



The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales

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(Received 31 August 1994; initial acceptance 21 December 1994;

final acceptance 6 July 1995; MS. number: A7082)

Abstract. Despite well-documented experimental evidence of echolocation in toothed whales, virtually nothing is known about the use and functional significance of cetacean sonar in the wild. Here, the patterns of echolocation sounds produced by killer whales, *Orcinus orca*, off British Columbia and Alaska are described. Two sympatric populations with divergent food habits differed markedly in sonar sound production. Individuals belonging to the fish-eating 'resident' population produced trains of characteristic sonar clicks, on average, 4% of the time, 27 times more often than marine mammal-eating 'transient' killer whales. The click trains of residents averaged 7 s, more than twice as long as the trains of transients. Click repetition rates within resident's trains were constant or changed gradually; within transient's trains they often fluctuated abruptly. Transients produced isolated single or paired clicks at an average rate of 12/h, four times as often as residents. In general, the isolated clicks and infrequent, short and irregular trains of transients were less conspicuous against background noise than the sonar of residents. This difference in acoustic crypticity may reflect a flexible response to the probability of alerting prey, because marine mammals have more acute hearing than fish in the frequency range of sonar clicks. In both populations, echolocation use per individual decreased with increasing group size, suggesting the sharing of information between group members. No relationships were found between echolocation activity and water clarity for whales of either population. Transient whales often travelled or foraged without discernibly echolocating, suggesting that passive listening provides cues for prey detection and orientation.

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Since the discovery of dolphin echolocation in the late 1950s (McBride 1956; Kellogg 1958), sonar has been experimentally investigated in many species of odontocetes. This research has aimed at determining the acoustic characteristics of echolocation signals, the patterns of signals used for different tasks, and the power of sonar to resolve objects under various conditions (see Au 1993). Using trained and blindfolded subjects and static target objects, experimenters have answered many fundamental 'what' and 'how' questions of sonar capability. 'When' and 'why' questions of sonar utility in the wild, however, have not been directly

addressed. Similarly, the possible role of passive listening as an alternative to sonar and vision (e.g. Norris 1967; Wood & Evans 1980; Evans & Awbrey 1988) has not been investigated.

Three sets of observations indicate that wild odontocetes may use echolocation less often or for different functions than was previously suspected. (1) Equipping fishing nets with acoustically reflective targets has generally been unsuccessful in reducing accidental entanglements (Evans & Awbrey 1988; Dawson 1991). (2) Recently captured or untrained dolphins are often unable to use echolocation effectively for simple tasks such as obstacle avoidance (Wood & Evans 1980). (3) In a well-controlled study, a blindfolded bottlenose dolphin pursued live fish without emitting echolocation sounds (Wood & Evans 1980), apparently orienting on swimming sounds alone. Because the advantages of echolocation to individuals living in dark or turbid environments seem

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apparent, these observations imply that liabilities also apply. These liabilities may include the costs of echolocation described for bats; that is, the stimulation of evasive responses in prey and the attraction of eavesdropping predators or competitors (Fenton 1980; Barclay 1982).

Here we report findings from a systematic study of the echolocation sounds of wild killer whales off Alaska and British Columbia. Two sympatric, non-associating populations that hunt distinctly different prey inhabit this region. These two populations provided a unique opportunity to compare the sonar sounds of whales engaged in different activities, to assess the flexibility of echolocation and its utility under varying conditions. We describe general differences in the patterns of echolocation use by each population, and how echolocation was affected by group size, activity and water clarity.

METHODS

Killer Whale Populations

Killer whales in Prince William Sound, Alaska, and along the coast of British Columbia have been the subjects of ongoing studies for 13 and 23 years, respectively. Almost all individuals have been identified and catalogued on the basis of natural markings and fin shape (Bigg et al. 1987; Heise et al. 1992; Ford et al. 1994), and their seasonal movements, diet, social structure and life-history parameters have been described (Stevens et al. 1989; Bigg et al. 1990; Nichol 1990; Olesiuk et al. 1990). Two sympatric non-associating forms, known as 'residents' and 'transients', inhabit these areas. Residents live in stable matrilineal groups (pods) of five to 40 individuals and forage principally or entirely on fish (Bigg et al. 1987). Transients form less stable associations than residents, but are typically seen in groups of two to 10 animals that feed principally or entirely on marine mammals (Bigg et al. 1987; Morton 1990). A third, rarely encountered assemblage of killer whales known as the 'off-shore' group has a range overlapping those of residents and transients in British Columbia (Ford et al. 1994), but was not included in this study.

Ford (1989) described three distinct types of vocalizations used by killer whales: whistles, calls and clicks. Whistles are highly variable pure-tone signals associated with social activity within

groups, and calls are pulsed signals that probably serve as long-term indicators of affiliation (Ford 1989). Clicks are short-duration, broadband signals that are used for echolocation by killer whales and other odontocetes (reviewed in Norris 1969; Watkins & Wartzok 1985; Au 1993; descriptions of click use by killer whales in Schevill & Watkins 1966; Diercks et al. 1971).

