

Sequential Habitat Use by Two Resident Killer Whale (*Orcinus orca*) Clans in Resurrection Bay, Alaska, as Determined by Remote Acoustic Monitoring

Harald Yurk,¹ Olga Filatova,² Craig O. Matkin,³
Lance G. Barrett-Lennard,¹ and Michael Brittain⁴

¹Vancouver Aquarium Marine Science Centre, P.O. Box 3232, Vancouver, BC, Canada V6B 3X8;
E-mail: yurk@zoology.ubc.ca

²Department of Vertebrate Zoology, Faculty of Biology, Moscow State University,
Vorobyovy gory 1/12, Moscow 119992, Russia

³North Gulf Oceanic Society, 3430 Main Street, Suite B1, Homer, AK 99603, USA
⁴P.O. Box 1936 Seward, AK 99664, USA

Abstract

Killer whales (*Orcinus orca*) are sighted regularly in coastal Alaska during the summer, but little is known about their movements through the area during the winter when weather and light limit the use of boat-based surveys. Acoustic monitoring provides a practical alternative because each extended resident killer whale family group or pod has a unique dialect that can be discerned by differences in their repertoires of stereotyped calls. The repertoires of resident killer whale pods in the northern Gulf of Alaska were updated from earlier studies, and the results used to determine the identity of pods that were recorded on remote hydrophones in Resurrection Bay, Alaska, in the fall, winter, and spring of 1999 to 2004. In total, seven pods of resident killer whales were identified acoustically, comprising four related pods from AB clan and three from AD clan. The frequencies of occurrence of the clans differed between the November to March recording period when AB clan occupied the area, and the April-May period when AD clan was predominant. The sequential use of this habitat during periods of relative prey scarcity has the effect of limiting intergroup resource competition and is consistent with earlier findings that demonstrated divergent resource specialization by sympatric killer whale populations.

Key Words: Killer whales, *Orcinus orca*, acoustic monitoring, behavior, habitat use, distribution, competition

Introduction

Cetaceans are highly mobile animals, and their movements can be difficult to predict. Many species are encountered only rarely and/or in

places or conditions that are not favorable for boat-based surveys. In most areas, more is known about cetacean distributions in summer than during winter (Ford et al., 2000; Scheel et al., 2001). Acoustic monitoring using stationary hydrophones can provide a practical alternative to boat-based surveys for vocally active species. Species studied with fixed hydrophones have included humpback whales (*Megaptera novaeangliae*) (Norris et al., 1999), bowhead whales (*Balaena mysticetus*) (Cummings & Holliday, 1985), blue whales (*Balaenoptera musculus*) (Stafford et al., 1998), and killer whales (*Orcinus orca*) (Morton & Symonds, 2002).

Members of an assemblage of North Pacific populations of fish-eating killer whales referred to as *residents* produce distinctive pulsed calls, whistles, and trains of echolocation clicks (Schevill & Watkins, 1966; Steiner et al., 1979; Ford, 1989) and are vocally active much of the time (Barrett-Lennard et al., 1996). The pulsed calls are characterized by abrupt shifts in pulse rates, which produce discrete call structures that are recognizable over great distances (Schevill & Watkins, 1966; Hoelzel & Osborne, 1986; Ford, 1989; Miller, 2006). Discrete call structures are group specific, making killer whales amenable to group identification through remote acoustic monitoring. Residents are characterized by a nested social structure comprising matriline containing a matriarch and all her descendents, pods containing a set of matrilines that associate frequently and use a common repertoire of stereotyped calls or group-specific dialect, clans containing related pods whose dialects include some similar calls, and populations or communities containing one or more associating clan (Ford, 1991, 2002a, 2002b). Despite overlaps in geographic range, all of these groups appear to be closed to immigration.

Dialects can therefore be used to unambiguously identify resident killer whale pods in passive acoustic monitoring studies in Alaska (Yurk et al., 2002).

Members of a second assemblage of North Pacific killer whale populations referred to as *transients* feed almost entirely on marine mammals (Ford et al., 1998). Transients and residents are genetically distinct (Stevens et al., 1989; Hoelzel & Dover, 1990; Barrett-Lennard, 2000) and differ greatly in behavior (e.g., Morton, 1990) and social organization (Baird & Whitehead, 2000). Transient killer whales can be distinguished from residents by their use of distinctively different call types (Deecke et al., 2005; Saulitis et al., 2005; Matkin et al., 2007). Regional transient communities can be distinguished by call type variants (Deecke, 2003); however, further acoustic subdivisions within populations analogous to clan- and pod-specific dialects in residents have not been identified. Transient killer whales use both calls and echolocation clicks much less often and less consistently than residents, making acoustic detection less reliable (Barrett-Lennard et al., 1996; Deecke et al., 2005; Matkin et al., 2007).

A third assemblage of killer whales referred to as *offshores* travels in larger groups and is also highly vocal and characterized by distinct calls (Ford, 2004). However, identification of call repertoires of this population is still incomplete (J. K. B. Ford, pers. comm., 2009). Although offshores occasionally enter the study area (Matkin et al., 1999), calls identified during this study could be unequivocally identified as either transient or resident calls. While it is possible that quiet offshore killer whales were missed, this is unlikely given the typical vocal behavior of these whales when encountered elsewhere.

Resident pods and two populations of transient killer whales, the AT1 and Gulf of Alaska (GOA) transients, are sighted regularly in Prince William Sound, Kenai Fjords, and in the adjacent Gulf of Alaska during the summer and have been the subjects of focused research since the mid-1980s (Matkin et al., 1999, 2008). Far less is known about the use of the above areas, including our study area, in the winter. Low daylight levels, short days, and difficult weather conditions limit the use of extensive boat-based winter surveys.

The value of acoustic monitoring in detecting killer whales was identified as early as the 1970s when the first systematic surveys of this species began. Several acoustic monitoring stations were established at remote locations, including light-houses along the British Columbia (BC) coast (Bigg et al., 1987), research out-stations such as Orcalab on Hanson Island, BC (Deecke et al., 2000; Weiß et al., 2007), field research sites in the

Crozet Islands (Guinet, 1991) and in the Pribilof Islands (Newman & Springer, 2008), and in wilderness parks such as the Glacier Bay National Park in Southeast Alaska (see list of projects in Yurk et al., 2001).

