastern Pacific waters have several features that are extremely unusual in mammals—they live in multi-generation matrilines from which there is no dispersal of either sex, matrilines have discrete group-specific dialects acquired by vocal learning, there is extensive nonreciprocal food sharing among all age/sex classes within matrilines, and females have prolonged post-reproductive periods that can last for decades. No doubt there are more unusual features in behavior and life history yet to be discovered in other ecotypes and regions.

Ecological specializations such as those seen in killer whales can be a mixed blessing. On the one hand, specialists may have a competitive advantage over generalists in foraging efficiency (as in the old adage, "jack-of-all-trades, master of none") (Kassen 2002). Through innovation and social learning, culturally driven specialization may lead to foraging strategies and tactics that are highly refined for a particular prey type. On the other hand, a high degree of specialization on a particular resource may lead to a reduced ability to efficiently exploit other kinds of prey. The culturally acquired knowledge and behaviors that make certain ecotypes adept at intercepting and catching seasonally migrating fishes such as salmon or herring would be ineffective for hunting marine mammals. Similarly, mammal-hunting specialists would be unlikely to have the acquired skills needed to be an adept fish predator. A specialist foraging strategy may be successful if abundance of the targeted resource is stable and predictable, but should its availability suddenly decline, specialists may be incapable of switching to alternative prey without a considerable reduction in foraging efficiency. Indeed, recent modelling of hypothetical specialist and generalist killer whale populations has shown that cultural specialization is adaptive in the short term and leads to increased fitness, whereas generalization is rarely adaptive. However, cultural evolution of specialization can lead to increased rates of group extirpation (Whitehead and Ford 2018).

It might be expected that a lifestyle based on learning and innovation would give killer whales the flexibility to adapt to fluctuating resource availability. But the cultural traditions of killer whales are deeply rooted and can be very resistant to change. An example is the vocal dialects of Resident killer whales. Clan-specific call repertoires in use today are, in most cases, little changed from those recorded as far back as the late 1950s (Ford 1991, unpubl. data). Despite decades of regular associations of pods from different clans, no diffusion or transfer of calls between them has taken place. The dietary specializations of ecotypes are also firmly fixed traditions. For example, three mammal-eating Transient killer whales that were live-captured and held temporarily in an ocean net pen refused to eat any fish offered to them daily for 2.5 months, by which time they were starving. On day 75, one animal died of malnutrition, but on the 79th day, the two remaining whales finally began to eat salmon that was provided to them and continued to do so until they were released back to the wild several months later, whereupon they resumed their mammal-hunting habits (Ford and Ellis 1999). In contrast, salmon-eating Resident killer whales readily ate fish offered to them within a few days of capture (the existence of ecotypes with different diets was not known to the captors at the time).

Sympatric salmon-eating Resident and mammal-eating Transient killer whale populations off the west coast of Canada have both been affected by fluctuations in the abundance of their prey (Ford et al. 2010). Resident killer whale survival and calving rates are correlated with availability of Chinook salmon, their primary prey species. Mortality rates increased sharply and reproduction decreased during several consecutive years of unusually low range-wide Chinook abundance in the 1990s. It appears that the whales either did not switch to alternative prey during this period or, if they did, it was insufficient to offset nutritional stress and its consequences. One population—the Southern Residents—remains critically endangered, and limited Chinook salmon availability is considered one of the main factors preventing recovery (Lacy et al. 2017). Transient killer whales were rare in coastal British Columbia when field studies began in the 1970s, likely because decades of predator control measures had seriously depleted their primary prey, harbor seals. It is likely that the whales either left the area or suffered decreased survival and reproduction in response to the removal of their food supply, as seen in Residents. Since then, harbor seal abundance has rebounded to historical levels, and Transients have experienced substantial population growth (Ford et al. 2007; Ford 2014).

Culturally driven foraging specialization appears to have resulted in the adaptive radiation of killer whales into a variety of ecological niches within the past 250,000 years (Riesch et al. 2012; Foote et al. 2016). However, cultural conservatism may limit the ability of these specialized ecotypes to adapt quickly to perturbations in their food supply over short time frames. But in some cases killer whales do seem to have the capacity for innovation in order to take advantage of a novel food supply—the abrupt onset of depredation behavior to take fish from a long-existing fishery is one such case. Hopefully, highly specialized killer whale ecotypes will have sufficient flexibility and resilience to withstand future changes in their ecosystem, especially where they arise from conflict with humans for the same food resources.

Acknowledgment Many thanks to John Durban, Eve Jourdain (Norwegian Orca Survey) and Jared Towers for kindly allowing use of their photographs.

