MARINE MAMMAL SCIENCE, 17(3):555–569 (July 2001)

DISTRIBUTION OF KILLER WHALE PODS IN PRINCE WILLIAM SOUND, ALASKA 1984–1996

D. SCHEEL[1]
Prince William Sound Science Center,
Box 705, Cordova, Alaska 99574, U.S.A.

CRAIG O. MATKIN
EVA SAULITIS
North Gulf Oceanic Society,
Box 15244, Homer, Alaska 99603, U.S.A.

ABSTRACT

Thirteen years of encounter data (1984–1996) were used to examine killer whale distribution within Prince William Sound, Alaska. Four patterns of area use were found, which comprised differences between resident pods and transient groups and differences among resident groups. Resident pods frequented large open passages, while transient groups used the narrow passages and bays in the southwest. This dichotomy likely reflects resident use of salmon and transient use of pinniped prey resources, as well as the different foraging strategies required for these prey types. Four resident pods (AB, AI, AJ, and AN) used Knight Island Passage more than other areas of the Sound; two (AE and AK) used all areas of the Sound more evenly. Use of the Sound by the AT1 transient whales declined in the latter part of the study. Nearshore foraging for pinniped prey by the AT1 transient whales was more common in areas where these whales spend a disproportionate amount of time, suggesting that these areas were critical foraging habitat for them. No similar pattern emerged for Open-water Foraging for cetaceans by AT1 whales, nor for foraging by the resident whales.

Key words: killer whale, *Orcinus orca,* habitat use, distribution, Alaska, Prince William Sound, foraging behavior.

Two distinct types of killer whales (*Orcinus orca*), termed "resident" and "transient," have been described in the North Pacific. Resident and transient whales differ in almost every known aspect of their ecology; however, specializations in foraging behavior are central to the distinctions between the two types. Resident whales eat fish and vocalize frequently while foraging, while

[1] Please direct correspondence to: David Scheel, Environmental Science Department, Alaska Pacific University, 4101 University Drive, Anchorage, Alaska 99508, U.S.A.; e-mail: dscheel@alaskapacific.edu.

transient whales eat marine mammals and are nearly silent while foraging (Morton 1990, Barrett-Lennard *et al.* 1996, Ford *et al.* 1998, Saulitis *et al.* 2000). Along the western coast of North America, resident whales are commonly seen in the spring to fall, feeding on salmon, but are generally seen less regularly in winter; while transient whales may be seen throughout the year but seldom remain at one locality for very long (Heimlich-Boran 1988, Morton 1990). Resident social structure is rigidly matrilineal and both male and female offspring remain with their mothers for life, while transient social structure is more fluid and remains to be completely described (Bigg *et al.* 1990, Matkin *et al.* 1999*a*). The two types do not travel together or otherwise occur together in social groups, nor interbreed, and they may be distinguished by mitochondrial DNA (Hoelzel and Dover 1991).

In some cases, differences in habitat use between resident and transient whales have been noted. In addition to the seasonal differences mentioned above, Heimlich-Boran (1988) noted that resident whales in Georgia Strait, British Columbia, usually traveled from headland to headland and foraged over high relief subsurface topography, while transient whales frequently entered bays and foraged in shallow protected areas, reflecting different strategies for the pursuit of salmon (*Oncorhynchus sp.*) *vs.* harbor seal (*Phoca vitulina richardsi*) prey. However, surprisingly little has been published on habitat use of killer whales, even for populations that have been intensively monitored for decades.

In Prince William Sound, Alaska, thirteen resident pods (approximately 278 individuals), along with at least two assemblages of transient whales, the AT1 and Gulf of Alaska (GOA) transients (approximately 55 individuals) have been identified as regular to rare visitors (Matkin *et al.* 1997). The distribution of killer whale pods in Prince William Sound has been previously discussed by Hall (1986) based on two years of aerial and small vessel observations (1976 and 1977). An additional thirteen years of at-sea observations and photographic identification data are now available (1984–1996). Using these data we tested three hypotheses. First, that resident pods and transient groups use different habitats within Prince William Sound. Second, that foraging behaviors are not evenly distributed in these waters. And third, that resident and transient whales have used these areas less frequently recently than in the past. Due to the scarcity of published information on this topic, these data may make a significant contribution to understanding patterns of habitat use by killer whales. Documenting the differences between resident and transient habitat use provides a foundation for understanding how the ecology of resident *vs.* transient whales can drive a differential response to spatially distributed environmental change, including changes in prey (*e.g.*, salmon or pinnipeds) and distribution or presence of environmental toxins (*e.g.*, an oil spill).

