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Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations

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Abstract Signal source intensity and detection range, which integrates source intensity with propagation loss, background noise and receiver hearing abilities, are important characteristics of communication signals. Apparent source levels were calculated for 819 pulsed calls and 24 whistles produced by free-ranging resident killer whales by triangulating the angles-of-arrival of sounds on two beamforming arrays towed in series. Levels in the 1–20 kHz band ranged from 131 to 168 dB re 1 μ Pa at 1 m, with differences in the means of different sound classes (whistles: 140.2 ± 4.1 dB; variable calls: 146.6 ± 6.6 dB; stereotyped calls: 152.6 ± 5.9 dB), and among stereotyped call types. Repertoire diversity carried through to estimates of active space, with “long-range” stereotyped calls all containing overlapping, independently-modulated high-frequency components (mean estimated active space of 10–16 km in sea state zero) and “short-range” sounds (5–9 km) included all stereotyped calls without a high-frequency component, whistles, and variable calls. Short-range sounds are reported to be more common during social and resting behaviors, while long-range stereotyped calls predominate in dispersed travel and foraging behaviors. These results suggest that variability in sound pressure levels may reflect diverse social and ecological functions of the acoustic repertoire of killer whales.

Keywords Communication · Ecology · Whistle · Pulsed call · Repertoire

Abbreviations SL: Source level · RL: Received level · SNR: Signal-to-noise ratio · TL: Transmission loss

Introduction

The amplitude at which a signal is produced, or source level, is of fundamental importance in communication systems, and acoustic signals have the potential to be produced over a wide range of levels (Loftus-Hills and Littlejohn 1971; Gerhardt 1975; Prestwich et al. 1989; Cynx et al. 1998; Bradbury and Vehrencamp 1998; Brumm 2004). For a signaler to benefit from an information transfer, it must produce signals at a sufficient level for an intended receiver to detect and decode the signal. However, signal levels attenuate during transmission from the source to the receiver, which must detect the signal in the presence of competing background noise. The benefits of information transfer, therefore, select for higher amplitude signals because they are more likely to be detected and decoded by an intended receiver (Wiley and Richards 1982). Energetic costs and the increased risk of detection by predators, prey, or social competitors are factors that may select for less intense signals (Prestwich et al. 1989; Ryan et al. 1982; Dabelsteen and Pedersen 1990; McGregor and Dabelsteen 1996).

Apparently in response to these balancing selective pressures, signals appear to be produced at the appropriate intensity for typical distances to target or intended receivers (Wiley and Richards 1982). Certain signal types within a repertoire may be selected to cover a large area while others function over short ranges, reflecting the context and motivation of the signaler (Rowell and Hinde 1962; Dittus 1988; Marten et al. 1977). Blackbirds (*Turdus merula*) switch from loud song to a quieter version of song in close range threat interactions with intruders (Dabelsteen and Pedersen 1990). Several recent studies have also shown that songbirds and non-human primates do not routinely maximize the amplitude of

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their songs, but adjust the source level in response to background noise (Sinnot et al. 1975; Cynx et al. 1998; Brumm and Todt 2002; Pytte et al. 2003; Brumm et al. 2004) and social competitors (Brumm and Todt 2004).

The range over which a signal can be detected, or 'active space', is not solely a function of its source level, but also the transmission loss the signal suffers between the signaler and the receiver as well as the detection threshold of the receiver in varying levels of background noise. Therefore, variation in source level cannot be assumed to directly result in a matching shift in active space. Techniques for estimating active space have been used for the territorial song display of the red-wing blackbird (*Agelaius phoeniceus*), which is produced at a level sufficient to be heard by neighboring red-wing blackbirds over a range of about two territories away (Brenowitz 1982). The active space of bottlenose dolphin (*Tursiops truncatus*) whistles is estimated to be much larger than that of bird song, partly due to reduced sound absorption in seawater (Janik 2000). Efficient acoustic signal propagation increases the potential for large communication networks to exist in the marine environment (Myrberg 1980; Janik 2005).

The goal of this study was to measure the sound pressure levels of pulsed calls and whistles produced by free-ranging resident killer whales, and estimate the maximum range they might be detected by conspecifics in different background noise conditions. Estimating active space links physiological measures of sound production and reception with acoustical ecology and habitat to quantitatively predict the distances over which social communication might take place. Because the active space of a signal relates to its function, analysis of source level and/or active space can be a useful tool to elucidate the function of signals in a repertoire (e.g. Marler 1973; Dittus 1988).

The vocal repertoire of killer whales consist of various burst-pulse calls and whistles (Schevill and Watkins 1966; Watkins 1967; Ford 1989; Ford 1991; Thomsen et al. 2001). The evidence is mixed whether the various signal types in the repertoire of resident killer whales reflect the activities or motivations of signalers, as is documented for many primate sounds (Dittus 1988; Hauser and Marler 1993). No whistle or call type correlates exclusively with any particular activity, but relative production rates of different call types and whistles vary with broad behavior metrics of the entire group (Bain 1986; Morton et al. 1986; Ford 1989; Thomsen et al. 2002). If the various sound types in the killer whale repertoire primarily serve a contact function of signaling group membership, as proposed by Ford (1989, 1991), one might expect little variation in the estimated active space of different sound types in the repertoire. Conversely, if sound-type production reflects the behavioral context or motivation of the signaler (Bain 1986; Morton et al. 1986; Ford 1989; Thomsen et al. 2002), one may expect to find diversity in the estimated active space of types depending on the context or behavioral state in which they tend to be produced.