Herein, findings are presented from a 5-y remote acoustic monitoring study in Resurrection Bay, Alaska, which focused on the identification of specific resident pods based on previously determined dialects (Yurk et al., 2002; Yurk, 2005). These findings shed new light on seasonal habitat use of specific resident and transient killer whales in the study area. The most novel finding, however, was that Resurrection Bay appears to be sequentially dominated by different clans of resident killer whales in the fall, winter, and spring of each year. The study also confirmed the feasibility, efficiency, and efficacy of remote acoustic identification and monitoring of groups of killer whales initially identified in boat-based studies.

Materials and Methods

Study Area and System Design

Resurrection Bay, on the southern end of Alaska's Kenai Peninsula, is a glacial fjord that opens into the Gulf of Alaska. It is divided by a narrowing at Caines Head into a protected inner bay with the town of Seward at its north end and an outer bay that gradually widens and opens to the Gulf of Alaska (Figure 1). Caines Head and the outer islands shelter the inner bay from the storms that regularly occur during a Gulf of Alaska winter.

In summer 1998, a remote hydrophone connected via a rugged steel-shielded cable to a radio transmitter (Cetacean Research Laboratory, Vancouver Aquarium Marine Science Centre, British Columbia, Canada) was installed off the south point of Halibut Cove, Fox Island (in Resurrection Bay; Figure 1, point 1). The transmitted FM signal carrying the whales' vocalizations could be monitored by research and other boats traveling in the area. Ambient and vessel noise were often a problem during the summer months because of heavy traffic by tourist and fishing vessels. In the fall and winter months, vessel noise became a less challenging issue, while noise generated by ocean swells and surf on cobble beaches in the outer bay became a serious impediment to acoustic monitoring (Figure 1). These conditions rendered the hydrophone ineffective for much of the winter season in this location, and it was moved to Thumb Point at the entrance to the inner bay in May 1999 (Figure 1, point 2).

This new location was protected from the noise of waves onto cobble beaches but still allowed a large portion of the outer bay to be monitored. This location provided all the acoustic data used in our

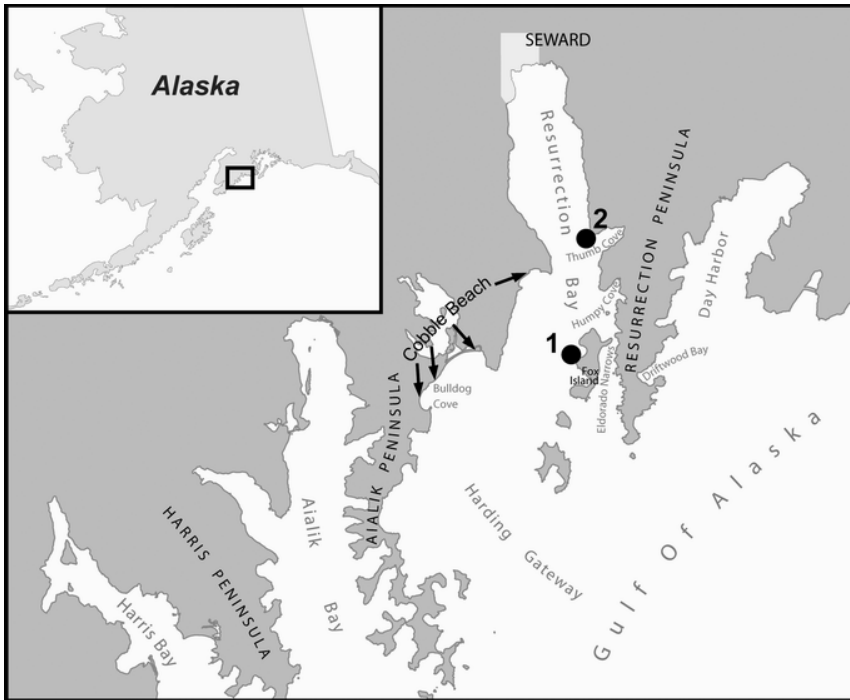


Figure 1. Study area and hydrophone locations (point 1: Fox Island; point 2: Thumb Point)

analysis. Sounds were recorded with an Offshore Acoustics omnidirectional hydrophone connected via cable to a microwave transmitter system (SeeMore Wildlife Systems, Homer, Alaska, USA) that transmitted signals to a receiver/recorder at the Alaska SeaLife Center in Seward.

The sensitivity of the hydrophone was $-154 \text{ dBV}/\mu\text{Pa} \pm 4 \text{ dB}$ at 100 Hz and the frequency response curve showed the following range: 5 Hz to 40 kHz, and was relatively flat up to 14 kHz (Offshore Acoustics). The hydrophone was weighted to the bottom with 80 kg of rocks in mesh netting attached to the cable 1.5 m from the hydrophone. A solid foam fishing-float was attached to the cable directly below the hydrophone to float it off the bottom. The rubberized, 1.9-cm-thick three-conductor cable followed the bottom and came to the surface, exiting the water in a protected area. We added a sheath of high-pressure hydraulic tubing with walls 9.5-mm thick over the wire in the intertidal area to protect the cable from chafing against rocks. The hydrophone was anchored in water 25 m deep.

The transmitter station at Thumb Point was situated on top of a large boulder approximately 5 m above maximum high water. This transmitter station included a microwave transmitter and antenna, three 80-W solar panels, one 100-W wind generator, and four 55 amp/h deep cycle batteries.

It also included a UHF-transceiver that allowed for remote power monitoring and on/off control of the system in the event of low power. Audio from the microphone was fed into an amplifier and then into a 2.4 GHz microwave transmitter. The transmitter had a reported frequency range of 150 Hz to 15 kHz, but the upper-frequency response of the cassette tape recorder used to record calls was limited to 8 kHz ($\pm 3 \text{ dB}$). A microwave signal was transmitted 6 nmi over water to a receiver at the Alaska SeaLife Center in Seward. The audio output of a microwave receiver was monitored opportunistically by an experienced technician (Michael Brittain), and a log was kept of beginning and ending times. During days when the hydrophone was monitored, the technician listened for an average of 6 h (SD 1.2 h). When calls were heard, the cassette tape recorder was manually activated and calls were recorded (mean: 37 min/recording day; SD 19 min). More details on data collection effort are presented in Figure 3.