Methods

The observations reported here are based on identification photographs and behavioral records made between 1984 and 1996, primarily from April to

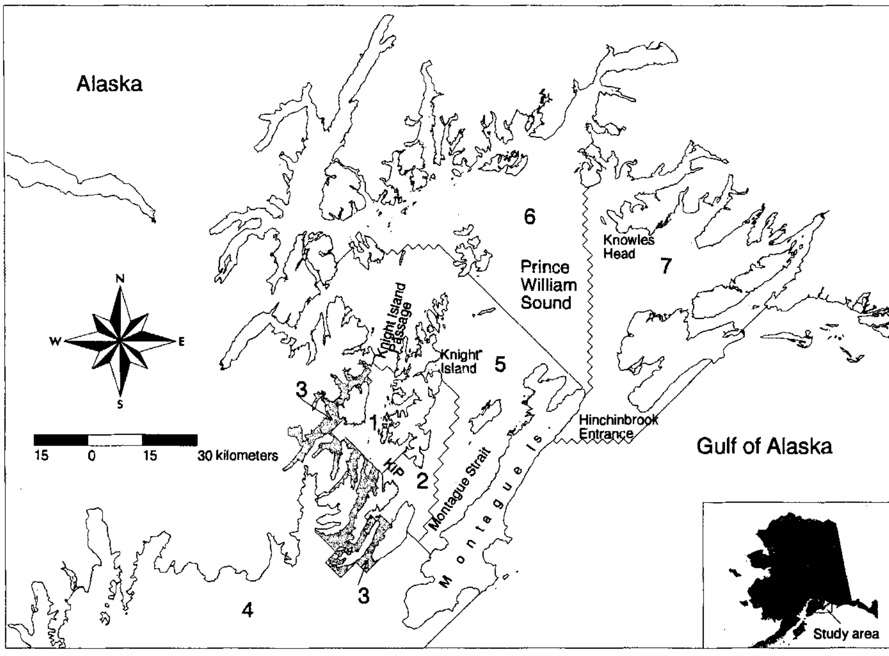

Figure 1. Zones used for analyses of encounter rates (see Table 1b and Methods for details). Zone 3 is shaded to make it easier to distinguish. KIP indicates Knight Island Passage.

October, over an area of approximately 3,500 km^2 in Prince William Sound, Alaska. Killer whales were located by visual searches, by acoustical monitoring, and by soliciting VHF radio reports from other vessels (see Matkin 1994 *et al.* for detailed methodology). Sit-and-wait searching was not a strategy used to detect whales, although acoustical monitoring was. Thus, searches were not systematic but relied on observer reports and familiarity with the area and with the behavior of the whales. For example, in the absence of radio reports from another vessel, searching was located in southwest Prince William Sound (zones 1–3, 5, Fig. 1), while searches in the northern or eastern Sound (zones 6, 7) and in Hinchinbrook entrance occurred most often in transit from Cordova or Valdez, on receipt of a report from another vessel, or as part of increased search effort in 1989–1990 (following the *Exxon Valdez* oil spill). Over the course of the study, a variety of vessels were used, nearly all eight meters or less in length and powered by either outboard or inboard/outboard motors. A vessel log and chart of the vessel track were kept for each day of operation, as well as a separate record detailing each encounter with killer whales and the whale track during the encounter. As whales could be encountered, and often were, at any time while a vessel was in the field, all vessel paths were recorded, including transit paths to and from port or camp, paths en route to a VHF report from another vessel, and paths while tracking whales. Specifics of each encounter were recorded, including date, time, duration, and location.

Table 1. Search effort and encounters with killer whale pods by year (a) and search effort by zone over all years (b).

(a) Year	Boat-days	Km searched[a]	Encounters[b]	(b) zone	Area (km^2)	Km searched[a]	Km searched/ km^2
1984	129	11,341	69	1	285	30,160	105.8
1985	60	4,452	48	2	359	28,018	78.0
1986	60	4,680	34	3	354	8,262	23.3
1987	29	2,057	22	4	6,404	5,817	0.9
1988	68	4,316	27	5	2,270	29,878	13.2
1989	206	16,181	88	6	3,542	11,430	3.2
1990	249	19,603	85	7	2,179	5,887	2.7
1991	188	15,651	54				
1992	136	10,492	69				
1993	79	5,591	40				
1994	87	6,321	32				
1995	125	11,066	63				
1996	92	7,700	32				
Total	1,508	119,451	663			119,452	

[a] Kilometers of search effort by all vessels. Note that this statistic and boat days, alternative measures of search effort, are strongly correlated ($R^2 = 0.986$).
[b] Encounters with killer whale groups.

Behavior was also recorded, as well as the time it occurred. However, the location of each behavior on the whale track was not noted. Position for vessel and whale paths were estimated from known landmarks. Within one mile of shore, estimates were likely more accurate (within one hundred meters) than when farther offshore (accurate within 0.5–1 km depending on distance from shore). Whales were approached and individually identified through left-side dorsal fin and saddle patch photography (Bigg *et al.* 1986, Matkin *et al.* 1994), and were grouped in pods as defined by Bigg *et al.* (1990) and Matkin *et al.* (1999*a*). Records, including all vessel and whale paths, were entered into a GIS database for analyses.