References

Baird RW, Dill LM (1996) Ecological and social determinants of group size in transient killer whales. Behav Ecol 7:408–416

Baird RW, Whitehead H (2000) Social organization of mammal-eating killer whales: group stability and dispersal patterns. Can J Zool 78:2096–2105

Baird RW, McSweeney DJ, Bane C, Barlow J, Salden DR, Antoine LRK, LeDuc RG, Webster DL (2006) Killer whales in Hawaiian waters: information on population identity and feeding habits. Pac Sci 60:523–530

Barrett-Lennard LG (2000) Population structure and mating systems of northeastern Pacific killer whales. Ph.D. dissertation. University of British Columbia, Vancouver

Barrett-Lennard LG, Ford JKB, Heise KA (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Anim Behav 51:553–565

Barrett-Lennard LG, Matkin CO, Durban JW, Saulitis EL, Ellifrit D (2011) Predation on gray whales and prolonged feeding on submerged carcasses by transient killer whales at Unimak Island, Alaska. Mar Ecol Prog Ser 421:229–241

Bigg MA (1982) An assessment of killer whale stocks off Vancouver Island, British Columbia. Report of the International Whaling Commission 32:655–666

Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. Report of the International Whaling Commission 12:383–405

Brent LJ, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP (2015) Ecological knowledge, leadership, and the evolution of menopause in killer whales. Curr Biol 25:746–750

Connor RC, Wells R, Mann J, Read A (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann J, Connor RC, Tyack P, Whitehead H (eds) Cetacean societies: field studies of whales and dolphins. University of Chicago Press, Chicago, pp 91–126

Deecke VB, Ford JKB, Slater PJ (2005) The vocal behaviour of mammal-eating killer whales: communicating with costly calls. Anim Behav 69:395–405

Deecke VB, Nykänen M, Foote AD, Janik VM (2011) Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. Aquat Biol 13:79–88

Duignan PJ, Hunter JE, Visser IN, Jones GW, Nutman A (2000) Stingray spines: a potential cause of killer whale mortality in New Zealand. Aquat Mamm 26:143–147

Durban JW, Fearnbach H, Burrows DG, Ylitalo GM, Pitman RL (2017) Morphological and ecological evidence for two sympatric forms of type B killer whale around the Antarctic Peninsula. Polar Biol 40:231–236

Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD, de Stephanis R (2016) Maternal kinship and fisheries interaction influence killer whale social structure. Behav Ecol Sociobiol 70:111–122

Filatova OA, Samarra FI, Deecke VB, Ford JK, Miller PJ, Yurk H (2015) Cultural evolution of killer whale calls: background, mechanisms and consequences. Behaviour 152:2001–2038

Foote AD, Newton J, Piertney SB, Willerslev E, Gilbert MTP (2009) Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. Mol Ecol 18:5207–5217

Foote AD, Morin PA, Pitman RL, Ávila-Arcos MC, Durban JW, van Helden A, Sinding MHS, Gilbert MTP (2013) Mitogenomic insights into a recently described and rarely observed killer whale morphotype. Polar Biol 36:1519–1523

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

Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can J Zool 69:1454–1483

Ford JKB (2014) Marine mammals of British Columbia. Royal BC Museum handbook, mammals of BC, vol 6. Royal BC Museum, Victoria, p 460

Ford JKB, Ellis GM (1999) Transients: mammal-hunting killer whales of British Columbia, Washington, and Southeastern Alaska. UBC Press, Vancouver, p 96

Ford JKB, Ellis GM (2006) Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. Mar Ecol Prog Ser 316:185–199

Ford JKB, Ellis GM (2014) You are what you eat: ecological specializations and their influence on the social organization and behaviour of killer whales. In: Yamagiwa J, Karczmarski L (eds) Primates and cetaceans: field research and conservation of complex mammalian societies. Springer, New York, NY, pp 75–98

Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb KC III (1998) Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can J Zool 76:1456–1471

Ford JKB, Ellis GM, Balcomb KC (2000) Killer whales: the natural history and genealogy of *Orcinus orca* in British Columbia and Washington, vol 102, 2nd edn. UBC Press, Vancouver

Ford JKB, Ellis GM, Durban JW (2007) An assessment of the potential for recovery of west coast transient killer whales using coastal waters of British Columbia. Research document 2007/088, Fisheries and Oceans Canada. Canadian Science Advisory Secretariat, Ottawa

Ford JKB, Ellis GM, Olesiuk PF, Balcomb KC (2010) Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? Biol Lett 6:139–142

Ford JKB, Ellis GM, Matkin CO, Wetklo MH, Barrett-Lennard LG, Withler RE (2011) Shark predation and tooth wear in a population of northeastern Pacific killer whales. Aquat Biol 11:213–224

