

Chapter 4

You Are What You Eat: Foraging Specializations and Their Influence on the Social Organization and Behavior of Killer Whales

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Abstract The feeding ecology of predators can have a profound effect on their life history and behaviour. The killer whale—the apex marine predator—has a cosmopolitan distribution throughout the world’s oceans. Globally, it is a generalist predator with a diverse diet, but regionally, different socially and genetically isolated killer whale populations can have highly specialized foraging strategies involving only a few types of prey. In the eastern North Pacific, the three sympatric killer whale lineages have distinct dietary specializations: one feeds primarily on marine mammals, another on salmon, and the third appears to specialize on sharks. These ecological specializations are associated with distinct patterns of seasonal distribution, group size, social organization, foraging behavior, and acoustic activity. Divergent foraging strategies may have played a major role in the social isolation and genetic divergence of killer whale populations.

Keywords Apex predator • Feeding ecology • *Orcinus orca*

4.1 Introduction

Ecological specialization is an important factor promoting the evolution of biological diversity and speciation (Futuyma and Moreno 1988; Robinson et al. 1996; Dieckmann and Doebeli 1999; Schluter 2001; Via 2001). Optimal foraging theory predicts that selection will generally favor dietary specialization, as specialists have a competitive advantage over generalists in foraging efficiency (as in the adage, “the jack-of-all-trades is the master of none”) (Stephens and Krebs 1986; Futuyma and Moreno 1988; Robinson et al. 1996). Such selection may drive the divergent evolution of a wide variety of adaptive traits involving morphology, physiology, and behavior of populations or subpopulations with different foraging strategies or in contrasting environments. Divergent selection between sympatric populations may lead to assortative mating, reproductive isolation, and, ultimately, speciation (Dieckmann and Doebeli 1999; Schluter 2001; Via 2001; McKinnon et al. 2004).

Killer whales, the largest of the dolphins (family Delphinidae), provide an exceptional opportunity to gain insight into the processes and outcomes of ecological specialization and divergence in a highly social and versatile mammalian predator. This species (only a single species, *Orcinus orca*, is currently recognized) is one of the most widely distributed mammals on the planet. It has a cosmopolitan distribution in all the world’s oceans, from the pack ice edges in both the Northern and Southern Hemispheres through the equatorial tropics (Ford 2002). Although rare in many regions, it is relatively common in cool, productive, high-latitude waters, particularly in nearshore areas. Despite their wide distribution, killer whales are not abundant, with a minimum estimated global population of 50,000, but probably not greatly more (Forney and Wade 2006). Killer whales occupy the top trophic position in the oceans and have no predators. As a species, killer whales could be considered generalist predators, with an extremely diverse array of more than 140

species of vertebrates and invertebrates—from small schooling fish to the largest of the cetaceans—recorded as prey (Ford 2009). However, field studies in several global regions have revealed that local populations can have remarkably specialized diets and may forage selectively for only a very small subset of the prey species that the predator is capable of consuming. In this chapter, we provide a description of three distinct killer whale lineages that co-occur in coastal waters of the northeastern Pacific, focusing in particular on the influence that ecological specialization appears to have had on their divergent lifestyles, including habitat use patterns, social structure, behavior, and use of underwater sound. We also provide a brief overview of how these lineages came to be identified and known in these waters and of recent work in other regions that suggests that ecological specialization is characteristic of this apex social predator.

4.2 Discovery of Killer Whale Lineages in the Eastern North Pacific

Before the 1970s, scientific understanding of the killer whale was poor and was based almost entirely on anecdotal or opportunistic observations rather than on dedicated scientific studies (Martinez and Klinghammer 1970). However, a live-capture fishery for killer whales that developed during the late 1960s in nearshore waters of southern British Columbia, Canada, and northern Washington State, USA, highlighted the need for basic abundance and life history data for management. As a result, in 1972 our late colleague, Michael Bigg, initiated field studies of killer whales in this area based primarily on the identification of individuals from photographs of natural markings on the whales' dorsal fin and grey "saddle patch" at the base of the fin. This technique was considered quite novel and unproven at the time, but Bigg quickly showed that it was an effective means of collecting reliable population abundance and life history data on these difficult-to-study animals (Bigg et al. 1976). We joined this field effort at different points in the 1970s and, working together with Bigg and our colleague Ken Balcomb in Washington State, broadened the study's scope to include social organization, foraging ecology, behavior, and vocalizations (Bigg et al. 1987).

By the late 1970s, it was apparent that two different types of killer whales coexisted in the region. One type, named "residents," lived in stable groups of 10 to 25 and were found reliably in predictable "core areas" throughout at least summer and fall. A second type was found in the same waters but only rarely and sporadically. These whales were observed alone or in small groups of 2 to 6, tended to swim close along shorelines, often erratically, and were never seen to mix with the larger "resident" groups. As it was thought that these whales were merely passing through the home ranges of the residents, they were named "transients" (Bigg 1982). Resident and transient killer whales were occasionally observed within a few hundred meters of each other but showed no obvious reaction to the presence of the other whales and did not intermingle. However, resident groups frequently mixed with other

residents and transients with other transients. Although residents and transients were clearly socially isolated, it was not certain what these two types represented. Initially it was thought that transients were individuals that had dispersed from resident groups, possibly in other regions, and were adopting a “low profile” behavior while transiting core areas of residents. However, subtle differences in dorsal fin shape and pigmentation suggested an underlying genetic distinction between them. As the number of observations of feeding grew in the early 1980s, evidence mounted that residents and transients were distinct ecotypes with fundamentally different diets—residents prey on fish and transients on marine mammals (Bigg et al. 1985, 1987). That these two types of whales specialize on such different kinds of prey helped explain the growing number of differences we observed in the movement patterns, social structure, vocalizations, and behavior of residents and transients.

