The Impact of Killer Whale Predation on Steller Sea Lion Populations in British Columbia and Alaska

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ABSTRACT

Steller sea lion populations in Alaska have declined precipitously over the last 25 years. Much research has been conducted on the role of anthropogenic factors in this decline. The retrieval of 14 sea lion flipper tags from a dead killer whale in 1992 underscored the need for a similar appraisal of predation. We used simulation models to examine (1) the extent to which killer whales contributed to the sea lion decline, and (2) the present effect of killer whale predation on depleted sea lion populations. We estimated the model parameters using three sources: a survey of researchers and mariners, the stomach contents of stranded killer whales, and killer whale identification photographs from several collections. The 126 survey respondents described 52 attacks including 32 reported kills. Eight out of 15 killer whale stomachs with identifiable contents contained marine mammals, and two contained Steller sea lion remains. The survey and stomach content data were consistent with earlier findings that only members of the transient killer whale population commonly prey on marine mammals. Based on identification photographs, we estimated that at least 250 transient killer whales feed in Alaskan waters. We ran Leslie matrix simulations under various assumptions concerning the functional responses of killer whales to changes in sea lion density. Our models suggest that killer whale predation did not cause the sea lion decline, but may now be a contributing factor. At present, approximately 18% of sea lions that die annually in Western Alaska may be taken by killer whales.

INTRODUCTION

The stomach of a dead killer whale that washed ashore in Prince William Sound in the summer of 1992 contained flipper tags from 14 Steller sea lions. Attacks and kills of sea lions by killer whales have been documented throughout Alaska and British Columbia (eg. Tomilin 1957, Rice 1968, Harbo 1975). and killer whale predation on otariids (eared seals) is commonly reported in other parts of the world (eg. Lopez & Lopez 1985, Guinet 1991, Hoelzel 1991). In view of concern over declining Steller sea lion populations in Alaska, we began a study to examine the role of killer whale predation in sea lion population dynamics. We sought answers to two questions. (1) What is the likelihood that killer whale predation contributed significantly to the recent decline of Steller sea lions in Alaska? (2) What is the present effect of killer whale predation on depleted sea lion populations in Alaska?

The study had four components. (1) Mariners were surveyed and asked to describe their observations of predatory and non-predatory interactions between killer whales and sea lions. (2) Data were compiled on killer whale diet based on the stomach contents of stranded whales from Alaska and British Columbia. (3) Photo-identification records were used to estimate the size of the mammal-eating 'transient' killer whale population from northern Washington to the Aleutian Islands. (4) Computer simulations were used to examine the potential impact of killer whale predation on Steller sea lion populations. These aspects of the study are presented in the following chapters. The remainder of the current chapter is a review of the natural history of Steller sea lions and killer whales.

STELLER SEA LIONS *(Eumetopias jubatus)*

Steller sea lions are the largest of the otariids and are sexually dimorphic (King 1983). Adult males average 3.0 m in length and 1,000 kg in weight, although individuals may weigh as much as 1120 kg; females average 2.4 m in length and 270 kg in weight, but weights to 350 kg have been recorded (Nowak 1991). Females may live for 30 years and males for 20 (Calkins and Pitcher 1982). Females attain sexual maturity between 3 and 6 years of age. Males become sexual mature between 3 and 8 years of age, but are not able to successfully defend breeding territories until they are about 10 years old (Pitcher and Calkins 1981). During the breeding season, which lasts from late May to early July, 65% of the sea lion population aggregates at rookery sites (Trites and Larkin 1995). In Alaska, there are 38 major rookeries (Loughlin et al. 1992), the majority of which are in remote locations. In addition *to* the rookery sites, there are 41 major and approximately 210 minor haul-out sites known in Alaska (Loughlin et al. 1992). In British Columbia there are three major breeding rookeries (Scott Islands, Kerouard Islands, and North Danger Rocks) and approximately 65 haul-out sites. Fifteen of these sites are occupied year-round, with the remainder typically occupied from August through May (Bigg 1985).

Males arrive at the rookeries in mid-May, and hold breeding territories that they defend from other males. The females arrive in June and shortly thereafter give birth to a single pup (Pitcher and Calkins 198 1, Bigg 1985). Pups weigh 16 to 23 kg at birth and are approximately 1 m in length (Calkins and Pitcher 1982). Females remain with their pups for the first 5 to 13 days then leave them to go to sea on short feeding trips. The pups remain on the rookery for about 28 days before they enter the water, and by mid-July they take to the water readily (Sandegren 1970). Typically adults and pups remain close to rookery sites until October, when they may disperse to haul-out sites for the winter. Merrick et al. (1994, cited in Merrick 1994) found that by six months of age, sea lions could travel up to 300 km on feeding trips. Sea lions disperse widely after the breeding season. For example, sea lions marked as pups on Marmot Island in the Gulf of Alaska have been observed in British Columbia as early as the first spring after branding (Met-rick 1994). One sub-adult male tagged in Oregon was observed at Cape St. Elias and at Marmot Island, Alaska, a distance of over 3,000 km (Merrick 1994).

The range of Steller sea lions extends along the coast from California to the Gulf of Alaska and the Bering Sea, and west to the Kurile Islands and Okhotsk Sea (Loughlin et al. 1984). The total worldwide population was estimated to be 116,000 sea lions in 1989, with 70% of the total concentration in Alaska (Loughlin et al. 1992). Reductions in Steller sea lion numbers were first detected in western Alaska in the mid 1970’s, but were not noted elsewhere until 1980 (Braham et al. 1980, Merrick et al. 1987, Trites and Larkin 1995). Between 1980 and 1992 the Aleutian Islands and Gulf of Alaska populations declined by over 65% (Trites and Larkin 1995) and continues to decline by about 5% per year (Merrick 1994). In 1994, the US population was estimated at 52,200 non-pups, with the majority of animals (61% or 31,900 animals) still found in the Gulf of Alaska and the Aleutian Islands (Merrick 1994). In 1994, 11,400 non-pups were counted in southeast Alaska, and 1,700 were counted in the Bering Sea. In British Columbia, 9,200 pup and adult sea lions were counted in 1994 (Peter Olesiuk, pers. comm.). In Oregon and California, 7,200 non-pup sea lions were counted (Merrick 1994). A review of the decline of Steller sea lions can be found in the *Recovery plan for the Steller Sea Lion* (NMFS 1992).

KILLER WHALES *(Orcinus orca)*

Killer whales are one of the most widely distributed mammals in the world (Ford et al. 1994a). They have been reported to prey on 36 species of marine mammals (Hoyt 1984, Jefferson et al. 1991, Matkin and Saulitis 1994). For prey such as pinnipeds, cetaceans, and some fish (eg. herring, salmon), it is often possible to document predation from surface observations and the collection of prey fragments at kill sites. Stomach contents of killer whale carcasses also provide useful information on diet. In the North Pacific, killer whales have been recorded feeding on twelve species of large cetaceans, five species of dolphins and porpoises, eight species of pinnipeds, sea otters (Matkin and Saulitis 1994), a moose (Kochman 1992). several species of seabirds and ducks (Odlum 1948, Scheffer and Slipp 1948, Ford and Ford 1981, Stacey and Baird 1989, Morton 1990, Stacey et al. 1990). and seventeen species of fish (Pacific Biological Station (PBS) unpubl. data).

Around the world, the movement patterns and distribution of killer whales are related to the movements and distribution of their prey. In Norway, killer whales arrive in the Vesteralen Islands area at the same time as herring (Simila and Ugarte 1991), and in Antarctic waters, in late November, at the same time as minke whales (Budylenko 1981). Condy et al. (1978) noted that the presence of killer whales off Marion Island, in the southern Indian Ocean, was synchronized with the hauling out of elephant seals and penguins. Killer whales were observed at Punta Norte, Argentina, only during the breeding season of their southern sea lion prey (Hoelzel 1991). In waters off Kamchatka, killer whales concentrated near seal and sea lion rookeries and were seen most often during periods of peak sea lion abundance (Tomilin 1957). Inhabitants of the Commander Islands described the close timing between the arrival of fur seals *(Callorhinus ursinus)* and killer whales (Tomilin 1957).

Resident, transient and offshore killer whales

The nearshore killer whales populations of British Columbia, southeast Alaska, and Prince William Sound have been studied systematically for many years, and key aspects of their social structure, population dynamics, foraging and acoustic behaviour have been described (Ford 1984, 1987, 1989, 1991, Bigg et al. 1985, 1987, 1990a, 1990b, Hoelzel 1990, Leatherwood et al. 1984, 1990, Morton 1990, Olesiuk et al. 1990, Barrett-Lennard 1992, Saulitis 1993, Baird 1994, Ford et al. 1994a, Barrett-Lennard et al. in press). Most individuals have been photographically identified, and classified as belonging to either the fish-eating *resident,* or the mammal-eating *transient* populations (Bigg et al. 1987, Ellis 1987, Heise et al. 1992, Ford et al. 1994a). These populations share a common range but do not associate, and differ markedly in social structure and vocal behaviour.

Residents live in matrilineal groups (pods) of five to 40 individuals and feed principally or entirely on fish (Bigg et al. 1985, 1987, Heimlich-Boran 1986, 1988, Jacobsen 1986, Nichol 1990). The movement patterns of residents have been correlated with the abundance of salmon in Puget Sound and in Johnstone Strait (Heimlich-Boran 1986, Nichol 1990). Transients are typically seen alone or in groups of two to 10, and feed principally or entirely on marine mammals (Bigg et al. 1985, 1987, Baird and Stacey 1988a, Morton 1990). Transients often travel nearshore and hunt silently or with minimal echolocation: residents spend more time in open water and use echolocation frequently (Barrett-Lennard et al. in press). The composition of transient groups may change over time, whereas there is no movement of individuals among resident groups (Bigg et al. 1990, Ellis unpubl. data).

A third assemblage of killer whales, tentatively known as the *offshore* population, has recently been recognized (Ford et al. 1994a,b). Little is known about the feeding habits and distribution of this group, although it has been observed feeding on fish (Ford unpubl. data), and is usually sighted well off the mainland coast, near the edge of the continental shelf (Ford et al. 1994b). Offshore whales are generally found in large, vocally active groups of 30 to 60 individuals, and they have not been seen associating with either resident or transient whales. Their vocal behaviour suggests that they do not hunt marine mammals by stealth as transients do (Barrett-

Lennard et al. in press). In addition, their large group sizes are above the range normally reported for transients By comparison, the largest group size reported for transients is 15 (Baird 1994).

It is important to consider feeding differences among killer whale populations when attempting to assess the impact of killer whale predation on a given prey species. In British Columbia and southeast Alaska there are approximately 364 residents, 200 offshores and 170 transients (Ford et al. 1994a,b, Ellis unpubl. data). Thus only 23% of the total population of killer whales known to travel in these waters consumes marine mammals.

OBSERVATIONS OF SEA LION PREDATION: A SURVEY OF MARINERS

Whatever else may be said of predation, it does draw attention.
(Errington 1946)

INTRODUCTION

Killer whales have commanded fearsome respect in most maritime cultures, and mariners have long traded anecdotal accounts of them attacking formidable prey, including whales, walruses and sea lions (eg. Harbo 1975). Yet despite their reputation as voracious predators, many observers have reported seeing killer whales in close proximity to potential prey, with no signs of aggression by the killer whales or flight by the prey. Attacks and non-aggressive interactions have also been widely reported in the scientific literature (eg. Mikhalev et al. 1981, Jefferson et al. 1991).

The list of prey taken by transient killer whales includes the Steller sea lion. In view of the dramatic decline in Steller sea lion numbers through much of their range, the mortality attributable to predation is of considerable interest. Data have not been systematically collected on killer whale predation rates on Steller sea lions, and indeed a project to do so would be both difficult and expensive. However, valuable information exists in the observations of mariners that work and travel in waters frequented by both killer whales and 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 success rate of observed attacks on sea lions, the age classes of sea lions taken, and the areas where predatory-type attacks occurred most often.

METHODS

We distributed a four-page questionnaire in 1993 and 1994 to approximately 250 mariners, including researchers, commercial fishermen, and tour boat operators. A copy of the questionnaire is included in Appendix 1. The results of these surveys were compiled to produce an account of the number of interactions observed between sea lions and killer whales, relative to the total amount of time mariners spent on the water. Mariners witnessing interactions between sea lions and killer whales were asked to describe their observations, including details on the number of animals involved, the age class of the sea lions, and the locations where interactions were observed. Interactions were separated into two categories: predatory and non-predatory. A non-predatory interaction was one in which killer whales and sea lions were observed in close proximity with no sign of aggression by the killer whales towards the sea lions. For ease of comparison, we expressed the interaction rate using the following

$$\textit{Interaction rate} = \frac{\text{Interactions } \textit{observed x } 100{,}000}{\textit{Number of observer hours for ail years}}$$

RESULTS

One hundred and twenty-six completed questionnaires were received. A summary of each response is presented in Appendix 2. Half of those who responded had spent 14 or more years on the coasts of British Columbia or Alaska (Table 2.1). The sighting effort of the respondents was highest in July (Figure 2.1), coinciding with the period that most Steller sea lion pups leave the rookeries (Sandegren 1970). Table 2.2 summarizes the attacks and kills (predatory interactions) reported by respondents, and details are included in Appendix 2. Table 2.3 summarizes the distribution of respondents and the number of interactions witnessed for all areas. Figure 2.2 shows the distribution of observer effort versus the interaction rate for all areas. Observer effort was highest in the Gulf of Alaska, but the highest rate of observed killer whale/ sea lion interactions was in the Aleutian Islands.

Of 492 reported interactions between killer whales and Steller sea lions, 90% were non-predatory in nature. These non-predatory interactions included two cases of sea lions harassing killer whales. Although predatory attacks were reported for only 10% of all interactions, 60% of these were lethal for the sea lion. The time spent by the whales during these attacks, and during consumption of the sea lion afterwards, ranged from 1 to 2 h. The majority of attacks and kills reported were of small adults (n=12). Only two pup kills were reported (Table 2.4). Figure 2.3 shows the non-pup sea lion population size (based on Merrick 1994) and the lethal interaction rate in Alaska. The greatest number of animals is found in the Gulf of Alaska, but the lethal interaction rate was highest in the Aleutian Islands.

Table 2.1 Experience and occupations of the 126 respondents to the killer whale/ sea lion interaction survey.

Experience of respondents		Occupations of questionnaire respondents	
Median no. years experience on the water (range l-58)	14	Researchers	50
Median no. days/year on the water	138	Fishermen/women	38
Median no. hours/day on the water	10	Tourboat operators	24
		Others	14

Table 2.2 Summary of interactions between killer whales and sea lions, as reported by 126 questionnaire respondents.

Number of interactions witnessed between killer whales and sea lions.	492	
Number of non-aggressive interactions	441	(89.6%)
Number of reported non-lethal attacks of sea lions by killer whales	19	(3.9%)
Number of reported kills of sea lions by killer whales	32	(6.5%)
Mean no. of interactions observed per 100,000 hours of sea time	12.3	
Mean no. of non-predatory interactions observed per 100,000 hours of sea time	11	
Mean no. of non-lethal attacks observed per 100,000 hours of sea time	0.47	
Mean no. of lethal attacks observed per 100,000 hours of sea time	0.8	
Mean no. of killer whale sightings observed per 100,000 hours of sea time	1100	
Median number of killer whale sightings per year per observer (range 0 to 150)	10	
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	

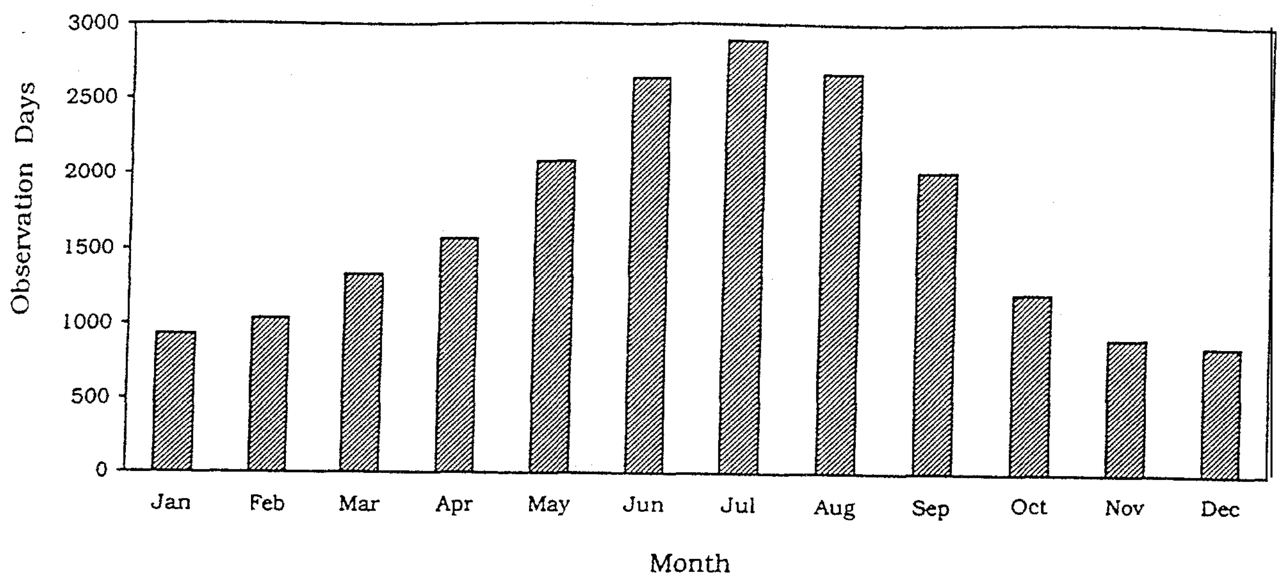

Figure 2.1 Number of observation days per month for all areas.