Call Analysis and Identification of Pods

Experienced observers are used for acoustic identification, which was made aurally and by comparing spectrograms. This method has demonstrated high reliability when distinguishing between calls of transient and resident killer whales, calls from different resident clans and

different resident pods, and for the identification of geographical differences in calls from different transient populations (Ford & Fisher, 1983; Ford, 1991; Deecke et al., 1999; Miller & Bain, 2000; Yurk et al., 2002; Saulitis et al., 2005) and is used in comparisons with other classification methods (Deecke & Janik, 2006). In particular, residents of the same matriline use specific call types as vocal signatures (dialects) to identify their matriline and pod (Ford, 1991; Deecke et al., 2000; Miller & Bain, 2000). Previous studies have provided catalogues of sound samples and spectrograms of group-specific calls and repertoires for each of the resident pods identified in this study, the AT1 transient group, and for some of the Gulf of Alaska transient groups (Yurk et al., 2002; Saulitis et al., 2005). These were updated using previously unpublished data, and sonograms of specific call variants that were essential in our analysis are shown in Figure 2.

Initially, recorded calls made by members of the resident and transient assemblages were separated. Resident calls were further subdivided by clan (AB or AD) following Yurk et al. (2002). Highly distinct dialects (Figure 2) made it possible to identify the clan even when the recording quality (signal-to-noise ratio) was poor.

AD clan calls were further divided by pod; AK, AD5, and AD16 pods are each distinguished by unique variants of AKS01 and AKS09 call types (Figure 2). A fourth AD clan pod, AE, produces distinctive AKS02 call types, but this pod was never identified in our recordings and has never been observed outside Prince William Sound during summer photographic surveys (Matkin et al., 1999).

The seven AB clan pods that were identified use a wider variety of call types but also share a greater number of similar sounding calls. So, for AB clan calls, the type and frequency of call types produced in an encounter was examined, and the pattern of occurrence of specific types was compared with the pattern of occurrence within the established repertoires of calls of AB clan pods. Although many AB clan pods use closely related call variants, it was possible to determine pod identities based on the unique patterns of use of specific call types. Unique call variants or calls occur more frequently in encounters that have more than one pod present (Yurk et al., 2002; Yurk, 2005). This is because some pods share many call types (e.g., AB, AJ, and AN pods). However, AB pod frequently uses the AKS14 call type, while this type is rarely found in AJ and AN pod recordings. Also, spectrographically, AKS14s produced by AJ and AN pods differ from those produced by AB pod. Other typical AB pod calls include a uniquely shaped AKS18 call type with deep

frequency modulations, a clearly distinct AKS11 call variant, and an AKS12 call type that has not been found in the repertoires of the other two pods (Figure 2).

Unique call types that distinguish AJ pod include AKS23 and AKS39. AJ pod also uses a distinct variant of AKS11 (Figure 2), also used for identification in this study. The AKS21 call along with specific variants of the AKS17, AKS18, and AKS22 call types were used to distinguish AN pod. AG pod can be distinguished from other AB clan pods by its use of the distinct AKS27 call type, and AF pod was distinguished by the use of the AKS16 call type, which has a unique upper-frequency component (Figure 2). The AI pod call dialect is very similar to that of AB pod; thus, calls cannot be easily assigned to either pod. However, AI pod does not use the AKS14 call type (Yurk et al., 2002), which is recorded during almost every encounter with AB pod in summer surveys and which occurred regularly in the remote recordings of this study.

If the recording quality was poor (i.e., the recording had a low signal-to-noise ratio, which was decided based on audible ambient noise in the recording and few visible sidebands in spectrograms of pulsed sounds), a particular pod was considered present only if at least two call types were recorded that distinguished the pod, or at least three calls of one distinct type in the same recording day but during different recording sessions. For example, during a 6-h period on the same day, three recordings were made, and in all three, a specific call type/variant was detected. In cases when less evidence was available, the presence of the pod was listed as "probable." If the recording quality was good, the presence of one distinct call or variant was generally sufficient to identify the pod.

Data Analysis

Using the approach described above, the presence of identified pods was confirmed during each recording session. A recording session usually contained one recording but could consist of more if these recordings occurred successively and were not separated by time intervals of more than one hour in the recording logbook. Presence of identified pods was determined during the recording sessions of each 24-h d for which there were recording sessions available. Actual residence time for pods was not estimated as killer whales are often silent when resting or traveling. The number of daily occurrences for each pod was calculated for each month across all years of acoustic monitoring in the context of monthly effort (hours of monitoring time).

