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FORAGING STRATEGIES OF SYMPATRIC KILLER WHALE (*ORCINUS ORCA*) POPULATIONS IN PRINCE WILLIAM SOUND, ALASKA

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ABSTRACT

Killer whales (*Orcinus orca*) feed on a wide variety of fish, cephalopods, and marine mammals throughout their cosmopolitan range; however, the dietary breadth that characterizes the species is not reflected in all populations. Here, we present the findings of a 14-yr study of the diet and feeding habits of killer whales in Prince William Sound, Alaska. Two non-associating forms of killer whale, termed *resident* and *transient* (Bigg *et al.* 1987), were identified. All prey seen taken by transients were marine mammals, including harbor seals (*Phoca vitulina*), Dall's porpoises (*Phocoenoides dalli*), Steller sea lions (*Eumetopias jubatus*), and harbor porpoises (*Phocoena phocoena*). Resident killer whales appeared to prey principally on salmon (*Oncorhynchus* spp.), preferring coho salmon (*O. kisutch*) over other, more abundant salmon species. Pacific herring (*Clupea pallasi*) and Pacific halibut (*Hippocampus stenolepis*) were also taken. Resident killer whales frequently were seen to interact in non-predatory ways with Steller sea lions and Dall's porpoises, while transients were not. Differences in the social organization and behavior of the resident and transient killer whales in Prince William Sound are discussed in the light of the dietary differences documented here.

Key words: killer whales, *Orcinus orca*, Prince William Sound, foraging, predation, behavior.

Killer whales (*Orcinus orca*) have been reported to feed on nearly every marine mammal species available to them throughout their cosmopolitan range (Hoyt 1984, Jefferson *et al.* 1991, Matkin and Saulitis 1994). Off the British Columbia and Washington State coasts, they have been observed to feed on 23 species of fish and squid (Ford *et al.* 1998). Once thought to be opportunistic predators (*e.g.*, Rice 1968), recent findings suggest that some killer whale populations exhibit dietary specializations. Two sympatric, non-associating killer whale populations, known as *resident* and *transient*, have been identified off British Columbia and Washington State (Bigg *et al.* 1987) and southeastern Alaska (Dahlheim *et al.* 1997). Resident killer whales in those regions feed exclusively on fish and squid; transients feed exclusively on mammals and occasionally take sea birds (Ford *et al.* 1998). The two forms also differ in seasonal distribution, social structure, behavior, and mitochondrial and nuclear DNA (Bigg *et al.* 1987, Stevens *et al.* 1989, Morton 1990, Hoelzel and Dover 1991, Hoelzel *et al.* 1998).

Two sympatric, non-associating forms of killer whale have also been identified in Prince William Sound, Alaska (Ellis 1987, Heise *et al.* 1992). These forms conform closely in behavioral characteristics to those identified off British Columbia (Bigg *et al.* 1987, Morton 1990, Ford *et al.* 1994). Although killer whales off British Columbia and Prince William Sound appear to belong to discrete populations (Matkin and Saulitis 1994, Matkin *et al.* 1997), the terms resident and transient have been applied to the Prince William Sound populations because of clear behavioral and dietary similarities (Ellis 1987, Heise *et al.* 1992).

At least three populations of killer whales, two of the transient type and one of the resident type, have been proposed for Prince William Sound based on DNA analysis (LB-L, unpublished data), social characteristics (Saulitis 1993, Matkin and Saulitis 1994) and acoustics (Saulitis 1993; Barrett-Lennard *et al.* 1996; ES, unpublished data). Prince William Sound resident killer whales travel in social groups called pods, containing 7–36 related individuals (Matkin *et al.* 1994, in press.). As is the case for British Columbian resident pods (Bigg *et al.* 1990), Prince William Sound resident pods exhibit long-term stability, with no immigration or emigration of members (Matkin *et al.*, in press). The minimum estimate of resident killer whales using Prince William Sound and adjacent waters was 446 in 1997 (Matkin *et al.* 1998). Of these, 202 individuals in nine pods are considered regular visitors (Matkin *et al.*, in press).

Residents use Prince William Sound waters most frequently during July, August, and September (Matkin *et al.* 1997), although they appear to make occasional visits to the area year-round (Matkin *et al.* 1998). Prince William Sound residents have been sighted as far west as Kodiak Island (Matkin *et al.* 1997). While residents most commonly seen in southeastern Alaska have been seen in the Sound, Prince William Sound residents have not been documented east of the Sound (Matkin *et al.* 1997).

At least two separate assemblages of transient killer whales use Prince Wil-

liam Sound, both of which consist of small groups that are more fluid in size and individual membership than are the resident pods (Matkin *et al.* 1994). The first assemblage, known as the AT1s, typically travels in groups of two to four individuals but occasionally travels singly or in groups of ten or more individuals (Saulitis 1993). In 1997 the AT1 transient assemblage contained 11 individuals (Matkin *et al.* 1998).

A second assemblage of transient killer whales occasionally enters Prince William Sound. These animals have not been seen associating with the AT1 transients (Matkin and Saulitis 1994) and differ from them in mitochondrial DNA sequences (LB-L, unpublished data) and acoustic characteristics (ES, unpublished data). This assemblage is referred to here as the Gulf of Alaska transients.