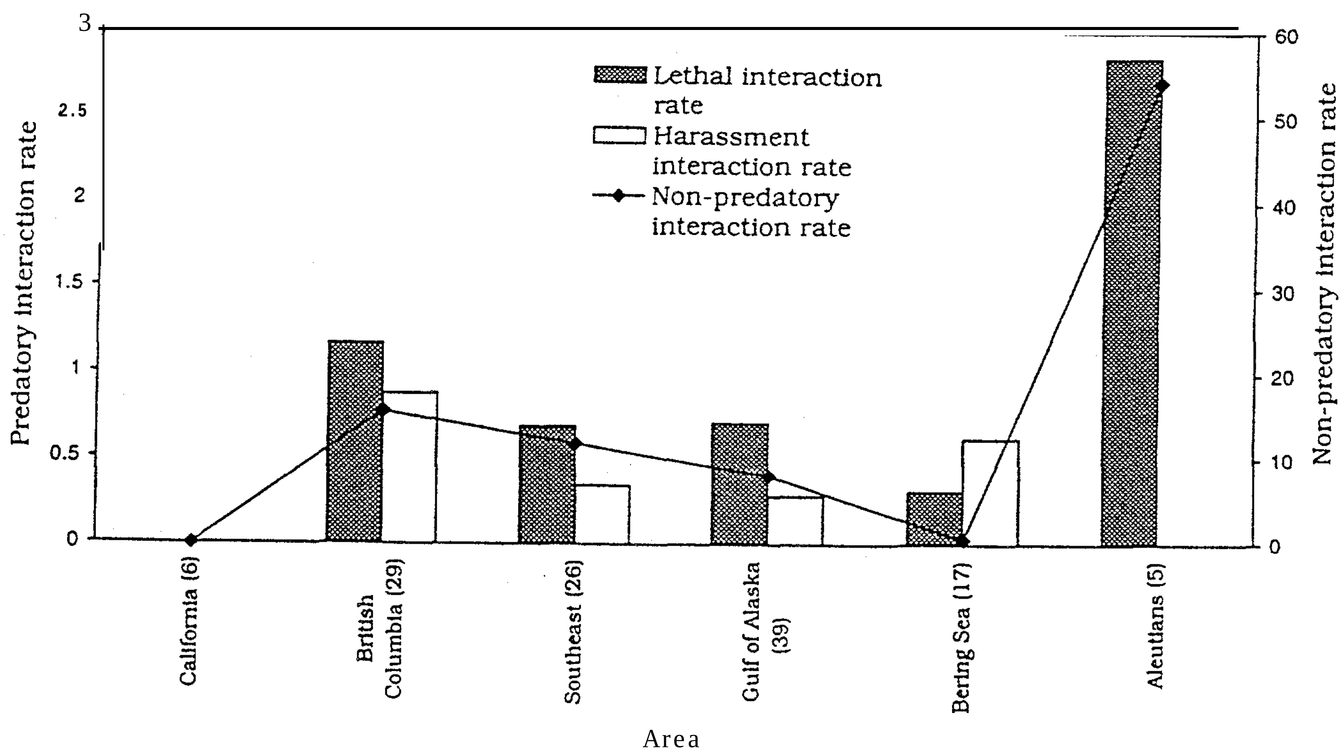

Figure 2.2 Predatory and non-predatory interaction rates for all areas. The number of observers in each area is shown in brackets.

Table 2.3 Observer effort and number of interactions witnessed for California, British Columbia and Alaska for all years.

Location	Type of Interaction: Non-predatory	Harass	Kill	Observer hours for all years	Number of Observers
California	0	0	0	59,962	6
BC	159	9	12	1,023,130	29
Southeast Alaska	102	3	6	865,592	26
Gulf of Alaska	112	4	10	1,409,636	39
Bering Sea	2	2	1	321,255	17
Aleutians	57	0	3	105,360	5
TOTAL	432	18	32	3,784,935	122

Table 2.4 Age classes of sea lions reported during predatory attacks by killer whales.

NON-LETHAL ATTACKS			LETHAL ATTACKS		
	# Attacked	Age Class		# Killed	Age Class
20 Reported Attacks:	0 (0 %)	Pups	32 Reported Kills:	2 (6 %>	pups
	3 (15%)	juveniles		5 (16%)	juveniles
	12 (60%)	adults		16 (50%)	adults*
	5 (25%)	not stated		9 (28%)	not stated

*in 16 reports of fatal attacks on adults. the majority of sea lions were small adults. In the single account of a large sea lion bull that was taken, 15-20 killer whales were present.

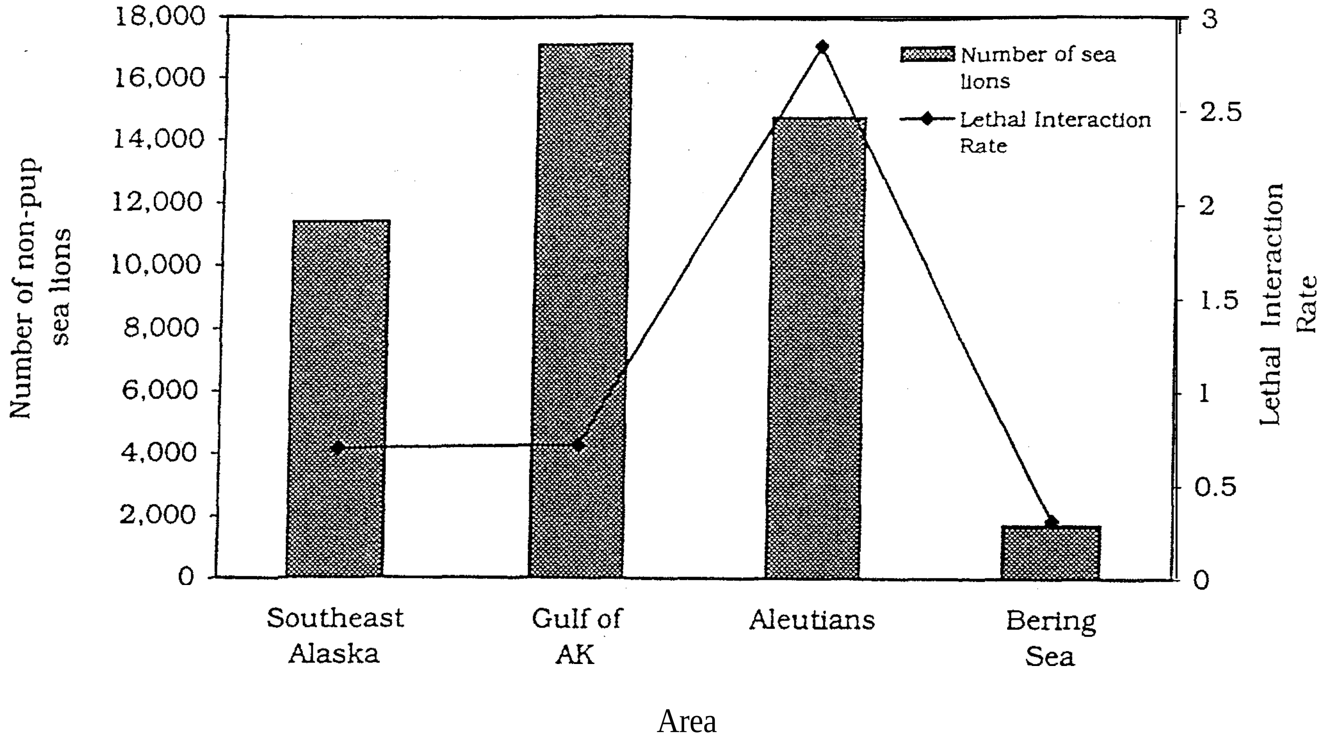

Figure 2.3 Number of non-pup sea lions in 1994 and the rate of observed lethal killer whale/ sea lion interactions for each geographical area in Alaska. Numbers of sea lions are from Merrick (1994) and were adjusted to account for missed sites and animals at sea, by the method of Loughlin et al. (1992).

DISCUSSION

Prior to initiating this study, we had the impression that some mariners had seen numerous attacks of sea lions by killer whales, yet in fact few of the questionnaire respondents had witnessed predatory attacks. The highest reported number of kills seen was four, by an observer working along the west coast of Vancouver Island. Indeed the average mariner surveyed spent over 8,100 hours on the water for each observation of an interaction between killer whales and sea lions, and 125,000 hours for each observation of a fatal attack on a sea lion (Table 2.2). These averages include responses from researchers conducting studies on either killer whales or sea lions, who were well situated to see interactions. The five authors of this report have spent a cumulative total of approximately 155,000 hours on the water searching for and observing killer whales, and only one has seen a fatal attack on a Steller sea lion.

The total number of observed interactions was highest in British Columbia (Table 2.3) but the interaction rates between killer whales and sea lions were highest in the Aleutians (Figure 2.2). This may be an artifact of the small number of observers from the Aleutians (n=5) and/ or the fact that all respondents from this area were researchers. In contrast, in the Gulf of Alaska, the interaction rate was much lower, despite the greater population of Steller sea lions (Figure 2.3). The difference may indicate greater predation pressure on sea lions in the Aleutians than in the Gulf of Alaska, or may be an artifact of the small number of observers from the area.

Based on the responses to the questionnaire distributed in this study, the majority of attacks and kills witnessed by mariners involved adult sea lions (Appendix 2, summarized in Table 3.5). However, these records are based on opportunistic observations of predation, rather than on detailed observations of killer whale foraging behaviour. Thus they may be biased in favour of predation on adult sea lions since these attacks are more visible. Observers reported that killer whales caused a great deal of splashing 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 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 underwater by killer whales (pers. obs., all authors). After a kill, blood, oil and/ or fragments of blubber are usually the only evidence of a fatal attack. Detecting these items usually requires an experienced observer with a boat that can manoeuvre across a suspected kill site. Differences in the conspicuousness of attacks depending on the age of prey is a potentially serious observing bias, and may largely explain why only two pup kills were reported.

We received killer whale identification photographs from several of the respondents, and in some cases were able to identify the whales present. All whales identified in groups involved in attacks on sea lions or other marine mammals were transients. The median group size reported for all killer whale sightings was 7.8, however the median size of groups that attacked Steller sea lions was four (Table 2.2). This difference may reflect the difference between the average sizes of resident and transient killer whale groups. In British Columbia the average group size is 5 to 50 for residents and 1 to 7 for transients (Bigg et al. 1987).

Few of the pinniped researchers who spent time on sea lion rookeries witnessed fatal attacks by killer whales. It is possible that killer whales foraging near sea lion haul-outs and rookeries may be particularly difficult to observe, since they likely hunt by stealth to avoid the risk of alerting their prey (Barrett-Lennard et al., in press). 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 time that killer whales took to kill and consume sea lions (l-2 h) was considerably longer than the mean handling time reported by Baird (1994) for harbour seals (28 minutes). This difference probably reflects the difference in size between the two prey species: a mature harbour seal weighs about 80 kg (Olesiuk and Bigg 1988) whereas an adult Steller sea lion weighs from 270 to over 1,000 kg (Nowak 1991). Approximate age categories were determined for 57 of the 72 harbour seal kills witnessed by Baird (1994). Sixty percent were pups, 19%

were juveniles and 21% were adults. Hoelzel (1991) reported that 54% of observed attacks on southern sea lions were of pups and 41% of the attacks were of adults. Adult southern sea lions are smaller than Steller sea lions, weighing between 140-350 kg (Nowak 1991). None of the observed attacks by killer whales of southern sea lion adults was successful (Hoelzel 1991). Lopez and Lopez (1985) investigated the intentional stranding of killer whales at Punta Norte, Argentina preying upon southern sea lions *(Otaria flavescens)* and southern elephant seals *(Mirounga leonina).* They also found that killer whales fed predominantly on pups and small juveniles.

Based on the patterns of killer whale predation on species similar to Steller sea lions, a strong case can be made that a higher proportion of pups are killed than is reflected in the questionnaire data. We suspect that killer whale predation on sea lion pups and juveniles peaks while animals are congregated at rookery sites. Several observers reported that killer whales spent more time near haulout and near-shore areas during the pupping season than during the rest of the year. Baird (1994) found that the majority of predation events he witnessed on harbour seals occurred during the weaning and post-weaning period. In view of the low number of interactions witnessed near sea lion rookery and haul-out sites, we recommend that pinniped and killer whale researchers make a concerted effort in future to note the behaviour of killer whales in these areas. Their observations should include scans of the water surface after seeing killer whales mill in the area, to look for blood or blubber fragments. Whenever possible, killer whales should be photographed, in order to determine whether they are resident, transient or offshore whales.

CONCLUSION

The observations and photographs provided by the survey respondents supported earlier evidence that killer whales preying on Steller sea lions belong to the transient population. Most of the observations of sea lion attacks by killer whales involved young adult sea lions. These events were highly conspicuous, and generally continued for periods exceeding 1 hr. Relatively few attacks of pups were described, probably because such events occur underwater and are of short duration, making them difficult to observe. The survey data suggest that the greatest predation pressure on Steller sea lions in Alaska occurs in the Aleutian Island region, and the least in the Gulf of Alaska. However, there was an unequal distribution of observer effort in these areas, and further study is warranted,

ANALYSES OF STOMACH CONTENTS OF KILLER WHALES IN ALASKA AND BRITISH COLUMBIA

INTRODUCTION

Killer whale prey ranges in size from herring to blue whales (Hoyt 1984, Jefferson et al. 1991, Matkin and Saulitis 1994), and killer whales have often been described as opportunistic predators (eg. Martinez and Klinghammer 1970, Dahlheim 1981, Matkin and 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 individuals are specific in their choice of prey and foraging strategies, although the species as a whole feeds on a variety of marine life. Studies in the eastern North Pacific have led to the identification of fish-eating resident and mammal-eating *transient* killer whales. In this chapter, we compile recent stomach content data for killer whales from this area, and report the relative frequency of occurrence of each identified prey type. We also review reports of stomach contents of killer whales from around the world.

Stomach Content Data from Around the World

Killer whales in other oceans have been documented to feed on a similar range of prey species as do killer whales in the North Pacific: fish, cephalopods, marine mammals, and birds. Analysis of stomach contents provides evidence that feeding specialization is common. Virtually all stomach. contents reported contained either marine mammals or fish, but not both (Zenkovich 1938, Tomilin 1957, Nishiwaki and Handa 1958, Betesheva 1961, Rice 1968, Jonsgard and Lyshoel 1970). For example, out of ten stomachs collected from the North Pacific by Rice (1968), two contained the remains of fish, six contained marine mammals, and two stomachs were empty. Evidence from Soviet whaling data suggests a similar diet separation 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 stomachs from the yellow killer whales contained fish, and 90% of the stomachs from the white animals contained marine mammals. Ivashin and Votrogov (1981) examined 362 stomachs, also taken from Antarctic killer whales. Sixty percent of stomachs contained only fish, 30% contained only minke whale *(Balaenoptera acutorostrata)* remains, 5% contained only squid, and 5% contained only pinnipeds. Of 28 killer whale stomachs taken in the southern Indian Ocean, 47% contained only minke whale remains, 36% contained both minke whales and pinnipeds, and 7% contained only pinnipeds (Mikhalev et al. 1981). Killer whale stomachs collected in April northwest of Bouvet Island, in the southern Atlantic, contained only dolphin remains (Budylenko 1981). An exception to the trend in stomach content data is in stomachs collected from killer whales in the Weddell Sea during the month of January: of nine stomachs examined, two contained a mixture of pinnipeds and fish (Mikhalev et al. 1981).

