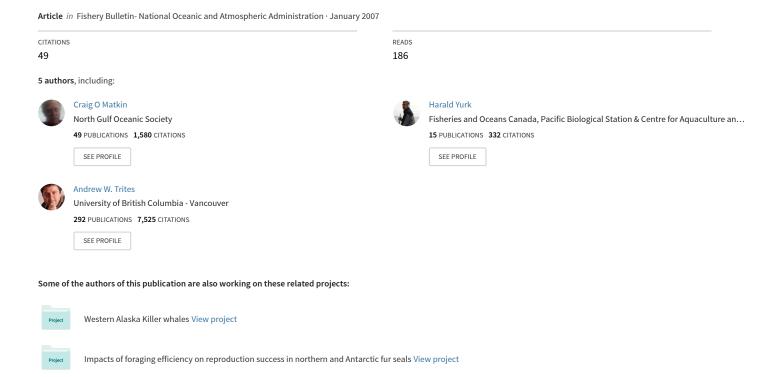
Ecotypic variation and predatory behavior among killer whales (Orcinus orca) off the eastern Aleutian Islands, Alaska



Abstract—From 2001 to 2004 in the eastern Aleutian Islands, Alaska, killer whales (Orcinus orca) were encountered 250 times during 421 days of surveys that covered a total of 22,491 miles. Three killer whale groups (resident, transient, and offshore) were identified acoustically and genetically. Resident killer whales were found 12 times more frequently than transient killer whales, and offshore killer whales were encountered only once. A minimum of 901 photographically identified resident whales used the region during our study. A total of 165 mammal-eating transient killer whales were identified, and the majority (70%) were encountered during spring (May and June). The diet of transient killer whales in spring was primarily gray whales (Eschrichtius robustus), and in summer primarily northern fur seals (Callorhinus ursinus). Steller sea lions (Eumetopias jubatus) did not appear to be a preferred prey or major prey item during spring and summer. The majority of killer whales in the eastern Aleutian Islands are the resident ecotype, which does not consume marine mammals.

Ecotypic variation and predatory behavior among killer whales (*Orcinus orca*) off the eastern Aleutian Islands, Alaska

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In 1992, flipper tags from fourteen Steller sea lions (*Eumetopias jubatus*) were found in the stomach of a killer whale (Orcinus orca) that had died in Prince William Sound (Heise et al., 2003). This discovery prompted considerable interest and speculation about the role that killer whales may have played in the decline and lack of recovery of Steller sea lions in western Alaska (Barrett-Lennard et al., 1995). Since the late 1970s, Steller sea lions in the Gulf of Alaska and Aleutian Islands have declined by over 80% (Merrick et al., 1987; Trites and Larkin, 1996; Loughlin and York, 2000; Winship and Trites, 2006). Similar sharp declines have also occurred among some populations of harbor seals (*Phoca vitulina*), northern fur seals (Callorhinus ursinus), and sea otters (Enhydra lutris) (York, 1987; Pitcher, 1990; Trites, 1992; Estes et al., 1998). Whether or not these declines are related to killer whales is currently the subject of considerable scientific debate (Springer et al., 2003; Trites et al.,

2006; DeMaster et al., 2006; Mizroch and Rice, 2006).

Most knowledge about killer whales in the North Pacific has been gathered between California and the northern Gulf of Alaska, where three distinct lineages of killer whales have been identified: fish-eating "resident" killer whales, which appear predictably in large groups from Washington to Alaska; marine mammal-eating "transient" killer whales, which appear infrequently and in smaller groups; and "offshore" killer whales, whose feeding habits are poorly known, but are thought to eat fish, including sharks (Matkin et al., 1999a; Barrett-Lennard, 2000; Ford et al., 2000; Saulitis et al., 2000). These groups are genetically and behaviorally distinct, but have overlapping geographic ranges and are considered as ecotypes because of their differences in diet. However, prior to our study, it was not known whether these lineage and ecotype distinctions extended to the northwestern Gulf of Alaska and the

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Aleutian archipelago, nor was much known about the extent to which killer whales prey on Steller sea lions and other species of marine mammals in these regions.

The goals of our study were 1) to determine whether the eastern Aleutian Islands are also home to the three lineages and ecotypes of killer whales that have been identified elsewhere in the northeastern Pacific; 2) to derive estimates of killer whale numbers for this region; and 3) to document the behaviour of killer whales foraging on marine mammals. Obtaining such information about killer whale numbers, diets, and hunting behavior is critical for resolving the role that killer whales may have played in the decline and lack of recovery of Steller sea lions and other species of marine mammals in western Alaska.

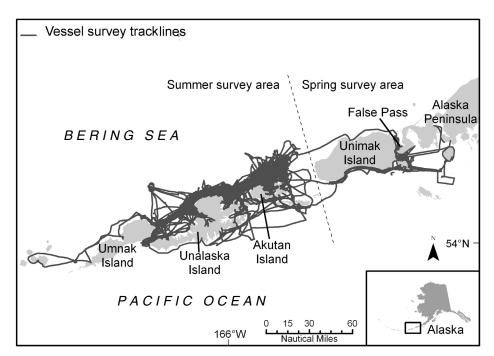


Figure 1

Tracks of the vessels during the surveys for killer whales (*Orcinus orca*) for the years 2001–2004. The vessels tended to return to areas that produced encounters with killer whales. The spring False Pass–Unimak Island surveys are distinguished from the summer Unimak Pass–Umnak Island surveys by the dashed line.

