

# Variation in call pitch among killer whale ecotypes

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Vocal structure can vary between populations due to variation in ecology-dependent selection pressures, such as masking by background noise and the presence of eavesdroppers. Signalers can overcome these obstacles to effective communication by avoiding frequencies that overlap with background noise or the audible range of eavesdroppers. In the Northeastern Pacific three “ecotypes” of killer whale coexist in sympatry, but differ from one another in their diet and habitat use. The minimum frequency ( $F_{\min}$ ) and the frequency containing the peak energy between 0 and 10 kHz ( $F_{\text{peak}}$ ) of a random sample of calls produced by a population of each ecotype was measured. The offshore ecotype produced calls with a significantly higher  $F_{\min}$  than the other ecotypes, which could be a strategy to avoid masking by low frequency chronic bandlimited wind noise found in the offshore environment. The resident ecotype produced calls with a significantly higher  $F_{\min}$  and  $F_{\text{peak}}$  than the transient ecotype. This could be to reduce detection by their salmonid prey, which has a narrow band, low frequency auditory range.

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## I. INTRODUCTION

Variation in vocalization structure can occur between populations or groups of the same species due to ecological differences such as background noise levels or habitat-dependent transmission properties, or the auditory range of eavesdropping competitors, predators, or prey (Hunter and Krebs, 1979; Rydell and Arlettaz, 1994; Slabbekoorn and Peet, 2003). Vocalizations may then undergo functional selection as the acoustic properties of an environment may favor vocalizations with particular characteristics, e.g., adjusting the frequency range of a signal so that it does not overlap with the frequency band of background noise or the auditory range of eavesdroppers (Rydell and Arlettaz, 1994; Slabbekoorn and Peet, 2003). In this study we compare the frequency parameters of calls produced by three sympatric killer whale ecotypes that differ in prey and habitat preference.

Three ecotypes of killer whale occur in sympatry in the Northeastern Pacific. The resident ecotype specializes in foraging on salmonid species; the transient ecotype specializes in foraging for marine mammals (Ford *et al.*, 1998; Saulitis *et al.*, 2000; Herman *et al.*, 2005). The majority of sightings of these two ecotypes are predominantly in coastal waters, however sightings are biased toward the summer months and less is known about their winter distribution (Ford *et al.*,

2000). Lastly the offshore ecotype, thought to be primarily piscivorous (Herman *et al.*, 2005; Krahn *et al.*, 2007), is most commonly sighted 15 km or more offshore and rarely found in coastal waters (Ford *et al.*, 2000). Each ecotype is distinct from the other two in both genotype (Hoelzel *et al.*, 1998; Barrett-Lennard, 2000) and phenotype (Ford *et al.*, 2000).

Killer whales maintain contact with conspecifics using stereotyped broadband calls (Ford, 1989). Call types are distinguishable by the frequency modulation contours (Ford, 1989; Deecke *et al.*, 1999; Yurk *et al.*, 2002). Calls have the potential to convey information on signaler’s sex, matriline and pod identity, behavioral state, direction of travel, and distance relative to the receiver (Ford, 1989, 1991; Deecke *et al.*, 2000; Miller and Bain, 2000; Miller, 2002; Nousek *et al.*, 2006; Miller *et al.*, 2007). There is strong evidence that call types are learned (Deecke *et al.*, 2000; Yurk *et al.*, 2002; Foote *et al.*, 2006). Call type dialects are found both within and between populations (Ford, 1991).

Previous studies have investigated variation in the acoustic behavior of resident and transient killer whales due to differences in the eavesdropping ability of their preferred prey species (Barrett-Lennard *et al.*, 1996; Deecke *et al.*, 2005). Background noise is another potential source of ecology-dependent variation in killer whale call structure. The character of ambient noise is likely to vary between the coastal and offshore habitats as it is highly correlated with wind speed (Knudsen *et al.*, 1948; Wenz, 1962; Wille and Geyer, 1984). In this study we compare the minimum frequency and the frequency of peak energy between 0 and 10 kHz of calls produced by pods from each ecotype and discuss how variation may relate to ecological variables such as background noise or the presence of eavesdroppers.

