

## Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts

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**Summary.** Vocalizations of free-ranging North Atlantic pilot whales were studied in different behavioral contexts to gain insight into the function and biological significance of different sound types. Simple whistles (with no frequency inflections) were heard more frequently when whales were “milling,” a restful behavior type. During “surface active” behavior, energetic, often coordinated activity probably representing feeding, many sound types, especially complex whistles (with more frequency inflections) and pulsed sounds, occurred with greater frequency than when this behavior was absent. Greater numbers of most whistle types were produced when whales were spread over a larger area and when more subgroups were present. Thus, in pilot whales, there is a significant relationship between their sounds and their behavior, with vocalizations possibly serving to maintain contact and coordinate movements of the herd.

be modified depending on the sender's “mood or emotional state” (Caldwell and Caldwell 1977).

Taruski (1976, 1979) examined the correlates of pilot whale whistling, though recordings were made from a broad area (ranging from Nova Scotia to Newfoundland) without considering group membership as a possible source of variation. Taruski (1976) described some 30 different whistle contours among North Atlantic pilot whales and, though he found the whistle repertoire graded, grouped these into seven broad classes.

The purpose of the study described here was to gain insight into the meaning and biological significance of the vocalizations of the North Atlantic pilot whale. Using concurrent visual and acoustic recordings over a period of several days, correlations between acoustic and behavioral variables were examined to study the relationships between vocalizations and context in pilot whales.

### Introduction

The relationship of a particular whistle form to a specific environmental or social context has not yet been conclusively demonstrated in any cetacean species (Herman and Tavolga 1980). Recent research (Partan et al. 1988) suggests, however, that bottlenose dolphins (*Tursiops truncatus*) may communicate behavior-specific information in their vocalizations. Most animal vocalizations are at least thought to have a communicative function (Sebeok 1977), which can often be broadly deduced from the context in which the sounds are made (Clark 1983; Silber 1986; Tyack 1981). While Caldwell and Caldwell (1965) believe that almost all of delphinid whistling can be attributed to a sender merely stating its identity by means of a “signature whistle,” even this whistle may

### Methods

A 13 m auxiliary ketch (inboard 45 h.p. diesel engine) with a crew of six scientists/sailors was used to follow pilot whales in the southern end of Conception Bay, Newfoundland (47°35' N, 53°05' W), from 24 to 31 July 1982. Every 30 min, behavioral observations were recorded on a data sheet while a 5-min long acoustic recording was made using a Uher 4200 Report Stereo tape recorder with towable Aquadyne AQ17 omnidirectional hydrophone and Barcus-Berry preamplifier. The system was flat from 20 Hz to 20 kHz.

Based on observations of pilot whales splitting up into small groups and later rejoining, the term “herd” is here used to mean the largest overall grouping of animals seen. The herd may then split up into a few (mean = 2.3, SD = 1.5,  $N = 190$ ) subgroups when spread out, usually consisting of 3–20 animals each. Observations were done only on the closest of these subgroups (or the herd, if in tight formation) subsequently referred to as the “focal group.” Mean focal group size was 17.8 animals with a SD of 18.5 ( $N = 195$ ). The behavior of the different subgroups seemed correlated, so that observations of the focal group were reliable predictors of the behavior of the whole herd.

Data gathered during each 5-min acoustic recording session included time of day, focal group size, estimated area over which the focal group was scattered ( $m \times m$ ), number of surrounding sub-

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groups seen, estimated speed of the whales (knots), and the estimated number of birds, usually gulls (Family Laridae), present with the whales (an indication of whales feeding). In addition, the behavior exhibited (directed swimming, milling, surface active) during the 5-min recording session was noted. Behavioral categories were defined as follows:

**Directed swimming** – coordinated movement by the focal group in a clearly defined direction, i.e., transiting, travelling.

**Milling** – lolling behavior during which no dominant heading could be discerned, and movement, if any, was slow.

**Surface active behavior** – very active, energetic behavior such as breaching (leaping from the water) or lunging (leaping forward just out of the water, dorsal side up). This behavior was almost always shown by the majority of the focal group simultaneously.

Based on identification photographs of individuals (Weilgart 1985), there was good reason to believe that these animals all belonged to the same overall herd. Whales were followed for a total of 118 h 55 min during which ca. 20 h of pilot whale vocalizations were recorded (236 5-min sessions).

Recordings were analyzed by ear to determine the number of whistles of each type, the number of pulsed sounds, and the degree of click activity heard during the first 4 min of each 5-min recording session. The overall impression of the quantity of clicks heard throughout the 4 min was rated qualitatively on a scale from 1 (few or none) to 3 (heavy clicking). Any sound that was not pure tone or narrow-band, but that was longer than 120 ms in duration (in contrast to clicks), was considered a pulsed sound (e.g., squawks, buzzes, moans, barks). Noisy and/or faint recordings were not used in the acoustic analysis (42 of the 236 sessions).

