VOCALIZATIONS OF THE NORTH ATLANTIC PILOT WHALE (GLOBICEPHALA MELAENA TRAILL) AS RELATED TO BEHAVIORAL AND ENVIRONMENTAL CONTEXTS

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Vocalizations of the North Atlantic Pilot Whale
(Globicephala melaena Traill)
as Related to Behavioral and Environmental Contexts

by

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ABSTRACT

Vocalizations of free-ranging North Atlantic pilot whales were studied in different behavioral and environmental contexts to gain insight into the function and biological significance of different sound types. Pilot whales in Conception Bay, Newfoundland, were followed for a period of a week, night and day. Concurrent visual and acoustic recordings were made, and correlations were examined between the different acoustic, behavioral, and environmental variables. Whistles were categorized into 7 types based on the aural impression of the whistles' contour.

Simple whistles (with no frequency inflections) were more common than complex whistles (more than 2 frequency inflections), which were rare. Simple whistles were heard when whales were milling, a restful behavior type which occurred over shallower water. In contrast, during surface active behavior, energetic coordinated behavior thought to be feeding, many sound types, especially complex whistles and pulsed sounds, increased in number. More clicking (thought to function in echolocation) was also heard. Greater numbers of most whistle types were

produced when whales were spread over a larger area and when more subgroups were present. During conditions of high wind speed and wave height (which produced much background noise), groups were larger and in tight formation with fewer surrounding subgroups present. Whales moved in a less unified manner when the group was larger and scattered over a greater area.

It was concluded that in pilot whales, complexity of sound and complexity of behavior (requiring a high level of coordination) were related. Vocalizations were thought to play an integral part in maintaining contact between group members and coordinating movements of the herd.

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CHAPTER 1 - INTRODUCTION

The purpose of this study was to gain insight into the meaning and biological significance of the vocalizations of the North Atlantic pilot whale Globicephala melaena (Traill 1809). This was done by studying the communicative act in different behavioral and environmental situations and examining relationships between sound types and the contexts in which they were produced.

The North Atlantic or long-finned pilot whale (known in Newfoundland as "pothead") is a sexually dimorphic odontocete, with adult males reaching an average length of 5.7 m and adult females, 3.4 m (Sergeant 1962). Pilot whales are characterized by a thick and bulbous forehead or "melon" which is especially prominent in adult males. No distinct beak is present. These whales are almost uniformly black, except for a ventral anchor-shaped patch of grayish-white (Leatherwood et al. 1976).

Pilot whales (Genus Globicephala) occur in all oceans of the world except the extreme polar waters. Distribution between these limits is more or less continuous with increasing abundance as one moves to tropical waters (Leatherwood & Dahlheim 1978). There are two different species of Globicephala: the short-finned pilot whale, G. macrorhynchus, is confined to more tropical and sub-tropical waters of the Atlantic, Pacific, and Indian Oceans, whereas the North Atlantic or long-finned pilot whale, G. melaena, is distributed throughout the North Atlantic, and also occurs in the Southern Hemisphere (Watson 1981).

Pilot whales are generally thought to migrate to higher latitudes in the summer (e.g. Leatherwood et al. 1976). G. melaena usually first enter Newfoundland bays during mid-July and most are gone by late October (Sergeant & Fisher 1957). Their movements closely parallel the movements of the short-finned squid Illex illecebrosus Le Sueur (Mercer 1975), on which they feed almost exclusively when in coastal waters (Sergeant & Fisher 1957). Pilot whales seem to feed in groups, since the degree of digestion was the same in members of the same herd examined after being driven ashore (Sergeant 1962).

These whales are often described as being among the most gregarious of cetaceans (e.g. Watson 1981). Kritzler (1952) felt that the tendency of pilot whales to form well-integrated social groups was more highly developed than in any other dolphin species he had observed. Pilot whales in Newfoundland may occur in herds of 200 or more, but in inshore bays, the average herd seems to be around 85 individuals (Sergeant 1962). These numbers, however, were obtained from animals driven ashore or naturally stranded. Pelagic herds comprise on average about 20 animals (Sergeant 1962), although this may be because the number of whales sighted at any one time is usually an underestimate of the total. Faroese pilot whalers, for instance, claim that the number of pilot whales seen above water is a small fraction of the actual herd size, once driven ashore (M. Moore, pers. comm.). (It should probably be noted here that authors often use the terms "herd", "pod", "school", or "group" interchangeably when referring to pilot whale aggregations. My usage will be defined in the Methods section).

Female pilot whales mature at ca. 6.5 years, as compared to 11 years for males, and have a mortality rate half that of the males (Sergeant 1962). In a typical herd, the average ratio of mature males to mature females is 1:3 (Sergeant 1962). This led Sergeant (1962) to conclude that the species must be polygynous.

They are also quite long-lived (maximum ages 40-50 years in males, 50-60 years in females (Sergeant 1962)). This longevity is conducive to the development of the intricate social relationships (e.g. reciprocal altruism, Trivers 1971) which Connor & Norris (1982) hypothesize for pilot whales (among other delphinids). Kasuya & Marsh (1984) propose that matrilineal kin groups may exist in G. macrorhynchus off Japan. They found that 25% of all mature females in the population studied were post-reproductive. Older females lactate longer than younger ones, with some nursing calves for up to 15 years after the birth of their last calf (Kasuya & Marsh 1984). Strong social bonds may also explain, in part, why Globicephala is the genus that most frequently mass strands (Geraci & St. Aubin 1979). Norris & Dohl (1980b) hypothesize that factors relating to the tight cohesion of the school may cause the whole herd to strand instead of perhaps just a single diseased individual.

The rich vocal repertoire of the pilot whale may reflect its highly social nature. Whistling species of cetaceans in general are large-school, communal foraging species, as opposed to the nonwhistlers, which are more solitary (Herman & Tavolga 1980). It has been suggested that the degree of complexity in the signal repertoire of an animal is often indicative of the complexity of the social system (Smith 1977).

Cetacean vocal emissions may be broadly divided into two categories: pure tone, narrow-band sounds (whistles or squeals) and sounds made of pulses which are usually of broad spectral composition (Caldwell & Caldwell 1977). These broad-band sounds, in turn, may be divided generally into; a) regular trains of clicks emitted in exploratory or environmental search situations, which are usually thought to function in echolocation ("clicks"), and b) rapid bursts of pulses often emitted in an "emotional" context ("pulsed sounds") (Caldwell & Caldwell 1977). These include sounds like barks, yelps, squawks, moans, cracks, etc.

Historically, it has been assumed that dolphin whistles function in social communication, and pulsed sounds, in echolocation (e.g. Schevill & Lawrence 1956). But since some pulsed sounds occur in social contexts, and because some social dolphin species don't whistle at all, vocal communication in these species is thought to occur through the use of pulsed sounds (Herman & Tavolga 1980). They have been observed to occur in situations of alarm, fright, or distress (Caldwell & Caldwell 1967), during copulatory behavior (Tavolga & Essapian 1957) or during chases and agonistic encounters (Caldwell & Caldwell 1967). Pulsed sounds are interesting because they have physical characteristics somewhat intermediate between clicks and whistles (broad-band, yet often show frequency modulation like whistles). They are thought to be clicks emitted at very high repetition rates (e.g. Busnel & Dziedzic 1966), but are perceived as quite different sounds by the human ear.

Cetacean whistles are typically either unmodulated pure tones or frequency-modulated pure tones of the mid- to upper-sonic range of frequency (5-15 kHz), and of 0.5 to 2 seconds in duration (Herman & Tavolga 1980). They have been hypothesized to be functional in the coordination, spacing, and movements of rapidly swimming individuals during communal foraging (Herman & Tavolga 1980). Since some dolphins can produce whistles and clicks simultaneously (Lilly & Miller 1961), they may be able to use whistles for maintaining vocal communication during food search by echolocation (Herman & Tavolga 1980). Caldwell & Caldwell

(1965) found that whistles have individual specificity, which may be of use in identifying herd members or assembling dispersed animals. They call these "signature whistles".

The relationship of a particular whistle form to a certain environmental or social context has not yet been conclusively demonstrated. However, a few generalizations can be made. Whistles tend to increase in rate under excited or stressful states like feeding or the anticipation of it, riding the bow wave of a vessel, being separated from familiar individuals, meeting another group of dolphins, or just in fully "alert", leaping or traveling, schools (Herman & Tavolga 1980).

Research on pilot whale vocalizations started in the 1960's. Schevill (1964) described whistles of G. melaena as ranging from 0.5–5.0 kHz in frequency, whereas those of G. macrorhynchus range from 2-12 kHz.

Busnel & Dziedzic (1966) recorded a variety of sounds from a free-ranging school of 11 pilot whales, one of which had been harpooned. They heard combinations of whistles and creaks, emitted simultaneously or sequentially, and characterized five signal types and several variants. They also noted abrupt frequency shifts and amplitude variations.

Globicephala were also found to produce double clicks (Busnel et al. 1971). Busnel and Dziedzic (1966) reported that they had recorded a wild G. melaena that had consistently emitted two different signals simultaneously. Caldwell & Caldwell (1969) confirmed this by recording a pilot whale in captivity which clearly had a double narrow-band emission. This capability of emitting two widely different whistles simultaneously has not been demonstrated in any other cetacean species.

Dreher & Evans (1964) observed 30 feeding pilot whales off California and concluded that the whistles recorded could be classified into 7 frequency contours. This is in contrast to the 15-19 different whistle contours they described for 3 other delphinids. These recordings, however, were brief and almost certainly not representative of the pilot whales' complete vocal repertoire. Dreher & Evans (1964) found that generally those contours most used by T. truncatus during feeding, were also used by Globicephala during feeding. The authors compare delphinid whistling to human language and believe that particular sounds have precise meanings. This view has since been highly contested (e.g. Caldwell & Caldwell 1977) and "has failed to receive analytic, experimental, or conceptual support" (Herman & Tavolga 1980).

Taruski (1976) described some 30 different whistle contours among wild North Atlantic pilot whales, and grouped these into 7 broad classes. He states that: "the whistle repertoire of the pilot whale (Globicephala melaena) is shown to be a continuum or matrix in which no mutually exclusive contour categories can be defined" (Taruski 1979). He also examined the correlates of pilot whale whistles. Taruski (1976) found that pilot whale whistling clearly varied with behavioral and environmental context. He suggested that the level of arousal in the whales may have accounted for some differences in whistle usage, but was unable to explain variations in other whistle parameters. All whistles analyzed by Taruski (1976) were random samples, recorded on three cruises that covered the area from Newfoundland south to Hudson Canyon. Pod membership was not considered and adjusted for, and recordings were made from very different areas (Nova Scotia and Newfoundland) and perhaps, from different populations.

McLeod (1982) also studied free-ranging pilot whales off Newfoundland but compared recordings of different pods to examine between-pod variability. He found that differences in whistles between different pods of the same area existed, but within-pod variability was not reliably assessed so that dialects could only be suggested, not proven. The purpose of McLeod's (1982) study was to create a catalog of wild pilot whale phonations, and no attempt was made to relate these to behavioral or environmental contexts.

Steiner (1981) examined the whistles from 5 species of dolphins in the western North Atlantic, one of which was Globicephala melaena. He found whistles to have consistent, species-specific characteristics based on results of multivariate discriminant analysis. G. melaena, which is taxonomically more distinct than the other 4 species studied, also had the most distinctive whistles. Moreover, since G. melaena is sympatric with the other species studied, Steiner (1981) reasoned that it would be especially important for this species to have highly characteristic whistles, if these are used for species-specific communication. Maximum frequency was suggested as the species-specific characteristic of the whistles, while whistle duration and number of inflection points were thought to be important for individual differentiation (Steiner 1981). Both Taruski (1976) and Steiner (1980) suggested that individual "signature" whistles may be present in G. melaena.

There have been few long-term studies of free-ranging cetaceans, in which sounds have been related to behavior. However, Tyack (1982) with humpbacks and Clark (1983) with right whales have greatly elucidated the functions and meanings of sounds by studying the natural contexts in which they are produced. "By combining such observations with knowledge of the social behavior and natural history of the species under study, ethologists have been able to create convincing adaptive explanations of systems of communication" (Tyack 1982). Tyack (1982) found that humpback whale groups responded differently to the songs and social sounds, respectively, of other humpbacks. The purpose of Clark's (1983) 18-month study on southern right whales was to correlate sounds with activities and to demonstrate the possible communicative functions of the sounds. He concluded that there are correlations between sounds and activities, and that the function of the sounds can be interpreted from the activities of the whales and the contexts in which the sounds were made.

Using data collected in inshore Newfoundland waters in 1982, I studied mainly the whistles, but also the pulsed sounds and clicks produced by North Atlantic pilot whales (G. melaena), and examined their relationship to various behavioral and environmental parameters. I observed and recorded only free-ranging pilot whales. Moreover, in light of the fact that between-pod dialects have been suggested in pilot whales (McLeod 1982), an attempt was made to follow only one herd of whales for as long as possible, through day and night. It was hoped that this would considerably reduce the sources of variation which troubled Taruski (1976). Only group movements and behavior could be used as contextual data since individual interactions were very difficult to detect. Group behavior, however, might be an accurate, if general, indication of the behavior of individual vocalizing animals, especially in a species which exhibits a high degree of behavioral coordination. Furthermore, many sounds have been hypothesized to have a function in group movements (Herman & Tavolga 1980).