Study Sites

We recorded killer whales in the following areas: (1) Prince William Sound, Alaska (60°05'N, 147°30'W) during May–August 1990, July–September 1991 and July–September 1992, (2) the central mainland coast of British Columbia (52°0'N, 127°50'W) during June 1991 and May 1992, and (3) Moresby Island, British Columbia (52°30'N, 131°0'W) during June–July 1992. All areas had relatively little vessel activity. Water clarity varied widely at the first and second sites with fluctuating run-off from rivers and glaciers.

Data Collection

All acoustic recordings and behavioural observations were made at sea from small (<12 m) vessels. We searched areas where killer whale sightings were common by scanning with 7 × 50 binoculars while travelling at approximately 15 km/h. If conditions permitted, we periodically put an observer on shore to scan from a high vantage point with binoculars or with a 20 × spotting scope. At approximately 1-h intervals we listened for vocalizing killer whales with a Sparten 60CX123 hydrophone lowered to a depth of 20 m. If vocalizations were heard, we attempted to find the whales using a directional hydrophone. Mariners and aviators often reported killer whale sightings to us via marine radio, enabling us to focus searches.

When we located killer whales (an 'encounter'), we slowly approached them to about 25 m and paralleled their course. We took identification photographs of each whale present, then moved 500 m ahead and shut off the vessel engine. We lowered a Bruel and Kjaer 8101 hydrophone to a depth of 25 m, and made recordings using a custom-built calibrated pre-amplifier and Nagra IV-SJ recorder running at 38 cm/s (system frequency response 25 Hz to 35 kHz ± 1 dB). We recorded 5-min sessions at hourly intervals, and

simultaneously made voice recordings of our observations on a separate track of the same tape.

Immediately after each recording session, we measured water clarity using a 20-cm Secchi disk with black and white quadrants. We lowered the disk on the shaded side of the vessel until it disappeared, raised it until it re-appeared, and recorded the average of the two depths. To assess whether water clarity varied with depth, we made an ambient light profile once per encounter using an Archer 276-116A photocell attached by a 30-m cable to a resistance meter. The photocell was weighted so that its light-sensitive surface was directed upwards. We took readings every metre as the cable was lowered. In water that was unstratified, the resistance readings increased evenly with depth; rapid changes in resistance indicated the presence of turbid layers.

Activity Categories

While recording, we noted the activities of the whales at the surface. We classified the most common activity observed during each session according to the behavioural categories listed below (modified from Ford 1989).

Foraging

Foraging by residents was indicated by erratic high-speed swimming, lunging, rapid circling and chasing fish at the surface. Foraging transients either swam along shorelines, entering bays and circling kelp patches and islets, or swam in dispersed formation across open areas. Fish scales, tissue, blood or blubber fragments were frequently seen at the surface when killer whales captured prey while foraging.

Travelling

Travelling killer whales swam in one or several groups on a consistent course at speeds exceeding 6 km/h. Individuals swam within a few body lengths of their neighbours in each group.

Slow-travelling

Slow-travelling whales swam in one or several groups on a consistent course at 3-6 km/h, and intermittently engaged in activities such as flipper or fluke slapping (striking flippers or tail flukes

on the water surface). The distances between individuals within a group often exceeded several body lengths.

Resting

Resting whales swam in one or several groups, moved at speeds less than 4 km/h, and surfaced in synchrony. Intervals between breaths were short and regular, and group members usually stayed within a single body length of their neighbours.

Socializing

Socializing whales made little directional progress and engaged in physical interactions such as chasing, rolling and thrashing. Surface activities were common, including breaching (leaping clear or partly clear of the water surface), spyhopping (vertical surfacing with the head lifted clear of the water) and flipper and fluke slapping.

Milling

Milling whales made little directional progress, and breathed at long, irregular intervals. Surfacing were not coordinated between group members. Surface activities such as those described above were rare.

Acoustic and Statistical Analysis

We analysed recordings using a Kay Elemetrics DSP-5500 real time sound analyser. The tapes were played back at reduced speed ($\frac{1}{8}$ to $\frac{1}{2}$ original speed, depending on the complexity of the sounds). During the analysis we simultaneously listened to the recordings and viewed a video display showing both a colour-enhanced, 512-point spectrograph with a 64-kHz bandwidth (compensated for tape speed) and a waveform trace, both in 4-s windows. We used the spectrograph to compare the frequency characteristics of clicks, and the waveform to help detect quiet clicks. Although the signal strength of the recordings declined above 35 kHz, usable information extended to 50 kHz and adequately covered the frequencies of killer whale clicks reported by Diercks et al. (1971) and Evans & Awbrey (1988).