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## II. METHODS

### A. Killer whale recordings

Recordings were collected from three populations of killer whale from the eastern North Pacific, one of each ecotype (transient, resident, and offshore). Recordings were made using a variety of recording devices, but all with a flat response between 0.1 and 10 kHz, the range in which all measured minimum frequencies fell.

The Southern Resident population is commonly sighted in the coastal waters of Washington State and British Columbia during the summer months, their winter distribution is known to range between Monterey Bay, CA and the Queen Charlotte Islands, BC. The population consists of three pods, J, K, and L pods, each of which has a distinctive call type repertoire (Hoelzel and Osborne, 1986; Ford, 1987, 1991). They share no call types in common with any other killer whale population in this study (Ford, 1987, 1991). A database of 278 recordings was analyzed from Haro Strait, WA and the neighboring waterways. Individual calls were isolated and saved as separate sound files. Thirty soundfiles of individual calls were then selected randomly, these were checked to confirm that the quality of the recording and signal-to-noise ratio was sufficient for measurements to be made and where this was not the case replacement soundfiles were chosen, also at random.

The West Coast Transient population is found from California to Southeast Alaska (Ford and Ellis, 1999). The West Coast Transient population has a single call type repertoire; however there are regional variations in call type usage (Deecke, 2003). They share no call types in common with any other killer whale populations in this study (Ford, 1987). Our recordings of the West Coast Transient population were also from Haro Strait, WA and neighboring waterways, a database of six recordings were analyzed and calls were isolated and selected in the same way as for the Southern Resident Population.

The offshore ecotype also has a large home range, and individuals sighted off the California coast have been resighted in the Bering Sea (Krahn *et al.*, 2007). A database of four recordings, from nonconsecutive encounters, totaling 81 min from relatively infrequent encounters with this ecotype in the coastal waters of Johnstone Strait, BC were analyzed. Three recordings were made in the same week, although on separate days, and were thus likely to be of the same group. Calls were isolated and selected as noted earlier. As recordings of all three ecotypes were made in the coastal waters around Vancouver Island during summer months, background noise levels should be similar in frequency characteristics and the suitability of calls for analysis based on their signal-to-noise ratio should be the same for all three ecotypes.

### B. Ecological variables

As the offshore killer whales were recorded during rare incursions into coastal waters, it was inappropriate to take the background noise levels from these recordings. Ambient noise levels and spectral profiles were measured from a coastal site (Haro Strait; 48°30'N, 123°08'W) and an off-

shore site (Bering Sea; 56°51'N, 164°03'W) using PAL (Passive Aquatic Listeners) recorders (Ma and Nystuen, 2005). The Haro Strait PAL was deployed from May to September 2005 in approximately 30 m of water. This location is a critical habitat for the Southern Resident population of killer whales (Ford *et al.*, 2000), and the whales were regularly sighted during the deployment period. This area is also commonly used by West Coast Transients during this period (Baird and Dill, 1995). The Bering Sea PAL was deployed May–September 2004 in approximately 70 m of water, offshores have been sighted in this area at this time of year (Zerbini *et al.*, 2007). Each PAL consisted of a low-noise wideband hydrophone (either an ITC-8263 or a Hi-Tech-92WB), signal preamplifier, and a recording computer (Tattletale-8). The nominal sensitivity of these instruments was  $-160$  dB relative to  $1 \text{ V}/\mu\text{Pa}$  and the equivalent oceanic background noise level of the preamplifier system is about 28 dB relative to  $1 \mu\text{Pa}^2 \text{ Hz}^{-1}$ . Bandpass filters were present to reduce saturation from low frequency sound (high pass at 300 Hz) and aliasing from above 50 kHz (low pass at 40 kHz). The PAL sampled at fixed intervals resulting in a time series of spectral level at 2 kHz, to coincide with the omnidirectional component of killer whale calls.