Members of the AT1 transient assemblage have been sighted year-round in Prince William Sound (Matkin and Saulitis 1994) and in Resurrection and Aialik Bays, west of Prince William Sound (Matkin *et al.* 1998). The Gulf of Alaska transients are seen infrequently in Prince William Sound; their range is unknown, though they have been seen as far west as Kodiak Island (unpublished data).

Potential marine mammal prey in Prince William Sound are Dall's porpoises (*Phocoenoides dalli*), harbor porpoises (*Phocoena phocoena*), humpback (*Megaptera novaeangliae*), minke (*Balaenoptera acutorostrata*), and gray (*Eschrichtius robustus*) whales, harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), and river (*Lutra canadensis*) and sea (*Enhydra lutris*) otters (Hood and Zimmerman 1986). Pacific herring (*Clupea pallasi*) and five species of Pacific salmon (*Oncorhynchus* spp.) are found in Prince William Sound, as are various bottom fish species, including Pacific halibut (*Hippocampus stenolepis*) and sablefish (*Anoplopoma fimbria*) (Hood and Zimmerman 1986).

In this paper we present fourteen years of data on the diet of resident and transient killer whales in Prince William Sound, Alaska, and compare our findings to those described for residents and transients of British Columbia. Finally, we discuss differences in social organization and behavior of resident and transient killer whales in Prince William Sound in light of their dietary specializations.

MATERIALS AND METHODS

Dietary and behavioral data were gathered concurrently with census data collected for a yearly killer whale population monitoring program in Prince William Sound from 1984 to 1996 (Matkin *et al.* 1998). The study area was approximately 3,500 km². Most effort was concentrated in the western part of the Sound (Fig. 1). All observations were made at sea from boats ranging in size from 4.7 to 12.8 m from late March through October.

Although months spent in the field varied among years, data collection occurred during July and August in all years of the study. Killer whales were located by visual searches, acoustic detection, and by responding to sighting reports from mariners.
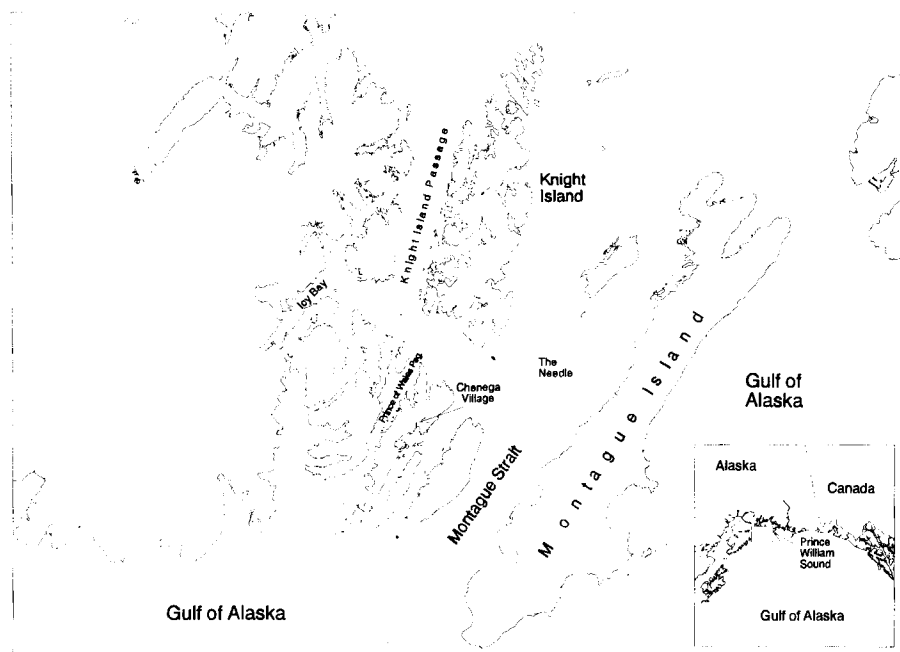
Figure 1. Study area in southwestern Prince William Sound, Alaska.

Killer whales were identified visually and from photographs taken of the left-side dorsal fin and saddle patch of each individual present using the method of photo-identification developed by Bigg *et al.* (1986). Individual resident killer whales were assigned to pods by analysis of association patterns among whales (Ellis 1987; Heise *et al.* 1992; Matkin *et al.,* in press). Because of their fluid group membership, transient killer whales were not assigned to pods.

Behavioral observations were made on a continuous basis by scanning the activities of the entire group (scan sampling; Altmann 1974). The beginning and end times of activity states and descriptions of the whales' specific behaviors, including evidence of predation, were recorded. The whales' behavior was categorized into four activity states: foraging, resting, traveling, and socializing (Dunbar 1988). These states were first defined for killer whales by Ford (1989) and have since been modified and used by Morton (1990), Felleman *et al.* (1991), and Barrett-Lennard *et al.* (1996), among others. In this study, the categories were defined as follows:

Socializing—Engaged in behaviors such as chasing, rolling, and aerial displays (*e.g.,* Jacobsen 1986) not related to feeding. Aerial displays included breaching, spy-hopping, and fluke- and flipper-slapping. Sexual behavior, indicated by erect penises, was also considered socializing. During socializing, vocal activity was high.