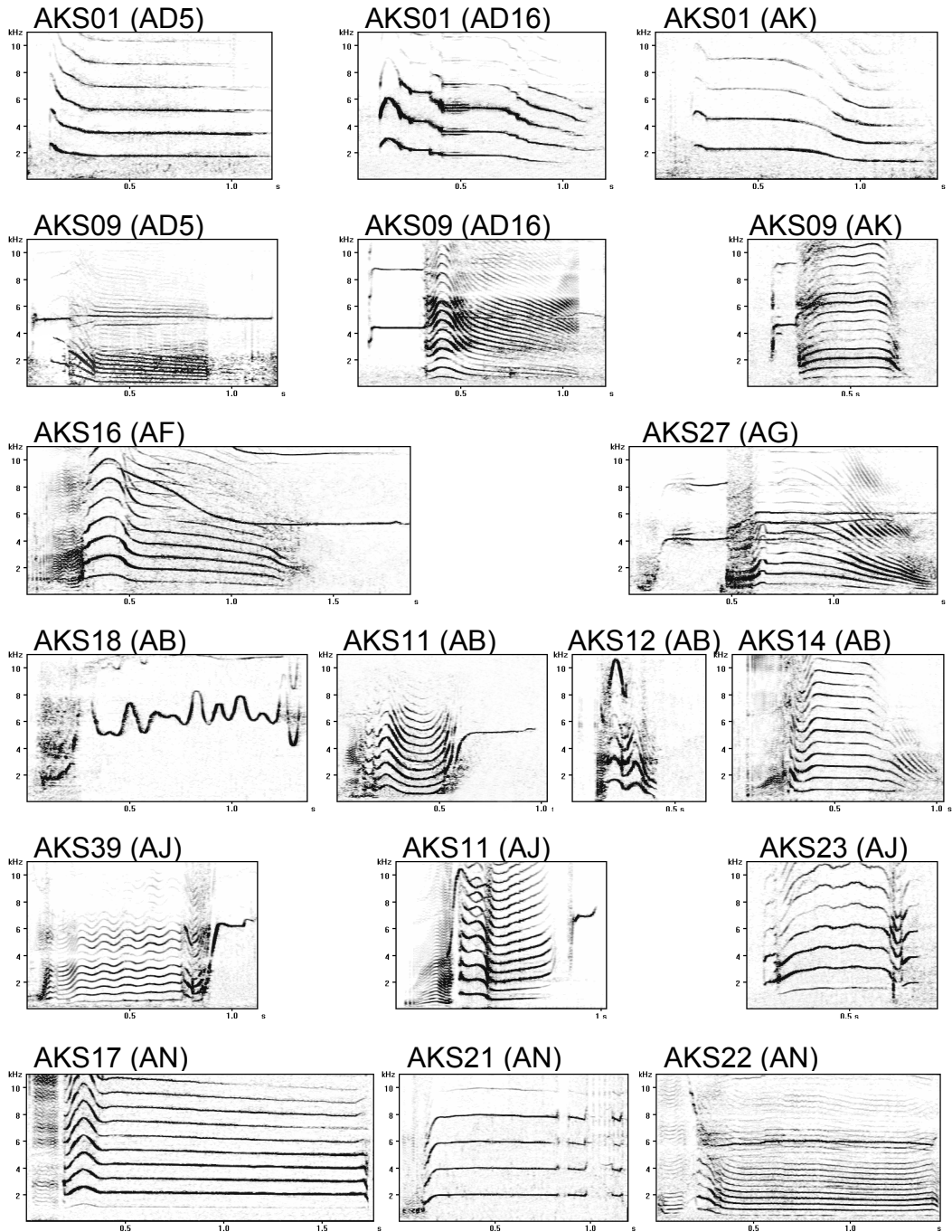


Figure 2. Updated sonograms of unique calls of resident killer whale clans and pods recorded in the study; clans do not share call types which allows distinction between AD5, AD16, and AK pods of AD clan from AB, AF, AG, AJ, and AN pods of AB clan (see Yurk et al., 2002, for details on repertoires).

The frequencies of occurrence of AD clan and AB clan during “winter” and “spring/fall” seasons was compared using the Yates Chi-square test assuming a homogenous occurrence pattern for each clan during each season as the null hypothesis. The frequency of AB, AJ, and AN pod occurrences was compared between each month from October through March using a standard Chi-square test again assuming homogenous occurrence for each pattern during each month of the recording period.

Results

Observation Effort

Beginning in fall 1999 and ending in spring 2004, the remote hydrophone at Thumb Point was monitored at regular intervals between early fall and late spring. Although the system broadcasted continuously, recordings were only made when the hydrophone was monitored by a technician and vocalizations were heard (Table 1).

Over a 5-y period, calls of seven different resident killer whale pods—AB, AJ, AN, AK, AD5, AD16, and AF pods—were identified, which are from two distinct killer whale clans: AB clan and AD clan (Yurk et al., 2002). Also, vocalizations of members of one distinct transient population, the AT1 group, were detected (Saulitis et al., 2005) (Table 2). Five resident pods (AB, AJ, AN, AK, and AD5) were recorded more than 10 times and

their patterns of occurrence were compared among the different months of monitoring.

To identify a potential pattern of use of Resurrection Bay by killer whales, a ratio was calculated expressing the time with killer whale recordings vs the total time of remote hydrophone recordings from September 1999 to May 2004. The percent time with calls present during different months is shown in Figure 3.

Although time periods with killer whale calls vs time periods without calls varied across months (Figure 3), no statistically significant difference in vocal activity was found among all monitored months (Kruskal-Wallis H test: $H = 5.6$, $p = 0.69$; Figure 4). In January of 2003, a higher median call rate (50% of monitored time contained calls) was detected than for any other month (Figure 4). However, since January was also the month with the lowest overall monitoring effort (hours that technician monitored hydrophone; Figure 3), it is not clear whether this pattern was typical of other years or a factor related to monitoring effort.

The occurrence of different pods varied among months. There was a strong co-occurrence of AB and AJ pods (AB clan pods) during the November to March periods (Figure 5, top). AK and AD5 pods (AD clan pods) were recorded together predominantly in May when AB clan pods were absent. AD5, however, was already present in April of many years, while AK pod was not detected until May annually. AN pod appeared to use the Bay

Table 1. Periods of monitoring and total recording time

Periods	Days of monitoring	Total hours of monitoring	Days with recordings	Hours of recording
5 Oct 1999 – 29 April 2000	94	490	8	6.75
20 Oct 2000 – 25 May 2001	120	811	20	22.50
03 Oct 2001 - 30 May 2002	173	1,294	53	30.75
11 Sept 2002 – 3 June 2003	151	808	38	15.00
7 Sept 2003 – 17 May 2004	187	1,210	64	29.25
15 Sept 2004 – 31 Dec 2004	49	203	3	0.90

Table 2. Number of days each pod (clan) was recorded during the periods of monitoring; TRA = Transient.

Clans	AB				AD			TRA
	AB	AJ	AN	AF	AK	AD5	AD16	AT1
5 Oct 1999 – 29 April 2000	8	7	0	1	0	0	0	0
20 Oct 2000 – 25 May 2001	7	3	7	0	3	14	0	1
03 Oct 2001 - 30 May 2002	36	25	19	5	9	8	1	1
11 Sept 2002 – 3 June 2003	23	21	6	0	1	6	0	0
7 Sept 2003 – 17 May 2004	28	26	13	0	2	0	0	2
15 Sept 2004 – 31 Dec 2004	1	1	1	0	0	0	0	0
Total	103	83	46	6	15	28	1	4