To measure the source intensity of a sound, it is necessary to measure the received sound pressure level of a signal and estimate its transmission loss from the source, which (at short ranges) is primarily a function of range. An established approach is to use multiple hydrophones to measure the range from the source to a calibrated receiver (Watkins and Schevill 1974; Watkins et al. 1997; Cato 1998; Janik 2000; Möhl et al. 2000). With this technique, source levels can be measured during normal behavior, although it can be difficult to observe the orientation of underwater signalers to measure to control for signal directionality. Killer whale calls are directional at higher frequencies (Miller 2002; Schevill and Watkins 1966; Bain and Dalheim 1994), so the received level of a sound depends on the orientation of the signaler. The term "apparent source level", used here, refers to source levels measured when signaler orientation is not known (Madsen et al. 2004). To measure apparent source levels of weak signals, the hydrophones must be positioned near the signaler and have a small inter-hydrophone spacing (e.g. Watkins et al. 1997). Such a small array, if immobile, will have a small coverage area through which animals could pass quite quickly. Larger arrays allow greater spatial coverage, but can only localize relatively intense sounds (e.g. Möhl et al. 2000). In such a case, mean source level represents only a mean of relatively intense sounds, depending on the array geometry (e.g. Janik 2000). To statistically examine the apparent source levels and estimated active space of sounds over a wide range of levels, I employed a novel towed two-beamformer array design that can be towed near animals, allowing a large 'coverage' area with a small (97 m) aperture array.

Materials and methods

Recordings were conducted in Johnstone Strait on September 1 and 7, 1998 while killer whales from several different pods were present. All recordings were taken in low noise conditions: sea state zero with no other vessels within a kilometer of the animals. The recording system consisted of two evenly spaced 8-element (2.6 m) beamforming arrays that were towed in series with an inter-array spacing of 97 m (Fig. 1). The arrays were towed parallel to the direction of movement of the whales at minimum speed (~1.5 m/s) to minimize noise generated by the ship. The signal from each hydrophone was recorded on a channel of two synchronized 16-bit Tascam 8-track digital recorders.

Data from the recorders were digitally transferred as wav files into computer using a precision conversion system that maintains channel synchronization on a sample-by-sample basis across both recorders. Signal analysis was carried out using custom Matlab software (see Miller and Tyack 1998 for details). The analog-signal to wav-file conversion was calibrated using tones measured on a calibrated LeCroy 9314AM oscilloscope. The hydrophone elements were Benthos AQ-2S hydro-

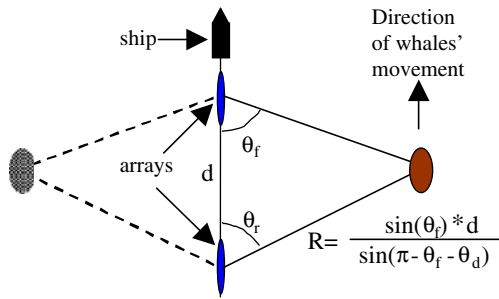


Fig. 1 Schematic of the research vessel and two-array system used to make calibrated recordings. Range from the rear array to a sound source is calculated using measured angles (θ , in radians) and the inter-array separation (d), which was 97 m. The *dashed lines* and lighter oval illustrate the consistency of the range estimate despite the left-right (and depth) ambiguity of the linear arrays

phones (nominal sensitivity: $-195 \text{ dBV}/\mu\text{Pa}$) attached to a custom WHOI preamp (43 dB gain flat from 100 Hz to 200 kHz).

The sensitivity of one hydrophone in the rear array was calibrated in-situ using a Brüel and Kjær (B&K) 8105 hydrophone and a B&K 2635 preamp set at a sensitivity of $-160 \text{ dBV}/\mu\text{Pa}$. The B&K hydrophone was attached next to the array hydrophone, and several loud sources were used to measure its sensitivity relative to the calibrated hydrophone. The relative sensitivities of the remaining elements were measured using a transient sound containing broadband energy from 1 to 20 kHz produced over 100 m from the array. The resulting measured sensitivity of $-152.7 \text{ dBV}/\mu\text{Pa}$ was consistent across hydrophones and closely matched the expected sensitivity based upon separate calibration of the pre-amplifiers and the nominal sensitivity of the hydrophones.

All whale sounds with a received sound pressure level at least 3 dB above background noise on the rear array were extracted from the recordings and a calibrated received spectrum was calculated from 1 to 20 kHz in 1/3-octave bands. One-third octave bands were used because they represent the logarithmic shape of auditory filters in the mammalian ear (Fletcher 1940). Calibrated spectra were calculated from the most intense subsection of each sound, and portions of the sound that were overlapped by extraneous sounds (such as echolocation clicks) or that were attenuated by surface diffraction were not included. The subsection used for the analysis was always greater than 100 ms in duration. The +3 dB criteria was implemented by assessing the background noise level just prior to the signal onset, and discarding signals where signal plus noise levels were < 5 dB greater than noise levels alone. The low-frequency cutoff of 1 kHz was chosen because killer whale hearing is much less sensitive below 1 kHz (Hall and Johnson 1972; Symanski et al. 1999), there is little energy in killer whale sounds below 1 kHz (Fig. 1; Ford 1987), and it is desirable to eliminate the low-frequency noise below 1 kHz in calculating RL. The high-frequency cutoff of

20 kHz bounded a 1/3-octave band and was chosen to reduce the effects of filter roll-off near the Nyquist frequency of 24 kHz.

Sounds were classified as whistles or calls based upon their harmonic structure (Watkins 1967). Calls were further classified to call type (Fig. 2; Ford 1987, 1991; Miller and Bain 2000). Any calls that did not clearly fall into one of the types described by Ford (1987) were classified as 'variable' calls.