In order to shed light on the relationships between pilot whale vocalizations, their visually observable behavior, and the surrounding environment, I made concurrent visual and acoustic recordings over a period of several days. Using these data, I was able to examine correlations between the different acoustic, behavioral, and environmental variables.

CHAPTER 2 - METHODS

A 13 m auxiliary ketch (with inboard 45 h.p. diesel engine), the Findrinny, was used to follow pilot whales in the southern end ~~of~~ Conception Bay, Newfoundland, from 24 - 31 July, 1982. We attempted to stay close (usually within 150 m) to the whales but approached them slowly and not directly, using only sail power whenever possible. Every attempt was also made to stay with the same group of whales for as long as possible. It was thought that by staying with the same general herd for a week and by sailing as much as possible, animals would habituate to our presence, and the disturbance we caused would be minimal. This in fact seemed to be true, as animals showed little fear of the boat and let us approach quite closely.

Six crew members were on board throughout most of the study. Watches were 4 hrs. long, around the clock, with 2 crew members on watch at one time. One crew member sailed the boat, constantly observing the whales, while, every 30 mins., the other entered these observations on a data sheet, made the acoustical recording, and plotted positions on a hydrographic chart. Acoustical recording was done every 30 min. for a duration of 5 min. when in the presence of pilot whales, as determined visually or acoustically.

Based on my observations of pilot whales splitting up into small groups and later rejoining, I have chosen the term "herd" to mean the largest overall grouping of animals seen. The herd may then split up into a few "podlets" or subgroups when spread out. These usually consisted of 3-20 animals. When following pilot whales, usually the largest or closest of these podlets (or the herd, if in tight formation) was chosen as the object of our observations. This was then called the "group", which may or may not have been surrounded by other podlets. The following parameters pertained only to the behavior of this group.

Data gathered during each 5 min. acoustical recording session included (underlined words indicate how variables will be referred to in the Results introduction): date, time of day, position (latitude and longitude), water depth (m), estimated number of animals in the group being followed (group size), estimated proportion of the group heading the same direction (%), estimated area over which the group was scattered (m x m), distance (m) whales were from the boat (estimated from the center of the group), estimated speed of the whales (knots), number of surrounding podlets seen, behavior (directional, milling, surface active, spyhopping--definitions follow), and the estimated number of birds present in conjunction with the whales (as an indication of feeding taking place).

"Area over which the group was scattered" was usually ca. 100 m x 100 m. In contrast, podlets were usually ca. 300-400 m apart from each other, although this parameter was not recorded. I mention it here to explain that the "number of podlets seen" is another index of the degree to which whales were scattered, but is on a larger scale than "area of the group". It, therefore, may also be the more sensitive variable of the two.

If the parameters I recorded varied over the 5 min. observation period, an average was used. Only the behavior exhibited during the 5 min. recording session was entered on the data sheet. All behavior categories occurring either simultaneously (by different members of the group) or sequentially (by the whole group) during these 5 mins. were recorded. Behavioral categories were defined as follows:

Directional behavior - coordinated movement by the group in a clearly defined direction, i.e. transiting, travelling.

Milling - lolling behavior during which no dominant heading could be discerned, and movement was slow, if the group was moving at all.

Surface active behavior - very active, energetic behavior which included at least one, and usually many, of the following: obvious feeding (squid seen in whales' mouths), leaping (jumping almost vertically, dorsal side up), breaching (leaping from the water, twisting, and splashing down on the back), lunging (leaping forward and barely out of the water, dorsal side up), streaking (fast swimming just below the surface, with rapid turns, in what seemed to be attempts to catch squid), and generally thrashing and splashing about at the surface. This behavior was almost always seen from the majority of the group simultaneously (Fig. 1).

Spyhopping - a specific behavior during which an animal would be oriented vertically with its head out of the water exposing its eyes. This is done slowly and is much less vigorous than surface activity. This behavior was recorded when at least one spyhop was seen (Fig. 2).

Environmental data were usually taken every 4 hrs. when following whales. Date, time, position, estimated wind speed (Beaufort scale), estimated cloud cover (%), estimated wave height (inches), and estimated swell height (inches) were recorded. During the entire study, environmental data were taken on 26 occasions.

Between recording sessions, additional behavioral notes were taken, and distinctively scarred or marked dorsal fins or individuals were photographed whenever possible, to identify individuals and clarify relationships between pods (see next paragraph for definition and assignment of pod numbers). Positions were plotted at each 5 min. session on a hydrographic chart and were estimated (accurate to at least 0.5 mi.) by features on land. Depth was determined using a Simrad Skipper 603 recording depth sounder on board. All sound recordings were made on a 2-track Uher 4200 Report Stereo tape recorder at a tape speed of 19 c.p.s.

Fig. 1. Surface active behavior. Note the large numbers of gulls present.

Fig. 2. Spyhopping behavior.

(flat frequency response from 20 Hz - 20 kHz). One track was used for whale sounds and the other for voice recordings marking the beginning and end of a recording session, by announcing time, date, position, and tape counter number. A towable Aquadyne AQ17 omnidirectional hydrophone with a Barcus-Berry preamplifier was lowered to a depth of ca. 10 m to record whale sounds. During recording sessions, the boat was hove-to or anchored to minimize water noise.

Whales were followed for a total of 118 hrs. 55 min. during which ca. 20 hrs. of pilot whale vocalizations were recorded (236 5 min. sessions). In addition, 7 rolls of 36 exp. and 3 rolls of 20 exp. 35 mm black & white (Tri-X or HP5) film were taken. Data collection needed to be interrupted six times owing to inclement weather or other reasons. After locating whales again following each interruption, a new pod identification number (1-7) was assigned (Table 1).

However, based on the identification photographs and because relatively few whales were in Conception Bay in 1982, there is good reason to believe that generally, these animals all belonged to the same overall herd. A preliminary analysis of the identification photographs revealed that 4 individual whales were resighted during the study. Whale #1 was photographed on 25 July, 11.30 h; 25 July, 16.15 h; 27 July, 08.35 h, and 27 July, 09.15 h, linking Pods 2 and 3 (Fig. 3). The longest time between

Table 1. "Pods" tracked in Conception Bay. A "pod" consists of a period during which constant acoustic or visual contact was maintained with pilot whales.

Pod No.	Observed From:	Observed To:	Hours Followed	Reason for Interruption	ID Photos Taken
1	24 July 18.30 h	24 July 21.05 h	2 h 35 min	Picked up New Crewmember	23
2	25 July 10.58 h	26 July 13.30 h	26 h 32 min	Dropped off Crewmember	67
3	26 July 16.02 h	27 July 17.36 h	25 h 34 min	Picked up Tapes and Crewmember	98
4	27 July 19.01 h	28 July 01.16 h	6 h 15 min	Lost Whales due to Storm	7
5	28 July 11.34 h	29 July 02.30 h	14 h 56 min	Lost Whales during Night	12
6	29 July 05.27 h	29 July 20.59 h	15 h 32 min	Anchored during Storm	59
7	30 July 16.29 h	31 July 20.00 h	27 h 31 min	End of Study	47

TOTAL 118 h 55 min

Fig. 3. Match of identified dorsal fins linking Pods 2 and 3. Whale #1 from 25 July, 16.15 h (top) was rephotographed on 27 July, 09.15 h (bottom), 41 hrs. later.

resightings was 45 hrs. 45 min. Whale #2 was photographed on 25 July, 12.05 h (Pod 2), and was rephotographed on 30 July, 16.20 h (Pod 7), 124 hrs. 15 min. later. This was the longest time between any match of this study. Whale #3 was photographed on 26 July, 16.15 h (Pod 3), and again, after 49 hrs. 35 min., on 28 July, 17.50 h (Pod 5)(Fig. 4). Whale #4 of Pod 7 was photographed 18 hrs. 55 min. apart--on 30 July, 18.20 h and on 31 July, 13.15 h. There were many other matches within pod numbers. The longest uninterrupted time we followed the whales was for 27 hrs. 31 min. during Pod 7.

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 (since some recordings fell short of the full 5 min.). Tapes were listened to at full-speed (19 c.p.s.). Qualitative categories were used for the degree of click activity, since clicks were impossible to count at this tape speed. The overall impression of the quantity of clicks heard throughout the 4 mins. was rated on a scale from 1 (few or none) - 3 (heavy clicking). Any sound that was not pure tone or narrow-band, but that was longer than 120 msec in duration (as opposed to clicks) was considered a pulsed sound. These squawks, buzzes, moans, barks, etc. were generally easy to distinguish from whistles (even though frequency modulation was sometimes present) and

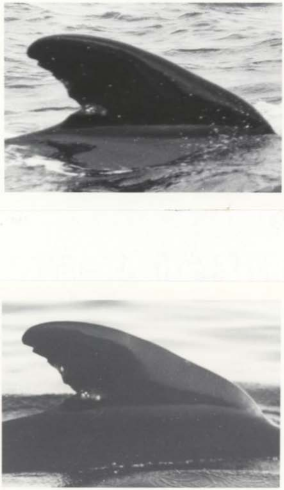


Fig. 4. Match of identified dorsal fins linking Pods 3 and 5. Whale #3 from 26 July 16.15 h (top) was rephotographed on 28 July, 17.50 h (bottom), 49 hrs. 35 min. later.

clicks (even though broad-band).

Whistle types were based on the 7 broad whistle categories defined by Taruski (1976). Statistical justification for this classification scheme is given in Appendix A (Test 2). Depicted here are stylized whistle contours. Actual examples of spectrogram tracings can be seen in Fig. 5.:

S1 - level frequency (——) - essentially no change in frequency throughout the entire duration of the whistle.

S2 - falling frequency (\ ) - a noticeable decrease in frequency throughout all or most of the duration of the whistle.

S3 - rising frequency (/) - a noticeable increase in frequency throughout all or most of the whistle.

S4 - up-down (∧) - a whistle in which frequency first rises, then falls.

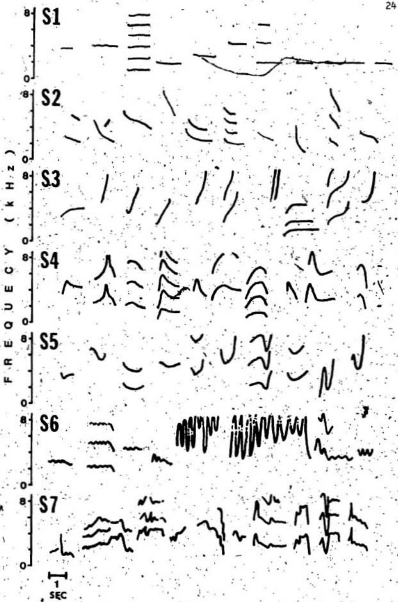
S5 - down-up (∨) - a whistle in which frequency first mostly falls, then rises.

S6 - waver () - a whistle in which there are at least 3 frequency inflections, but the frequency excursions are generally symmetrical about some mean.

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.

Summary statistics of characteristics (such as maximum

Fig. 5. Tracings of spectrograms for whistles of each category, S1 - S7. The x-axis represents time and the y-axis, frequency (in kHz). Measurements for Reliability Test 3 were performed on these spectrograms. For information on how spectrograms were made, see Methods section of Reliability Test 2.


S1
S2
S3
S4
S5
S6
S7
8
0
FREQUECY (kHz)
1 SEC

frequency, duration, etc.) of each whistle type are presented and discussed in Appendix A (Test 3, Table 13).

Like Taruski (1976), whistles S1-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. Pulsed sounds are also considered complex sounds because of their acoustical complexity (broad-band yet sometimes with frequency modulation), following Clark (1983).

Each 4 min session during which vocalizations were quantified was also ranked according to the quality of the recording and the confidence of the aural analysis. Rating categories with their quality codes were (* indicates categories used in vocalization analysis; numbers in parentheses indicate number of sessions (n) and percentage of the total 236 sessions):

*1) no problems in hearing or categorizing sounds (111 - 47.0%)

*2) minor interfering noise (e.g. water noise, boat sounds, etc.) (33 - 14.0%)

3) major interfering noise (e.g. outboard motors, radio interference from nearby ships) (25 - 10.6%)

*4) high rates of whistling so that categorization of whistles became difficult (15 - 6.4%)

*5) very high rates of whistling so that categorization may be unreliable (12 - 5.1%)

*6) sounds that were fairly distant (23 - 9.7%)

7) sounds that were very distant so that accuracy might be a problem (5 - 2.1%)

8) sounds that were distant with interfering noise in addition (10 - 4.2%)

9) high rates of whistling with interfering noise (2 - 0.8%)

Vocalization parameters that were subjected to analysis for each 4 min. session were: the number of S1, S2, S3, S4, S5, S6, and S7 whistles, the number of pulsed sounds, the rating of click activity, and the total number of whistles in the 4 min. session. Whenever these vocalization parameters were involved in the following statistical analyses, only selected data with quality codes 1, 2, 4, 5, or 6 were used. Since there was hardly any difference in reliability between sessions without problems and sessions with problems (such as quality codes 2, 4, 5, 6) (see Appendix A, Tables 10, 11, 12), only those quality codes were eliminated from analysis which represented a major bias by factors external to the whales (like noise, distance). A total of 14,183 sounds (whistles + pulsed sounds) were aurally categorized, but because of the elimination of sessions with certain quality codes, only 13,173 sounds were used in the analysis. Those analyses which did not include sound variables used all data regardless of quality code.