To our surprise, in the early 1990s we discovered a third type of killer whale, named “offshores,” in British Columbian waters (Ford et al. 1992; Ford et al. 2000). These whales have slightly different fin shapes than residents and transients and appear to be somewhat smaller in body size. Offshore killer whales generally prefer the outer continental shelf, and it was only when we expanded our study area to include these waters that we found these whales. Residents and transients also use these outer waters, and offshores have recently made more frequent appearances in nearshore areas (Dahlheim et al. 2008). Despite their mostly sympatric distribution, all three killer whale types maintain social isolation from each other (Ford et al. 2000). From the few available observations of predation by offshore killer whales and their patterns of behavior and vocal activity, it appears that they are primarily or entirely fish feeders with a probable specialization on sharks (Ford et al. 2000, 2011; Jones 2006; Dahlheim et al. 2008).

In addition to our own long-term studies in British Columbia and Washington State, numerous other researchers have undertaken fieldwork on various aspects of the life history, ecology, and behavior of killer whales, both in our study area and in adjacent coastal waters. Over the years, these efforts have together provided a much improved understanding of the divergent ecological specializations of residents and transients and the role these have played in defining the lifestyles of these lineages.

4.3 Population Delineation of Lineages

Resident, transient, and offshore killer whale lineages are sympatric in coastal waters of the eastern North Pacific from California to the Aleutian Islands in Alaska. Molecular studies have confirmed what earlier observations suggested—that the three lineages are genetically distinct and gene flow between them is minimal or absent (Stevens et al. 1989; Hoelzel et al. 1998; Barrett-Lennard 2000; Morin et al. 2010). At least two of these lineages—residents and transients—are represented by multiple discrete populations of typically a few hundred individuals. Four populations have been described for residents (Matkin et al. 1999; Ford et al. 2000; Matkin et al. 2007a). Each population ranges over roughly 1,300- to

1,800-km sections of coastline that overlap substantially. Despite overlapping distribution, each population generally occupies rather discrete areas, especially during summer and fall. Groups of resident whales from adjacent populations have been observed in close proximity on a few occasions, but no intermingling has taken place. However, groups belonging to the same population frequently join and travel together, occasionally forming large multigroup aggregations that may persist for several days. DNA fingerprinting indicates that mating takes place between groups within each resident population, and intermating between populations is extremely rare (Barrett-Lennard 2000).

Transient killer whales are subdivided into at least five regional populations, each typically composed of 100–300 individuals (Bigg et al. 1987; Black et al. 1997; Ford and Ellis 1999; Matkin et al. 1999, 2007a). Groups of transients within each population regularly intermingle and, in contrast to residents, they will also associate with members of adjacent transient populations during the infrequent occasions when they roam into the range of another population (Ford and Ellis 1999; Ford et al. 2007). Offshore killer whales appear to consist of a single population of at least 250 animals that ranges widely over the continental shelf, from southern California to the eastern Aleutian Islands, Alaska (Ford et al. 2000; Matkin et al. 2007a; Dahlheim et al. 2008). The extent of potential movements beyond the continental shelf for any of these whales is unknown because of the lack of field effort in offshore waters.

4.4 Dietary Specialization

Gaining insight into the feeding habits of free-ranging cetaceans is difficult because predation usually takes place underwater and out of sight. We have studied the diets of resident, transient, and offshore killer whales using three different methods: (1) direct observation of predation when it takes place at the surface, (2) collection of prey fragments left in the water column following a kill, and (3) recovery of prey remains from the stomachs of beach-cast carcasses. Others have also used chemical analyses of skin and blubber biopsy samples collected from killer whales to infer diet from stable isotope ratios, fatty acids, and levels of various types of contaminants (e.g., Krahn et al. 2007).

Surface observations and identification of prey fragments from kills indicate that the diet of resident killer whales in British Columbia (Fig. 4.1) consists primarily of teleost fishes, in particular the Pacific salmonids (*Oncorhynchus* spp.) (Fig. 4.2: Ford et al. 1998; Saulitis et al. 2000; Ford and Ellis 2006). Non-salmonid fishes such as lingcod (*Ophiodon elongatus*), Dover sole (*Microstomus pacificus*), and Pacific halibut (*Hippoglossus stenolepis*) have also been identified from predation events, but these represent less than 3 % of observed kills. A surprising result of our prey fragment sampling has been the pronounced preference that residents have for Chinook salmon (*Oncorhynchus tshawytscha*). In total, more than 70 % of identified salmonid kills have been Chinook, despite this species being one of the least



Fig. 4.1 A male resident killer whale surfaces following capture of a Chinook salmon, the primary prey species of this ecotype. (Photograph by M. Malleeson)

common of the five salmonid species available in the whales' habitat (Ford and Ellis 2006). Chinook predominated in our samples even when other salmonids, such as sockeye (*O. nerka*) and pink (*O. gorbuscha*) salmon, were far more abundant in foraging areas during summer spawning migrations, outnumbering Chinook by as many as 500 fish to 1 (Ford et al. 1998; Ford and Ellis 2006). Chum salmon (*O. keta*) are significant prey during a short period in the fall, but Chinook still appear to be taken preferentially. Prey remains recovered from beach-cast carcasses of residents are generally consistent with our observations of predation. Chinook salmon has been identified in most stomach contents to date, and various non-salmonids and squid have also been represented occasionally (Ford et al. 1998).

