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Original article

Ecological aspects of transient killer whales *Orcinus orca* as predators in southeastern Alaska

Marilyn E. Dahlheim & Paula A. White

In this study we present empirical data on predator numbers, movements and area usage, and predation obtained from tracking transient killer whales *Orcinus orca* throughout the inland waters of southeastern Alaska, USA. During 1991-2007, we documented 155 transient killer whales via photo-identification methodology within the large study area (27,808 km^2). Transient killer whales were distributed throughout southeastern Alaska and were present during all seasons, although not all individuals were seen every year. Resighting data suggested that within southeastern Alaska, maternal groups may partition area usage of their environment. By following whales for 1,467 km, we calculated a mean travel speed of 7.2 km/hour with mean daily movements of 134 km $\pm$ 88 km/24 hours and ranging within 59-240 km/24 hours. Photographic matches demonstrated that most of the transient killer whales (86%) identified in southeastern Alaska also utilized British Columbia and Washington State waters. In contrast, photographic matches between whales in southeastern Alaska and whales seen off of California, USA, were rare, suggesting that different transient killer whale stocks occupy these two regions. Transient killer whales preyed upon Dall's porpoise *Phocoenoides dalli*, Pacific white-sided dolphins *Lagenoryhncus obliquidens*, harbor porpoise *Phocoena phocoena*, minke whales *Balaenoptera acutorostrata*, Steller sea lions *Eumetopias jubatus*, harbor seals *Phoca vitulina* and seabirds. Potential prey species that were available, but not targeted, included humpback whales *Megaptera novaeangliae*, elephant seals *Mirounga angustirostris* and sea otters *Enhydra lutris*. Prey-handling techniques varied depending on the prey being targeted with no evidence of prey specialization. During 114 encounters totaling 332.5 hours of direct observations of transient killer whales, we documented 36 predation events for a calculated kill rate of 0.62 prey items/24-hour period/whale. The data we present in this article provide a foundation of transient killer whale ecology aimed at improving our ability to understand the impact of transient killer whale predation on southeastern Alaska prey populations.

Key words: area usage, kill rates, marine predator, prey handling, prey selection, southeastern Alaska, transient killer whales

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Knowledge of predator life history, prey selection and kill rates is essential when assessing the ecological role of a predator in an ecosystem. Long-term research in terrestrial systems exemplifies the efforts of biologists to understand the complexities of predator-prey relationships (Harrington & Paquet 1982, Sinclair & Arcese 1995, Sinclair et al. 2003, Packer et al. 2005). In terrestrial systems, researchers utilize a wide variety of equipment and methods when studying predators (Mills 1996, Gese 2001). In contrast, when studying predation in marine systems, researchers encounter significant challenges due to limitations in the types of equipment and methods available for data collection. In the case of killer whales *Orcinus orca*, locating and tracking these highly mobile marine predators for extended periods of time and over a geographically large range can be both problematic and costly. Observations of predation events are often opportunistic and are limited to daylight hours. Predation may also occur well below the surface. Given that whale faeces and/or prey remains do not persist in the environment for any length of time, food habit studies by means of collecting scats or recovery of carcasses present unique challenges (Whitehead et al. 1989, Whitehead 1996, Jarman et al. 2002, Hanson et al. 2010). Not withstanding these difficulties, questions regarding the ecological role of killer whales as predators on marine mammals are currently of great interest particularly in the eastern North Pacific. Specifically, the recent declines of some Alaskan marine mammal populations, coupled with the high-profile nature of these predators, has led to speculation and debate regarding the 'top-down' impact of transient killer whale predation on other species (Estes et al. 1998, Springer et al. 2003, Williams et al. 2004, DeMaster et al. 2006, Mehta et al. 2007, Wade et al. 2008, 2009).

North Pacific killer whales have been categorized into three eco-types (i.e. resident, offshore and transient) differing in several aspects of morphology, ecology, behaviour and genetics (Bigg et al. 1987, Baird & Stacey 1988, Hoelzel et al. 1998, 2002, Dahlheim et al. 2008). Although killer whales consume a wide variety of prey species (Jefferson et al. 1991), eco-types are associated with dietary specialization: resident and offshore whales eat fish whereas transient whales prey on marine mammals (Baird & Dill 1995, Ford et al. 1998, Ford & Ellis 1999, Dahlheim et al. 2008). Popular literature characterizes the spectacular and dramatic nature of transient killer whales' attacks on cetaceans (Silber & Brown 1991, Pitman & Chivers 1999, Scutro 2004). Although previous studies provide valuable insights into this species' predatory behaviour, they are limited in that they were conducted at specific sites where single species of prey are concentrated, have been of short duration or have relied on opportunistic sightings of predation events (Dahlheim & Towell 1994, Baird & Dill 1995, Matkin & Dahlheim 1995). Long-term studies that operate over large spatial and temporal scales may more accurately describe the ecological variability of these highly mobile predators throughout a complex ecosystem.