The stomach contents of stranded killer whale carcasses have also provided valuable dietary information. Unfortunately, such opportunities occur relatively infrequently, perhaps partly due to low killer whale mortality rates. For resident whales in British Columbia, mortality rates range from 0.011 for adult females to 0.018 for juveniles to 0.039 for adult males (Olesiuk et al. 1990). In addition, killer whale carcasses generally sink (Zenkovich 1938). From 1973 to 1987 in British Columbia, only 14 carcasses were recovered, of which 8 were neonates (Olesiuk et al. 1990). In Alaska, twenty killer whale strandings were recorded between 1975 and 1987 (Zimmerman 199 1).

RESULTS

Table 3.1 lists the stomach contents of 22 killer whale carcasses from the eastern north Pacific. This includes five killer whale carcasses that have washed ashore since 1990 in the waters around Prince William Sound, Alaska. Fourteen of the carcasses discussed were found in British Columbia, the remaining were in Alaska. Six of the 22 stomach contents contained fish, 8 contained marine mammal remains and the rest were either empty or contained an insufficient quantity of prey fragments to provide reliable feeding information. Table 3.2 summarizes the stomach contents of eight whales that contained marine mammals and were likely transients. The remains of harbour seals were found in all eight of these stomachs, and seven of the stomachs contained more than one prey species. Whale and porpoise fragments were the next most commonly found prey. Sea lion and bird remains were found with equal frequency. Appendix 3 is a detailed summary of the material recovered from the killer whale stomach from Culross Island in 1990.

Several stomachs contained seal and sea lion whiskers. To determine how many prey these whiskers represented, we divided the total whisker count by the average number of whiskers present on a single animal. As whisker counts were not easily found in the literature, we present the raw data used to determine the average number of whiskers per seal and sea lion in Appendix 4. The whisker count yielded a higher number of predated animals than did the number of bone fragments, claws or teeth. Also of interest in this study is the recovery of 15 Steller sea lion flipper tags from a killer whale stomach (two of the tags were from one sea lion). The tags were applied to pups in 1988 and 1989, on Marmot Island, as part of a study by the National Marine Mammal Laboratory, Seattle, WA. Appendix 5 lists the tag number and year of tagging of each animal. Researchers reported that killer whales were not observed in the area at the time of tagging (D. Calkins, pers. comm.).

For comparison with our findings, the frequency of attacks and kills of southern sea lions reported by Hoelzel (1991) is presented in Table 3.3. Although Hoelzel witnessed 96 attacks on adult sea lions, none was fatal, whereas 39% of the 209 attacks on pups were fatal. Table 3.4 presents data from Matkin and Saulitis (1994) which summarizes the number of documented non-lethal and fatal killer whale attacks on all Alaskan marine mammal species.

Table 3.1. Stomach contents of killer whales from British Columbia and Alaska. (Area: PWS= Prince William Sound; SEA= Southeast Alaska. ID= alpha-numeric identification number, listed where known. Sources: PBS = Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, BC.).

YEAR	AREA	FORM (ID)	STOMACH CONTENTS	Source
KNOWN RESIDENTS AND/OR WHALES WITH STOMACHS CONTAINING FISH REMAINS				
1973	Vancouver Is., BC	Resident(B04)	empty, halibut hook embedded in lower lip	PBS
1977	Victoria, BC	Resident (L8)	fishing lure and fish scales	K. Balcomb/PBS
1986	Port Renfrew BC	Resident(L66)	4 fishing hooks, 2 chinook	PBS
1989	Tofino, BC	Resident (L14)	2 fish hooks, 1 salmon sp.	PBS
1990	Malcolm Is. BC	Resident (A09)	18 Chinook salmon, 1 salmon sp., 15 lingcod 5 greenling, 8 English sole, 2 sanddab, 2 Dover sole, 2 starry flounder, 1 rex sole, 1 rock sole, 1 curlfin sole, 1 staghorn sculpin, 1 great sculpin, 1 sablefish	PBS
1994	Burke Channel BC	Resident (A53?)	1 salmon sp., halibut hook	K.Heise
KNOWN TRANSIENTS AND/OR WHALES WITH STOMACHS CONTAINING MARINE MAMMAL REMAINS				
1976	Tofino, BC	?	2 harbour porpoises, 20 harbour seals (based on 394 claws), unidentified pinniped whiskers	PBS
1979	Boundary Bay, BC	Transient (O1)	unidentified cetacean, elephant seal, harbour seal, 2 white-winged scoters, squid	PBS
1981	Bamfield, BC	?	harbour seal, gray whale, cormorant	PBS
1989	Tlell, BC	?	harbour seal flippers and unidentified teeth	J. Fulton/PBS
1990	Culross Is. PWS	?	bones, whiskers and hair from adult and juvenile harbour seal, 18 teeth (13 confirmed harbour seal, 5 probable harbour seal), 1 Dall's porpoise (Appendix 3)	L. Barrett-Lennard & K. Heise
1990	Beartrap Bay, PWS	Transient (AT19)	empty	K.Wynne
1991	Cape St. Elias Gulf of AK	?	Sub-adult sea lion including skull, harbour seal, Dall's porpoise	K.Wynne

Table 3.1 cont.. Stomach contents of killer whales from British Columbia and Alaska.

Year	Area	Form (ID)	Stomach Contents	Source
1992	Montague Is. PWS	?	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	E. Saulitis
1992	Cook Inlet AK	?	Regurgitated 1 harbour seal flipper and pieces of beluga while stranded.	D.Bain
OFFSHORE WHALES				
1994	Barnes Lake SEA	Offshore	Crab shell and eel grass	D.Bain
UNKNOWN				
1987	Moresby Is. near Victoria, BC	? (male)	empty	PBS
1987	Uclelet, BC	? (calf)	empty	PBS
1989	Burke Channel, BC	?	2 fish eye lenses, 1 halibut hook and gangion,	PBS
1991	Montague Is. PWS	?	2 circle hooks with gangion and stainless steel snap, small pieces of plastic	L. Barrett-Lennard & K. Heise
1993	Manley Is.	?	Fish eye lens, feather fragment	L. Barrett-Lennard, G. Ellis & Tom
Smith				
1993	St Pauls Is. Pribilofs	(young male)	500g bull kelp, 1 very large squid or medium sized octopus beak, 1 medium sized squid beak, 1 common murre	A. Springer & M. Williams

* Stomach contained 15 tags from 14 Steller sea lions (two tags were from the same animal).

Table 3.2. Summary of prey recovered from eight killer whale stomachs containing marine mammals.

Prey Species	Number of Stomachs (n=8)
Harbour seal	8 (100%)
Porpoise	3 (38%)
Whale	3 (38%)
Sea lion	2 (25%)
Elephant seal	1 (13%)
Bird	2 (25%)
Squid	1 (13%)

Table 3.3 Age classes of southern sea lions attacked by killer whales in Argentina and of Steller sea lions attacked by killer whales in this study.

	Hoelzel 1991. (southern sea lions)		This study (Steller sea lions)	
	Non-lethal Attacks	Kills	Non-lethal Attacks	Kills
Pups	127 (53.8%)	82 (99%)	0 (0%)	2 (6%)
Subadults	13 (5.5%)	1 (1%)	3 (15%)	5 (16%)
Adults	96 (40.7%)	0 (0%)	12 (60%)	16 (50%)
Not Stated			5 (25%)	9 (28%)
Total	236	83	20	32

Table 3.4 Incidences of attacks on and/or predation of Alaskan marine mammals by killer whales from previously published data (modified from Matkin and Saulitis 1994).

Species	No. Attacks	No. Kills	No. Stomachs	Total
Dall's porpoise (*Phocoenoides dalli*)	10	1	1	12
Harbour porpoise (*Phocoena phocoena*)	2	4	3	9
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	2	0	0	2
Beluga (*Delphinapterus leucas*)	3	9	1	13
Baird's beaked whale (*Berardius bairdii*)	0	0	1	1
Cuvier's beaked whale (*Ziphius cavirostris*)	0	0	1	1
Short-finned pilot whale (*Globicephala macrorhynchus*)	0	0	1	1
Sperm whale (*Physeter macrocephalus*)	1	0	0	1
Humpback whale (*Megaptera novaeangliae*)	4	0	0	4
Gray whale (*Eschrichtius robustus*)	5	4	1	10
Minke whale (*Balaenoptera novaengliae*)	2	5	0	7
Right whale (*Eubalaena glacialis*)	2	0	0	2
Sei whale (*Balaenoptera borealis*)	0	0	1	1
Fin whale (*Balaenoptera physalus*)	4	3	1	8
Bowhead whale (*Balaena mysticetus*)	2	1	0	3
Ringed Seal (*Phoca hispida*)	0	0	1	1
Bearded seal (*Erignathus barbatus*)	0	0	3	3
Northern fur seal (*Callorhinus ursinus*)	1	2	2	5
Harbour seal (*Phoca vitulina*)	7	9	7	23
Steller sea lion (*Eumetopias jubatus*)	12	4	2	18
Northern elephant seal (*Mirounga angustirostris*)	1	0	3	4
Pacific walrus (*Odobenus rosmarus divergens*)	3	6	1	10
Sea otter (*Enhydra lutris*)	2	2	0	4

DISCUSSION

Stomach contents

Stomach content analysis gives clear evidence of the prey species eaten by killer whales. Less clear is the relative importance of prey, since identifiable remains such as bones, claws and whiskers may be digested and expelled at different rates. If prey are not swallowed whole, the parts eaten may influence the analysis results. 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 (Appendix 3). Had digestion proceeded much further, it is unlikely we would have detected porpoise in the stomach as the material would have deteriorated beyond recognition. Tomilin (1957) reported that killer whales often ate only the fluke portion of porpoises. The Culross Island whale also had seal skin in its stomach, yet on other occasions, killer whales have removed and discarded the skin of harbour seals before consuming the seals (Barrett-Lennard, Ellis, Heise, unpubl. data).

The results presented in Table 3.1 support the segregation of killer whales into at least two forms, those that eat fish (residents) and those that eat marine mammals (transients). One transient whale (recovered in 1979 in Boundary Bay, BC) contained squid as well as parts of several marine mammals and birds. The squid may have been the prey of one of the marine mammals or birds, or it may have been taken directly by the killer whale. A second whale (collected in St. Paul Island in 1993) of unknown population status, contained bird and cephalopod remains. Thus, while it is possible that transients occasionally feed on cephalopods, there is no indication that they take fish. Likewise there is no evidence that residents take any warm-blooded prey.

Little diet information is available on the offshore form of killer whale that has recently appeared along the coast of British Columbia. The stomach contents reported here from the killer whale recovered from Barnes Lake in southeast Alaska suggest that they do not prey on marine mammals, as no bones were recovered. However, this observation should be interpreted cautiously, as the animal had been trapped in the lake for several weeks prior to death, and may have had time to expell or digest completely and remains of its usual prey. Offshore whales have been observed apparently feeding on salmon off the Queen Charlotte Islands (John Ford pers. comm.).

Harbour seals were found in all eight stomachs that contained marine mammal remains and were the predominant prey item, followed by porpoises and other cetaceans (Table 3.2). The stomach of one killer whale contained the remains of 20 harbour seals, a second stomach contained the remains of 18 harbour seals and all other transient stomachs contained the remains of at least one harbour seal. Similarly Ford et al. (in prep.) found that the majority of predation by transient killer whales witnessed by mariners from Frederick Sound, Alaska, to the Gulf Islands in British Columbia, involved harbour seals (58%). Only 11% were kills of sea lions (both California and Steller). From a review of the prey items of killer whales in Alaska by Matkin and Saulitis (1994), harbour seals and beluga whales were the most commonly reported marine mammal prey (summarized in Table 3.4 in this study). The two killer whale stomachs that contained Steller sea lions were the same as those described in more detail in Table 3.2.

Of the 18 Steller sea lion/ killer whale interactions listed by Matkin and Saulitis (1994), only 6 (33%) involved sea lion mortality, whereas 70% (16) of 23 harbour seal/ killer whale interactions were fatal attacks. In addition to the attacks on marine mammals, Matkin and Saulitis also presented 51 reports of predation on fish and 10 predatory attacks by killer whales on seabirds. These results are similar to those of Jefferson et al. (1991) who reviewed killer whale interactions with marine mammals from around the world and found that in the northern hemisphere, harbour seals were the most commonly reported prey species.

Prey sharing

Although two of eight transient whale stomachs contained Steller sea lion remains (Table 2), it is unlikely that individual killer whales kill and consume an entire sea lion. Prey sharing is probably common, as suggested by the observation in Chapter 2 that sea lions were attacked by groups of transient killer whales. Hoelzel (1991) reported observing food-sharing directly in at least 34 of 83 predations of southern sea lions by killer whales and had indirect evidence that over 70 % of prey were shared. As southern sea lions are smaller than Steller sea lions (adult males weigh 200-350 kg, adult females weigh about 140 kg), it is likely that food-sharing takes place at least as often when killer whales consume Steller sea lions. Baird (1994) reported that killer whales foraging for harbour seals off Vancouver Island did so in groups averaging 3.3 whales. He observed food-sharing in 51 percent of all harbour seal kills witnessed.

Age classes and the success rate of attacks

Of special interest in this study were the stomach contents recovered from the killer whale in Prince William Sound in 1992 with tags from 14 Steller sea lions in its stomach (Table 3.1, Appendix 5). Two of the tags were consecutively numbered, suggesting that the pups may have been captured by the killer whale near the time of tagging. However, pups normally remain on shore until about 28 days old. D. Calkins (pers. comm.) reported that immediately after the tagging and branding process in 1988 and 1989 on Marmot Island, few sea lions went into the water, As well, killer whales were not seen in the area at the time of tagging. An alternative but less parsimonious explanation may be that the sea lion pups dispersed from the rookery as a group, and were attacked by the killer whale somewhere between Marmot Island and Prince William Sound.

It is possible that individual killer whales may specialize in hunting certain species of mammalian prey. For example, Saulitis (1993) reported specialization in the “AT1” group of transient killer whales in southwestern Prince William Sound, Alaska. They seem to forage primarily for Dall’s porpoises and harbour seals, and frequently pass close to Steller sea lions without initiating any obvious interactions. A less commonly seen group of transient killer whales in Prince William Sound (the “AC group”) has been observed attacking Steller sea lions (R. Corcoran, C. Thoma, T. Edwards, pers. comm.). Possible hunting specialization has also been observed in southern British Columbia, where certain groups of transients appear to forage specifically for harbour seals (Baird 1994), largely ignoring the Steller and California sea lions that haul out in the same area. Baird also found that individual killer whales varied in their foraging behaviour, in that some hunted along shorelines most often and others hunted offshore (see also Saulitis 1993, Barrett-Lennard et al. in press).

Hoelzel (1991) found that the capture rate of southern sea lions varied markedly among individual killer whales. One whale had a 100% success rate attacking southern sea lions (n=7 observations), a second whale had a 57% success rate (n=28) and a third whale had a 0% success rate (n=6). The method of attack also strongly affected the success rate. Of 319 attacks witnessed, only 83 (26%) were successful, and except for one animal, all animals killed were pups (summarized in Table 3.5). Lopez and Lopez (1985) found that killer whales fed predominantly on pups and small juvenile southern sea lions *(Otaria flavescens)* and southern elephant seals *(Mirounga leonina).* These two studies in Argentina, combined with the stomachs containing sea lion tags and the observations reported in the previous chapter of killer whales near rookery sites, suggest that predation may be an important component in pup and juvenile mortality.

CONCLUSION

Our review of the stomach contents of 22 killer whales has substantiated the field observations of diet differences between residents and transients; killer whales are specialists on either marine mammals or fish. Six whale stomachs were empty, and six others were of known resident whales and./ or contained fish remains. Harbour seals were found in all eight killer whale stomachs that contained marine mammals, and Steller sea lions were found in two of these stomachs.

TRANSIENT KILLER WHALE POPULATION ESTIMATE FOR THE EASTERN NORTH PACIFIC

INTRODUCTION

Killer whales are remarkably variable in the shapes of their dorsal fins and in their pigmentation patterns. This makes it relatively easy to identify individuals from good quality black-and-white photographs. Killer whale photo-identification studies have been ongoing in British Columbia and northern Washington State for 23 years (see Bigg et al. 1987, Ford et al. 1994a for overview). These studies have shown clearly the existence of at least three distinct non-associating forms of killer whale: fish-eating *residents*, mammal-eating *transients*, and an as yet poorly understood group provisionally called *offshores.* Prior to the photo-identification studies of the late 1970's, it was commonly thought that thousands of killer whales lived along the B.C. coast. By 1987, only 250 residents and 80 transients had been counted in northern Washington and the southern half of the British Columbia coast, and it was apparent that the entire population was in the hundreds, not thousands (Bigg et al. 1987). Surveys have continued in southern B.C. and northern Washington, and more northerly parts of the mainland British Columbia coast. These efforts have now identified a total of 734 whales, comprising 364 residents, 170 transients, and approximately 200 offshores (Bigg et al. 1987, Ellis unpubl. data, Ford et al. 1994 a,b,).

