

Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska

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Abstract: Killer whales, *Orcinus orca* (L., 1758), in the North Pacific are classified as three genetically distinct ecotypes: residents (fish-eaters), transients (mammal-eaters), and offshores (probable fish-eaters). Within the transient ecotype, three putative subpopulations have been identified by genetic analysis: West Coast transients, Gulf of Alaska transients, and AT1 transients. Here, we examine the behavior and vocalizations of the AT1 transients, which are found only in the Prince William Sound/Kenai Fjords region, to determine if their acoustic behavior distinguishes them from other genetically distinct transient subpopulations. We identified 14 discrete, pulsed calls in the vocal repertoire of the AT1 transients. These calls were entirely different than those of West Coast and sympatric Gulf of Alaska transients. Despite their large call repertoire, AT1 transients were silent most of the time, utilizing a foraging strategy of stealth, acoustic crypsis, and passive listening for locating marine-mammal prey. Unlike resident killer whales, AT1 transient vocalization types were context specific. For example, lone AT1 transients produced long-distance, high-amplitude pulsed calls in stereotyped sequences to locate other AT1 whales. In contrast, hunting individuals emitted low-amplitude pulsed calls to maintain contact with group members. The repertoire and call-usage patterns of the AT1 transients are consistent with genetic evidence that they are a unique, reproductively and socially isolated subpopulation in danger of extinction.

Résumé : Les orques, *Orcinus orca* (L., 1758), du Pacifique nord se répartissent en trois écotypes génétiquement distincts : les résidents (piscivores), les vagabonds (mangeurs de mammifères) et les orques du large (probablement piscivores). Trois sous-populations putatives ont été identifiées par analyse génétique dans l'écotype des vagabonds : les vagabonds de la côte ouest, les vagabonds du golfe de l'Alaska et les vagabonds AT1. Nous examinons ici le comportement et les vocalises des vagabonds AT1 qui se retrouvent seulement dans la région du détroit du Prince-William et des fjords de Kenai afin de déterminer si leur comportement acoustique les distingue des autres sous-populations génétiquement distinctes de vagabonds AT1. Nous avons identifié 14 appels à impulsions séparés dans le répertoire des vagabonds AT1. Ces appels sont complètement différents de ceux des vagabonds de la côte ouest et de ceux des vagabonds sympatriques du golfe de l'Alaska. Malgré leur riche répertoire d'appels, les vagabonds AT1 sont silencieux la plupart du temps et utilisent une stratégie alimentaire impliquant la sournoiserie, la dissimulation acoustique et l'écoute passive pour localiser les mammifères marins qui leur servent de proies. Contrairement aux orques résidents, les vagabonds AT1 ont des types de vocalises associés au contexte. Par exemple, les vagabonds AT1 solitaires produisent des appels à impulsions de longue distance et de grande amplitude en séquences stéréotypées afin de localiser d'autres épaulards AT1. Au contraire, les individus en chasse émettent des appels à impulsions de faible amplitude afin de maintenir un contact avec les membres du groupe. Le répertoire et les patterns d'utilisation des appels des vagabonds AT1 s'accordent avec les données génétiques pour établir qu'il s'agit d'une sous-population particulière, isolée reproductivement et socialement et en danger de disparition.

[Traduit par la Rédaction]

Introduction

In the coastal waters of the eastern North Pacific, killer whales (*Orcinus orca* (L., 1758)) occur in three sympatric, genetically distinct, nonassociating ecotypes: residents (or

fish-eaters), transients (or mammal-eaters), and offshores (Bigg 1982; Matkin et al. 1999; Ford et al. 2000). The three ecotypes are distinguished not by the extent of their ranges but by their feeding behavior and genetics. Resident killer whales travel in groups of regularly associating, stable

Received 4 November 2004. Accepted 24 June 2005. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 8 September 2005.

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matrilines (Bigg et al. 1987). Group-specific vocal dialects have been described for residents in southern Alaska (Yurk et al. 2002), the inside waters of British Columbia (Ford 1991), and the North Atlantic (Moore et al. 1988; Strager 1995).

Mammalian dialects are vocal traditions of sympatric or neighboring groups or subpopulations (Conner 1982; Ford 2002) and differ from geographically varying repertoires, which are vocal differences resulting from isolation between groups or subpopulations (Conner 1982; Lynch 1996). Resident killer whales are thought to use dialects as vocal identifiers of their matrilines (Ford 1991; Deecke et al. 2000; Miller and Bain 2000). Resident pods with similar dialects are genetically related (Barrett-Lennard 2000; Yurk et al. 2002).

Transient killer whales travel in less stable associations of two to six whales and sometimes alone (Ford and Ellis 1999). Unlike residents, transients sometimes emigrate from their maternal groups (Ford and Ellis 1999; Baird and Whitehead 2000). Moreover, most aspects of transient behavioral ecology, including feeding habits, range, and vocal repertoire, differ markedly from that of residents. It thus seems probable that patterns of transient acoustic behavior would also differ.

Three mammal-eating subpopulations have been identified in the North Pacific through mitochondrial and nuclear microsatellite DNA analysis: the West Coast subpopulation, which ranges between southeastern Alaska and southern California; the Gulf of Alaska subpopulation, which ranges from southeastern Alaska to at least Kodiak Island; and the AT1 subpopulation, which ranges from Prince William Sound to Kenai Fjords, Alaska (Barrett-Lennard 2000). Genetic analyses suggest no female dispersal and very restricted male-mediated gene flow among these subpopulations (Barrett-Lennard 2000).

The West Coast transient subpopulation (219 individuals; Ford and Ellis 1999) has a vocal dialect distinct from residents, including those occupying the same geographic areas (Ford and Hubbard-Morton 1990). Deecke (2003) identified 13 discrete pulsed calls in the West Coast transient repertoire. Whales in each region produced 9–11 call types, with 3 call types occurring over the entire range (over 2500 km). In comparison, the northern British Columbia resident subpopulation (216 individuals; Ford et al. 2000) produced 44 call types (Ford 1991). Until now, no studies have ascertained whether the culturally and acoustically distinct subpopulations found in resident killer whales also exist for transients.

Three functionally distinct vocalization types have been described for killer whales: clicks, pulsed calls, and whistles (Schevill and Watkins 1966; Diercks et al. 1971, 1973; Steiner et al. 1979; Awbrey et al. 1982; Ford 1989). Clicks are brief sound pulses typically emitted in series and used primarily for echolocation (Schevill and Watkins 1966; Ford 1989; Barrett-Lennard et al. 1996). Rapidly repeated clicks result in tonal sounds with rich harmonic structure known as pulsed calls and are thought to be used for behavioral coordination and group recognition (Ford 1989, 1991; Miller et al. 2004). Pulse repetition rates are reflected in a pulsed call's harmonic structure (Ford 1989). In contrast, whistles are tonal

sounds with little or no harmonic structure (Dahlheim and Awbrey 1982; Ford 1989) that are used primarily in social contexts in which animals are in close proximity to one another (Ford 1989; Thomsen et al. 2002).

Killer whales produce three types of pulsed calls. Discrete (stereotyped) pulsed calls are distinguishable spectrographically and by ear (Ford 1984; Bain 1986; Deecke et al. 1999) and fall into distinctive structural categories. These calls make up the group or population's vocal dialect or repertoire and are emitted consistently by all whales in a group over time (Ford 1989). Variable calls are miscellaneous calls that are not consistent in spectral structure (Ford 1989). Aberrant calls are distorted discrete calls emitted when killer whales engage in "excited" activities, such as socializing or feeding (Ford 1989).