Pod Encounter Rates Corrected for Search Effort

Search effort was measured as kilometers that each vessel traversed. Kilometers searched and vessel-days were highly correlated (Table 1a), indicating that the average miles searched per day was consistent throughout the study and that either measure of search effort would yield similar results. We divided the study area into seven zones (Fig. 1), based on the distribution of search effort. Areas of dense search effort (*e.g.*, zones 1, 2; Fig. 1, Table 1b) were divided into small zones; areas of sparse search effort (*e.g.*, zones 4, 6, 7) were made into larger zones to increase the sample size of encounters within sparsely searched zones. Zone boundaries were chosen to (1) separate areas of dense and sparse effort (*e.g.*, zone 2 from 5); (2) keep geographically similar areas in a single zone (*e.g.,* the southwest bays and passages form zone 3, while outside waters form zone 4); and (3) separate geographically distinct areas (*e.g.,* eastern Sound in zone 7 from northwestern and central Sound in zone 6). Zones were large except in the southwestern Sound (zones 1–3) where search effort was most intense (Table 1). For each year, we then tabulated the number of encounters with killer whale groups that started within each zone. This number of encounters, divided by the kilometers of effort within that zone, was the encounters-per-unit effort. All encounter rates in this paper, therefore, refer to rates of encounters with known killer whale groups, and not with numbers of individual whales encountered. The composition or size of these groups may have changed over the duration of the study. Encounter rates were an indicator of the frequency of finding whale groups in a particular zone, and were assumed to indicate how commonly groups used different areas of the Sound.

Our analyses of area use consider the AT1 group separately from other transients that also traverse the area and have been collectively known as the Gulf of Alaska (GOA) transients. The separation of these two groups was based on their lack of association, as well as genetic separation (Matkin *et al.* 1999*b*; Barrett-Lennard, unpublished data). For resident pods, we limited our analyses to pods with more than 50 encounters over the study period and, thus, examined the distribution of the six most frequently encountered resident pods (hereafter referred to as major resident pods): AB, AE, AI, AJ, AK, and AN, the latter of which split into two pods, AN10 and AN20, in 1991. For analyses here, we include only sightings of AN10 after the split (there was only a single sighting of the AN20 group in the period 1992–1996). With this exception, all encounters with major resident pods, AT1 transients, and the GOA transients are included in our distribution analyses. We calculated encounter-rates-per-unit effort by year and by map zone, and compared the period 1984–1989 (hereafter referred to as the 1980s) with 1990–1996 (referred to as the 1990s). These year groupings were chosen to divide the available data roughly in half, as there were insufficient data to analyze years individually. We evaluated the distribution of social groups across map zone and decades using a multivariable analysis of covariance (MANCOVA) with Wilk's lambda as the test statistic, and kilometers-of-effort as a covariate to account for search effort. For groups where encounter rates differed significantly by zone, we used a *post hoc* Tukey's Honestly Significant Differences multiple comparisons test to identify differences. Tukey's HSD properly accounts for the multiple comparisons being made, so that any further correction (such as the Bonferroni adjustment) is not necessary. In this and subsequent analyses, no statistical difference does not conclusively indicate that differences do not exist, as the data may be too sparse or variable to detect biologically real differences.

Foraging Behavior

Whales were followed and their behavior recorded as opportunity permitted. Behaviors were classified as Travel (movement on a consistent compass course;

group members surfaced and dove synchronously), Rest (slower than normal movement; maternal units were in close association [<1 body length from neighbors] and synchronous in movement and breathing), Social (interaction between individuals, including sexual behaviors, chasing, rolling, breaching, spy-hopping, fluke and flipper slapping), or Foraging (any activity related to search for, pursuit of, capture, and consumption of prey). Foraging was broken down into sub-behaviors: Feeding (prey seen in the mouth of a whale or surface indications of prey such as blood, oily sheen, or fish scales); and for resident pods, Foraging for Fish (tight circling, rapid erratic movement, and lunges often accompanied by echolocation); or for transient whales, Open-water Foraging for Mammals (milling or slow travel when at the surface >1 km offshore, silent dives of ten or more minutes duration, and underwater movements of >1 km between surfacing) and Nearshore Foraging (movement following contours of the shoreline often within 20 m of shore, and entering small bays, narrow channels, and exploring rock outcrops or shoal areas).

Foraging sub-behaviors were not reliably distinguished in the field before 1987, and we therefore restricted analyses of behavior to 1987 and later years. Although the path of each encounter and the duration of behaviors were recorded, the specific locations of different behaviors were not. The distance traveled by whales was tabulated from the GIS database, and the zone in which most of this distance ($>50\%$) occurred was designated the "behavior zone" for that encounter (to distinguish this special use from any zone that contained a portion of the encounter). Encounters where no single zone contained $>50\%$ of the path length were designated as behavior zone 9 (a separate classification). Behaviors were analyzed based on behavior zone and, for the periods 1987–1991 and 1992–1996, it was necessary to combine years because of small sample sizes. The sampling period for behavioral data was shorter than for distributional data, and the time periods were chosen simply to divide the available data roughly in half. We calculated the proportion of each encounter duration that was spent in Foraging activities other than Feeding. We did not include Feeding because we were interested in the choices whales make about where to acquire prey, rather than the effect of habitat on the time taken to consume prey already obtained. For the same reason, we analyzed behaviors as the time-proportion of encounters (each encounter weighted equally) rather than analyzing time-weighted behaviors (a time budget). Thus, each observation bout (encounter) represents an independent sample of where whales were found foraging, and we avoid the problems of non-independence of sequential behaviors and of potential bias in encounter length by geographic location. Proportions were arc-sin transformed and their distribution analyzed by time period and behavior zone using ANOVAs on the arc-sin transformed proportions. Major resident pods that were similar in their area-use patterns (see Distribution Results and Table 3), were combined for analyses of behavior (AB, AI, AN, and AJ were considered together, as were AE and AK). GOA transient whales were excluded from analyses of behavior because foraging observations for these groups were too sparse for meaningful analyses.