Analysis was performed using SPSS procedures NONPAR CORR for Kendall and Spearman correlation coefficients, CROSSTABS for Cramer's V chi-square tests, NPAR TESTS for Mann-Whitney U tests, and BREAKDOWN for analysis of variance. For the principal component analysis, SPSS-X procedure FACTOR was used. The following Results section specifies to which statistical test(s) data were subjected. Tests were always 2-tailed except when stated otherwise. In order to normalize data based on counts, for the analyses of variance, square-root transformations were performed on the following variables: number of S1, S2, S3, S4, S5, S6, and S7 whistles, whistle total number, number of pulsed sounds, group size, number of podlets, and number of birds. Because of the relatively slow changes in weather and sea state, environmental data (wind speed, cloud cover, wave height, and swell height) were linearly interpolated between the 26 actual observations, for every 30 mins. when a recording session took place. Time of day was recoded into 2-hr. intervals, starting with the 0601-0800 hr. interval (dawn).

In this study, classification of whistle types was done on the basis of whistle contour. This may be very different from how a whale perceives or interprets these whistles. The whale may use many parameters of the whistle besides merely its contour. Indeed, it might even find my categories meaningless (see Chabot (1985), for a discussion of the classification of whale sounds). However, it makes some sense that the whale's perception of a sound and my own are more similar than the perception of the whale and the output of the spectral analyzer. Nuances of sound that are not demonstrable on a sonogram or spectrogram are detected by the human ear (Busnel 1966). The spectral analyzer also has other limitations--it cannot process rapid fluctuations in frequency like a waver (S6) often produces, unless tape speed is drastically reduced. A machine, however, is more reliable and objective in its analysis. The greatest drawback in categorizing whistles by ear is subjectivity. While the classification of a whistle's contour by its spectrogram or visual appearance is also subjective, it can be an improvement on categorization by ear. Because of the practical difficulties and time requirements of spectrally analyzing over 13,000 whistles (as opposed to Taruski's (1976) 822 whistles), I have chosen analysis by aural impression. Observer or "listener" reliability in the classification of vocalizations was, however, tested in the following ways:

1) self-reliablity

2) reliability between myself and another observer

3) reliability between myself (and the other observer) and spectrograms

These tests are described in Appendix A, and comments are made on the more interesting by-products of the analyses.

CHAPTER 3 -RESULTS

3.0 Introduction

Variables (defined in Methods) were divided up into 4 categories: 1) Sounds, 2) Behavior, 3) Contextual Variables, and 4) Environmental Variables, in the following manner:

Sounds	Behavior	Context	Environ.
Whistle Types	Directional	Area	Depth
S1	Milling	Group Size	Time
S2	Surface Active	No. of Podlets	Cloud Cover
S3	Spyhopping	Proportion	Swell Ht.
S4		Speed	Wave Height
S5		No. of Birds	Wind Speed
S6		Distance	
S7		Date	
Pulsed Sounds		Pod I.D. No.	
Clicks			
Whistle Total No.			

Relationships within categories and between different categories were examined. Specifically, these comparisons or correlations were made (given with their respective section numbers):

3.1. Sounds with each other

3.2. Sounds with behavior

3.3. Sounds with contextual variables

3.4. Sounds with environmental variables

3.5. Behavior with contextual variables

3.6 Behavior with environmental variables

3.7. Contextual variables with each other

3.8 Contextual with environmental variables

3.9. Environmental variables with each other

Behavioral types (listed above) were not compared with each other because data were insufficient to draw meaningful conclusions. While the comparison of environmental variables to each other was not directly pertinent to this thesis, it may help elucidate other correlations with environmental variables and more fully describe conditions during the study.

All sections in which behavior is discussed compared the presence to the absence of the respective behavior with regard to a given variable. In all the following sections, those relationships which were not mentioned can be assumed to be not statistically significant at $p<.10$. Results pertaining to whistle S7 should be taken with some caution as there were indications of slight problems in reliability with this whistle type because of its high variability (see Appendix). Summary statistics of all variables are available in Tables 2 (continuous variables) and 3 (categorical variables).

Table 2. Summary statistics for continuous variables. Only selected data (with quality codes 1, 2, 4, 5 and 6) were used for sound variables (S1–S7, pulsed sounds, whistle total). Proportion = proportion of whales heading dominant direction, Area = area over which whales were scattered, Distance = distance whales were from the boat.

Variable	N	Mean	SD	Units
S1	194	4.68	6.25	Whistles
S2	194	12.50	11.01	Whistles
S3	194	12.99	10.61	Whistles
S4	194	9.14	9.39	Whistles
S5	194	6.54	7.61	Whistles
S6	194	10.91	12.03	Whistles
S7	194	4.51	7.55	Whistles
Pulsed Sounds	194	6.64	7.58	Sounds
Whistle Total	194	61.28	35.33	Whistles
Area	193	13,005.00	40,293.86	Sq. m
Distance	201	114.5	113.8	m
Group Size	195	17.83	18.52	Whales
No. of Birds	194	4.56	16.86	Birds
No. of Podlets	190	2.31	1.52	Podlets
Proportion	187	79.28	26.70	%
Speed	191	2.72	1.13	Knots
Cloud Cover	26	67.23	44.64	%
Depth	189	116.8	61.27	m
Swell Height	26	1.23	4.76	inches
Wave Height	26	2.87	2.49	inches

Table 3. Summary statistics for categorical variables. Only selected data (with quality codes 1, 2, 4, 5 and 6) were used for click scale.

Click Grade	N=194
1	33.0%
2	28.9%
3	38.1%

Quality Code	N=236	
1	No Problems	47.0%
2	Minor Noise	14.0%
3	Major Noise	10.6%
4	High Rates of Whistling	6.4%
5	Very High Rates of Whistling	5.1%
6	Distant	9.7%
7	Very Distant	2.1%
8	Distant with Noise	4.2%
9	High Rates of Whistling with Noise	0.8%

Behavior	N	Present	Absent
Directional (D)	195	77.9%	22.1%
Milling (M)	195	25.1%	74.9%
Surface-Active (SA)	195	20.5%	79.5%
Spyhopping (H)	195	3.6%	96.4%

Date	N=236
24 July	2.5%
25 July	10.6%
26 July	17.8%
27 July	19.1%
28 July	11.0%
29 July	16.1%
30 July	6.8%
31 July	16.1%

Time	N=236
6-8 h	6.4%
8-10 h	6.4%
10-12 h	8.9%
12-14 h	10.6%
14-16 h	8.5%
16-18 h	11.0%
18-20 h	12.7%
20-22 h	10.6%
22-24 h	5.9%
0-2 h	7.6%
2-4 h	5.1%
4-6 h	6.4%

Pod No.	N=236
1	2.5%
2	22.0%
3	21.2%
4	5.5%
5	12.3%
6	13.6%
7	22.9%

Windspeed - Beaufort	N=26
0	11.5%
1	23.1%
2	34.6%
3	15.4%
4	0.0%
5	11.5%
6	3.8%

3.1 Sounds with each other

[Spearman corr. coeff.]

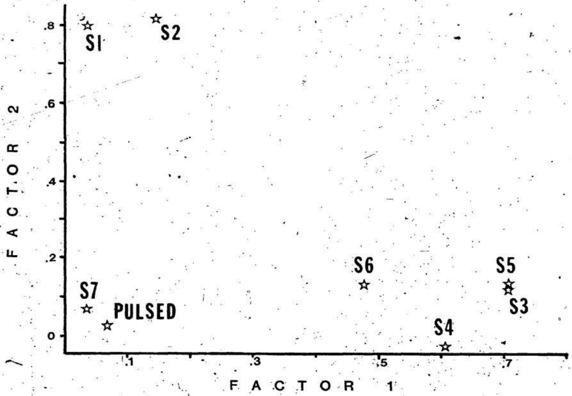
All sounds were correlated with each other at least at the .10 level, and most correlations of sounds were very highly significant ($p<.01$) (Table 4). Most highly correlated were pulsed sounds with clicks (.61, $p<.01$). The lowest correlations were S1 with pulsed sounds (.12, $p<.10$), S7 with clicks (.12, $p<.10$), and S1 with clicks (.13, $p<.10$). Overall, whistle types S1, S2, and S7 tended to be less highly correlated with other sounds. In contrast, the whistle types which were generally most highly correlated with other sounds were S3 and S6. The whistle total of each 4 min. session was also highly significantly correlated with the clicks (.38, $p<.01$) and number of pulses (.59, $p<.01$) occurring in that session.

Principal Component Analysis (Fig. 6) (also used by Clark (1982) in his classification of right whale sounds) revealed that whistle types S1 and S2 tended to happen together in the same session, but that they did not usually occur in conjunction with other whistle types. A similar situation was found with whistle type S7 and pulsed sounds. The occurrence of whistle types S3 and S5 tended to parallel each other very closely in the same session, and these whistles were very significantly correlated with one another

Table 4. Spearman correlation coefficients relating clicks, pulsed sounds [Pulse], whistle types S1-S7, and whistle total [Total] (S1+S2+S3+S4+S5+S6+S7).
+ = P<0.10, * = P<0.05, ** = P<0.01. N=194

Pulse	.61**							
S1	.13+	.12+						
S2	.19**	.16*	.38**					
S3	.42**	.39**	.32**	.23**				
S4	.30**	.28**	.27**	.24**	.44**			
S5	.31**	.24**	.35**	.32**	.49**	.32**		
S6	.35**	.42**	.22**	.38**	.43**	.47**	.43**	
S7	.12+	.25**	.29**	.27**	.25**	.33**	.25**	.32**
Total	.38**	.39**	-	-	-	-	-	-
	Clicks	Pulse	S1	S2	S3	S4	S5	S6

Fig. 6. Principal Components Analysis for whistle types S1-S7 and pulsed sounds. In this graph, sounds plotted close together tended to occur together in the same session. Only selected data with quality codes 1, 2, 4, 5, and 6 were used. N = 194.


FACTOR 2
.8
.6
.4
.2
0
FACTOR 1
.1
.3
.5
.7
S1
S2
S7
PULSED
S6
S4
S5
S3

(.49, p<.01). Both also tended to happen together with whistles S4 and S6.

3.2 Sounds with behavior

[Mann-Whitney U test; Cramer's V chi-square with clicks]

The most common behavior was directional behavior (Fig. 7). While pilot whales were exhibiting directional behavior, their output of various whistle types was either not significantly different or was less, than when directional behavior was absent (Fig. 8). Mean numbers of S1 whistles (p<.05) and S2 whistles (p<.01) were significantly lower when directional behavior was taking place. There was no significant difference in the whistle total number (p>.10)

In contrast, when whales were milling, numbers of S1 (p<.01) and S2 (p<.01) whistles increased, on average, relative to when whales were not milling. There was also a tendency for S7 whistles to occur more often (p<.10) during milling than in its absence.

During surface active behavior, the most vigorous and energetic behavior type observed, several sound types, especially the more complex whistles, increased in number over instances when this behavior was not present. In particular, pulsed sounds (p<.01), S4 whistles (p<.01), S6 whistles (p<.01), and, to a lesser extent, S7 whistles (p<.05) increased. A greater degree of clicking (Cramer's

Fig. 7. Relative frequencies of behavior types. The percentage of time each behavior (D - directional, M - milling, SA - surface active, H - spyhopping) was present is indicated. Because behavior types were not mutually exclusive, total percentages do not equal 100 %. Sample sizes (number of 5 min. sessions in which the respective behavior was present) are given at the top. The total number of 5 min. sessions in which behavior was scored was 195.

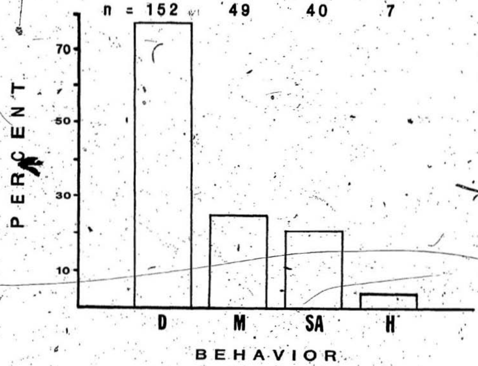
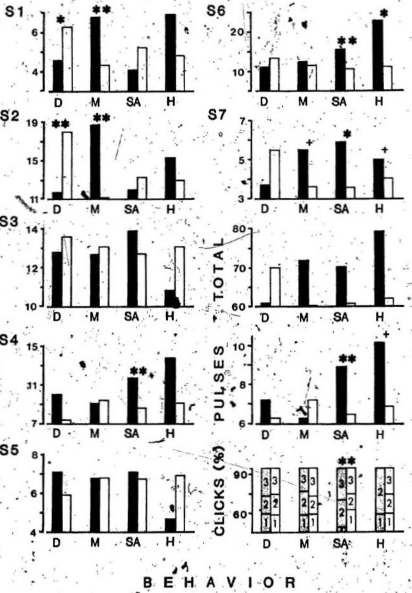

n = 152
49
40
7
70
50
30
10
PERCENT
D
M
SA
H
BEHAVIOR

Fig. 8. Relationships of sound variables (S1-S7 whistles, whistle total numbers, pulsed sounds and clicks) to behavior (D - directional, M - milling, SA - surface active, H - syphopping). Black or grey bars indicate the presence of the behavior, white bars, its absence. Mean counts over 5 min. sessions are represented for all variables except clicks. Significance, however, was based on non-parametric tests. Click scale: 1 - few or no clicks, 2 - medium click activity, 3 - heavy clicking. Cramer's $V = .251$, $p < .01$ for clicks with surface active behavior. Sample sizes are as follows (presence/absence of behavior): D = 126/35,
M = 39/122, SA = 36/125, H = 7/154.
+ = $p < .10$, * = $p < .05$, ** = $p < .01$.