Sonar pulses usually occurred in regular series of three or more clicks separated by intervals of less than 2 s, referred to as click trains. We used a

digital stopwatch during the analysis to record the beginning and end time of each click train. The individual pulses in any given click train were typically consistent in frequency structure, but differed from clicks in other trains, as reported for narwhals, *Monodon monoceros* (Ford & Fisher 1978). This frequency signature made it possible to distinguish the overlapping trains of different individuals. If the whales were widely dispersed or travelling rapidly during a recording session, it was sometimes difficult to determine whether certain trains had ended or faded into background noise. If this ambiguity occurred, we discarded the data from the session. Similarly, we did not analyse some sessions because ambient noise was loud enough to potentially mask quiet clicks.

Early in the study, two distinct types of click trains were apparent. The first had a click repetition rate that remained constant for the duration of the train, or that changed in a smoothly graded fashion; the second had a click rate that changed abruptly. To describe this dichotomy quantitatively, we defined 'regular' trains as ones in which the duration of all adjacent inter-click intervals differed by less than 10%; in 'irregular' trains at least one pair of adjacent intervals differed by 10% or more. Almost all trains fell clearly into one category or the other; in cases of uncertainty we paused the playback recorder and analyser and measured click intervals on the spectrographic display.

We counted the percentage of trains that were irregular for each session. These data were normalized by arcsine square root transformation, and mean percentages for transient and resident killer whales were compared using *t*-tests. We summed the durations of all click trains, calculated the mean durations for each session, and used *t*-tests to compare the grand means for resident and transients.

We devised a simple echolocation use index (*EI*) to quantify the use of click trains. This was the average percentage of time that an individual whale present during a recording session emitted click trains, calculated as follows:

$$EI = 100 \frac{d}{sn}$$

where *d* is the sum of the durations of all the click trains, *s* is the recording session duration, and *n* is the number of whales present (referred to

hereafter as group size). We arcsine-square-root-transformed *EI* values for statistical testing and used the log of group size. Mean *EI* values were compared by *t*-test. We examined the effect of behavioural activity and group size on *EI* using an ANCOVA, and used a planned contrast analysis (Wilkinson 1990) to test whether echolocation was more strongly associated with foraging than with other behavioural activities.

In addition to clicks occurring within trains, we sometimes detected single clicks or closely spaced pairs of clicks that were not part of any series. These clicks were acoustically similar to those occurring within trains, and are referred to as 'isolated clicks'. We used *t*-tests to compare the mean number of isolated clicks produced per h per whale by residents and by transients.

To measure the click repetition rates of echolocation trains, we selected a subsample of sessions and trains using random number tables. The spectrograph of each train was then paused on the monitor while we measured its duration and number of clicks. The repetition rate of a train was calculated as the number of clicks it contained minus one, divided by the duration of the train.

In many instances we analysed more than one recording session from the same encounter. To ensure that recordings were statistically independent, we selected sessions for analysis that were separated by a distinct change in behaviour. Thus, if an encounter consisted of 3 h of foraging followed by 2 h of resting and then 3 h of foraging, we analysed at most one session from each of the three activity periods. On occasion we analysed concurrent transient foraging sessions that were separated by a kill and feeding session or by a transition between foraging modes (e.g. a change from nearshore to offshore foraging). All statistical tests are two-tailed.

RESULTS

Killer Whale Encounters

We encountered killer whales 111 times, and spent an average of 5 h observing and recording per encounter. By comparing the photographs taken during the encounters with catalogues of identified killer whales (Bigg et al. 1987; Ellis 1987; Heise et al. 1992), we determined that residents from 11 pods were present 85 times, transients from six groups were present 23 times,

and uncategorized killer whales were present three times. Residents and transients were never seen together. Fewer transient than resident killer whales were present per encounter (on average, 4.6 and 18.0, respectively), and transients were generally dispersed over smaller areas than residents.

Detectability of Echolocation Sounds

We were able to detect echolocation clicks from approaching killer whales up to or beyond 3 km; under most conditions we could distinguish complete trains when the animals were within 1 km. When a group passed the boat, clicks quickly dropped in volume, and detection became unreliable within 500 m. This directional effect was most evident in the high frequency part of the sound spectrum, as previously reported for killer whales and other odontocetes (Schevill & Watkins 1966; Diercks et al. 1973; Au 1993). It was our consistent qualitative impression that residents' clicks were more intense than transients', despite the fact that the larger size of resident groups meant that the average hydrophone-to-whale distance was usually greater for residents than transients. Nevertheless, resident groups were at times sufficiently dispersed that echolocation trains were difficult to distinguish from background noise, and we discarded data from more resident than transient sessions during analysis. We successfully analysed 88 sessions of transient and 74 of resident killer whales.