Materials and methods

Following the research method used to collect information on killer whales in other regions (Matkin et al., 1999a; Ford et al., 2000), five types of data were gathered: photo-identification pictures of individuals and groups, acoustic recordings of killer whale calls, skin tissue samples for genetic analysis, prey samples, and accounts of predation. Additionally, we documented the presence of potential marine mammal prey. Analysis of these data allowed the determination of killer whale ecotypes and a description of killer whale feeding habits.

Field methods

Boat-based surveys over a wide geographic range occurred during June-September 2002-2004 from Unimak Pass to Samalga Pass, and surveys over a relatively small range occurred in May and early June 2003-2004 in the False Pass-Unimak Island region. Surveys in the broader region traversed 19,686 nautical miles and were focused in the Bering Sea within twenty miles of the shoreline between Unimak Pass and eastern Umnak Island (Fig. 1). The 2003-2004 False Pass-Unimak surveys traversed 1970 miles in Ikatan Bay and along the Pacific shore of Unimak Island. We operated in areas of suspected high killer whale density according to information provided by local fishermen and researchers from the National Marine Mammal Laboratory (NMML) (Dahlheim, 1997) during previous transect

surveys that covered broader regions. We modified our surveys each season to cover the areas that were most productive in providing killer whale encounters.

The research was conducted from aluminum-hull fishing vessels (powered by diesel inboard engines) ranging from 10 to 14 meters in length. Survey effort varied by year with a total of 372 days from 2001 to 2003 from the Unimak Pass to Samalga Pass in summer and a total of 49 survey days in 2003 and 2004 in the False Pass-Unimak Island region in spring (Table 1). All sightings of marine mammals during vessel surveys were recorded and the number of individuals was estimated to determine the relative abundance of potential prey items.

Photographs of the left side of dorsal fins and saddle patches of killer whales were taken with a Nikon F-100 camera (B and H Photo, New York, NY) equipped with either fixed 300-mm lenses or 100-300 zoom lenses and loaded with Fuji Neopan ASA1600 black and white film (B and H Photo New York, NY). These photographs were checked against existing photo-catalogues of Alaskan killer whales (Dahlheim, 1997; Matkin et al., 1999a) and other unpublished photographs. Tissue samples of at least one whale in each group were collected for genetic analysis and biopsy when weather and behavior of the whales permitted close approach. These samples were collected by using lightweight darts and an airpowered rifle (Barrett-Lennard et al., 1996). The outer skin portion of the samples was used for genetic analysis, and the underlying blubber portion was used for

Table 1

Survey effort (in days) and number of encounters with resident and transient killer whales (*Orcinus orca*) in the eastern Aleutians (2001–2004). "Survey days" are the days spent looking for whales; "Miles" are given in nautical miles.

Year	Dates	False Pass–Unimak Island region (single vessel 2003–2004)				Eastern Aleutians (Single vessel 2001, two vessels 2002–04)				
		Survey days		Encounters			G		Encounters	
			Miles	Resident	Transient	Dates	Survey days	Miles	Resident	Transient
2001		_	_			19 Jun– 18 Aug	16	835	13	1
2002		_	_	_		17 Jun– 24 Aug	188	6599	57	4
2003	16 May– 3 Jun	18	642	0	13	10 Jun– 31Aug	108	6321	49	4
2004	4 May– 3 Jun	31	1328	0	32	7 Jun– 9 Sep	130	6766	70	7
Total		49	1970	0	45		372	20,521	189	16

contaminant analysis, lipid and fatty acid, and stable isotope analysis (see Herman et al., 2005). Genetic analysis involved sequencing the entire mitochondrial control region (see Barrett-Lennard [2000] for details). Acoustic recordings were made when whales were vocalizing and ambient noise levels permitted using an Offshore AcousticsTM (Offshore Acoustics, Nanaimo, British Columbia) hydrophone with a built-in preamplifier and a Sony WM-D6C (B and H Photo, New York, NY) cassette recorder. This system had a frequency response of 10 Hz to 8 KHz (±3 dB).

Single, continuous observation periods with killer whales were termed encounters. During these vesselbased observation periods, the location of the killer whales was plotted at approximately 5-min intervals by using a global positioning system (GPS) linked to a computer with NobletecTM (Nobletech, Beaverton, OR) navigational software. Time spent in different behavioral states (e.g., feeding, socializing, resting, traveling) was recorded on data sheets. Whales were observed continuously during encounters, and any signs of possible predation were recorded. During behavioral observations, marine mammal kills were confirmed only when marine mammal parts were observed in the mouths of the whales, or when bits of blubber, skin, or viscera, hair were collected, or blood or oil was observed on the surface of the water. Predation on fish was confirmed by observations of fish in the mouths of whales or by collecting and inspecting floating parts. To document the potential marine mammal prey in the region during the period of the study, we recorded the time, location, and number of all marine mammals sighted.

Analytical methods

Photo-identification All photographic negatives were examined over a light table with an 8.0 power PeakTM (B

and H Photo, New York, NY) magnification loop. Identifiable individuals were recorded and assigned a unique alphanumeric name in order to be tracked throughout the study. Whales that could not be positively re-identified were not assigned a name. From this photographic database, the actual number and identity of individual killer whales and groups of whales present for each encounter were determined. Because some of the photographs were of poor quality, these photographs were rejected from further analyses; thus not all the whales encountered were identifiable.