The vocal behavior of resident killer whales has been studied extensively; that of transients is less well known. Transients are silent most of the time and difficult to observe owing to their hunting strategy of stealth (Morton 1990; Guinet 1992; Barrett-Lennard et al. 1996; Deecke et al. 2005). Their vocal behavior appears to be constrained by the acute hearing abilities of their prey (Barrett-Lennard et al. 1996; Deecke et al. 2005), and most vocal activity occurs only after marine-mammal kills and during social activity (Morton 1990; Deecke et al. 2005).

The small size of the AT1 subpopulation and its limited range create an unusual scenario in which all individuals in the subpopulation are familiar with one another because they regularly interact both physically and acoustically, a situation markedly different than that of the West Coast transients. In 1984, 22 AT1 transients were identified through photo-identification (Heise et al. 1992). Nine animals disappeared immediately following the 1989 *Exxon Valdez* oil spill and sightings of remaining individuals have declined (Matkin et al. 1999). Furthermore, the population of their primary prey species, the harbor seal (*Phoca vitulina* L., 1758), has declined drastically (Frost et al. 1999). In 2004, the AT1 subpopulation was designated as depleted under the US Marine Mammal Protection Act.

Here, we address two questions: (1) do AT1 transients possess a vocal repertoire distinct from that of other transient subpopulations and (2) is there a relationship between the vocalizations and behaviors of AT1 transients? We describe the vocal repertoire of AT1 transients, compare it with that of West Coast and Gulf of Alaska transients, and attempt to interpret the communicative function of their calls.

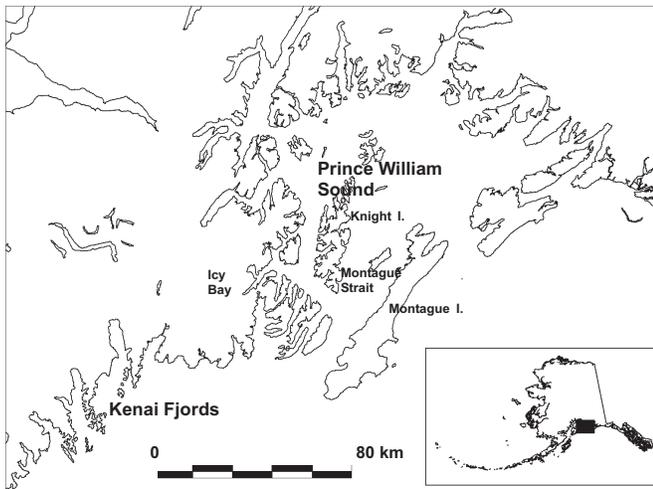
Methods

Study area and data collection

The study was conducted from May through September 1988–1992, in southwestern Prince William Sound, Alaska, an area of approximately 3500 km² (Fig. 1). Southwestern Prince William Sound is known historically as a foraging area for transient killer whales (Hall 1986; von Ziegeler et al. 1986; Leatherwood et al. 1990).

All observations were made at sea from a 6.1-m skiff with an 80-horsepower (1 horsepower = 746 W) outboard motor. We located killer whales by visual searches, by responding to VHF sighting reports by mariners, and rarely, by acoustic de-

Fig. 1. The study area located in Prince William Sound, Alaska.



tection. Each individual in the group was identified by fin shape and natural markings using a photographic catalogue (Heise et al. 1992). To confirm field identifications, photographs of each individual were taken using the method developed by Bigg et al. (1986). Following photo-identification, we moved at least 200 m ahead of the whales, shut off the engine and lowered an Offshore Acoustics hydrophone with a built-in preamplifier to a depth of 30 m. We began acoustic sampling and concurrently determined behavior by visually scanning all individuals in the group (scan sampling; Altmann 1974) and assigning an activity state to the group. Activity states were easily distinguished from one another by such characteristics as the directionality and synchronization of surfacings, speed of travel, presence of aerial and percussive behaviors, and interactions with prey (see below). We were able to confidently assign an activity state to the entire group because group sizes were small (2–12 individuals) and surface behaviors of individuals in the group were coordinated. Recordings were made using type 11 tapes in a Sony Professional WM-D6C cassette recorder (i.e., Ford 1989; Barrett-Lennard et al. 1996; Yurk et al. 2002). This system had an effective frequency response of 40 Hz to 15 kHz (± 3 dB). After the whales passed the research boat and were oriented away from the hydrophone, we repositioned the boat approximately 200 m ahead of them and began a new acoustic and behavioral sampling period. Behavioral data linked to tape counter numbers and beginning and end times of the sampling period were notated on data sheets. We repeated this procedure as long as weather, light conditions, and the behavior of the animals permitted (up to 24 h).

Activity state categories

Activity state categories were modified from Jacobsen (1986), Ford (1989), Barrett-Lennard et al. (1996), and Saulitis et al. (2000), and are defined as follows:

- **Socializing** — killer whales engaged in chasing, rolling and aerial displays such as breaching, spy-hopping, and fluke- and flipper-slapping (Jacobsen 1986).
- **Milling** — each killer whale surfaced independently of the others, both in timing and in direction of movement. They did not travel, and surface displays were not seen.

- **Open-water foraging** — killer whales searched for prey at least 1-km offshore. Surfacings of the whales were not synchronized or unidirectional and were interspersed by dives of 10 min or longer during which the whales often traveled a kilometre or more (Saulitis et al. 2000). Mean group size in offshore foraging was 5.4 whales (± 2.6 , $N = 16$). Most attacks on Dall's porpoises, *Phocoenoides dalli* (True, 1885), occurred following periods of offshore foraging (Saulitis et al. 2000).
- **Nearshore foraging** — killer whales slowly traveled within 20 m of shore, typically following the contours of the shoreline, entering bays and narrow passages, and circling islets (Saulitis et al. 2000). Mean group size in nearshore foraging was 3.3 whales (± 1.4 , $N = 30$). Most kills made during this behavior were of harbor seals (Saulitis et al. 2000).
- **Group travel** — killer whales swam in a line-abreast pattern in one or more groups, moving in a consistent direction at speeds of up to 6 km/h (Barrett-Lennard et al. 1996). They typically swam within a few body lengths of their neighbors.
- **Lone whale travel** — encounters with lone transients.
- **Resting** — the killer whales' movements and breathing patterns were closely synchronized, and they moved at speeds of < 3 km/h (Ford 1989). Resting whales were grouped in presumed maternal units and typically surfaced within a body length of their neighbors (Jacobsen 1986).
- **Attack on marine mammals** — pursuit or capture of other marine mammals often involved high-speed chases, aerial leaps, or repeated dives in one area.
- **Feeding on marine mammals** — this was determined by seeing prey in the mouths of killer whales or by repeated diving in one area in the presence of patches of blood, oil, and (or) prey remains, often in association with feeding birds.

Acoustic repertoire description

We identified the discrete call repertoire by first transcribing all recordings onto data sheets using symbolic representations that reflected the calls' tonal shifts (after Ford 1989). We then selected examples of each call type for analysis by examining real-time spectrograms (frequency vs. time plots) on a Kay Elemetrics DSP-5500 sonograph analyzer, using a frequency range of 0–8 kHz and a filter bandwidth of 40 Hz. Audible call characteristics and structural differences visible on the spectrogram were used to distinguish call types. Several studies have documented the reliability of aurally and visually (by examination of spectrograms) categorizing killer whale calls (i.e., Ford 1984; Bain 1986; Deecke et al. 1999; Yurk et al. 2002).

