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Examining the evidence for killer whale predation on Steller sea lions in British Columbia and Alaska

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Abstract

The discovery of flipper tags from 14 Steller sea lions (*Eumetopias jubatus*) in the stomach of a dead killer whale (*Orcinus orca*) in 1992 focused attention on the possible role of killer whale predation in the decline of Steller sea lions in western Alaska. In this study, mariners in British Columbia and Alaska were surveyed to determine the frequency and outcome of observed attacks on sea lions, the age classes of sea lions taken, and the areas where predatory attacks occurred. The 126 survey respondents described 492 killer whale/sea lion interactions, of which at least 32 were fatal attacks on the sea lion. The greatest rate of observed predation occurred in the Aleutian Islands. The stomach contents of dead and stranded whales also were examined. Stomachs that were not empty contained only fish or marine mammal remains, but not both. This supports earlier evidence of dietary segregation between fish-eating *resident* and marine mammal-eating *transient* killer whales in Alaska. Steller sea lion remains were found in two of 12 killer whale stomachs examined from Alaska between 1990 and 2001. Stomach contents from two *offshore* killer whales provided the first direct evidence that this third form of killer whale feeds on fish.

Key words: Steller sea lions, *Eumetopias jubatus*, killer whales, *Orcinus orca*, predation, stomach contents, harbour seals, Alaska, British Columbia, questionnaire.

Introduction

Since 1980, the Steller sea lion (*Eumetopias jubatus*) population in the Aleutian Islands and the Gulf of Alaska has declined by 80% (Trites & Larkin, 1996, Ferrero *et al*., 2000). In 1992, a killer whale (*Orcinus orca*) was discovered with tags from 14 Steller sea lions in its stomach. This, combined with other recent work indicating that killer whales could be responsible for the decline of sea otters over large areas of western Alaska (Estes *et al*., 1998), prompted an examination of the evidence for killer whale predation on Steller sea lions. We used two methods to examine this question: an analysis of the stomach contents of dead killer whales, and a questionnaire survey of mariners who had the opportunity to observe interactions between sea lions and killer whales.

Killer whales

Killer whales often have been described as opportunistic predators (Dahlheim, 1981, Matkin & Leatherwood, 1986). In the last twenty years; however, long-term study of killer whale populations in various geographical areas has changed this view. One of the most significant findings has been that populations are specific in their choice of prey and foraging strategies (Baird, 1994; Barrett-Lennard *et al*., 1996; Saulitis, 1993; Saulitis *et al*., 2000). Long-term studies in the eastern North Pacific have led to the identification of fish-eating *resident* and mammal-eating *transient* killer whales (Bigg *et al*., 1987; Ford *et al*., 1994, 1998, 2000; Ford & Ellis, 1999; Matkin & Saulitis, 1994; Matkin *et al*., 1999; Barrett-Lennard & Ellis, 2001). Genetic analyses has revealed that in Alaskan waters there are at least two subpopulations of resident killer whale (northern British Columbia residents and Alaska residents) and three subpopulations of transient killer whale (Gulf of Alaska transients, west coast transients and AT1 transients, Barrett-Lennard & Ellis, 2001). The AT1 transients are found primarily around Prince William Sound and Kenai Fjords and number approximately 11 animals (Matkin *et al*., 1999). The west coast transients range between California and southeast Alaska and over 200 have been identified in the waters between Washington and Alaska (Ford & Ellis, 1999).

Approximately 60 Gulf of Alaska transients have been identified (Ford & Ellis, 1999), although this number is expected to increase as a result of current research effort in the area (Barrett-Lennard, unpublished data). A third poorly-known population of at least 200 killer whales, referred to as *offshores* has also been identified (Ford *et al*., 2000; Barrett-Lennard & Ellis 2001). Their range is not known, and their diet is thought to include fish because they travel in large groups and are acoustically active.

In this study, we report on the stomach contents recovered from 12 killer whales in Alaska from 1990 to 2001. Opportunities to examine killer whale stomach contents occur relatively infrequently, perhaps partly due to low mortality rates (annual mortality rates for resident killer whales range from 0.011/year for adult females to 0.039/year for adult males, Olesiuk *et al*., 1990). In addition, killer whale carcasses generally sink (Zenkovich, 1938). From 1973 to 2000 in British Columbia, only 24 killer whale carcasses were recovered, of which eight were neonates (Olesiuk *et al*., 1990; Barrett-Lennard, unpublished data), although approximately 167 resident whales and an unknown number of transients died over this same period (Ford *et al*., 2000). To date, stomach contents have only been recovered from one known transient in British Columbia (Ford *et al*., 1998, Barrett-Lennard unpublished data).