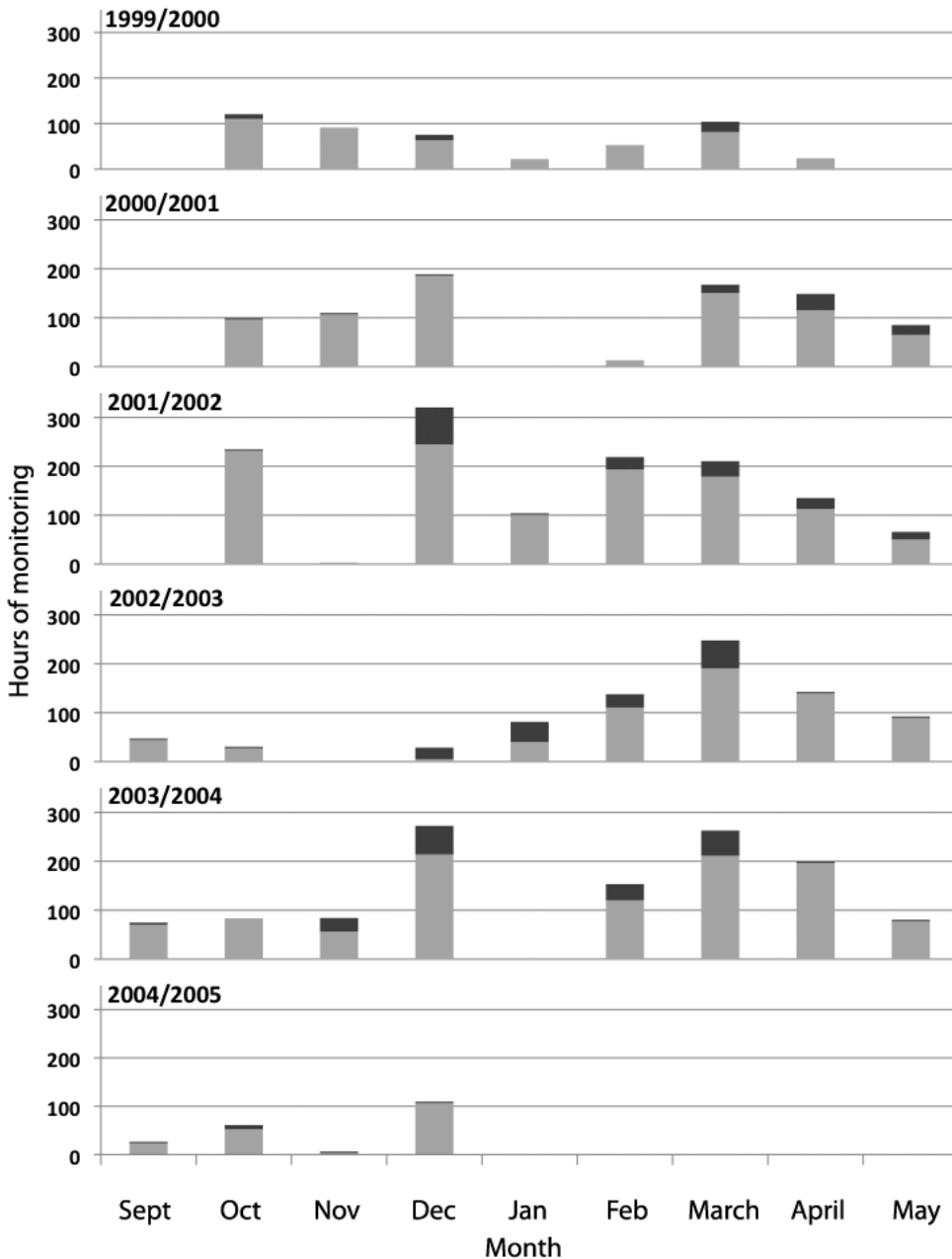


Figure 3. Monitoring effort and acoustic detections of killer whales; bar height indicates total hours monitoring effort per month, and the areas of light shading indicate number of hours during which killer whales were detected acoustically.

during similar times as AB and AJ pods, but AN whales were recorded less frequently. A comparison of the occurrence of the two clans during the “winter” periods (November-March) and “spring/fall” periods (April-May and September-October) revealed statistically significant differences (Yates $\chi^2 = 130.98$, $df = 1$, $p < 0.001$). Thus,

recordings during the November to March periods were dominated by AB clan whales (mostly AB, AJ, and AN pods), while AD clan whales (AD and AK pods) dominated the recordings during April and May (Figure 5). Within-clan differences in occurrence for the three commonly recorded AB clan pods (AB, AJ, and AN) were not significant,

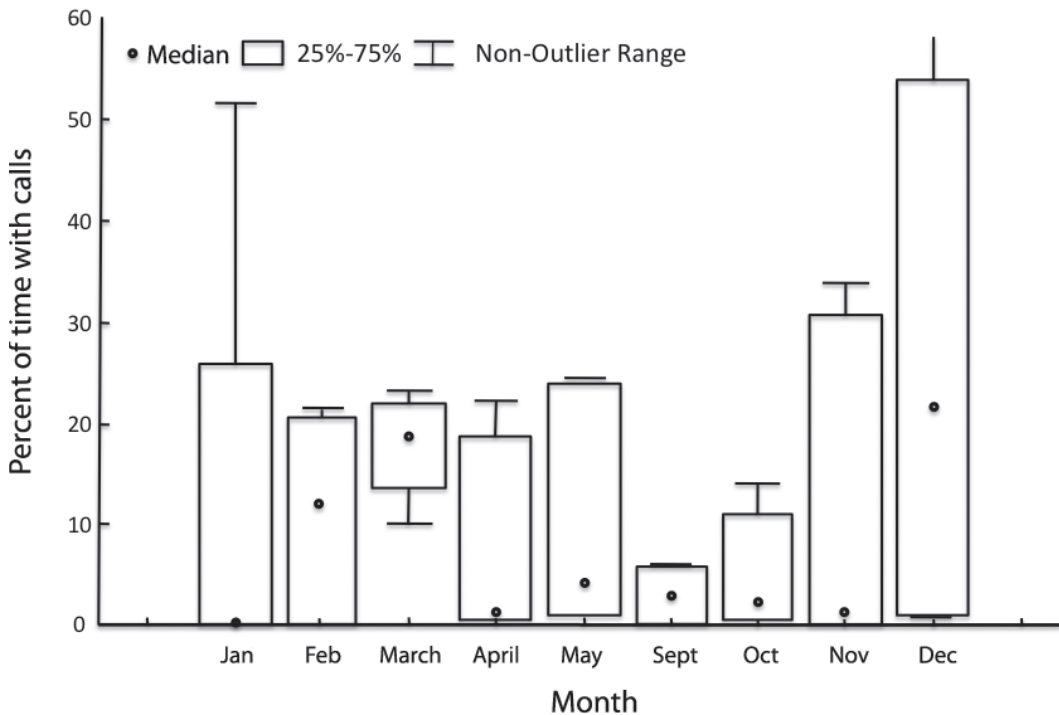


Figure 4. Percentage of monitored periods during which killer whales were detected acoustically by month for all years; the upper and lower limits of the boxes indicate the 3rd and 1st quartiles, respectively, and the bars indicate the range of 95% of the observations (not including outliers).

and AB pod was the most frequently recorded pod during the winter.