Acoustics We inspected acoustic recordings for the presence of discrete calls by listening to tapes and monitoring real-time spectrograms using Cool Edit 2000™ (Syntrillicum Software Corp., Phoenix, AZ) sound manipulation software. Calls were analyzed following the protocol of Ford (1991) and Yurk (2005). Killer whales produce a variety of different types of vocalizations that can be described as clicks, whistles, and calls (Ford, 1989). Calls are the most common type of vocalization, occurring in over 90% of all encounters with vocalizing killer whales. These pulsed vocalizations occur as either signals of a frequently repeated acoustic pattern or as signals of variable acoustic pattern (Ford, 1991). Discrete calls were chosen for this analysis because they retain their recognizable acoustic structure for many years and likely for many generations (Yurk, 2005). Recognized calls were digitized at a 44.1-kHz sampling rate with a 16-bit sample size and further analysed spectrographically using Canary 1.2.4 sound analysis software (Cornell Laboratory of Ornithology, Ithaca, NY). The spectrographic analysis was done by using fast-Fourier transformations (FFT) of time series of the recorded sound pressure waves with sizes of 1024 points for each analyzed time series. The FFT identifies the composing sine waves in sound pressure waves of acoustic signals and allows spectrographic representations of the sound frequency versus time and pressure. Spectrograms were produced with an 87.5% overlap of the analyzed time series. Resulting spectrograms had a time resolution of 2.9 milliseconds and a frequency resolution of 43 Hz.

We categorized calls by ear and by visual inspection of distinct upper and lower frequency components of the sound spectrum (UFC and LFC, respectively), as described by Miller and Bain (2000) and Yurk et al. (2002). When categorizing the calls as distinct, particular attention was given to 1) the existence and contour shapes of UFCs; 2) LFC contour shapes; 3) LFC segmentation (elements separated by silent intervals); and 4) the component structure (elements within the LFC arising from abrupt shifts in contour and not separated by silent intervals) of the LFCs (Ford, 1991; Yurk, 2005).

The three known ecotypes of killer whales inhabiting waters off British Columbia and southern Alaska (resident, transient, and offshore) are acoustically distinguishable by 1) vocalization rate; 2) the occurrence of different discrete calls; 3) the syllables used in calls; and 4) the production rate and characteristics of echolocation clicks. Transient killer whales, which appear to rely on passive listening to catch their marine mammal prey, vocalize less frequently than resident killer whales (Deecke et al., 2005). Transients rarely use echolocation clicks, in contrast to resident and offshore killer whales (Deecke et al., 2005). All calls of transient killer whales are distinct from the calls of resident whales by 1) an audible quavering of the fundamental sound frequencies (instead of a crisp appearance of these sound frequencies that is typical of calls from resident killer whales), and 2) a distinctively lower amount of different call syllables and a distinct order of these syllables compared to those in calls of resident killer whales (Yurk, 2005). Transient and resident killer whales are distinguishable from offshore killer whales by their use of unique call types (Yurk, 2005). We determined whether the encountered whales fell into discrete acoustic groups and, if so, whether those acoustic groups were similar to any of the acoustic groups observed in British Columbia and southern Alaska. Analysis was completed by Yurk (2005), independent of knowledge of genetic differences and social associations among groups. Call rates were estimated from field estimates of killer whale group sizes for each encounter.

Genetics DNA was extracted from the skin portion of the biopsies using proteinase K digestion, phenol and chloroform purification, and ethanol precipitation using standard procedures (Sambrook et al., 1989)

We obtained mtDNA sequences using the following procedure: 1) the entire D-loop region was PCR-amplified by using custom-designed primers that annealed to the flanking tRNA-Thr and 12s-rRNA regions (Barrett-Lennard, 2000); 2) the PCR product was purified with QIAQuick® spin columns (Qiagen, Valencia, CA) following protocols supplied by Qiagen, Ltd. (Valencia, CA); 3)

a sequencing reaction was performed with Fs-Taq® (Applied Biosystems, Foster City, CA) system reagents and protocols supplied by Applied Biosystems, Ltd. (Foster City, CA); and 4) the sequence was resolved on an Applied Biosystems 377 (Applied Biosystems, Foster City, CA) automated DNA sequencer. Because the sequence was too long (950 bases) to be entirely resolved in one direction, sequencing reactions were run from each end of the amplified fragment. We visually checked the output graphs from the automated sequencer and corrected the computer-generated sequences accordingly. We also used the approximately 400-base overlap in the sequences of opposite directions to check for errors. As a final check of accuracy, we overlaid each output graph with a reference graph on a transparent sheet, and scanned the two graphs for differences. We then aligned unique sequences using the program CLUSTAL-W (European Bioinformatics, Cambridge, UK) (Thompson et al., 1994).

Results

Summary of survey effort and encounters with killer whales

On 250 occasions, groups of one or more killer whales were encountered during the surveys that covered a total of 22,491 miles in 421 days in the eastern Aleutians and False Pass-Unimak Island area (Table 1). The majority of survey effort and encounters occurred west of Unimak Pass during summer; surveys in False Pass-Unimak Island area were not initiated until 2003. From approximately half of our encounters with groups of killer whales in both regions, we obtained genetic samples or acoustic recordings (Table 1). Killer whales of the offshore ecotype were encountered only once (in 2003) and both acoustic and genetic samples were obtained during this encounter.

Use of acoustic data, genetic analysis, and group association to infer lineage

Genetic and acoustic analyses revealed the presence of three killer whale populations. As described in more detail below, one population clustered genetically and acoustically with resident killer whales ranging from Puget Sound, Washington to Kenai Fjords, Alaska, and a second population clustered with transient killer whales from the same general area. Accordingly, those two groups were provisionally classified as a resident killer whale group and a transient killer whale group, respectively. The third population clustered genetically with offshore killer whales sampled off British Columbia, and were provisionally classified as an offshore killer whale group. Acoustic comparison was not possible in the case of offshore killer whales because of a scarcity of recordings.