Every discrete pulsed call that was portrayed clearly on the sonograph's monitor was used for measurement of call characteristics. Using Ford (1987) as a model, we measured duration (ms), whistle component frequency (upper frequency component), and frequency intervals between sidebands (harmonics) (Hz). The distance between sidebands reflects the pulse repetition rate (Watkins 1967). Some calls were separated into segments by identifying sudden shifts in pulse repetition rates or silent intervals (Ford 1984; Yurk et al. 2002). Descriptive statistics were calculated for all discrete

call measurements. To measure the amount of variability in each structural component, we calculated the coefficient of variation (CV) for each call type ($CV = SD/\text{mean} \times 100$; Ford 1987). The acoustic repertoire of discrete calls was compared with that of West Coast transients and Gulf of Alaska transients, both aurally and spectrographically. Our conclusions were verified by H. Yurk and V. Deecke, University of British Columbia.

Counts of whistles and variable and aberrant calls were made but not analyzed spectrographically because of their extreme variability. Likewise, echolocation clicks were not analyzed because the frequency response of our recording equipment could not reliably detect their higher frequency components (see Barrett-Lennard et al. 1996).

Statistical analysis of call associations

On several occasions, we encountered male AT1 transients traveling alone. We were surprised to discover that these individuals were highly vocal and that they appeared to emit certain discrete pulsed calls in predictable sequences that were interspersed by silent periods. To investigate this, we tallied the number of times a given call was followed by itself and by each of the other calls for every continuous series of calls. To examine which pairs of calls tended to be produced together, we tested the null hypothesis that the probability of a specific call being produced was independent of the call immediately preceding it by examining transition frequency and probability matrices (Kemeny et al. 1959; Davis 1973; Lewis and Gower 1980), and tested for independence of call production using the log-likelihood ratio (G statistic) (Zar 1984).

To determine whether single killer whales emitted sequences of more than two calls, we conducted a Markov chain analysis (Davis 1973). Markov chains are sequences in which a given state (call) is dependent, in a probabilistic manner, on preceding states (calls) (Kemeny and Snell 1960; Davis 1973; Lewis and Gower 1980). Using results of the log-likelihood ratio test, we chose call transitions that occurred more than expected (had the highest G statistics). From these transitions, we constructed all possible three- and four-call sequences and calculated their expected probabilities (after Gehrich 1984). We compared the three- and four-call sequences with the highest expected probabilities of occurring to what we observed, but because of our small sample sizes and the complexity of interpreting multi-dimensional contingency tables, we did not conduct statistical analyses (Steel and Torrie 1960).

Finally, we raised the one-step transition probability matrix to increasingly higher powers until the rows of the matrix were identical (row convergence) as another way of examining whether single killer whales emitted calls in a random or stereotyped manner (Davis 1973). When the matrix is raised to the " n th" power, the resulting matrix represents the expected probability of progressing from one call to another in " n " steps. When row convergence is reached, the probability of occurrence of a call is independent of the initial call. The number of steps required to reach row convergence represents the degree of randomness in a particular call sequence.

Analysis of call and activity state relationships

To test the null hypothesis that the call types emitted by killer whales did not differ among activity states, counts were made of each vocalization type in each sampling period. If more than one activity was observed in a sampling period, the sampling period was partitioned by activity, and counts of each vocalization type were noted for each activity state. Thus, within each activity state, vocalization counts were independent; however, some counts in different activity states came from the same encounter. Since we tested for differences in vocalization counts between activity states, our approach is conservative. Six activity states and six call types were selected. We eliminated rare activities and vocalizations and activities in which vocalizations were never heard. The counts of each vocalization type were divided by the duration (min) of the sampling period. The rate was divided by the number of whales present for an estimate of calling rate/whale. These data were arcsine transformed (see Zar 1984) and used to test the null hypothesis that there was no difference in the proportion of the six call types within each of the six activity types using one-way ANOVAs by the general linear models (GLM) procedure and Scheffé's multiple contrasts (Zar 1984; after Ford 1989). The relationship between vocalizations and behavior was further examined using contingency tables.

Results

Vocal repertoire

We observed members of the AT1 subpopulation during 227.6 h and recorded 6344 calls (545 samples) during 4622 min of acoustic sampling time. We recorded clicks in 7% of samples. Whistles made up 38.9% of all vocalizations recorded. Pulsed calls made up over half of the vocal repertoire (61.1% of all calls recorded). We recorded 1241 variable pulsed calls (19.6% of total calls), and aberrant pulsed calls were recorded in 6% of the vocal samples.

Fourteen discrete pulsed call types were identified (Fig. 2) and were the most common calls recorded in this study (41.5% of total calls). We analyzed 882 discrete calls, with an average of 5.29 characteristics measured per call (range 2–10).

Aural and spectrographic comparisons between AT1 transient and West Coast transient repertoires yielded no matches (for sonograms see Deecke et al. 2005). Likewise, AT1 transients shared no discrete calls with Gulf of Alaska transients recorded in the same area (Fig. 3). However, the Gulf of Alaska transient call classifications presented here are still tentative. Not enough recordings have been made to unequivocally verify all of their discrete call types (H. Yurk, personal communication).

Call associations for lone males

Two AT1 males were recorded while traveling alone, which provided a unique opportunity to identify with certainty the individual producing a particular sequence of calls. During the three encounters involving lone males, 488 discrete pulsed calls were recorded. Lone males repeated some calls more often than expected, and others, less often than expected ($p < 0.001$; Table 1) and produced only 8 of

Fig. 2. Sonograms of the 14 discrete, pulsed calls of the AT1 subpopulation of killer whales, *Orcinus orca*.