Table 2. The number of encounters in which each pod or group was seen, 1984 to 1996 (n = 638 encounters, some of which contained multiple pods).

Pod	n
AT1	160
GOA	24
All residents	461
AB	220
AE	145
AI	168
AJ	56
AK	89
AN	147

Results

Surveys resulted in a total of 1,508 boat-days of search effort and 663 encounters with 19 different killer whale groups over 13 yr (Table 1a). The most intense searching was conducted in western Montague Strait and Knight Island Passage. These areas were designated as zone 1 (Fig. 1; encompassing southwestern Knight Island Passage, immediately around southwestern Knight Island where researchers maintained a base camp during most years of study), and as zone 2 (Fig. 1; including eastern Knight Island Passage and western portions of Montague Strait, the remainder of the most intensely searched area). The outer, central, and eastern areas of the Sound (zones 4, 6, 7, respectively) received relatively sparse coverage. The remaining two zones, zone 5 around northern and eastern Knight Island complex, and zone 3 in the southwest bays and passages, received intermediate levels of effort (Table 1b). Encounters involving the six major resident pods, the AT1 group, or any of the GOA transient groups made up 96% (n = 638 encounters) of all encounters (Table 2).

Distribution

For all major resident pods and transient groups, encounters increased with search effort and were affected by zone and decade (Table 3, over-all MANCOVA). Average encounter rates varied greatly year to year with no significant differences between decades, except that encounter rates were generally higher in the 1980s than the 1990s for AT1 group, and higher in the 1990s than 1980s for AE pod (Table 3, univariate results). For AT1 group, encounter rates during the 1980s were less than 0.1 per 100 km searched in 1984, but were more than twice that in 1985, 1988, and 1989. In contrast, encounter rates for this group were below 0.1 per 100 km searched in 1991, 1994, and 1996; and did not rise above 0.2 per 100 km searched at any time during the 1990s. For AE pod in the 1980s, there were only two years when encounter rates were higher than 0.1 per 100 km searched (1985 and 1986), while encounters were at least that high in six of seven years in the 1990s.

Table 3. Results of a MANCOVA showing overall and univariate effects of zone and decade on encounters with six resident pods and AT1 and GOA transient groups (see text for details).

Analysis	source	df	Approximate F	P	Effect[a]	(HSD)
MANCOVA	Effort[b]	8, 75	22.67	0.001	+	
	Zone	48, 373	2.21	0.001	see univariate tests	
	Decade	8, 75	2.98	0.006	see univariate tests	
AB (Resident)	Zone	6	5.68	0.001	2174536	(3.27)
	Decade	1	1.77	0.187	NS	
AI (Resident)	Zone	6	5.86	0.001	2174536	(2.38)
	Decade	1	0.50	0.482	NS	
AJ (Resident)	Zone	6	2.41	0.034	2143765	(1.39)
	Decade	1	1.39	0.242	NS	
AN (Resident)	Zone	6	5.14	0.001	2147365	(2.80)
	Decade	1	0	0.985	NS	
AE (Resident)	Zone	6	4.01	0.001	1257463	(1.73)
	Decade	1	4.15	0.045	90s > 80s	
AK (Resident)	Zone	6	1.45	0.205	NS	
	Decade	1	0	0.994	NS	
AT1 (Transient)	Zone	6	4.16	0.001	1376452	(2.17)
	Decade	1	9.36	0.003	80s > 90s	
GOA (Transient)	Zone	6	3.22	0.007	5346721	(0.87)
	Decade	1	1.15	0.286	NS	

[a] Plus indicates that effort was positively correlated with encounter rates. Zone numbers appear ordered from most to least encounters (after effects of effort and decade have been accounted for); bars connect zones that were not significantly different (Tukey's Honestly Significant Differences multiple comparisons test, HSD in parentheses).
[b] The effect of effort in each univariate comparison was significant ($F > 5.52$, df = 1, $P < 0.021$) however the individual statistics were not listed to save space.