Ford JKB, Reeves RR (2008) Fight or flight: antipredator strategies of baleen whales. Mammal Rev 38(1):50–86

Ford MJ, Parsons KM, Ward EJ, Hempelmann JA, Emmons CK, Hanson MB, Balcomb KC, Park LK (2018) Inbreeding in an endangered killer whale population. Anim Conserv. https://doi.org/10.1111/acv.12413

Foster EA, Franks DW, Mazzi S, Darden SK, Balcomb KC, Ford JKB, Croft DP (2012) Adaptive prolonged postreproductive life span in killer whales. Science 337:1313–1313

Guinet C (1991) L'orque (*Orcinus orca*) autour de l'Archipel Crozet comparaison avec d'autres localités. Rev Ecol (Terre Vie) 46:1991

Guinet C (1992) Comportement de chasse des orques *Orcinus orca* autour des Îles Crozet. Can J Zool 70:1656–1667

Guinet C, Bouvier J (1995) Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. Can J Zool 73(1):27–33

Guinet C, Domenici P, De Stephanis R, Barrett-Lennard L, Ford JKB, Verborgh P (2007) Killer whale predation on bluefin tuna: exploring the hypothesis of the endurance-exhaustion technique. Mar Ecol Prog Ser 347:111–119

Guinet C, Tixier P, Gasco N, Duhamel G (2014) Long-term studies of Crozet Island killer whales are fundamental to understanding the economic and demographic consequences of their depredation behaviour on the Patagonian toothfish fishery. ICES J Mar Sci 72:1587–1597

Hoelzel AR (1991) Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning and foraging strategy. Behav Ecol Sociobiol 29:197–204

Hoelzel AR, Moura AE (2016) Killer whales differentiating in geographic sympatry facilitated by divergent behavioural traditions. Heredity 117:481–482

Hoelzel AR, Hey J, Dahlheim ME, Nicholson C, Burkanov V, Black N (2007) Evolution of population structure in a highly social top predator, the killer whale. Mol Biol Evol 24:1407–1415

Iñíguez, M., Tossenberger, V.P., and Gasparrou, C. 2005. Socioecology of killer whales (*Orcinus orca*) in northern Patagonia, Argentina. Unpublished paper to the IWC Scientific Committee, 9 p. Ulsan, Korea, June 2005. (SC/57/SM5)

Ivkovich T, Filatova OA, Burdin AM, Sato H, Hoyt E (2010) The social organization of resident-type killer whales (*Orcinus orca*) in Avacha Gulf, Northwest Pacific, as revealed through association patterns and acoustic similarities. Mammalian Biology-Zeitschrift für Säugetierkunde 75:198–210

Jourdain E, Vongraven D, Bisther A, Karoliussen R (2017) First longitudinal study of seal-feeding killer whales (*Orcinus orca*) in Norwegian coastal waters. PLoS One 12(6):e0180099

Kassen R (2002) The experimental evolution of specialists, generalists, and the maintenance of diversity. J Evol Biol 15:173–190

Lacy RC, Williams R, Ashe E, Balcomb KC III, Brent LJ, Clark CW, Croft DP, Giles DA, MacDuffee M, Paquet PC (2017) Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Sci Rep 7:14119

Lopez JC, Lopez D (1985) Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. J Mammal 66:181–183

Matkin CO, Saulitis E (1994) Killer whale (*Orcinus orca*): biology and management in Alaska. Prepared for US Marine Mammal Commission by North Gulf Oceanic Society, Homer, AK

Matkin CO, Testa JW, Ellis GM, Saulitis EL (2014) Life history and population dynamics of southern Alaska resident killer whales (*Orcinus orca*). Mar Mamm Sci 30:460–479

Miller PJO, Shapiro AD, Tyack PL, Solow AR (2004) Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. Anim Behav 67:1099–1107

Moore SE, Francine JK, Bowles AE, Ford JKB (1988) Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. Rit Fiskideildar 11:225–250

Morin PA, Archer FI, Foote AD, Vilstrup J, Allen EE, Wade P, Durban J, Parsons K, Pitman R, Li L, Bouffard P, Abel Nielsen SC, Rasmussen M, Willerslev E, Gilbert MTP, Harkins T (2010) Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. Genome Res 20(7):908–916

Morin PA, Parsons KM, Archer FI, Ávila-Arcos MC, Barrett-Lennard LG, Dalla Rosa L, Duchêne S, Durban JW, Ellis GM, Ferguson SH, Ford JKB, Ford MJ, Garilao C, Gilbert MTP, Kaschner K, Matkin CO, Peterson SD, Robertson KM, Visser IN, Wade PR, Ho SYW, Foote AD (2015) Geographic and temporal dynamics of a global radiation and diversification in the killer whale. Mol Ecol 24:3964–3979