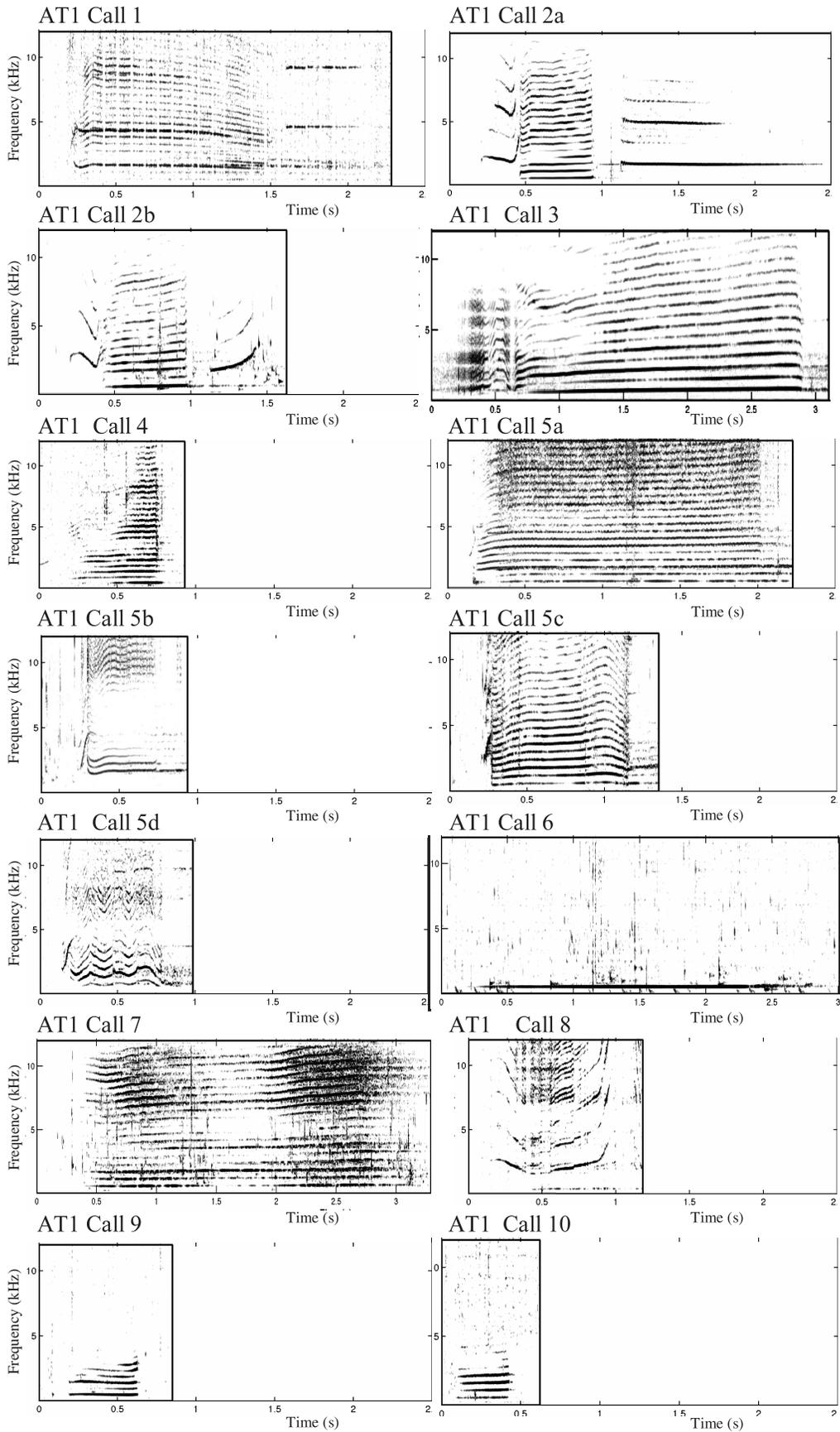


Fig. 3. Tentative classifications of some Gulf of Alaska (GOA) transient killer whale calls recorded in the Kenai Fjords/Prince William Sound region.

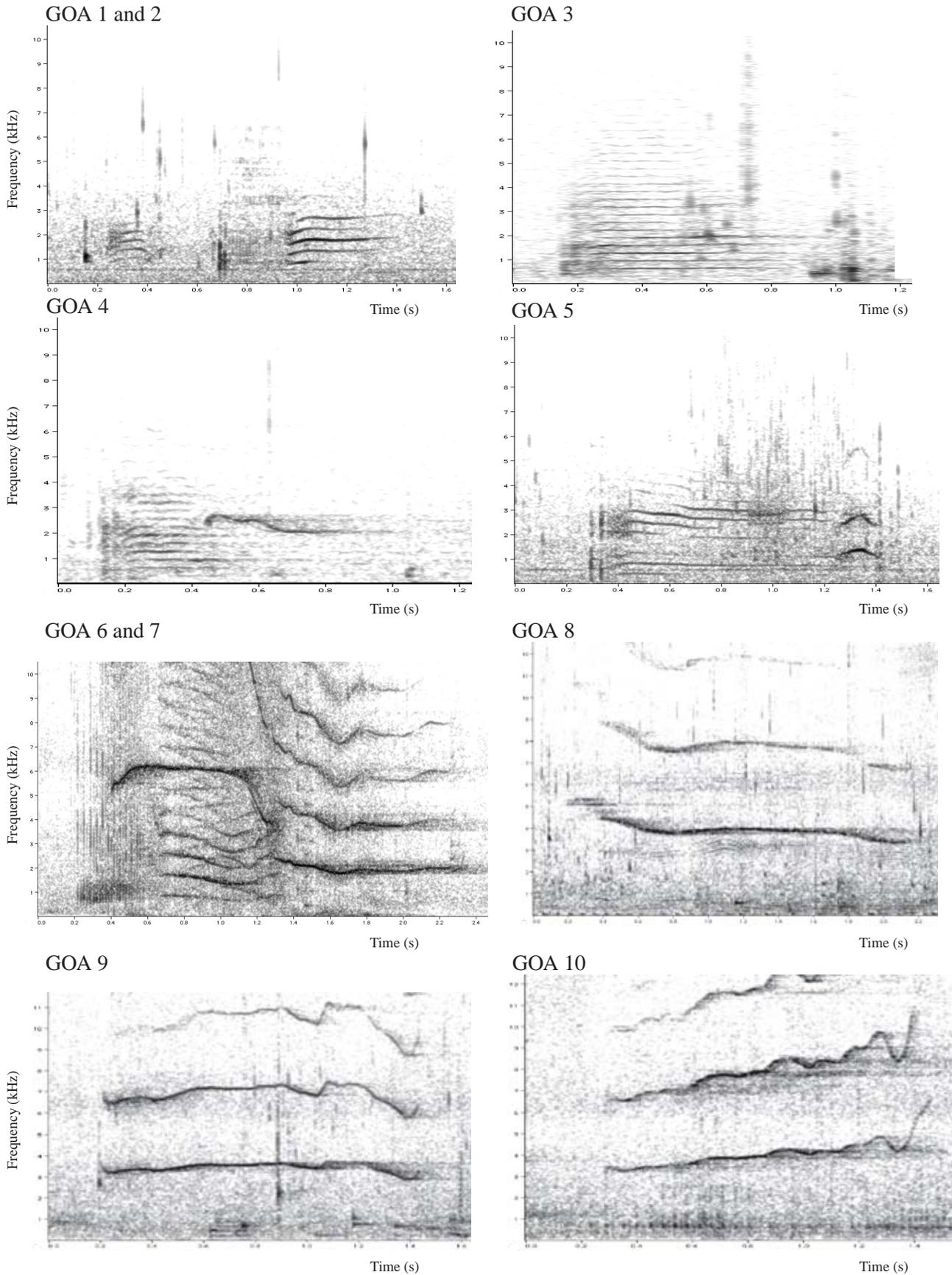


Table 1. Partial *G* statistics for diagonal elements of the transition probability matrix reflecting which calls tended to be repeated more than expected by lone AT1 transient killer whales, *Orcinus orca*.

Call repetition	Observed probability	Expected probability	<i>n</i>	Observed – expected probabilities	Partial <i>G</i> statistic
1–1	0.188	0.254	22	–	74.7
2–2	0.732	0.154	52	+	124.5
3–3	0.462	0.057	12	+	4.6
4–4	0.067	0.033	1	+	0.7
5a–5a	0.095	0.109	10	–	31.8
5b–5b	0.540	0.109	27	+	45.7
5c–5c	0.438	0.104	21	+	33.8
8–8	0.929	0.061	26	+	13.9

Note: Overall *G* statistic = 471.4, *df* = 7, *p* < 0.001, *n* = 171 pairs of repeated calls.

Table 2. Partial *G* statistic results for the transition probability matrix for calls made by lone AT1 transient killer whales showing which calls tended to follow other calls more than expected.

First call	Second call							
	1	2	3	4	5a	5b	5c	8
1	–	–	0	0	0	+	+	0
2	–	++	0	+	–	0	0	0
3	–	0	++	+	0	0	0	0
4	0	0	0	0	+	0	0	0
5a	++	–	0	0	0	–	0	0
5b	–	0	0	0	0	++	0	0
5c	–	0	0	0	+	0	++	0
8	0	0	0	0	0	0	0	++

Note: Overall *G* statistic = 134.0, *df* = 63, *p* < 0.001, *n* = 460 call transitions. The minus indicates that the partial *G* statistic is less than –1, zero indicates that the partial *G* statistic is between 1 and –1, one plus indicates that the partial *G* statistic is greater than or equal to 1 and less than 10, and two pluses indicate that the partial *G* statistic is 10 or greater.

14 AT1 call types. Call sequences occurred in predictable patterns and were significantly linked to the calls that immediately preceded them (*p* < 0.001; Table 2). For example, calls 1 and 5a occurred together more often than expected, and calls 1, 2, 3, 5b, 5c, and 8 were repeated more often than expected (Table 2).