Steller sea lions

There are two genetically distinct populations of Steller sea lions in the eastern North Pacific (Bickham *et al*., 1996). The eastern population is found from California to Cape Suckling (144°W, Fig. 1) and generally has been increasing (Trites & Larkin 1996, Calkins *et al*., 1999). The western Alaskan population, which has shown a dramatic decline over the past 30 years (Loughlin *et al*., 1992; Trites & Larkin, 1996; Sease *et al*., 2001) is found west of Cape Suckling. Numerous hypotheses have been advanced to explain the decline, including shooting or entanglement (Trites & Larkin, 1996), reduction in the quantity or quality of food (Trites & Larkin, 1992, Castellini, 1993; Merrick *et al*., 1997; Rosen & Trites, 2000), disease and parasites (Spraker *et al*.,1993), and an overall decline in the carrying capacity of the Bering Sea (National Research Council, 1996; Trites *et al*., 1999). It is also possible that predation may have caused the decline, although prior to this study this hypothesis received little attention.

Observations of attacks on and kills of sea lions by killer whales have been documented throughout Alaska and British Columbia (e.g., Tomilin, 1957; Rice, 1968; Harbo 1975; Ford & Ellis, 1999), and killer whale predation on otariids (eared seals) is commonly reported in other parts of the world (e.g., Lopez & Lopez, 1985; Guinet, 1991; Hoelzel; 1991). However, data have not been systematically collected on killer whale predation on Steller sea lions. In this study, we surveyed mariners to obtain information on the frequency with which killer whales and sea lions were observed in proximity, the outcome of observed attacks on sea lions, the age classes of sea lions taken and the areas where predatory-type attacks were observed. We used this information or 'ecological knowledge' (Huntington, 2000) as a method of acquiring information on the extent to which killer whales prey on Steller sea lions.

Materials and Methods

Stomach contents

The stomach contents of 12 killer whales stranded in Alaska between 1990 and 2001 were examined for fragments of prey that could be identified to species. Species identifications were confirmed by Pacific Identifications Inc. of Victoria, B.C. the late Francis (Bud) Fay (University of Alaska, Fairbanks), Elaine Humphries (University of British Columbia, Vancouver) and William A. Walker (Natural History Museum of Los Angeles County, Los Angeles). We attempted to identify each dead killer whale using photographs from previously published catalogues (Bigg *et al*., 1987; Dahlheim *et al*., 1997; Ford *et al*., 1994, 2000; Ford & Ellis, 1999; Heise *et al*., 1992; Matkin *et al*., 1999) and from unpublished photographs held by the Pacific Biological Station (PBS), Department of Fisheries and Oceans, Nanaimo, B.C. and the North Gulf Oceanic Society, Homer, Alaska. Genetic analyses were successful on seven of the 12 killer whale carcasses following methods described in Barrett-Lennard (2000), to determine whether the whales were from the resident, transient, or offshore population. The minimum number of pinniped prey was calculated by counting the number of teeth, claws, and whiskers recovered. We estimated a minimum of 70 whiskers (>5 cm long) per animal for both harbour seals (*Phoca vitulina*) and sea lions, based on specimens held by PBS and whisker counts published in Scammon (1874).

Mariner's survey

We distributed a four-page questionnaire in 1993 and 1994 to approximately 250 mariners in British Columbia and Alaska, including researchers, commercial fishermen, and tour boat operators. The results of those surveys were compiled to produce an account of the number of interactions observed between sea lions and killer whales relative to the

Table 1. Stomach contents of killer whales from Alaska (Area: PWS=Prince William Sound; SEA=Southeast Alaska, AK=Alaska).

Year	Area	Population*	Stomach Contents
Known transient and/or whale with stomach containing marine mammal remains			
1990[1]	Culross Island PWS	AT 1 Transient (G) male	Bones, whiskers and hair from adult and juvenile harbour seal, 1 Dall's porpoise dorsal fin.
1990[2]	Beartrap Bay, PWS	AT 1 Transient (G,P)	Empty.
1991[2]	Cape St. Elias Gulf of AK	?	Sub-adult sea lion including skull, harbour seal, Dall's porpoise skull.
1992[3]	Montague Island PWS	G of AK Transient (G)	15 Steller sea lion tags, 480 sea lion whiskers, harbour seal claws (8 hind, 6 fore) and 20 harbour seal whiskers, bullet, halibut hook, 29 small & 27 large sea lion claws.
1993[4]	Cook Inlet AK	?	Regurgitated 1 harbour seal flipper and beluga skin and blubber while stranded.
2000[5]	Orca Inlet PWS	AT 1 Transient (G,P)	At least 3 harbour seals, (1 adult female, 1 male, 1 pup female), three harbour seal flipper tags (from 1 adult female and 1 pup).
2001[5]	Hinchinbrook Island PWS	?	Harbour seal flipper, fur and claws from at least 2 harbour seals, bull kelp (*Nereocystis*) (over 6 kg).
2001[6]	Izembeck Lagoon Bering Sea	?	Bird feathers (4), harbour seal (fur, 2 claws and 1 whisker), river otter bones and fur, sand and small rocks.
Known offshore whales			
1994[7]	Barnes Lake SEA	Offshore male (G,P)	Crab shell, sculpin and eel grass.
1994[7]	Barnes Lake SEA	Offshore female (G,P)	Salmonid bones.
Known resident whale			
1991[1]	Montague Island PWS	Resident (G)	2 circle hooks with gangion and stainless steel snap, small pieces of plastic.
Unkown whale			
1993[8]	St Pauls Island Bering Sea	(unknown young male)	500 g bull kelp, 1 very large squid or medium sized octopus beak, 1 medium sized squid beak, 1 common murre.