With the exception of AK pod, all major resident pods tended to use Knight Island Passage (zones 1, 2) more than other areas of the Sound (Fig. 2). Area-use patterns were especially similar for resident pods AB, AI, and AN (Table 3). Collectively, these three pods were recorded in southwest bays and passages (zone 3) only 14 times (4.6% of 303 encounters), only once (0.3% of encounters) in the northwestern Sound, eight times (2.6%) in the central Sound, once (0.3%) in the eastern Sound and 12 times (4.0%) in the area of Hinchinbrook Entrance. All other encounters were in the southwestern Sound, primarily Knight Island Passage and Montague Strait (zones 1, 2, 5). Among major resident pods, the pattern exhibited by these three pods was most different from that of pod AK, which showed no statistical preference for any of

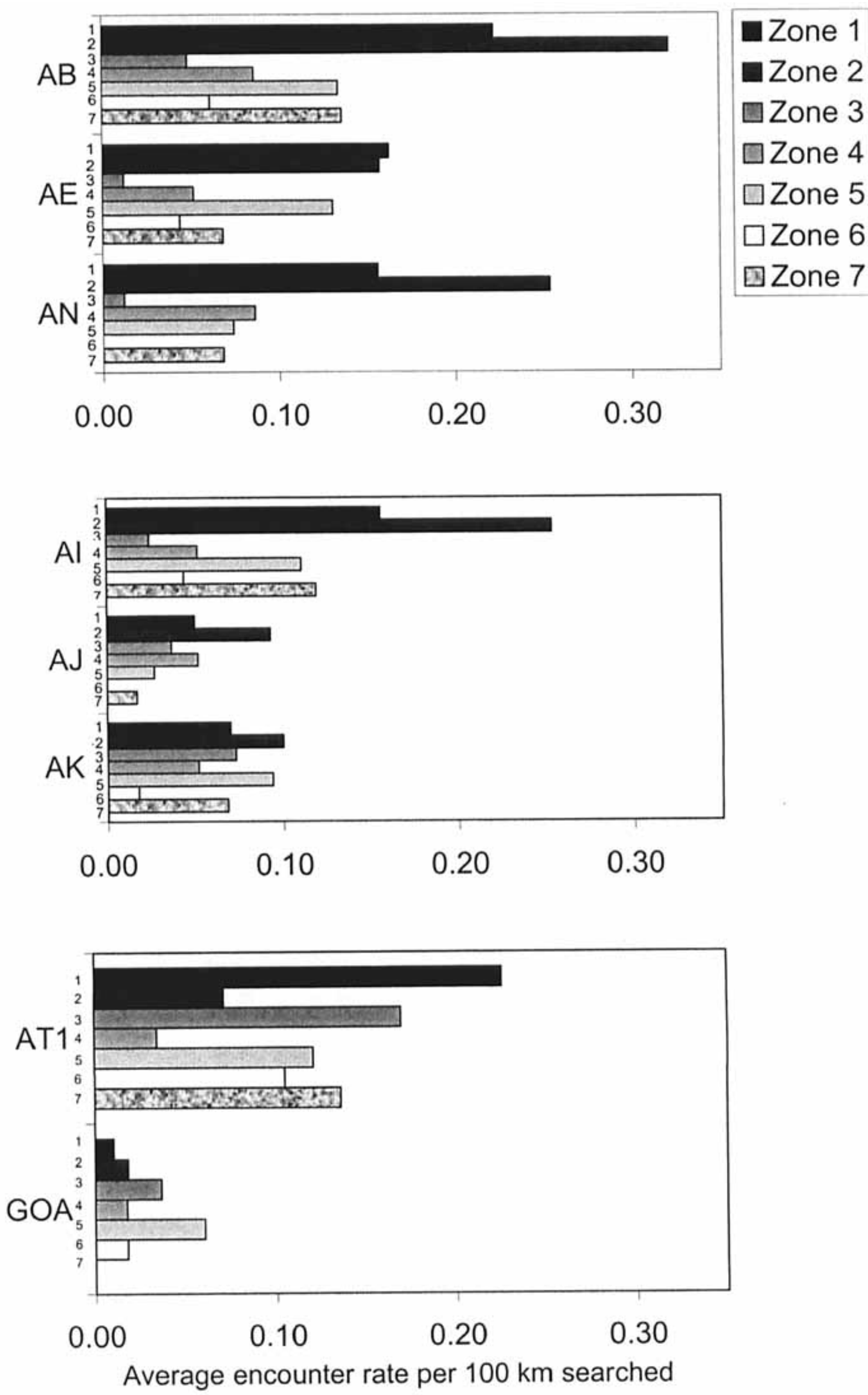

Figure 2. Encounter rates with major resident pods and AT1 and GOA transient groups in zones 1–7. Numbers for each bar indicate the zone for which encounter rates are shown.

the zones (Fig. 2, Table 3). Of the two remaining major resident pods, AE was more similar to the AK pattern of no strong preference for a particular portion of the study area. For AE pod, slightly higher use in the most-frequented zones (1, 2) was not significantly different from use in the least-used zone (zone 3) in pairwise comparisons using Tukey's Honestly Significant Difference (Table 3). Pairwise comparisons, as in this case, may fail to reject a null hypothesis even when the overall statistic can reject it based on the larger overall sample size. Finally, the pattern shown by AJ pod was similar to but less dramatic than that of pods AB, AI, and AN. Area use by AJ pod was greatest in zones 1 and 2, and the most-frequented and least-frequented zones were significantly different (Table 3). Although all six major resident pods used zone 3 in transit, none showed a pattern of regular occurrence in these passages or the southwestern bays.