Of the large number of potential three- and four-call sequences (including call repetitions) that could be generated from eight calls types, only a few were actually produced by single killer whales (Table 3). Observed and expected conditional probabilities differed for all of the three- and four-call sequences (Table 4). The most common three-call sequence was 2–2–2, which made up 11.46% of all three-call sequences (Table 4).

In the Markov chain analysis, row convergence was reached in 78 steps, confirming that patterns of call production of single killer whales were stereotyped. The squared and cubed matrices confirmed that multiple repetitions of call 2 occurred more often than expected. The probability of moving from call 2 to call 2 in two steps (sequence 2–2–2) had the highest expected probability (0.55) and the observed probability (0.66) was higher than expected. Likewise, the observed probability of sequence 2–2–2–2 was higher (0.53) than expected (0.39).

Table 3. The number of distinct three- and four-call sequences (including repetitions) produced by lone AT1 transient killer whales.

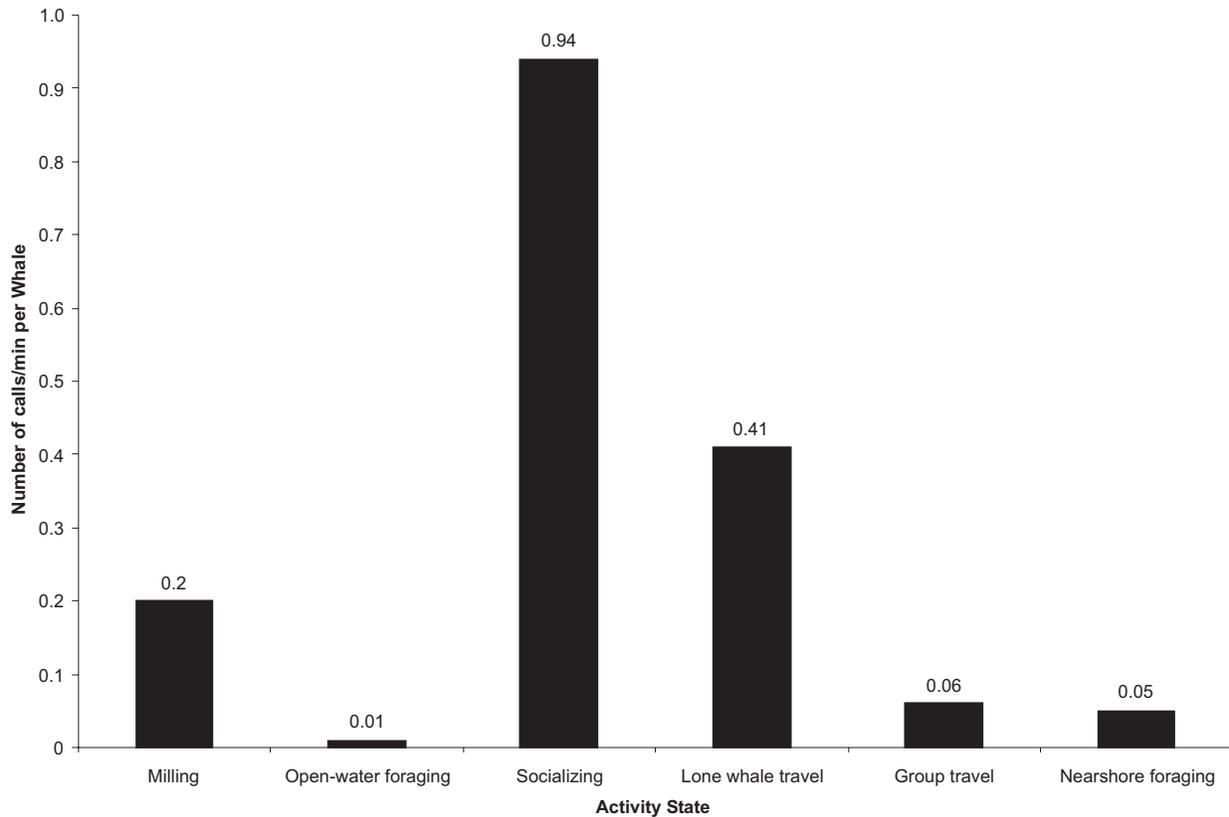
First call of sequence	Number of three-call sequences	Number of four-call sequences	<i>n</i>
1	20	36	117
2	11	17	71
3	5	5	26
4	5	7	15
5a	18	31	105
5b	13	15	50
5c	12	17	48
Total	84	128	432
Number of potential sequences	512	4096	

Analysis of relationships between vocalizations and activities

The calling rate for six activity states is shown in Fig. 4. The calling rate was highest during socializing (Fig. 4), a rare behavior that made up only 9% of the AT1 activity budget (Fig. 6). In fact, 73% of all calls recorded in this study occurred during this activity state. A majority of those calls were whistles, which are close contact social signals (Ford 1989; Thomsen et al. 2002; Fig. 5). Whistles, which have frequencies well within the hearing range of transient killer whale prey, were never heard during foraging or when whales were recorded alone. Vocalizations were rare during foraging and group travel, with rates of <0.1 calls/min per whale (Table 5).

For analysis of relationships between vocalizations and behaviors, we used the six activities in which the killer whales spent most of their time and six calls that had sufficient sample sizes (Table 5). Because the low-amplitude calls (calls 9 and 10) were always heard together, we grouped them under the name “quiet calls” for these analyses.

The mean calling rate of the six vocalization types differed significantly in nearshore foraging, socializing, and lone whale travel (Table 5). Calls other than quiet calls appeared to be suppressed during nearshore foraging. Calls 1 and 2 and whistles occurred significantly more than other calls during socializing and this was the only behavior in which whistles were heard more often than expected. Group

Fig. 4. Calling rate (number of calls/min per killer whale) in each activity state.**Table 4.** Observed and expected conditional probabilities of the most common ($n > 6$) three- and four-call sequences given by lone AT1 transient killer whales and the overall percentage of the sequences in the lone whale data set.

Sequence	Observed probability	Expected probability	n	Percent occurrence
2-2-2	0.66	0.17	33	11.46
5c-5a-5b	0.32	0.26	10	3.47
5b-5b-5b	0.31	0.16	8	2.78
5b-5a-1	0.25	0.15	8	2.78
1-5a-1	0.23	0.16	18	6.25
5a-1-5c	0.21	0.13	16	5.56
5a-1-5a	0.21	0.16	17	5.90
5a-1-5b	0.20	0.14	16	5.56
2-2-2-2	0.53	0.39	23	9.06
5b-5b-5b-5b	0.27	0.16	7	2.76
5c-5a-1-5c	0.26	0.05	7	2.76
5a-1-5a-1	0.22	0.11	16	6.30

travel, offshore foraging, and milling had no significant differences in calling rate per whale. Killer whales were silent during group travel and offshore foraging. However, milling had a more uniform distribution of calls than did any of the other behaviors (Fig. 5). This may be due to the fact that milling, rather than being a distinct behavioral category, often occurs during other activities such as feeding on marine mammals, resting, foraging, and socializing.

Contingency table analysis substantiated the results of the ANOVAs; namely, that the frequency of the six calls was

not independent of behavioral state (χ^2 test, $\chi^2 = 2060.7$, $p < 0.001$). The most highly correlated call/activity state was quiet calls/nearshore foraging. Whistles occurred less than expected in all activities except in socializing.