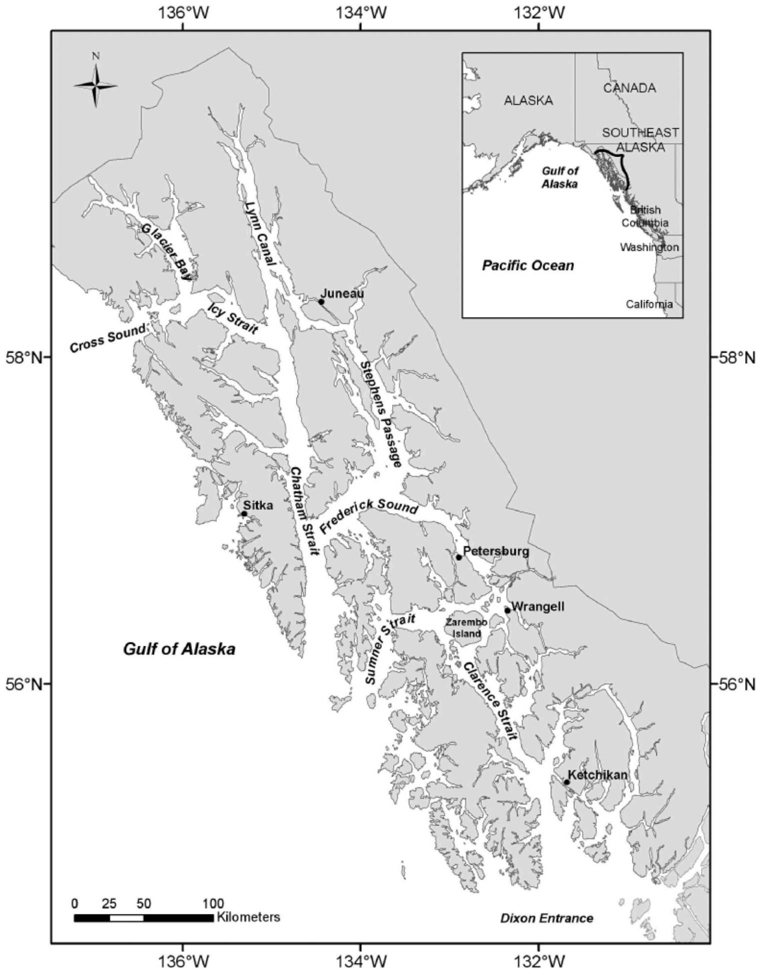
In this article, we summarize data on southeastern Alaska, USA, transient killer whales collected over a 27,808 km^2 area spanning a 17-year period. Our research objective was to examine ecological parameters of transient killer whales critical to bolstering our understanding of their role as predators in southeastern Alaska. Our specific objectives were to: 1) quantify predator numbers and distribution, 2) examine frequency of occurrence, area usage and movements, 3) record predator*prey interactions and 4) calculate a kill rate/day/whale for southeastern Alaska transient killer whales.

Material and methods

Between 1991 and 2007, researchers from the Alaska Fisheries Science Center, National Marine Mammal Laboratory (NMML), conducted dedicated cetacean surveys throughout the inland waters of southeastern Alaska (Fig. 1). All major inland waters were surveyed each year including: Lynn Canal, Icy Strait, Chatham Strait, Stephens Passage, Frederick Sound, Sumner Strait and Clarence Strait. Whenever possible, smaller bodies of water (i.e. bays, inlets and passages) and areas exposed to the open ocean (Cross Sound and Dixon Entrance) were also surveyed. The extent of area coverage for each survey was dependent on weather and cruise duration. For all cruises, minor changes in the ship's course were made to maximize survey coverage and reduce the detrimental effect of weather or sea conditions on our ability to find animals. An overview of survey effort by region is provided in Figure 2(A-C).

We initiated surveys in 1991 and conducted them aboard the 28.3-m long National Oceanic and Atmospheric Administration (NOAA) ship John N. Cobb. Between 1991 and 1993, and again in 2007, we conducted three trips per year: one in spring (April-May), one in summer (June-July) and one in fall (September-October). From 1994 to 2006, we conducted two trips per year, one either in spring or summer and the other in fall. In total, 38 cruises were completed with nine cruises occurring during spring (April-May; 116 days), 14 during summer (June-July; 173 days) and 15 during fall (September-October; 195 days). During each survey, observers kept a constant watch when the vessel was underway and recorded all cetaceans seen. Observers were stationed on each side of the vessel and used 7×50 binoculars to scan for marine mammals. The observer's identity and weather conditions were noted at the beginning and end of each observer

Figure 1. The defined southeastern Alaska study area.



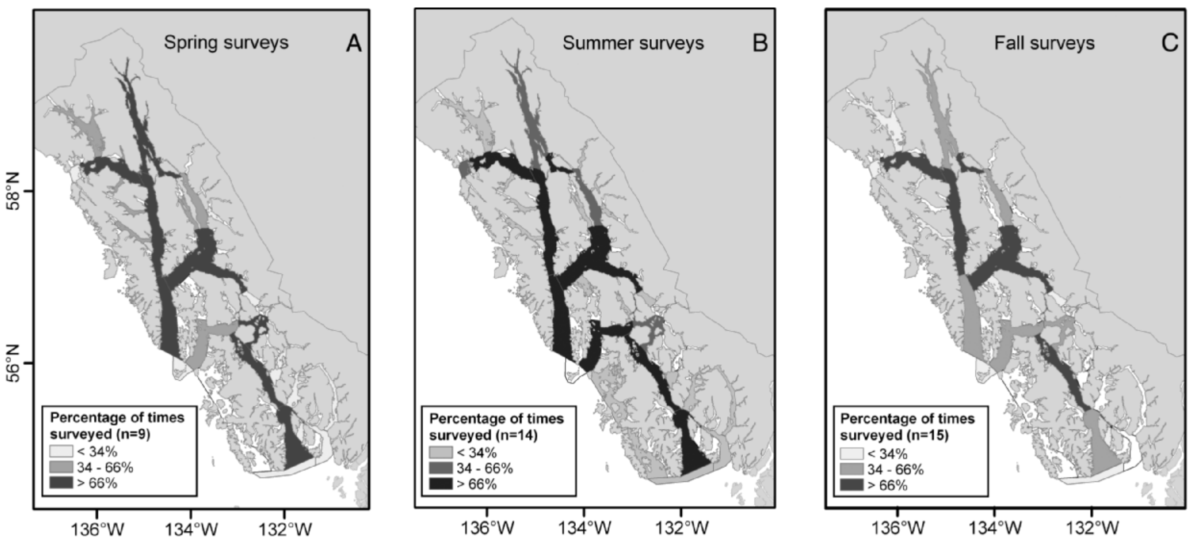


Figure 2. Survey effort in spring (A), summer (B) and fall (C) in southeastern Alaska during 1991-2007. The areas are grouped into three categories based on the percentage of time that the area was surveyed; i.e. < 34%, 34-66% and > 66%. From Dahlheim et al. 2009.

watch (1.5-2.0 hours in duration) or when conditions changed. For all cruises, watches were terminated when conditions reached or exceeded Beaufort wind force scale of four.