*Method of determining population identity in brackets: G=genetic analysis. P=Photo-identification. In the case of genetic identification it was possible to determine if the whale was a Gulf of Alaska transient (G of AK) or an AT transient (as per Matkin *et al*., 1999).

Sources:

1. Kathy Heise and Lance Barrett-Lennard (University of British Columbia, Dept. of Zoology, Vancouver, B.C. V6T 1Z4).
2. Kate Wynne (Alaska Sea Grant Program, 118 Trident Way, Kodiak Island, AK 99615).
3. Eva Saulitis (North Gulf Oceanic Society, 60920 Mary Allen Ave., Homer, AK 99603).
4. David Bain (Six Flags Marine World, Vallejo, California 94589).
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6. Donna Willoya and Liana Jack (Alaska Sea Otter and Steller Sea Lion Commission, 6239 B St#204, Anchorage, AK 99518).
7. David Bain (address above) and Rich Ferrero (National Marine Mammal Lab, NMFS, Seattle, WA 98115).
8. Alan Springer and Mike Williams (University of Alaska, Fairbanks, AK 99775).

total time mariners spent on the water. We asked mariners who witnessed interactions between sea lions and killer whales to describe their observations, including details on the number of animals involved, the age class of the sea lions, the locations where interactions were observed, and the length of time the interactions lasted. We did not solicit information on interactions between killer whales and other marine mammal species. Interactions between killer whales and sea lions were separated into two categories: predatory and non-predatory. A non-predatory interaction was one in which killer whales and sea lions were observed swimming in close proximity with no sign of aggression by the killer whales towards the sea lions. A predatory interaction involved the killer whales behaving

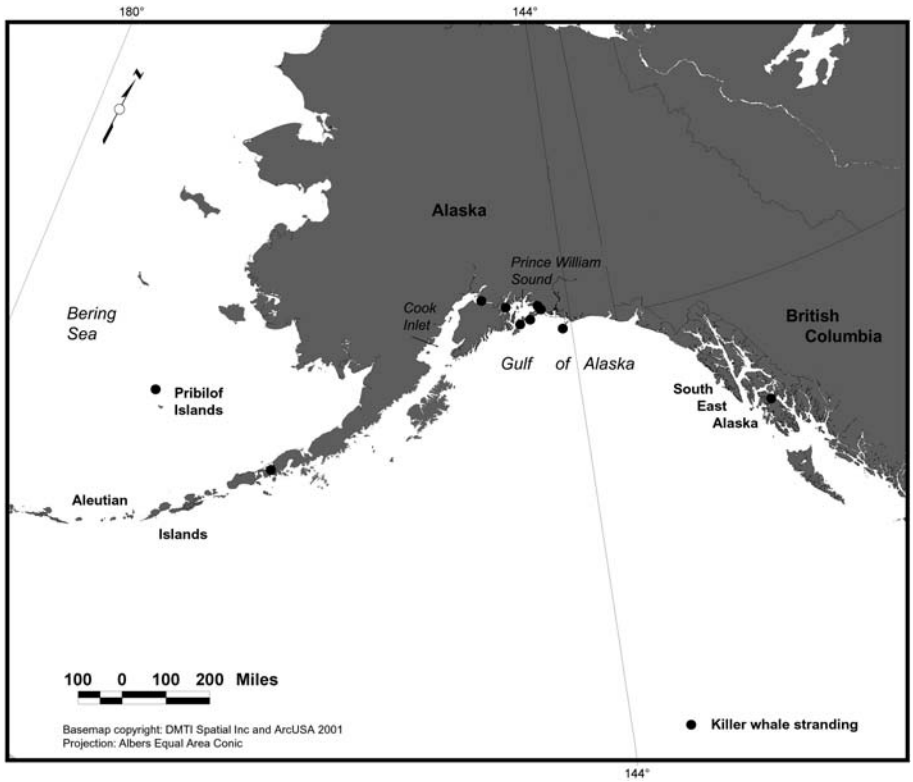

Figure 1. The study area showing place names in the text and the locations where killer whale stomach contents were recovered (see Table 1). In two cases (Barnes Lake, southeast Alaska, and on Montague Island, Prince William Sound), killer whales were found in close proximity, which is why only 10 strandings appear on the map. Gulf of Alaska transients have been seen in southeast Alaska, but not in British Columbia, and their range into offshore waters is unknown (Ford & Ellis 1999). The AT1 transients are generally found around Prince William Sound. The 144°W longitude marks the dividing line between the western (declining) and eastern populations of Steller sea lions.