Source level calculation

The source level (SL) in dB re $1 \mu\text{Pa}$ at 1 m of each sound was calculated as:

$$\text{SL} = \text{RL} + 20 \log(R) - k,$$

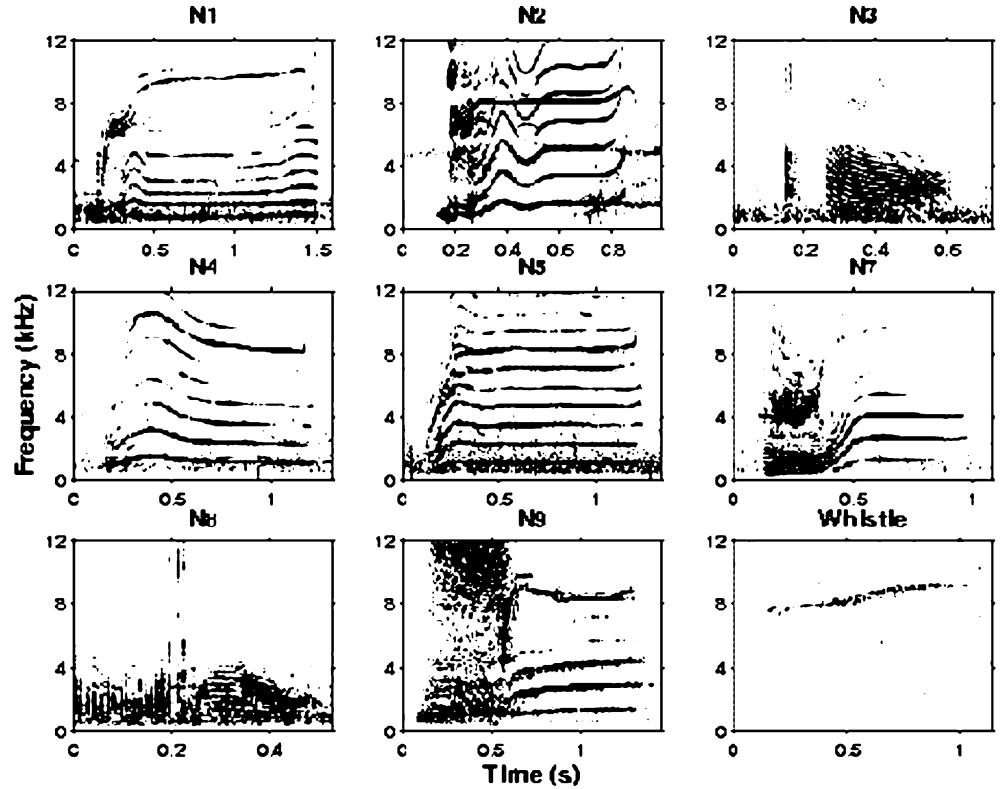
where RL is the received level in dB, R is the measured range from the vocalizing whale to the center of the rear array, and k is the near-field anomaly which represents the mean contribution to the field of the multiple bottom and surface reflections. A calibrated source spectrum was calculated for each 1/3-octave band, which was summed to calculate the broadband source level.

This simple transmission loss equation is valid when range is less than water depth and short enough that frequency-dependent absorption can be ignored (Marsh and Shulkin 1962; Urick 1981). In sea-state zero, k is estimated by Marsh and Schulkin (1962) to be 5.4 dB at 2.0 kHz and 3.8 dB at 8.0 kHz (which is the primary energy band in killer whale calls). Since the ranges used here are only the shortest of the possible valid range (to 400 m rather than to 3,000 m), the proportion of energy in the reflections versus direct path should be corrected to be somewhat less than the typical value given by Marsh and Shulkin. Thus, this study set the value of k to be equal to 3 dB.

The -3 dB value reflects the expectation that transmission loss will not be that fully predicted by spherical spreading. This value specifically subtracts non-correlated broadband energy that arrives at the receiving hydrophone after being reflected from the sea surface (Charif et al. 2002) assuming that the path lengths of the direct and surface paths are roughly identical, that reflection from the surface is lossless, and that the reflection will not destructively or constructively interfere with the direct path. Frequency-specific interference was clearly apparent in portions of some of the analyzed signals, and such portions of the sounds were specifically not included in the source level calculation. While the transmission-loss equation used to calculate apparent source level was probably not exact for all sounds analyzed, it is unlikely to be strongly biased and should be within $\sim 3 \text{ dB}$ for sounds measured at the ranges reported here.

Range from the rear array to the vocalizing animal was calculated by intersecting the angles-of-arrival of the sound on the two in-series beamforming arrays (Fig. 1).

Fig. 2 Spectrograms of the eight most common call types recorded and a whistle. Note that call types N1, N2, N4, N5 and N9 all contain a separately modulated high frequency component, while call types N3, N7 and N8 do not. The effective filter bandwidth was 97 Hz



The angle-of-arrival was calculated for each array using a broadband frequency-domain beamforming algorithm that measures the amount of energy coming from each direction at each frequency (Miller and Tyack 1998; Thode et al. 2000b). This technique does not obtain a 3-D localization of a sound because the linear arrays cannot resolve the left-right (and depth) ambiguity. However, the range estimate is valid for any position or depth of the signaler. With an inter-array spacing of 97 m, 0 and +3 dB signal-to-noise ratio requirements for the front and rear arrays, respectively, and background noise near 90 dB in the 1–20 kHz band, the lower limit of apparent source levels measurable by this system is roughly 127 dB at 1 m. At the greatest range from the rear array from which sounds were analyzed (410 m), sounds with an apparent source level below 142 dB at 1 m would have insufficient SNR (signal-to-noise ratio) to be analyzed, and may be underrepresented in the sample.