Foraging—Engaged in search for, pursuit, capture, and consumption of prey. Fish foraging was indicated by echolocation (Barrett-Lennard *et al.* 1996) and sporadic tight circling and lunging by individual whales (Ford 1989, Hoelzel

1993). During fish foraging, the whales were widely dispersed, either singly or in small groups (Barrett-Lennard et al. 1996). Marine mammal foraging was indicated when whales swam individually or in small groups close to shore, entering bays and circling islets (Saulitis 1993, Baird and Dill 1995) or when they milled and slowly traveled through areas of open water in a widely dispersed formation without echolocation (Saulitis 1993, Barrett-Lennard et al. 1996).

Traveling—Swimming in a line-abreast pattern in one or more groups, moving in a consistent direction at speeds of over 6 km/h (Barrett-Lennard et al. 1996). Individuals typically swam within a few body lengths of their neighbors.

Resting—Movements and breathing patterns closely synchronized and moving at speeds much slower than those of traveling whales (<4 km/h) (Ford 1989, Barrett-Lennard et al. 1996). Resting whales were commonly grouped in maternal units (Matkin et al., in press). Individuals typically surfaced within a single body length of their neighbors (Barrett-Lennard et al. 1996).

During behavioral scans, the presence of potential prey in the vicinity of killer whales was noted, and the number, species, and behavior of potential prey animals was described. Non-predatory interactions with killer whales were defined as occasions when potential prey animals chased, followed, or intermingled with killer whales without a predatory response by the whales. Harassment was indicated when potential prey animals exhibited an avoidance or alarm response in the presence of nearby killer whales, when killer whales chased, followed, or lunged at potential prey without making a kill, or when, following an attack, a kill was suspected but could not be confirmed.

Marine mammal kills were confirmed by observations of marine mammal parts in the whales' mouths, bits of blubber, skin, viscera, hair, and/or blood in the water, and/or oil slicks in the vicinity of milling whales. The species identity of marine mammal prey was usually determined during observations of attacks and chases. Fish predation was confirmed by observations of fish in the whales' mouths or fish scales in the water at the kill site.

When successful predation was suspected, an observer on the research vessel's bow scanned the area and retrieved fish scales or other prey fragments using a long handled dip-net. Scale samples were identified to species at the Fish Aging Laboratory, Pacific Biological Station, Nanaimo, BC.

Separate activity budgets were developed for residents and transients based on data from 1988 to 1996. These budgets were compared using contingency analysis (Zar 1984).

RESULTS

The data presented here represent 662 encounters with killer whales from 1984 to 1996, 196 of which were with transients and 466 with residents. Of the transient encounters, 174 were with AT1 transients and 22 with Gulf of Alaska transients. Residents and transients were never seen together in the

Table 1. Percentage of time spent in each activity state for resident and transient killer whales in Prince William Sound, Alaska, 1988–1996, based on 1,914 h of observation of residents and 515 h of observation of transients. Proportion of time spent in each state differed significantly between two whale types (contingency test, chi-square = 11.97; df = 3; $P < 0.01$).

	Rest	Travel	Forage	Socialize
Transient	4.1	38.5	50.0	7.4
Resident	17.6	35.2	35.5	11.7

same encounter. Behavioral data were collected during 2,429 h of observation, 515 with transients and 1,914 with residents.

Resident and transient behavioral budgets were significantly different (Table 1). Transients spent more time foraging and less time resting than residents. Residents and transients both spent the majority of their time traveling and foraging.

Foraging behaviors were distinctly different, depending upon whether the whales were hunting for mammals nearshore, hunting for mammals offshore, or searching for fish. We described these three types of behaviors as follows:

Open water foraging for mammals—Whales generally farther than 1 km offshore. When hunting at the surface, they milled or traveled slowly, and movements of individual whales were not synchronized. The whales traveled for a km or more beneath the surface at times, often during dives of 10 min or longer duration. When prey was detected, often a coordinated chase involving all whales in the group ensued, and prey was shared among group members. All porpoise kills occurred during open-water foraging.

Nearshore foraging for mammals—Whales generally remained within 20 m of shore, entering bays and narrow passages, and circling islets. Individuals typically separated from one another, traveling along different parts of the shoreline. All but three harbor seal kills occurred during nearshore foraging.

Foraging for fish—Only residents were observed foraging for fish. During this type of foraging, echolocation clicks were heard, and the whales were often dispersed over several square km. When foraging for salmon, chases often occurred at the surface and were indicated by tight circling and lunges by individual whales.

Only transient killer whales were seen foraging for marine mammals. Thirty-one marine mammal kills by transient killer whales were documented. Transients preyed almost exclusively upon Dall's porpoises and harbor seals (Table 2). Only one other species, the harbor porpoise, was documented as prey. Most of the unidentified marine mammals preyed upon by killer whales ($n = 7$) were described as unidentified porpoises ($n = 4$); the remaining prey items were unidentified marine mammals ($n = 2$) or unidentified pinnipeds ($n = 1$).

Most harbor seal kills ($n = 11$) occurred beneath the water's surface and were detected by the appearance of blubber fragments and oil on the surface. Consequently, it was not possible to determine how long these attacks lasted.

Table 2.   Diet of transient killer whales in Prince William Sound, Alaska based on thirty-one documented kills, April–October, 1984–1996.