Sample size was too small for a statistical comparison of difference in occurrence of AD clan pods, and there was no obvious trend in occurrence among AD5 and AK pods between years other than the later arrival of AK pod (Figure 5). AD5 pod was the most commonly recorded pod from this clan and occurred about twice as often as AK pod (AD5 pod: 28 times; AK pod: 15 times). AD16 pod was recorded only once in May 2002.

Calls of two other groups were recorded as well but at much lower rates of occurrence. The resident killer whale pod AF (AB clan) was detected six times during the study period: once in March 2000, four times in December 2001, and once in May 2002. Transients from the AT1 population were detected four times during the study: once in November 2000, once in March 2002, once in December 2003, and finally in March 2004.

Discussion

Most remote acoustic monitoring of cetaceans has focused on determining species occurrence and relative regional and seasonal abundance (Stafford et al., 1998; Burtenshaw et al., 2004; Mellinger

et al., 2006; Moore et al., 2006). Remote acoustic monitoring of killer whales has differed from the typical application in that, for many studies, the focus was on determining group identity or inferring behavior (Bigg et al., 1987; Morton & Symonds, 2002; Newman & Springer, 2008). The remote acoustic monitoring of killer whales in Resurrection Bay was effective in determining not only the presence of killer whales but in identifying different killer whale assemblages, and in the case of resident killer whales, determining patterns of use for particular clans and pods over extended winter periods when vessel surveys are difficult. These distinctions are possible because killer whale matriline and pods maintain distinct call dialects (Ford & Fisher, 1983) that are passed between generations and are remarkably stable over periods of at least 50 y (Ford, 1991, 2002b).

In Johnstone Strait, BC, acoustic monitoring of killer whales with fixed hydrophones has helped researchers describe movements and communicative behavior of killer whales (Bigg et al., 1987; Deecke et al., 2000; Yurk et al., 2001; Weiß et al., 2007). In most cases, trained observers monitor the hydrophones in real time. However, in more recent projects, scientists (J. K. B. Ford, pers. comm., 2000, 2009) have applied automated killer

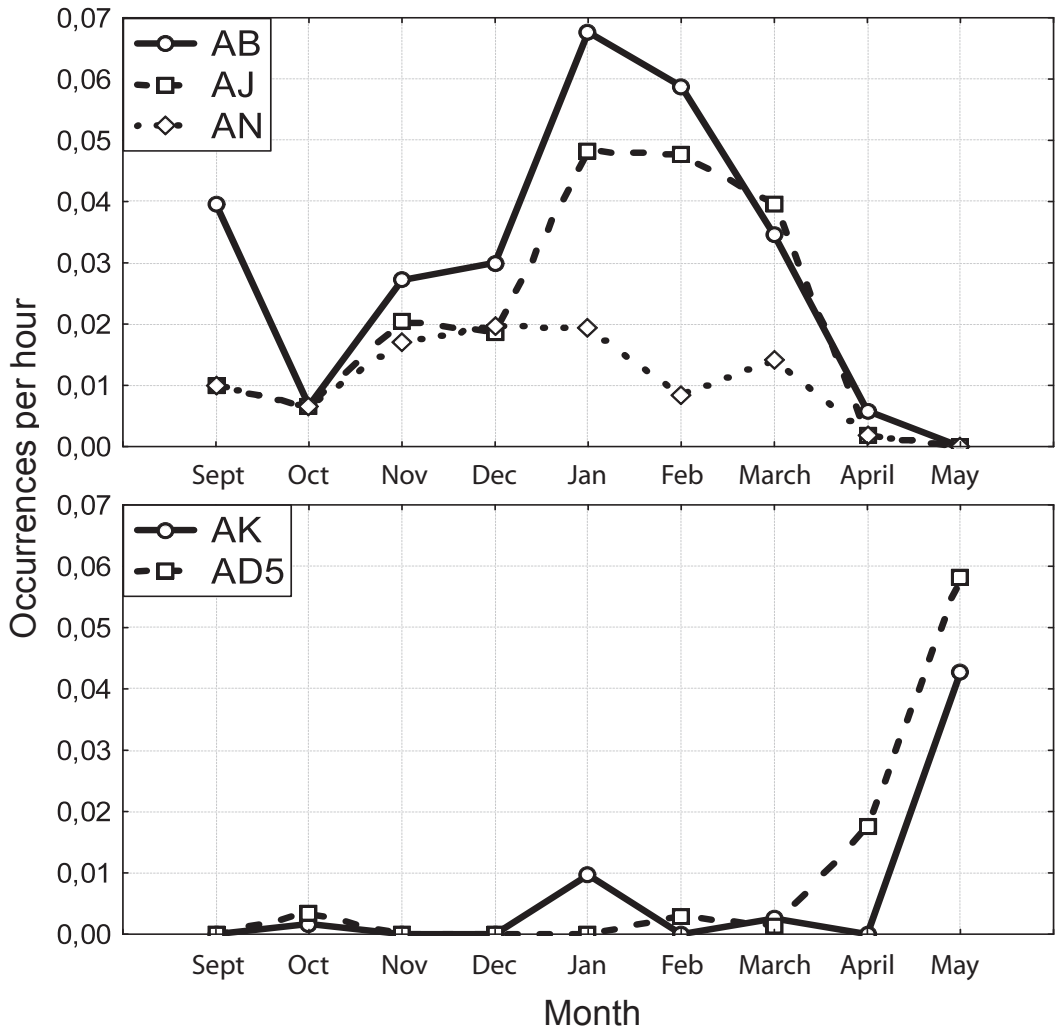


Figure 5. Number of acoustic detections of AB clan (top section) and AD clan (bottom section) whales per hour of monitoring in Resurrection Bay during 1999-2004

whale call recognition systems via cell-phone and long-term recording via fixed remote recording packages to remote acoustic monitoring of killer whales in British Columbia.