The accuracy of the range estimate was calibrated using a sound source deployed from a stationary boat. Several simultaneous acoustic and visual fixes were taken as the two-array system was driven past the sound source. Visual fixes were taken using a laser-range finder and a hand-held compass as well as by ship's radar. At each of these points the range error was calculated and expressed as the source level error that would result from the range error. Calibration results of eight separate passes showed that range errors contribute less than ± 3 dB error to the source level estimate over a 500×200 m² body of water on both sides of the array (Fig. 3). Animal sounds that came from outside the

calibrated region were excluded from analysis. Because range errors should not be correlated with errors in transmission loss, the apparent source levels presented here should typically be accurate to within ± 3 dB.

Active space estimation

The active space of each sound was estimated as the maximum range at which its apparent source level minus transmission loss exceeded the whale's detection threshold in at least one 1/3-octave band under different background noise conditions. The scenarios modeled were sea-state zero and sea state six background noise, which have been well characterized and summarized for naturally occurring sea states (Knudsen et al. 1948). In sea state zero, noise levels range from 44 dB re $1 \mu\text{Pa}^2/\text{Hz}$ at 1 kHz to 20 dB at 20 kHz (see also Erbe 2002). Noise levels in sea state six are roughly parallel, in frequency, to those at sea state zero, but are about 26 dB higher.

The relatively simple transmission-loss equation used for calculation of source level ignores propagation effects that become prominent over longer distances. The appropriate empirically derived equation for intermediate-range transmission loss in a shallow environment is:

$$\text{TL} = 15 \log(R) + \alpha R + \alpha_T \left(\frac{R}{H-1} \right) + 5 \log(H) + 60 - k_L,$$

where TL is the transmission loss (dB), R is the range (km), α is the absorption coefficient of seawater, H is a

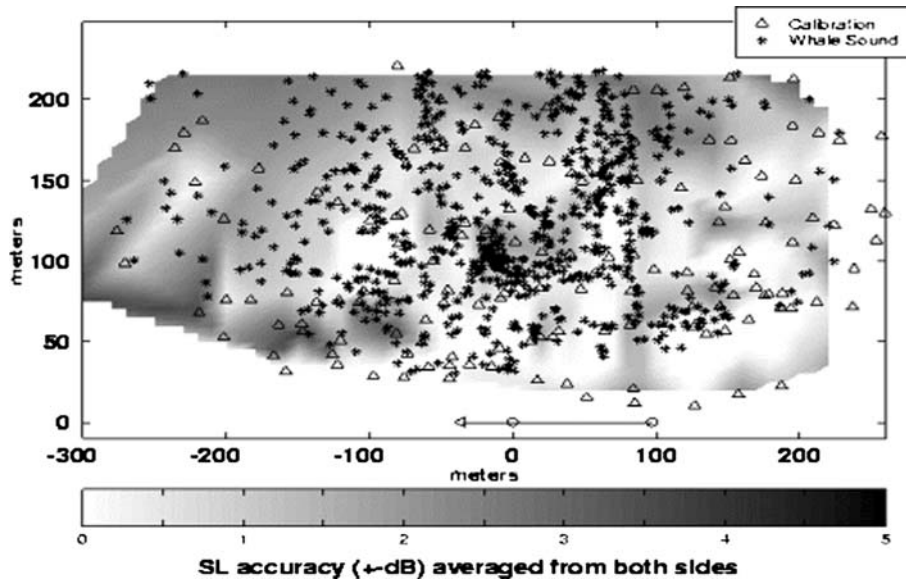


Fig. 3 Calibration results of the range measurement of the two-array system. The front array is centered on (0,0) and the rear array on (97,0). The *triangle* symbols mark where calibration measurements were taken and the *asterisk* symbols mark the position of all killer whale sounds for which an apparent source level was calculated. Calibration measures were taken on both sides of the array system, but are plotted together because the left-right

ambiguity is not resolvable using this linear array system. The *grayscale* background is the interpolated range error on source level (in dB) between measured points. Note that all sounds were within or near the calibrated region, and that the range error did not exceed ± 3 dB in the region from which apparent source levels were calculated

function of water depth, α_T is the shallow-water attenuation coefficient and k_L is a near-field anomaly (Marsh and Shulkin 1962). The absorption coefficient was calculated using an empirically-derived formula (Francois and Garrison 1982). The values for α_T and k_L assuming a sand bottom (Erbe 2002) and sea states zero or five, as well as the equation to calculate H based on a water depth of 100 m are given in Marsh and Shulkin (1962). This equation accounts for spreading loss, frequency-dependent absorption, and surface/bottom interactions.

Transmission loss was subtracted from the source spectrum in each 1/3-octave band at range steps of 100 m. A signal was judged to be detectable by another killer whale when the received level in at least one 1/3-octave band exceeded the hearing threshold of killer whales or 6 dB below the background noise level, whichever was greater. There are few measurements of the hearing abilities of killer whales in noise (Bain and Dalheim 1994) and no explicit measurements of critical ratios, so I used Fletcher's (1940) equal power assumption with a correction for binaural hearing capabilities to estimate a detection threshold in noise (Erbe 2002). Bain and Dalheim (1994) found that masking sources needed to be 4–40 dB more intense to mask natural calls when they were placed to the side or behind an animal. Similar results have been found for human ability to detect speech in cluttered environments (Kidd et al. 1998). Sea generated noise arrives from broad azimuth angles, while the conspecific call arrives from one direction primarily. There is also evidence that humans and birds can use energy in different harmonic bands to improve

detection thresholds (Hall et al. 1984; Klump and Langemann 1995), which is ignored here. Thus, the -6 dB signal to ocean-noise criterion adopted here is a best-guess given current information. New information on the ability of killer whales to detect calls in background noise would be useful to assess the validity of this criterion.