Prey species	# Killed
Dall's porpoise	12
Harbor seal	10
Harbor porpoise	2
Unidentified mammal	7
Total	31

Sea birds were often observed investigating kill sites. In contrast, highly visible surface chases were noted during Dall's porpoise kills. These attacks lasted up to 43 min. Transients spent 22.2% of their time nearshore foraging and 27.8% of their time offshore foraging, suggesting that they spent a slightly higher percentage of time hunting for Dall's porpoises than for harbor seals.

Forty-three harassments of marine mammals by transient killer whales were documented (Table 3). Transient killer whales were never observed preying on fish; however, in one instance, an AT1 individual chased a salmon beneath the research vessel. Most harassments were of Steller sea lions ($n = 14$) and harbor seals ($n = 12$). Of the 14 Steller sea lion harassments, 4 were by AT1 transients and 10 by Gulf of Alaska transients. All harbor seal kills and harassments documented in this study were made by AT1 transients.

On 11 occasions, two individuals of the Gulf of Alaska transient population were observed near a Steller sea lion haul-out on the Needle, a rocky islet in Prince William Sound (Fig. 1). The sea lions were harassed during each of these observations; however, no kills were observed.

Sixty-three scale samples were collected from fish kills made by resident killer whales in five years of the study (1991–1992; 1994–1996). Ninety-four percent of the samples were from coho salmon (*O. kisutch*) (Table 4). The rest of the samples were from chinook (*O. tshawytscha*) and chum (*O. keta*) salmon. Twelve samples were collected from unidentified resident whales. About half of the scale samples ($n = 29$) were collected in August. On 38 occasions,

Table 3.   Number of harassments of potential prey by AT1 and Gulf of Alaska (GOA) transients in Prince William Sound, Alaska, 1984–1996.

Species	AT1 transients	GOA transients	Total
Harbor seal	12	0	12
Dall's porpoise	4	2	6
Steller sea lion	4	10	14
Humpback whale	6	0	6
Sea otter	2	1	3
River otter	1	0	1
Salmon	1	0	1
Total	30	13	43

Table 4. Salmon species preyed on by resident killer whales in Prince William Sound, July–September, 1991–1996 based on analysis of sixty-three scale samples collected from individual killer whales (41 photographically identified; 10 identified to pod; 12 unknown) representing seven pods.

Pod	# Coho	# Chinook	# Chum	Total
AB	14	0	0	14
AN	2	1	0	3
AI	3	0	0	3
AE	20	0	0	20
AJ	4	0	0	4
AK	3	0	2	5
AD	1	1	0	2
Unknown	12	0	0	12
Total	59	2	2	63

predation on fish by resident killer whales was observed but scale samples were not collected. Thirty-six of these kills were of salmon, one was of herring, and one was of halibut.

Resident killer whales interacted non-aggressively with marine mammals on 66 occasions, 47 of which involved Dall's porpoises and 16 involved Steller sea lions. Interactions with a humpback whale and with a minke whale were each documented once. The minke whale swam among resident killer whales for more than three hours. On one occasion, a sea otter swimming among resident killer whales appeared agitated and rolled itself into a tight ball; the whales ignored it. Dall's porpoises were observed swimming with resident killer whales, engaging in apparent play behaviors with killer whale calves, and surfacing rapidly just in front of killer whales, sometimes making physical contact. One recognizable Dall's porpoise remained with the AB resident pod from May through September in 1984. Steller sea lions interacted with residents on 13 occasions by surfacing among them, porpoising towards them or by nipping at them. Interactions occurred during all four general killer whale activity states and involved all resident pods.

DISCUSSION

This study confirmed that resident and transient killer whales in Prince William Sound exhibited distinct dietary preferences, as Ford *et al.* (1994, 1998) found in residents and transients off British Columbia and Washington State. Transients in Prince William Sound were observed feeding exclusively on marine mammals, while residents were observed feeding exclusively on fish. Despite their sympatric distributions, the two forms did not associate.

The stomach contents of five killer whale carcasses recovered in or near Prince William Sound reflect the same pattern of feeding segregation (Barrett-Lennard *et al.* 1995; KH, unpublished data). Likewise, for carcasses found off British Columbia, no stomachs that contained mammal remains also contained fish remains (Ford *et al.* 1998). Stomach content analyses from other regions

also indicate dietary preferences for either fish or mammals (Betesheva 1961; Berzin and Vladimirov 1983).

Although transient killer whales in Prince William Sound prey almost equally on harbor seals and Dall's porpoises, off British Columbia and southeastern Alaska, harbor seals are clearly preferred over other prey species. Ford *et al.* (1998) reported that 67% of observed kills by British Columbian and southeastern Alaskan transients were of harbor seals, while only six percent were of Dall's porpoises. Baird (1994) reported that over 95% of observed transient kills off southern Vancouver Island were of harbor seals. Dall's porpoise attacks were more prolongued and vigorous than those of harbor seals. In our study, they lasted up to 43 min and involved high speed chases and aerial leaps. Dall's porpoise attacks have lower success rates (39%; Ford *et al.* 1998) than harbor seal attacks (90%–100%; Baird 1994, Ford *et al.* 1998).