Audiograms of key prey species were taken from the literature and compared with the mean minimum frequency from the 30 calls measured. The current published data on the predominant species that constitute the diet of offshore killer whales are not as detailed as for the other two ecotypes. Therefore we focused only on transient and resident killer whales. Resident killer whale calls were compared with an audiogram for Atlantic Salmon *Salmo salar* (Hawkins and Johnstone, 1978) as a literature search found no audiogram for Chinook salmon *Oncorhynchus tshawytscha*, the preferred prey species of the Southern Resident population based on observations, prey fragment sampling, and stomach contents analyses (Ford *et al.*, 1998; Ford and Ellis, 2006). Transient killer whale calls were compared with audiograms for the harbor porpoise *Phocoena phocoena* (Kastelein *et al.*, 2002), and harbor seal *Phoca vitulina* (Kastak and Schusterman, 1998), their two most common prey species based on observation and stomach contents analyses (Baird and Dill, 1996; Ford *et al.*, 1998).

### C. Acoustic and statistical analysis

Recordings were digitized using Soundforge software at 44.1 kHz and analyzed using Canary 1.2.4. Spectrograms and energy spectra were produced with a filter bandwidth of 88.24, FFT size 1024, and 87.5% overlap. We measured  $F_{\min}$ : the lowest frequency on the spectrogram, and  $F_{\text{peak}}$ : the frequency with highest amplitude between 0 and 10 kHz. Using the measurement panel in Canary, we were able to measure frequency parameters to a resolution of 0.01 kHz. We used analysis of variance (ANOVA) tests to compare the  $F_{\min}$  and  $F_{\text{peak}}$  of the call samples from each population (Fig. 1).

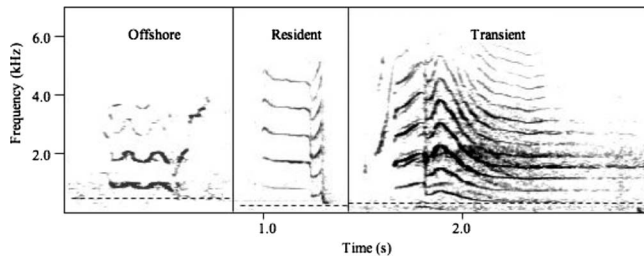


FIG. 1. Spectrograms of examples of calls of each ecotype of NE Pacific killer whale (filter bandwidth of 88.24, FFT size 1024, 87.5% overlap). Dashed lines indicate the  $F_{\min}$  variable measured.

### III. RESULTS

#### A. Frequency variation between ecotypes

Our selection of 30 resident calls was extracted from 28 recordings from nonconsecutive encounters totaling 512 min, and calls from all 3 pods (J, K, and L) were included. The selection of 30 transient calls came from 6 recordings, each from nonconsecutive encounters totaling 219 min. Last, 30 offshore calls were selected from 4 recordings totaling 80 min. There was significant variation between the three ecotypes in mean  $F_{\min}$  (ANOVA:  $F_{2,87}=38.23$ ,  $p < 0.0001$ ; Fig. 2). A post hoc  $t$ -test indicated the offshore ecotype produced calls with a significantly higher minimum frequency ( $\bar{x} \pm SE = 0.89 \pm 0.24$  kHz,  $N=30$ ) than the resident ( $\bar{x} \pm SE = 0.55 \pm 0.33$  kHz,  $N=30$ ;  $t=4.738$ ,  $p < 0.0001$ ) and transient ecotypes ( $\bar{x} \pm SE = 0.34 \pm 0.06$  kHz,  $N=30$ ;  $t=12.141$ ,  $p < 0.0001$ ). The difference between the resident and transient mean  $F_{\min}$  was also significant ( $t=3.014$ ,  $p=0.0038$ ). There was also significant variation in the  $F_{\text{peak}}$  between ecotypes ( $F_{2,87}=4.511$ ,  $p=0.014$ ; Fig. 2). A post hoc  $t$ -test showed that the resident ecotype mean  $F_{\text{peak}}$  ( $\bar{x} \pm SE = 1.88 \pm 1.02$  kHz) was significantly higher than the mean  $F_{\text{peak}}$  of the transient ecotype ( $\bar{x} \pm SE = 1.28 \pm 0.42$  kHz;  $t=2.919$ ,  $p=0.0042$ ) but not the offshore ecotype mean