The auditory threshold at the center of each 1/3-octave band was obtained by fitting a third-order polynomial curve to the auditory threshold points reported in the literature (Hall and Johnson 1972; Symanski et al. 1999). This threshold comparison assumes that the energy in a band of noise that is just audible is equal to the threshold energy of the pure tone at the center of the band, as appears to be the case for human speech (Hawkins and Stevens 1950). Because killer whale hearing becomes less sensitive at low frequencies, the detection threshold was always hearing-threshold limited below 9 and 5 kHz in sea-states zero and six, respectively (see also Janik 2000).

Results

I recorded killer whale sounds for a total of 5 h on two different days from five different pods (Table 1), though effort was focused on animals from pods A1 and A5. Because the arrays were towed parallel to the direction of movement of the whales and sounds were localized broadside to the array (Fig. 1), animals most often surfaced with a sideways orientation to the receiver. It is

Table 1 Group composition and sample size from recording effort

Date	9/1/98	9/8/98
Pods present	A1, A5	A1, A5, B1, C1, I15
No. of animals	12	46*
Hours recorded	2	3
Calls analyzed	334	485
Whistles analyzed	15	9

The same 12 animals present on 9/1/98 were also present on 9/8/98
 *The number of animals on 9/8/98 were estimated based upon identified groups as all individuals were not separately identified

therefore reasonable to consider the apparent source levels to primarily represent off-axis levels, with occasional sounds from animals oriented directly toward or away from the receiver.

The same 12 animals from pods A1 and A5 were present on both recording days and the arrays were positioned to obtain sounds primarily from these animals. The animals were traveling in subgroups and vocally active throughout both recording sessions. Although I could not identify the individual producing each sound, calls were often produced by whales in multiple locations in clear vocal exchanges (Miller et al. 2004), so the sample contained calls produced by multiple individuals in the group. The apparent source levels of 819 pulsed calls and 24 whistles were measured. Of

the 819 pulsed calls, 60 did not clearly correspond to one of the call types defined by Ford (1987) and were classified as variable calls.

Apparent source levels

The apparent source levels in the 1–20 kHz band of all sounds ranged from 131 to 168 dB at 1 m (Fig. 4). Whistles had the lowest mean (\pm SD) apparent source level (140.2 ± 4.1 dB re $1 \mu\text{Pa}$ at 1 m), followed by variable calls (146.6 ± 6.6 dB), with stereotyped calls being the most intense (152.6 ± 5.9 dB). These differences by sound type were statistically significant ($F_{2,840} = 76.1$, $P < 0.0001$, Tukey post-hoc $P < 0.0001$). Sounds were occasionally observed on only one array when animals were quite close, suggesting that some sounds were produced below the threshold of 127 dB to be localized with the system. All of these faint sounds were either whistles or variable calls, none were stereotyped calls.

Within the stereotyped calls, the eight most common call types produced by pods A1 and A5 accounted for 618 of the 759 stereotyped calls. Significant differences in apparent source level were found across types ($F_{7,611} = 54.6$, $P < 0.0001$), with a mean of 156.5 and 145.4 for the most (N4) and least (N3) intense call types, respec-