In Prince William Sound, Alaska, photo-identification research has been ongoing for 13 years, and resident and transient populations have been well described (Ellis 1984, 1987; Heise et al. 1992). However, few systematic surveys have been undertaken in western Alaska (Dahlheim and Waite 2993, Dahlheim 1994). Aerial surveys, such as those conducted by Leatherwood et al. (1983) and Brueggeman et al. (1987), have been useful for determining distribution and relative abundance of killer whales, yet population estimates based on these surveys have large confidence intervals. This is because of the difficulties associated with quantifying the probability of individuals being double-counted. Such surveys also provide little or no information on feeding ecology and stock identity, and thus are of limited utility to a study such as this.

Association patterns have proven to be one of the most unequivocal methods for distinguishing between residents and transients. In over 20 years of research in British Columbia and Alaska, transient killer whale groups have been seen associating regularly with other transient groups, and resident pods have been observed in association with other residents. If a whale is seen travelling with a group of transients, it has not been seen later associating with residents. With the exception of one aggressive interaction (Ellis unpubl. data), residents and transients have never been seen associating.

Vocal behaviour is also a reliable method for distinguishing between residents and transients. However, this information is rarely collected except by those studying killer whale acoustics, and recordings were not available for use in this study. The morphology of the dorsal fin and characteristics of the saddle patch pigmentation (gray area below the dorsal fin) are also used to distinguish residents and transients (Baird and Stacey 1988b, Ford et al. 1994a), but these designations are more subjective than the previous two methods and require judgement by those experienced in photo-identification.

METHODS

To estimate transient population size in Alaska, data were drawn from photo-identification studies from British Columbia, southeast Alaska and Prince William Sound (Bigg et al. 1987, Ellis 1984, 1987, Heise et al. 1992, Ford et al. 1994b), and from databases maintained by the Pacific Biological Station (PBS, Department of Fisheries and Oceans, Nanaimo, B.C.) the North Gulf Oceanic Society (NGOS, Homer, Alaska), and the National Marine Mammal Laboratory (NMML, National Marine Fisheries Service, Seattle, WA). Individually identified killer whales from the PBS and NGOS databases had been previously categorized as resident, transient, or offshore based on association patterns and vocal characteristics.

Recent summaries of the NMML photographic database (Dahlheim and Waite 2993, Dahlheim 1994) did not distinguish between resident and transient killer whales. However, NMML kindly allowed two of the authors of this report (Barrett-Lennard and Ellis) to view the NMML collection of identification photographs to estimate the number of transient whales within Alaska. These authors screened the NMML photographs for matches with whales identified in the PBS and NGOS databases. Whales that had not been previously identified but were travelling with matched whales were classified by association. For example, if unmatched whale *a* was photographed by NMML while travelling with whale *b*, and *b* had been previously identified as a transient, then we classified *a* as a transient as well. If it was not possible to classify individuals by association, then they were distinguished as either resident or transient based on dorsal fin morphology and saddle patch pigmentation pattern. To test the consistency of these classifications, author Heise and J. Ford (Vancouver Aquarium) repeated the classification of resident or transient status independently, using good quality photocopies of the photographs.

RESULTS

A summary of the results of the review of published and unpublished material on killer whale population size is presented in Table 4.1. The killer whale population size in the eastern North Pacific is at least 1,345 whales, including 258 identified transients. Estimates of transient numbers in Prince William Sound and in British Columbia and southeast Alaska were obtained from previously published reports (Bigg et al. 1987, Heise et al. 1992, Ford et al. 1994a,b). Examination of the southeast Alaska photographic database held by NMML yielded no new identifications of adult killer whales. However, a total of 35 transients were identified from the NMML photographs taken in the waters west of Prince William Sound. Two of these transient whales were identified by association with previously identified transients, but 33 were new individuals and were considered transient-type based on morphology. Ford and Heise's independent designations of residents and transients matched those provided by Ellis and Barrett-Lennard in all cases.

Table 4.1. Killer whale population estimates for Alaska and British Columbia, by region.

REGION	POPULATION ESTIMATE (Proportion of total) Resident	Transient	Offshore	TOTAL	REFERENCE
Southeast Alaska[1], B.C., and Washington	364 (49%)	170 (23%)	200(28%)	734	Ford et al. 1994a,b, Ellis unpubl. data
Prince William Sound	28.5 (84%)	55 (16%)		340	Heise et al. 1992. Ellis unpubldata
Western Alaska[2]	238 (88%)	33 (12%)		271	Dahlheim 1994, NMML database
TOTAL	887 (66%)	258 (19%)	200 (15%)	1,345	

[1]East of 142° W longitude [2]West of 142°W longitude

DISCUSSION

Our principal objective was to determine the number of transient killer whales in Alaska. As can be seen from Table 4.1, although 340 whales have been individually identified in the waters of Prince William Sound, only 55 are transients (16%). This is similar to the situation in western Alaska, where 33 out of 27 1 whales (12%) are transient type. In British Columbia and south-east Alaska, where over 755 whales have been identified, 170 animals are of the transient form (23%). The higher transient-to-resident ratio in southern waters relative to northwestern waters may simply reflect differences in the survey methods and effort that have been applied in the two areas. However, photographic studies of killer whales in Prince William Sound have been ongoing since the mid-1970's, yet the proportion of transients found there is substantially less than the proportion of transients found in the British Columbia killer whale population.

Examination of the NMML photographs taken in southeast Alaska during surveys in 1992 and in 1993 did not yield any new adult animals that had not previously been identified. No transient individuals have been sighted both in western Alaska and in southeast Alaska or British Columbia. This was surprising given the large distances transient whales in British Columbia are known to travel. For example, two individual transient killer whales photographed in Glacier Bay, Alaska, were subsequently resighted off Monterey Bay, California, a distance of over 2,600 km (Goley and Straley 1994).

CONCLUSION

Based on reviews of both published and unpublished material, we estimate a transient population size of 170 whales from Washington to southeast Alaska, and 88 whales for Prince William Sound and western Alaska, for a total of 258 animals. As transients are known to range over 2,600 km, it is unlikely that 258 transients would be found at one time in Alaskan waters. No individual transients have been sighted in both the western and eastern parts of the study area. The ratio of identified transients to identified residents is highest in southern waters, and lowest in western Alaska.

STELLER SEA LIONS AND KILLER WHALES: A SIMULATION STUDY

INTRODUCTION

Three possible causes of the dramatic decline of Steller sea lions in Alaska have attracted attention in recent years: (1) shooting or entanglement in fishing gear (Trites and Larkin 1992, Trites 1995); (2) diseases and parasites (Spraker et al. 1993); and (3) reductions in the quality or availability of food (Trites and Larkin 1992, Castelleni 1993, Fritz et al. 1993). Most researchers have considered that predation mortality is probably small, and an insignificant factor in the decline. In 1992, however, flipper tags from 14 Steller sea lions were found in the stomach of a single dead killer whale in Prince William Sound. This incident raised concern that predation may in fact be more significant in sea lion population dynamics than previously thought, and may have exacerbated or even caused the decline.

In this chapter, simulation models are used to examine the potential impact of killer whale predation on sea lion populations in British Columbia and Alaska. The exercise provides estimates of the effect of this predation under differing assumptions about predator and prey behaviour, and across ranges of parameter estimates. At the end of the chapter, we discuss the model results in the context of the ecology and distribution of both the predator and the prey, and comment on the types of data that would improve the precision of the impact estimates.

SIMULATION MODELS

We used a deterministic age-structured model with population observations at discrete time intervals (Leslie 1945) as a common framework throughout the analysis, and modified it to incorporate different assumptions about predation patterns. The key parameters used in the model were (1) the number of transient killer whales, (2) the food consumed by each, (3) the proportion of their diet supplied by sea lions, (4) the initial sea lion population size, and (5) the intrinsic growth rate of sea lion populations. We varied the values of these parameters within ranges that were based on information from previous chapters, from the literature, and from census data.

Two simplifying assumptions were common to all versions of the model. Fist, we assumed that sea lion populations have the potential to grow exponentially, without density dependent limiting mechanisms. We made this assumption because we were most concerned with the behaviour of the model at low population densities, and because mechanisms of density dependence are poorly understood in pinnipeds (Trites 1990). Second, we did not include numerical responses of killer whales to changes in sea lion numbers. Transient killer whales take a variety of alternative prey (Chapter 3), and thus are buffered against the depletion of any single prey species. In addition, the slow generation time of killer whales (Olesiuk et al. 1990) means that any increase in killer whale numbers in response to increases in sea lion population growth would be minor in the time frame of the model.

Model structure

The sea lion population data were stored in a matrix of 2 sexes and 3 1 cohorts representing yearly age increments. Young of the year, (pups) were assigned an age of 0. The number of sea lions of a given sex alive in a cohort of age x at time t was designated $N_{g,x,t}$ where g designated gender (g=l for males and g=2 for females). The age structure used at the starting point of the model was from York (1990). Pups were introduced into the model each year by multiplying the number of females in each cohort by the age-specific fecundity, b_X (from Calkins and Pitcher 1982). An equal sex ratio of pups was assumed, therefore

$$N_{g,0,t} = 0.5 \sum_{x=1}^{30} b_x N_{2,x,t} \quad . \tag{1}$$

To advance cohorts from one year to the next, we used age- and sex-specific survival rates, $s_{g,x}$ (from York 1990; re-scaled by Trites and Larkin 1992). These survival rates resulted in zero population growth. Growth was set by multiplying the survival rates by the intrinsic rate of population increase *(r)*, where $rs_{g,x}$ was limited to a maximum value of 1. Thus, in the absence of predation the number of sea Lions of each sex in cohorts 1 to 30 was

$$N_{g,x,t} = r N_{g,x-1,t-1} s_{g,x-1} \quad (x>0), \tag{2}$$

and the total population at the end of the pupping season in any given year, P_t , was

$$P_t = \sum_{g=1}^{2} \sum_{x=1}^{30} r N_{g,x-1,t-1} s_{g,x-1} + \sum_{x=1}^{30} r b_x N_{2,x-1,t-1} s_{2,x-1} \, . \tag{3}$$

We added terms to the basic model above to simulate (I) non-age-specific predation, (2) age-specific predation, and (3) age-specific, frequency-dependent predation. Each of these modified models is described below.

Model 1: Non-age specific predation.

This model had two key assumptions. First, a fixed proportion of a transient killer whale's diet, *d*, was composed of sea lions. Second, killer whale predation was not age- or sex-specific. **Thus,** sea lions from a sex-age class were preyed on in proportion to the ratio of the size of that class to the entire population size. Assuming that *m* kg/day of marine mammals were eaten per transient killer whale, the biomass in kg of sea lions consumed annually *(C)* by a population of *K* transient killer whales was

$$C = 365 \, mdK \, . \tag{4}$$

The total biomass in kg of sea lions alive at a given time, B_t, was calculated as folIows:

$$B_t = \sum_{g=1}^{2} \sum_{x=0}^{30} N_{g,x,t}\, w_{g,x} \ , \qquad (5)$$

where $w_{g,x}$ is the average weight of individuals by age-and-sex category (Figure 5.1). The number of sea lions of an age-and-sex category that were consumed in a given year, $c_{g,x,t}$, was

$$c_{g,x,t} = N_{g,x,t}\, C \,/\, B_t \qquad (6)$$

Thus, age-sex classes were advanced from one year to next as follows

$$N_{g,x,t} = r\, N_{g,x-1,t-1}\, s_{g,x-1} - c_{g,x-1,t-1} , \qquad (7)$$

and pups were introduced into the population as in equation 2.

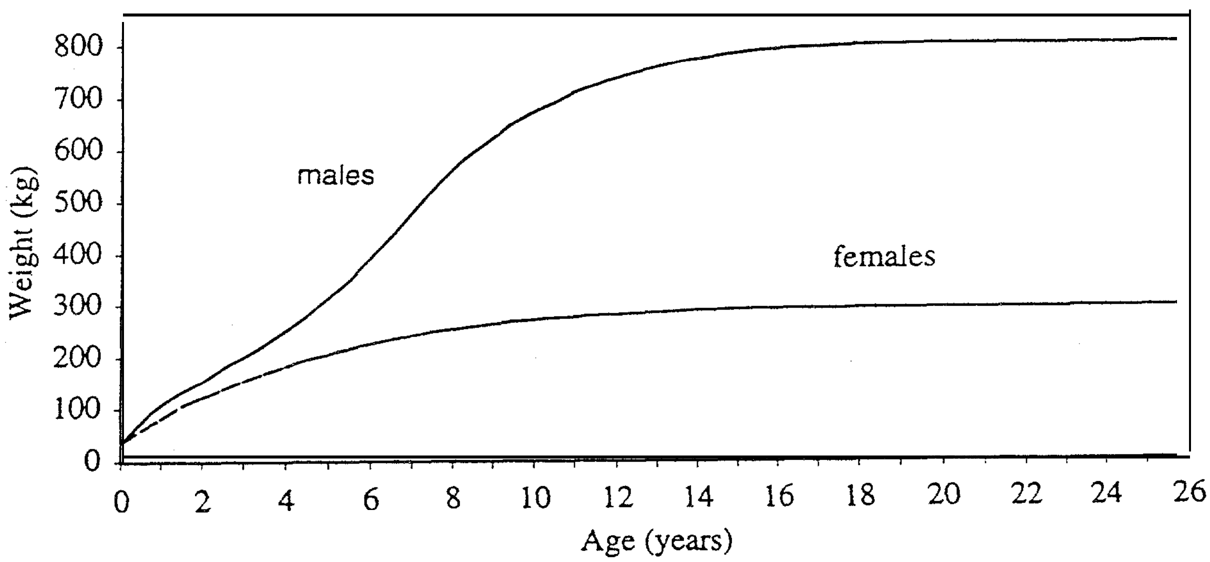

Figure 5.1 Average weights for male and female Steller sea lions from ages 0 to 30 years. The curves are based on age-length regressions for Steller sea lions from the Golf of Alaska (McLaren 1993), with length converted to mass by scaling the allometric relationships in Trites and Bigg (in press), and corrected slightly based on data in Calkins and Goodwin 1988.

Model 2: Age-specific predation.
As with Model 1, this model assumed that a fixed proportion of a transient killer whale's diet was made up of sea lions, and that killer whale numbers remained constant. Thus, the value of C was the same as in Model 1. The vulnerability of sea lions to predation, however, varied with age. A vulnerability parameter, v_x , was set to a value of 1 for pups, reduced to a value of 0.2 for adults, and increased back to 1 for very old sea lions (Figure 5.2). Both sexes were considered equally vulnerable at each age. To determine the number of sea lions consumed in each age-sex class, we first calculated $Z_{g,x,t}$, the number of sea lions in each class weighted by their vulnerability:

$$Z_{g,x,t} = v_x N_{g,x,t} \,. \qquad (8)$$

We then substituted $Z_{g,x,t}$ for $N_{g,x,t}$ in equations 5 and 6. Individuals moved from one age class to the next as shown in equation 7, using the new values of $c_{g,x,t}$.

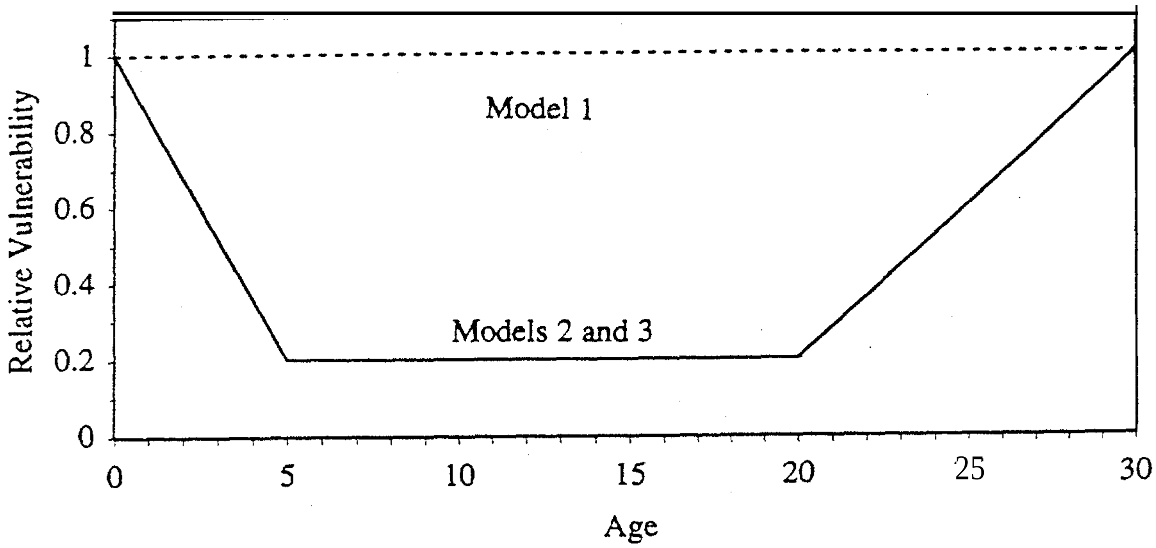

Figure 5.2 Relative vulnerability of Steller sea lions from ages 0 to 30 years to predation by transient killer whales. Model 1 assumes that predation is not age specific, models 2 and 3 assume that vulnerability varies with age.