Characteristics of Clicks and Trains

Isolated clicks and those occurring within trains were broadband pulses with peak energy ranging from 4 to 18 kHz. Measurable energy usually

extended to 35 kHz and occasionally to 50 kHz, the upper limit of the recording system. These peaks and ranges are somewhat lower than those reported by Awbrey et al. (1982) for Antarctic killer whales. The difference, however, may be artefactual, because recorded frequency characteristics depend on the distance and orientation of whales relative to the hydrophone. Because the hearing of killer whales extends beyond 100 kHz (D. E. Bain, unpublished data, cited in Bain & Dahlheim 1994), we paid careful attention to the upper frequency portion of the spectrographic display for evidence of the lowest components of very high frequency clicks. We found no indication of such clicks in the 162 sessions analysed.

Isolated clicks were initially very difficult to distinguish against background noise. Indeed, early in the analysis we missed these sounds entirely. With experience, however, we recognized isolated pulses closely resembling those found in click trains. No similar sounds were detected in control recordings made in the study areas when whales were absent. Most isolated clicks were single pulses; however, we recorded some double pulses with inter-click intervals of 100 ms or less.

The characteristics of resident and transient click trains are summarized in Table I, and examples of each are shown in Figs 1 and 2. The percentage of irregular click trains was approximately 18 times higher for transients than residents, whereas the click trains of residents were more than twice as long, on average, as those produced by transients. During spectrographic analysis we noted that residents' click trains were consistently louder in relation to background noise than the trains of transients. Because we did

Table I. Characteristics of resident and transient killer whale click trains and isolated clicks

	Resident	Transient	<i>P</i>
Percentage of irregular trains*	3.44 ± 1.08 (70)	63.10 ± 8.13 (27)	<0.001
Click train duration* (s)	7.22 ± 0.54 (70)	2.80 ± 0.49 (27)	<0.001
Echolocation index (all data)	4.24 ± 0.51 (74)	0.16 ± 0.04 (88)	<0.001
Echolocation index* (non-zero data)	4.48 ± 0.53 (70)	0.51 ± 0.12 (27)	<0.001
Mean number of isolated clicks/h per individual	2.80 ± 0.83 (74)	11.86 ± 3.58 (88)	0.024

All values are $\bar{X} \pm SE$, and are followed by the number of recorded sessions in parentheses. The click train durations are the grand means of the average click train durations for each session. *P*-values refer to *t*-tests for equality of means.

*Sessions with no click trains were excluded when calculating these values.

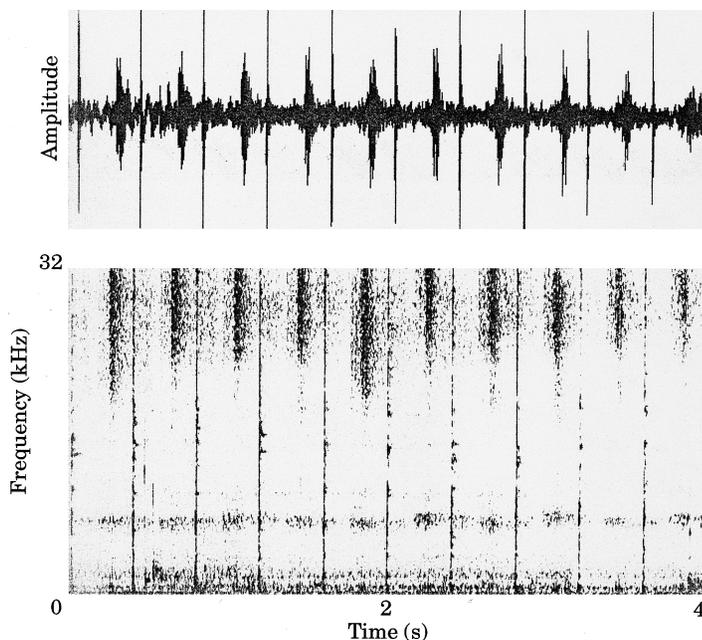


Figure 1. Waveform and spectrogram of 4 s of a resident killer whale click train. Clicks are narrow vertical lines on the spectrogram plot; the wide shaded areas extending up from 20 kHz are click echoes, probably from a large diffuse target such as a kelp bed.

not know the distance from the hydrophone or the orientation of the whales producing clicks, we did not systematically quantify click intensity.

The distributions of click repetition rates for residents and transients were not normally distributed, and are not statistically analysed. The median click repetition rates for residents and transients were similar: 7.081 per s and 6.131 per s ($N=32$ and 23, respectively). The maximum rate, however, was 126 per s for residents compared to 19 per s for transients, and 15% of the resident trains exceeded 20 per s. We qualitatively noted that slow click trains were louder than fast ones for transients, and that residents' clicks were louder and more variable during foraging than during other activities.