Resident, transient, and offshore killer whales have never been observed interacting socially in the ar-

eas where they were previously identified and studied (Puget Sound to Kenai Fjords), and no interaction was observed in our study between the genetically or acoustically distinguished groups. Therefore, it was possible to infer the population status from the group-association patterns of individuals for which there was no genetic or acoustic data. Animals observed in association with whales of known genetic or acoustic type were assumed to be of that same type. We did not use diet as a criterion for classification to avoid circular reasoning (evidence of dietary differences between populations becomes tautological if diet is used to define populations).

Acoustic analysis During 31 of 39 encounters in which we recorded killer whale vocalizations and did not collect genetic samples, the use of distinct calls, use of echolocation clicks, and the call rate were consistent with attributes of resident killer whale vocalizations from other regions of the Northeast Pacific (Table 2) (Yurk, 2005). All encounters had average call rates of three calls or more per minute, and strings of echolocation clicks were abundant across encounters. During these encounters, 23 structurally distinct calls were identified. Seven calls showed no obvious similarities to calls recorded elsewhere in the northeast Pacific and 15 had structural similarities, sharing some call components with calls used by killer whales that regularly occur in the northern Gulf of Alaska. However, no call from these encounters was identical to any call of the known killer whale call repertoires.

The resident-type killer whales encountered in western Alaska possibly belong to groups that are distinct from the groups of resident killer whales in other regions of Alaska because no call syllables or call patterns (sequence of syllables) between groups were found to match. Resident killer whales learn their distinct call structures in their maternal group, in which they remain for life, and call structures remain stable and group-specific for more than one generation (Ford, 1991; Yurk et al., 2002). However, because we do not know the complete call repertoires of killer whales in western

Table 2

Location and number of encounters that produced recordings of killer whales (*Orcinus orca*) used in our acoustic analyses from 2001 through 2004 in the Eastern Aleutians and False Pass, Alaska.

Year	Location	Number of encounters
2001	Unalaska	3
2002	Unalaska, Akutan Island Umnak Island	, 31
2003	False Pass	2
2004	False Pass	3
Total		39

Alaska we cannot be sure that we will not find complete call-type matches in the future.

In eight killer whale encounters that did not yield genetic samples (five from False Pass and three from other areas in the eastern Aleutians), vocal activity or average call rate was considerably lower than the three calls per minute that are typical for residents, and was closer to one or less than one call per minute, which is typical for transient killer whales from other areas of the northeast Pacific (Deecke et al., 2005; Saulitis et al., 2005). Furthermore, all recorded calls showed typical characteristics of transient type calls, such as the quavering of the fundamental sound frequencies and the lower number of call syllables compared to those in calls from resident killer whales.

The three encounters that were not from the False Pass region (Table 2) contained three distinct calls that were structurally similar but did not show identical order of syllables or identical syntax to calls used by members of the AT1 transient community. The AT1 transient community is thought to be limited to the Prince William Sound and Kenai Fjords region and to use a distinct call repertoire (Saulitis et al., 2005).

In the recordings made during five encounters in the False Pass region in 2003 and 2004 (Table 2), 14 distinct calls were identified in more than one of the recording sessions. Thirteen of these 14 distinct calls were identified from recordings made during two encounters in 2003. Ten of these 13 calls were also recorded during 3 encounters with killer whales in May 2004 in the same area. Thus, although the majority of calls recorded in 2004 were already identified in 2003, one new distinct call was found. This high number of same distinct-type calls is typical for transient killer whales (Deecke, 2003). Call repertoires of resident killer whales are generally much larger, and this larger repertoire is likely responsible for the detection of several new calls from newly encountered whales in recordings from consecutive years (Ford, 1991; Yurk, 2005). All call types recorded in the False Pass region appeared to be distinct from calls recorded from transient killer whales in other regions of the North Pacific. However, some structural similarity (in the form of matching call components) was found for some of the 14 calls recorded in our study and for the calls recorded from a transient community that inhabits waters along the west coast of North America. These results may indicate that the transient killer whales we encountered in the eastern Aleutians comprise one or more unique populations or communities that show some acoustic similarity with transient killer whales found in other regions of the

Genetic analysis A total of 93 skin samples were collected from 2001 through 2004 by using biopsy darting techniques. Separation of ecotypes based on mtDNA haplotype (Barrett-Lennard, 2000) showed that 47 of the 93 samples were of transient-type lineage, 42 were of the resident-type lineage, and 4 were of the offshore-type lineage. Preliminary classifications of lineages based

on morphology and behavior and determined from field observations and photographs were consistent with the genetic analysis. For the 26 encounters that yielded both genetic and acoustic data, the two kinds of data provided identical classifications of lineage.

All 35 killer whales sampled in the False Pass-Unimak Island region had transient haplotypes. Eight of the nine samples collected in the area in 2003 had the GAT1 haplotype, which was first identified in transient killer whales from the northern Gulf of Alaska area in or near Kenai Fjords and Prince William Sound. The remaining sample contained the AT1 haplotype, formerly sequenced only in members of the AT1 transient population of the Prince William Sound area. In 2004, 14 of 26 killer whales sampled in the False Pass-Unimak Island area had the GAT1 haplotype, and the remainder had a GAT2 haplotype, a similar but not identical haplotype known to exist at a low frequency in the Gulf of Alaska transient killer whale population (Barrett-Lennard, 2000). Eleven of the 12 transient whales sampled in the summer months during 2001-2004 in the eastern Aleutians had the GAT1 haplotype, and the remaining one had the GAT2 haplotype.

Ecotypic parameters

Resident killer whales During a majority of our encounters, resident killer whales tended to be found and to travel along or near the 200-meter depth contour (Fig. 2A). This contour corresponds to a steep drop-off from the coastal shelf.