Based upon field observations and the results of statistical analyses on the relationship between activity states and call types, the vocalizations of the AT1 group were grouped into four functional categories:

- Loud calls — high-amplitude, discrete, long-distance communication calls that could be heard up to several kilometres away (calls 1, 4, and 5a-5d).
- Foraging calls — low-amplitude, stereotyped pulsed calls (calls 6, 9, 10) emitted when hunting. In contrast to calls 9 and 10, which are very short, call 6 had an average length of >3 s and a much lower frequency (rarely exceeding 600 Hz) than any other AT1 call (Fig. 2).
- Social calls — whistles, variable, and aberrant calls, which were emitted by groups of killer whales engaged in non-hunting behaviors. These calls were most common during socializing, when whistles made up 46.3% and variable calls made up 18.4% of the total calls heard. Socializing occurred after marine-mammal kills, when groups of whales joined together, and during sexual activity.
- Echolocation clicks — clicks occurred only during feeding on marine mammals, socializing, milling, and fish pursuit. These high-amplitude clicks, which resembled bangs, machine gun bursts, or loud claps, were given singly or in irregular sequences and were radically different from the cryptic clicks described by Barrett-Lennard et al. (1996). The click trains described for resident killer whales (Ford 1989) were not heard.

Fig. 5. Frequency of occurrence of call types for each behavioral category of killer whales. Q, quiet calls (calls 9 and 10 combined); V, variable calls; W, whistles.

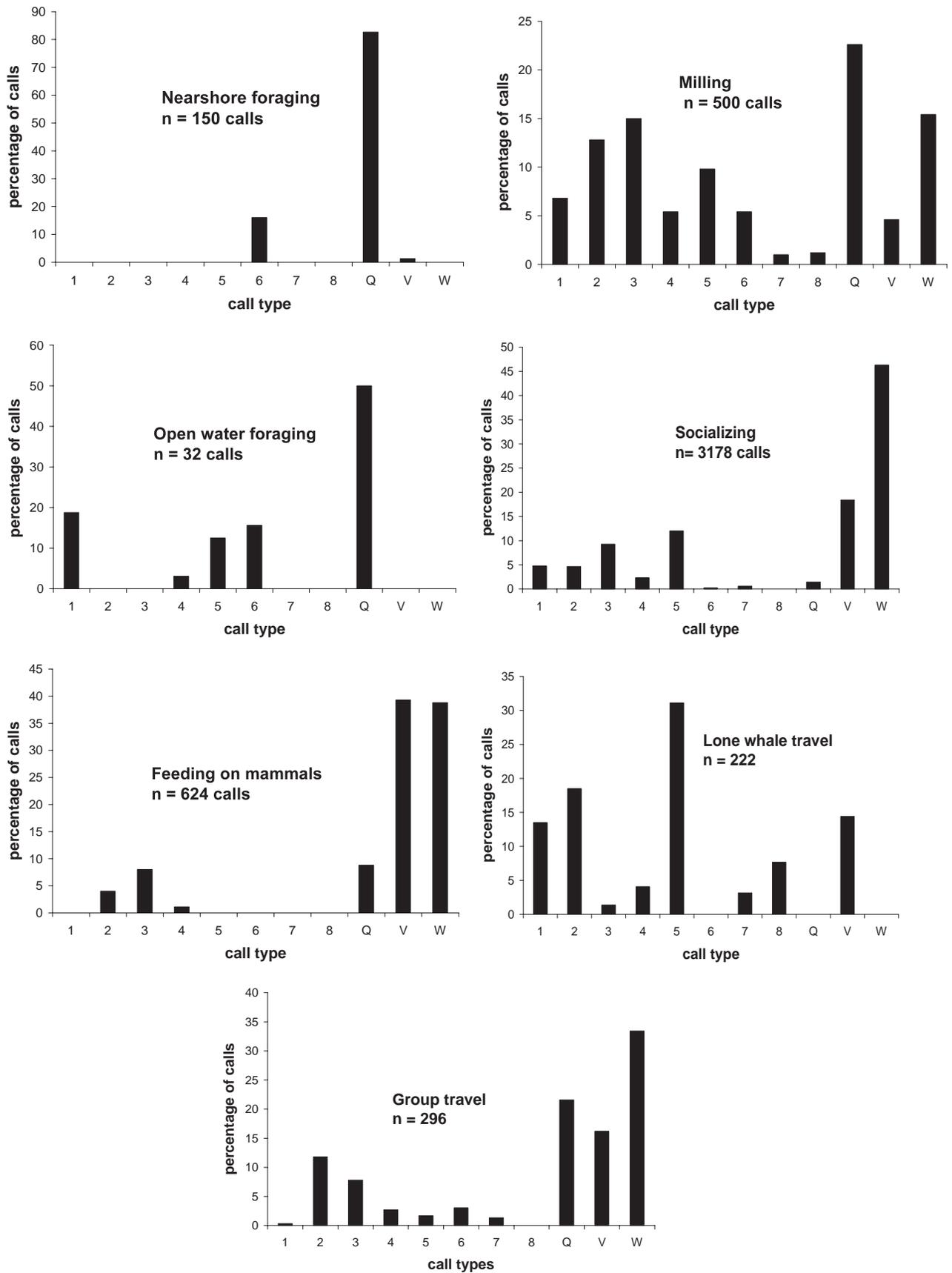
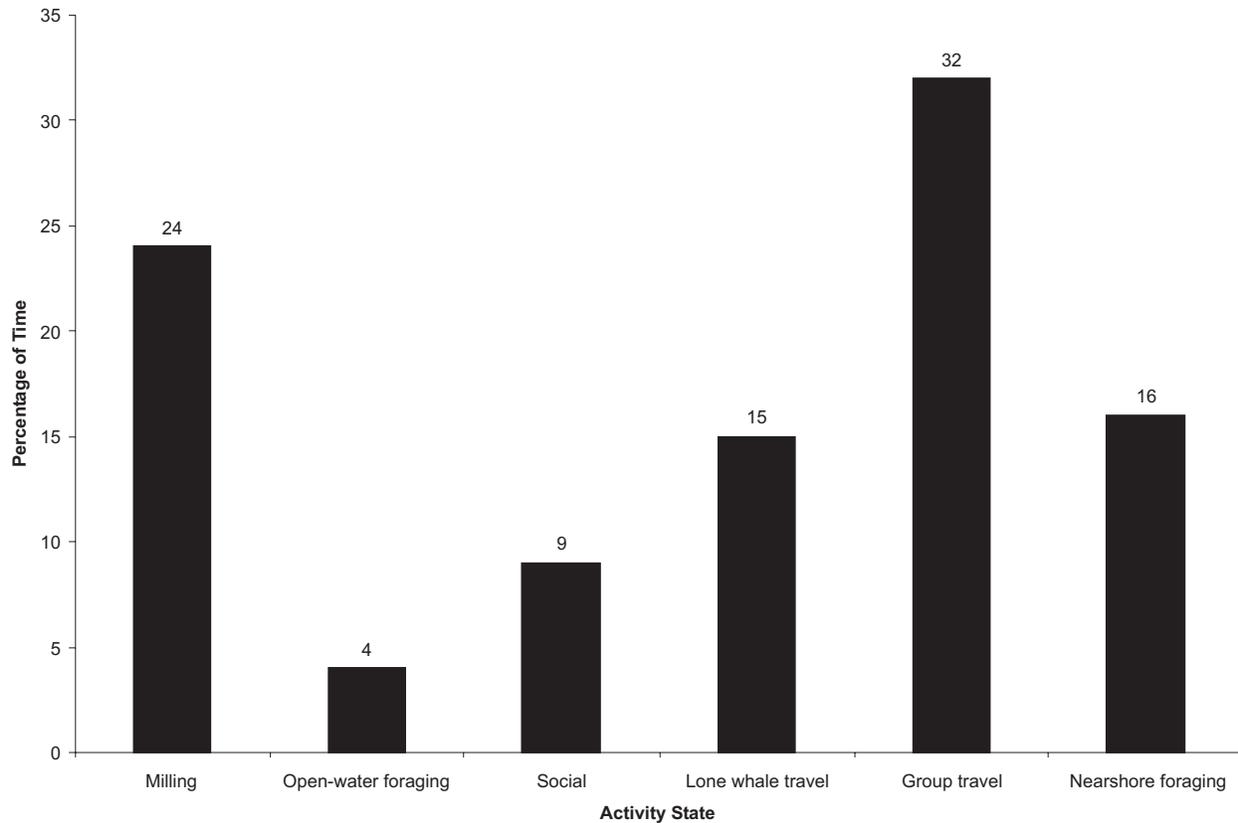


Fig. 6. Percentage of time spent by the AT1 subpopulation of killer whales in each of six activity states.