Echolocation Use

Overall use of echolocation

We detected click trains in 95% of the analysed resident killer whale sessions, and in 31% of the transient sessions. The difference in average *EI* values (Table I) meant that a resident killer whale was 27 times more likely to be producing a click

train at any time than a transient. Significant differences still existed when we calculated mean *EIs* based solely on the sessions with detectable click trains (Table I). In this case, residents' mean *EI* exceeded transients' by a factor of nine. In contrast, isolated clicks were used four times more frequently by transients than residents.

Effects of whale activities and group size

Figure 3 shows the mean *EI* and the number of sessions analysed for each behaviour category. The number of sessions analysed provides only an approximate behaviour budget, because we were sometimes unable to analyse recordings made when the whales were widely dispersed or swimming rapidly. Transients spent more time foraging than residents, and were never observed socializing. Residents travelled infrequently and rested more often than transients. Differences in the echolocation indexes of transients and residents were consistent for all behaviour categories.

For resident killer whales, the ANCOVA showed no evidence that the relationship between group size and *EI* differed between activities, ($F_{4,62}=1.454$, $P=0.277$). *EI* differed significantly

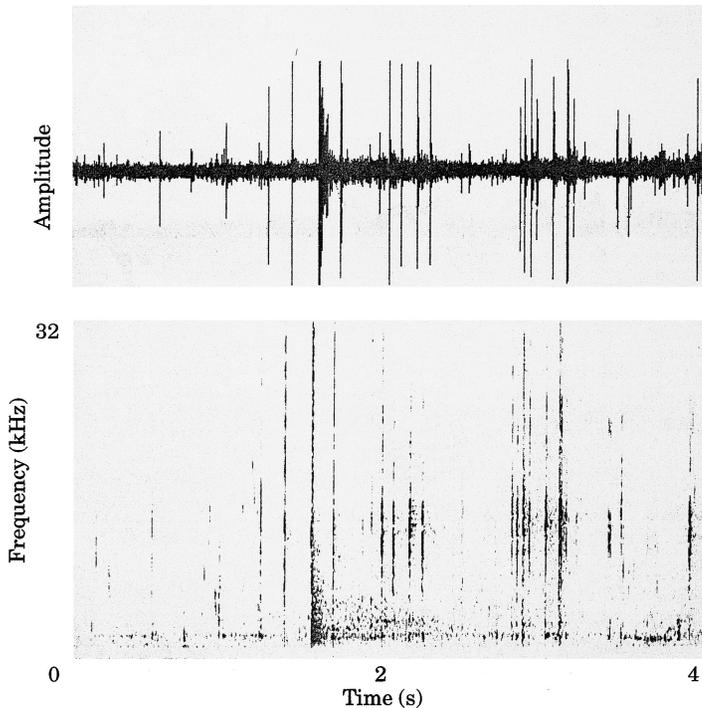


Figure 2. Waveform and spectrogram of 4 s of a transient killer whale echolocation click train. Note the uneven spacing between clicks.

between activities when adjusted for group size ($F_{5,67}=2.898$, $P=0.020$), and there was a significant negative correlation between group size and EI (Fig. 4; $F_{1,67}=4.060$, $P=0.048$). The adjusted mean EI was significantly higher for foraging whales than for resting, socializing, milling and slow-travelling whales combined ($F_{1,67}=9.171$, $P=0.003$). To ensure that the relationship between group size and EI did not result from our failing to detect sonar from distant individuals in large groups, we did an ANOVA in which we excluded all recordings of groups spread over more than approximately 1 km^2 . The result supported our previous finding ($F_{1,56}=4.35$, $P=0.042$).

For transient killer whales, an ANCOVA based on the entire data set yielded no evidence that EI is related to either activity or group size ($F_{3,82}=0.388$, $P=0.762$; $F_{1,82}=1.690$, $P=0.197$, respectively). Similarly, separate ANOVAs failed to relate either factor to EI ($F_{4,83}=0.370$, $P=0.829$; $F_{1,86}=1.928$, $P=0.169$, respectively). When we excluded the observations with $EI=0$ from the analysis, ANCOVA probabilities and an ANOVA relating EI and activity were also not

significant at $P=0.05$, but an ANOVA supported a negative relationship between group size and EI ($F_{1,25}=7.405$, $P=0.012$).

Effect of foraging areas

We noted differences in foraging behaviour between transient killer whales patrolling coastlines and those seeking prey in open water, similar to the differences reported by Saulitis (1993). Transients near shore typically swam in tight groups, rounding headlands or entering bays rapidly without surfacing. We saw 15 confirmed and nine probable kills of harbour seals near reefs, shoals or rocky shores during this study. Offshore, transients travelled 200–300 m apart and preyed on Dall's porpoises, *Phocoenoides dalli*, and on harbour porpoises, *Phocoena phocoena*. We confirmed that kills took place in three out of six pursuits of groups of one to four Dall's porpoises; two pursuits of single harbour porpoises ended with probable kills (Barrett-Lennard 1992). Both mean EI and isolated click production were greater for transient killer whales foraging along