Approximately 92% of the encounters with killer whales during our summer surveys from Unimak Pass to Umnak Island were with whales determined by genetics, acoustics, or group association to be of the resident ecotype; however, this ecotype was not encountered in the spring surveys east of Unimak Pass (Table 1). A minimum of 901 resident whales used the Eastern Aleutians during the study; this count was based on individuals identified from photographs taken from 2001 through 2004. Of these individuals, 143 were seen only once during the study, and the remainder were repeatedly identified. The number of new, previously un-photographed whales observed each year declined from 534 whales in 2002 to 211 whales in 2003, to 156 whales in 2004 (Table 3). The decline in new whale sightings each year may indicate that we have identified the majority of whales that use this area during the summer months; however, there may be hundreds of whales that occasionally use the area but have not been encountered. The study area is likely only a portion of the range of the identified resident whales; several whales were matched with individuals seen in photographs taken in the Pribilof Islands over 200 miles to the west.

The numbers of individuals that could be positively identified in each resident ecotype encounter ranged from 4 to 109. A total of 347 whales were placed in 82 tentative matrilines which consisted of a reproductive female and her offspring of both sexes. These matrilines

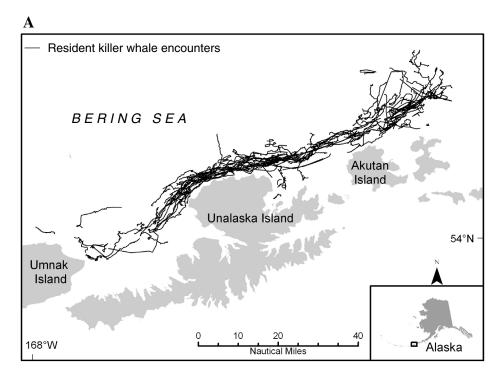
Table 3Number of sightings of individual resident killer whales (*Orcinus orca*) in the eastern Aleutians from June to September, 2001 through 2004.

Year	Previously identified whales	New whales identified	Total whales identified
2001	0	38	38
2002	38	496	534
2003	268	211	479
2004	334	156	490
Total		901	

were determined from repeated association of individuals in both photographs and field observations. This method of determining matrilines was demonstrated effective in other population studies of resident killer whales (Bigg et al., 1990; Matkin et al., 1999b). Most of the matrilines comprised two generations (mother and offspring), although some included a probable grandmother. All matrilines were of consistent composition and maintained their structure over the course of the study, which has been the case in all other resident populations studied to date (Matkin et al., 1999a; Ford et al., 2000). The structure of the population was inferred from 41 groups of one or more matrilines that appeared to be longer-term associations. These groups could be considered as tentative pods (as defined by Bigg et al., 1990). Twenty-one of these groups, containing 266 whales, were sighted frequently enough that basic age and sex classes could be determined. These groups contained 65 adult males (24.4%), 105 females or immature males (39.5%), and 96 juveniles and calves (36.1%). These proportions of males, females and immature males, and juveniles and calves are comparable to those observed in other resident populations in Alaska and British Columbia (Leatherwood et al., 1990).

There was no evidence that resident killer whales consumed marine mammals. Whales belonging to the resident ecotype were observed consuming fish only during infrequent observations of predation (halibut were identified from samples, and salmon were probable from visual observations only). Much of the predation by resident killer whales was not visible at the surface and therefore prey samples could not be obtained. Resident whales were the only killer whales observed removing fish from the lines of commercial fishermen and observed following and feeding on fish discards from trawlers.

Transient killer whales A total of 165 individual killer whales were determined to be transients from encounters during 2001–2004 (Table 4). A majority of these whales (114) were photographed during the May–June field work in the False Pass–Unimak Island region in



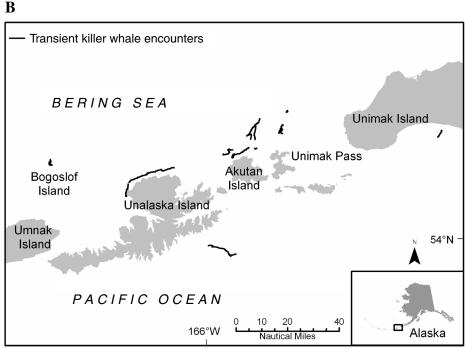


Figure 2

Tracks of the vessels during times that the vessels accompanied groups of killer whales (*Orcinus orca*) 2002–2004. (A) tracks of vessels following resident killer whales in the Eastern Aleutians during summer; (B) tracks of vessels following transient killer whales in the Eastern Aleutians during summer; (C) tracks of transient killer whales near False Pass- Unimak Island during spring.

2003 and 2004 (Fig. 2B). The remaining 51 individuals were photographed during the summer field season when encounters with transient killer whales were relatively

infrequent in the eastern Aleutians from Unimak Pass west to Umnak Island (Fig. 2C). There were only six transient whales (less than 4% of the total identified)

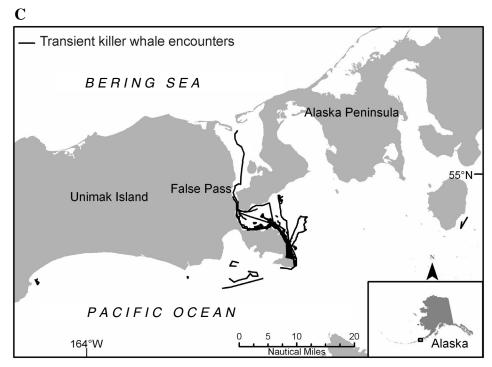


Figure 2 (continued)

Table 4

Number of individual transient killer whales (Orcinus orca) identified by region and by year. And the overlap of individuals between regions.