When killer whales were encountered, 1-2 skiffs (e.g. a 7-m rigid-hull inflatable equipped with a 115-hp outboard engine or a 5-m Boston whaler with a 90-hp engine) were launched. During an encounter (~ a sighting of one or more killer whales), we noted the number of whales and the start and end time and location. Each individual whale was photographed and its behaviour was noted. When weather prohibited launching of the skiff(s), researchers collected data from the support vessel.

Natural markings (e.g. saddle patch pigmentation or dorsal fin shape and/or nicks on the fin) allowed for individual identification of transient killer whales (Dahlheim et al. 1997, Ford & Ellis 1999, Ford et al. 2000). Southeastern Alaska whales are assigned alphanumeric designations (e.g. AL13; Dahlheim et al. 1997). Researchers in British Columbia use a different naming system (e.g. T designations; Ford & Ellis 1999). Both sets of identification numbers are provided here for cross-reference purposes. We used photo-identification methodology to obtain overall counts and to collate information on individual/group life histories. Identification of killer whales as belonging to the transient eco-type was first evaluated in the field by observing morphological features characteristic of each eco-type (Dahlheim et al. 1997, Ford et al. 2000). Skin samples from at least one member of each group were obtained via biopsy darting. Genetic analysis confirmed the eco-type classification.

Social organization among transient killer whales is known as 'fission-fusion' and is characterized by periodic loose associations of animals (Holekamp et al. 1997, Ford & Ellis 1999, Baird & Whitehead 2000). Mothers and their offspring (i.e. maternal groups) show a strong tendency towards lifelong associations and, thus, form the basic unit within killer whale society (Dahlheim et al. 1997, Ford & Ellis 1999, Baird & Whitehead 2000). In this study, assignment of individuals to maternal groups was based on published data for transient killer whales provided by Dahlheim et al. (1997) and Ford & Ellis (1999). Maternal groups typically contain six or fewer individuals that travel and feed in close association with one another (Dahlheim et al. 2009). Although all members of the population are rarely seen together, maternal groups may join temporarily to form larger groups (Table 1). Due to the dynamic nature of fission-fusion societies, we considered the occurrence of maternal groups and adult males separately.

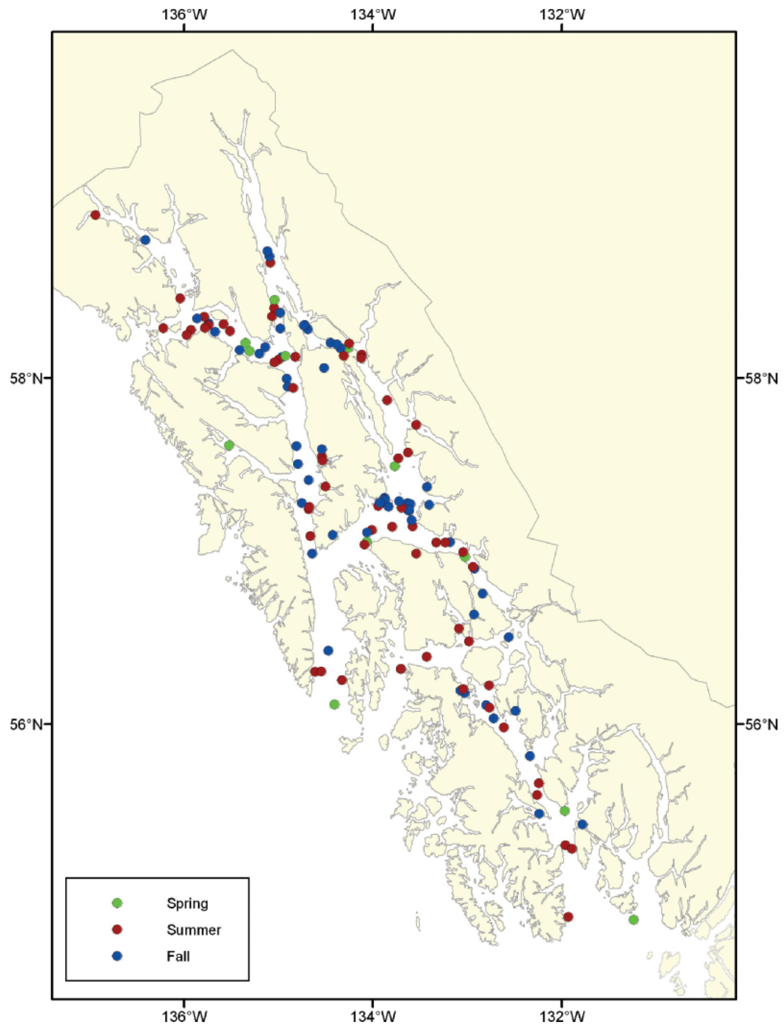
In addition to the data from our dedicated survey, other sources of photographic data were available for review. These included published literature (Leatherwood et al. 1984, Ellis 1984, 1987, Matkin & Dahlheim 1995, Ford & Ellis 1999) and photographs and videotapes submitted to the NMML by contractors, fishermen, researchers, private boaters and whale watching companies working throughout southeastern Alaska. These supplementary sources were used to examine distributional patterns, record occurrence in winter, and document prey species targeted.

We examined the distributional patterns of

Table 1. Prey species targeted by southeastern Alaska transient killer whales and a description of their predatory behaviour and group size.