In this study, a single experienced observer (Michael Britton) monitored the hydrophone in real time and decided when to record vocalizations (Table 1). This eliminated potential inconsistencies in the ability of automated systems to recognize killer whale vocalizations in noisy environments. Calls of transient (mammal-eating) killer whales were recorded only four times during the 5 y of study. In all four cases, transient calls belonged to the AT1 transient population. This small population numbered 22 whales prior to the 1989 Exxon Valdez oil spill. It now contains

only seven individuals and is considered depleted under the Marine Mammal Protection Act (Matkin et al., 2008). Based on summer surveys, the AT1 range includes only the Prince William Sound/Kenai Fjords region (Saulitis et al., 2005). Data collected here extends our knowledge of AT1 winter distribution and indicates this pod might be found in the Kenai Fjords region year-round. The lack of recordings of the GOA transient population during this study could reflect their absence in Resurrection Bay during the monitoring period (September to May). GOA transients also tend to vocalize less frequently than AT1 transients (Saulitis et al., 2005) and might not have been detected by the hydrophone or observer. Also, the location of the hydrophone in this study may have

avored the recording of resident killer whales over transients, while placement of hydrophones elsewhere (e.g., near pinniped haulouts) might have yielded additional transient vocalizations.

For resident killer whales, the remote hydrophone data suggest that AB and AD clans segregate seasonally, with AB clan present in winter months and AD clan present in spring. Boat-based observations during the spring and early summer supported this segregation that was revealed by remote hydrophone monitoring. The AB clan pods identified by acoustic monitoring were absent from photographic data collected from the Kenai Fjords in May through early July with sporadic appearances that began at the end of July and continued on into the September/October period (Matkin et al., 2003; Matkin, unpub. data). Conversely, AD5 and AK pods (AD clan members) were regularly encountered in Kenai Fjords in May and early June. Although pods from these two acoustic clans are known to mix during the summer and fall months (Matkin et al., 1999, 2003), coinciding with the resident killer whale breeding season (Bigg et al., 1990), these study results suggest there is segregation at other times of the year. Mating is common between members of different clans (Barrett-Lennard, 2000); and to a lesser degree, it occurs between distantly related pods of the same clan (Yurk, 2005).

In this study area, Pacific salmon (*Onchorynchus* sp.) return to nearshore waters in the summer and early fall months, providing the primary prey for resident killer whales (Saulitis et al., 2000). This collection of prey might make large social aggregations possible. Prey availability is considerably reduced during the late fall and winter months when returning spawning salmon are not available. This may limit food sharing and cooperation to close relatives as expected under inclusive fitness theory (Hamilton, 1964), thereby explaining the winter segregation of killer whale clans. Chinook salmon (*O. tshawytscha*) are caught by sports fishermen in all months of the year in Resurrection Bay (D. Dubuc, pers. comm., 2007). However, in winter, they are the only salmon species available and are feeding in the area rather than returning to spawn. These "feeder" Chinook salmon might constitute a limited but important winter food source for resident killer whales. The seasonal exclusion of one clan from the area likely reflects inter-clan competition during periods of food shortage.

An even more interesting question presented by these findings is why one clan should have predominant use of the area during one seasonal period of resource limitation but leave Resurrection Bay when spawner Chinook salmon begin to return in the spring, thus allowing another clan to move into the area. One possible explanation for this pattern is that another as yet unidentified feeding

area is more productive than Resurrection Bay and therefore more attractive to AB clan whales in the spring season. In any case, the reduction of competition implied by sequential habitat use is consistent with resource partitioning by residents and transients, which also has the effect of limiting intergroup competition.

Remote hydrophone monitoring in winter months is an effective tool for assessing resident killer whale distribution in winter and assessing habitat use by specific pods and clans. A properly designed network of remote listening stations could be used to track the wide-ranging movements of resident pods and clans and potentially provide group specific data on important winter range and behavior.

Acknowledgments

Primary funding for this work was provided by the Alaska SeaLife Center, and monitoring equipment was provided by John Ford and the Cetacean Research Laboratory, Vancouver Aquarium Marine Science Centre. The microwave transmission station was designed by Daniel Zatz and maintained by Rich Kleinheader and Konrad Schaad of SeeMore Wildlife Systems. Acoustic analysis facilities were provided by the Vancouver Aquarium, and hydrophones were provided by Offshore Acoustics. Eva Saulitis provided review and comments.

Literature Cited

- Baird, R. W., & Whitehead, H. (2000). Social organization of mammal-eating killer whales: Group stability and dispersal patterns. *Canadian Journal of Zoology*, 78, 2096-2105.
- Barrett-Lennard, L. G. (2000). *Population structure and mating patterns of killer whales, Orcinus orca, as revealed by DNA analysis*. Ph.D. thesis in Zoology, University of British Columbia, Vancouver.
- Barrett-Lennard, L. G., Ford, J. K. B., & Heise, K. A. (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., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1987). *Killer whales: A study of their identification, genealogy and natural history in British Columbia and Washington State*. Nanaimo, BC: Phantom Press. 79 pp.
- Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb III, K. C. (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*, 383-405.
- Burtenshaw, J. C., Oleson, E. M., Hildebrand, J. A., McDonald, M. A., Andrew, R. K., Howe, B. M., et al.