S1
6
4
*
**
D M SA H
S6
20
10
**
*
D M SA H
S2
19
15
11
**
**
D M SA H
S7
7
5
3
+
*
+
D M SA H
S3
14
12
10
D M SA H
TOTAL
80
70
60
D M SA H
S4
15
11
7
**
D M SA H
PULSES
10
8
6
**
+
D M SA H
S5
8
6
4
D M SA H
CLICKS (%)
90
60
**
3 3 2 2 1 1
D M SA H
BEHAVIOR

V=.25, p<.01) was heard in conjunction with surface active behavior. Whistle total, however, did not increase significantly (p>.10).

Spyhopping was accompanied by an increase in whistle type S6 (p<.05). There was also, on average, a tendency for greater numbers of whistle type S7 (p<.10) and pulsed sounds (p<.10) to be heard during spyhopping.

3.3 Sounds with contextual variables

[Kendall corr. coeff.]

When whales were spread over a greater area, whistle types S1 (.13, p<.05), S2 (.12, p<.05), S6 (.13, p<.05), and S7 (.13, p<.05) increased in number (Table 5). The whistle total, in general, tended to be greater when whales covered a greater area (.10, p<.10).

Surprisingly, whistle total was not correlated with group size (p>.10). The only whistle type which showed a slight tendency to increase with increasing numbers of whales present was S2 (.10, p<.10). Indeed, fewer clicks (-.27, p<.01) and slightly fewer pulsed sounds (-.11, p<.10) were heard when there were more whales present.

Very different results were obtained when considering the number of podlets present. Here, most whistle types increased in number when more podlets were observed. There was a very significant positive correlation between the

Table 5. Kendall correlation coefficients relating sound variables (whistle types S1-S7, whistle total numbers [Total], pulsed sounds [Pulse], and clicks) with contextual variables (area over which whales were scattered, group size, number of podlets, proportion of the group heading the same direction, speed of the whales, and distance whales were from the boat), with sample sizes (N).
+ = P<0.10, * = P<0.05, ** = P<0.01.

	Area	Group Size	No. of Podlets	Propn.	Speed	Distance
N	159	161	156	153	157	167
S1	.13*	.08	.04	-.10	.09	.01
S2	.12*	.10+	.09	-.19**	-.03	-.02
S3	.02	-.00	.17**	-.05	.08	-.10+
S4	-.00	-.05	.18**	.00	.08	-.10+
S5	.06	-.07	.15**	-.01	.06	-.03
S6	.13*	-.01	.22**	.01	.13*	-.11*
S7	.13*	-.01	.15*	-.11+	.12+	-.06
Total	.10+	.03	.22**	-.05	.13*	-.10+
Pulse	.07	-.11+	.29**	.01	.03	-.16**
Clicks	.07	-.27**	.32**	.02	.11+	-.24**

number of podlets and whistles S3 (.17, $p<.01$), S4 (.18, $p<.01$), and S6 (.22, $p<.01$). This correlation was also present with whistles S5 (.15, $p<.05$) and S7 (.15, $p<.05$), but less significantly so. Whistle total was very significantly correlated with the number of podlets present (.22, $p<.01$), in contrast to the situation with group size. The whales' output of pulsed sounds (.29, $p<.01$) and clicks (.32, $p<.01$) also increased with greater numbers of podlets seen.

The greater the proportion of whales travelling in the same direction, the fewer S2 whistles were heard (-.19, $p<.01$). In other words, when whales were moving in a more coordinated group, they produced fewer S2 whistles. They also tended to emit fewer S7 whistles (-.11, $p<.10$).

Greater total whistle numbers were heard when whales were moving faster (.13, $p<.05$). In particular, whistle S6 (.13, $p<.05$) increased in number with the speed of the whales. Whistle type S7 (.12, $p<.10$) and clicks (.11, $p<.10$) showed similar tendencies in this direction.

The number of birds present was not significantly related to acoustic output of any kind ($p>.10$).

As expected, fewer whistles in total were heard when whales were more distant, although the correlation was only marginally significant (-.10, $p<.10$). Clicks, which are thought to be highly directional (e.g. Norris et al. 1961; Norris & Evans 1966; Evans et al. 1964) and to have high attenuation rates (due to higher frequency content), were heard less when distances were greater (-.24, p<.01). Fewer pulsed sounds were also heard when whales were further away (-.16, p<.01). Other whistles were also negatively correlated with distance from the boat, but the significance was only marginal. These were S3 (-.10, p<.10), S4 (-.10, p<.10), and S6 (-.11, p<.05) whistles.

[Analysis of variance; with clicks, used Cramer's V chi-square]

There was a significant difference in mean whistle total between different days (p<.01)(Fig. 9). Mean whistle total was particularly low on the first day of the study (July 24). The last two days (July 30 and 31) were also quite low in mean total whistle number. In the cases of July 24 and 30, however, sample sizes were small. Click activity also varied from day to day (Cramer's V=.286, p<.01)(Fig. 10). The pattern was very erratic, with no clear trend apparent. July 25 and 28 were peaks in click activity, and a marked low occurred on July 30.

Pod identification number, being closely related to date, varied similarly. Mean whistle total varied significantly (p<.01) between different pods (Fig. 9). The lowest mean number of whistles were heard from Pods 1 and 4, but sample sizes were unusually small for these groups.

Fig. 9. Variations in whistle total numbers over days (stars) and pod identification numbers 1 - 7 (bars representing the amount of time the pod was followed). Means of square-rooted counts are presented. Sample sizes for each date are indicated below the corresponding date. F-values for 7 d.f. are 6.34 (p<.01) for days, and 9.13 (p<.01) for pod number (6 d.f.).

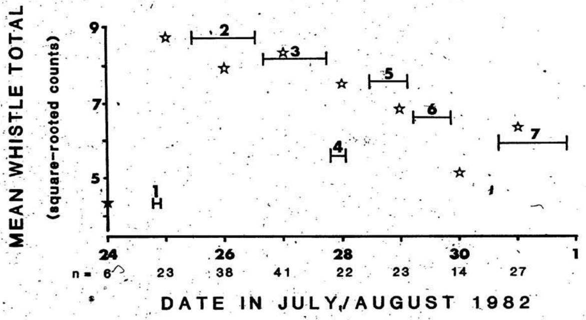
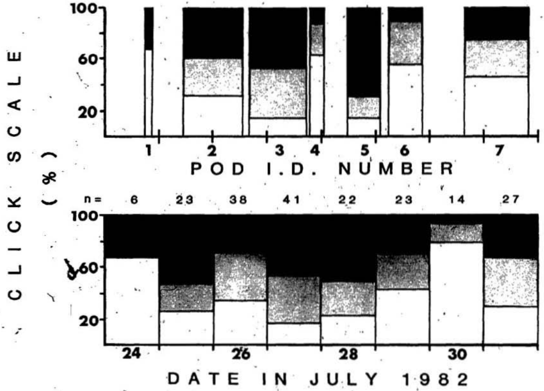

MEAN WHISTLE TOTAL
(square-rooted counts)
9
7
5
1
2
3
4
5
6
7
24
26
28
30
1
n = 6
23
38
41
22
23
14
27
DATE IN JULY/AUGUST 1982

Fig. 10. Variations in degree of click activity over pod identification numbers (top) and days (bottom). In the top figure, the width of the bars signifies the amount of time the pod was followed, being superimposed over date corresponding to the bottom figure. Click scale is given in percent of each of the following categories: 1 - few or no clicks (represented by white), 2 - medium click activity (gray), and 3 - heavy clicking (black). Sample sizes are shown above the corresponding date. Cramer's V = .304 ($p<.01$)(top) and Cramer's V = .286 ($p<.01$)(bottom).


CLICK SCALE
(%)
100
60
20
1
2
3
4
5
6
7
POD I.D. NUMBER
n =
6
23
38
41
22
23
14
27
100
60
20
24
26
28
30
DATE IN JULY 1982

Click activity was particularly low in Pods 4 and 6, whereas Pod 5 formed a conspicuous peak in the extent of clicking heard (Fig. 10). This difference in click activity between pods was significant (Cramer's V=.304, p<.01).

3.4 Sounds with environmental variables

[Kendall corr. coeff.]

Greater total numbers of whistles were heard over deeper water (.15, p<.01)(Table 6). Specifically, whistle types S1 (.15, p<.05), S5 (.23, p<.01), and S6 (.14, p<.05) were more frequently produced when whales were in deeper water. With increasing depth, a greater amount of click activity also took place (.17, p<.01).

[Analysis of variance; with clicks, used Cramer's V chi-square]

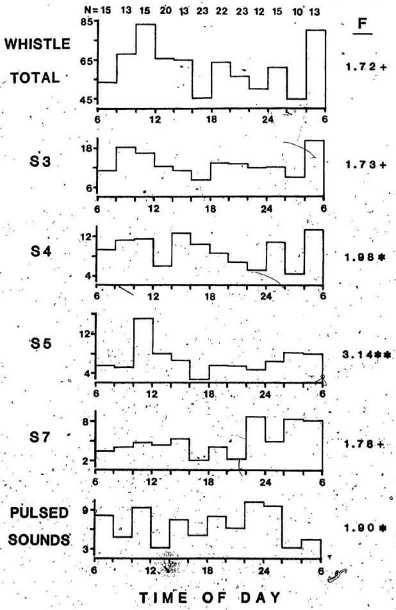
There was a tendency for the total number of whistles to vary diurnally (p<.10)(Fig. 11). On average, a slight trend towards more whistles during midday (08.00-16.00 hrs.) and early morning (04.00-06.00 hrs.) could be detected, with a peak at the 10.00-12.00 hr. interval. In general, fewer mean numbers of whistles were heard from 16.00-04.00 hrs. during darkness.

Whistle type S3, since it was the most commonly heard

Table 6. Kendall correlation coefficients relating sound variables (whistle types S1-S7, whistle total numbers [Total], pulsed sounds [Pulse] and clicks) with environmental variables (water depth, cloud cover, swell height, wave height, and wind speed), with sample sizes (N). + = P<0.10, * = P<0.05, ** = P<0.01.

	Depth	Cloud Cover	Swell Height	Wave Height	Windspeed
N	149	186	186	186	186
S1	.15*	.03	.10+	.05	-.04
S2	.08	-.03	.06	-.06	-.11+
S3	.05	.03	.00	-.12*	-.09+
S4	.06	.04	.02	-.06	-.03
S5	.23**	.16**	.10+	-.07	-.14*
S6	.14*	.10+	.12*	-.02	-.09
S7	.00	.10+	-.00	-.03	-.06
Total	.15**	.11*	.06	-.04	-.07
Pulse	-.01	-.07	.08	-.20**	-.16**
Clicks	.17**	-.17**	.13+	-.25**	-.23**

Fig. 11. Diurnal variations in vocalizations (whistle total numbers, S3, S4, S5, and S7 whistles, and pulsed sounds). True means are represented although significance was based on numbers with square-root transformations. Sample sizes for all histograms are indicated on the top. F-values for 11 d.f. are given on the right-hand side.
+ = $p<.10$, * = $p<.05$, ** = $p<.01$.


N= 15 13 15 20 13 23 22 23 12 15 10 13
F
WHISTLE TOTAL
85
65
45
1.72 +
S3
18
6
1.73 +
S4
12
4
1.98 *
S5
12
4
3.14 **
S7
8
2
1.78 +
PULSED SOUNDS
9
3
1.90 *
6
12
18
24
6
TIME OF DAY

whistle, showed roughly a similar trend to that of whistle total. Mean values of S3 were higher, for the most part, from early morning to noon (04.00-12.00 hrs.) than they were from afternoon to night (12.00-04.00 hrs.). Especially high numbers of this whistle were heard from 04.00-06.00 hrs., on average. Over all time periods, though, differences in means were only marginally significant ($p<.10$).

A very erratic pattern was exhibited by whistle type S4 with respect to time of day. In general, mean whistle numbers were higher around noon, but at the 12.00-14.00 hr. interval, there was a marked dip. A peak in mean whistle numbers occurred between 04.00-06.00 hrs. Differences in means of the 12 time periods were significant ($p<.05$).

Diurnal variations in whistle type S5 were more significant than in any other sound ($p<.01$). A clear maximum in mean numbers occurred in the 10.00-12.00 hr. time interval, and a minimum, in the 16.00-18.00 hr. time period. Means at other time periods were fairly similar.