It is most probable that the whales' preference for different salmonids—and other prey species for that matter—is proportional to their relative profitability. Chinook are by far the largest of the Pacific salmon, commonly reaching sizes of more than 20 kg, and they tend to have the highest lipid content of the salmonids, enhancing their net energy density. Chum salmon are the second largest salmonid and can reach 10 kg or more. The much smaller sockeye and pink salmon seem to be of little interest to the whales, despite their brief but often great abundance during summer.

In striking contrast to resident killer whales, transient killer whales (Fig. 4.3) have only been observed to hunt and consume endothermic prey, primarily marine mammals and occasionally seabirds. In British Columbia, Washington State, and Southeast Alaska, the most frequent prey species by far (about 50 % of kills) is the harbour seal (*Phoca vitulina*), a small (average, 60–80 kg) pinniped that is common throughout nearshore waters of the region (Fig. 4.2) (Ford et al. 1998; Matkin et al.

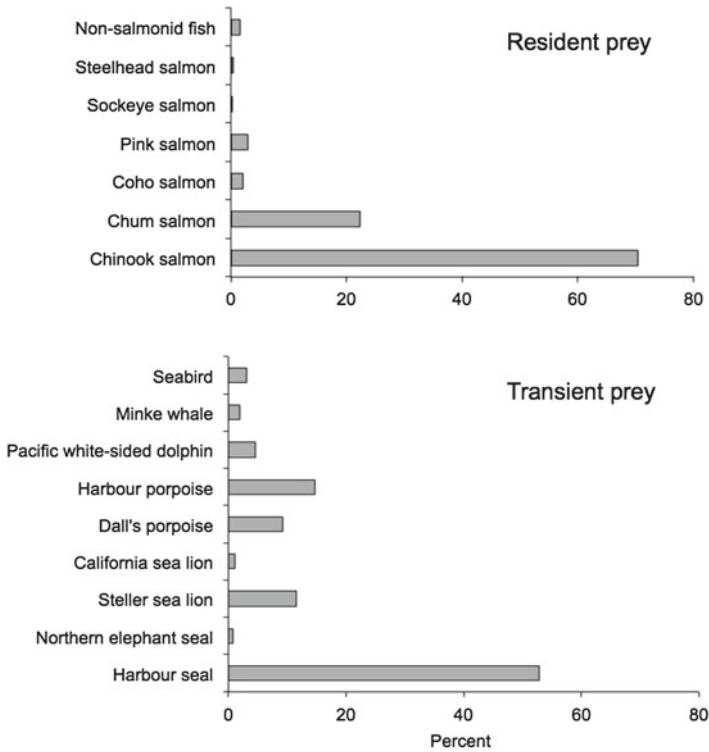


Fig. 4.2 Frequency distribution of prey species observed to be consumed by resident (*top*, $n=439$ kills) and transient (*bottom*, $n=251$ kills) killer whales in coastal waters of British Columbia, Washington State, and southeastern Alaska. [Data from Ford et al. (1998), Ford and Ellis (2006), and Ford and Ellis (unpublished data)]

2007a, b). Harbour porpoise (*Phocoena phocoena*) and Dall’s porpoise (*Phocoenoides dalli*) together make up about one-quarter of observed kills, with the remainder composed of Steller sea lions (*Eumetopias jubatus*), California sea lions (*Zalophus californianus*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), minke whales (*Balaenoptera acutorostrata*), northern elephant seals (*Mirounga angustirostris*), and various seabird species (Ford et al. 1998, 2005). Swimming deer (*Odocoileus hemionus*) and moose (*Alces alces*) have on rare occasions been reported to be killed by killer whales in the region, almost certainly transients (Pike and MacAskie 1969; Matkin et al. 1999). Seabirds do not seem to be an important prey item of transient killer whales. Only a minority of seabirds that are harassed and killed by transients are ultimately consumed: most are abandoned. Interaction with seabirds usually involves juvenile whales and may represent play behavior that ultimately functions to develop prey handling skills (Ford et al. 1998; Saulitis et al. 2000). Transients have not been observed to take any fish species, nor have any fish remains been identified in stomach contents of beach-cast carcasses of transients (Ford et al. 1998; Saulitis et al. 2000; Heise et al. 2003).



Fig. 4.3 A female transient killer whale hunting for the preferred prey of this ecotype, harbour seals. (Photograph by J. Towers)

There is little evidence that transient individuals or matriline specialize on particular types or species of marine mammals, despite the very different tactics needed to capture and kill them (harbour seals versus Dall's porpoise, for example; Ford et al. 1998). Our long-term monitoring of transient predation has shown that the variety of prey species taken by particular individuals or groups is strongly correlated with the cumulative number of predation events documented for those animals (Ford et al. 1998). Predation of minke whales by transients in our study area is uncommon, but a particular matriline (the T18 group) has been involved in more cases than one would expect by chance (Ford et al. 2005; J.K.B.F. and G.M.E., unpublished data). This matriline also hunts more typical prey, such as harbour seals and porpoises. There are no records of transients in our study area having successfully killed large whales such as adult gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*), or blue (*Balaenoptera musculus*) whales. Indeed, foraging transients rarely show any reaction to these potential prey species despite their frequent presence in their vicinity (Jefferson et al. 1991). This indifference is likely related to the difficulty in catching the fast-swimming fin and blue whales and the risk of injury posed by defensive responses from gray and, especially, humpback whales (Ford and Reeves 2008). Gray whale calves and juveniles, however, are frequently targeted by foraging transients in central California (Ternullo and Black 2002) and around the eastern Aleutian Islands, Alaska (Barrett-Lennard et al. 2005; Matkin et al. 2007).