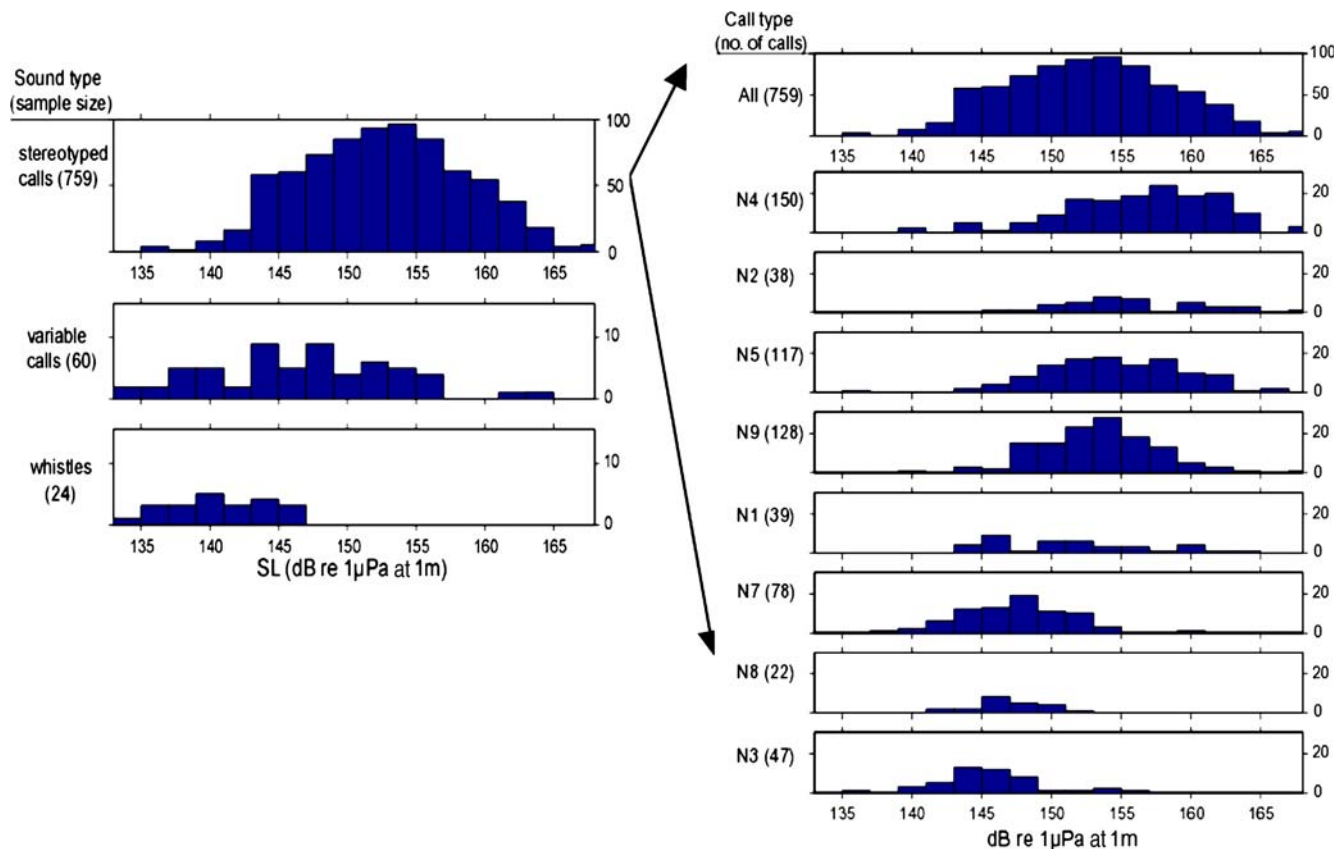


Fig. 4 Left: the apparent source levels of stereotyped calls, variable calls and whistles. Right: source levels of the eight most common stereotyped calls recorded from pods A1 and A5 (see Fig. 2). Note the diversity of average source level among the different sound types

tively (Fig. 4). Clustering using Tukey post hoc probability of 0.01 resulted in four clusters, suggesting diversity in the level of different call types. Though differences were statistically significant, calls of the same type were produced over a rather wide range of source levels, with standard deviations ranging from 2.7 to 5.4 dB for call types N8 and N4, respectively.

Estimated active space

In sea-state zero noise conditions, estimated active space of all sounds ranged from 1.9 to 25.8 km (Fig. 5). Whistles had the smallest average estimated active space (6.4 ± 2.4 km), followed by variable calls (7.8 ± 3.7 km), with stereotyped calls having the largest average estimated active space (11.0 ± 4.7 km). The mean estimated active space of stereotyped calls was greater than that of variable calls and whistles ($F_{2,840} = 23.40$, $P < 0.001$, Tukey post hoc $P < 0.001$), but the contrast between variable calls and whistles was not statistically significant (Tukey post hoc $P = 0.46$). Significant differences across the eight most common call types were also apparent ($F_{7,611} = 31.77$, $P < 0.0001$), with a mean of 12.8 ± 4.7 km and 6.1 ± 1.6 km for the longest (N2) and shortest range (N3) call types, respectively. Clustering using Tukey post hoc probability of 0.01 resulted in two clear clusters: a long-range cluster consisting of call types N2, N4, N1, N9, and N5 (combined mean of 12.4 ± 4.3 km), and a short-range cluster consisting of call types N7, N8 and N3 (combined mean of 6.8 ± 3.1 km). Note that all the call types in the long-range cluster contain a separately-modulated high

frequency component, while all those in the short-range cluster do not.

Source level, detection threshold, and water depth variables were perturbed for the long and short-range call groups to determine the sensitivity of the model to the input variables. As expected, the active space estimate was equally sensitive to perturbations in source level and detection threshold. A 6 dB increase in source level (or decrease in threshold) resulted in increases in estimated active space of 26 and 37% for long- and short-range call types, respectively, while a 6 dB decrease in source level (or increase in threshold) resulted in a corresponding decrease of 24 and 30%. Increasing water depth to 500 m resulted in increases of estimated active space of 16 and 9% for long- and short-range call types, respectively, while decreasing water depth to 20 m resulted in corresponding decreases of 25 and 19%.

Relative to the sea-state zero scenario, estimated active space in sea state six noise conditions was 75%, 83% and 91% lower for combined stereotyped calls, variable calls and whistles, respectively (Fig. 5, top). Within the eight most common stereotyped calls (Fig. 5, bottom), sea state six conditions resulted in reductions of 74% and 81%, respectively for long and short-range call types. The percentage reduction in estimated active space was smallest for the most intense calls, and greatest for the lower-intensity whistles.