Year —					
	False (May-		Eastern A (July-Se	Overlan of individuals	
	Total whales	New whales	Total whales	New whales	Overlap of individual between regions
2001	_	_	5	5	_
2002	_	_	18	18	_
2003	84	84	25	18	2
2004	75	30	22	16	4
Total		114		51	6

that were common to both regions and time periods, although the regions are geographically adjacent (Figs. 1 and 2). In the second year, 2004, in False Pass–Unimak Island, 74 whales were identified and 45 (60%) had been photographed the previous year. In the Unimak Pass–Umnak Island surveys in both 2003 and 2004, only about 28% of the whales identified had been previously photographed in the region.

Offshore killer whales Only one encounter, which occurred in the eastern Aleutians (10 July 2003), was with killer whales identified by genetic and acoustic data as the offshore ecotype. We photographed 54 offshore killer whales in this encounter, although not all whales

present were photographed. A total of 44 of these offshore whales had been previously photographed off British Columbia, Washington State, and Kenai Fjords, Alaska, and 10 had not been previously photographed (Ellis¹).

Description of the marine mammal prey base

Although we did not measure the actual abundance of potential marine mammal prey, we recorded sightings of all marine mammals and calculated average group

¹ Ellis, G. 2005. Unpubl. data. Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia, Canada V9T 6A7.

 Table 5

 Number of sightings, harassments, and observed kills of known marine mammal prey species of killer whales (Orcinus orca).

	Prey species						
Prey species	Total no. of sightings	Average group size	No. of harassments	No. of observed kills	No. observed to have escaped		
Gray whale (May–June only)	18^{I}	1.4	19	18	1		
Dall's porpoise	521	3.9	3	0	3		
Steller sea lion	153	53.4	1	1	0		
Humpback whale	834	4.1	0	1	0		
Northern fur seal	388	4.2	5	4	1		
Minke whale	42	1.2	2	2	0		
Harbor porpoise	18	4.9	0	0	0		
Harbor seal	82	9.6	0	0	0		
Sea otter	94	3.7	0	0	0		
California sea lion	2	1.0	0	0	0		
Fin whale	15	2.2	0	0	0		
Sperm whale	7	1.6	0	0	0		
Baird's beaked whale	10	9.4	0	0	0		
Total			31	26	5		

¹ This number comprises only live whales; most kills were already dead when observed and were not included in these sightings.

size as an indication of the relative availability of potential prey (Table 5). During the 346 survey days in the eastern Aleutians in June-September 2002-2004, the largest number of pinniped sightings was of northern fur seals (375 sightings), which were frequently encountered as single individuals resting at the surface, or were observed on the rookery at Bogoslof Island. Steller sea lions (124 sightings) were counted during our repeated monitoring of rookeries and haulouts in the region, resulting in a relatively large average group size (53.4 sea lions) but were encountered only occasionally off the rookeries. Other pinnipeds included harbor seals (73 sightings), which were primarily observed hauled out in small groups of less than 30 individuals, and two sightings of individual California sea lions (Zalophus californianus). Sea otters were observed on 81 occasions. The most frequently encountered cetacean was the humpback whale (Megaptera novaeangliae; 834 sightings), followed by Dall's porpoise (Phocoenoides dalli; 521 sightings). Less frequently observed species were minke whales (Baleanoptera acutorostrata; 42 sightings), fin whales (Baleanoptera physalus; 15 sightings), sperm whales (*Physeter macrocephalus*; 7 sightings), and Bairds beaked whales (Berardius bairdii; 10 sightings).

During 49 survey days in the False Pass-Unimak Island region in May and early June 2003-2004, Steller sea lions were the most frequently ncountered pinniped (29 sightings), although some fur seals (13 sightings) and harbor seals (9 sightings) were also observed. Sea otters were also present (13 sightings). The most frequently encountered cetaceans were gray whales (18 sightings) and harbor porpoises (*Phocoena phocoena*;

18 sightings). Other cetaceans sighted in this region were minke whales (3 sightings) and humpback whales (1 sighting).

Predation on marine mammals

Predation on or harassment of marine mammals was observed on 31 occasions and was attributed solely to the transient killer whale ecotype. Attacks that did not yield proof of a kill (i.e., tissue, blood, or prey in the mouth) were considered harassments. Gray whales (Eschrichtius robustus) were the most frequently taken species (Table 5), with 19 apparent harassments, of which 18 resulted in kills, observed in False Pass in 2003 and 2004 (May to early June). In all but one case, the gray whale was already dead and was being consumed when we found the whale. The only other predatory event during this period was a single harassment of Steller sea lions that were hauled out. During the summer season in the eastern Aleutians (Unimak Pass-Umnak Island), northern fur seals were the most frequently harassed prey; four of the five observed harassments resulted in kills. Other species included Dall's porpoises (harassed on three different occasions), two minke whales (harassed and killed), one Steller sea lion (harassed and killed), and one humpback whale (harassed).

Discussion

Our analysis indicates that the three killer whale ecotypes in the eastern North Pacific also are found in the eastern Aleutian Islands. All killer whales examined by acoustic or genetic analysis could be placed unequivocally in the resident, transient, or offshore lineage.

Resident killer whales

A vast majority of the whales observed in the eastern Aleutians during summer were determined to be of the resident ecotype. Our minimum estimate of 901 whales is as high as any density of resident killer whales in any region of the eastern North Pacific studied to date (Matkin et al., 1999a; Ford et al., 2000).