Low harbor seal numbers may account for the fact that Prince William Sound transients consistently prey on a species more difficult to capture than harbor seals. Harbor seal counts during the molting season in the Gulf of Alaska and Aleutian Islands declined by 19% from 1989 to 1995 (Hill *et al.* 1997). Harbor seals in Prince William Sound declined by 60% from 1984 to 1996 (Frost *et al.* 1997). The most recent population estimate of harbor seals in Prince William Sound is 5,300 (Frost *et al.* 1997). In contrast, harbor seal numbers in British Columbia, southeastern Alaska and Washington State have been increasing at 12% per year since 1970 (Olesiuk *et al.* 1990).

Most dietary observations during this study were made during the summer months. Transient feeding behavior may change seasonally, as prey availability changes. For example, juvenile Steller sea lions become more abundant in Prince William Sound with the arrival of herring in early spring.[1] Observers have documented transient killer whales preying upon Steller sea lions during that time (Barrett-Lennard *et al.* 1995; KH, unpublished data). Barrett-Lennard *et al.* (1995) estimated that Steller sea lions make up 15% of the diet of transient killer whales in Alaska. Steller sea lions make up 7% of kills by transient killer whales off British Columbia, Washington State, and southeastern Alaska (Ford *et al.* 1998).

Our results suggest, however, that Steller sea lion predation may be more common for Gulf of Alaska transients than it is for AT1 transients. Gulf of Alaska transients harassed Steller sea lions more frequently than did AT1 transients (Table 3). A Gulf of Alaska transient carcass contained 14 Steller sea lion tags, while neither of two carcasses identified as AT1 transients contained sea lion remains (LB-L, unpublished data; Barrett-Lennard *et al.* 1995). Gulf of Alaska transients were observed killing Steller sea lions in northern Prince William Sound (Barrett-Lennard *et al.* 1995). Despite the fact that AT1 transients were observed far more frequently than were Gulf of Alaska tran-

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[1] Personal communications from Richard Corcoran, Prince William Sound Aquaculture Corporation, Cordova, AK 99574, July 1996; Dean Rand, Discovery Charters, Box 1500, Cordova, AK 99574, April 1995.

sients, AT1 transients were never seen foraging around Steller sea lion haulouts or attacking or preying upon Steller sea lions.

Steller sea lion predation may involve considerable risks to killer whales due to the large size and aggressive nature of adult sea lions. Off British Columbia and Alaska, Steller sea lion attacks often last for 1–2.5 h before the prey is killed (Baird and Dill 1995, Barrett-Lennard *et al.* 1995, Ford *et al.* 1998). Steller sea lions were observed charging toward both resident and transient killer whales in this study. Specialization on a particular prey species such as the Steller sea lion may develop when successful capture requires highly developed hunting skills and involves substantial risk to the whales. For example, killer whale calves off the Crozet Archipelago learn from their mothers the technique of intentional stranding to capture pinnipeds, a sophisticated and apparently high-risk behavior (Guinet and Bouvier 1995).

Transient killer whales off British Columbia and southeastern Alaska occasionally harass and prey upon sea birds (Ford *et al.* 1998), while this behavior has never been observed in Prince William Sound. Because sea bird predation primarily involves subadult whales and is unlikely to provide a significant food source (Ford *et al.* 1998), it has been suggested to function as a means of developing hunting skills in juveniles (Matkin and Dahlheim 1995, Ford *et al.* 1998). The AT1 transient assemblage contains no juveniles or calves for which such training would be advantageous. Additionally, sea bird predation may simply reflect a regional cultural difference between the two populations.

Data on harassments of marine mammals by killer whales suggest that the diet of Prince William Sound transient killer whales is more diverse than indicated by observed kills alone and may reflect their potential year-round diet. In addition to observed harassments (Table 3), there have been reliable reports of killer whales attacking humpback whales in Prince William Sound.[2] Harbor porpoises may also make up a larger percentage of the transient killer whale diet than is reflected in our data, since very little field effort occurred during times of harbor porpoise abundance (early spring; CM, ES, personal observations). Fifteen percent of kills by transient killer whales off British Columbia, Washington State, and southeastern Alaska were of harbor porpoises (Ford *et al.* 1998).

Prince William Sound resident killer whales exhibited a strong selectivity for coho salmon during July and August. Coho salmon are present, feeding in nearshore waters, from May through December,[3] and may provide a consistent food source for most of the year.

In British Columbian waters, however, similar methods yielded few samples of coho scales, even though coho are more abundant there than in Prince William Sound (Ford *et al.* 1998). There, resident killer whales feed preferentially on chinook salmon, which are the largest and most energy-rich of the

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[2] Personal communications from Nancy Naslund, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Ankorage, AK 99501, June 1994; Paul Kompkoff, Chenega Bay, AK 99574, June 1995, (commercial fisherman).

[3] Personal communication from Slim Morstad, Alaksa Department of Fish and Game, Cordova, AK 99574, December 1998.

five Pacific salmon species (Ford *et al.* 1998). In British Columbia chinook salmon are a year-round prey source for residents (Ford *et al.* 1998).

Seasonal bias may account for the small number of chinook scales in our sample. Chinook salmon are rare in southwestern Prince William Sound during July and August,[3] when most of our scale samples were collected. The presence of any chinook salmon scales in this sample is therefore significant. In May and June large runs of chinook salmon enter the Copper River Delta adjacent to Prince William Sound, and commercial fisherman report frequent killer whale sightings off the Copper River during that time,[4] while few resident pods are encountered in Prince William Sound during the same months. Chinook salmon are present in Prince William Sound in late fall and winter.[3]

Sockeye salmon contain the second highest amount of fat of the five Pacific salmon species (Sidwell 1981, Exler 1987). Although they are available from May through July in Prince William Sound, no sockeye predation was documented in this study. Off British Columbia and Washington State, sockeye salmon make up only 3% of documented kills (Ford *et al.* 1998).