Model 3: Age-specific, density-dependent predation.
This model had the same form as Model 2, except that the annual biomass of sea lions consumed by transient killer whales, C , depended on total sea lion numbers. We modelled two kinds of dependence relationships: Types II and III, in Helling's (1959) classification of functional responses (Figure 5.3). The following equation replaced equation 4:

$$C_t = 365mKD_t, \tag{9}$$

where D_t is the functional response, expressed as the proportion of a transient killer whale's diet supplied by sea lions.

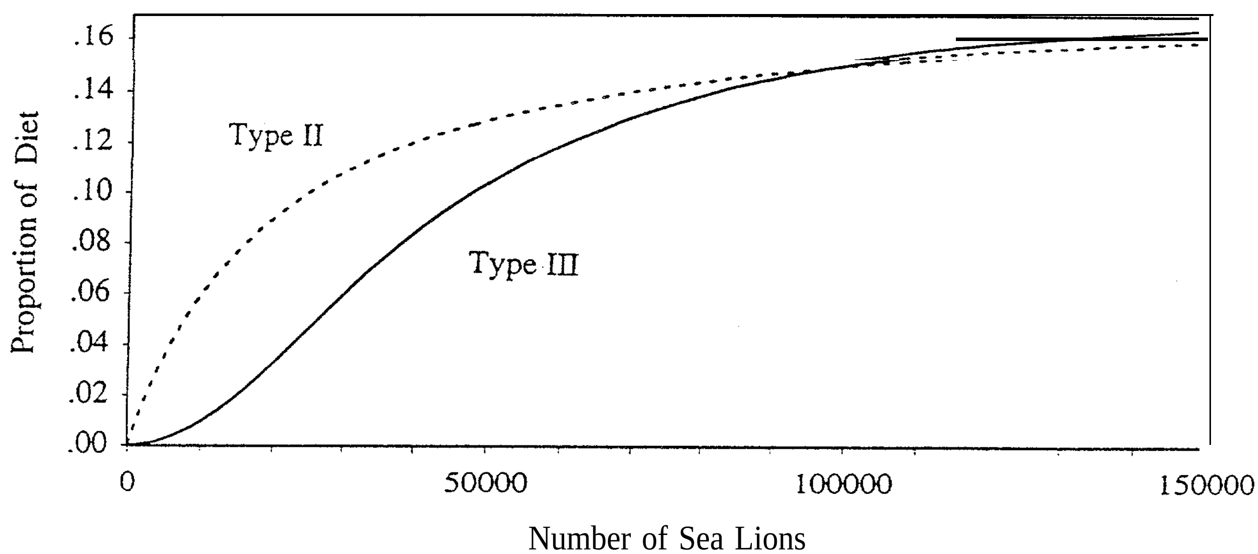

Figure 5.3 Hypothetical relationships between the proportion of Steller sea lions in the diet of transient killer whales and sea lion density. Holling's (1959) Type II and Type III functional responses are shown, where: (Type II) $D = 0.18-(0.18/(1+P/20000))$, and (Type III) $D = (N/100000)^2/(1+(N/100000)^2/.177)$, where D is the proportion of Steller sea lions in the diet and P is the sea lion population size. For both response relationships, D = .15 when P = 100,000.

PARAMETER ESTIMATES

Transient killer whale numbers

Transient killer whale numbers were based on the analysis of photo-identification data described in Chapter 4. Of the 258 identified transients from Alaska and British Columbia, 88 were photographed in Prince William Sound or further west, and the remainder were photographed from Glacier Bay east to British Columbia. No individuals were matched between both areas, thus, we refer to them here as the western and eastern transient assemblages, and place the dividing line at approximately 142° west longitude. The counts for each region probably include some individuals that have died since last being photographed. However, in the absence of data on population trends in transient killer whales, we assume that the population is approximately stable, and that these deaths have been compensated for by births.

Because few unknown transients have been sighted in British Columbia and southeast Alaska in recent years during extensive surveys, we believe that our count is close to the true number inhabiting the region. Transient killer whales known from southeast Alaska and British Columbia have been sighted as far south as California (e g. Goley and Straley 1994). However, these sightings are rare, and Alaska and British Columbia are thought to be core areas for these transients. We estimated for the sake of the model that approximately 125 (75%) members of the eastern assemblage are within the inshore waters of British Columbia and southeast Alaska at any given time.

In the waters west of Prince William Sound sighting effort is low, and some transient groups have been sighted only once. Thus, our count is probably somewhat lower than the actual number of transients inhabiting the area. To allow for the existence of presently unknown transient killer whales in the western assemblage, we used an estimate of 125. The combined total estimate used in the simulations for the coastal waters from southern British Columbia to the Aleutian Peninsula was 250.

Transient killer whale food consumption

Few data exist on either the caloric requirements of transient killer whales or the age/sex structure of their populations. We estimated food consumption rates using data from three sources: (1) consumption rates of fish by captive killer whales of known age and sex (Kriete 1995), (2) the estimated sex/age structure of a stationary population of resident killer whales (Olesiuk et al. 1990), and (3) the caloric value of the marine mammal prey of transient killer whales (summarized in Perez 1990). We derived estimated daily food consumption rates for whales of each sex in each age category (ages 0.5 to 60.5 years for males and 0.5 to 90.5 years for females) from Kriete's regression relationships, and multiplied each value by the proportion of the killer whale population estimated by Olesiuk to be in the corresponding age and sex category. The resultant values were summed to obtain an overall feeding rate of 84.3 kg fish/day/whale, or 176,000 kcal/whale/day. Figure 5.4 shows the age structure used, and the percentages of total consumption taken by the whales in each age/sex category.

The caloric content of the small pinnipeds that comprise the majority of the diet of transient killer whales is on the order of 3000 kcal/kg (obtained by averaging the values for northern fur seals and ringed seals summarized in Perez 1990). Dividing 176,000 kcal/day by 3000 kcal/kg gives a food consumption rate of 58.7 kg/day. The energetic requirements of wild killer whales hunting marine mammals is, however, likely to be substantially higher than that of captive whales being fed fish. We therefore applied a correction factor of 25%, giving an estimated feeding rate of 220,000 kcal /day, or 73 kg/day for transient killer whales. Baird (1994) estimated that wild transient killer whales consumed 62 kcal/day per kg of body weight when foraging for harbour seals. Dividing our caloric intake estimate by Baird's consumption by weight estimate gives an average killer whale weight of 3550 kg. This figure is reasonable in light of data on (1) the weights of captive whales

(Kriete 1995) and (2) the sex/age distribution in Figure 5.4, suggesting that our estimate and that of Baird are in approximate agreement.

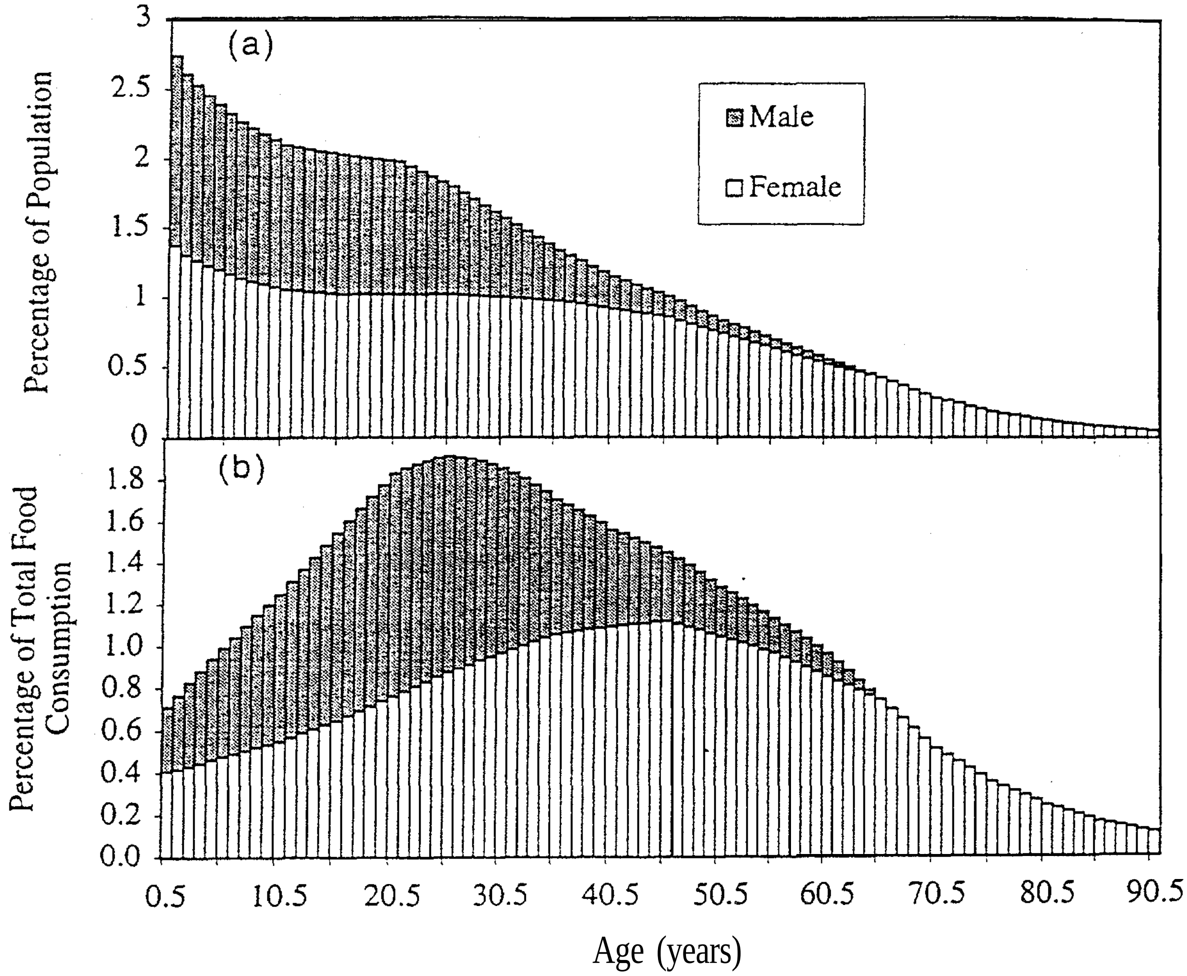

Figure 5.4 The estimated percentage of killer whales in each age/sex category in a stationary population (a; adapted from Olesiuk et al. 1990), and the total consumption taken by whales of each age/sex category (b). The figure shows, for example, that females between 40 and 41 years of age consume approximately 1.1% of the food eaten by a population of killer whales.

Sea lion population size

Sea lion populations have been censused periodically in Alaska and British Columbia since the mid 1950's. Between 1960 and the late 1970s the Steller population in Alaska numbered between 200,000 and 250,000 pups and adults (Loughlin et al. 1989, Trites and Larkin 1995), with the majority of animals concentrated in the Gulf of Alaska and along the Aleutian Islands. The population began to decline in the early 1970s in the eastern Aleutians (Braham et al. 1980), and declines were also noted elsewhere in the Gulf of Alaska and western Aleutians by 1979-8 1. The declines in each of these areas has continued to the present day. In 1994 the Steller population in the Gulf of Alaska and further west numbered approximately 42,500 (the product of Merrick's estimate of 33,600 non-pups and Trites and Larkin's pup correction factor of 1.27; Merrick 1994, Trites and Larkin 1995). In southeast Alaska the population has increased slightly in recent years, and in 1994 numbered approximately 14,500 animals (Merrick 1994, Trites and Larkin 1995). The estimated population in British Columbia in 1994 was 9,200 (P. Olesiuk, Canadian Department of Fisheries and Oceans, unpublished data). Thus, the number of Steller sea lions east of the Gulf of Alaska and north of Washington state was approximately 23,700; and the combined total for Alaska and British Columbia was 68,700. To consider the role of predation past and present, and to predict its effect should sea lion populations continue to decline, we used population numbers ranging from 200,000 to 10,000 in the simulation model.

Intrinsic growth rate of sea lion populations
Sea lion populations increased by approximately 4%/ yr in western Alaska from 1956 to 1967, and at the same rate in south-eastern Alaska from 1956-1992 (Trites and Larkin 1995). We therefore used 4%/ yr as a point estimate of the intrinsic population growth rate in the simulations, however we also investigated the behaviour of the models for growth rates to 8%.

Proportion of sea lions in the diet of transient killer whales
We estimate that between 10 and 15% of the diet of transient killer whales consists of sea lions, based on both the observed kill rates of sea lions by transient killer whales and the stomach contents of stranded killer whales presented in previous chapters. It is apparent, however, that there is a considerable uncertainty in this estimate. For example diet preferences may change seasonally and may vary between transient individuals or groups, and changes in the abundance of alternate prey, such as harbour seals, may affect the proportion of sea lions eaten by transient killer whales. Thus, in one simulation exercise we observed how different estimates of the rate of sea lion consumption affected the model predictions. When point estimates of the consumption proportions were required in other simulations, we used a value of 12.5%. For the Model 3 simulations, we used functional response curves that gave a predation rate of 15% for a sea lion population of 100,000, as shown in Figure 5.3.

SIMULATION RESULTS

In our initial simulations, we examined the effects of predation pattern on the growth trajectories of Steller sea lion populations. The model predicted that a sea lion population with an initial size of 100,000 animals would decline most rapidly with age-specific and density-independent predation of the type described in Model 2, becoming extinct in approximately 25 yrs (Figure 5.5). If predation was neither age-specific nor density-dependent as in Model 1, the rate of decline was slower (extinction at 56 yrs). The age-specific, Type II functional response model produced a rapid decline until very small population sizes, and resulted in extinction after 27 years. The Type III functional response model showed a gradual decline to a population of 9,000 over 50 years.

In the next set of simulations, we examined how changes in predation pressure affected the model results. We repeatedly ran simulations for a given sea lion population size while changing the size of the transient population. When a transient population size was found that maintained sea lion numbers at a constant level, the number of transients was recorded, the sea lion population size was incremented by 5000, and the process was repeated.

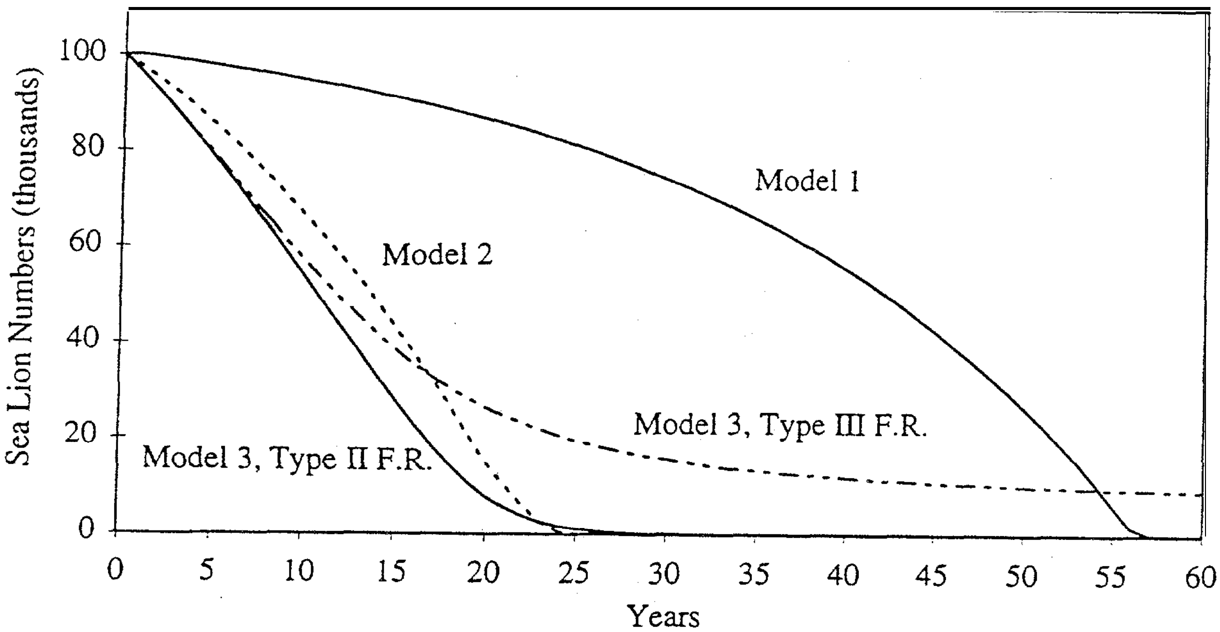

Figure 5.5 Sea lion population trajectories under four predation models (described in text). The following parameter values were used: transient killer whale numbers, 250; killer whale consumption rate, 74 kg/day; initial sea lion numbers, 100,000; sea lion intrinsic population growth rate, 4%; proportion of sea lions in transient killer whale diet, 0.125 for Models 1 and 2, as in Figure 5.3 for Models 3 Type II and 3 Type III.