These patterns of area use by the major resident pods differed from those of the AT1 transient group or the combined GOA transient groups, which used a larger portion of Prince William Sound than resident pods AB, AI, AN, or AJ and were more likely to be encountered in zone 3. The AT1 group also used the mid- and eastern-Sound waters (zones 6, 7; Fig. 2) more commonly than any other group. The GOA transients used areas almost exclusively in southern or eastern Montague Strait (zones 4, 5; Fig. 2), the north tip of Montague Island (zone 5), and in Hinchinbrook entrance.

Distribution of Foraging Behaviors

Foraging for Fish made up a greater proportion of sample time with AB, AI, AN, and AJ pods in the period 1987–1991 than in the period 1992–1996, but there were no significant differences between behavior zones in the incidence of this foraging behavior (Fig. 3; ANOVA: time period, df = 1, $F = 5.41$, $P = 0.021$; behavior zone, df = 7, $F = 0.44$, $P = 0.876$). The same pattern was found for pods AE and AK considered together: the occurrence of Foraging for Fish was greater for the 1987–1991 time period than during the 1992–1996 period, but there were no significant differences among behavior zones (Fig. 3; ANOVA: time period, df = 1, $F = 4.17$, $P = 0.042$; behavior zone, df = 7, $F = 1.17$, $P = 0.318$).

In contrast, for the AT1 group the occurrence of Nearshore Foraging was significantly greater on encounters that occurred predominantly in zones 1 and 3 and less on encounters predominantly in zones 2 and 5 (Fig. 3; ANOVA: behavior zone, df = 7, $F = 2.16$, $P = 0.043$). No differences were found for this behavior by time period (ANOVA: df = 1, $F = 0.18$, $P = 0.670$). There were no significant differences in the occurrence of Open water Foraging for Mammals across behavior zones or time periods for this group (ANOVA: time period, df = 1, $F = 0.01$, $P = 0.923$; behavior zone, df = 7, $F = 0.65$, $P = 0.710$).

Discussion

Most individual killer whales from pods considered in this study are known only from Prince William Sound and surrounding waters. The Sound is a

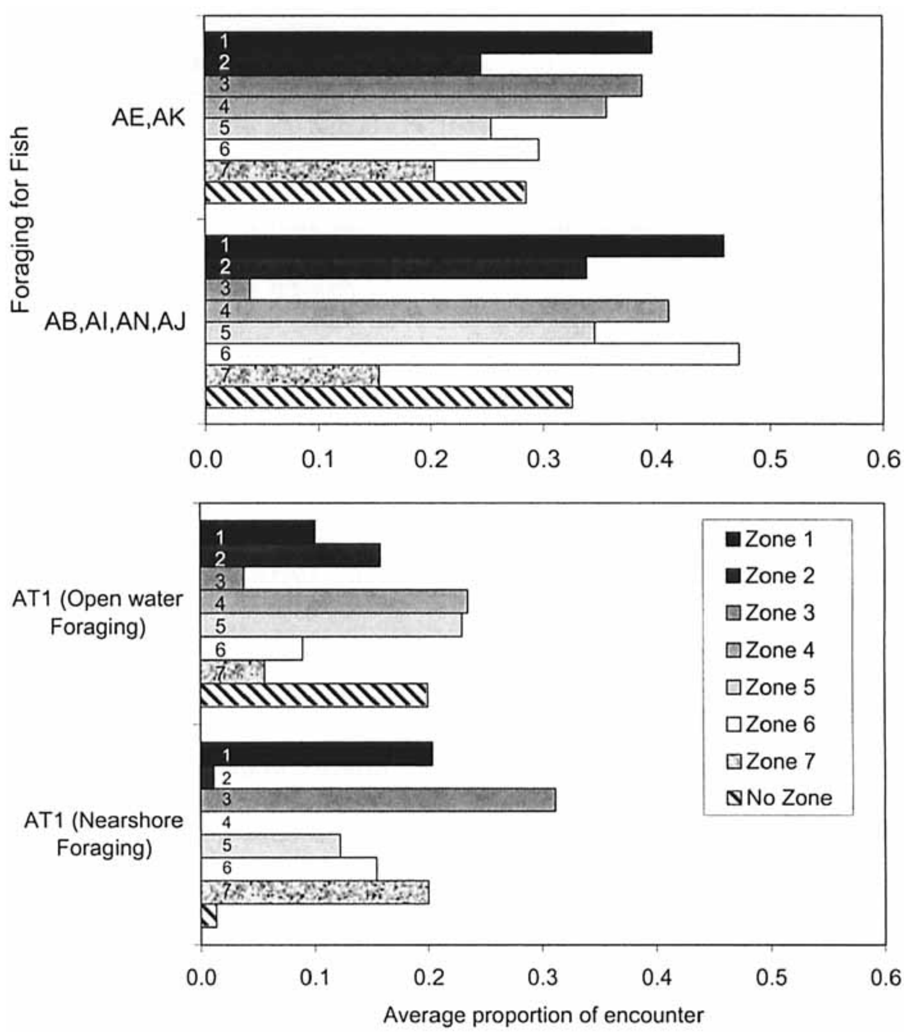

Figure 3. (Top panel) Incidence of Foraging for Fish behavior by zone in which greater than 50% of encounter occurred, and (bottom panel) incidence of Transient Nearshore Foraging and Open-water Foraging for Mammals by the zone in which greater than 50% of encounter occurred (see Methods for details). Numbers for each bar indicate behavior zone for which behavior rates are shown.

relatively small area, 200 km at its widest, and resident killer whales are known to have ranges in excess of 750 km (Biggs *et al.* 1990, Matkin *et al.* 1997). It is therefore not surprising that every group examined was recorded at least occasionally throughout Prince William Sound, as well as to the west of the Sound in the waters off the Kenai Peninsula.