Offshore killer whales are the least known of the three lineages in the region. They have been observed consuming a probable Pacific halibut (Jones 2006) and possibly blue sharks (*Prionace glauca*) and Chinook salmon (Dahlheim et al. 2008).

Stomach contents of a killer whale identified as an offshore by mtDNA analysis included two carcharinid sharks and two opah (*Lampris regius*, a large pelagic teleost fish; Morin et al. 2006). Recently, we observed offshore killer whales feeding on multiple Pacific sleeper sharks (*Somniosus pacificus*) (Ford et al. 2011). A diet consisting largely of sharks, with their abrasive skin, might explain the extreme tooth wear that appears to be common in offshore killer whales (Ford et al. 2011). Stable isotope ratios and fatty acid profiles determined from skin and blubber biopsy samples also suggest that the diet of offshore killer whales is distinct from that of either resident or transient lineages (Herman et al. 2005; Krahn et al. 2007).

4.5 Social Organization

Similar to most delphinids, killer whales are highly social, group-living animals. However, the social structure of resident, transient, and offshore killer whales differs considerably, and these differences appear to be related to and are likely determined by their respective ecological specializations. Resident killer whales live in matrilineal groups that are exceptionally stable in composition. A typical matriline is composed of an older female, her sons and daughters, and the offspring of her daughters. Because longevity of females can reach 80 years and females have their first viable calf at about 14 years (Olesiuk et al. 2005), a matriline may contain as many as four generations of maternally related individuals. More than 30 years of demographic data have demonstrated that dispersal from the matriline is virtually absent in resident killer whales—both males and females remain in their natal group for life (Bigg et al. 1990; Ford et al. 2000; Ellis et al. 2007). In no case has an individual whale been observed to leave its matriline and join another on a long-term basis, other than in a few rare cases involving orphans.

Members of resident matrilineal groups travel together and they seldom separate by more than a few kilometers or for more than a few hours. Contact is maintained among matrilineal members by the exchange of discrete, stereotyped underwater calls that are unique to the group (Ford 1989, 1991; Miller et al. 2004). Matrilineal groups frequently travel in the company of certain other matrilineal groups that are closely related, based on high degrees of call similarity, and likely shared a common maternal ancestor in the recent past. Matrilineal groups that spend the majority of their time together are designated as pods (Bigg et al. 1990). Pods are less stable than matrilineal groups, and member matrilineal groups may spend days or weeks apart. However, matrilineal groups still spend more time with others from their pod than with those from other pods. In British Columbia, resident pods are on average composed of three matrilineal groups (range = 1–11; Ford et al. 2000), with a mean total size of 18 whales (range = 2–49; Ford et al. 2000). Residents often form large temporary aggregations involving multiple matrilineal groups and pods, especially at times when prey densities are high.

A level of social structure above the resident pod is the clan, which is defined by patterns of call similarity. Clans are composed of pods that share a portion of their repertoire of stereotyped calls. Different clans have no calls in common. Pods

belonging to a clan are likely descendants of an ancestral pod, and their acoustic similarities reflect this common heritage. Call repertoires are traditions passed on across generations by vocal learning, and calls actively or passively change in structure or use over time. Calls are retained within the lineage because of the lack of dispersal from matriline. Clans are sympatric, and the two to nine pods that make up each clan frequently travel together as well as with pods from different clans (Ford 1991; Yurk et al. 2002).

Transient killer whale society lacks the closed, strictly matrilineal structure seen in residents. Transients usually travel in groups of two to six individuals, much smaller than the typical size of resident matriline and pods. In contrast to residents, offspring often disperse from the natal matriline for extended periods or permanently (Bigg et al. 1987; 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 groups. These young females usually give birth to their first calf shortly after dispersing. Once dispersed, these females may rejoin their natal matriline occasionally, but generally only for brief periods after they have calves of their own. Male dispersal does take place, but the pattern is less clear because of uncertainty in the status of many individuals in the population. The range of transients appears to extend beyond our study area, possibly into offshore waters, and gaps of many years can occur between sightings of individuals (Ford and Ellis 1999; Ford et al. 2007). There are numerous cases of mothers and a single adult son staying together for decades, but few where a mother and more than one adult son have persisted. Male siblings may disperse from these groups at puberty, but if so they must leave our study area as none has been resighted after disappearing from the natal group, either as a member of another group or as a lone individual. All lone adult males found in the study area appear to have lost their mothers through mortality. These individuals often travel alone or associate with a variety of different transient matriline, but rarely with other lone males. The associations of transient matriline 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 a subregion or portion of the population (Ford 1984; Deecke et al. 2005).

The typically small size of transient groups is likely a result of the foraging strategy of this lineage. Transients generally hunt other marine mammals with stealth: they swim quietly to prevent detection by their acoustically sensitive prey, and attack using the element of surprise (Ford 1984; Barrett-Lennard et al. 1996). 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 harbour seals (Baird and Dill 1996).

As with most details of their life history and behavior, the social organization of offshore killer whales is poorly understood. Their group sizes tend to be relatively large, certainly much larger than those of transients, and possibly larger on average

than residents. Groups of 2 to 100 or more individuals have been documented in encounters with offshores off the coast of British Columbia, with about half involving 20 or more individuals. These larger groups probably represent temporary gatherings of smaller social units, possibly related to prey density as in residents. We have documented persistent bonds lasting more than a decade between females and adult males, which likely represent mothers and their adult sons. However, we have not observed long-term associations between reproductive females, as seen in the multi-generation matriline of residents. This finding suggests a dynamic society with dispersal from the natal matriline as in transients, but frequent formation of larger aggregations as in residents.