Figure 5.6 shows the number of transient killer whales capable of maintaining a state of zero growth in different-sized populations of sea lions, under the assumptions of each model. Consumption rates were not varied in this exercise. However, consumption rate effects may be easily inferred from the figure, because changing the number of transients by a given factor was exactly equivalent to changing consumption rate by the same factor. As expected, when functional responses are not included, the number of transient killer whales required to prevent growth in a sea lion population increased linearly with sea lion numbers. The Type II functional response model was also approximately linear over the range of sea lion numbers used. The Type III functional response model, however, showed that the number of transients that could prevent Sea lion population growth was least when sea lions numbered approximately *42,000.*

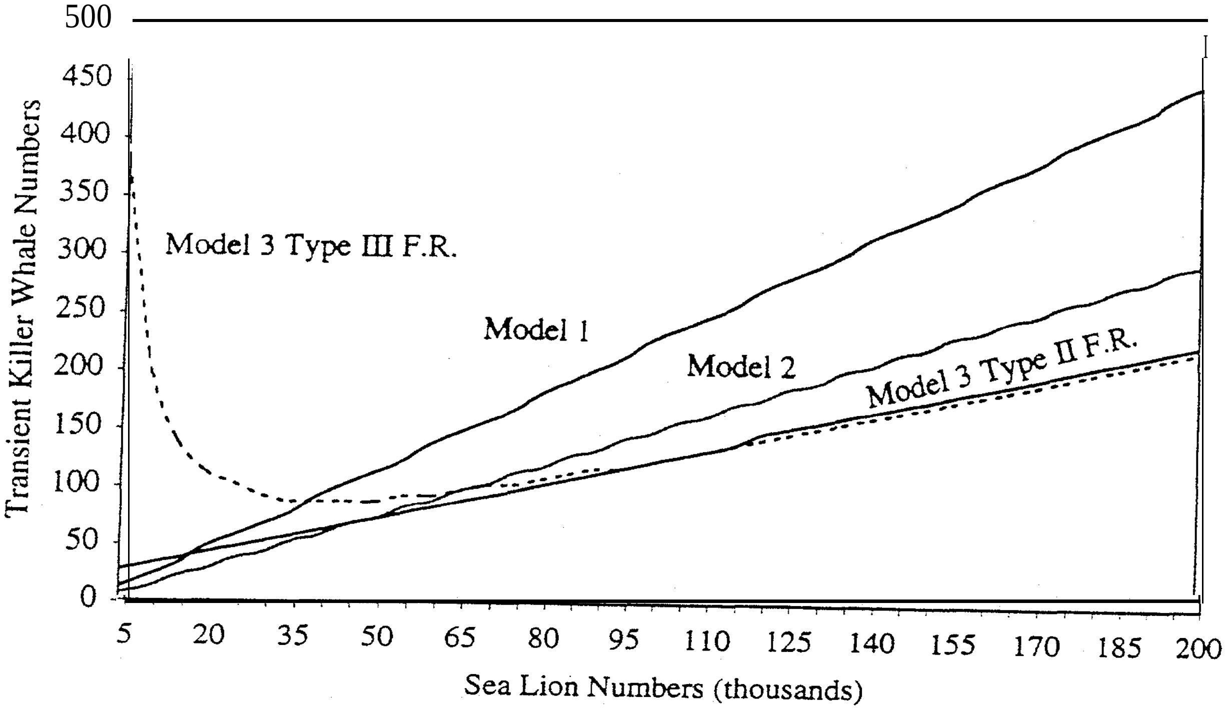

Figure 5.6 Transient killer whale numbers ensuring zero growth of sea lion populations, under four predation models. Parameter values as in Figure 5.5.

Next, we examined the effects of changes in *r* on the model results. Here, we used the age-specific, Type III functional response predation model, and *r* values of 4,6, and 8% (Figure 5.7). The finding that sea lion populations of approximately 42,000 required the least number of transients to maintain a growth rate of zero was true for each value of *r*. According to this simulation, a transient killer whale population of 125 transient killer whales is capable of limiting growth in a sea lion population only if $r < 1.06$, whereas a population of 250 animals can theoretically prevent population growth even if $r = 1.08$.

In the next simulation exercise, we examined the effect of variation in transient killer whale diet on the predictions of the age-specific, Type III functional response model (Model 3 Type III). It is clear from the structure of the model that changing the proportion of the diet of killer whales made up of sea lions is equivalent to changing the number of transient killer whales by a similar factor. However, we present the model predictions in this way because they make readily apparent the killer whale number/ diet combinations that are theoretically capable of preventing sea lion population growth (Figure 5.8).

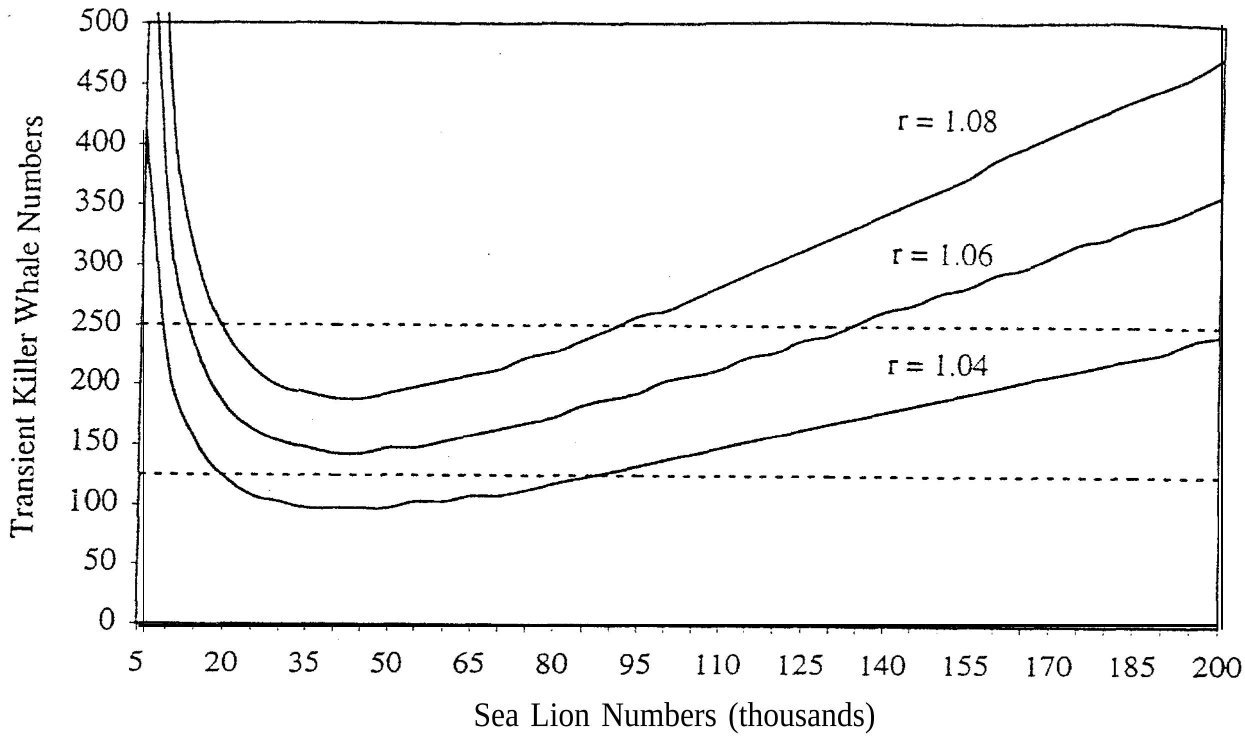

Figure 5.7 Transient killer whale numbers ensuring zero growth of sea lion populations: effect of sea lion intrinsic growth rates. Simulations are based on and an age-specific, Type III functional response model (Model 3 Type III, see text), Parameter values as in Figure 5.5.

Finally, we examined the percentage of total mortality accounted for by predation in a declining sea lion population (Figure 5.9) We started with an initial population of 200,000 sea lions and reduced it by 5% per year, similar to the rate of decline seen in western Alaska sea lion stocks over the past 20 years. Total mortality was calculated as 0.5 $P_t + K_t$, where P_t is the population size and K_t is the number of deaths required to cancel the births occurring during the year. The number of births occurring per year is estimated by .2154 P_t (based on Trites and Larkin 1992). Predation was assumed to be age-specific with a Type III functional response (Model 3), thus the total number of sea lions killed by predators declined throughout the simulation. However, the *proportion* of total mortality accounted for by predation increased until the sea lion population had declined to approximately 42,000. At that population size, 125 transients (the estimated number in western Alaska) accounted for 18% of the sea lion deaths occurring annually.

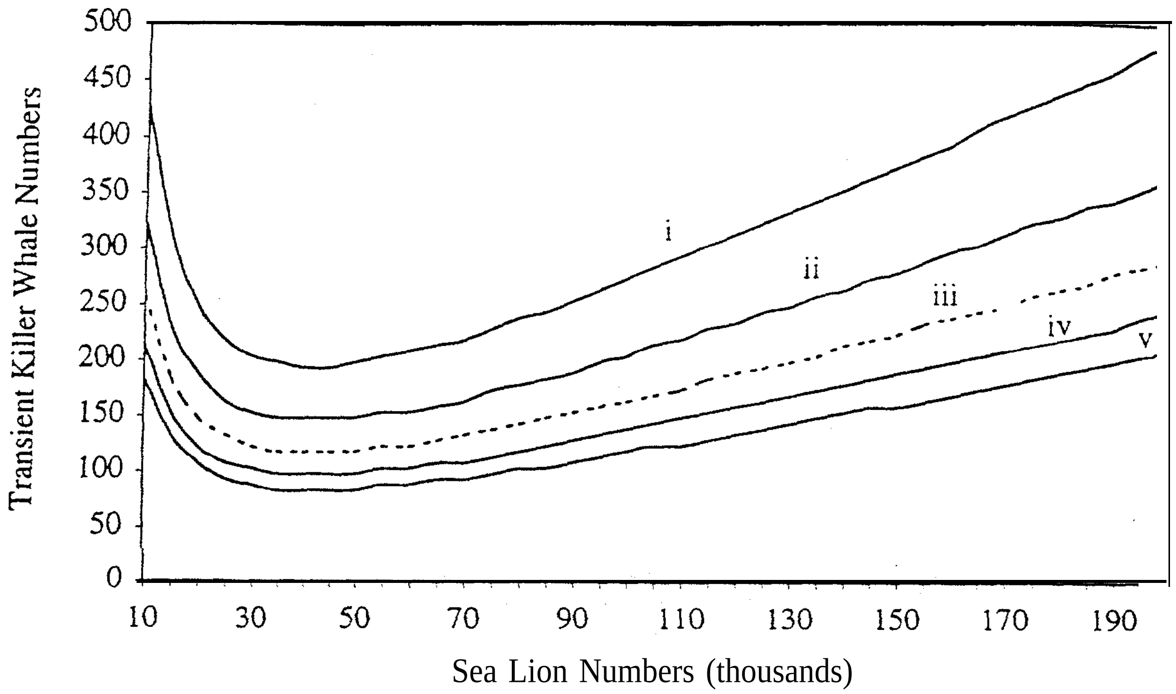

Figure 5.8 Transient killer whale numbers ensuring zero growth of sea lion populations: effect of transient killer whale diet. Simulations are based on an age-specific, Type III functional response model (Model 3 Type III, see text). From (i) to (v), the proportion of the diet of transient killer whales provided by sea lions is 7.5, 10.0, 12.5, 15.0 and 17.5 % respectively, when the number of sea lions is 100,000.

DISCUSSION

The simulation models presented in this chapter are subject to the normal limitations of mathematical models: they are no better than the assumptions they are built on or than the parameters they are given. Their principle value is to focus research by suggesting new hypotheses or by testing the logical consistency of old ones. In particular, the results of deterministic models such as those presented here should be interpreted cautiously when developing conservation strategies: we hope that they provide insight into real processes, but they cannot account for real world complexity and stochasticity. With that disclaimer in mind, the model results suggest that killer whale predation in western Alaska may be a substantial component of total sea lion mortality when sea lion populations are at their present levels. In the remaining section of this paper, we discuss the simulations in the light of sea lion and killer whale ecology, biology, and geographic distributions.

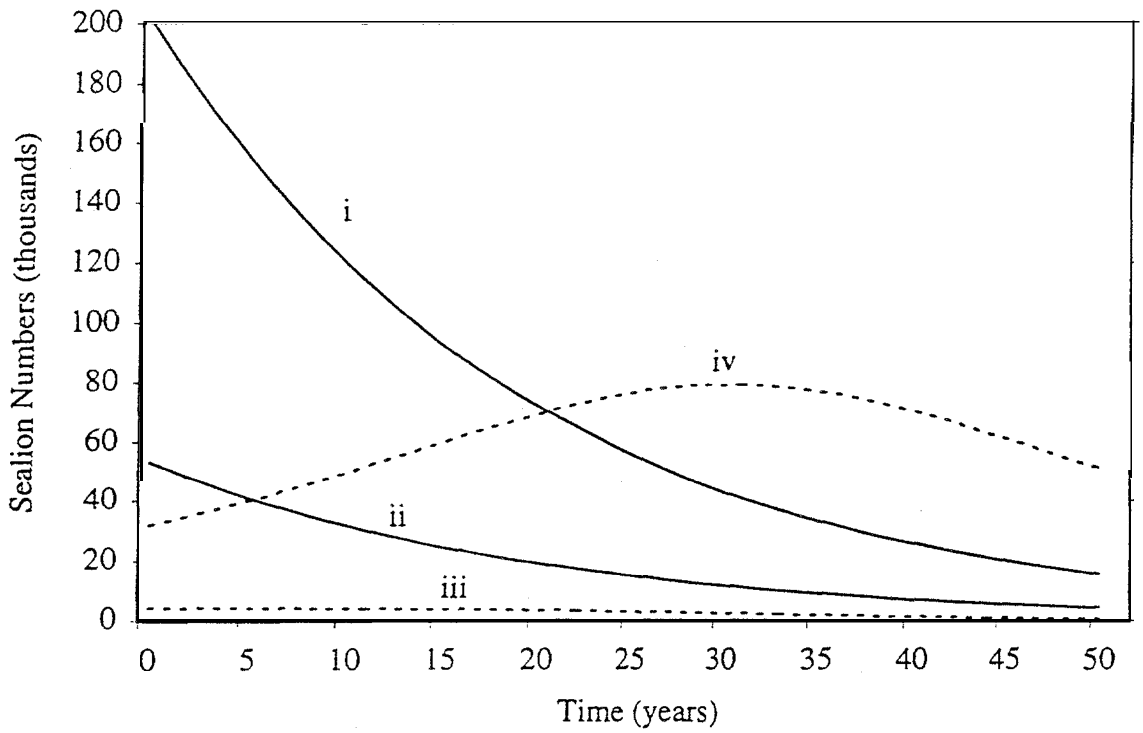

Figure 5.9 Sea lion mortality accounted for by killer whale predation. Shown are (i) sea lion numbers declining at 5%/ yr , (ii) total sea lion mortality/ yr (5% of the population plus births of the year, see text), (iii) the total number of sea lions consumed per year by killer whales, and (iv, plotted on the left axis) the proportion of total mortality accounted for killer whale predation. The assumed predation pattern is age-specific with a Type III functional response (Model 3 Type III). The assumed number of transient killer whales is 125.

The demographics of killer whale predation on sea lions.

The models predict that the impact of killer whale predation on sea lion populations is greatest when whales favour pups, juveniles and very old individuals. This effect is driven by the differential mortality of young sea lions, as few individuals are expected to live long enough to experience senescent increases in their vulnerability to killer whales. Unfortunately, neither the stomach content data nor the observational data tell a clear story regarding the age classes of sea lions taken by killer whales. One stomach contained flipper tags from 14 sea lions that had been tagged between 3 and 4 years previously, and thus were certainly not adults when eaten. The fact that no bones were found in the stomach suggests that the sea lions had not been eaten recently. However, the principal difficulties in interpreting all stomach content data are that we do not know the extent to which the consumption of skeletal elements depends on the size of the prey taken, or how long such items are retained in the stomach.