Whistle types were based on the seven broad whistle categories defined by Taruski (1976). Actual examples of spectrogram tracings can be seen in Fig. 1. Spectrograms were produced using a real-time Ubiquitous Spectrum Analyzer, Model UA-6B. Mean numbers and standard deviations of each whistle type per 4-min recording session ( $n=194$ ) are given in parentheses for each category:

S1 – level frequency (4.68, SD=6.25).

S2 – falling frequency (12.50, SD=11.01).

S3 – rising frequency (12.99, SD=10.61).

S4 – up-down: frequency first rises, then falls (9.14, SD=9.39).

S5 – down-up: frequency first falls, then rises (6.54, SD=7.61).

S6 – waver: a whistle with at least 3 symmetrical frequency inflections (10.91, SD=12.03).

S7 – multiple humps: a whistle in which there are at least 3 asymmetrical frequency inflections. This category was used as a catch-all category for a wide variety of multiple-humped whistles (4.51, SD=7.55).

The mean total number of whistles per 4-min session was 61.26 (SD=35.33). The number of pulsed sounds heard per session averaged 6.64 (SD=7.58).

As in Taruski (1976), whistles S1 to S3 are considered and referred to in the following results and discussion as simple whistles, while whistles S4, S5, and especially S6 and S7 are classed as complex whistles based on the number of frequency inflections they exhibit.

A total of 13173 sounds (whistles + pulsed sounds) were aurally categorized. Observer or “listener” reliability in the classification of vocalizations was tested in the following ways on a subsample of the data and found acceptable (Weilgart 1985): (1) consistency of repeated analyses by the same listener; (2) consistency between two different listeners; (3) consistency between listeners and spectrograms.

Correlations were performed using Kendall correlation coefficients ( $\tau$ ). Since the three behavioral categories were not mutually exclusive (more than one behavior type may have been observed from the focal group during the 5-min session), comparisons in vocal output were made between the presence and absence of a particular behavior type. Mann-Whitney U tests were used to test the significance of differences between mean numbers of sounds heard per session during the presence and absence of a given behav-

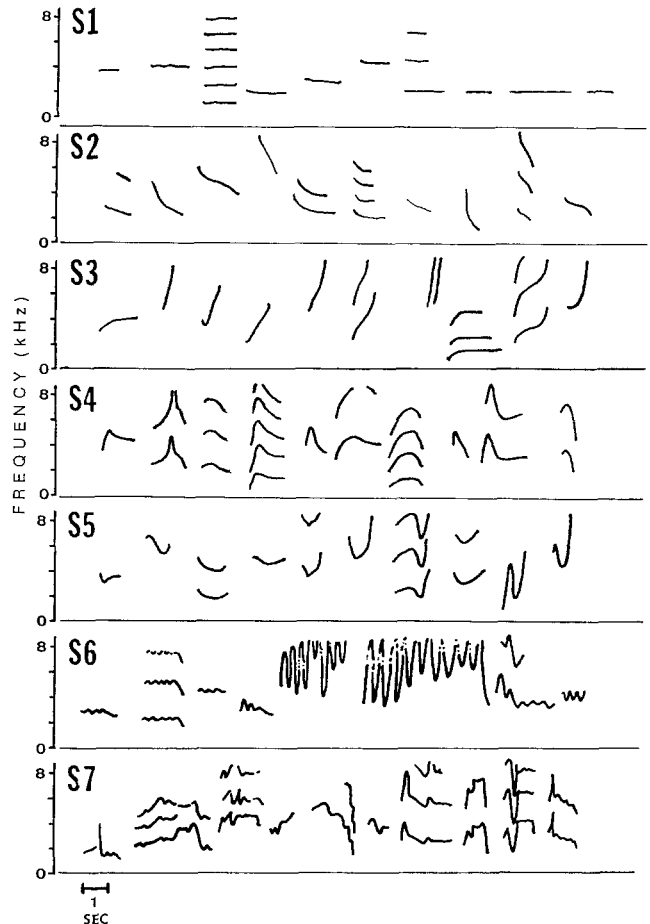


Fig. 1. Tracings of spectrograms for whistles of each category, S1–S7. The x-axis represents time and the y-axis, frequency (in kHz)

ior type. The Cramer's V chi square test was used similarly for comparisons of the categorical rating of click activity with behavior. Tests were always 2-tailed.

## Results

Mean numbers of S1 whistles (Mann-Whitney U test,  $P<0.05$ ) and S2 whistles ( $P<0.01$ ) were significantly lower during directed swimming than in its absence (mean numbers in presence and absence of directed swimming, respectively: S1: 4.6, 6.3 (per 4-min session); S2: 11.7, 18.0;  $N=126, 35$ ). In contrast, when whales were milling, numbers of S1 ( $P<0.01$ ) and S2 ( $P<0.01$ ) whistles increased, on average, compared to when whales were not milling (means in presence and absence of milling, respectively: S1: 6.8, 4.3; S2: 18.7, 11.2;  $N=39, 122$ ). During surface active behavior, the most vigorous and energetic behavior type observed, several sound types, especially the more complex whistles, increased in number compared to when this behavior was not present. In particular, pulsed sounds ( $P<0.01$ ), S4 whistles ( $P<0.01$ ), S6 whistles ( $P<0.01$ ), and, to a lesser degree, S7 whistles ( $P<0.05$ ) increased in number (means in presence and absence of surface active behavior, respectively: pulsed: 8.9, 6.5; S4: 11.6, 8.6; S6: 15.5, 10.5;

S7: 5.9, 3.6;  $N=36, 125$ ). A greater amount of clicking (Cramer's chi-square  $V=0.25, P<0.01$ ) was heard in conjunction with surface active behavior than in its absence (presence and absence of surface active behavior, respectively: 1 (few clicks): 9%, 36% of all sessions; 3 (many clicks): 49%, 40%;  $N=36, 125$ ). Whistle total number, however, did not increase significantly ( $P>0.10$ ) during surface active behavior.