Our data indicate that the eastern Aleutian resident killer whales comprise a distinct population, but evidence is equivocal at this time. No repeated associations have been recorded between eastern Aleutian residents and those photographed off Kodiak Island north and eastward, despite extensive field effort and examination of photographic databases for matches. However, at least one group of resident killer whales has been photographed in both regions (Durban²). Acoustic analysis indicates that resident whales sampled in the eastern Aleutians have call repertoires distinct from other well-known resident populations described from Kenai Fjords through Washington State. However, on the basis of structural similarities among calls from these regions, it can not be ruled out that some social contact occurs or that these whales share a recent common ancestry. The structure of some call syllables appears to change quickly in a climate of diminishing social contact (Deecke et al., 2000), whereas the overall syllable type and the syntax of syllables in calls remains stable for a longer period of time (Ford, 1991; Yurk, 2005). Genetic samples taken in the eastern Aleutians revealed only the NR haplotype, whereas those from Kodiak Island waters and in Kenai Fjords yielded a mixture of NR and southern resident haplotypes (SR haplotypes) (Barrett-Lennard, 2000). An examination of nuclear alleles is needed to clarify the relationship between eastern Aleutian residents and other resident killer whales in other regions of the North Pacific.

Offshore killer whales

Only one group of whales was determined to be of the offshore ecotype, with 54 individuals identified in a single encounter. Most (44) of the individuals identified in that encounter had been identified in other regions, including southern British Columbia and Kenai Fjords, Alaska, indicating that there is a single wide-ranging population in the eastern North Pacific. This ecotype is not known to consume marine mammals and the only reported stomach contents are salmonid bones, crab shell, sculpin, and eelgrass (Heise et al., 2003).

Transient killer whales

Transient killer whales, as determined in our analyses, were the only whales observed consuming marine mammals and were not seen feeding on fish or engaging in behaviors associated with fish-feeding in other areas (Ford and Ellis, 1999; Saulitis et al., 2000). This observation supports findings in other regions that indicate transient killer whales are a distinct ecotype specializing in marine mammal prey and comprise a subset of the total whales found in any region (Matkin et al., 1999b; Ford et al., 2000). Most of the 165 transient individuals identified in our study were present only in spring and early summer when gray whales were migrating. We documented only 51 different transient individuals in late summer, at which time their appearance was sporadic and they seemed to leave the region for periods of weeks or longer.

Transient killer whales in the eastern Aleutians display a unique call repertoire that is distinct from from the repertoire of transient killer whales in other regions. Therefore, the eastern Aleutian group may represent a separate population. Other than three whales photographed near the Barren Islands by NMML in 2001 (Durban²), and resighted east of Unalaska Island in 2002; no other transient whales from this area have been photographed north and east of the Shumagin Islands. The results of mitochondrial DNA analysis are equivocal because the three haplotypes we identified all occur in waters of the northern Gulf of Alaska. Again, extensive examination of nuclear alleles and comparison with those from other regions will be needed to clarify population structure.

For example, more detailed genetic analysis of eastern Aleutian transient killer whales exhibiting the AT1 haplotype has shown that they have dissimilar nuclear alleles from those of the threatened AT1 population of Prince William Sound and Kenai Fjords (Barrett-Lennard³). This finding indicates that the similarity of their haplotypes reflects historical lineage sorting rather than a recent descent from a common maternal ancestor. Because haplotypes reflect maternal lineages, the co-occurrence of two haplotypes in the transient whale aggregations encountered in the False Pass-Unimak Island area during spring supports the idea that distinct matrilines that may not associate at other times of year join to form these aggregations.

The small overlap (3.6% of the individuals) between transient killer whales encountered west of Unimak Pass in summer and transient killer whales observed in spring in the False Pass–Unimak Islands area indicates there is further seasonal and spatial structuring in the population. The large percentage of new transient killer whales encountered in each year of summer studies, compared to the lower percentage of resighted individu-

² Durban, J. 2005. Unpubl. data. National Marine Mammal Lab, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

³ Barrett-Lennard L. 2005. Unpubl. data. Vancouver Aquarium, 845 Aviso Rd, Vancouver, BC, Canada.V6G

als in the spring, indicates that a smaller percentage of the summer whales have been identified. A survey of nearshore waters from the Gulf of Alaska to the Aleutian Islands revealed that the highest densities of transient killer whales were from the Shumagin Islands through the eastern Aleutian Islands, and an estimated abundance of 226 (CV=0.45) transient killer whales were present west of the Shumagin Islands in summer (Zerbini et al., 2006).

Transient killer whales near False Pass in May were concentrated on the Pacific Ocean side of Unimak Island and in Ikatan Bay, where gray whales pass along a shallow shelf and water depth rarely exceeds 70 meters (Fig. 1). Reports from mariners and pilots have indicated that other areas around Unimak Island and along the Bering Sea coast (e.g., Cape Lutke and the coastline near Nelson Lagoon) may also be points of interception of gray whales by killer whales. Our own surveys (Fig. 2B) indicate that transient killer whales inhabit a wide area around Unimak Island and the tip of the Alaska Peninsula, where we recorded kills of gray whales at Deer Island (110 km northeast of False Pass) and Cape Lutke (140 km southwest of False Pass).

Despite uncertainties regarding the range of transient killer whales, it is evident that they are numerous, concentrated, and consistently present in the spring from Unimak Pass eastward. Gray whales have been previously reported as killer whale prey (Matkin and Saulitis, 1994); however, the extent to which transient killer whales were focused on gray whale predation during May-June around Unimak Island has not been previously described. Although subsequent surveys in these areas during summer (C. O. Matkin, unpubl. data; Durban².) have identified some of the same whales as those identified in the spring, most of the whales do not remain in these nearshore waters. It is not known whether these transient whales move offshore and disperse, follow the gray whales into the Bering Sea, or move into other unstudied regions.