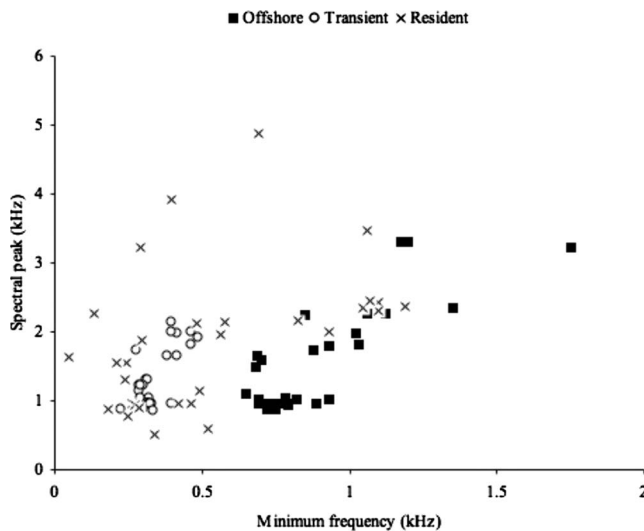


FIG. 2.  $F_{\min}$  (the lowest frequency detectable on the spectrogram) plotted against  $F_{\text{peak}}$  (the frequency with highest amplitude between 0 and 10 kHz) of a random sample of 30 calls each recorded from resident, transient, and offshore Pacific killer whale ecotypes.

TABLE I. Sound budgets from nearshore and offshore sites. Peaks represent short transient sounds such as whale calls.

	Dominant sound source (% of time present)				
	Ships	Wind	Rain	Peaks	
Nearshore Pacific (Haro Strait)	23	53	8	12	
Offshore Pacific (Bering Sea)	1	85	6	7	
	Sound pressure density spectrum levels 2 kHz (db relative to $1 \mu\text{Pa}^2 \text{Hz}^{-1}$ )				
	Ships	Wind	Rain	Peaks	Mean
Nearshore Pacific (Haro Strait)	$63 \pm 7$	$55 \pm 6$	$58 \pm 8$	$59 \pm 8$	$58 \pm 8$
Offshore Pacific (Bering Sea)	$72 \pm 5$	$60 \pm 7$	$64 \pm 6$	$62 \pm 7$	$60 \pm 8$

$F_{\text{peak}}$  ( $\bar{x} \pm SE = 1.55 \pm 0.76$  kHz;  $t=1.421$ ,  $p=0.161$ ). There was also no significant difference between the transient and offshore mean  $F_{\text{peak}}$  ( $t=1.703$ ,  $p=0.0939$ ).

#### B. Ecological correlates

By examining the spectral characteristics of the sound, it was possible to identify the source (see Ma and Nystuen, 2005) and produce a sound budget for each location, including the percentage of time that a particular source is present and the loudness of that source (Table I). The mean ambient noise levels were higher overall at the offshore site and wind noise was the main contributor and almost constant. Wind noise was only present at the coastal site approximately half of the time and then was lower in sound level than the offshore site. The noise from nearby ships were the loudest events detected and broadband in frequency range, this loud, broadband noise source was present more of the time in the coastal site, but was temporally variable. The higher  $F_{\min}$  of the offshore ecotype would therefore be consistent with the hypothesis that persistent low frequency ambient noise will select for higher pitch calls. However this is not the case for our measurements of  $F_{\text{peak}}$ .

Although the mean minimum frequency of resident killer whale calls was above the auditory range of salmonids, the  $F_{\min}$  ranged to as low as 0.13 kHz and a number of calls overlapped with the peak hearing range of salmonids (Hawkins and Johnstone, 1978; Fig. 3). However even the minimum  $F_{\text{peak}}$  (0.508 kHz) measured from the 30 resident calls was above the auditory range of salmonids (0.03–0.40 kHz; Hawkins and Johnstone, 1978). All the measured  $F_{\min}$  and  $F_{\text{peak}}$  values for transient killer whale calls overlapped with the hearing range of harbor seal and harbor porpoise, their preferred marine mammal prey (Fig. 3).