The diurnal pattern of complex whistle type S7 was quite unusual, compared to the above-mentioned ones. It was roughly similar to other whistles in that, on average, more S7 whistles were heard from 08.00-16.00 hrs. than from 16.00-22.00 hrs. However, most whistles were heard from 22.00-06.00 hrs., on average. This whistle, then, unlike other whistles, was most common during the night. Differences, however, were only marginally significant (p<.10).

Pulsed sounds showed a significant difference with time of day (p<.05). The diurnal variations of these sounds were characterized by fluctuations, in which no trends were immediately apparent. Highest means in pulsed sounds occurred in time periods 10.00-12.00 hrs. and 22.00-02.00 hrs., thus sharing some similarity with whistle S7 in their nocturnal prevalence.

Click activity did not vary with time of day (p>.10).

[Kendall corr. coeff.]

More total whistles were heard when skies were more cloudy (.11, p<.05)(Table 6, p. 50). In particular, numbers of S5 whistles were higher when cloud cover was greater (.16, p<.01). Whistles S6 (.10, p<.10) and S7 (.10, p<.10) showed only a tendency to increase with cloud cover. Click activity, however, was greater under clear skies (-.17, p<.01).

Swell height was not significantly correlated with whistle total number (p>.10), but there was a marginally significant increase in numbers of S1 (.10, p<.10) and S5 (.10, p<.10) whistles, and in click activity (.13, p<.10) with higher swells. Significantly greater numbers of whistle type S6 were also heard with an increase in swell height (.12, p<.05).

While wave height was not significantly correlated with total numbers of whistles heard ($p>.10$), fewer pulsed sounds ($-.20$, $p<.01$) and clicks ($-.25$, $p<.01$) were heard when waves were higher. Counts of whistle type S3, in addition, were negatively correlated with wave height ($-.12$, $p<.05$).

As with wave height, wind speed was negatively correlated with particularly pulsed sounds ($-.16$, $p<.01$) and clicks ($-.23$, $p<.01$). There was a tendency for fewer S2 ($-.11$, $p<.10$) and S3 ($-.09$, $p<.10$) whistles to be heard at higher wind speeds. Fewer S5 whistles ($-.14$, $p<.05$) were heard when it was windier, but whistle total was not affected ($p>.10$).

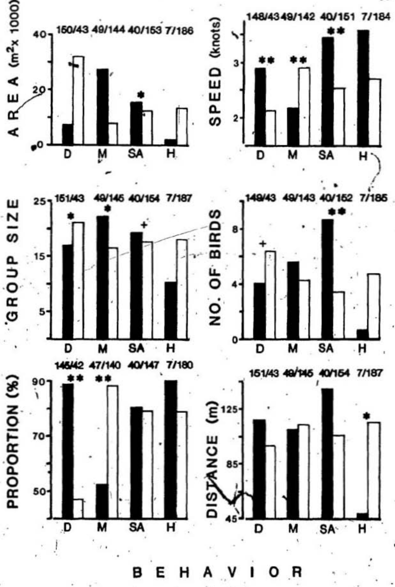
3.5 Behavior with contextual variables

[Mann-Whitney U test]

Only while engaged in surface active behavior were whales spread over a significantly greater area ($p<.05$)(Fig. 12). This was despite a tendency for group sizes to be smaller during surface active behavior ($p<.10$). Group sizes were smaller ($p<.05$) when directional behavior took place, but when milling, larger numbers of whales were present ($p<.05$).

The number of podlets did not vary significantly relative to the behavior of the followed group ($p>.10$).

Fig. 12. Relationships of contextual variables (area over which whales were scattered, group size, proportion of the group heading the same direction, speed of the whales, number of birds present, and distance whales were from the boat) to behavior (D - directional, M - milling, SA - surface active, H - spyhopping). Black bars indicate the presence of the behavior; white bars, its absence. In all bar graphs, means are represented. Significance, however, was based on nonparametric tests because of non-normal distributions. Especially "area" and "group size" were very skewed and kurtotic. The means presented here thus have limited value. Sample sizes are indicated above each bar (presence/absence of behavior). + = p<.10, * = p<.05, ** = p<.01 indicate differences between values during the behavior and during its absence.


AREA (m^{2}x 1000)
150/43 49/144 40/153 7/186
40
20
0
*
D M SA H
SPEED (knots)
148/43 49/142 40/151 7/184
3
2
** ** **
D M SA H
GROUP SIZE
151/43 49/145 40/154 7/187
25
15
5
* * +
D M SA H
NO. OF BIRDS
149/43 49/143 40/152 7/185
8
4
0
+ **
D M SA H
PROPORTION (%)
145/42 47/140 40/147 7/180
90
70
50
** **
D M SA H
DISTANCE (m)
151/43 49/145 40/154 7/187
125
85
45
*
D M SA H
BEHAVIOR

During directional behavior, a greater proportion of the whales were heading the same direction ($p<.01$). This is not remarkable, since directional behavior was defined in this way. While milling, whales were moving less in unison with each other than when not milling, with a smaller proportion of the group moving in the same direction ($p<.01$).

Pilot whales moved faster when engaged in directional behavior ($p<.01$) and surface active behavior ($p<.01$). In contrast, whales moved significantly more slowly when milling ($p<.01$) than in its absence.

A significantly greater number of birds was present while surface active behavior took place than when it did not ($p<.01$). During directional behavior, fewer birds tended to be present ($p<.10$).

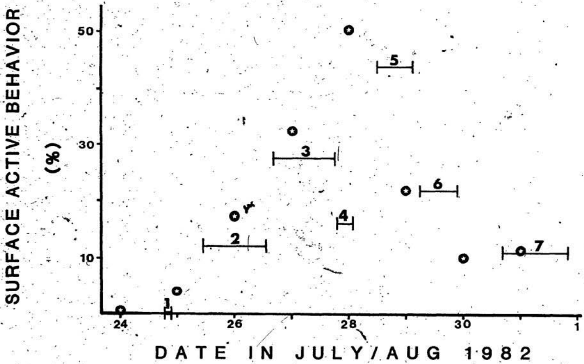
More spyhopping was seen when whales were closer to the boat ($p<.05$).

[Cramer's V chi-square]

Surface active behavior was the only behavior which varied significantly from day to day (Cramer's V=.334, $p<.01$). From Fig. 13, it seems that surface active behavior increased steadily until it reached a peak on 28 July. It then, steadily, decreased in relative occurrence until 30 July when it levelled off to 31 July.

Surface active behavior was also significantly related

Fig. 13. Variations in surface active behavior over days (stars) and pod identification numbers (bars representing the amount of time the pod was followed). Percentages of time surface active behavior was present are given. Sample sizes are as follows for 24-31 July: 6, 24, 29, 34, 20, 37, 10, 35. Cramer's V = .334 ($p<.01$) for date; and .282 ($p<.05$) for pod number.


SURFACE ACTIVE BEHAVIOR
(%)
50
30
10
24
26
28
30
1
DATE IN JULY/AUG 1982
1
2
3
4
5
6
7

to the pod identification number (Cramer's $V=.282$, $p<.05$)(Fig. 13), probably because of the close relationship between pod number and date. Here, the relative occurrence of surface active behavior peaked with Pod 5, and formed a smaller peak with Pod 3. There was a dip between the two peaks at Pod 4, which had a small sample size.

3.6 Behavior with environmental variables

[Mann-Whitney U test; with time of day and windspeed, used Cramer's V chi-square]

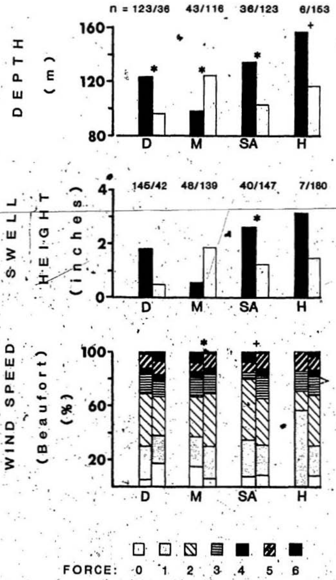
Whales were over deeper water when engaged in directional behavior ($p<.05$) and surface active behavior ($p<.05$)(Fig. 14). Spyhopping also tended to occur over deeper water ($p<.10$). Milling, however, took place over significantly shallower water ($p<.05$) than did the absence of milling.

No diurnal variations in any behavior were significant ($p>.10$).

Cloud cover showed no significant relationship to behavior ($p>.10$).

Swells were significantly higher when surface active behavior occurred ($p<.05$), than when it did not. Wave height, however, bore no significant relationship to behavior ($p>.10$).

Fig. 14. Relationships of environmental variables (water depth, swell height, and wind speed) to behavior (D - directional, M - milling, SA - surface active, H - spyhopping). The left-hand bars of each pair (indicated black in the upper two diagrams) represent the presence of the behavior; right-hand bars (white, in the upper two diagrams), its absence. Means are represented for depth and swell height, although significance was based on non-parametric tests. Cramer's V = .265, p<.05 for wind speed and milling, and .247, p<.10, for surface active behavior. Sample sizes are given above graphs (presence/absence of behavior). The lower two graphs have the same sample sizes. + = p<.10, * = p<.05, ** = p<.01.


n = 123/36
43/116
36/123
6/153
DEPTH
(m)
160
120
80
*
*
*
+
D
M
SA
H
145/42
48/139
40/147
7/180
SWELL HEIGHT
(inches)
4
2
0
*
D
M
SA
H
WIND SPEED
(Beaufort)
(%)
100
60
20
*
+
D
M
SA
H
FORCE:
0
1
2
3
4
5
6

[Cramer's V chi-square]

Wind speed was significantly related to milling behavior (Cramer's V=.265, p<.05)(Fig. 14). When there was very little or no wind (Force 0) or strong wind (Force 6), whales were more frequently seen to be milling.

There was a tendency for surface active behavior to vary with wind speed (Cramer's V=.247, p<.10). In wind speeds less than Force 3 or during Force 6, surface active behavior was more frequently observed.

3.7 Contextual variables with each other

[Kendall corr. coeff.]

As expected, larger groups were scattered over a greater area (.20, p<.01)(Table 7). The smaller the area over which whales were spread, the more they moved in unison with one another, i.e. with a greater proportion of whales heading the same direction (-.25, p<.01). Whales also moved faster when scattered over larger areas (.15, p<.01)]. The greater the area the group of whales covered, the more birds were seen (.21, p<.01). Whales covered greater areas during the earlier days of the study (-.14, p<.01).

The greater the number of animals in the group being followed, the fewer surrounding podlets were seen (-.25, p<.01). With larger group sizes, coordination between animals broke down, i.e., a smaller proportion of the group

Table 7. Kendall correlation coefficients relating contextual variables (area over which whales were scattered, group size, number of podlets, proportion of the group heading the same direction, speed of the whales, number of birds present, and date), with each other. Sample sizes (N) are given in parentheses.
+ = P<0.10, * = P<0.05, ** = P<0.01.

	Area	Group Size	No. of Podlets	Prop'n	Speed	No. of Birds
Group Size	.20** (193)					
No. of Podlets	-.06 (180)	-.25** (180)				
Proportion	-.25** (187)	-.22** (187)	-.05 (175)			
Speed	.15** (191)	.04 (191)	-.02 (178)	.17** (186)		
No. of Birds	.21** (192)	.16** (193)	.04 (179)	-.12* (187)	.11+ (190)	
Date	-.14** (193)	-.00 (195)	-.05 (190)	-.03 (187)	-.07 (191)	.06 (194)

travelled in the same direction ($-.22$, $p<.01$). More birds were present when there were more whales in the group ($.16$, $p<.01$).

Whales moved faster ($.17$, $p<.01$) and fewer birds were present ($-.12$, $p<.05$) when whales moved more in unison, with a greater proportion of the group heading the same direction. In general, fewer birds tended to be seen when the whales' speed was greater ($.11$ $p<.10$).

3.8 Contextual with environmental variables

[Kendall corr. coeff.]

When whales were over deeper water, group sizes were significantly smaller ($-.16$, $p<.01$), but more surrounding podlets were present ($.18$, $p<.01$)(Table 8). Whales were also found over greater depth earlier in the study ($-.47$, $p<.01$).

[Analysis of variance]

Group size varied according to time of day ($p<.01$), with mean numbers being larger from 10.00-22.00 hrs. (Fig. 15). Slight peaks in group size occurred at the 12.00-14.00 hr. and 18.00-22.00 hr. time intervals. Sample sizes, however, were low for time periods 22.00-04.00 hrs. in this analysis and in the following 3 analyses of time with number

Table 8. Kendall correlation coefficients relating contextual variables (area over which whales were scattered, group size, number of podlets, proportion of the group heading the same direction, speed of the whales, number of birds present, and date), with environmental variables (water depth, cloud cover, swell height, wave height, and wind speed). Sample sizes (N) are given in parentheses. + = P<0.10, * = P<0.05, ** = P<0.01.