4.6 Seasonality and Habitat Use

All three lineages of killer whales are found in coastal waters of the northeastern Pacific throughout the year, but there are significant differences in their seasonality and patterns of habitat use. The seasonal movements of resident killer whales are closely tied to those of their primary prey. Several studies have demonstrated correlations between resident whale occurrence in nearshore waters and the aggregate abundance of multiple salmon species migrating through nearshore waters to coastal spawning rivers in British Columbia and Washington State (Heimlich-Boran 1986; Guinet 1990; Nichol and Shackleton 1996). However, these analyses were undertaken before it was known that these whales forage selectively for Chinook salmon and shun the smaller but much more abundant pink and sockeye salmon (Ford et al. 1998; Ford and Ellis 2006). Correlations of whale occurrence with these abundant salmonids are thus incidental, and the whales are instead attracted by migrating Chinook salmon, which pass through these migratory corridors in lower numbers but concurrently with the smaller species. Movements of resident killer whales in this area during October and November are clearly associated with fall migrating chum salmon, which the whales do consume (Nichol and Shackleton 1996; Ford and Ellis 2006). Interestingly, a different population of resident killer whales in south-central Alaska moves into Prince William Sound during midsummer, where they forage extensively for coho salmon (*Oncorhynchus kisutch*) (Saulitis et al. 2000). Neither Chinook nor chum salmon are common in this area at this time of year, although these same whales feed on Chinook and chum salmon in other areas and times of year (C. Matkin, personal communication).

During winter and spring, resident whales mostly vacate their summer habitat in nearshore waters and appear to range widely along the outer exposed coast. It is likely that the whales maintain their focus on Chinook salmon prey during this time of year. Most other salmonid species are pelagic and unavailable to the whales during this time of year, but nonmigratory or early spawning runs of Chinook are found in these outer coast waters (Ford and Ellis 2006). Residents may also increase their consumption of non-salmonid species such as Pacific halibut during winter and spring.

Compared to residents, transient killer whales have a relatively uniform pattern of occurrence in nearshore waters throughout the year, likely because their primary prey species—harbour seal, harbour porpoise, Dall’s porpoise, and Steller sea lion—are nonmigratory and available in all months of the year. However, there is an interesting seasonal peak in local occurrence along the west coast of North America that appears to coincide with the pupping season of harbour seals. In Glacier Bay, the northern limit of the range of the so-called “West Coast” transient population ($\sim 58^{\circ}30'N$ latitude), transient whale occurrence peaks in June and July (Matkin et al. 2007). Near the southern extent of their range, around Vancouver Island ($\sim 48^{\circ}$ to $51^{\circ}N$ latitude), there is an obvious peak in occurrence during August and September (Baird and Dill 1995). Both these periods coincide with local peaks of pupping and weaning of harbour seals, which exhibits a latitudinal cline in timing along the West Coast (Temte et al. 1991). Pups are likely easy and abundant prey for transients, and the whales appear to move in accordance with their seasonal availability.

Offshore killer whales appear to exhibit a diffuse seasonal shift in distribution along the West Coast of North America. The majority of sightings in the southern portion of their known range, off central and south California, have been recorded during fall and winter (September to March; Dahlheim et al. 2008). Sightings in Alaska, the northern portion of the range of offshore killer whales, have taken place only during April to September, but there is minimal observer effort during winter in this area (Dahlheim et al. 2008; C. Matkin, personal communication). Off British Columbia, roughly the latitudinal midpoint of their range, sightings of offshores have been recorded in all months. Without a better understanding of the primary prey species of offshore killer whales, it is not possible to interpret the significance of this apparent seasonal distribution shift.

Differences are also apparent in finer-scale patterns of habitat use by the three killer whale lineages. Residents congregate during summer and fall in core feeding areas in locations where geography and tidal currents act to concentrate migratory salmon (Heimlich-Boran 1988; Nichol and Shackleton 1996; Saulitis et al. 2000; Ford 2006). During the peak of salmon abundance, the majority of matriline in a resident population may gather in these core areas, and individual matrilines or pods may spend weeks in a relatively restricted area that the whales could transit in a day or two. There are distinctions among the movement patterns of different resident pods within a population’s overall range. Although most resident groups may be observed in most parts of the range, particular pods and matrilines have preferred areas that they frequent more often than other groups (Osborne 1999; Ford 1991, 2006; Ford et al. 2000; Hauser et al. 2007), likely because of the benefit of foraging in familiar areas where individuals have experience in locating local concentrations of prey.

While in their core summer feeding areas, resident killer whales spend 50–65 % of their time foraging (Heimlich-Boran 1988; Ford 1989; Morton 1990). Between foraging bouts, the whales group together and socialize or rest, which together represent about 30–40 % of their time. In at least two resident populations, the whales may also spend considerable time rubbing their bodies on certain

shelving, pebble beaches that have been used traditionally for many years (Ford 1989; Matkin et al. 1999).