Targeted species	Transient killer whale predatory behaviour	Group size
Dall's porpoise	High-speed chase of short duration; prey hit from underneath with whale's rostrum; prey thrown high into the air. Highly visible event.	3-25 whales
Pacific white-sided dolphin	High-speed chase of longer duration than that observed for Dalls porpoise, prey hit from underneath with whale's rostrum; prey thrown high into the air. Highly visible event.	7-15 whales
Harbor porpoise	Matched pace with porpoise from behind; prey swallowed quickly after a short duration chase. No aerial behaviours. Subtle event.	2-5 whales
Harbor seal	Prey dragged or captured below surface; either consumed quickly and/or 'played with' for a longer duration. Subtle event.	1-6 whales
Steller sea lion	High-speed attack with whales on their sides as they pass prey; prey hit with whale's tail; tail slapping continues for periods of up to one hour. Prey often thrown in the air. Highly visible event.	6-15 whales
Minke whale	Long duration, prey dragged below surface; prey attacked dorsally near blowhole region & held down by tail stock. Highly visible event.	5-10 whales
Birds	Prey followed on surface or grabbed from below and quickly consumed. Subtle event.	Varied
Fish	Fast swimming at water's surface in tight circle formations.	Varied

Figure 3. Distribution of transient killer whales in southeastern Alaska based on National Marine Mammal Laboratory's dedicated survey data for spring, summer and fall during the period 1991-2007.



transient killer whales within southeastern Alaska by plotting the locations of all encounters using ArcView Geographic Information System (GIS; ESRI; Redlands, California). We used resightings between years to examine the annual presence of different maternal groups in southeastern Alaska. We also examined finer-scale differences in area usage and movements within southeastern Alaska by plotting all of the resighting locations for each maternal group separately. To document occurrence of individuals or maternal groups outside of southeastern Alaska, we compared our photographs to catalogues of eastern North Pacific killer whales (Heise et al. 1991, 1993, Black et al. 1997, Dahlheim 1997, Matkin et al. 1999, Ford & Ellis 1999).

We tracked whales from behind at relatively slow speeds and at close distances (i.e. < 150 m) to avoid disrupting their normal behaviour or the behaviour of their potential prey, and to ensure that all predation events were documented. When a change in whale behaviour was noted, possibly indicating a predation event (e.g. overt directional changes, increased swimming speeds, longer submerged times, splashing and aerial displays), we positioned our vessel closer to the whales and recorded the prey species being targeted, the location of the event, as well as predator group size, and prey-handling techniques. While tracking transient killer whales, we recorded all predatory behaviour including 'harassments' (i.e. directed chase ending in unsuccessful capture) and 'kills' (i.e. capture and consumption of prey; Baird & Dill 1995, Ford et al. 1998). A 'kill' was defined as a direct observation of prey either in the whales' mouths or incapacitated at the surface, severely injured prey seen bleeding profusely combined with the presence of blood,

AK ID	BC ID	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
Maternal Groups																										
AL3	T85	X	X				X	X	X		X	X			X									X		X
AH	T93		X			X		X	X	X	X	X		X				X								
AL4	T85		X				X	X	X	X	X	X			X			X								
AM2	T2		X				X	X	X	X	X		X													
AL10	T71		X				X	X				X			X		X	X				X				
AL 7	T49		X					X	X			X		X		X					X					
AL8	T49		X					X	X			X				X			X				X	X		
AL13	T124						X	X	X		X	X			X			X	X			X	X			
AL14	T124						X	X	X		X	X			X			X	X			X	X			
AO2	T88						X		X	X				X			X	X		X		X		X		
AQ4	T91							X	X		X	X	X	X	X			X	X							
AQ3	T75							X	X		X	X	X		X			X	X	X			X			X
AQ31	T79							X	X		X			X	X	X	X	X	X	X						
AQ33	T73							X	X		X			X	X		X	X	X	X	X					
AL42	T100							X		X	X	X		X	X	X		X	X	X	X					
AL41	T100							X		X	X	X		X	X		X					X				
AM21	T64							X		X		X	X	X	X	X		X		X		X	X		X	
AQ10	T68							X			X		X							X					X	X
AM24	T104							X			X					X	X	X		X		X	X	X	X	
AM22	T64							X				X	X		X		X	X				X			X	
AO10	T133							X																		
S1	T46							X																		
AQ7	T75								X		X	X	X		X			X		X				X		
AM33	T116								X		X			X												
AM31	T36								X								X									
O5	T13									X																
AQ8	T75										X	X	X		X				X	X						
AV10	T34										X	X											X	X		
AA	T111										X					X						X	X			
S3	T26										X					X						X	X			
AV30												X							X				X			
AV52	T125											X														
AQ61	T166														X	X	X	X								X
A020															X	X			X			X		X	X	
AV61	T171														X											
A030																X										
AV34																			X							
T37	T37																						X			
T23	T23																								X	
T23C	T23C																								X	
T18	T18																								X	
Males																										
AH4	T96		X			X		X	X	X	X	X		X		X										
AH5	T97		X			X		X	X	X	X	X		X		X		X				X				
AH1	T93		X			X		X	X	X				X				X					X			
AL5	T48		X				X	X		X	X				X											
AM1	T1		X				X		X	X	X															
AL9	T51		X					X		X	X					X				X			X	X		

Figure 4. Annual resightings of maternal groups and adult males. The maternal group membership is defined in Dahlheim et al. (1997) and Ford & Ellis (1999). Both the southeastern Alaska (AKID) and British Columbia (BCID) identification numbers are provided as both naming systems are currently in use. Data prior to 1989 are from Leatherwood et al. (1984). Whales AM1, AL1, AM4, AA1 and F1 have not been seen in more than 15 years and are presumed dead.

		YEAR																								
AK ID	BC ID	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
Males																										
AL1	T83		X																							
AL40	T40				X	X	X	X		X	X	X														
AQ30	T66					X		X	X		X	X														
AQ2	T72					X		X	X			X		X					X	X				X		X
AO1	T88						X		X	X				X			X	X		X		X		X		
AM4	T2A						X																			
AM30	T82							X	X	X	X					X	X									
AM20	T63							X	X	X		X	X		X		X	X							X	
AQ1	T92							X	X		X	X	X	X	X			X	X				X			
AQ32	T74							X	X		X			X	X	X	X	X	X	X						
AL43	T102							X		X	X	X			X		X	X	X	X	X					
AQ11								X			X		X													X
AM23	T103							X			X					X	X	X		X		X	X	X	X	
AO10	T133							X																		
AV1	T162								X																	
O4	T14									X																
AL17	T85A										X	X			X									X		X
AA4	T113										X					X						X	X			
AA5	T114										X					X										
AA1	T110										X															
F1	T105											X		X												
AV50	T126											X														
AV51	T128											X														
AQ60	T165														X	X	X	X								X
AV60	T170														X											
AV35																			X							
AV36																			X							
T148	T148																						X			

Figure 4. continued.

blubber, muscle tissue, internal organs or an oil slick on the water's surface. We divided the total number of hours spent following transient killer whales by the total number of kills observed to calculate a kill rate as follows:

Kill rate = number of kills/number of hours followed.