The frequency of encounters with most major resident pods did not differ significantly between the 1980s (1984–1989) and the 1990s (1990–1996). Differences were found only for the AE pod, which was more frequently encountered in the 1990s. However, these analyses examined only the frequency of encounters with the major resident pods, and did not consider the number of individual whales present at each encounter nor the presence of other less well known resident pods that entered the Sound on occasion and traveled with the major resident pods. In particular, the decline in the size of AB pod from 36 to 22 individuals following the *Exxon Valdez* oil spill (Matkin *et al.* 1999a) was not considered. Also, in 1990 AN pod split into AN10 and AN20 pods and the 28 whales in the AN20 pod were no longer encountered in the Sound. Our results indicate that the six major resident pods continued to use the Sound consistently over the years, even while the number of resident whales present in some pods declined (Matkin *et al.* 1999*a*). In addition, the number of other resident pods using the Sound may have declined and resulted in an overall decline in use of Prince William Sound by resident killer whales (Matkin *et al.* 1999*c*).

The transient AT1 group frequented the Sound less often in the 1990s than in the 1980s (Table 3). These animals seldom traveled as a single unit and were generally encountered in groups of 2–6 whales. The total number of AT1 whales declined from 22 to 11 during the early 1990s following the *Exxon Valdez* oil spill (Matkin *et al.* 1999*b,c*). In addition, harbor seals, the primary prey of the AT1 group, have also declined during this period (see discussion of behavioral data, below) and these killer whales may have been forced to increase their foraging range in response to the decrease in harbor seal numbers.

From the onset of the study in 1984, the primary focus of this research has been photo-identification. Data on distribution of killer whales were not collected in a systematic format designed to answer specific questions regarding changes in distribution. Thus, the uses of the data to examine distribution are limited and must be approached with caution. However, biases are minimized when data are stratified by search effort (as here) or by sighting density (Edwards and Kleiber 1989). Spatial biases may occur if a unit of search effort in one area of the Sound is not as efficient as the same effort in another area. Because researchers concentrated search effort in areas where they were most successful at sighting whales, it seems likely that any spatial bias would be towards underestimating use in areas where search effort was lowest (zones 4, 6, 7; Table 1). However, we note that sightings per unit effort in these zones do not appear unusually low (Fig. 2, Table 3). Temporal biases may occur if observers over time became more skilled and more familiar with the areas used by whales. Temporal biases are likely to favor an increase in sightings per unit effort over time, a trend found for AE pod, but opposite to that detected for the AT1. With these caveats in mind, the direction of potential bias allows us more confidence of the effect in the AT1 group, but perhaps less for AE pod.

We found several general patterns of spatial use among eight different resident pods and transient groups. A major difference was apparent between resident- and transient-type whales. This partitioning of habitat between residents which occurred in the wider entry waterways of the western Sound

(Montague Strait and Knight Island Passage), and transients which were more often found in the narrow bays and passages (zone 3), reflects dietary preferences. Salmon migration pathways enter the Sound at Montague Strait and run up passages along the western side of Knight Island, and resident whales feed on the salmon across the width of these channels (Saulitis *et al.* 2000). However, foraging tactics on pinnipeds appear to require careful searching of areas very close to shorelines (Saulitis *et al.* 2000), perhaps because pinnipeds are most vulnerable as they enter or leave haul-out sites. Data on the distributions of salmon, pinniped, or cetacean prey within the Sound have yet to be published.

In British Columbia transient whales exhibited group-specific foraging behavior: some transient groups seldom foraged in nearshore areas while others spent up to 50% of their time foraging nearshore (Baird and Dill 1995). Members of the AT1 group spent similar amounts of time in nearshore and offshore foraging (Fig. 3). Our analyses were consistent with the interpretation that killer whale distributions reflect their foraging needs, at least in some cases. For example, Nearshore Foraging for the AT1 group (Fig. 3) was significantly more common in the southwest bays and passages (zone 3), along the western side of Knight Island (zone 1), and in zone 7, the same areas where this group spends a disproportionate amount of its time (Fig. 2) suggesting these areas were critical foraging habitat for these whales. However, no similar pattern emerged for Open-water Foraging for Mammals behavior for the AT1 group. For the resident groups, foraging behaviors were no more likely in the most commonly used zones than they were elsewhere. Although we found a decrease from the 1980s to the 1990s in the proportion of time major resident pods in the Sound spent foraging, there was no evidence that foraging behavior accounts for differences between the AB, AN, AI, and AJ grouping of resident pods and the AE and AK grouping. It should be noted that although members of all these pods intermix at times, the AB, AN, AI, and AJ pods are genetically distinct (Mt DNA) from the AE and AK pods (Matkin *et al.* 1999*b*; Barrett-Lennard *et al.*, unpublished data).