In contrast to resident whales, transient killer whales typically do not remain for long in any particular location. They are almost constantly on the move, swimming from one prey hotspot to the next. Because of their apparent reliance on stealth for capturing marine mammals, it is no doubt more productive for transients to hunt elsewhere once potential prey is alert to their presence. By covering 75–150 km of coastline per day, transients tend to undergo more frequent extensive travel throughout their range than do residents. Nonetheless, as with residents, at least some transient groups have preferred areas within the overall population range, where local knowledge of the location of pinniped haulouts or predictable concentrations of small cetaceans may serve to improve hunting efficiency (Ford and Ellis 1999). Compared to residents, transients dedicate considerably more time to foraging and traveling (>75 % of their activity budget: Morton 1990; Baird and Dill 1995). Socializing and resting activities, which comprise about one-third of the activity budget for residents, are seldom exhibited by transients (<10 % of activities; Morton 1990; Baird and Dill 1995; Barrett-Lennard et al. 1996; Deecke et al. 2005). Beach rubbing has not been reported for transients.

Details of habitat use by offshore killer whales are not yet clear because of the comparatively infrequent encounters with this population. Long-distance movements appear to be undertaken frequently by offshore whales. Several identified individuals have been observed at the extremities of the population's known range, which extends more than 4,000 km from the Aleutian Islands to Southern California (Dahlheim et al. 2008). Any potential habitats that may be used preferentially by a subset of the offshore population, and what prey species may drive their movements, have yet to be described.

4.7 Foraging Behavior

The distinct diets of killer whale lineages are associated with corresponding contrasts in their foraging behavior. When foraging, members of a resident killer whale matriline or pod spread out, often over areas of several square kilometers, with individuals or small subgroups diving and surfacing independently while swimming generally in the same direction. They maintain contact and likely coordinate movements through the frequent exchange of loud underwater calls, which are effective to ranges of 10–25 km (Ford 1989; Miller et al. 2004; Miller 2006). When foraging in coastal inlets, channels, and straits, individuals and small maternal groups usually forage along the shoreline, while other whales, particularly mature males, forage alone farther from shore and in deeper water. Foraging resident whales dive for 2–3 min (Ford 1989; Morton 1990) to depths typically less than 30 m, but occasionally to more than 150 m (Baird et al. 2005a). These depths are similar to those used by their primary prey species, Chinook salmon (Candy and Quinn 1999).

Foraging resident killer whales find prey using echolocation, which may be effective for detecting Chinook salmon at ranges of 100 m or more (Au et al. 2004). By foraging in loosely dispersed groups, the detection rate of scattered salmon is likely enhanced. However, residents whales do not appear to cooperatively herd or capture prey. Rather, prey capture is undertaken primarily by individuals with occasional cooperation from offspring, siblings, or other close matrilineal kin. The majority of salmonid prey items captured by adult females and subadults are brought to the surface, where they are broken up for sharing within the matriline or for provisioning young offspring (Ford and Ellis 2006). Adult males usually capture and consume salmonid prey alone.

In contrast to residents, transient killer whales forage in near silence in an apparent attempt to minimize detection by their acoustically sensitive marine mammal prey (Ford 1984; Morton 1990; Barrett-Lennard et al. 1996; Deecke et al. 2005). Transients rarely exchange underwater calls while hunting for prey (Deecke et al. 2005), and echolocation click production is also greatly suppressed (Barrett-Lennard et al. 1996). Both pinniped and cetacean prey have excellent hearing abilities at the frequencies used by killer whales for calling and echolocation and could detect and potentially evade approaching transients if they were to vocalize (Barrett-Lennard et al. 1996; Deecke et al. 2005). As vocalizing would likely incur high costs in terms of reduced rates of prey capture, transients appear to depend on passive listening to detect and approach prey from a distance, likely cueing on the animals' vocalizations or swimming noises (Barrett-Lennard and Heise 2006). There is little cost associated with the production of underwater sounds for resident whales because salmonids and most other fish have relatively low hearing sensitivity to such frequencies and are unlikely to detect approaching whales at a distance (Barrett-Lennard et al. 1996; Deecke et al. 2005).

Transient killer whales employ two fairly distinct modes of foraging: nearshore and open water. When foraging nearshore, the whales swim in relatively tight groups and follow the contour of the shoreline, round headlands, and enter bays without hesitation (Morton 1990; Barrett-Lennard et al. 1996). They often circle small islets and reefs, particularly those that serve as pinniped haulouts. Resident whales, in contrast, forage along more direct routes, usually swimming from headland to headland. Dive durations of foraging transient whales are typically twice the duration of the 2- to 3-min dives of residents, and may exceed 10 min (Morton 1990). Nearshore foraging is generally associated with capture of pinniped prey, particularly harbour seals (Baird and Dill 1995; Barrett-Lennard et al. 1996; Saulitis et al. 2000). When foraging in open water, transient groups spread out over a larger area, with individuals swimming several hundred meters apart, often roughly abreast. Most prey captured during open water foraging are porpoises or dolphins, but seals or sea lions may also be taken (Barrett-Lennard et al. 1996; Saulitis et al. 2000).

Transients share the majority of their prey (Baird and Dill 1995), likely to an even greater extent than do residents because of the larger body masses of most marine mammal prey items. Transient group members frequently use cooperative hunting tactics to catch and subdue their prey (Baird and Dill 1995; Ford et al. 1998). Predation on Steller sea lions, for example, can be extended events that

may entail risk of injury to the attacking whales. These prey can be large (up to 1,000 kg in males) with sizeable canine teeth that can inflict significant wounds during defensive or retaliatory actions. Groups of transient killer whales attack single sea lions in open water by circling the animal so as to prevent it from reaching shore, while individuals take turns rushing toward the prey and ramming it or striking it with their tail flukes. This action may continue for 1–2 h until the animal is sufficiently debilitated so that it can be safely grasped, drowned, and shared among group members. Transients may also hunt fast-swimming Dall's porpoise using a cooperative "tag team" tactic where individuals take turns chasing the prey animal to exhaustion. Transients have been also observed to herd groups of 50+ Pacific white-sided dolphins into confined or shallow bays where individuals can be readily captured. Transients hunt these difficult-to-capture species in significantly larger groups than when foraging for the smaller harbour seals (Ford et al. 1998). These groups often represent temporary associations of smaller, stable social units.