Discussion

AT1 transient dialect

AT1 transients share no discrete call types with either West Coast or sympatric Gulf of Alaska transients. Likewise, AT1 transient calls differ from those of sympatric Southern Alaska residents. Using the definition put forth by Conner (1982) and Ford (2002) that mammalian dialects are distinct vocal traditions of sympatric or neighboring populations or groups, we propose that the AT1 call repertoire is a dialect. However, the degree of vocal variation among transient subpopulations differs profoundly from that of resident killer whales, which exhibit pod-specific dialects within populations — specifically, lack of call sharing by members of the same population.

Genetic and acoustic studies have shown that maternal relatedness is reflected in the degree of call sharing among resident killer whale pods (Barrett-Lennard 2000; Yurk et al. 2002). The more closely related the resident pods, the more call sharing observed (Yurk et al. 2002). In this study, the lack of overlap in the discrete call repertoires of AT1 transients, other transients, and residents suggests that they are socially isolated. The AT1 transients have a single mitochondrial haplotype (Barrett-Lennard 2000). Their separation from other transients appears to be the oldest and most complete of the three subpopulations; consequently, Barrett-Lennard (2000) suggests that the isolation of the AT1 subpopulation is likely to result in its extinction, as currently only eight individuals remain and no calf recruitment has been observed since 1984 (Matkin et al. 2003). Barrett-

Lennard (2000) proposed that transient subpopulations are cohesive social units and that individuals rely on acoustic recognition to maintain (or avoid) contact. The ability of killer whales to maintain long-term cultural traditions such as feeding specializations makes subpopulation cohesion advantageous (Barrett-Lennard 2000). We never observed AT1 transients associating with other sympatric transients or residents. While Gulf of Alaska transients were uncommon visitors to our study area, residents were observed regularly.

Genetic isolation of subpopulations can lead to variation in vocal dialects (Krebs and Kroodmsa 1980). Likewise, social isolation can lead to divergence in dialect through errors in call reproduction and in call innovation and extinction (Ford 1991). Genetic evidence suggests that the AT1 transients have been separated from other transients for many generations (Barrett-Lennard 2000); our acoustic results reflect this separation. Unlike transients, resident pods with different vocal dialects frequently mix, and dialects conveying pod affiliation may facilitate their social interactions (Ford 1991) and inbreeding avoidance, i.e., mating with acoustically dissimilar individuals (Barrett-Lennard 2000; Yurk et al. 2002). The distinct dialect of the AT1 transients may, in contrast, facilitate a lack of mixing with other transients.

We identified 14 discrete pulsed calls in the AT1 transient dialect; Deecke (2003) catalogued 13 discrete pulsed calls in the West Coast transient dialect. Although one must be careful when comparing absolute dialect sizes across subpopulations owing to fine differences in categorization methods, we feel confident in arguing that the size of the AT1 dialect is consistent with that of a much larger population. The AT1

Table 5. Mean calling rate (number of calls/min) per killer whale for six categories of calls during six behaviors, with one-way ANOVA results.

Behavior	Call category						Total	Whistle	Quiet call (calls 9 and 10 combined)	p	Scheffé's multiple contrast result
	2	3	5a	6	9	10					
Milling	0.05	0.02	0.03	0.02	0.07	0.01	0.20	0.1780			
Nearshore foraging	0.00	0.00	0.00	0.00	0.05	0.00	0.05	0.0001	Quiet call > all others		
Socializing	0.05	0.12	0.12	0.00	0.07	0.58	0.94	0.0001	Whistle > all others; 2, 3, >5a, 6, quiet call		
Group travel	0.02	0.01	0.00	0.00	0.02	0.01	0.06	0.1750			
Lone whale travel	0.12	0.03	0.14	0.02	0.10	0.00	0.41	0.0059	Whistle < 1, 3		
Open-water foraging	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.1300	Whistle > 2, 5a		
Total	0.24	0.18	0.29	0.04	0.32	0.60	1.67				

subpopulation, which numbered only 22 in 1984, is much smaller than the West Coast subpopulation, and it has a much smaller range. Consequently, all members of the AT1 subpopulation are likely to be within frequent acoustic contact with one another. Furthermore, as their numbers and range are small, social bonds among members of the AT1 subpopulation may be stronger than those within other transient subpopulations, favoring the retention of a complex dialect and communication system.

More significantly, AT1 transients have a high microsatellite DNA diversity, suggesting that the subpopulation in Prince William Sound may be made up of maternal groups that, at one time, were part of a much larger population that ranged over a larger area (Barrett-Lennard 2000). The number of calls in the AT1 transient dialect supports this theory. Indeed, transients with the AT1 haplotype have recently been discovered in the Bering Sea and Russia; however, nuclear microsatellite analysis indicates that there have been no recent matings between those individuals and the AT1 transients (L.G. Barrett-Lennard, unpublished data).

Barrett-Lennard (2000) suggests that the higher genetic diversity in transients than residents implies that they may receive some limited gene flow from other killer whale subpopulations. Despite theoretical mating opportunities with sympatric Gulf of Alaska transients and residents, the lack of recruitment in the AT1 transient subpopulation indicates that they are indeed reproductively isolated, as suggested by their unique vocal dialect, or that other factors are impeding their reproductive success.

Acoustic behavior of AT1 transients

While AT1 transients were silent most of the time, males traveling alone were often quite noisy, producing stereotyped sequences of loud discrete calls over extended periods. These vocalizations, each between 1 and 4 s long, were rarely produced in other behavioral contexts. They contrasted markedly with quiet hunting calls, which averaged less than 0.5 s long. East and Hofer (1991) suggest that long calls provide more accurate directional information than short calls.

Directionality is also influenced by a call's frequency. Quiet hunting calls exhibited no harmonic energy above 4 kHz, whereas loud calls were rich in harmonic energy well above 6 kHz (Fig. 2). Miller (2002) demonstrated that the higher frequency harmonics of killer whale calls (>5 kHz) are more directional than lower frequency harmonics owing to the size of whale's melon, which limits the size of wavelengths it can focus. This mixed directionality likely allows receivers to perceive the orientation of signalers and to coordinate their activities accordingly (Miller 2002). Likewise, spinner dolphin, *Stenella longirostris* (Gray, 1828), whistle harmonics increase in directionality with frequency (Lammers et al. 2003). Lone killer whales making long discrete pulsed calls changed orientation frequently, apparently vocalizing in more than one direction to make contact with other whales. Moreover, several of these calls contained high-frequency whistle components, which are directional and also can convey information about a caller's orientation (Miller 2002) and possibly its identity.