Pink salmon are the smallest and lowest in fat content of the five Pacific salmon species (Exler 1987, Sidwell 1981). While they comprised 15% of scale samples collected at sites of killer whale predation off British Columbia and Washington State (Ford *et al.* 1998), there was no pink salmon predation documented in Prince William Sound, despite extremely large returns of pink salmon. A bias against the collection of pink salmon scales may exist since the scales are much smaller than those of other species and may be more difficult to observe in the water. We feel that this bias is not sufficient, however, to account for the complete absence of pink salmon scales in our sample and believe that coho salmon are preferentially selected over pink salmon when both species are present.

Our data may reflect only those fish kills that were made near the surface. Data on resident killer whale interactions with the Prince William Sound commercial longline fishery indicate that killer whales exhibit prey selectivity for particular bottom fishes (Matkin and Saulitis 1994). Resident killer whales selectively remove sablefish and halibut from longline gear while leaving Pacific cod (*Hippoglossus stenolepis*) and other bottom fish species untouched.

While direct comparisons among activity budgets of killer whales from different areas are not feasible due to observer bias and variations in definitions of behavioral categories, the overall trends in differences between residents and transients in Prince William Sound are similar to those observed off British Columbia and Washington State (Ford 1989, Morton 1990, Baird 1994, Felleman *et al.* 1991). Transients forage and travel more than residents, and residents socialize and rest more than transients. In the case of both residents and transients, traveling and foraging behavior are difficult to distinguish, and may, in fact, overlap in function. Most killer whale activity during foraging

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[4] Personal communication from Dan Bilderback, P. O. Box 734, Cordova, AK 99574, September 1997, (commercial fisherman).

and traveling occurs beneath the water's surface. In all areas where they have been studied, residents spend 58%–72% of their time traveling and foraging, while transients spend between 88.5%–94.5% of their time traveling and foraging (Ford 1989, Morton 1990, Baird 1994, Felleman *et al.* 1991, this study).

Different prey choices among populations of killer whales are accompanied by different foraging strategies and social structure. For example, killer whales off both Argentina and the Crozet Archipelago in the southern Indian Ocean, have adopted the technique of intentional stranding in order to capture pinnipeds at haul-out sites (Lopez and Lopez 1985, Hoelzel 1991, Guinet and Bouvier 1995). Other odontocete species exhibit considerable intraspecific variability in hunting techniques, group size and social organization. Bottlenose dolphins (*Tursiops truncatus*) exist in nearshore and offshore forms in most parts of their range and have been found to adapt their foraging techniques to a wide range of prey types (Shane *et al.* 1986, Bel'kovich *et al.* 1991). The results of this study provide further evidence that sympatric killer whale populations with different dietary preferences exhibit different social organizations and behavioral strategies.

The extent of behavioral flexibility in hunting strategies within local populations of killer whales is unknown. Most studies are carried out during spring, summer, and fall, when killer whales are seen predictably in an area and are feeding on seasonally abundant prey. Little is known of killer whale feeding behavior when they leave these more easily accessible areas or when winter weather precludes observational research.

The AT1 population's use of two distinct foraging strategies to hunt harbor seals and Dall's porpoises exhibits behavioral flexibility, as does the resident killer whales' exploitation of bottom fish available on commercial longline gear. Specializations may be expressed seasonally or when particular prey species in an area are abundant and reliably encountered. The decline in Steller sea lion and harbor seal numbers in the Gulf of Alaska may result in killer whales using different strategies to exploit alternative species such as sea otters in the Aleutian Islands (Hatfield *et al.* 1998, Estes *et al.* 1998).

The flexibility in the foraging behavior of killer whales, however, appears to be limited. There is no evidence that transients switch to fish feeding and residents switch to mammal feeding, even seasonally. The differing reactions of potential marine mammal prey species to resident and transient killer whales provide further evidence that feeding preferences for fish and mammals are maintained. The radically different strategies employed in fish-foraging and in mammal-foraging may limit behavioral flexibility and maintain the dietary specializations of residents and transients. For example, the specialized hunting techniques required for salmon feeding, including refinement of echo-location ability (Barrett-Lennard *et al.* 1996) and learning of prey avoidance responses, are clearly different than those required for hunting marine mammals. The same factors that promote hunting success for fishes may decrease hunting success for marine mammals. For instance, large group sizes of resident killer whales may enhance hunting success for salmon, through the shar-

ing of echolocation information over wide areas to locate patchily distributed salmon schools (Barrett-Lennard *et al.* 1996), while small group sizes may enhance the hunting success of transients, which depend upon stealth to capture marine mammal prey (Baird and Dill 1996). Passive listening, rather than echolocation, may be employed in the detection of prey by transients (Saulitis 1993, Barrett-Lennard *et al.* 1996). Switching between foraging tactics may also be prohibited by the extent of learning required to efficiently master each hunting technique (Baird *et al.* 1992).