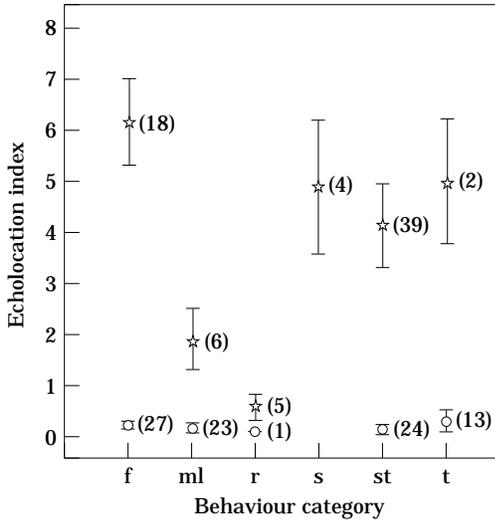


Figure 3. Mean echolocation index values for resident and transient killer whales, by behavioural activity. Stars and circles refer to residents and transients, respectively. Bars are standard errors and the number of sessions analysed in each category are in parentheses. Abbreviations: f=foraging, ml=milling, r=resting, s=socializing, st=slow travelling, t=travelling.

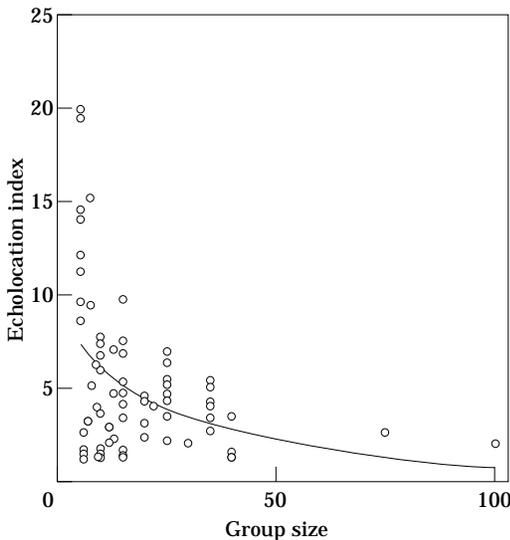


Figure 4. Echolocation index as a function of group size for resident killer whales. A logarithmic regression line is fitted to the data.

shorelines than for those in open water (Table II). No similar area-specific behaviour patterns were apparent with resident killer whales.

Water clarity

Ambient light levels declined evenly with depth at all three locations. Because there was no evidence of stratification, the Secchi disk transparencies (range 1.4–12.0 m, median=7.8 m) were taken as reliable indicators of relative water clarity. Echolocation index levels were independent of Secchi disk transparency for both residents ($F_{1,66} < 0.001$, $P = 1.00$) and transients ($F_{1,76} = 0.54$, $P = 0.46$) when recordings from all behavioural activities were combined. Similarly, there was no relationship between *EI* and water clarity when behaviour patterns were analysed separately.

DISCUSSION

The Cost of Echolocation

Transient and resident killer whales differ markedly in travel patterns, dive intervals and group sizes. Transients travel along shorelines more frequently, have longer average dive times and live in smaller groups than residents (Morton 1990). Because whales travelling near shore risk stranding or collision with the bottom, transients require more precise and more frequently updated positional information than do residents. The long average dive time of transients restricts their opportunities to acquire this information by visual reference to above-surface features, relative to residents. Because group members are likely to share information (Norris & Dohl 1980), the small group sizes of transients may require each transient individual to obtain more information directly from the environment than does each resident. These arguments suggest that transients should use echolocation more frequently than residents. The opposite finding that we report here suggests that the cost of echolocation may be substantially higher for transients than residents.

Differences in the cost of echolocation for the two forms of killer whale may result from differences in the abilities of their prey to detect and respond to sonar sounds. Most fish species have very low auditory sensitivity above 3 kHz (Hawkins & Johnstone 1978; Hawkins 1986) and thus are unlikely to detect much energy from killer whale clicks. Marten et al. (1988) tested the reactions of 13 species of bony fish to high-intensity

Table II. Echolocation indexes and isolated click production of transient killer whales in nearshore and offshore waters

	Nearshore (N=57)	Offshore (N=26)	P
Mean echolocation index (EI)	0.23 ± 0.07	0.02 ± 0.01	0.016
Mean number of isolated clicks/h per individual	12.76 ± 2.56	1.30 ± 0.52	0.004

Means are shown ± SE. P-values are for *t*-tests for equality of means. Five recorded sessions during which the whales were intermediate distances from shore were not included in this analysis.

sonar from bottlenose dolphins and detected no behavioural reactions. Astrup & Møhl (1993) reported responses of cod, *Gadus morhua*, to artificial high frequency clicks only at very high sound pressure levels. Thus, the cost of echolocation for fish-eating residents, in terms of the risk of alerting their fish prey, is probably low.