A significantly greater number of birds was present while surface active behavior took place than when it did not ( $P<0.01$ ).

Greater total whistle numbers were heard when whales were moving faster (Kendall's  $\tau=0.13, P<0.05$ ). In particular, whistle S6 ( $\tau=0.13, P<0.05$ ) increased in number with the speed of the whales. Total numbers of whistles per 4-min session were *not* correlated with focal group size ( $P>0.10$ ). This may reflect that occasionally we recorded and counted sounds from the whole herd or various other subgroups besides just the focal group. When the area over which the focal group was spread was greater, however, whistle types S1 ( $\tau=0.13, P<0.05$ ), S2 ( $\tau=0.12, P<0.05$ ), S6 ( $\tau=0.13, P<0.05$ ), and S7 ( $\tau=0.13, P<0.05$ ) increased in number. The number of subgroups seen is another more large-scale index of the degree to which whales were scattered. There was a very significant positive correlation between the number of subgroups and whistles S3 ( $\tau=0.17, P<0.01$ ), S4 ( $\tau=0.18, P<0.01$ ), S5 ( $\tau=0.15, P<0.05$ ), S6 ( $\tau=0.22, P<0.01$ ), and S7 ( $\tau=0.15, P<0.05$ ). Whistle total numbers were very significantly correlated with the number of subgroups present ( $\tau=0.22, P<0.01$ ), in contrast to focal group size, which showed no relationship to whistle total (see above). The number of animals in the focal group and the number of surrounding subgroups showed a significant inverse relationship ( $\tau=-0.25, P<0.01$ ).

## Discussion

The results obtained, together with observations of apparent feeding, suggest that feeding was generally taking place during surface active behavior. It was the only behavioral category in which greater click activity was heard and more gulls were seen. Clicks have long been implicated in echolocation (Kellogg et al. 1953; Norris et al. 1961; Norris 1969), and in captive dolphins, feeding sessions are characterized by fast, very intense, continuous clicking (e.g. Dreher 1966).

Pilot whale feeding may sometimes require a high level of coordination between group members. Information needed for this behavior appears to be transmitted by pulsed sounds and complex whistles S4, S6, and S7. Saayman et al. (1973) suggest that acoustic communication probably plays an important role in the highly organized fish herding procedures of *Tursiops aduncus*. In general, when pilot whales were moving at higher speeds, regardless of behavior, whistle total, as well as numbers of whistle S6, increased. Again, this may imply that the coordination necessary at or for higher speed is mediated by means of whistles, in particular complex ones.

Clark (1983) found that in right whales, the complexity of the sounds made was directly related to the complexity of the social context. Taruski (1976) related high proportions of complex whistles in pilot whales to high arousal situations, such as excitement (which corresponded approximately to our "surface active"). Similarly, McLeod (1982) found an increase in complex whistles in pilot whales after the broadcast of killer whale (*Orcinus orca*) phonations.

In contrast to the vigorous displays of surface active behavior, milling seemed to be more of a restful state. Speed was slower during milling, and a smaller proportion of whales was moving in the same direction. Also, unlike surface active behavior, during milling more simple whistles were heard. Directed swimming appeared intermediate both in terms of energetic expenditure and the complexity of the whistles produced.

There was no variation in whistling rate with focal group size, yet almost all whistle types and their total increased in number with more surrounding subgroups present. Focal group size and the number of subgroups present varied inversely, suggesting that animals all belonged to the same general herd, whether in one large group or divided up into many small subgroups. Acoustic communication between subgroups of the same herd may be very important in coordinating actions of the whole herd. Inter-subgroup distances (usually ca. 300–500 m) may reflect this, since these distances were similar to the maximum ranges over which we could hear whistles. The hypothesis that whistles function as contact calls is further supported by the discovery that more whistles of certain types were heard when a focal group of whales was spread over a greater area. Whether a herd is separated into many subgroups or whether individuals in a single group are more dispersed, sound may be used to maintain contact and coordinate movements. Norris and Dohl (1980) have theorized that the unified actions of spinner dolphin (*Stenella longirostris*) schools, when spread out over large expanses of water, are acoustically mediated.

In conclusion, pilot whale whistling may be used to maintain contact with group members and coordinate and integrate the movements of the herd. The simplest whistle types are emitted during low activity, restful behavior, while the more complex whistle types and pulsed sounds occur when behavior is vigorous and energetic, and seems to involve more complex coordination among individuals of the group.

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