According to the reports of observers (Chapter 2), small adult sea lions make up the category most commonly attacked by killer whales. This observational data is probably biased, however, because the killing of adult sea lions is likely to involve longer handling times than is the killing of pups. Baird (1994) reported a mean handling time for adult sea lions and elephant seals that was five times longer than that of harbour seals, which are similar in size to young sea lions. Attacks on adult sea lions often involve a great deal of very visible surface activity (Chapter 2). Sea lion pups, like harbour seals, may usually be killed underwater, providing little evidence to observers.

Two lines of inferential evidence suggest that sea lion pups may in fact be disproportionately vulnerable to transient killer whales. First, observers reported often seeing small groups of killer whales near sea lion rookeries (Chapter 2), where they would have access to pups entering the water. Second, in a study of a similar species *(Otario flavescens),* where direct observations of predation by killer whales were possible, Hoelzel (1991) reported that of 209 pups attacked, 82 were killed, while during the same period 96 adults were attacked, all unsuccessfully.

In summary, the available data, along with inferential evidence, suggests some biasing of predation towards younger members of the population, but the extent of that tendency is unknown. According to the simulations, this age selectivity means that the impact of killer whale predation on Steller sea lion populations is greater than would be predicted by consumption rates alone.

Functional and numerical responses in killer whale predation patterns

In classical predator-prey theory, when the abundance of a prey species declines below a certain level, it becomes unprofitable for a predator to continue to search for that prey. When this occurs, specialist predators may emigrate or die off (numerical responses), and generalist predators may switch to alternate prey (functional response).

We have no evidence of a numerical response by transient killer whales to declines in Steller sea lion numbers. Unfortunately, however, the data regarding the numbers and the population identity of killer whales is least complete in western Alaska, where Steller sea lion declines have been most extreme (Loughlin et al. 1992). It is possible that there was some emigration of so-called western assemblage transient killer whales into southeast Alaska and British Columbia from the mid- to late 1980s, as the number of “new” transient killer whales identified per year increased during that period (G. Ellis, unpubl. data). However, it seems more parsimonious to attribute these new sightings to a co-incident increase in sighting effort in British Columbia, including new surveys in areas such as the Queen Charlotte Islands (Ford et al. 1994b).

A stronger case can be made in favour of functional responses. Because transient killer whales take a variety of marine mammal prey, it seems reasonable that some form of prey switching would occur as sea lion numbers decline. Harbour seals, known to be important components of the diet of transient killer whales, are a likely alternate prey. Because harbour seals are often found in the same areas as sea lions, transients hunting them are likely to be able to continue to take sea lions that would not otherwise be profitable to hunt. Thus, a form of 'apparent competition' (Holt and Lawton 1994) may exist, where an increase in harbour seals in a local area attracts transient killer whales that in turn cause a decline in the sea lion numbers.

The shape of the functional response curve has been shown to have important consequences for the effects of predation on prey populations (Yodzis 1994). Is it most reasonable to assume a Type II or Type III functional response in the case of killer whale predation on sea lions? If, as described above, killer whales can effectively use harbour seals to subsidize a continuing hunt for sea lions, a Type II functional response is expected, with high levels of sea lion predation even at low sea lion densities. For this to occur, harbour seals would need to be relatively abundant. In western Alaska, however, there is evidence that some harbour seal populations are in severe decline (Castellini 1993, Hoover-Miller 1994).

If harbour seals are not abundant, transient killer whales are likely to shift their concentration from sea lions to species that live further offshore, such as dolphins, porpoises, mysticete whales, fur seals and elephant seals. In this case a Type III functional response curve might be expected, where killer whales cease actively searching for sea lions as sea lion abundance declines, but continue to prey on sea lions opportunistically when they are encountered by chance. Yodzis (1994) argued that Type III functional responses are likely to exist when prey exist in refugia, and when predators have a search image for prey. Both conditions apply to this system: haulout and rookery sites constitute refugia against killer whales (Barrett-Lennard et al., in press), and the selectivity of killer whales for particular prey (Ford et al. in prep) make it likely that they have well-developed search images for prey.

The models in this chapter showed that a transient population of 250 individuals could theoretically drive a population of 100,000 sea lions to extinction in somewhat over 30 years, assuming the depensatory predation of a Type II functional response. If, as we have argued, killer whales show a Type III functional response, sea lion populations are expected to equilibrate at a level determined by the shape of the functional response curve. If presently depleted harbour seal populations were to begin to recover, the initial consequences for sea lions could be increased predation, as nearshore hunting would be "subsidized". However, as harbour seal numbers increased further, killer whales would be expected to focus hunts on harbour seals alone, ultimately reducing the predation pressure on sea lion populations.

We have not considered the possibility that transient killer whales shift to a fish diet when marine mammal prey are depleted. The stomach contents of stranded killer whales (Chapter 3) provides evidence that the dichotomy in prey types between resident and transient killer whales is very strong. The group sizes, hunting techniques, and echolocation strategies used when foraging for fish and for marine mammals are different and perhaps quite incompatible (Barrett-Lennard et al. in press). Furthermore, in many years of systematic study in Alaska and British Columbia, there have been no positive observations of transients feeding on fish. Thus, while we cannot rule out the possibility that transients that are extremely food stressed take fish as an alternate to marine mammals, we believe that such switching is rare.

Differences in the impact of killer whale predation on eastern and western sea lion populations.
In the part of Alaska west of 142° W longitude, we estimated that there were on the order of 125 transients and 42,500 Steller sea lions at the end of the pupping season in 1994. Based on the Type III functional response plotted in Figure 5.3 and an intrinsic growth rate of 4%/ yr, it can be seen from Figure 5.5 that this number of transients is, theoretically, more than that required to cause the sea lion population to decline. Taking slopes from Figure 5.5, we can determine that 250 transients would cause this population to decline at 7.7%/ yr, thus the predicted instantaneous rate of decline for 125 transients is 3.8%/yr. This compares with an actual rate of decline of approximately 5% /yr.

East of 142° W longitude and north of Washington State, there are approximately 23,700 sea lions and 125 transient killer whales. With the same assumptions as those above the model predicts that predation should be capable of holding these sea lion populations at a growth rate close to zero (Figure 5.6). In fact, these populations are increasing slightly (on the order of 2% per year, Olesiuk, unpubl. data, Trites and Larkin 1995).

Predation mortality as a percentage of total mortality, past and present.
Using the 1994 population estimate of 42,500 Steller sea lions for Alaska and British Columbia, the age-specific, Type III functional response predation model accounts for about 18% of the total annual mortality of Steller sea lions in western Alaska (Figure 5.9). Historically, killer whale predation was a much smaller component of overall mortality. For example, when the Alaska/ British Columbia population was 200,000 sea lions, the annual mortality due to killer whales was on the order of 2%/ yr according the model assumptions, which was about 9% of the total annual mortality of a stationary population.

CONCLUSIONS

Present rates of decline in sea lion populations in Alaska and British Columbia are similar to those predicted by simulation models in which killer whale predation is assumed to be age-specific and subject to a Type III functional response. The impact of predation is predicted to have been less at greater population sizes, however, and the models do not explain the initial decline of Steller sea lions in Alaska. Under the model assumptions, killer whale predation is unlikely to drive sea lion populations to extinction, and in south-eastern Alaska and British Columbia it may hold sea lion numbers at or near present levels. In western Alaska, however, the decline could continue until sea lions are at about half their present levels. At present, roughly 18% of the sea lions that die annually in western Alaska do so as a result of killer whale predation, according to the model. Thus, changes in other mortality factors could reverse the current trend.

Changes in harbour seals population sizes may affect the rate at which killer whales take sea lions. For instance, if seals are abundant, as in British Columbia, killer whales may include a relatively small proportion of sea lions in their diet, and if seals are scarce, transients may move offshore to hunt cetaceans. At some intermediate level, however, a situation of apparent competition may arise, where seal predation makes it profitable for killer whales to hunt near shore, resulting in increased predation on sea lions.

A better understanding of the impact of killer whale predation on Steller sea lion populations requires more precise knowledge of the age-specificity and seasonality of killer whale predation patterns. Continued effort should be put into retrieving and analysing the stomach contents of killer whale carcasses, into carefully monitoring the behaviour of killer whales near sea lion rookeries, and into monitoring the survival of sea lion pups during their initial time at sea.

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Appendix 1. STELLER SEA LION AND KILLER WHALE INTERACTION QUESTIONNAIRE

Please return this questionnaire by December 3 1, 1993 to:

Lance Barrett-Lennard
North Pacific Universities Marine Mammal Consortium
Fisheries Centre, University of British Columbia
Room 18, Hut B-3, 6248 Biological Sciences Road
Vancouver, B.C. Canada V6T 1Z4

1. Your name:

2. On average, how frequently have you seen killer whales in your area? *(for example: "never", "'once every two months", "twice per month", etc.)*

3. On average, how many killer whales have you seen at a time? *(for example: "1", "5 to 10", "variable from 2 to 20", etc.)*

4. Were there sea lion haulout or rookery sites in your area?

   If so, please answer the following:

   a) What were the approximate locations of the sites?

   b) How frequently did you pass within view of them?

   c) How many sea lions would you estimate attended them?

   d) If you live south of Alaska: were these sites inhabited by *(check)*
      Steller sea lions?
      California sea lions?

Don't know

5. Estimate the number of sea lions you saw in a typical day, week, or month *(for example: "none", "5 per day", "5 per week", etc.).*

6. Have you seen killer whales close to sea lions but not attacking or chasing them? How often? If so, please describe the incident or incidents below. *(include if possible the time of year and location, how many killer whales and sea lions were seen, how the whales and sea lions behaved, etc. Please attach additional pages if necessary).*

7. If you have seen killer whales chase or attack sea lions please describe each incident in as much detail as possible. *(Include if possible the time of year and location, the number of killer whales and sea lions that were in the area and the number actually involved in the interaction, whether the sea lions were adults, juveniles or pups, whether you saw any evidence that any of the sea lions were killed or injured, etc. Please attach additional pages if necessary).*

The following section will help us to determine how common killer whale/sea lion interactions are, and when and where they are most likely to be observed. It will also provide a check of current killer whale and sea lion population estimates.

8. What kind of activities have you carried out when on or by the sea *(eg. commercial fishing, recreation, research, place of residence, etc.)?*

9. In which marine areas have you spent the majority of time *(eg. Prince William Sound, Bristol Bay, Queen Charlotte Sound, etc.)?*

10. a) Please list the years that you spent significant time on or by the sea? *(for example: "1985-1991, inclusive").*

b) How many days per month have you spent on or by the sea in a typical year?

January	___	July	___
February	___	August	___
March	___	September	___
April	___	October	___
May	___	November	___
June	___	December	___

d) On average how many hours per day did you spend in view of the water?

_____ hours/day

11. Can you recommend anyone else to whom we should send this questionnaire? If so, please provide names and addresses.

12. Do you have photographs or video footage of sea lion killer whale interactions that might provide information on the size or number of sea lions or the identity of the killer whales (based on fin shape and saddle patch pigmentation)? If so, might we examine them? *(Please check one box).*

[ ] No.

[ ] Yes, enclosed, please return by __________

[ ] Yes, I will send separately.

[ ] Yes, but I do not wish to send. *(If you are willing, please suggest other ways we might examine them).*

13. Would you like to receive a summary of our results when they are complete?

[ ] No, not necessary.

[ ] Yes.

If so, please fill in below:

Name:
Address:

Zip or Postal Code:

Telephone: ( )
Facsimile: ( )
E-mail:

Appendix 2. Summary of each of the 126 responses to the sea lion questionnaire. (Note: BC = British Columbia QCI = Queen Charlotte Islands. PWS = Prince William Sound, ** = information not provided)

Viewer's principal location	Viewer's activity	Number of years on water	Hours/ year viewing	Haulouts seen how often per year?	Sea lion numbers on haulout	Estimate of # of sea lions seen per year.	Killer whale sightings per year of observing	Mean killer whale group size	Non-predatory interaction	Whales harass sea lion(s)	Whales kill sea lion(s)	Comments
Aleutians	research	10	3840	12	30-300	660	20	10.0	1			Watched a group of killer whales chase 20 sea lions
Aleutians	research (pinnipeds)	5	240	4	200	17,000	3	3.0	2			First interaction lasted 20-30 min, yet no evidence of harassment, in Ugamak, Aleutians; 2nd interaction lasted 10 min, killer whales swam by and sea lions were agitated, no evidence of attack or kill, in Kodiak island area.
Aleutians	research (pinnipeds)	24	300	20	**	**	16	5.0	10		3	Only has vague recollections of kills.
Aleutians	research affiliate	19	1440	7	many '000'	4500	16	10.0	24			Has never seen an attack, despite extensive experience.
Aleutians	research (seabirds)	13	2400	120	50-200	15,000	36	7.5	20			No predatory interactions witnessed despite constant observation in rookery area Mar21- Oct 20.
Baffin Bay	research (whales)		0				0.2					
BC (QCI)	fishing	5	720	16	20-40-2000	1,000	7	6.0				
BC (QCI)	recreation	15	48	4	20-50	200	3	3.0	1			Occurred in Skidegate Inlet, 1 killer whale with 4-6 sea lions in area but no interaction
BC (QCI)	home	1	336				9	3.0				
BC (QCI)	tourboat	5	460	70	25-300	4,450	15	20.0	2	2		Killer whales chased sea lions twice, but did not catch them; has also seen killer whales chase harbour and Dall's porpoises
BC (QCI)	fishing	49	1638	10	40-50	530	5	6.0				
BC (Vancouver Is.)	tourboat (whale-watching)	8	1456	50	0-1500	5130	150	8.0	10			
BC (Vancouver Is.)	tourboat	25	680	100	50-2000	28,000	3	5.0	2		2	Reports 1 attack on California sea lion by 3-5 killer whales, 1 attack on unknown species of sea lion by 7 killer whales, both were fatal attacks for the sea lions involved.
BC (Vancouver Is.)	tourboat (whale-watching)	15	1080			30	100	25.0				
BC (Vancouver Is.)	tourboat (whale-watching)	15	1320	12	12-50	375	75	20.0		1		
BC (Vancouver Is.)	tourboat (whale-watching)	20	1670				140	20.0	9	0	1	Six transients (all female) killed 1000 lb sea lion over 1 1/2 hours.
BC (Vancouver Is.)	research (pinnipeds)	15	4380	57	10-40	2,920	24	7.5	20	1	1	Non-predatory interactions occurred when residents swam by Eden Island; in Oct. 1984, 11 transients killed sea lions; 3 transients also attacked 3 sea lions, but sea lions swam off unharmed.
BC (Vancouver Is.)	parks service	5	1440			4	90	7.0				Never seen attack but has seen resident killer whales attack a Dall's porpoise.
BC (Vancouver Is.)	fishing	24	560	2	30 - 50	30	60	7.5				
BC (Vancouver Is.)	tourboat	3	480	80	0-1,000	9,500	84	45.0	10			
BC (Vancouver Is.)	search and rescue	42	4800	12	100-1500	5,000	5	4.0	1		1	Summer '93, killer whales appeared to take 1-2 sea lions, could only see blood
BC (Vancouver Is.)	research (whales)	8	744	40	1500	16,000	120	8.0	25		2	Both kills were also witnessed by tour boats, as killer whales killed 1 California sea lion each time at Bleecher Bay, BC
BC (Vancouver Is.)	research (whales)	8	744	40	1500	16,000	120	8.0				
BC (Vancouver Is.)	search and rescue	6	48	12	100-1500	3600	6	10.0				