aggressively towards the sea lions by chasing or attacking them. We expressed the interaction observation rate using the following index:

$$\textit{Interaction Index} = \frac{\textit{Number of interactions observed}}{\textit{Total number of observer hours for all years} \times 10^5}$$

Results

Stomach contents

Table 1 lists the stomach contents of 12 killer whale carcasses that washed ashore in Alaska between 1990 and 2001, and the locations of these carcasses is shown in Figure 1. Four killer whales were individually identifiable from photographs; two as *transients* (AT1 and AT 19 from the AT1 transient subpopulation) and two as *offshores* (Graeme Ellis, personal communication[1]). Genetic analyses of seven carcasses revealed that two animals were *offshores*, one an Alaskan resident from AB pod, and four animals were *transients* (Barrett-Lennard, 2000). Genetic analyses were attempted on the two whales recovered in 2001, but the samples were too degraded for successful extraction of DNA. Harbour seal parts were found in all seven of the stomachs that contained marine mammal remains, and Steller sea lion parts were found in two. Fifteen Steller sea lion flipper tags (including two with the same number) from 14 Steller sea lions were found in the stomach of a killer whale found dead on Montague Island, Prince William Sound in 1992. All sea lions had been tagged on Marmot Island in 1987 (4), 1988 (9) and 1990 (1) as part of a

[1]Graeme Ellis, Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, BC. April 2001.

Table 2. Interactions between killer whales and sea lions between 1935 and 1993 as reported by 126 questionnaire respondents.

Number of killer whales/sea lion interactions witnessed	492
Number of non-aggressive interactions (%)	441 (89.6%)
Number of reported non-lethal attacks by killer whales (%)	19 (3.9%)
Number of reported kills of sea lions by killer whales (%)	32 (6.5%)
Number of interactions observed/100 000 h of sea time	12.3
Number of non-predatory interactions observed/100 000 h of sea time	11.0
Number of non-lethal attacks observed/100 000 h of sea time	0.5
Number of lethal attacks observed/100 000 h of sea time	0.8
Number of killer whale sightings observed/100 000 h of sea time	1100
Median number of killer whale sightings/year/observer (range 0–150)	10.0
Median killer whale group size for all sightings (range 1 to 45)	7.5
Median killer whale group size for all predatory interactions (range 2 to 20)	4.0

Table 3. Observer effort and number of interactions reported in each area between 1935 and 1993.

Location	Type of Interaction			Observer hours	Number of observers
	Non-predatory	Harass	Kill		
California, Washington, and Oregon	0	0	0	59 962	7
British Columbia	168	10	12	1 023 130	29
Southeast Alaska	102	3	6	865 592	27
Gulf of Alaska	112	4	10	1 409 636	40
Bering Sea	2	2	1	321 255	18
Aleutians	57	0	3	105 360	5
Total	441	19	32	3 784 935	126

long-term study[2]. Two of the tags were consecutively numbered.[3] If the sea lions were eaten shortly before the killer whale's death, the maximum age of most of the sea lions was four or five years when consumed. All of the tags were equally encrusted with a blackish substance that had to be scraped-off for the numbers to be read. The killer whale stomach recovered in the summer of 2000 in Prince William Sound contained tags from two female harbour seals that were tagged earlier in the year in the same area. One seal weighed 25.9 kg and the other 48.9 kg at the time of tagging[4].

Survey responses

We received 126 completed questionnaires from mariners. Fifty respondents were researchers, 38 were commercial fishers, 24 were tourboat operators, and the remaining were considered as 'others', including float plane pilots and recreational boaters. Mariner experience on the water ranged from 1 to 58 years, with a median of 14 years, 138 days per year, and 10 h per day, and a mean of 14.3 years, 156 days per year, 10.3 h/day. The peak of sighting activity occurred in July. Table 2 summarizes the attacks and kills (predatory interactions) reported by respondents. Because the data for the number of killer whale sightings and group sizes were strongly skewed, we report the median results, as well as the range. Observers saw small groups of killer whales most often, but occasionally larger groups of up to 45 animals were seen. Table 3 summarizes the regional geographic distribution of respondents from California to Alaska and the number of interactions witnessed in each area.

Of 492 reported interactions between killer whales and Steller sea lions, 441 (89.6%) were non-predatory in nature. Those non-predatory interactions included two cases of sea lions harassing killer whales. Although predatory attacks were reported for only 10% of all interactions, over 60%

[2]Tom Loughlin, National Marine Mammal Laboratory, NMFS, Seattle, WA, and Don Calkins, Alaska Sea Life Centre, Seward, AK. April 2001.

[3]Tag Numbers 108, 174, 240, 305, 412, 429, 430, 439, 485, 507, 545, 589, 630, and 806.

[4]Kathy Frost, Alaska Department of Fish and Game, Fairbanks, Alaska. November 2000.

Table 4. Reported age classes of southern sea lions in Argentina (Hoelzel, 1991) and of Steller sea lions in British Columbia and Alaska attacked by killer whales (this study).