Discussion

The apparent source levels of all measured sounds ranged from 131 to 168 dB re 1 μ Pa at 1 m, with statisti-

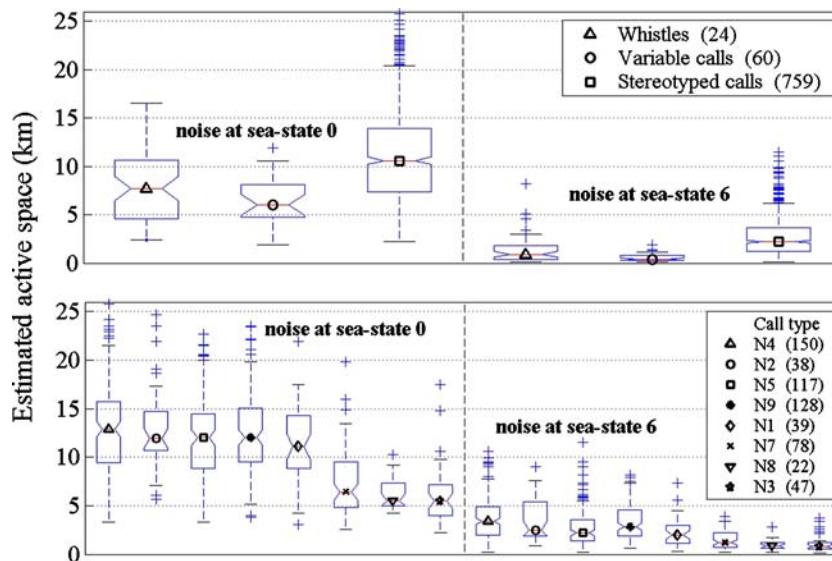


Fig. 5 Box plots of estimated active space of whistles, variable calls, and group stereotyped calls (top), and stereotyped calls classified by type (bottom) in sea-state zero (left half of both panels) and sea state six (right half) background noise scenarios. The center of each box is the median value, and the upper and lower box borders are the first quartiles of the data. The whiskers extend to

the most extreme datum within the inter-quartile range defined by the box borders, and more extreme data are plotted as symbols. Note the bimodal structure of the estimated active space. The short-range sound class includes whistles, variable calls and call types N3, N7, and N8. The long-range sound class consists of stereotyped call types N1, N2, N4, N5 and N9

cally significant differences in the levels of different sound types in the repertoire (Fig. 4). Supported by similar results from the active space model (Fig. 5), the acoustic repertoire of this group of resident killer whales can be partitioned into two primary groups: 'long-range' sounds including call types N4, N2, N5, N9 and N1 (all contain a separately-modulated high-frequency component), and 'short-range' sounds including whistles, variable calls, and call types N7, N8 and N3 (all without a high-frequency component). Relative to low-noise sea-state zero conditions, the estimated active space of whistles, variable calls and stereotyped calls was 91%, 83% and 75% less in sea-state six, respectively, suggesting that repertoire diversity in active space is preserved or possibly enhanced under higher noise conditions.

The range of apparent source levels reported here is similar to those reported for other large delphinids (Watkins et al. 1997; Fish and Turl 1976; Janik 2000). Erbe (2002) used the received level of 105–124 dB as a minimum estimate of killer whale call source levels. Adding 40 dB of transmission loss for whales sighted roughly 100–200 m away during those recordings, Erbe's (2002) results are consistent with those reported here. The whistles in my sample were more intense than whistles produced by resting spinner dolphins in Hawaii (109–125 dB at 1 m; Watkins and Schevill 1974), but were less intense than those reported for traveling spinner dolphins (mean 150–154 dB; Lammers and Au 2003). Whistles produced by bottlenose dolphins in Moray Firth (134–169 dB) were more intense than the whistles reported here, but were quite consistent with the overall range of sound source levels in this study (Janik 2000). Whistles were roughly 10 dB less intense than burst-pulse sounds in a sample of sounds collected from the melon-headed whale (Watkins et al. 1997).

Despite statistically strong differences across sound types, the range of apparent source levels within each type was large, with > 20 dB between the most and least intense exemplars in many cases (Fig. 4). Only about 3 dB of variability is expected from errors in range measurement or inaccuracies in the transmission loss model. Though signalers may have the ability to modify the source level of a sound depending on their motivation, there may be other features of sound production that add variability to apparent source levels. As killer whale calls are directional at high frequencies (Schevill and Watkins 1966; Bain and Dalheim 1994; Miller 2002), apparent source level should vary as a function of signaler orientation, which we could not control or measure. During the recordings, most whales surfaced with a sideways orientation to the array, so the average values measured here are certainly below the on-axis source level. Some analyzed calls contained clear high-frequency components, so were likely to be from individuals oriented more directly toward the array (Miller 2002). Additional variation could be due to individual differences in body size, which varies greatly with age and sex of killer whales (Matkin and Leatherwood

1986). Source levels appear to increase with body size across cetacean species (Patterson and Hamilton 1967; Cummings and Thompson 1971; Thode et al. 2000a; Cummings and Holliday 1985; Schevill and Watkins 1972; Cummings et al. 1968; Dawbin and Cato 1992).

The results of the active space estimation suggest that killer whales may be able to detect communication sounds produced by conspecifics over large distances in quiet conditions. Overall estimated active space ranged from 1.9 to 25.8 km in sea-state zero conditions. The maximum estimated active space closely matches maximum active space estimates of 20–25 km calculated for a bottlenose dolphin whistle using the same transmission loss model in sea state zero conditions (Janik 2000). While observers have anecdotally noted cases in which killer whales apparently reacted to sounds of other whales greater than 10 km distant, carefully controlled observations or experiments to measure the distances over which killer whales react to conspecific sounds are lacking.

The active space model estimates the distance over which communication may occur, and is useful to demonstrate diversity within the repertoire, but its accuracy is limited by the lack of information on detection thresholds of calls in noise. This simple model using average conditions ignores variability in the statistics of background noise, propagation conditions, and physiological characteristics of signalers and receivers that undoubtedly lead to a much larger scale of variability in the true active space of each communication signal. Sensitivity analyses suggest that the active space estimates fluctuate by roughly $\pm 30\%$ with ± 6 dB changes in SL or auditory sensitivity. Water depth of 100 m assumed in the model is valid over many near-shore areas that killer whales inhabit, but active space estimates increase in deeper water, and decrease in shallower water, due to loss from surface and bottom reflection (Marsh and Shulkin 1962). The depths of the signaler and receiver themselves also influence signal propagation, with lower frequencies being relatively more attenuated when signalers or receivers are near the surface (Mercado and Frazer 1999).