### IV. DISCUSSION

Interpopulation variation in  $F_{\min}$  could have resulted from a number of factors and could be functional or an epiphenomenon of the learning process (Slater, 1986, 1989). For example this variation could facilitate population identity

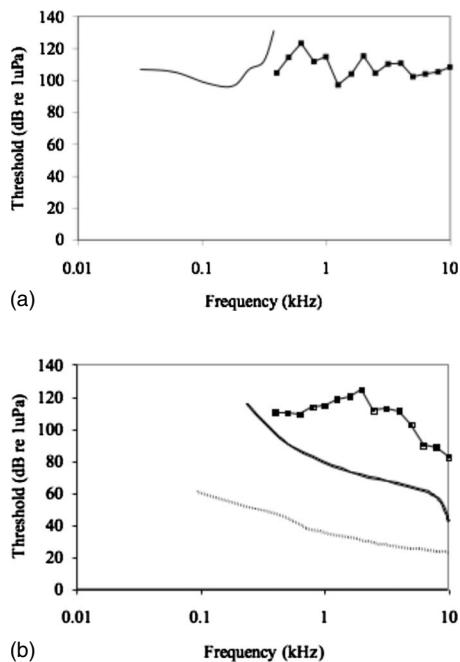


FIG. 3. (a) Audiogram of the Atlantic salmon *Salmo salar* (Hawkins and Johnstone, 1978) and one-third octave received levels (dB) up to 10 kHz of the most common resident call type (SI) from our sample, estimated to have been recorded <500 m from source based on surface observations, and on-axis based on the number of visible harmonics (see Miller, 2002). (b) Audiogram up to 10 kHz of the harbor porpoise *Phocoena phocoena* (solid line; Kastelein *et al.*, 2002), and harbor seal *Phoca vitulina* (dashed line; Kastak and Schusterman, 1998), and one third octave received levels (dB) of the most common transient call (WCT07) from our sample, estimated to have been recorded <500 m from source based on surface observations and on-axis based on the number of visible harmonics (see Miller, 2002).

(Yurk, 2005). However, the frequency modulations of call types within pod specific call type repertoires achieve this regardless of the frequency range of the fundamental (Yurk *et al.*, 2002). The structure of killer whale call types is known to shift randomly over time by a drift mechanism (Deecke *et al.*, 2000), which could lead to interpopulation variation in  $F_{\min}$ . However, the range of  $F_{\min}$  from published call type repertoire catalogues of other resident ecotype populations is very consistent in their  $F_{\min}$ , e.g., Kamchatka Residents  $0.5 \pm 0.2$  kHz (Filatova *et al.*, 2004), Northern Residents  $0.4 \pm 0.3$  kHz, Southern Residents  $0.5 \pm 0.3$  kHz (Ford, 1987) and similar to our random 30 calls from the Southern Resident population. This suggests that some common ecological or contextual factor may have led to directional convergence in  $F_{\min}$ .

Although ambient noise is likely to vary greatly spatially and temporally due to local conditions and our two sites are not expected to be representative, generic coastal and offshore sites, our measurements do conform to the general prediction that offshore waters will have higher levels of low frequency noise due to wind noise (Knudsen *et al.*, 1948; Wenz, 1962; Urick, 1983; Wille and Geyer, 1984). Wind noise is frequency dependent, decreasing 5 dB per octave with increasing frequency between 0.5 and 5.0 kHz (Wenz, 1962), therefore the offshore into ecotype's use of high pitch calls, in terms of  $F_{\min}$ , may avoid masking by low frequency wind noise. A previous comparison of the calls recorded