In every instance, loud calling began when the separated killer whales were well out of visual range of each other. Aggregations (larger than those used for hunting) of AT1

transients suggest that affiliations between all members of this group are important. Loud calls may aid in bringing dispersed groups of whales together for social purposes, and perhaps, for food-sharing (Guinet 1992).

Why do AT1 males produce stereotyped call sequences? If lone transients were simply trying to locate other group members and to advertise their identity, wouldn't one repeated call with a high-frequency whistle component be sufficient? West Coast transients traveling alone emit two call types (J. Ford, personal communication). Similarly, long-distance communication in many primate groups is accomplished with only a few calls (Horr 1972; Mackinnon 1974; Byrne 1981; Brown and Waser 1984; Dittus 1984; Masatata and Biben 1987). In contrast, lone AT1 males emitted several discrete call types, suggesting that call sequences encode multiple pieces of information (such as the caller's sex, motivational state, or distance from the receiver) or that multiple calls enhance the effectiveness of long-distance communication. Call sequences can convey more information over greater distances than can tonal characteristics alone. Although nuances of pitch and tone quality are rapidly lost through attenuation of sound, pulse repetition rate and stereotyped patterns of call emission are not lost as readily (Waser 1982).

Loud calling was a relatively rare behavior in AT1 transients. AT1 killer whales spent almost 90% of their time foraging and traveling (Saulitis et al. 2000), behaviors characterized by silence. A traveling or foraging whale emitted <1.2 calls every 20 min. Maintaining silence while foraging and traveling is clearly advantageous for transient whales, whose marine-mammal prey can easily detect their calls (see Deecke et al. 2002). On the other hand, foraging must be accompanied by a degree of coordination because prey capture is a group activity and food is shared (Baird and Dill 1996).

Quiet calls may function to allow coordination of AT1 killer whales while they maintain acoustic crypsis from potential prey. Quiet calls were emitted intermittently and unpredictably during foraging, reducing their detectability. Detection thresholds in harbor seals, one of their primary prey, are enhanced by repetition of sounds (Turnbull and Terhune 1993). Quiet calls were low in amplitude and short in duration compared with other AT1 calls, further reducing detectability, as low frequencies eliminate directional cues (Miller 2002). At the same time, their stereotyped harmonic structure may help foraging killer whales maintain contact. Guinet (1992) describes very quiet "short distance contact calls" used when killer whales were hunting marine mammals off the Crozet Archipelago.

Some marine-mammal prey of AT1 transients, including harbor seals and harbor porpoises, *Phocoena phocoena* (L., 1758), are known to have good underwater hearing as low as 1 kHz (Schusterman et al. 1972; Wolski et al. 2003). Deecke et al. (2005) argues that limited vocal communication is the primary strategy used by transients to avoid detection by prey. However, the use of call 6, a foraging call with a frequency that rarely exceeded 600 Hz and a length of >3 s, by AT1 transients suggests that that frequency shifting, in addition to limitation of vocal communication, may be a strategy that transients use to avoid detection by prey while still maintaining acoustic communication with one another.

A curious finding of our study was that AT1 transients

called at a higher average rate (0.28 calls/min per whale) than did West Coast transients (0.05 calls/min per whale). Several factors may account for this difference. AT1 transients, within their limited range, can maintain vocal contact with all subpopulation members, something that is impossible for West Coast transients. While AT1 transients hunted in presumed maternal groups, during social activity, aggregations of two or more groups were common. Like West Coast transients (Morton 1990; Deecke et al. 2005), AT1 transients produced sounds at higher rates during and after kills, when most social activity took place. Deecke et al. (2005) suggested that food calling was unlikely to be advantageous for West Coast transients because all members of their social groups were usually present during an attack. Calling could attract unrelated transients and thus not increase individual fitness. In the case of the AT1 transients, individual fitness may be increased by maintaining strong social bonds within the entire subpopulation. Gulf of Alaska transients were rare visitors to Prince William Sound, and thus, risk of acoustically attracting them to food sources was minimal.

Another factor that may account for the higher calling rates of AT1 transients was that their entire behavioral repertoire occurred in a limited area of patchy harbor seal and Dall's porpoise abundance. Moreover, harbor seals were often killed in enclosed bays and narrow channels, where transmission of calls was limited by bathymetry. West Coast transients were studied in areas of high prey abundance, as well as higher transient killer whale densities. Their cost of calling may be higher because nearby prey, as well as non-related animals, can more easily be alerted to their presence.

The context specificity of AT1 transient calls suggests that they use their vocalizations in different ways than do residents. Since these two forms differ in almost every aspect of their ecology, this result is not surprising. Resident killer whales produce all of their discrete calls during all of their behaviors, although the frequency distribution of these calls differs among behaviors (Morton et al. 1986; Ford 1989). Unlike transients, residents do not need to suppress their vocalizations while hunting, as the fish they prey on cannot hear in the frequency range of killer whale vocalizations (Hawkins and Johnstone 1978). Like residents, the frequency distribution of AT1 transient vocalizations differed among behaviors; however, some of those vocalizations, such as quiet calls, loud calls, and whistles, were context-specific and reflective of particular aspects of their foraging ecology and social system.

In summary, the AT1 transients conform to general trends observed in other transient subpopulations in the North Pacific, including dietary specialization on marine mammals (Ford et al. 1998; Saulitis et al. 2000) and hunting strategies that rely on passive listening, stealth, and acoustic crypsis (Barrett-Lennard et al. 1996; Deecke et al. 2005), yet their patterns of call usage are unique. Their acoustic behavior appears to have evolved around two seemingly incompatible necessities: remaining silent to successfully find food and calling loudly to find each other.

Acknowledgments

Without the tolerance of the AT1 transients, we would not

have been able to carry out this study. We acknowledge also the tolerance and hard work of many field assistants and colleagues: M. James, E. Weintraub, C. Schneider, M. Hare, L. Larsen, S. Sikemma, P. Bill, O. von Ziegesar, D. Grimes, K. Balcomb-Bartok, R. Angliss, E. Miller and especially J. Lyle, L. Barrett-Lennard, K. Heise, and M. Freeman. We benefitted greatly from the guidance of J. Kelley and M. Castellini and from the example of the late M. Bigg. We thank J.K.B. Ford for use of his sound analysis laboratory and for his pioneering work on killer whale acoustics. We thank the mariners and residents of Prince William Sound for their assistance, especially M. Eleshansky, P. Selanoff, S. and D. Selin, J. and N. Lethcoe, H. Kalve, D. Rand, D. Janka, and D. Grimes. We thank the AFK Hatchery for logistical help, especially E. Prestegard, R. Corcoran, M. Somerville, S. Mariner, and C. Pratt. We thank Chenega Village for logistical support, especially G. and L. Evanoff, M. and C. Eleshansky, and P. Kompkoff. Additional recordings of AT1 transients were provided by J. Francine, of Hubbs Research Institute, and by L. Barrett-Lennard and K. Heise. We thank G. Ellis of the Pacific Biological Station for identifying killer whales from photographs. The development of our ideas benefitted greatly from discussions with L. Barrett-Lennard, K. Heise, C. Guinet, V. Deecke, H. Yurk, and R. Baird. For invaluable advice on statistical analyses we thank P. Quang, E. Murphy, M. Ayers, J. Testa, S. Hills, and J. Miller. Funding for this research was supplied by the Alaska Sea Grant College Program (with special thanks to R. Dearborn), the American Museum of Natural History, the International Women's Fishing Association, the Fairbanks Business and Professional Women's Association, the North Gulf Oceanic Society, and the Exxon Valdez Oil Spill Trustee Council. We thank L. Barrett-Lennard, V. Deecke, H. Yurk, M. Gratz, S. Cosens, and an anonymous reviewer for comments on the manuscript.

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