	Southern sea lions		Steller sea lions	
	Non-lethal attacks	Kills	Non-lethal attacks	Kills
Pups	127 (54%)	82 (99%)	0 (0%)	2 (6%)
Subadults	13 (6%)	1 (1%)	3 (16%)	5 (16%)
Adults	96 (41%)	0 (0%)	11 (58%)	16 (50%)
Not Stated			5 (26%)	9 (28%)
Total	236	83	19	32

were lethal for the sea lion. The duration of the predatory attack, combined with the time taken to consume the sea lion, ranged from 1–2 h. The majority of attacks and kills reported were on small adult sea lions (n=27). Only two pup kills were reported (Table 4). Pinniped researchers rarely observed predatory interactions between killer whales and Steller sea lions, and only one fatal attack was reported, by a pinniped researcher in the Priblof Islands. The sea lion was consuming a fur seal pup when it was attacked by the killer whales.

Discussion

Diets of killer whales

Given recent concern over the decline of Steller sea lions in western Alaska, it is noteworthy that only two of the twelve killer whale' stomachs examined in this study contained Steller sea lion remains. Of special interest were the 15 flipper tags from 14 Steller sea lions that were recovered from a whale that was genetically identified as a Gulf of Alaska *transient* (Table 1). Two of the tags had the same number. All of the tags were equally encrusted with a black substance (possibly due to a chemical reaction with stomach acids) suggesting that the sea lions were not killed recently. Two of the recovered tags were consecutively numbered, which is interesting given that 800 sea lion pups were tagged in total on Marmot Island[5]. However, it is not possible to confirm whether the sea lions were eaten by the killer whale shortly after tagging, or whether they were taken individually or as a group sometime later. Pups normally remain on shore for the first month of life. T. Loughlin (personal communication[6]) reported that few sea lions went into the water immediately after the tagging and branding process in 1987 and 1988 on Marmot Island, and that killer whales were not seen in the area at the time of tagging. It is possible that the sea lion pups dispersed from the rookery as a group, which was then attacked by the killer whale somewhere between Marmot Island and Prince William Sound. One of the sea lions, tagged in 1990, was at most two years old at the time it was killed by the killer whale.

Harbour seals were the predominant prey item found in all seven killer whales stomachs that contained marine mammal remains, and they are likely a more important prey item for killer whales than are Steller sea lions. In a review of killer whale interactions with marine mammals from around the world, harbour seals were the most commonly reported prey of killer whales in the northern hemisphere (Jefferson *et al*., 1991). Most predation by west coast transients witnessed by mariners from Frederick Sound, Alaska to Washington State also involved harbour seals (58%, Ford *et al*., (1998). Only 9% were kills of sea lions (both California and Steller). The most common marine mammal prey of killer whales in Alaska reported by Matkin & Saulitis (1994) were harbour seals and beluga whales (*Delphinapterus leucas*). Possible hunting specialization by transient killer whales on harbour seals has been observed in southern British Columbia, where certain groups of transients appear to forage specifically for them (Baird & Dill, 1995), largely ignoring the Steller and California sea lions that haul-out in the same area. A similar situation could occur in Alaska. Members of the AT1 transient group, primarily seen in southwestern Prince William Sound and Kenai Fjords, seem to forage primarily for Dall's porpoises (*Phocoenoides dalli*) and harbour seals (Saulitis *et al*., 2000). They frequently pass by Steller sea lions without initiating any obvious interactions. The Gulf of Alaska transients are less commonly seen in Prince William Sound, but some of its members (the AC group, based on Heise *et al*., 1992) have been observed attacking Steller sea lions there (R. Corcoran,

[5,6]Tom Loughlin, National Marine Mammal Laboratory, NMFS, Seattle, WA, April 2001.

C. Thoma, T. Edwards, personal communication[7]). The one Gulf of Alaska transient identified in this study had Steller sea lion remains in its stomach (Table 1).

Our results support Bigg *et al.*'s (1987) segregation of killer whales into at least two forms, those that eat fish (*residents*) and those that eat marine mammals (*transients*). Fish remains were not found in any of the stomachs containing marine mammal remains. However, the relative importance of prey species determined from stomach content analysis should be interpreted cautiously, because parts of the body such as skin, flesh, bones, claws, and whiskers can be digested and expelled at different rates. If prey are not swallowed whole, the parts eaten may influence the analysis. For example, the whale recovered from Culross Island in 1990 had the tail fluke and patches of skin from a Dall's porpoise in its stomach, yet contained no porpoise bones. Had digestion continued much further, it is unlikely we would have identified porpoise as a food item. Interestingly, Tomilin (1957) reported that killer whales often ate only the fluke portion of porpoises. Prey sharing amongst killer whales, as described by Guinet *et al.* (2000) and Pitman *et al.* (2003), may also influence which portions of a carcass are consumed by a killer whale. The whale in this study recovered from Culross Island had seal skin in its stomach, yet on other occasions, killer whales have been observed removing and discarding the skin of harbour seals before consuming them (Barrett-Lennard, Heise, unpublished data). Interpretation of the data is further complicated because the cause of death could not be determined for any of the whales and it is possible that the animals were not feeding normally at the time of death. However, our results are consistent with observed kills by transients in British Columbia reported by Ford & Ellis (1999).