Hourly kill rates were multiplied by 24 hours to obtain a daily rate. The daily rate was then divided by the average group size for southeastern Alaska transient killer whales (Dahlheim et al. 2009) resulting in a calculation of daily kill rate per whale.

Results

Combining the results of our dedicated surveys with supplementary data, we identified 155 transient killer whales within the inland waters of southeastern Alaska. Over the past decade, calf production has been primarily responsible for the observed increase in the number of identified killer whales. Thus, discovery of previously unidentified or 'new' adult whales in the area is now rare. Transient killer whales were encountered throughout the study area and were seen in all three seasons sampled (Fig. 3). Supplementary sources confirmed their presence during every month of the year to include the winter season. The frequency at which different maternal groups and/or individual adult males were resighted varied on an annual basis (Fig. 4). Out of 41 maternal groups and 29 adult males, 73% of the maternal groups (N = 30) and 69% of the adult males (N = 20) were seen throughout the years. The mean number of years in which the same whales were resighted was 7.03 ± 2.60 years for maternal groups and 6.60 ± 2.54 years for adult males. The mean interval between resightings of the same whales was 2.16 ± 1.70 years (N = 97 intervals).

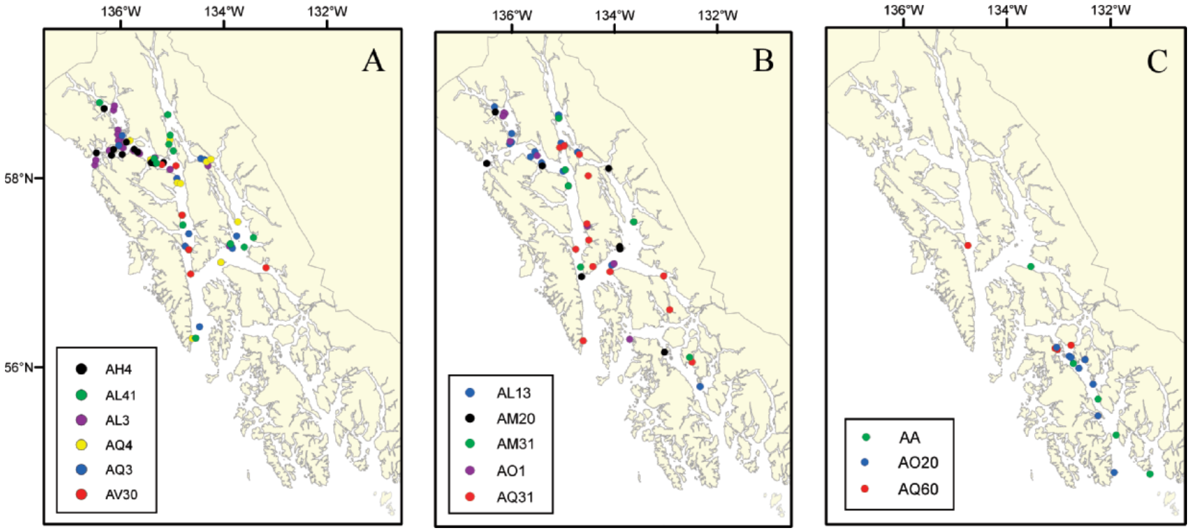


Figure 5. Area usage depicted for 14 maternal groups of transient killer whales in southeastern Alaska of which six groups, only seen in the northern part of the study area, are shown in A), five groups primarily seen in the northern part of the study area with infrequent occurrence in the southern part of the study area are shown in B) and three groups observed most often in the southern part of the study area are shown in C).

We documented eleven maternal groups and nine adult males in southeastern Alaska only once during our study.

Resighting data suggested that within southeastern Alaska maternal groups may partition area usage of their environment. Of 14 maternal groups seen multiple times, six groups were only seen in the northern part of the study area (i.e. Chatham Strait, Frederick Sound, Stephens Passage, Lynn Canal and Icy Strait; Fig. 5A). We observed five groups most frequently in the northern part of the study area although each group had one sighting in either Sumner or Clarence Strait (see Fig. 5B). The remaining three groups were found most frequently in the southern part of the study area (i.e. Clarence Strait and Sumner Strait; see Fig. 5C).

On a broader geographical scale, photographic comparisons confirmed that a large percentage (86%; N=134) of the southeastern Alaska transient killer whales have also been documented in British Columbia and Washington State waters. In contrast, no matches were found between animals seen in our study with those listed in the photographic catalogues available from Prince William Sound (N = 54 whales; Matkin et al. 1999) or the Gulf of Alaska, the Aleutian Islands and the Bering Sea (N = 154 whales; Dahlheim 1997, NMML unpub. data 2001-2003). Of 21 whales identified from southeastern Alaska none have yet been observed in any other region.

Out of 114 encounters with transient killer whales, 84 had associated start and end times and locations for a total of 264.5 hours and 1,467 km of track line, respectively (Fig. 6). The mean duration of encounters was 3.15 ± 3.1 hours and the range was 0.25-19 hours. Mean travel speed was 7.2 ± 5.8 km/hour and the range 0.2-33.5 km/hour. Two maternal groups were resighted multiple times during a single cruise. The mean daily movements of these groups averaged 134 km ± 88 km/24 hours (range 59-240 km/24 hours) with one group moving 380 km in 192 hours and another group moving 234 km in 100.5 hours (Fig. 7).