Viewer's principal location	Viewer's activity	Number of years on water	Hours/ year viewing	Haulouts seen how often per year?	Sea lion numbers on haulout	Estimate of # of sea lions seen per year.	Killer whale sightings per year of observing	Mean killer whale group size	Non-predatory interaction	Whales harass sea lion(s)	Whales kill sea lion(s)	Comments
BC (Vancouver Is.)	tourboat	16	1242	205	3-300	20,500	7	7.5	1			Sea lions hauled out on an unusual location while killer whales were in area, no other activity seen.
BC (Vancouver Is.)	tourboat (whale-watching)	26	1368	150	2-20	4500	12	4.5				
BC (Vancouver Is.)	tourboat (whale-watching)	34	8760	100	10-100	9,100	50	4.0	40		4	Says typically bull killer whales do the attacking, and that he has seen 1 male killed and 3 females killed in the past 4 years.
BC (Vancouver Is.)	tourboat	9	1578	195	0-12	1,170	22	3.0	3			Killer whales go near haul out but ignore sea lions.
BC (Vancouver Is.)	research (sea otters)	14	3640	30	200-1000	6,200	7	10.0	2			
BC (Vancouver Is.)	research (whales)	20	368			50	48	13.0	10	2		Non-predatory interactions were with groups of resident whales; in harassments 3 killer whales attacked 1 subadult sea lion; 5 whales attacked 1adult sea lion but it was not killed (Steller sea lions) in both cases.
BC coast	research (whales)	14	2000	12	60-1000	2,500	45	10.0	10	1		2 female whales isolated 300kg sea lion, repeatedly hitting it with tails, while sea lion moved closer to gp of 50-60 sea lions, whales then left & 20 min later killed a harbour seal, occurred off Harmac in Nanaimo, BC.
BC coast	research (pinnipeds and whales)	25	2064				72	40.0	10	3	1	Three to six killer whales typically chase after California sea lion, but has only seen fatal attack once.
BC coast	research (whales)	14	1960	12	15-400	3,000	25	8.0	10			
BC coast	tourboat	9	2860	32	2-700	3200	15	18.0	1			
BC coast	tourboat	6	1440	16	25-300	1600	15	15.0	2			Has observed that when killer whales are in the area, sea lions haul out.
Bering Sea	research	13	280	2	2500	2725	0.0796	9.0				Has seen killer whales attack beluga but not sea lions.
Bering Sea	research (pinnipeds and whales)	12	352	3	200-900	1500	3	4.0				
Bering Sea	fishing	30	480	1	20	20	3	5.0				
Bering Sea	research (pinnipeds)	8	540	2		80	0.28	2.0				
Bering Sea	fishing	29	623	4	10-70	315	5	2.0				Has seen killer whales chase after fur seal pups when working around the Pribilofs.
Bering Sea	home	38	720	1	900-1,000	12,000	1	3.0				
Bering Sea	research (pinnipeds)	5	798	16	200-1000	6300	0.6	3.5	2			Researcher on sea lion rookery.
Bering Sea	research (pinnipeds)	3	920	2	150	200	2	3.0				Has seen killer whales and fur seals in close proximity, but never sea lions.
Bering Sea	research	1	978	11	350-1000		0	0.0				
Bering Sea	fishing	27	1440	2	200-300	500	2	15.0				
Bering Sea	research	1	1515	48	40-140	1000	3	5.0		1		Five killer whales involved in attack on 1 sub-adult sea lion. Killer whale calf unsuccessfully chased the sea lion and the sea lion out swam it.
Bering Sea	fishing	15	1920	2	**	13	1.5	2.5				
Bering Sea	researcher (pinnipeds)	4	2160	120	100-300	24,000	1	5.0		1		Four whales involved in attack of 1 sea lion, 90 walruses also went into the water near the whales, later researcher saw 3 adult sea lions swimming against shore, but quickly became too dark to see what happened to them.
Bering Sea	fishing	20	2160			24	1.5	4.5				

Viewer's principal location	Viewer's activity	Number of years on water	Hours/ year viewing	Haulouts seen how often per year?	Sea lion numbers on haulout	Estimate of # of sea lions seen per year.	Killer whale sightings per year of observing	Mean killer whale group size	Non-predatory interaction	Whales harass sea lion(s)	Whales kill sea lion(s)	Comments
Bering Sea	tourboat	11	8640	1	40-60	162	6	5.0				
Bering Sea	fishing	24	406			40	3	7.5				
Bering Sea	research (pinnipeds)	19	856	107	?	?	1	5.0			1	Has seen 1 predation in 18 years, but says the 1000lb male sea lion was eating a fur seal pup at the time it was eaten by 5 killer whales. Also reports that when killer whales are in the area, they generally pass well offshore.
California	research (pinnipeds, seabirds, whales)	16	120	24	10-800	4800	2.5	4.5				
California	research (pinnipeds)	8	216	48	1000	14,400	0.143	5.0				Great white sharks might be important predators on sea lions in California.
California	research (pinnipeds)	15	288	12	10-300	1200	0	0.0				
California	research (pinnipeds)	7	2142	90	300	27,000	0	0.0				
California	research	12	2400	240	150-400	12000	1.5	5.0				
California	research (pinnipeds and whales)	10	820	7	10-200	1400	1.5	20.0				
Gulf of Alaska	recreation	25	90	1	25	400	0.05	5.0		1		5-6 killer whales chased 20-30 sea lions across Bear Cove, a mix of ages of sea lions. Saw no evidence of kill.
Gulf of Alaska	research	16	552		110,000	110,000	1.5	17.0	2			Has never seen predatory attacks, but twice watched 8 killer whales swim around haul out at least 3 times, then leave, without attacking (over 200 sea lions on land, and 'many' in water). Both incidents occurred in southeast Alaska.
Gulf of Alaska	research (pinnipeds)	11	1140	ea 1/yr***	**	**	22.5	1.0	10			Has seen range of responses of sea lion to killer whales, from intimidation to aggression.
Gulf of Alaska	fishing	10	1500	20	75	170	5	10.0	40			Usually when sees killer whales and sea lions together, both species are interested in feeding on herring or salmon.
Gulf of Alaska	fishing	15	1704	21	20-100		24	10.0	1			
Gulf of Alaska	fishing	23	1860			775	6	8.0			2	kill#1, 4-6 killer whales took 2 sea lions in Kodiak Harbour, Apr 1993; kill #2 July 1984, Wide Bay, Kodiak, pack of whales took several sea lions.
Gulf of Alaska	tourboat	25	4320	12	1-2	140	24	22.0				
Kodiak	home	7	730			365	75	3.0	4			Killer whales circled sea lion, did not attack.
Kodiak	recreation	15	1008	2.5	300-1000	360	2.5	3.0				
Kodiak	fishing	21	2808	3	*# Marmot	650	3	15.0				
Kodiak	fishing	15	2880				2	6.0				
Kodiak	fishing	13	4320				24	40.0				Has heard of second hand accounts but has never witnessed a kill.
Kodiak	research (pinnipeds)	4	540	30	*=# on Mai	18,000	0					A researcher on rookery, but never seen attacks or harassment of sea lions by killer whales.
Kodiak	pilot	8	4320	365	100-500	36500	3.5	3.0	1		4	Two kills were small pups at Marmot, 2 were of small adults in Kodiak; kills were confirmed.
Kodiak	fishing	25	3276			365	36	10.0	2	1		Occurred near Shelikof Strait, 2 killer whales chased 1 large sea lion, sea lion swam away.
Oregon	fishing	21	3942			1100	9	5.0		2		Six whales each time killed and or maimed 4-5 sea lions of all sizes, incidents occurred off Newport, OR.

Viewer's principal location	Viewer's activity	Number of years on water	Hours/ year viewing	Haulouts seen how often per year?	Sea lion numbers on haulout	Estimate of # of sea lions seen per year.	Killer whale sightings per year of observing	Mean killer whale group size	Non-predatory interaction	Whales harass sea lion(s)	Whales kill sea lion(s)	Comments
PWS	fishing	18	1120	3	20-150	1050	16	17.5		1		4 killer whales surrounded 2 adult (?) female sea lions, swam around and around them, occasionally hitting them with a fin or tossing them with their tails, watched for 45 min., whales were trying to exhaust sea lions. Observer then left area.
PWS	tourboat	7	1200	134	3-200	6560	16	3.0	10		2	Sea lions always vigilant when killer whales swim by can buoy (seen 10 times); 1 juv sea lion was chased by 2-3 killer whales (AC's), and later a skinned sea lion was recovered (June '94); also has account of 2-3 whales playing with dead sea lion.
PWS	fishing	13	1200	72	80	30-8000	24	20.0	2			Comments that the number of sea lions seen on a daily basis has declined from 60-80 per day in the early 1980's in PWS down to 2-3 per week in the 1990's.
PWS	research	11	1512	15	5-300	1620	12	5.0				Has published second-hand accounts of killer whales attacking sea lions, but has never witnessed it.
PWS	research (whales)	9	1554	8	50-1,000	2570	92	40.0	5			Extracted 14 sea lion tags from killer whale stomach.
PWS	fishing	20	1638	13	25-250	700-3500	70	40.0	3			Has seen sea lions and AT transients in close proximity twice, with no predation by killer whales, also watched AK-pod residents ignore sea lions on rubbing beach.
PWS	fishing	13	1800	36	100	675	30	30.0				
PWS	tourboat	34	1826	186	20-50	4,550	50	10.0				
PWS	tourboat	26	2672	10	200	1650	150	20.0	8			Has stayed in area of killer whales and sea lions for 1-2 hours, yet has not seen any sign of transients attacking sea lions.
PWS	fishing	35	3792		n/a	1900	10	10.0				
PWS	fishing	9	4320			1450	12	15.0				Although killer whales and sea lions travel in same waters, has not witnessed any type of interaction, either predatory or otherwise.
PWS	recreation	8	4320	4.5	250	1500	24	4.5	5			
PWS	fishing	11	4320	2.5	500	180	12	3.0				
PWS	fishing	46	4320			900	3	1.0				
PWS	research	5	240			40	20	7.5				
PWS	tourboat	16	1030	103	5-300	1,030	20	8.0	3	1	1	8 whales attacked 1 sub-adult sea lion and skinned it, killer whales were very active 8 whales also went by sea lion that was breathing heavily, but they lost the sea lion as it went alongside boat, mariner took it back to haul-out buoy.
PWS	tourboat	24	2478	135	1-100	3000	120	8.0	2			Has second hand story of killer whale pulling sea lion off can buoy 9.
PWS	research (whales)	15	686	4	75-300	1150	10	18.0	10			Watched transients around Cape Elrington sea lion haulout, but has not seen any attacks or interactions.
PWS	research (whales and pinnipeds)	6	2880	20	200-2500	3750	12.5	40.0				Necropsied a 30' whale with a juvenile sea lion in its stomach, occurred off Cape St. Elias.
PWS	recreation	17	1472	1	100	240	6	7.0			1	1 injured sea lion with 4 orcas in area, 20 sea lions also in area, saw blood and teeth marks, sea lion near death? Happened while on Dark Is, Shuyak/Kodiak area in 1964, and lasted about 1 1/2 hrs. Other sea lions were very agitated.
PWS	research (marine mammals and birds)	2	1380	4	15	600	10	7.0				
PWS	research (sea otters)	4	584	24	5-400	146	10	7.5	3			
PWS	fishing	18	8592	52	150-300	10,400	52	15.0	1			Has only watched killer whales eat fish.
Russia	research (pinnipeds)	9	432	10	300-400	3,500	0.44	2.0				Has seen predation on harbour seals, but never on sea lions.

Viewer's principal location	Viewer's activity	Number of years on water	Hours/ year viewing	Haulouts seen how often per year?	Sea lion numbers on haulout	Estimate of # of sea lions seen per year.	Killer whale sightings per year of observing	Mean killer whale group size	Non-predatory interaction	Whales harass sea lion(s)	Whales kill sea lion(s)	Comments
Russia	research (pinnipeds)	12	456	18	4000	?	120	5.0				Describes a second-hand account of 1 subadult male being taken by group of whales and batted about like a football, witnessed by captain of fish-processing boat
Southeast Alaska	tourboat	40	4320	36	150 - 300	2000	2	5.5	1			The non-predatory interaction occurred the 1 time 30 whales came into area. Has watched Steller's harass juvenile humpback whales, actually taking bites out of them.
Southeast Alaska	research (pinnipeds)	3	364	91	1000-3000	91000	4	7.5	2			Has seen sea lions haul out to avoid whales, but never seen killer whales chase whales; researcher on rookery.
Southeast Alaska	research (whales)	16	334	14	2-100	810	24	20.0	10		1	Sea lion was large adult, sex unknown, interestingly a humpback whale was nearby and followed sea lions and killer whales.
Southeast Alaska	research (pinnipeds)	1	592	123	500	30,750	2	1.0	1			
Southeast Alaska	recreation	18	636	1	50-100	100	2	25.0	3			
Southeast Alaska	research (pinnipeds)	6	1280	160	4,500	720,000	22	5.0	3			5-7whales seen feeding in kelp, no interest in sea lions, sea lions occasionally jumped in water, whales occasionally tail slapped and breached as a group close to shore.
Southeast Alaska	research (whales)	2	1395	15	150-200	1860	6	10.0				Never seen sea lion attacks, but has seen attacks on humpbacks and porpoises.
Southeast Alaska	fishing	1	1800			1,800	2	7.5				
Southeast Alaska	fishing	59	1980	70	30-200	700-10,00	18	11.0	1		1	Saw 15-20 whales, the small ones attacked a big bull sea lion that was bleeding and flailing. Also has second hand report of kill on Fairweather ground, and has reports of sea lions chasing humpbacks.
Southeast Alaska	home	1	2196	54	0 -50	140	0	7.5	20		1	Has often seen killer whales and sea lions together without incident.
Southeast Alaska	fishing	23	2470	40	15-100	1765	11	5.0	0	1		Uncertain if kill: whales went close to sea lion and sea lion disappeared but no attack was seen. Has also seen whales attack Dall's porpoises and harbour seals.
Southeast Alaska	fishing	1	2484	12	20-30	345	24	7.5				
Southeast Alaska	fishing	7	2700	80	100-300	800	2	5.5	1			Watched 12 killer whales herd sea lions that were trapped against a steep sided shoreline, but no animals were attacked.
Southeast Alaska	fishing	5	8760	120	50 -100	600	2	6.0				
Southeast Alaska	research (pinnipeds)	19	1164	45	20000 tot	20,000	6	17.0	10			Has often seen killer whales in close proximity to young pup sea lions (2-4wks old), but with no response to sea lions by whales.
Southeast Alaska	fishing	18	1960				1	3.0				
Southeast Alaska	tourboat	14	1320	55	45	700	18	9.0	15		1	4-5 killer whales killed 1 800lb female sea lion, killer whales in area for 1-2 hrs.
Southeast Alaska	research (pinnipeds)	22	660	10	10-Hazy #	700-10,00	30	7.5	3			
Southeast Alaska	fishing	24	1650	0		2,000	22	7.0	10			Has seen killer whales chase harbour seal chases but never sea lions.
Southeast Alaska	fishing	11	1568	12	12-300	350	48	10.0				Reports second-hand account of sea lion feeding on herring being attacked by a few killer whales, killing several sea lions. Was also reported in local newspaper and by several locals.
Southeast Alaska	fishing	23	6744	120	5 -100	900	12	25.0	1			Says sea lions are often nervous when killer whales are in the area. He passes haulouts daily in summer.
Southeast Alaska	fishing	33	2448	16	30-100	600	6	4.0	2	1		The sea lion that was atticked had first been shot by humans.
Southeast Alaska	research (whales)	18	368	24	1-100	92	28	15.0	4	1	1	
Southeast Alaska	tourboat	10	1512	126	20-200	3850	10	9.0	15		1	Female sea lion was pulled off rocks and killed by 2 whales in Lynn Canyon haulout. They tossed it a few minutes, submerged and moved out of sight, sea lion appeared lifeless. In non-predation, a few whales pass within 1/2-3/4 mile of haulout.
Southeast Alaska	fishing	9	600			36	0					
Southeast Alaska	tourboat	11	978			1050	9	3.0				
TOTALS		1897	232194	4675			2914		441	21	32	

Appendix 3: Material recovered from the stomach of a killer whale carcass on Culross Island, Prince William Sound, Alaska in May 1990.

Species	Identifiable remains	Comments
Harbour seal	r. humerus	juvenile*
	r. scapula	juvenile*
	r. ulna (proximal 3/4)	juvenile*
	r. radius (proximal 1/2)	juvenile*
	1. tibia (shaft only)	
	occipital condyle	
	r. metacarpal 5	adult
	r. metacarpal 4	adult
	r. metacarpal 3	adult
	medial cuneiform	
	2 left & right upper canines	adult, matching
	2 left & right lower canines	adult, matching
	1 lower canine	adult
	8 post-canine teeth	very eroded
	65 nails	probable harbour seal
	134 whiskers	
	skin and fur	
Dall's porpoise	tail fluke & pieces of skin	
Unknown	5 very eroded canines	possible harbour seal or fur seal
	2 fibula shafts	
	loose fur	

* bones were juvenile in size, but were flexible and somewhat eroded; may have been from adult animal

Appendix 4: Whisker counts of harbour seals and sea lions.

Species	Sex-Age Class	Whisker Number	Source
Steller Sea Lion	M Adult	52 (>5 cm)	PBS
	M Adult	62	Scammon 1874
	F Adult	70	" "
	M Juvenile	71	" "
	F Yearling	71	" "
	F Newborn	71	" "
Harbour Seal	? Adult	80 (40>5 cm)	PBS
	? Adult	70 (40>5 cm)	PBS
	? Adult	60-70	Scammon 1874

Scammon calls these seals 'leopard seals' *(Phoca pealii?* Gill). but based on their abundance and distribution (along the western coast of North America to the Kurile Islands) he was probably referring to harbour seals *(Phoca vitulina).*

Appendix 5: Steller sea lion tag numbers recovered from a killer whale carcass on Montague Island, Prince William Sound in 1992. All animals were tagged as pups on Marmot Island.

Year of Tagging	Tag Numbers
1987	108, 174, 240, 305
1988	412, 429, 430, 439, 485, 485, 507, 545, 589, 630
?	806