In contrast to fish, the pinniped and cetacean prey of transient killer whales have acute hearing to frequencies beyond 30 kHz (Møhl 1968; Andersen 1970; Terhune 1988), well within the range of killer whale sonar clicks. Seals that are alerted to the presence of transient killer whales may leave the water, move into shallow areas, or take refuge in kelp patches or on the bottom; sea lions may leave the water, aggregate into tight defensive clusters, or swim away at high speed (personal observations). Porpoises may also swim away from transients at high speed on erratic courses (personal observations), and dolphins and grey whales have been reported to move into shallow water when killer whales were nearby (Baldrige 1972; Würsig 1989). The acute hearing and anti-predatory behaviour of cetaceans and pinnipeds would appear to make echolocation costly for mammal-eating transients.

Our finding that transients echolocated more when near shore than when offshore may reflect a balance between the risks of stranding or collision and the costs of echolocation described above. Lower hearing sensitivity or vigilance of seals relative to porpoises and camouflaging noise from waves striking the shore may also make echolocation less costly inshore than offshore.

Sonar Characteristics

Relative to residents, transients used short and irregular echolocation trains composed of clicks that appeared structurally variable and low in

intensity. Sequences of short duration sounds that are irregular in timing and frequency structure more closely resemble random noise than do regular sequences. Thus, marine mammals would be less likely to detect transient than resident echolocation trains against background noise. Transients near shore may echolocate mainly for orientation as argued above, rather than for prey detection. Fenton (1984) described similar behaviour by bats that use echolocation to avoid obstacles but use other cues to detect prey. When near shore, quiet clicks are likely to provide good positional information, because topographic features are large and produce strong echoes.

Compared to click trains, isolated clicks could only provide crude information (Norris 1967). We suggest that they provide spatial 'snapshots' with little risk of alerting potential prey. Our difficulty in recognizing isolated clicks while listening to slowed recordings may be indicative of the problems faced by acoustically vigilant porpoises or pinnipeds. Killer whales foraging for elephant seals in the Indian Ocean, like the transients in our study, produced isolated clicks but very few click trains or calls (Guinet 1992).

Maximum distances between echolocating killer whales and their acoustic targets may be inferred from their click repetition rates. In experimental studies, echolocating bottlenose dolphins, *Tursiops truncatus*, and false killer whales, *Pseudorca crassidens*, allowed sufficient time after each click for an echo to return, plus a short lag, before emitting the next click (Morozov et al. 1972; Roitblat et al. 1990; Thomas & Turl 1990). If killer whales do the same, the repetition rates reported here indicate maximum target distances ranging from 6 to 480 m for residents and 40 to 800 m for transients. Close-range echolocation by residents may be used to assess and select fish and to track individual fish during pursuit. The

repetition rates of transients suggest that they rarely use sonar trains to assess, detect or track nearby prey, but rather to locate distant obstacles or prey. Our qualitative observation that transients decreased click intensities at higher click repetition rates suggests that they match sound levels to target distances, which would reduce their risk of warning prey.

Behavioural Contexts of Sonar Use

Results presented here and in Ford (1989) suggest that echolocation is used by resident killer whales for orientation and for locating and/or catching prey, and that the function of other vocalizations is primarily social. In this study, residents used echolocation most frequently during foraging. In contrast, Ford (1989) reported the highest call and whistle rates during socializing, and described residents foraging for periods longer than 1 h without using calls. Ford also noted that the first call in a series seemed to trigger responses from scattered group members; in this study, click trains did not appear to elicit responses. Travelling residents also had relatively high average echolocation index levels in this study, suggesting a possible function of echolocation in orientation and navigation. Our observation that click repetition rates seemed more variable during foraging than during travelling suggests that residents track targets through different ranges when foraging, and scan with echolocation when travelling.

Social factors appeared to constrain echolocation use under certain circumstances. For example, on two occasions residents that were approached by transients abruptly stopped calling, grouped up tightly and travelled away without echolocating.

We suggest two reasons why transients use little echolocation even when not foraging. First, transients may be alert for opportunistic encounters with prey even when not actively searching. During two encounters, transient groups that did not appear to be actively searching began rapid pursuits of dolphins that surfaced nearby. Second, the vigilance responses of potential prey may be persistent, and thus may reduce the hunting success of transients in the future. During this study we observed seals leaving the water and remaining ashore for more than 9 h after non-hunting killer whales passed nearby.

Group Size and Sonar Use

The negative correlation between sonar use and group size for resident killer whales suggests that sonar information is shared, which could occur in at least three ways. First, information obtained by echolocation may be communicated directly. Second, by monitoring the echolocation of group members, individuals may be able to infer the location of foraging hotspots, as reported in bat colonies (Wilkinson 1992). Third, killer whales may be able to interpret the echoes of clicks produced by other group members. Scronce & Johnson (1976) showed that a blindfolded captive bottlenose dolphin could detect a target using artificially produced clicks from a sound projector.