	Water Depth	Cloud Cover	Swell Height	Wave Height	Wind Speed
Area	.05 (157)	.06 (185)	.07 (185)	.00 (185)	-.10+ (185)
Group Size	-.16** (158)	.20** (187)	-.08 (187)	.14** (187)	.19** (187)
No. of Podlets	.18** (158)	-.08 (188)	.28** (188)	-.31** (188)	-.26** (188)
Proportion	.10 (152)	-.03 (179)	.04 (179)	.05 (179)	-.05 (179)
Speed	.02 (155)	.03 (183)	.21** (183)	.12* (183)	.11+ (183)
No. of Birds	-.01 (157)	-.06 (186)	.06 (186)	-.03 (186)	-.02 (186)
Date	-.47** (189)	-	-	-	-

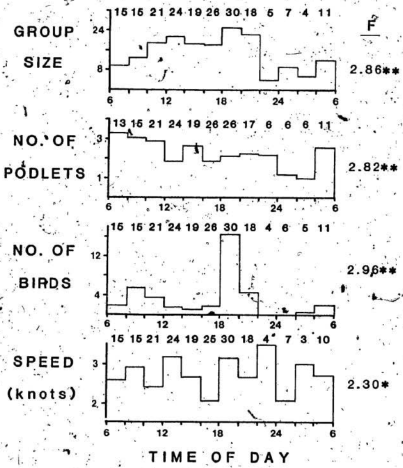


Fig. 15. Diurnal variations in contextual variables (group size, number of podlets, number of birds, and whale's speed). True means were presented although significance was based on numbers with square-root transformations. Sample sizes are indicated above each corresponding bar. F-values for 11 d.f. and their significance are given on the right-hand side. * = p < .05, ** = p < .01.

of podlets, speed, and number of birds, respectively, because these parameters could usually not be reliably assessed at night.

Diurnal differences in the number of podlets seen were significant (p<.01). Higher mean numbers of podlets were observed during the morning (06.00-12.00 hrs.) than at other times. Although the speed of the whales varied with time (p<.05), no trend could be discerned in the fluctuations of Fig. 15. Whales were on average slowest, however, during the 16.00-18.00 hr. time period. The number of birds present was related to time of day (p<.01). A very high peak occurred at the 18.00-20.00 hr. time interval, and a much lower peak, during the 08.00-10.00 hr. time period.

[Kendall corr. coeff.]

Group sizes were larger when there was more cloud cover (.20, p<.01)(Table 8). Whales were moving faster (.21, p<.01) and more podlets were seen (.28, p<.01) during higher swells. With greater wave height, whales were also moving faster (.12, p<.05), but fewer podlets were observed (-.31, p<.01) and group sizes were larger (.14, p<.01). This was also the case at higher wind speeds: whales tended to go faster (.11, p<.10), fewer podlets were seen (-.26, p<.01), and groups were larger (.19, p<.01). In addition, whales tended to be spread over a smaller area during high winds

(-.10, p<.10), despite larger groups.

3.9 Environmental variables with each other

[Kendall corr. coeff; with windspeed, Cramer's V chi-square]

While whales were over greater depth, skies were cloudier (.14, p<.01), swells were higher (.29, p<.01), but there tended to be less wind (-.09, p<.10)(Table 9). Wind speed varied diurnally (Cramer's V=.334, p<.01)(Fig. 16), with higher winds more common during the afternoon and late evening (14.00-22.00 hrs.) than at other times. Winds were calmest in the early morning, especially during 04.00-08.00 hrs.

When there was more cloud cover, waves were higher (.33, p<.01) and wind speed was greater (.29, p<.01)(Table 9). Wave height was naturally highly affected by wind speed (.61, p<.01), in contrast to swell height, which decreased with higher winds (-.11, p<.05).

3.10 Summary

The rates at which different sound types were heard within sessions correlated very significantly with each other, although this was less the case with simple whistles S1 and S2. S1 was especially weakly correlated with clicks and pulsed sounds. Whistles S1 and S2 were heard more often

Table 9. Kendall correlation coefficients relating environmental variables (cloud cover, swell height, wave height, and wind speed) with each other.
+ = $P<0.10$, * = $P<0.05$, ** = $P<0.01$.

	Cloud Cover	Swell Height	Wave Height
Swell Height	.05		
Wave Height	.33**	-.04	
Wind Speed	.29**	-.11*	.61**

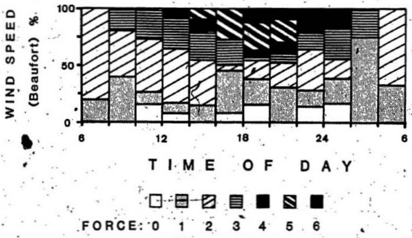


Fig. 16. Variations in wind speed (Beaufort scale) with time of day. Cramer's V = .33, $p<.01$.

during milling but less often during directional behavior. During milling, group sizes were larger, and whales were moving more slowly, over shallower water. The opposite happened during directional behavior: groups were smaller with a greater proportion moving in the same direction, at greater speeds, over deeper water. S2 was different from other sound types in that only this whistle was associated with the variable "proportion of the group heading the same direction".. More S2 whistles were heard when whales were moving less in unison, with fewer animals heading the same direction, as was more common during milling. Generally, whales moved in a less unified manner when the group was larger and scattered over a greater area. More birds were also present during these conditions.

Simple whistles S2 and S3 were, on average, the most common whistles heard overall. However, S3, unlike S2, was relatively highly correlated with other sound types, especially with intermediate whistle S5. Both S3 and S5 whistles did not show significant associations with any of the behavioral states measured in this study. Like all sounds except S1 and S2, they both increased in number when more podlets were present, which occurred over deeper water and when group size was smaller. Of all sound types, numbers of S5 increased most with water depth and showed the most statistically significant diurnal variations. This whistle was most common in the late morning to noon time period, and least common in the late afternoon. Other whistles showed similar diurnal trends, with acoustic output usually higher during early morning (04.00-06.00 hrs.) and in the hours before noon (10.00-12.00 hrs). Pulsed sounds and complex S7 whistles, in contrast to the other whistles, tended to be heard more at night.

Surface active behavior was the only behavior during which intermediate whistle S4 increased in number. Complex S6 whistles, which were very significantly correlated with other sound types, also increased with surface active behavior and, to a lesser extent, with spyhopping. Especially more S6 whistles were heard when more podlets were present. Complex whistle type S7, while also heard more often in conjunction with surface active behavior, was distinguished from S6 in that it was one of the whistles least correlated with other sound types, in general. Pulsed sounds and S7 whistles tended to occur together in the same session and, throughout the analysis, showed similar trends. Pulsed sounds, more than any other sound type, increased in number when more podlets were seen. They were heard more often when surface active behavior was observed during which time the whales were moving faster and more birds were seen. Clicks were strongly correlated with pulsed sounds and increased with surface active behavior. More click activity was heard when group sizes were smaller, skies were clearer, and when whales were over deeper water.

Whistle total was not related to group size at all. Instead, the number of surrounding podlets present had a greater bearing on the total number of whistles heard during each 4 min. session. Whales also tended to produce more whistles in total when over deeper water, where more surface active behavior took place. Surface active behavior seemed to show a clear trend over days, peaking on 28 July, midway through the study. Earlier in the study, whales were found over greater depth.

More podlets were observed during the morning when group size was lower than at other times. Fewer podlets and larger group sizes occurred, however, during storm conditions of high wind speed and wave height. Whales moved faster with higher swells.

In general, simpler whistles tended to be heard more during low-activity, restful behavior, while complex whistles occurred more in conjunction with very energetic, coordinated behavior. Simpler whistles were generally more common, whereas complex sounds such as S7 whistles and pulsed sounds, were heard only rarely. Rates of overall whistling seemed to be especially high when whales were spread out with podlets widely separated.

CHAPTER 4 - DISCUSSION

Introduction

After mentioning the limitations and problems with the data, I will present background information on acoustic communication, the physics of sound transmission, and its relationship to pilot whale sounds. I will then discuss contact calls and, based on physical and other characteristics, theorize which sound type might function as such in pilot whales. Graded acoustical systems and their correlates will be reviewed, and rules relating sound structure to motivation in mammals will be presented to offer possible "meanings" of various pilot whale sounds.

Results of my analysis are then directly discussed at length, relating vocalizations to behavior, environment, and other contexts. Discussions of variations in feeding behavior and of signature whistles are also given.

Data constraints

Before proceeding further, it is important to note constraints on the interpretation of these data. They are based on the assumption that the vocalizations heard during a recording session were emitted by the same animals from which behavioral and contextual data were taken. In other words, were we hearing the same whales we were observing, or did these sounds come from another fairly close podlet?

Podlets were usually at least 300 m further from us than the group we were following, so differences in sound amplitude often convinced us of the source of the sounds. Moreover, the behavior of different podlets seemed correlated so that observations of the group we were following were, in general, reliable predictors of the behavior of the surrounding podlets. Otherwise, little could be done to ease this uncertainty.

There are many sources of variation when studying whales in the wild. So little could be seen of the whales and their individual interactions at sea that I was forced to use group behavior, a comparatively crude measurement of individual behavior. In addition, many parameters had to be estimated. These factors contributed to considerable "noise" in the data. This was reflected in some relatively low correlation coefficients (<.2) of the results. They were statistically significant, however, due to large sample sizes (ca. 195-236). Because of the way the data needed to be collected, I believe these low, but significant, correlations represented real effects.

Acoustic communication

Communication, or "the process in which actors use specially designed signals or displays to modify the behaviour of reactors" (Krebs & Davies 1981), can take place using a variety of channels, determined, to a large extent, by ecological and social circumstances. Acoustic signals have the advantage that they can be used in habitats or conditions where vision is restricted. They can also be transmitted over relatively long distances, especially in water where the speed of sound is approximately 4.5 times faster than in air (Giancoli 1980). In social situations, when complex information must often be relayed over a short period of time, the auditory channel is particularly useful. Sound is easily modulated--enormous numbers of signals can be broadcast by rapid changes in frequency, duration, and harmonic structure (Krebs & Davies 1981). In addition, sounds can be patterned sequentially to greatly increase information content (Herman & Tavolga 1980).

Animal sounds can be readily classified into ecological categories dealing with: 1) food problems, 2) avoidance of predators, 3) reproduction, and 4) group movements (Collias 1960). Pilot whales probably do not suffer substantial losses due to natural predators, although little is known (Sergeant 1962). While many sounds may be associated with reproductive behavior, only data pertaining to general group behavior were collected for this thesis. Nevertheless, it seems probable that the greater part of the vocal repertoire of the pilot whale is devoted to "food problems" and the frequently related "group movements". Since pilot whales are faced with the problem of catching one of the fastest and most evasive marine creatures, squid (e.g. Clarke 1983), it is not surprising that complex behavioral routines (e.g. cooperative feeding) have developed as a consequence. Acoustic signals, then, because of their potential to transmit large amounts of complex information independent of visual range, seem especially appropriate means by which to mediate coordinated actions of pilot whales.

Sound transmission

The major problems in the transmission of sound are identified by Wiley & Richards (1978) to be: 1) attenuation--the sound gets lost in the background noise, and 2) degradation--distortion of the sound in its passage through the environment. In a scattering environment, attenuation effects along the axis of propagation can be lessened by the use of a sound with wider radiation from the source, than one with a more narrowly beamed broadcast (Wiley & Richards 1978). Wiley & Richards (1978) reason that tonal signals, which focus energy in a narrow band of frequencies but are not very directional, permit a greater received signal/noise ratio, and so, extend the range of effective transmission. Especially frequency-modulated upsweeps (like whistle S3) are least likely to be lost in background noise because sounds with these characteristics contrast most with the physical features of usual ocean ambient noise (Watkins & Schevill 1979). A frequency upsweep might also permit a receiver to estimate its distance from the source by comparing intensities of high and low frequency components of a signal (Tolstoy & Clay 1966; Wiley & Richards 1978). Tonal signals have the additional advantage for long-range communication in that both frequency and amplitude modulation can be used to encode information. In particular, Wiley & Richards (1978) conclude that "for rapidly transmitting large amounts of information to maximum range, signals should consist of tones modulated in frequency".

Therefore, whistles, as pure-tone sounds, seem well suited for much of pilot whale communication. Clicks, which are often thought to be highly directional (e.g. Norris et al. 1961; Norris & Evans 1966; Evans et al. 1964), have their energy spread over a wide range of frequencies. They would therefore be more quickly submerged within the background noise. If, however, the position of the receiver is accurately known, narrow-beam clicks may be effective in overcoming transmission problems (Wiley & Richards 1978). Such directional sound sources also reduce the effects of reverberation (Wiley & Richards 1978), which may be a problem in shallow water (Murchison 1980). However, Wiley & Richards (1978) state that "because wide spectrum signals must rely on amplitude modulation to encode information, such signals would permit the transmission of little information in long-range communication". Therefore, clicks as wide spectrum signals probably do not have the capacity to encode nearly as much information as do the frequency-modulated whistles. Moreover, it is unlikely that the position of the receiving whale is known if the water is murky and whales are spread out. In any case, it may be advantageous to communicate to the school as a whole, in many directions, as opposed to a particular individual. This would seem to be especially true for the contact call, which is one of the commonest categories of calls (Brown 1975). It is given between members of a pair, family, brood, or flock to help keep the social unit together (Brown 1975). In pilot whales, a contact call would probably have to cover the largest distances in the greatest number of directions, i.e. be omni-directional as whistles are.