from killer whales in the high ambient noise waters of the Ross Sea (Urick, 1983) found they were higher in minimum frequency than Pacific Resident calls (Awbrey *et al.*, 1982) and that Ross Sea killer whales seasonally use an "acoustical niche" outside the frequency range of leopard seal vocalizations (Mossbridge *et al.*, 1999). Inter and intraspecies comparisons of other odontocetes have also found that offshore species or populations have higher pitched whistles and concluded that this may be to reduce masking by ambient noise (Ding *et al.*, 1995a, b). However, this does not explain the significant difference in  $F_{\min}$  between the resident and transient ecotypes, which are both found in coastal waters such as Haro Strait. Additionally, the full range of each ecotype is not fully known and resident and transient ecotypes may spend more time in offshore waters during the winter when there are fewer sightings in nearshore waters (Ford *et al.*, 2000).

Ship noise was the loudest sound source in both environments and was more persistent in the coastal environment (Table I). However, ship noise, although most intense at low frequencies, can be broadband between 0 and 10 kHz and could mask the entire omnidirectional component of killer whale calls (Bain and Dahlheim, 1994). A change in frequency would therefore not compensate for such broadband masking. Foote *et al.* (2004) reported an antimasking strategy of increasing call duration in the presence of boat noise by killer whales, which had developed within a decade concurrent to an increase in vessel traffic. They suggested that this would decrease call detection and perception thresholds through increased redundancy. Any vocal response may therefore depend upon both the temporal (e.g., transient or chronic) and spectral properties (e.g., narrowband or broadband, low or high frequency) of noise.

Deecke *et al.* (2005) reviewed the costs and limitations to transient killer whales of producing call types outside the broadband auditory range of their main prey species, which included the increased attenuation of higher frequencies and the reduced directionality of low frequencies. The first of these costs would be negligible if resident killer whales produced calls not overlapping with the low-frequency narrowband hearing range of salmonids (Hawkins and Johnstone, 1978), and may explain the difference in  $F_{\min}$  between the resident and transient calls. Some resident killer whale calls did contain energy below 400 Hz, which would therefore be detectable by salmonids, at least at close range, but calling while foraging does not appear to be constrained in resident killer whales (Deecke *et al.*, 2005). Frequency is just one factor when considering the active space of a signal, the hearing threshold of the receiver is also important. Salmonids have poor hearing even at the peak of their audible range (Hawkins and Johnstone, 1978) and the distance over which salmonids can detect killer whale calls would be considerably less than marine mammals. As our recordings were not made with a calibrated hydrophone and the exact distance between the signaler and hydrophone were not known, it is not possible to precisely quantify the distance that salmon could detect a resident killer whale calls. However, Fig. 3 indicates that within approximately 500 m, detection

of resident killer whale calls would be limited by the hearing threshold in salmonids but easily detectable by harbor porpoise *Phocoena phocoena* and harbor seal *Phoca vitulina*. The higher  $F_{\text{peak}}$  of resident calls compared to transient calls may also be a strategy to reduce detection by salmonid prey. However the ratio of energy in the first two harmonics can be sex-dependent (Miller *et al.*, 2007), therefore, differences between ecotypes in  $F_{\text{peak}}$  in our samples could be due to a bias in recording predominantly calls produced by adult male residents and female transients (see Miller *et al.*, 2007).

Differences between habitats in wind noise or the selection pressure from eavesdropping prey would be consistent over time scales that would allow genotypic selection of call frequency. However, the plasticity of killer whale vocal behavior (Foote *et al.*, 2004, 2006) would enable call structure to be changed over ontogenetic time scales. Active selection of the vocal repertoire could be rapidly achieved by the dropping of call types with lower frequencies and increasing the usage of call types with higher frequencies, or by a spectral shift of existing call types.

Future recordings using multihydrophone arrays to localize the individual calling will help to control for potentially confounding variables such as sex, body size, and context, which we were unable to account for. Further within-population comparisons between recordings with different background noise levels may also reveal short-term changes to call structure in response to temporal variations in ambient noise, such as that noted by Foote *et al.* (2004), to boat noise. Combining recordings of killer whales with known dietary specialization and measurements of ambient noise, as we have done in this study, from new locations would help further understand the role of ecology in shaping killer whale call structure.

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