- (2004). Acoustic and satellite remote sensing of blue whale seasonality and habitat in the Northeast Pacific. *Deep-Sea Research II*, 51, 967-986.
- Cummings, W. C., & Holliday, D. V. (1985). Passive acoustic location of bowhead whales in a population census off Point Barrow, Alaska. *The Journal of the Acoustical Society of America*, 78(4), 1163-1169.
- Deecke, V. B. (2003). *The vocal behaviour of transient killer whales (Orcinus orca) communicating with costly calls*. Ph.D. thesis in Biology, University of St. Andrews, St. Andrews, Scotland. 138 pp.
- Deecke, V. B., & Janik, V. M. (2006). Automated categorization of bioacoustic signals: Avoiding perceptual pitfalls. *The Journal of the Acoustical Society of America*, 119(1), 645-653.
- Deecke, V. B., Ford, J. K. B., & Slater, P. J. B. (2005). The vocal behaviour of mammal-eating killer whales: Communicating with costly calls. *Animal Behaviour*, 69(2), 395-405.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (1999). Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects. *The Journal of the Acoustical Society of America*, 105(4), 2499-2507.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Animal Behaviour*, 60(5), 629-638.
- Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, 67, 727-745.
- Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, 69, 1454-1483.
- Ford, J. K. B. (2002a). Killer whales. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *The encyclopedia of marine mammals* (pp. 669-676). New York: Academic Press.
- Ford, J. K. B. (2002b). Dialects. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *The encyclopedia of marine mammals* (pp. 322-323). New York: Academic Press.
- Ford, J. K. B. (2004). *The role of acoustics in defining killer whale populations and societies*. Paper presented at the Killer Whale Taxonomy Workshop, La Jolla, CA. 14 pp.
- Ford, J. K. B., & Fisher, H. D. (1983). Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. In R. Payne (Ed.), *Communication and behavior of whales* (pp. 129-161). Boulder, CO: Westview Press.
- Ford, J. K. B., Ellis, G. M., & Balcomb, K. C. (2000). *Killer whales: The natural history and genealogy of (Orcinus orca) in the waters of British Columbia and Washington*. (2nd ed.). Vancouver: UBC Press.
- Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S., & Balcomb III, K. C. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, 76, 1456-1471.
- Guinet, C. (1991). Comportement de chasse des orques (*Orcinus orca*) autour des îles Crozet. *Canadian Journal of Zoology*, 70, 1656-1667.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, 12, 1-52.
- Hoelzel, A. R., & Dover, G. A. (1990). Genetic differentiation between sympatric killer whale populations. *Heredity*, 66, 191-195.
- Hoelzel, A. R., & Osborne, R. W. (1986). Killer whale call characteristics: Implication for cooperative foraging strategies. In B. C. Kirkeveld & J. S. Lockard (Eds.), *Behavioral biology of killer whales* (pp. 373-403). New York: Alan R. Liss, Inc.
- Matkin, C. O., Ellis, G. M., Olesiuk, P., & Saulitis, E. L. (1999). Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound. *Fishery Bulletin*, 97(4), 900-919.
- Matkin, C. O., Barrett-Lennard, L. G., Yurk, H., Ellifrit, D., & Trites, A. W. (2007). Ecotypic variation and predatory behavior among killer whales (*Orcinus orca*) off the eastern Aleutian Islands, Alaska. *Fishery Bulletin*, 105, 74-87.
- Matkin, C. O., Saulitis, E. L., Ellis, G. M., Olesiuk, P., & Rice, S. D. (2008). Ongoing population level impacts on killer whales following the Exxon Valdez oil spill in Prince William Sound, Alaska. *Marine Ecological Progress Series*, 356, 269-281.
- Matkin, C. O., Ellis, G. M., Barrett-Lennard, L. G., Yurk, H., Saulitis, E. L., Scheel, D., et al. (2003). *Photographic and acoustic monitoring of killer whales in Prince William Sound and Kenai Fjords: Exxon Valdez Oil Spill Restoration Project final report*. Homer, AK: North Gulf Oceanic Society.
- Mellinger, D. K., Stafford, K. M., & Fox, C. G. (2006). Seasonal occurrence of sperm whale (*Physeter macrocephalus*) sounds in the Gulf of Alaska, 1999-2001. *Marine Mammal Science*, 20(1), 48-62.
- Miller, P. J. O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A*, 192, 449-459.
- Miller, P. J. O., & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, 60(5), 617-628.
- Moore, S. E., Stafford, K. M., Mellinger, D. K., & Hildebrand, J. A. (2006). Listening for large whales in the offshore waters of Alaska. *BioScience*, 56(1), 49-55.
- 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, Special Issue 12*, 245-248.
- Morton, A. B., & Symonds, H. K. (2002). Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, *Canada ICES Journal of Marine Science*, 59, 71-80.
- Newman, K., & Springer, A. M. (2008). Nocturnal activity by mammal-eating killer whales at a predation hot

- spot in the Bering Sea. *Marine Mammal Science*, 24(4), 990-999.
- Norris, T. F., McDonald, M., & Barlow, J. (1999). Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *The Journal of the Acoustical Society of America*, 106(1), 506-514.
- Saulitis, E. L., Matkin, C. O., & Fay, F. H. (2005). Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska. *Canadian Journal of Zoology*, 83, 1015-1029.
- Saulitis, E. L., Matkin, C. O., Barrett-Lennard, L. G., Heise, K., & Ellis, G. (2000). Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science*, 16(1), 94-109.
- Scheel, D., Matkin, C. O., & Saulitis, E. L. (2001). Distribution of killer whale pods in Prince William Sound, Alaska 1984-1996. *Marine Mammal Science*, 17(3), 555-569.
- Schevill, W. E., & Watkins, W. A. (1966). Sound structure and directionality in *Orcinus* (killer whale). *Zoologica*, 51, 70-76.
- Stafford, K. M., Fox, C. G., & Clark, D. S. (1998). Long-range acoustic detection and localization of blue whale calls in the northeast Pacific Ocean. *The Journal of the Acoustical Society of America*, 104(6), 3616-3625.
- Steiner, W. W., Hain, J. H., Winn, H. E., & Perkins, P. J. (1979). Vocalizations and feeding behaviour of the killer whale (*Orcinus orca*). *Journal of Mammalogy*, 60, 823-827.
- Stevens, T. A., Duffield, D. A., Asper, E. D., Hewlett, K. G., Bolz, A., Gage, L. J., et al. (1989). Preliminary findings of restriction fragment differences in mitochondrial DNA among killer whales. *Canadian Journal of Zoology*, 67, 2592-2595.
- Weiß, B. M., Symonds, H. K., Spong, P., & Ladich, F. (2007). Intra- and intergroup vocal behaviour in resident killer whales, *Orcinus orca*. *The Journal of the Acoustical Society of America*, 122(6), 3710-3716.
- Yurk, H. (2005). *Vocal culture and social stability in resident killer whales (Orcinus orca)*. Ph.D. thesis in Zoology, University of British Columbia, Vancouver. 126 pp. Retrieved February 23, 2010, from www.marine-mammal.org/pdfs/Yurk%202005.pdf.
- Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, 63(6), 1103-1119.
- Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B., Spong, P., Symonds, H. K., Matkin, C. O., et al. (2001). Remote acoustic monitoring of killer whales: Advantages and current limitations. *14th Biennial Conference of the Biology of Marine Mammals*. Vancouver, BC: Society for Marine Mammalogy.