The distribution of most, if not all, transient killer whales that we identified undoubtedly extends well beyond our survey area. Technical advances in satellite and radio tagging procedures that could be applied to killer whales would aid considerably in understanding the movements and range of transients in this region. Without a better understanding of the range of these whales, it is impossible to fully assess their impact on prey populations.

Northern fur seals appear to be an important prey for killer whales from late June to September west of Unimak Pass. This finding is based on observed kills compared to kills of other species. A substantial number of the fur seals sighted in summer were likely associated with the recently established and expanding fur seal rookery on Bogoslof Island. This population increased rapidly from 898 pups in 1992 to 5096 pups in 1999 (Angliss and Lodge, 2004). Additionally, peak numbers of migrating fur seals pass through Unimak Pass into the Bering Sea in June on their way to the

Pribilof Islands and then migrate back to the Pacific in peak numbers during October-November (Bigg, 1990).

Northern fur seals have long been indicated as an important prey for killer whales in the Pribilof Region (Hanna, 1923; Zenkovich, 1938; Tomilin, 1957). However, their importance as prey in the eastern Aleutians has not been previously documented and may have developed with the growth of the Bogoslof rookery. This geographic region presents an opportunity to examine the effects of killer whale predation on an apparently stable or increasing population of fur seals—a species that is declining in other areas.

Minke whales made up a substantial proportion of summer predation despite the relative low frequency with which they were sighted, and the apparent difficulty that killer whales have in capturing this fast swimming species in open water (Ford et al., 2005). Minke whales appear to be a minor part of the diet of killer whales from Washington State to northern southeastern Alaska (Ford et al., 2005).

We observed the harassment of a humpback whale by killer whales once; during the attack, other humpback whales rapidly converged on the attackers and appeared to drive the killer whales away. No injuries were apparent. Harassments of humpbacks have been reported in other regions of Alaska (Saulitis et al., 2000), but did not result in a kill or apparent injury. Photographs of scars indicate that most killer whale attacks on baleen whales target young animals, probably calves on their first migration from low-latitude breeding and calving areas to high-latitude feeding grounds (Mehta⁴).

Although none of the attacks that we observed on Dall's porpoises resulted in confirmed kills, Dall's porpoises could be a significant prey as has been indicated in other regions (Ford et al., 1998; Saulitis et al., 2000); however, more observations are needed. Harbor seals were conspicuously absent from our prey observations despite also being an important prey in other regions of Alaska (Saulitis et al., 2000; Matkin et al., in press). Harbor seals are found in relatively low numbers in the eastern Aleutians.

Although Steller sea lions were observed as prey on one occasion and were harassed on another, they did not appear to be a primary target of the transient killer whales we observed during our spring and summer surveys. Whether or not they are an important prey during other seasons (fall and winter) is not known and will require additional study or the application of other methods to be fully assessed.

Although our study was limited by a small sample size in the summer, it provided significant information on the distribution of transient killer whale prey and the importance of fur seals in the killer whale diet during summer west of Unimak Pass and the importance of grey whales in killer whale diet during spring from Unimak Pass east. An increase in sample size of ob-

⁴ Mehta, A. 2005. Unpubl. data. Woods Hole Oceanographic Institute, Woods Hole, MA 02543-1050.

served kills is therefore important to develop greater confidence and detail in estimating the composition of killer whale diets.

Our seasonal bias towards spring and summer leaves uncertainty about killer whale diets during fall and winter. In this regard, analytical techniques that include identification of fatty acids, stable isotopes, and contaminants may prove useful when coupled with field observations to obtain a more complete picture of the feeding habits of killer whales during these seasons (Herman et al., 2005).

Conclusions

Our work underscores the importance of determining lineages and ecotypes of killer whales before making assumptions regarding feeding habits and potential impact of killer whales on prey populations. Although there may be well over 100 marine mammal-eating transient killer whales that aggregate in False Pass–Unimak Island region to feed on gray whales in spring, the majority of the killer whales present in summer are fish-eating residents. In the summer, marine-mammal-eating transients are far less abundant than in spring.

Our study indicates that the diet of transient killer whales off the eastern Aleutian Islands contrasts with the diets of transient killer whales in other parts of the North Pacific. In British Columbia, for example, transient killer whale diet is composed primarily of harbor seals (Ford et al., 1998), whereas both harbor seals and harbor porpoise are the primary prey of killer whales in northern Glacier Bay and Icy Strait region of southeastern Alaska (Matkin et al., 2005). Further north, in Prince William Sound and Kenai Fjords, the dominant prey of the AT1 transient killer whales are harbor seals and Dall's porpoises (Saulitis et al., 2000). Only in the Gulf of Alaska (Kenai Fjords) has predation by some Gulf of Alaska transient killer whales apparently focused on sea lions (Matkin et al., 2005).

Killer whale feeding behavior needs to be examined on a region-by-region basis, as well as seasonally. Experience in other regions of the North Pacific has shown that estimated population sizes, life history parameters, and dietary information can be obtained with a concerted long-term research effort. Our study has demonstrated that the eastern Aleutians also support the presence of three killer whale ecotypes, as has been previously described along the Pacific Coast of North America. It also has developed minimum estimates of the numbers of transient and resident killer whales that use the region and has provided information that may indicate that grey whales and northern fur seals are important prey items in this region at certain times and in certain areas. Steller sea lions were not a primary prey during our spring and summer surveys. Whether or not killer whales are impeding population recovery of Steller sea lions in the eastern Aleutian Islands cannot be answered decisively, nor can the effect that killer whales may be having on other species in this region

as yet be ascertained. Answers to these and other questions are expected to become clearer as the observational database for killer whales is expanded and the data for regions within the North Pacific are compared.

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