While distinct fish-eating and mammal-eating populations of killer whales appear to be a common feature in the North Pacific and in other regions such as Antarctica (Berzin and Vladimirov 1983), it can be expected that populations of killer whales in each area have developed hunting tactics and dietary specializations that reflect the local distribution, abundance, and predictability of resources.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49: 227–265.

BAIRD, R. W. 1994. Foraging behaviour and ecology of transient killer whales (*Orcinus orca*). Ph.D. thesis, Simon Fraser University, Vancouver, British Columbia. 157 pp.

BAIRD, R. W., AND L. M. DILL. 1995. Occurrence and behavior of transient killer whales: Seasonal and pod-specific variability, foraging behavior, and prey handling. Canadian Journal of Zoology 73:1300–1311.

BAIRD, R. W., AND L. M. DILL. 1996. Ecological and social determinants of group size in transient killer whales. Behavioral Ecology 7:408–416.

BAIRD, R. W., P. A. ABRAMS AND L. M. DILL. 1992. Possible indirect interactions between transient and resident killer whales: Implications for the evolution of foraging specializations in the genus *Orcinus*. Oecologia 89:125–132.

BARRETT-LENNARD, L. G., K. HEISE, E. SAULITIS, G. ELLIS AND C. MATKIN. 1995. The impact of killer whale predation on Steller sea lion populations in British Columbia and Alaska. Unpublished report. Available from North Pacific Universities Marine Mammal Research Consortium, University of British Columbia, Vancouver, British Columbia.

BARRETT-LENNARD, L. G., J. K. B. FORD AND K. A. HEISE. 1996. The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. Animal Behavior 51:553–565.

BEL'KOVICH, V. M., A. V. AGAFONOV, O. V. YEFREMENKOVA, L. B. KOZAROVITSKY AND S. P. KHARITONOV. 1991. Searching and hunting behavior in the bottlenose dolphin (*Tursiops truncatus*) in the Black Sea. Pages 38–77 *in* K. Pryor and K. S. Norris, eds. Dolphin societies: Discoveries and puzzles. University of California Press, Berkeley, CA.

BERZIN, A. A., AND V. L. VLADIMIROV. 1983. A new species of killer whale (Cetacea, Delphinidae) from Antarctic waters. Zoolologicheskiy Zhurnal 62:287–295 (in Russian).

BETESHEVA, E. I. 1961. Pitanie promyslovykh kitov Prikuril'skogo raiona (Food of commercial whales in the Kuril region). Trudy Instituta Morfologiya Zhivotnykh Akademiya Nauk SSSR 34:7–32. In Russian. (Abstract translated *in* Biological Abstracts 43:469).

BIGG, M. A., G. M. ELLIS AND K. C. BALCOMB III. 1986. The photographic identification of individual cetaceans. Whalewatcher: Journal of the American Cetacean Society 20:10–12.

BIGG, M. A., G. M. ELLIS, J. K. B. FORD AND K. C. BALCOMB III. 1987. Killer whales: A study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press, Nanaimo, BC.

BIGG, M. A., P. F. OLESIUK, G. M. ELLIS, J. K. B. FORD AND K. C. BALCOMB III. 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 (Special Issue 12):386–406.

DAHLHEIM, M. E., D. K. ELLIFRIT AND J. D. SWENSON. 1997. Killer whales of Southeast Alaska: A catalogue of photo-identified individuals. Marine Mammal Laboratory, Alaska Fisheries Center, NMFS, NOAA, Seattle, WA. 79 pp.

DUNBAR, R. I. M. 1988. Primate social systems. Comstock Publishing Associates, Ithaca, NY.

ELLIS, G. 1987. Killer whales of Prince William Sound and Southeast Alaska: A catalogue of individuals photoidentified, 1976–1986. Hubbs Sea World Research Institute Technical Report 87-200, San Diego, CA. 76 pp.

ESTES, J. A., M. T. TINKER, T. M. WILLIAMS AND D. F. DOAK. 1998. Killer whale predation on sea otters links oceanic and nearshore ecosystems. Science 282:473–476.

EXLER, J. 1987. Composition of foods: Finfish and shellfish products. U.S. Dept. Agriculture Handbook 8–15.

FELLEMAN, F. L., J. R. HEIMLICH-BORAN AND R. OSBORNE. 1991. The feeding ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. Pages 113–147 *in* K. Pryor and K. S. Norris, eds. Dolphin societies: Discoveries and puzzles. University of California Press, Berkeley, CA.

FORD, J. K. B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67:727–745.

FORD, J. K. B., G. M. ELLIS AND K. C. BALCOMB III. 1994. Killer whales: The natural history and genealogy of *Orcinus orca* in the waters of British Columbia and Washington State. University of British Columbia Press, Vancouver, BC.

FORD, J. K. B., G. M. ELLIS, L. G. BARRETT-LENNARD, A. B. MORTON, R. S. PALM AND K. C. BALCOMB III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

FROST, K. J., L. F. LOWRY, J. M. VERHOEF AND S. J. IVERSON. 1997. Monitoring, habitat use, and trophic interactions of harbor seals in Prince William Sound. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 95064). Available from Alaska Department of Fish and Game, Division Wildlife Conservation, Fairbanks, AK.

GUINET, C., AND J. BOUVIER. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. Canadian Journal of Zoology 73:27–33.

HATFIELD, B. B., D. MARKS, M. T. TINKER, K. NOLAN AND J. PIERCE. 1998. Attacks on sea otters by killer whales. Marine Mammal Science 14:888–894.