Moura AE, Kenny JG, Chaudhuri RR, Hughes MA, Reisinger RR, De Bruyn PJN, Dahlheim ME, Hall N, Hoelzel AR (2015) Phylogenomics of the killer whale indicates ecotype divergence in sympatry. Heredity 114:48

Olesiuk PF, Ellis GM, Ford JKB (2005) Life history and population dynamics of northern resident killer whales (*Orcinus orca*) in British Columbia. Research Document 2005/045. Canadian Science Advisory Secretariat, Fisheries & Oceans Canada, Ottawa, ON

Pitman RL, Durban JW (2012) Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. Mar Mamm Sci 28:16–36

Pitman RL, Durban JW, Greenfelder M, Guinet C, Jorgensen M, Olson PA, Plana J, Tixier P, Towers JR (2011) Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters. Polar Biol 34(2):303–306

Pitman RL, Ensor P (2003) Three forms of killer whales (*Orcinus orca*) in Antarctic waters. J Cetacean Res Manag 5(2):131–140

Pitman RL, Fearnbach H, Durban JW (2018) Abundance and population status of Ross Sea killer whales (*Orcinus orca*, type C) in McMurdo Sound, Antarctica: evidence for impact by commercial fishing? Polar Biol 41:781–792

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

Saulitis E, Matkin C, Barrett-Lennard L, Heise K, Ellis G (2000) Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. Mar Mamm Sci 16:94–109

Scammon CM (1874) The marine mammals of the north-western coast of North America: described and illustrated; together with an account of the American whale-fishery. JH Carmany, San Francisco

Similä T, Ugarte F (1993) Surface and underwater observations of cooperatively feeding killer whales in northern Norway. Can J Zool 71:1494–1499

Similä T, Ugarte F (1999) Patterns in social organisation and occurrence among killer whales photo-identified in northern Norway. European Research on Cetaceans 12:220. In: Evan PGH, Parsons ECM (eds) Proceedings of the twelfth annual conference of the European Cetacean Society, Monaco, 20–24 Jan 1998. Artes Graficas Soler, Valencia

Similä T, Holst JC, Christensen I (1996) Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. Can J Fish Aquat Sci 53:769–779

Simon M, Ugarte F, Wahlberg M, Miller L (2006) Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. Bioacoustics 16:57–74

Strager H (1995) Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. Can J Zool 73:1037–1047

Stredulinsky EH (2016) Determinants of group splitting: an examination of environmental, demographic, genealogical and state-dependent factors of matrilineal fission in a threatened population of fish-eating killer whales (*Orcinus orca*). MSc thesis. University of Victoria, BC

Tavares SB, Samarra FI, Miller PJ (2017) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behav Ecol 28:500–514

Ternullo R, Black N (2002) Predation behavior of transient killer whales in Monterey Bay, California. In: Fourth international Orca symposium and workshop. CEBC-CNRS, Villiers en Bois, pp 156–159

Tixier P, Gasco N, Guinet C (2014) Killer whales of the Crozet Islands: photoidentification catalogue 2014. Villiers en Bois: Centre d'Etudes Biologiques de Chizé-CNRS, vol 10, p m9. https://www.researchgate.net/publication/268978107_Tixier_et_al_CROZET_KILLER_WHALES_PHOTO_ID_CATALOGUE_2014_POSTER

Tosh CA, De Bruyn PJ, Bester MN (2008) Preliminary analysis of the social structure of killer whales, *Orcinus orca*, at subantarctic Marion Island. Mar Mamm Sci 24:929–940

Towers JR, Ellis GM, Ford JKB (2015) Photo-identification catalogue and status of the northern resident killer whale population in 2014. Canadian Technical Report of Fisheries and Aquatic Science 3139:vi + 75

Visser IN (2000) Orca (*Orcinus orca*) in New Zealand waters. Ph.D. dissertation, University of Auckland, New Zealand

Visser IN, Smith TG, Bullock ID, Green GD, Carlsson OG, Imberti S (2008) Antarctic Peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. Mar Mamm Sci 24:225–234

Whitehead H, Ford JKB (2018) Consequences of culturally-driven ecological specialization: killer whales and beyond. J Theor Biol 456:279–294

Wright BM, Stredulinsky EH, Ellis GM, Ford JKB (2016) Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*. Anim Behav 115:81–95

Yano K, Dahlheim ME (1995) Behavior of killer whales *Orcinus orca* during longline fishery interactions in the southeastern Bering Sea and adjacent waters. Fish Sci 61:584–589

Yurk H, Barrett-Lennard L, Ford JKB, Matkin CO (2002) Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. Anim Behav 63:1103–1119