Predation was directly observed in 36 of the 114 encounters. We positively identified prey species taken during 19 (53%) of the 36 observed events. In the remaining 17 events where prey could not be reliably identified, we documented that a kill had been made using the criteria as described above. Transient killer whales were documented depredating several different species of marine mammals (Fig. 8). Prey species included Dall's porpoise *Phocoenoides dalli*, Pacific white-sided dolphins *Lagenoryhncus obliquidens*, harbor porpoise *Phocoena phocoena*, minke whales *Balaenoptera acutorostrata*, Steller sea lions *Eumetopias jubatus* and harbor seals *Phoca vitulina*. Seabirds and fish were

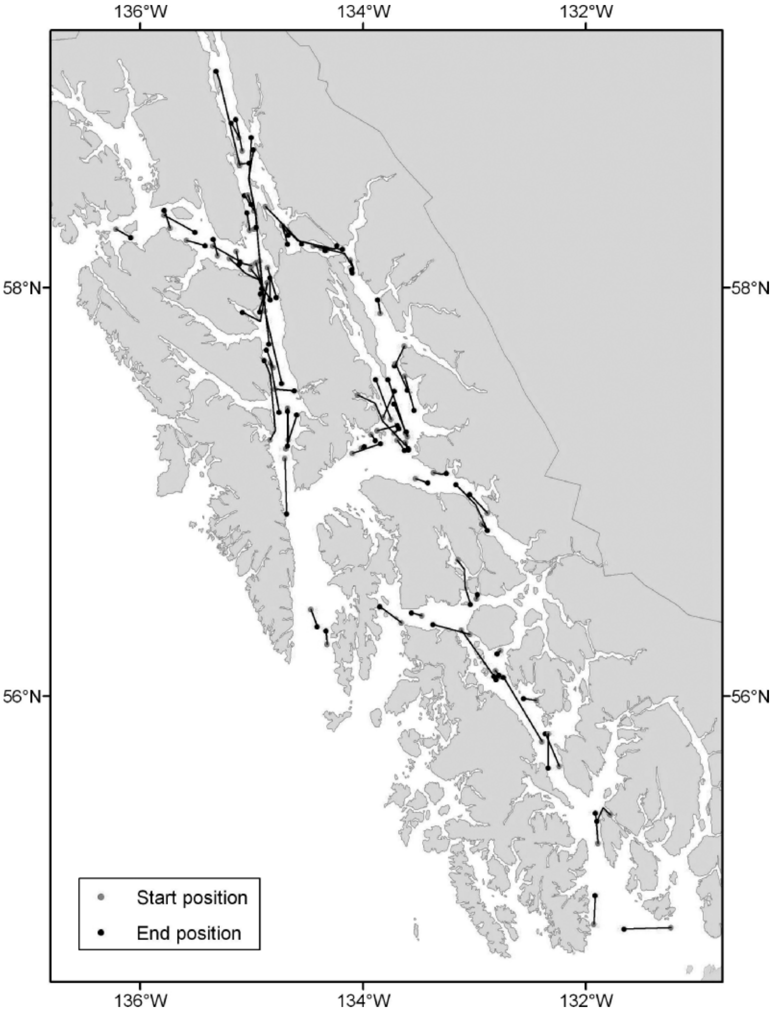


Figure 6. Track lines from start to end positions of transient killer whales in southeastern Alaska based on National Marine Mammal Laboratory's dedicated survey data during 1991-2007.

also harassed, however, we could not positively determine if these prey items were actually consumed.

Transient killer whales employed different prey-handling techniques depending on the prey species being targeted (see Table 1). Despite observed differences in prey handling, we found no evidence of prey specialization. The same individuals or groups were observed, consuming a variety of prey species. Group size is reported as a range, because sample sizes for predation on each prey species were too small to determine if whale group size correlated with prey being targeted.

Kill rates were calculated from 114 encounters and 332.5 hours spent following transient killer whales (i.e. 36 encounters with predation and 78 encounters with no predation observed). From these data we calculated a daily kill rate per transient killer whale of 0.62 ± 0.25 prey items/24-hour period/whale (range: 0-1.3 prey items/24-hour period/whale).

Discussion

Transient killer whales were found in southeastern Alaska throughout the year and occupied a variety of habitats that included open-strait environments, near-shore waters, bays and inlets, and ice-laden waters near tide water glaciers. Dahlheim et al. (2009) recently reported a seasonal pattern of occurrence in southeastern Alaska with transient killer whales more abundant in the summer. Temporal movements in and out of southeastern Alaska are likely related to seasonal availability of prey. For example, an increase in the number of transient