HEISE, K., G. ELLIS AND C. MATKIN. 1992. A catalogue of Prince William Sound killer whales, 1991. North Gulf Oceanic Society, Homer, AK.

HILL, P. S., D. P. DEMASTER AND R. J. SMALL. 1997. Alaskan marine mammal stock assessments, 1996. NOAA Technical Memorandum NMFS-PFSC-78. 150 pp.

HOELZEL, A. R. 1991. Killer whale predation on marine mammals at Punta Norte, Argentina: Food sharing, provisioning and foraging strategy. Behavioural Ecology and Sociobiology 29:197–204.

HOELZEL, A. R. 1993. Foraging behavior and social group dynamics in Puget Sound killer whales. Animal Behavior 45:581–591.

HOELZEL, A. R., AND G. A. DOVER. 1991. Genetic differentiation between sympatric killer whale populations. Heredity 66:191–195.

HOELZEL, A. R., M. E. DAHLHEIM AND S. J. STERN. 1998. Genetic variation among killer whales (*Orcinus orca*) in the eastern North Pacific, and genetic differentiation between foraging specialists. Journal of Heredity 89:121–128.

HOOD, D. W., AND S. T. ZIMMERMAN. 1986. The Gulf of Alaska: Physical and biological resources. OCS Study MMS 86–0095. 655 pp. Available from NTIS, U.S. Department of Commerce, Springfield, VA 22161.

HOYT, E. 1984. Orca, the whale called killer. Camden House, Ontario.

JACOBSON, J. K. 1986. The behavior of *Orcinus orca* in Johnstone Strait, British Columbia. Pages 135–185 *in* B. C. Kirkevold and J. S. Lockard, eds. Behavioral biology of killer whales. Alan Liss, Inc., New York, NY.

JEFFERSON, T. A., P. J. STACEY AND R. W. BAIRD. 1991. A review of killer whale interactions with other marine mammals: Predation to co-existence. Mammal Review 22:151–180.

LOPEZ, J. C., AND D. LOPEZ. 1985. Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. Journal of Mammalogy 66:181–183.

MATKIN, C. O., AND E. SAULITIS. 1994. Killer whale (*Orcinus orca*): Biology and management in Alaska. Unpublished report. Available from U.S. Marine Mammal Commission, 1825 Connecticut Avenue, Washington, DC 20009.

MATKIN, C. O., G. ELLIS, M. DAHLHEIM AND J. ZEH. 1994. Status of killer whales in Prince William Sound, 1984–1992. Pages 141–162 *in* T. Loughlin, ed. Marine mammals and the *Exxon Valdez*. Academic Press, San Diego, CA.

MATKIN, C. O., D. MATKIN, G. M. ELLIS, E. SAULITIS AND D. MCSWEENEY. 1997. Movements of resident killer whales between southeastern Alaska and Prince William Sound, Alaska. Marine Mammal Science 13:469–475.

MATKIN, C. O., D. SCHEEL, G. ELLIS, L. BARRETT-LENNARD, H. JURK AND E. SAULITIS. 1998. Annual report of the comprehensive killer whale investigation. Unpublished report to EVOS Trustee Council. 59 pp. Available from Exxon Valdez Oil Spill Trustee Council, 641 G Street, Suite 401, Anchorage, AK 99501.

MATKIN, C. O., G. ELLIS, P. OLESIUK AND E. SAULITIS. In press. Association patterns and inferred genealogies of resident killer whales (*Orcinus orca*) in Prince William Sound, Alaska. Fishery Bulletin, U.S.

MATKIN, D. R., AND M. E. DAHLHEIM. 1995. Feeding behaviors of killer whales in northern southeastern Alaska. Pages 246–253 *in* D. R. Engstrom, ed. Proceedings of the Third Glacier Bay Symposium, 1993. National Park Service, Anchorage, AK.

MORTON, A. B. 1990. A quantitative comparison of the behavior of resident and transient forms of killer whale off the central British Columbia coast. Report of the International Whaling Commission (Special Issue 12):245–248.

OLESIUK, P. F., M. A. BIGG AND G. M. ELLIS. 1990. Recent trends in the abundance of harbour seals, *Phoca vitulina,* in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 47:992–1003.

RICE, D. W. 1968. Stomach contents and feeding behavior of killer whales in the eastern North Pacific. Norsk Hvalfangst-Tidende 57:35–38.

SAULITIS, E. 1993. The behavior and vocalizations of the AT group of transient killer whales in Prince William Sound, Alaska. M.S. thesis, University of Alaska, Fairbanks, AK. 193 pp.

SHANE, S. H., R. S. WELL AND B. WÜRSIG. 1986. Ecology, behavior and social organization of the bottlenose dolphin: A review. Marine Mammal Science 2:23–63.

SIDWELL, V. D. 1981. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks and their products. NOAA Technical Memorandum NMFS F/SEC-11. 432 pp.

STEVENS, T. A., D. A. DUFFIELD, E. D. ASPER, K. G. HEWLETT, A. BOLZ, L. J. GAGE AND G. D. BOSSART. 1989. Preliminary findings of restriction fragment differences in mitochondrial DNA among killer whales (*Orcinus orca*). Canadian Journal of Zoology 67:2592–2595.

ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.