The feeding ecology of the third form of killer whales known as *offshores* is less well understood. Ford *et al.* (2000) suggested that offshore killer whales feed principally on fish, because they travel in large groups and are acoustically active. The stomach contents recovered from the two offshore killer whales in this study provide concrete evidence that they do eat fish. One whale had salmon bones in its stomach, and the other had sculpin (family Cottidae), as well as some pieces of crab shell and eelgrass. These whales were part of a larger group of ten whales that were trapped in Barnes Lake, Alaska for six to ten weeks before they died. Harbour seals were also present in the lake while the whales were there (Bain, personal observation), yet were apparently not eaten by the two whales that died.

Evidence from stomach content analysis of killer whales around the world provides evidence that feeding specialization of killer whales is common; virtually all stomach contents reported contained either marine mammals or fish, but not both (Zenkovich, 1938; Tomilin, 1957; Nishiwaki & Handa, 1958; Betesheva, 1961; Rice, 1968; Jonsgard & Lyshoel, 1970). Evidence from Soviet whaling data also suggest segregation between fish-eating and mammal-eating killer whales in the Antarctic (Berzin & Vladimirov, 1982). Of 785 killer whales collected, 629 (80%) were of a smaller 'yellow' form found near shore and 156 (20%) were of a larger 'white' form found further offshore. Ninety-nine percent of the stomach contents from the yellow killer whales were fish, and 90% of the stomach contents from the white animals were marine mammals. Ivashin (1981 in Mikhalev *et al.*, (1981)) reported on 362 killer whale stomachs. Sixty percent contained only fish, 30% contained minke whale (*Balaenoptera acutorostrata*) remains, 5% contained squid, and 4% contained pinnipeds.

Mariner's survey

Surprisingly, few of the questionnaire respondents witnessed predatory attacks by killer whales on Steller sea lions, and many reports were second or third-hand accounts (Table 2). The highest number of kills reported by an observer was four, and this individual worked along the west coast of Vancouver Island, and had spent almost 300 000 h on the water and had over 1700 sightings of killer whales over the course of his career. Mariners spent an average of 8100 h on the water for each observation of a killer whale/sea lion interaction and 125 000 h for each observation of a fatal attack on a sea lion (Table 2). These averages include responses from researchers conducting studies on either killer whales or sea lions, who were well-situated to see interactions. At the time of the survey, the five authors of this paper had spent a total of approximately 155 000 h on the water searching for and observing killer whales, and none saw a fatal attack on a Steller sea lion. Collectively, we observed 28 non-predatory interactions and only one case of harassment of sea lions by killer whales.

The questionnaire results indicated that the majority of attacks and kills witnessed by mariners involved adult sea lions (Table 4). However, the fact that these records are based on opportunistic observations of predation, rather than on detailed observations of killer whale foraging behaviour, could have biased the study in favour of predation on adult sea lions since such attacks are highly visible. Killer whales caused a great deal of splashing

[7]Rich Corcoran, Solomon Gulch Fish Hatchery, Valdez, AK. April 2001.

during attacks of adult sea lions, by breaching on or near the sea lions, and by slashing at them with their tail flukes. This conspicuous activity generally lasted over 1 h and was therefore likely to attract the attention of passing mariners. By comparison, attacks of younger sea lions were probably much less obvious. Harbour seals, which are similar in size to small sea lions, are usually killed under water by killer whales. Blood, oil and/or fragments of blubber are usually the only evidence of a fatal attack on harbour seals.

We received killer whale identification photographs from several respondents and in some cases identified the whales concerned. All whales identified in attacks on sea lions or other marine mammals were transient killer whales. The median group size for all killer whale sightings was 7.5; however, the median size of groups that attacked Steller sea lions was four (Table 2). In British Columbia, this difference could reflect the difference between the average sizes of resident (5–50) and transient (1–7) killer whale groups (Bigg *et al*., 1987). In southern Alaska, transients seldom travel in groups larger than five animals (Matkin *et al*., 1999).

Pinniped researchers who have spent time on sea lion rookeries rarely witnessed killer whale attacks. It is possible that transient whales foraging near sea lion haul-outs and rookeries may be particularly difficult to observe, since they hunt by stealth to avoid the risk of alerting their prey (Barrett-Lennard *et al*., 1996). Indeed, the only pinniped researcher to observe a fatal attack on a Steller sea lion was on a fur seal rookery at the time, and the sea lion was preoccupied consuming a fur seal pup when it was attacked by the killer whales.