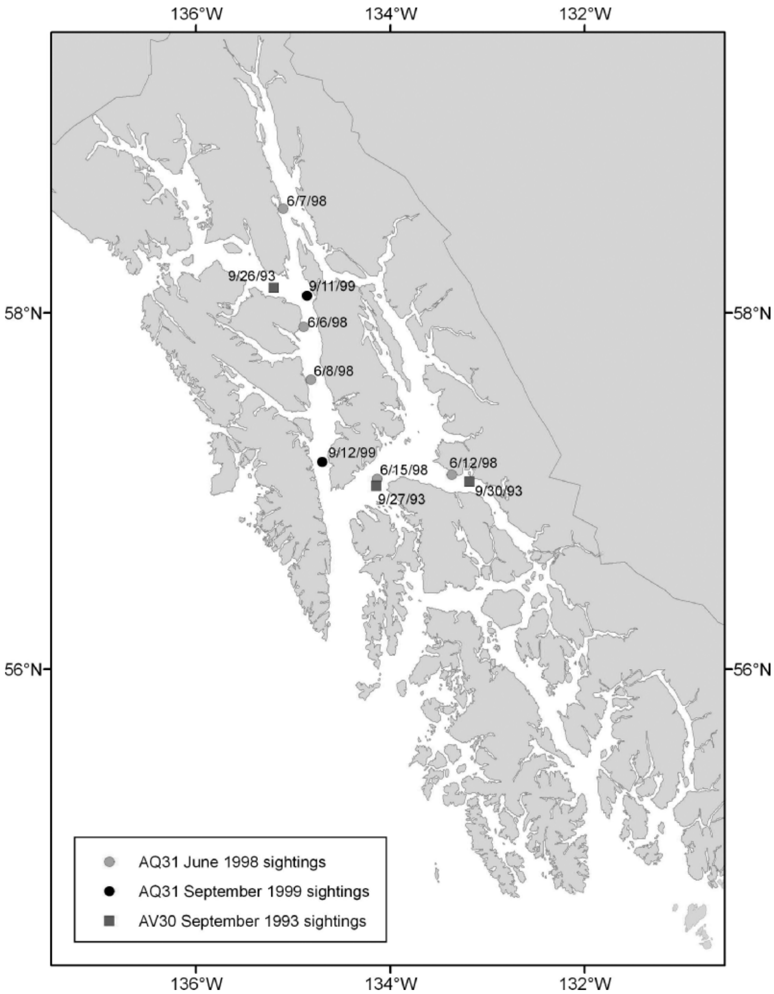


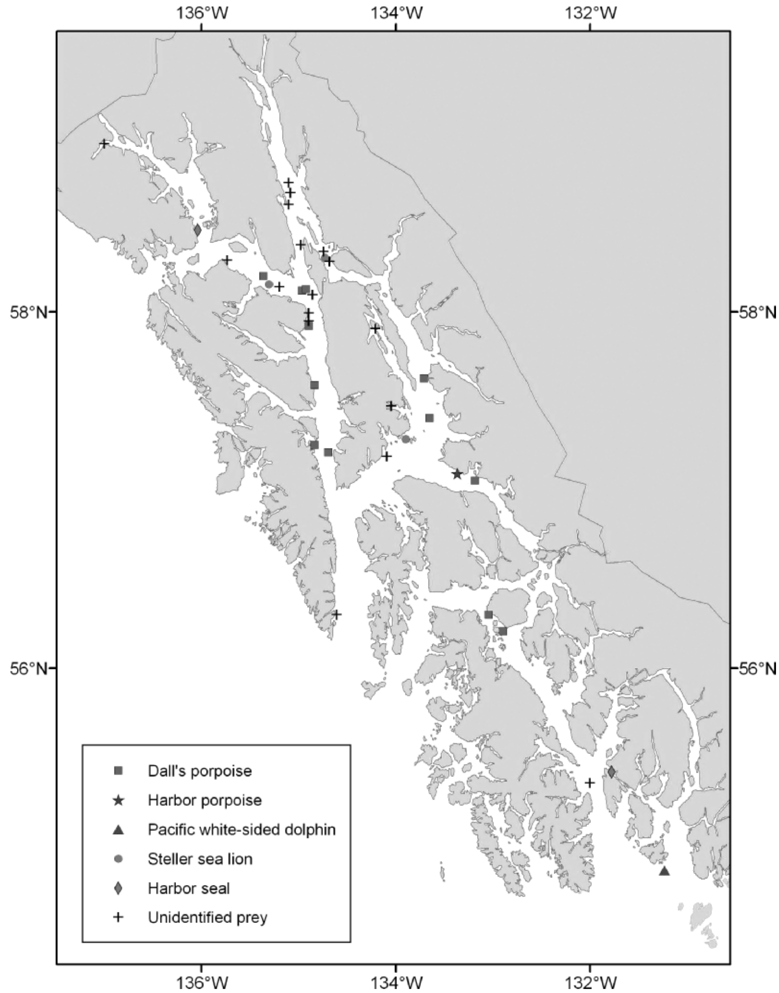
Figure 7. Resighting locations of two maternal groups (AQ31 in June 1998 and in September 1999, and AV30 in September 1993) of transient killer whales. For each group, multiple resightings occurred over the span of several days.

killer whales in the fall off southern Vancouver Island, British Columbia, has been linked to harbor seal pupping times (Baird & Dill 1995). Along the Californian coast, transient killer whale sightings show a bimodal pattern that coincides with seasonal concentrations of prey; increasing in spring during the northbound migration of gray whale *Eschrichtius robustus* cow-calf pairs and again in the fall during an increased abundance of pinnipeds (Nancy Black, pers. comm., Monterey Bay Cetacean Project).

The average time that predators spend traveling through an area is an important ecological parameter with regards to impact on local prey populations. Our quantification of whale movements with regards to speed, distance and direction augment previous studies that reported travel speeds only as categorical variables (Deeke et al. 2005). Travel speeds would be expected to vary with whale behaviour. Pistorius et al. (2002) reported swimming speeds of 11.9-14.4 km/hour when killer whales were patrolling the beaches at subantarctic Marion Island in the Indian Ocean. Higher rates of speed used during the pursuit of prey may not be representative of killer whale swimming speeds when engaged in different behaviours (e.g. resting, milling, socializing and traveling). In contrast, we calculated a mean travel speed from a large number of direct observations of whales engaged in a variety of behaviours that included, but were not limited to, hunting.

Whereas sightings document species distribution, it is our ability to recognize individual whales during subsequent encounters that is fundamental to refining our knowledge regarding how different maternal groups utilize the region over space and time. Some transient killer whales spent considerably more time in southeastern Alaska than did

Figure 8. Location of predation events coded by six prey species and unidentified prey based on National Marine Mammal Laboratory's dedicated survey data during 1991-2007.



others, both on an annual and multi-year basis. Moreover, within southeastern Alaska some maternal groups preferentially utilized different areas including a well-defined separation between the northern and southern parts of the study area. This pattern cannot be attributed to effort because surveys would have an equal chance of detecting all whales present in the area. Both the temporal and spatial patterns observed suggest that transient killer whales partition their use of resources in the southeastern Alaska ecosystem. Area partitioning may reduce conspecific competition. Year-round effort or remote-sensing techniques (e.g. radiotelemetry and satellite tags) are needed to fully document seasonal shifts and resolve finer-scale questions regarding home range and core area usage of individual whales or groups.