4.8 Acoustic Communication

As do most delphinids, killer whales have a well-developed acoustic communication system. However, as noted earlier, the types and extent of vocalization show major differences among lineages. Resident killer whales frequently exchange strident calls from stable repertoires of a dozen or more call types. These learned call types or their variants are specific to clans, pods, and matriline, and thus encode the matrilineal genealogy of individuals (Ford 1991). This specificity likely enhances the effectiveness of these calls as intragroup contact signals, especially when whales are dispersed and traveling in association with other matriline or pods. These group-specific dialects may also play a role as a behavioral mechanism to prevent inbreeding. As there is no dispersal from the natal matriline, resident killer whales would be at considerable risk of inbreeding without a reliable means of distinguishing between kin and non-kin mating partners. Group-specific call repertoires appear to serve such a function (Ford 1991), and genetic studies have shown that resident whales mate with individuals that are outside the pod or clan and are acoustically dissimilar (Barrett-Lennard 2000).

Although transient killer whales spend much of their time foraging for marine mammals in silence, they become highly vocal while attacking and consuming their prey (Ford 1984; Deecke et al. 2005). Calling at such times likely carries little cost as stealth is no longer needed, and it may help coordinate cooperative attack tactics within the group or serve other social functions after the kill is made. Similar to resident killer whales, transients have repertoires of distinctive stereotyped call types. Unlike residents, however, these repertoires generally do not differ among groups. As there is dispersal from the natal matriline in this ecotype, 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.

The fish-eating offshore killer whales are as vocal as resident killer whales. Preliminary analyses indicate that offshores produce stereotyped calls that are distinct from any of those of residents or transients, but it is not yet known whether any calls are specific to particular groups. As our understanding of the social dynamics of this poorly known lineage improves, patterns of call use should become clearer.

4.9 Specializations in Other Regions

Field studies in other global regions have provided additional evidence that ecological specializations are typical of most killer whale populations. Although these populations are not as well known as resident and transients in the eastern North Pacific, it is apparent that at least in some cases their specializations have had similar influences on patterns of social structure, behavior, and vocal activity. Off the northern coast of Norway, a population of killer whales moves seasonally in relation to their primary prey, the Atlantic herring (*Clupea harengus*) (Similä 1997). In coastal fjords where herring congregate in high densities during fall and winter, 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. Once the school is concentrated, individuals dive under the school and strike it with their tail flukes. Fish stunned directly by the physical blow from the flukes or the associated loud cavitation sound are then eaten individually (Similä and Ugarte 1993; Simon et al. 2005). These herring-eating killer whales appear to live in matrilineally organized pods similar in size to those of fish-feeding resident killer whales, but it is not known whether they share the same extreme stability (Similä 1997). They are highly vocal and have pod-specific call repertoires as observed in resident killer whales (Strager 1995), which would suggest a stable pod structure.

In the Strait of Gibraltar, a small population of killer whales appears to specialize on predation of bluefin tuna (*Thunnus thynnus*) as the fishes enter and exit the Mediterranean Sea during their breeding migration (Reeves and Notarbartolo di Sciara 2006). To catch these swift tuna, the whales employ an endurance-exhaustion technique involving protracted chases at swimming speeds of 12–14 km/h for periods of 30–40 min (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.

On the coast of Patagonia, Argentina, a small population of killer whales uses a novel, but risky, hunting technique that involves intentional stranding in the shallows to capture young southern sea lions (*Otaria flavescens*) and southern elephant seals (*Mirounga leonina*) at the water’s edge (Lopez and Lopez 1985). Whales hunt cooperatively and share their prey with others in the group (Hoelzel 1991). A similar beaching tactic is used by killer whales in the sub-Antarctic Crozet Islands when hunting southern elephant seal pups (Guinet 1992). As do mammal-hunting transients in the northeastern Pacific, whales in both these Southern Hemisphere

locations have small group sizes, hunt mostly in silence, and appear to locate prey by passive listening (Guinet 1992; J.K.B.F., unpublished data).

Three distinct forms of killer whales—known as types A, B, and C—have been described in circumpolar waters of the Antarctic (Pitman and Ensor 2003). These sympatric forms differ in pigmentation patterns, genetic structure (mtDNA sequences), patterns of habitat use, and diet (Pitman and Ensor 2003; Krahn et al. 2008; LeDuc et al. 2008). Type A killer whales are found mostly in ice-free waters where they apparently feed mainly on cetaceans, particularly Antarctic minke whales (*Balaenoptera bonaerensis*). Type B whales forage primarily in loose pack ice and appear to specialize on seals. These whales exhibit a novel hunting tactic in which group members coordinate their swimming movements to create a large wave that washes seals off ice floes (Visser et al. 2008). Type C whales inhabit dense pack ice and appear to be fish feeders, having been observed preying on Antarctic toothfish (*Dissostichus mawsoni*) (Pitman and Ensor 2003; Krahn et al. 2008). They are substantially smaller than other Antarctic killer whales, with adults approximately 1–3 m shorter in length than type A individuals (Pitman et al. 2007). Type C whales tend to have larger group sizes than mammal-hunting types A and B, which is consistent with the pattern of group sizes versus prey type in the northeastern Pacific. Unfortunately, too little is known about these Antarctic ecotypes to determine whether ecological specialization has influenced their social structure, behavior, and acoustics in ways similar to those of lineages in other regions.