The pattern of killer whale predation on species similar to Steller sea lions, and the remains of sub-adult sea lions found in two of the twelve killer whale stomachs, suggest that a higher proportion of pups and juveniles may be killed than are reflected in the questionnaire data. More research is needed to determine whether killer whale predation on Steller sea lions has significant population level effects. We suspect that killer whale predation on sea lion pups and juveniles peaks while animals are congregated at rookery sites. The peak of sighting activity of killer whales and of observer activity occurred in July, coinciding with the period when most Steller sea lion pups leave the rookeries (Sandegren, 1970). Several observers reported that killer whales spent more time near haul-out and near-shore areas during the pupping season than during the rest of the year. Researchers in other areas and on other species have reported that pups are most frequently taken by killer whales (Baird, 1994 harbour seals; Hoelzel, 1991 southern sea lions *Otaria flavescens*; Lopez & Lopez, 1985 southern sea lions and southern elephant seals *Mirounga leonine*). In view of the low number of interactions witnessed in the eastern North Pacific, we recommend that researchers make a concerted effort in the future to note the behaviour of killer whales around Steller sea lions, particularly in areas where sea lion populations are declining. Observations should include scans of the water surface after seeing killer whales mill in the area (to look for blood or blubber fragments) and if possible identification photographs of killer whales should be made. Such efforts could provide valuable insight into the question of whether or not transient killer whales are responsible for the decline of Steller sea lions in western Alaska.

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Literature Cited

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

Baird, R. W. & L. M. Dill. (1995) Occurrence and behaviour of transient killer whales: seasonal and pod-specific variability, foraging behaviour and prey handling. *Canadian Journal of Zoology* **73,** 1300–1311.

Barrett-Lennard, L. G. (2000) Population structure and mating patterns of killer whales (Orcinus orca) are revealed by DNA analysis. Ph.D. Thesis, University of British Columbia, Vancouver, B.C. Canada. 97 pp.

Barrett-Lennard, L. G., Ford, J. K. B. & Heise, K. (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour* **51,** 553–565.

Berzin, A. A. & Vladimirov, V. L. (1982) A new species of killer whale (Cetacea, Delphinidae) from Antarctic waters. *Zoologicheskii Zhurnal* **62,** 287–295.

Betesheva, E. I. (1961) Pitanie promyslovykh kitov Prikuril'skogo raiona (Food of commercial whales in the Kurile region). *Tr. Inst. Morfol. Zhivotnykh Akad. Nauk SSSR* **34,** 7–32. In Russian. (Abstract translated in Biological Abstracts 43(1), entry 469.

Bickham, J. W., Patton, J. C. & Loughlin, T. R. (1996) High variability for control-region sequences in a marine mammal: implications for conservation and maternal phylogeny of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammalogy* **77,** 95–108.

Bigg, M. A., Ellis, G. M., Ford, J. K. B. & Balcomb III, K. C. (1987) *Killer Whales: a Study of their Identification, Genealogy, and Natural History in British Columbia and Washington State.* Phantom Press, Nanaimo, B.C. 79 pp.

Calkins, D.G, McAllister, D. C., Pitcher, K. W. & Pendleton, G. W. (1999) Steller sea lion status and trend in Southeast Alaska: 1979–1997. *Marine Mammal Science* **15,** 462–467.

Dahlheim, M. E. (1981). A review of the biology and exploitation of the killer whale, *Orcinus orca*, with comments on recent sightings from Antarctica. *Report of the International Whaling Commission* **31,** 541–546.

Dahlheim, M. E., Ellifrit, D. K. & Swenson, J. D. (1997) Killer whales (*Orcinus orca*) of Southeast Alaska: A catalogue of photo-identified individuals. National Marine Mammal Laboratory, National Marine Fisheries Service. 7600 Sand Point Way, N.E. Seatttle, WA. 98115. 79 pp.

Estes, J. A., Tinker, M. T., Williams, T. M, & Doak, D. F. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282,** 473–476.

Ferrero, R. C., DeMaster, D. P., Hill, P. S., & Muto, M. (2000) Alaska Marine Mammal Stock Assessments 2000. National Marine Mammal Lab, AFSC, NMFS, NOAA, 176 pp. Available from NMML, 7600 Sand Point Way, N.E. Seatttle, WA. 98115.

Ford, J. K. B. & Ellis, G. M. (1999) *Transients, Mammal-hunting Killer Whales.* UBC Press, Vancouver, B.C. 102 pp.

Ford, J. K. B., Ellis, G. M. & Balcomb III, K. C. (1994) *Killer Whales: the Natural History and Genealogy of Orcinus orca in British Columbia and Washington.* UBC Press: Vancouver. 102 pp.

Ford, J. K. B., Ellis, G. M. & Balcomb III, K. C. (2000) *Killer Whales: the Natural History and Genealogy of Orcinus orca in British Columbia and Washington.* UBC Press, Vancouver, B.C.. Second Edition. 104 pp.

Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S. & Balcomb III, K. C. (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.

Guinet, C. (1991) Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Canadian Journal of Zoology* **69,** 2712–2716.

Guinet, C., Barrett-Lennard, L. G. & Loyer, B. (2000). Co-ordinated attack behavior and prey sharing by killer whales at Crozet Archipelago: Strategies for feeding on negatively-buoyant prey. *Marine Mammal Science* **16,** 829–834.