Contact calls

Based on the physical characteristics mentioned above, the most likely whistle to function as a contact call (if indeed one exists for the pilot whale) would be S3. As a whistle, it is omni-directional; and as a frequency upsweep, it could presumably be heard above the background noise over the greatest range (Watkins & Schevill 1979), and moreover, might allow the receiving whale to estimate its distance from the caller (Tolstoy & Clay 1966; Wiley & Richards 1978). It was also the most common whistle, was most correlated with other whistle types, and was not associated with any particular behavior. Contact calls would presumably have these characteristics. They would need to be simple (less affected by degradation), present during all coordinated behavior, and frequently emitted since they carry information of rapidly changing conditions which must continuously be updated. It might be expected that such a call would be highly correlated with other whistle types, since other information besides simply location may need to be exchanged. A form of whistle S3 was also suggested to serve as a contact call by McLeod (1982) who found that this whistle was especially prevalent in recently stranded pilot whales which had been towed back out to sea. Clark (1983) suggested that the "up" call in right whales, also a frequency upsweep and the most common sound the whales made, functioned as contact call. Dreher & Evans (1964) found a frequency upsweep like whistle S3 also to be the most common whistle in the repertoire of captive bottlenosed dolphins, and associated it with search behavior.

Generally, in animal commmunication, the most frequent signal carries the least amount of information and shows the highest redundancy (Schleidt 1973). In the case of the contact call, little more than the sender's location (and possibly identity) need be transmitted. Schleidt (1973) theorizes that a contact call should be just loud enough to carry over the maximal safe distance to be away from the next neighbor. He further suggests that if these calls control group cohesion, an increase in ambient noise should decrease the spacing in the group, or be compensated by an increase in signal strength. This may explain why pilot whales were found to "huddle" into larger groups and form fewer podlets during storm conditions of high wind speed and wave height, which adversely affected the range of signal transmission. In contrast, whales were spread out into more podlets during the morning when conditions were calmest (and thus, with least background noise present (Albers 1965)).

Graded signals.

Taruski (1976) found that there were no clear mutually exclusive pilot whale whistle types. He noted that whistle shapes could be arranged in a continuum such that any particular whistle could be derived from any other, through a series of intermediates. This is in agreement with my results (Appendix A, Test 3a). Pilot whale whistles, then, seem to clearly be graded signals. Such sound types also occur in many primate species, including the chimpanzee (Marler 1977). Primate species, in which most or all of the vocal repertoire consisted of a single graded acoustical system, were characterized by the absence of territoriality, greater group size (30-50 animals), and more complex troop organization resulting from the presence of several adult males (Marler 1977). The closest correlation between discretely organized and graded vocal repertoires occurred with territoriality. Non-territorial primates seemed more likely to develop graded vocalizations (Marler 1976). The above features of primate species with graded signals may also pertain to pilot whale social life. Territoriality would seem unnecessary and impractical for pilot whales (oceanic food resources could not feasibly be defended (Brown 1975)) and indeed, there is no evidence that it exists. Pilot whales show evidence of complex social organization, with more than one adult male usually present in a pod (Sergeant 1962).

Green & Marler (1979) also propose that graded signals would be more prevalent in social species in which individuals are familiar with their fellow group members. If interactants are experienced at communicating with each other, signals would not have to be as complete or discrete. Green & Marler (1979) believe that porpoises and whales, in addition to primates, may exhibit these social characteristics.

Marler (1972) theorizes that graded sounds would tend to be used more at relatively close ranges, where back-up visual cues, for instance, could be provided to decrease ambiguity. Graded sounds, while more liable to misinterpretation than discrete signals, allow for the communication of more refined information (Marler 1976). They have the potential for conveying subtle and complex information about the state or mood of the vocalizer, for instance. However, Marler (1976) makes an important point--

we do not know how graded sounds are perceived by the receiver. In human speech, even though the sounds may be graded, they are nevertheless perceived categorically (Liberman et al. 1961). Until we understand the perceptual processing of graded sounds (whether categorical or continuous), their communicative significance will remain hidden (Marler 1976). So, even though the vocal repertoire of the pilot whale appears very complex, whistles may be "categorized" by the receiver into a relatively small number of signal types. These, however, may or may not correspond to my classification based on whistle contour. The pilot whales may even by using acoustic parameters that we do not yet use in our analysis.

Motivation-structural rules in mammalian sounds

My principal aim in this thesis was to examine the social context in which sounds were made to gain insight into their function and significance. However, it is interesting to note that, generally speaking, the mere physical structure of sounds may give clues to the motivation underlying their use (Morton 1977). This general rule mostly pertains to close contact sounds, but may also operate on some long-distance or broadcast calls, especially those made by species living in groups (Morton 1977). Morton (1977) proposed several rules, of which only those pertinent to this thesis are presented in the following:

1) In birds and mammals, "harsh" (covering a wide frequency band), relatively low frequency sounds are used when the vocalizer is hostile. In contrast, higher frequency, more pure tone-like sounds are emitted when the animal is frightened, appeasing, or friendly.

2) The higher the frequency used, the more fearful or friendly the sender; the lower the frequency, the more hostile the vocalizer.

3) The greater the sound's harshness, the greater is the aggressive motivation of the sender; the more pure tone-like, the more fearful or friendly, regardless of the frequency range used.

4) Sounds rising in frequency, regardless of the sound's quality, signify decreasing hostility or increasing appeasement or fear. Sounds decreasing in frequency indicate an increasingly hostile motivation.

5) A sound whose frequency rises and falls equally or is frequency constant (but midrange in the overall frequency range) reflects conflict of motivation to approach or withdraw from a stimulus. A stimulus of "interest" has been received by the sender.

6) Species that often join in groups, especially mixed species groups, have a prevalence of high frequency, pure tonal sounds in their repertoire, compared with species more aggressive to conspecifics which have harsher close contact calls.

7) A species with a greater complexity of social interactions will evolve sound signals containing a more complete range of sound qualities, representing finer gradations in motivation.

Since I was unable to study individual interactions between whales, I could not determine which sounds were close contact sounds and which were associated with group behavior. Therefore, most of the above hypotheses could not be assessed with my results. However, pulsed sounds, which are more "harsh-sounding" than the pure tonal whistles, are thought to occur in aggressive contexts, based on studies on captive cetaceans (Overstrom 1983). Clark (1983) also felt that the "pulsive calls" of southern right whales were aggressive signals directed at other members of the group. Whistles S6 (wavers) or S1 could be interpreted as reflecting conflict of motivation, based on Point #5, but no evidence is available to support this. A preliminary analysis suggests that in situations of fear, such as when stranded pilot whales were towed out to sea, simple whistles, mainly S3 whistles, were heard. It is unlikely, however, that all S2 (decreasing in frequency) whistles indicate mounting hostility, and that all S3 (increasing in frequency) whistles reflect increasing appeasement or fear. In long-distance situations, S3 whistles seem to simply function as contact calls, whose frequency contour is more a result of environmental selection pressures favoring enhanced transmission properties (see above). It is clear, however, that pilot whales have a prevalence of pure tonal sounds (whistles) and are gregarious. They are also a species with apparently fairly complex social interactions and a correspondingly complete range of sound qualities.

Relationships between vocalizations and behavior

My study suggests that within one species, the pilot whale, complexity of sound and complexity of behavior also seem to be related. The very energetic surface active behavior, during which squid were sometimes cooperatively corralled (see next section), was accompanied by more sound types increasing in number than any other behavior. Interestingly, these sounds were also the most complex ones--pulsed sounds or whistles with more frequency inflections. This is in contrast to milling, a low activity, more restful behavior during which whales were less coordinated in their direction of movement. Here, simple whistles were the sounds increasing in number. Norris & Dohl (1980a) found that, in resting schools of spinner dolphins, complex phonations were nearly absent, and indeed, schools were mostly silent.

Directional behavior, opposite to milling in most ways but not as energetic as surface active behavior, showed no particular whistle type dominantly associated with it.

Instead, those simple whistles which increased with milling, decreased with directional behavior. One should remember that if a significant effect is found with regard to milling, the opposite trend would be expected in directional behavior, and vice versa, since these two behavior types comprised most of all observations.

Clark (1983) also found that, in right whales, the complexity of the social context was directly related to the complexity of sounds made. He stated that "sounds with the simplest and most predictable structure were associated with long distance contact situations while the highly variable, acoustically complex sound types were associated with groups of socially active whales". Taruski (1976) related high proportions of complex whistles in pilot whales to high arousal situations, such as excitement (which corresponded approximately to what I call "surface active"), and stress and fear caused by a pilot whale drive during which whales were killed. Similarly, McLeod (1982) found an increase in complex whistles in pilot whales after broadcast of killer whale phonations. Caldwell et al. (1970), however, suggested the opposite to be true for bottlenosed dolphins--high arousal or emotion were related to simpler whistles. General whistling rates in delphinids have also been reported to increase during stressful situations, when animals are excited, or in relation to feeding (Caldwell & Caldwell 1977; Norris & Dohl 1980a; Herman & Tavolga 1980), in contrast to my data which do not show an overall increase in whistle total.

Surface active behavior and feeding

Surface active behavior was the only behavioral category in which more birds were seen and greater click activity was heard. Speed was also greater during surface active behavior. These results suggest that feeding was taking place when this behavior was observed. Moreover, it was clearly seen how, on one occasion, whales moved at a high speed in single file, formed a ring, and then spiralled together to tighten their circle. After this corralling had presumably produced a concentration of squid in the center, whales were seen to engage in the typical surface active displays of lunging, leaping, breaching, and streaking through the squid school (Fig. 1, p. 15). Several times squid could be seen in the mouths of breaching whales or in the beaks of gulls which dove into the school. Such herding of squid by the whales may bring the squid fairly close to the surface or may injure them, making them accessible to the gulls, which explains why more birds were seen in conjunction with surface active pilot whales. Often whales were first sighted by the large concentrations of birds above them. Saayman & Tayler (1979) also found that the presence of gulls scavenging fish in conjunction with high-speed chasing and jumping of dolphins, was characteristic of humpback dolphins feeding close to the surface. Since clicks have long been implicated in echolocation (Kellogg et al. 1953; Norris et al. 1961; Norris 1969), it is reasonable that more clicking would be heard in feeding situations, to aid in prey detection. In captive dolphins, feeding sessions are characterized by fast, very intense, continuous clicking (Dreher 1966; Caldwell & Caldwell 1967).

Corralling of the kind described above, and perhaps pilot whale feeding in general, seem to require a high level of coordination between group members. Information needed for this complex behavior appears to be transmitted by complex sounds--pulsed sounds, and whistles S4, S6, and S7. Relatively uncommon sounds, such as pulsed sounds and whistle S7, would be expected to convey more complex information (Moles 1963). Free-ranging dolphins are reported to emit specific sounds at particular stages of feeding during the herding of fish (Morozov 1970). Saayman et al. (1973) also suggest that acoustic communication probably plays an important role in the highly organized fish herding procedures of <u>Tursiops aduncus</u>. When whales were moving at higher speeds in general, 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.

Milling behavior

In contrast to the vigorous displays of surface active behavior, milling seems to be more of a restful state. Speed was slower during milling, and a smaller proportion of whales was moving in the same direction. Groups were larger in number, and whales were found over shallower water during this behavior. Norris & Dohl (1980) similarly found spinner dolphins to rest over inshore shallow areas. They propose that this is a protective adaptation, allowing the resting school to place a protective bottom close beneath it and a shore nearby on one flank. If protection is indeed important, this may explain why milling occurred when groups were larger, assuming there is safety in numbers (Bertram 1978). Whistle S2 was especially closely associated with milling behavior. When groups were larger, regardless of behavior, less click activity was heard. It may be that other whales can benefit from a group member scanning the environment by clicks, thereby relieving some whales from the task of echolocating. Perhaps only a few individuals need to echolocate for the group. It may also be that less clicking occurs in the "safe" conditions of large group size and shallow water because whales need not be as alert to their surroundings.

Directional behavior

During directional behavior, smaller numbers of whales were moving more quickly and with more coordination relative to their direction, over deeper water, with fewer birds associated with them. These conditions are almost directly opposite those that occurred during milling. Taruski (1976) also found 'lolling' (milling) and 'transiting' (directional behavior) in pilot whales quite different and was surprised not to find differences in their whistles relative to these behavior types. My analysis did reveal differences (fewer simple whistles heard), probably because of a larger sample size over a longer time period with less variation in pods (Taruski (1976) used pods from different geographical locations).

Vocalizations and group size or aggregation

Contrary to expectations, no whistle type increased in number when more animals were present. There was no variation in whistling rate with group size. This could mean that only a few key members of the group emitted most of the whistles. Clark (1983) considered this to be the case with the pulsive sounds of right whales. It is quite possible that there are large differences between individuals in vocal output, as Caldwell & Caldwell (1967) have observed. Taruski (1976), however, found large pilot whale herds to have a much higher whistling rate than small herds. This has also been found with captive bottlenosed dolphins, Tursiops truncatus, where as the size of the group increases, the number of phonations/animal/hour tends to increase geometrically rather than arithmetically (Caldwell & Caldwell 1967). As mentioned previously, the possibility that podlets other than the followed group were recorded cannot definitely be ruled out though.