Transients frequently suppressed the use of click trains altogether. The negative correlation between echolocation and group size based on the sessions containing at least one click train, however, suggests that information is transferred between members of transient groups. The intermittent and low-intensity nature of transient sonar makes it unlikely that echo sharing is a common mode of information exchange. Rather, we suggest that information is probably transferred by some type of direct signalling. Indeed, isolated clicks may function partly as signals between group members.

Vision, Echolocation and Passive Listening

The lack of significant associations between echolocation index and water clarity for either residents or transients advises caution in extrapolating the results of echolocation experiments in captivity. Echolocation does not appear to take over where vision leaves off. In a study designed to examine echolocation use by a blindfolded dolphin during the capture of live fish, the dolphin repeatedly located and approached fish without producing any detectable echolocation sounds (Wood & Evans 1980). The experiment demonstrated that delphinids can detect, track and catch fish using non-visual external cues such as swimming sounds. This type of experiment has not been repeated on other odontocetes, but sound production by many fish species is well documented (Myrberg 1981; Hawkins 1986), and many species of cetaceans may make use of this source of information. In particular, sounds may be the principal cues used by non-echolocating mysticete whales to locate schools of small fish in turbid water.

Norris et al. (1961) also found evidence that echolocation and vision are not directly substituted. In their study, a bottlenose dolphin retrieved dead fish both when blindfolded and in clear water without a blindfold. Evans & Awbrey (1988) observed wild bottlenose dolphins using intense echolocation while feeding on dead fish in clear water. In the present study, foraging residents also used echolocation even in relatively clear water.

Transient killer whale attacks on Dall's porpoises were not preceded by echolocation in this study. Because the whales detected the porpoises well beyond underwater visual range, and were not observed scanning visually above the surface, passive listening appears to be the most likely detection mechanism. Dall's porpoise echolocation is centred on frequencies of 135–149 kHz (Au & Jones 1991) and thus may not be detectable by killer whales, which have little sensitivity above 105 kHz (Bain & Dahlheim 1994). With our recording equipment we detected the underwater sounds generated by porpoises surfacing and breathing up to 25 m away under quiet ambient conditions, and transients may make use of such sounds at much greater distances.

Transients foraging in open water show a tendency at times to avoid proximity to engine-powered vessels (personal observations; E. L. Saulitis, personal communication), which may be a response to the masking effect of engine noise. On three occasions we observed transients initiating pursuit of Dall's porpoises immediately after the study vessel's engine was shut off, and G. M. Ellis (personal communication) has reported similar observations. It appeared in each instance that engine noise impaired the whales' ability to detect their prey.

Implications for Echolocation in other Odontocetes

The patterns of sonar use by resident and transient killer whales indicate that echolocation is (1) both flexible and facultative, (2) constrained by inter- and intraspecific factors and (3) not obligately linked to conditions affecting vision. In other odontocetes, high echolocation costs may arise from the risk of attracting predators (especially killer whales), and not from the risk of alerting fish or cephalopod prey. Predator attraction costs are likely to be lower for schooling than

for solitary odontocetes, owing to protective properties of schools (Norris & Schilt 1988). We predict, therefore, that limited, cryptic and context-dependent echolocation is used by solitary odontocete species, and by individuals of gregarious species that are separated from their schools. As with transient killer whales, passive listening is probably important for orientation and prey detection to all odontocetes that are constrained in their use of echolocation. Finally, because most odontocete individuals probably do not scan constantly with echolocation, we predict that entanglements of cetaceans in fishing nets will be more effectively reduced by fitting nets with active sound-generating devices than with sonar reflectors.

ACKNOWLEDGMENTS

The late Michael Bigg helped us plan this project, and blessed it with his insight and enthusiasm. Jamie Smith was our principal advisor throughout. C. Matkin, O. von Ziegesar and E. Saulitis made possible the work in Prince William Sound. G. Ellis conducted the photo-identifications. We thank G. Barrett-Lennard, J. Kimmel, A. Reid, L. Saville and J. Smith for assistance in the field. Discussions with D. Bain, R. Baird, G. Ellis, C. Guinet, C. Matkin, A. Morton, E. Saulitis, T. Simila and J. Watson helped to shape our ideas and sharpen our focus. We thank C. Clark, A. Lotem, D. Westcott and two anonymous referees for helpful comments on drafts of the paper. Others who assisted were D. Burles, M. Dahlheim, P. Domenici, D. Ludwig, P. Matthews, S. Heard, W. Hochachka and D. Ward. The research was supported by the Canadian Natural Sciences and Engineering Research Council, the North Gulf Oceanic Society, and the Vancouver Aquarium. L. Barrett-Lennard received personal support from the British Columbia Science Council. Finally, we thank Parks Canada and the U.S. National Marine Mammal Laboratory for facilitating our research in the Queen Charlotte Islands and Prince William Sound, respectively.

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