Harbor seal numbers in Prince William Sound have declined by 63% from 1984 through 1997, a decrease that was exacerbated by the *Exxon Valdez* oil spill (Frost *et al.* 1999). Harbor seals are the primary prey of the AT1 transient group (Saulitis *et al.* 2000). It is possible that a decline in prey availability accounts for the general decline in encounter rates with the AT1 group (Table 3). These whales appeared to use the Sound heavily for foraging, as the frequency of Nearshore Foraging is highest for AT1 whales in the areas where they most often occur. Nearshore Foraging is exhibited when whales are hunting pinniped prey, primarily harbor seals (Saulitis *et al.* 2000).

Killer whale distributions may also depend on the locations of favored rubbing beaches or other resources, although there is no evidence to support or refute such a claim. Differences in foraging behavior or in the distribution of prey seem likely to account for area-use differences between residents and transients. In British Columbia two genetically distinct, non-associating resident communities exist whose ranges seldom overlap (Bigg *et al.* 1990, Ford *et al.* 2000), and it may be that distinct ranges resulted from competition and the specialization of each community on different salmon runs. Although we found two different patterns of area use among genetically distinct, occasionally associating groups of resident whales in the Sound, these patterns overlap strongly (Table 3) and are apparently not similar to the geographic distinction between communities in British Columbia. We found no evidence from analyses of foraging behavior that would account for the differences in area use among the resident pods in the Sound that we examined.

In light of increased discussion of marine reserves and habitat protection, this study is a first attempt to define specific marine habitats important for wide ranging Odontoceti such as killer whales. Although killer whale distribution in relation to salmon abundance has been examined in Puget Sound (Heimlich-Boran 1986), there has been no attempt in other areas of the North Pacific to define important killer whale habitat. In Prince William Sound, killer whales are predictably found inshore, at least seasonally, as are their prey. Such an approach may have application to other Odontoceti where data are available.

Acknowledgments

We thank Lance Barrett-Lennard, Lloyd Lowry, and one anonymous reviewer for comments on drafts of this manuscript. The research described in this paper was supported by the Oil Spill Recovery Institute and the *Exxon Valdez* Oil Spill Trustee Council. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council.

Literature Cited

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

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

Bigg, M. A., G. M. Ellis and K. C. Balcomb III. 1986. The photographic identification of individual cetaceans. Whalewatcher: Journal of the American Cetacean Society 20:10–12.

Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford and K. C. Balcomb III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission (Special Issue 12):383–405.

Edwards, E. F., and P. M. Kleiber. 1989. Effects of nonrandomness on line transect estimates of dolphin school abundance. Fishery Bulletin, U.S. 87:859–876.

Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm and K. C. Balcomb. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

Ford, J. K. B., G. M. Ellis and K. C. Balcomb III. 2000. Killer whales 2nd edition. University of British Columbia Press, Vancouver, BC.

Frost, K. J., L. F. Lowry and J. M. Ver Hoef. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. Marine Mammal Science 15:494–506.

HALL, J. D. 1986. Notes on the distribution and feeding behavior of killer whales in Prince William Sound, Alaska. Pages 69–83 *in* B. C. Kirkevold and J. S. Lockard, eds. Zoo Biology Monographs. Volume 1. Behavioral biology of killer whales. Alan R. Liss, New York, NY.

HEIMLICH-BORAN, J. R. 1988. Behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. Canadian Journal of Zoology 66:565–578.

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

MATKIN, C. O., G. M. ELLIS, M. E. DAHLHEIM AND J. ZEH. 1994. Status of killer whales in Prince William Sound, 1985–1992. Pages 141–162 *in* T. R. Loughlin, ed. Marine mammals and the Exxon Valdez. Academic Press, San Diego, CA.

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

MATKIN, C. O., G. M. ELLIS, P. OLESIUK AND E. L. SAULITIS. 1999*a*. Association patterns and genealogies of resident killer whales (*Orcinus orca*) in Prince William Sound, Alaska. Fishery Bulletin, U.S. 97:900–919.

MATKIN, C. O., G. ELLIS, E. SAULITIS, L. BARRETT-LENNARD AND D. MATKIN. 1999*b*. Killer whales of southern Alaska. North Gulf Oceanic Society, Homer, Alaska.

MATKIN, C. O., G. ELLIS, L. BARRETT-LENNARD, H. YURK, D. SCHEEL AND E. SAULITIS. 1999*c*. Comprehensive killer whale investigation. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 98012), North Gulf Oceanic Society, Homer, Alaska. Available from Exxon Valdez Oil Spill Trustee Council, 641 G Street, Suite 401, Anchorage, AK 99501.

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

SAULITIS, E., C. MATKIN, K. HEISE, L. BARRETT-LENNARD AND G. M. ELLIS. 2000. Foraging strategies of sympatric killer whale (*Orcinus Orca*) populations in Prince William Sound, Alaska. Marine Mammal Science 16:94–109.

Received: 9 December 1999
Accepted: 29 December 2000