4.10 Conclusions

The killer whale is a highly versatile social predator that has evolved to successfully occupy a variety of specialized ecological niches in the world's oceans. In so doing, this species has assumed a variety of distinct lifestyles that have been shaped by these ecological specializations. In the eastern North Pacific, the three killer whale lineages have distinct patterns of seasonal distribution, group size, social organization, foraging behavior, and acoustic activity, which can be related to their preferred type of prey and the strategies the animals use to acquire it. Some similar patterns are apparent among killer whales in other regions, although a lack of field data prevents a more complete assessment of the parallels between ecotype and life history or behavior for these populations.

Although different killer whale lineages may be genetically distinct, there is no evidence that dietary preferences result from any genetic predisposition. Globally, there is no congruence between killer whale ecotype and genotype (Hoelzel et al. 2002; LeDuc et al. 2008). Instead, ecological specializations appear to represent behavioral traditions that likely evolved independently in different regions. It is plausible that ecological divergence could arise in sympatry with, for example, the innovation of a novel foraging tactic in a particular matriline that allowed predation on a new type of prey. If this matriline and its descendants became further specialized on this prey type, rates of association with other groups that do not adopt this

new diet may diminish over time, leading to social segregation and reproductive isolation. Such a process could lead ultimately to speciation. Resident and transient killer whale lineages in the northeastern Pacific have been suggested to represent incipient species (Baird et al. 1992) and Antarctic type A, B, and C killer whales to represent distinct species (LeDuc et al. 2008).

There are still many questions concerning ecological specialization in killer whales that remain to be answered. For example, to what extent might specializations constrain a lineage's ability to switch to alternative prey species in a changing environment? The preferences for fish and marine mammal prey exhibited by resident and transient killer whales, respectively, are extremely strong, and there is no evidence that one ecotype ever switches to the prey type of the other or has the behavioral flexibility to do so. Marine mammals in coastal waters of the northeastern Pacific can discriminate between lineages and will flee from transients but show indifference to residents (Ford and Ellis 1999; Deecke et al. 2002), suggesting that if residents ever hunt marine mammals, it must occur extremely rarely. The suite of specialized behaviors that make resident killer whales adept at locating and catching Chinook salmon likely would be ineffective for hunting marine mammals. Transients would similarly be ill equipped to adopt a fish-feeding lifestyle.

The extent of dietary flexibility of killer whales has implications for their potential role in driving marine ecosystem dynamics. It has been proposed that a shift to sea otter predation by mammal-hunting killer whales in the Aleutian Islands resulted in a precipitous decline in sea otter abundance that started in the mid-1980s (Estes et al. 1998). This shift is thought to be a response to reduced availability of the whale's presumed primary prey in the region, harbour seals and Steller sea lions. In an extension of this hypothesis, Springer et al. (2003) postulated that the decline of sea otters was the last in a series of population collapses of prey species of mammal-hunting killer whales in the northern Gulf of Alaska that was triggered by the decimation of the great whales by industrial whaling in the nineteenth and twentieth centuries. This hypothesis has been challenged on various grounds (Trites et al. 2007; Wade et al. 2007), particularly because there is no evidence that the great whales (especially adults) have ever played an important role in the diet of killer whales (Mizroch and Rice 2006; Ford and Reeves 2008). Although it may be possible that predation by killer whales could result in depletion of targeted prey species, dietary specializations could have significant constraints on the directions that subsequent prey shifts may take.

To date, most ecologically specialized killer whale populations, including sympatric fish-eating and mammal-eating ecotypes, have been described in highly productive cold temperate or polar waters, likely the result of the diversity of abundant prey types available in these high latitudes, which has provided the opportunity for niche partitioning. It may well be that killer whales in less productive tropical or subtropical waters are generalist predators that include a greater variety of prey in their diets (Baird et al. 2005b). For example, a high incidence of killer whale teeth scars on humpback whales using breeding grounds off the west coast of Mexico suggests that predation in this area, especially on calves, may be extensive (Steiger et al. 2008). This prey resource is seasonal, however, as humpbacks only occupy

these breeding grounds for 3 to 5 months in winter. Because there is no evidence that killer whales follow migrating humpback whale mothers and calves to their high-latitude feeding grounds, it is likely that the predators shift to alternative prey species for the remainder of the year.

Globally, killer whales form a mosaic of distinct populations, some overlapping and others geographically discrete, that are ecologically specialized to greater or lesser degrees. Each population is likely to have foraging tactics, activity patterns, social organization, and acoustic behavior that have been shaped by its dietary specialty. Highly specialized populations can be expected to have lifestyles that are closely adapted to their foraging strategy, whereas more generalist populations may be relatively less constrained by any particular prey type. In certain regions, such as the northeastern Pacific, some parts of this mosaic are becoming fairly clear. In other regions, such as the Antarctic, a fascinating picture is emerging but significant knowledge gaps remain to be filled. In regions where killer whales are little studied, such as in sparsely inhabited tropical waters, there is much yet to be discovered. Only when all the components of this global mosaic of killer whale populations have been described will we have a complete appreciation of the range of ecological specializations and lifestyles of this multifaceted and resourceful predator.

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