Harbo, R. (1975) Lunch with killers. *Pacific Diver* **1,** 21–22, 43.

Heise K., Ellis, G. M. & Matkin, C. O. (1992) *A Catalogue of the Killer Whales of Prince William Sound.* Homer, Alaska: North Gulf Oceanic Society. 51 pp.

Hoelzel, A. R. (1991) Killer whale predation of marine mammals at Punta Norte, Argentina: food sharing, provisioning and foraging strategy. *Behavioural Ecology and Sociobiology* **29,** 197–204.

Huntington, H. P. (2000) Using traditional ecological knowledge in science: methods and applications. *Ecological Applications* **10,** 1270–1274.

Jefferson, T.A., Stacey, P. J. & Baird, R. W. (1991) A review of killer whale interactions with other marine mammals: predation to coexistence. *Mammal Review* **22,** 151–180.

Jonsgard, A. & Lyshoel, P. B. (1970) A contribution to the biology of the killer whale, *Orcinus orca*. *Nytt Magasin for Zoologi* **18,** 41–48.

Lopez, J. C., & Lopez, D. 1985. Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting near shore. *Journal of Mammalogy* **66,** 181–183.

Louglin, T. R., Perlov, A. S. & Vladimirov, V. A. (1992) Range-wide survey and estimation of total number of Steller sea lions in 1989. *Marine Mammal Science* **8,** 220–239.

Matkin, C. O., Ellis, G. M., Saulitis, E., Barrett-Lennard, L. G. & Matkin, D. (1999) *Killer Whales of Southern Alaska.* North Gulf Oceanic Society. Box 15244. Homer, Alaska, 99603. 96 pp.

Matkin, C. O. & Leatherwood, S. (1986). General biology of the killer whale, *Orcinus orca*: a synopsis of knowledge. Pages 35–68 In: B. C. Kirkevold & J. S. Lockard (eds.) *Behavioral Biology of Killer Whales*. Alan R. Liss, Inc., New York, NY 457 pp.

Matkin, C. O. & Saulitis, E. L. (1994) Killer whale, *Orcinus orca*, biology and management in Alaska. U.S. Marine Mammal Commission, Washington, D.C. 46 pp.

Mikhakev, Y. A., Ivashin, M. V., Savusin, V. P. & Zelenaya, F. E. (1981) The distribution and biology of killer whales in the Southern Hemisphere. *Report of the International Whaling Commission* **31,** 551–566.

Nishiwaki, M. & Handa, C. (1958) Killer whales caught in coastal waters off Japan. *Science Report of the Whales Institute, Tokyo* **13,** 85–96.

Olesiuk, P. F. & Bigg, M. A. (1988) Seals and sea lions on the British Columbia coast. Department of Fisheries and Oceans, Nanaimo, B.C. 12 pp.

Olesiuk, P. F., Bigg, M. A. & Ellis, G. M. (1990) Life history and population dynamics 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,** 209–243.

Pitman, R. L., O'Sullivan, S. & Mase, B. (2003) Killer whales (*Orcinus orca*) attack a school of pantropical dolphins (*Stenella attenuata*) in the Gulf of Mexico. *Aquatic Mammals* **29(3)**, 321–324.

Rice, D. W. (1968) Stomach contents and feeding behavior of killer whales in the eastern North Pacific. *Norsk Hvalfangst-Tid.* **57,** 35–38.

Sandegren, F. E. (1970) Breeding and maternal behaviour of the Steller sea lion (*Eumetopias jubatus*). M.Sc. Thesis. University of Alaska, Fairbanks, AK. 138 pp.

Saulitis, E. L. (1993) The vocalizations and behavior of the ''AT''-group of killer whales (*Orcinus orca*) in Prince William Sound, Alaska. M.Sc. Thesis. University of Alaska, Fairbanks, AK. 209 pp.

Saulitis, E., Matkin, C. O., Barrett-Lennard, L. G. Heise, K. & Ellis, G. M. (2000) Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science* **16,** 94–109.

Scammon, C. M. (1874) The Marine Mammals of the North-western Coast of North America. reprinted by Dover: New York. 319 pp.

Sease, J. L., Taylor, W. P., Loughlin, T. R. & Pitcher, K. W. 2001. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1999 and 2000. *NOAA Technical Memorandum* NMFS-AFSC-122. 60 pp.

Tomilin, A. G. (1957) *Cetacea*. Vol. 9. In: V. G. Heptner (ed.) Mammals of the U.S.S.R. and adjacent countries. Izd. Akad. Nauk SSSR, Moscow. 756 pp. (Translated from Russian by the Israel Program for Scientific Translations, Jerusualem, 1967)

Trites, A. W. & Larkin, P. A. (1996) Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956–1992: How many were there? *Aquatic Mammals* **22,** 153–166.

Zenkovich, B. A. (1938) On the *Grampus* or killer whale (*Grampus orca* Lin.). *Priroda* **4,** 109–112.