The proportion of whales common to southeastern Alaska/British Columbia and Washington State was large suggesting that movements between these areas are relatively common. In contrast, Black et al. (1997) reported only four photographic matches of transient killer whales occurring between central California and southeastern Alaska. This represents only 3% of the 105 individual whales identified from central California (Black et al. 1997). Similarly, only six matches have been made between central California and British Columbia (Black et al. 1997, Ford & Ellis 1999). Based on the extensive research effort put forth in southeastern Alaska, British Columbia, Washington State and central California, one would predict a higher percentage of matches if whales were moving frequently among these areas.

Studies on mtDNA restriction patterns provide evidence that eastern temperate North Pacific transient killer whales occupying different regions are genetically distinct (Stevens et al. 1989, Hoelzel

1991, Hoelzel & Dover 1991, Hoelzel et al. 1998, 2002). Currently, National Marine Fisheries Service recognizes three different populations or stocks of North Pacific transient killer whales which occur in: 1) the Gulf of Alaska, the Aleutian Islands and the Bering Sea, 2) Prince William Sound to the Kenai Fjords and 3) California to southeastern Alaska (Angliss & Allen 2009). Given the lack of movements documented over the last two decades of transient killer whales between the inland waters of southeastern Alaska/British Columbia/Washington State and the coastal waters off central California, we propose that transient killer whales occurring off California be considered as a different stock and managed accordingly.

Wide-ranging movement patterns coupled with a demonstrated ability and willingness to shift between prey species allow transient killer whales to capitalize on seasonally or locally abundant prey. Dietary scope has been associated with predators that utilize an active, as opposed to a sit-and-wait, style of hunting (Rosenheim et al. 2004). Highly mobile predators such as transient killer whales most likely have diets that also vary regionally depending upon local prey resources. For that reason, Matkin et al. (2006) suggested that killer whale feeding behaviour be examined on a region-by-region basis. When comparing our study with research conducted in British Columbia (Baird & Dill 1995, Ford et al. 1998) and Prince William Sound (Saulitis et al. 2000), we found that transient killer whales targeted similar species and diversity of prey. Conversely, interesting differences exist when comparing prey selection by southeastern Alaska transient killer whales to other areas. Specifically, some species that have been harassed or killed in other regions have not been targeted as prey in southeastern Alaska e.g. humpback whales off the coast of Columbia in the South Pacific (Florez-Gonzales et al. 1994), elephant seals in British Columbia (Baird & Dill 1996) and sea otters in the Aleutian Islands (Estes et al. 1998). Although predation on sea otters has been reported in Prince William Sound (Hatfield et al. 1998), no predation on sea otters was observed during our study. It is possible that predation on sea otters may have gone undetected due to their relatively small size and their close proximity to the shore.

The lack of predation on humpback whales in southeastern Alaska has been previously noted (Dolphin 1987) and is particularly intriguing because humpbacks with attending calves occur in high numbers throughout the study area each year. Why killer whales do not exploit this seemingly abundant resource remains unknown, but these observations are consistent with the findings of Mehta et al. (2007), who examined the occurrence of killer whale scars on humpback whales and concluded that most attacks are directed at calves prior to their arrival in high latitudes. Given the conspicuous nature and lengthy attacks documented during observations of killer whales preying on large whales and large pinnipeds, it is unlikely that kills on humpback whales or elephant seals would have gone undetected (Mehta et al. 2007). Despite the fact that we spent considerable time with resident whales (410 hours in 85 encounters) and to a lesser extent with offshore whales (28 hours in four encounters) over the same time period (Dahlheim et al. 2008, 2009), these two eco-types were never observed pursuing or eating marine mammals.

Prey-handling techniques varied depending upon the prey being targeted with no evidence to support prey specialization. Similar findings were reported for transient killer whales in British Columbia (Baird & Dill 1995, 1996, Ford et al. 1998) and Prince William Sound (Saulitis et al. 2000).

We averaged kill rate across all prey species to illustrate a larger pattern of predatory behaviour. We did not attempt to calculate species-specific kill rates given our sample sizes. Our calculations were based on a 24-hour period, however, the nocturnal behaviour of transient killer whales remains unclear. Two previous studies that utilized radio-tracking to examine killer whale behaviour at night produced conflicting results (Erickson 1978, Robin Baird, unpubl. data, Cascadia Research Collective). Furthermore, our calculations assumed that individual killer whales eat every day, although most large carnivores do not. The blubber layer found in killer whales, which acts as a fat reserve for most cetacean species, suggests that killer whales do not need to eat every day. The range in the observed daily kill rate (0-1.3 prey items/24-hour period/whale) may be reflective of the prey species and age class being targeted (Baird & Dill 1995, 1996, Williams et al. 2004). Meals consisting of smaller prey items or those containing less nutritional value would need to be consumed at a higher rate. Likewise, transient killer whales of different sex and age classes will differ in their food intake requirements (Williams et al. 2004). Seasonal or regional differences in kill rate may also vary with prey abundance (Hanby et al. 1995). Predators often temporarily increase their kill rate and consumption when high concentrations of prey are encountered (Kruuk 1972).

In conclusion, as predators that are present year-round preying upon a diversity of species, transient killer whales play an integral role in shaping the southeastern Alaska marine ecosystem. Documenting shifts in area usage by individually recognizable whales may serve as an indicator of ecosystem health and may be a valuable tool in gauging environmental change. This may be especially useful in detecting changes in number and/or distribution of prey populations, e.g. small cetaceans that may be more difficult than killer whales to monitor directly. The ecological plasticity of transient killer whales may mask an underlying dependence on local resources. Our efforts to document area usage improves our ability to work towards conserving the full range of habitats utilized by these wide-ranging marine predators and may help to identify areas and resources important to transient killer whale survival. Recognizing the high degree of exchange of transient killer whales that occurs between southeastern Alaska waters and British Columbia and Washington State waters is also crucial to developing species-wide management plans especially with regards to international boundaries as they relate to marine environmental policies and protection laws.

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