Directionality of signal transmission and hearing sensitivity are also expected to influence active space (Bain and Dalheim 1994). Although I could not directly observe the orientation of signaling animals in this study, most sounds were likely received from an off-axis orientation with some sounds produced by animals facing directly toward or away from the array. Thus, the mean active space estimated in this study is likely to be intermediate to the extremes when an animal is facing directly toward or away from the receiver. While the radiation pattern of killer whale calls has not been measured, the high-frequency component of stereotyped call types are directional, with differences of > 6 dB for animals moving toward, versus away from, a receiver (Miller 2002). Assuming the 1–5 kHz band is omnidirectional, front-to-back differences of at least $\pm 30\%$ in active space can be predicted. Actual front-to-back

differences are probably greater than this as the 1–5 kHz frequency band may not be omni-directional. The orientation of the receiving animal is also likely to be an important factor in the shape of active space in animals with directional hearing (Bain and Dalheim 1994). Receiver directivity has been measured at high frequencies for dolphins (Au 1993), but little information is available for the low frequencies at which killer whale calls are produced (Bain and Dalheim 1994).

Estimated active space decreased strongly in noisy sea state six conditions, with short-range sound relatively more affected than the long-range stereotyped calls. Strong predicted impacts of naturally-occurring noise may imply mechanisms to adaptively modify signals in response to background noise would be selectively advantageous. Mossbridge and Thomas (1999) found that frequency modulations of Antarctic killer whale calls shifted away from the 2.8 to 3.8 kHz band seasonally used by calling leopard seals. Killer whales in three different pods increased the duration of their most common call type in the presence of boat noise (Foote et al. 2004). It is important to emphasize that the source levels reported here were produced in sea state zero conditions with little nearby vessel traffic, except the research vessel itself. Given the documented compensatory mechanisms in call frequency and duration, it seems plausible that killer whale may also have mechanisms for amplitude regulation of their calls in noise (Cynx et al. 1998; Brumm and Todt 2002; Brumm et al. 2004). Measurement of the source level of sounds produced by killer whales in varying noise conditions could test this possibility.

The result that sound pressure levels and active space estimates can be used to partition the acoustic repertoire of resident killer whales into at least two sound classes is strongly corroborated by observations of sound-type production in different behavioral states of killer whale groups. Resident killer whales do not appear to produce any sound type exclusively in association with a particular behavioral category, but do alter the rates of sound-type production in different behavior states (Bain 1986; Morton et al. 1986; Ford 1989; Thomsen et al. 2002). Thomsen et al. (2002) found that resident killer whales produced short-range whistles and variable calls most commonly in socializing contexts, while stereotyped calls predominated in foraging and travel contexts. In his study of behavior and sound production of pods A1, A4, and A5, Ford (1989) found significant increases in the production of the short-range whistles, variable calls, and the N3 call type during beach-rubbing, socializing, and group-resting behaviors. In these behavioral states, animals tend to be closely spaced and interactions between group members appear to be primarily affiliative. The intense, long-range call types N2, N4, N5, and N9 were used more during behaviors where group members are dispersed, including traveling, foraging, when different pods were meeting, or in large aggregations of animals (Ford 1989, pp 737). In a study of two captive whales from A5 pod, call-type clusters associated with

high activity levels (assessed by respiration rate) included call types N4, N2, and N9, while lower-activity clusters contained call types N7, N8, N3 and whistles (Bain 1986). Though there is a clear division in both the estimated active space and behavioral context of production of long-range and short-range sound classes, it is interesting that these animals have a repertoire of sound types within each class. Thus, the functional aspect of active space described here does not fully explain why killer whales produce a repertoire of whistles and burst pulse calls (Ford 1989).

The precise function(s) of calling by killer whales remains unknown. Ford (1989, 1991) proposed that discrete stereotyped call repertoires function primarily to maintain pod cohesion and coordinate activities. Individuals within groups regularly exchange calls, often immediately matching the call type produced by another individual (Miller et al. 2004). Such interactive calling behavior suggests that communication is at least partly directed to other killer whales within the group. Given that group members rarely separate by more than a few kilometers, why should resident killer whales produce calls that can be detected at much greater distances? The simple explanation that signalers should simply always maximize signal level seems inconsistent with the result of this study which demonstrates that killer whales often produce calls with less active space than their maximum capability.

The ability of a killer whale to detect a conspecific at tens of kilometers may be a consequence of the signal level required for detailed information (group membership, Ford 1991; direction of movement, Miller 2002) to be reliably transferred over shorter typical separation distances to intended receivers within the group (McGregor and Dabelsteen 1996). Alternatively, calling may have inter-group functions such as spatial competition (Miller and Bain 2000) or mate attraction (Yurk et al. 2002) that select for longer-range signals. In the fjord-like inland waters of the coastal NE Pacific, with numerous islands, continuous sections of water are often considerably shorter than the estimated active space of calls. In such a habitat, a direct signal path may often be as important as ‘staying within range’ for members of stable social groups to maintain acoustic contact with each other. If the intended receivers of killer whale calls are the members of other groups, we might expect calling to occur in ‘hot-spots’ where acoustic propagation conditions are good or from which there exists a direct path to larger areas of killer whale habitat. A detailed analysis of the geography of call production by these mobile animals may help elucidate intra-group and inter-group functions of calling.

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