In marked contrast, almost all whistle types and their total increased in number with more surrounding podlets present. Group size and the number of podlets present varied inversely, suggesting that animals all belonged to the same general herd, whether in one large group or divided up into many small podlets. McLeod (1982) heard very similar phonations from two podlets separated by less than 1 km which led him to believe that these were a part of the same (larger) herd. Acoustic communication between podlets of the same herd may be very important in integrating actions of the whole herd. Inter-podlet distances (usually ca. 300-500 m) may reflect this, since these distances were similar to the maximum ranges over which we could hear whistles. This idea is further supported by the discovery that more whistles of certain types were also heard when a group of whales was spread over a greater area. Whether a herd is separated into many podlets or whether individuals in a single group are more dispersed, sound plays a major role in maintaining contact and coordinating movements. Norris & Dohl (1980a) have theorized that the unified actions of spinner dolphin schools when spread out over large expanses of water are acoustically mediated. When distances between whales are less, vision, also well developed in many cetaceans (Madsen & Herman 1980), can assume some of the communication "load".

Behavior related to environmental context

Over greater depth, the herd broke up into more podlets with a corresponding decrease in group size. As above, greater total numbers of whistles were heard. Surface activity and directional behavior also occurred over greater depth. Since both surface activity and click activity increased with depth, feeding may have taken place over deeper water. There was no relation between directional behavior and the number of podlets seen, but group sizes were smaller when directional behavior was observed. It may be that when the whales are travelling, smaller groups are preferred because they are more easily coordinated. Coordination with respect to direction of movement was indeed found to break down, both with larger groups and with groups spread over larger areas (which were also usually larger). During the less active milling behavior, however, unified behavior appears not as necessary and larger groups may even be somewhat advantageous as a protective device.

Very definite "huddling" occurred during storm conditions of increased wind speed, wave height, and cloud cover--group size increased, the area groups were scattered over decreased, and fewer podlets were seen. As previously mentioned, when spread out both over greater area and into more podlets, whales rely heavily on the acoustic channel of communication. During conditions of high wave height and wind speed, some whistle types, and especially the broad-banded, more directional sounds like pulsed sounds and clicks (the ones also most influenced by distance), were more quickly lost in background noise. Such interferences in transmission can be reduced by moving closer together. Other additional advantages in tighter formations, such as hydrodynamic ones, should not be ruled out though.

Variations with time of day

No consistent diurnal trends in pilot whale vocalization or behavior were discovered. Taruski (1976) also found few differences in whistle parameters with respect to time of day. In captive Tursiops truncatus, most vocal activity occurred an hour or so before sunrise, while least phonations were generally heard from 21.00-03.00 hrs. (Powell 1966). Feeding schedule, however, influenced vocal activity and these results to some extent (Powell 1966). Saayman et al. (1973) found no clear relationship between whistling rate in captive T. aduncus and time of day, although less vocalizations tended to be heard in the early morning and at night. My results agree more with Powell (1966) in that there was a slight trend for vocal activity to be high during early morning. In general, a weak pattern of higher whistling rates around midday emerged. "Codas", sperm whale sounds which occur mostly in social contexts, were also heard more often during midday when groups were largest (Whitehead et al. 1983). More pilot whale podlets were seen during morning hours, and the corresponding increase in vocalizations observed otherwise (regardless of diurnal variation), was mildly apparent for that time of day. Group size showed peaks around noon and in the hours before sunset. This agrees with observations by Sergeant (1962) who found pods to gather together before nightfall. Quite surprisingly, click activity showed no relation to time of day. It was expected that, since the pilot whales' prey, the squid Illex illecebrosus shows distinct diurnal vertical migration (Palmer & O'Dor 1978), more feeding, and therefore, more echolocating would take place during the night when squid would be nearer the surface. There is some evidence that sperm whales which also feed on squid, do so during the night (Whitehead et al. 1983).

Sound types

Highest correlations occurred between different sound types. Since all these correlations were positive, apparently no category of sound was used in isolation, i.e. in the absence of the other sound types. Sounds almost never showed opposing trends in a given context, with one whistle type increasing as another decreased, for instance. In very general terms, simpler sounds tended to be more common, while complex sounds like whistle S7 and pulsed sounds were rarer. Again, these rarer sounds would be expected to contain more information than simply the location and identity of the sender (Moles 1963). Pulsed sounds have been implicated in "emotional" contexts, especially aggressive ones (Clark 1983; Overstrom 1983), in accordance with Morton's (1977) generalized rules. Pulsed sounds are very highly correlated with clicks and indeed, are thought to be clicks emitted at very high repetition rates (e.g. Busnel & Dziedzic 1966).

Signature whistles

Based on studies on captive animals, some authors believe that almost all of delphinid whistling can be attributed to merely a sender stating its identity by means of a "signature whistle" (Caldwell & Caldwell 1965). This whistle may be modified according to the mood or emotional state of the sender but basically remains the same whistle, repeated over and over again (Caldwell & Caldwell 1977). Taruski (1976) suggested that 5 of his 7 pilot whale whistle categories may function as signature whistles mainly because these whistle types were common and some whistles were identical. Steiner (1980) found that individual signature whistles appeared to be present in pilot whales, and I have also come across whistles that looked identical on spectrograms. In the course of following the same general herd of pilot whales day and night for a week, I would conclude, though, that while these signature whistles may exist in pilot whales to some extent, behavior and context are much more intimately related to vocalization. Because pilot whales emitted different types of sounds according to their behavior, and moreover, because the complexity of the sound paralled the complexity of the behavior, more information must be transmitted besides merely the emitter's identity. It is possible, however, that in a simple tank environment, only a small subset of the individual's entire repertoire may be used.

Summary of contexts of vocalizations

In summary, whistles S1 and especially S2, were associated with milling, a restful behavior. Unlike all other sounds, these did not increase with the number of podlets present. Whistle S3 was suggested as a contact call. This is in contrast to Taruski (1976) who thought whistle S5 functioned in herd cohesion, since it was most common at dawn and at night. While I also found that whistle S5 showed the most significant diurnal variations, these did not coincide with those of Taruski (1976). Whistle S5 was most frequently heard during the late morning to noon. This whistle also increased most in number with depth, compared to other sound types. Whistles S4, S6, and S7 and pulsed sounds were associated with surface active behavior, which was possibly feeding. Dreher (1966) demonstrated that when a triple-humped whistle (like S6) was broadcast to captive dolphins, a high degree of excitement was aroused in the group, which responded with intense echolocation and a high rate of whistling. "Search whistles" in the shape of S3 were particularly heavily used (Dreher 1966). While this might suggest a feeding situation, no conclusions can be drawn. Pulsed sounds (and possibly whistle S7) are theorized to occur in "emotional" contexts (Caldwell & Caldwell 1977), based on previous studies on captive dolphins, and on their relative rareness. Clicks are widely believed to function in echolocation (useful in exploratory or search situations and prey detection), and, in this study, were indeed associated with what were thought to be feeding situations.

Conclusion

In conclusion, most pilot whale whistling is probably devoted to maintaining contact with group members and coordinating and integrating the movements of the herd. Simplest sounds were emitted during low activity, restful behavior, while more complex sounds occurred when behavior was vigorous and energetic, and seemed to involve more complex coordination among individuals of the group. This acoustically mediated unified behavior may be especially adaptive in feeding situations such as the corralling of squid, and probably evolved as a consequence of exploiting an evasive and fast-moving food source.

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APPENDIX A

TEST 1: SELF-RELIABILITY

In the self-reliability test, I aurally analyzed a subset of 20 randomly chosen 4 min. recording sessions in the same way I had done 16 months earlier in the original analysis using all 236 sessions (see Methods). Correlations between the first (original analysis) and second counts were very highly significant (Spearman corr. coeff.), except for whistle S1 when the correlations were fair, $p \approx .05$ (Table 10). There seemed to be a clear correspondence between the 2 analyses, although regression lines either did not go through the origin, or have a slope of 1, or both, for whistles S2, S3, S5, and S6, as they should have had if the correspondence had been statistically 1:1 (Table 11).

TEST 2: RELIABILITY BETWEEN MYSELF AND ANOTHER OBSERVER

Methods

To determine whether analysis of whistle types can be reliably counted by ear, a blind experiment was run using an independent volunteer. The observer trained for 2.5 days by listening to pilot whale tapes (not the ones used in this

Table 10. Examination of self-reliability in categorizing sounds. The original analysis (first count) was compared with a re-analysis (second count) using Spearman correlation coefficients. Significant values indicate correlations between first and second counts. Correlations were carried out using all 20 sessions (left hand side of Table) and a subset of only the "best" recording sessions--those of quality code 0--(right hand side of Table).

	USING ALL 20 SESSIONS		USING 14 "BEST" SESSIONS	
	r	Sig.	r	Sig.
S1	.549	.012	.528	.052
S2	.562	.010	.762	.002
S3	.793	.001	.754	.002
S4	.743	.001	.604	.022
S5	.871	.001	.910	.001
S6	.926	.001	.910	.001
S7	.713	.001	.796	.001
Pulsed	.908	.001	.931	.001

Table 11. Examination of self-reliability in categorizing sounds. Linear regressions were calculated of the second counts, from the reanalysis, on the first, original, counts. These regressions were tested against the null hypotheses that the slope of the lines was 1, and the intercept 0. Significant values indicate that the calculated lines were significantly different from those of the null hypothesis. Tests were carried out using all 20 sessions (left hand side of Table) and a subset of only the 14 "best" recording sessions--those of quality code 0--(right hand side of Table). * = $P<0.05$, ** = $P<0.01$. Tests are 2-tailed t tests.

	USING ALL 20 SESSIONS		USING 14 "BEST" SESSIONS	
	Slope(=1?)	Intercept(=0?)	Slope(=1?)	Intercept(=0?)
S1	.758	.951	.824	.554
S2	.549**	6.063**	.718**	3.783**
S3	.566**	4.293**	.536**	3.857**
S4	1.069	- .096	1.013	- .207
S5	.688**	- .709	.788**	-1.147
S6	.638**	.279	.643**	- .248
S7	.742**	.381	.901	- .716
Pulsed	.930	1.896*	1.121	.466
Total	.802**	5.510	.783**	5.007

analysis) to learn to categorize sounds. I gave her a short demonstration on how I would classify the sounds. We then began with the last tape and worked backwards, using only the first and third sessions of each tape (every other one). The observer and I sat with the Uher tape recorder between us in a very dimly lit room. We drew the contours of the whistles as they were heard. Simultaneously, spectrograms, portraying sound contours on a vertical axis of frequency and horizontal axis of time, were produced. The session was ended when I felt enough obvious whistles (around 5 - 10) had been heard, i.e. each run was for an indefinite length, usually between 15 sec. - 45 sec.). We also commented on the quality of the tape or sounds. 24 sessions out of 133 were discarded due to lack of sounds and/or poor tape quality, yielding 109 sessions in total.

To more easily compare our results with the spectrograms, several times during a session, one of us would mark the output (using the beam-finder on the oscilloscope, which would show up as a black line on the spectrogram) and announce this. For improved resolution on the spectrum analyzer, the sounds were played (and listened to for the aural test) at 1/2 real time. Spectrograms were made using a Ubiquitous Spectrum Analyzer, Model UA-6B, a Tektronix 5103N monitor oscilloscope, and a Nihon Kohden oscilloscope camera. Frequency was displayed on the y-axis of the oscilloscope, while the x-axis was held stationary, and reels of 35 mm photographic paper were moved along the x-axis at a rate of 2.5 mm/sec. The memory period was 100 msec. and sound intensity (z-axis) was indicated by modulating the intensity of the beam (intensity scale was logarithmic). The frequency display was linear, and the analysis range of 0 - 5 kHz gave an actual output of 0 - 8.75 kHz (due to reduced tape speed). Bandwidth was 10 Hz. Temporal resolution was 40 spectra/sec. Since sounds lasted about 1.5 sec., this is roughly 60 spectra/sound. A blinking LED with a frequency of 1 flash/sec was positioned above the oscilloscope screen and appeared on the spectrograms, where it was used for time measurements (e.g. whistle duration).

To analyze the results, I made up a catalog of the whistle contours the observer drew (24 different types) (Fig. 17), and a catalog for my whistle contour drawings (20 different types) (Fig. 18). An attempt was made to split up the whistle types so that categorizing the whistle contours would be as objective and unambiguous as possible. I went through all the sessions and categorized our whistle contour drawings using our respective catalogs. I also rated sessions based on the tape or sound quality comments, with the following quality codes: 0 - O.K., 1 - slightly to fairly faint, 2 - faint, 3 - very faint, 4 - background noise (engine, water, or radio noise), 5 - very noisy, 6 - many whistles, 7 - noisy and distant, 8 - many sounds and

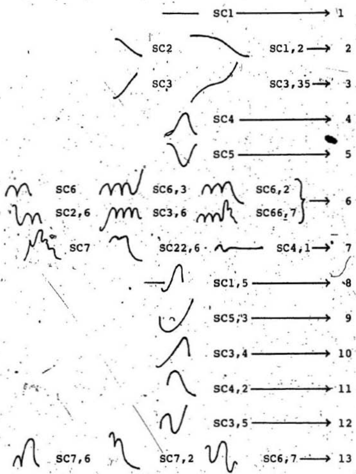

Fig. 17. Catalog of the observer's whistle contours (left), and the categories into which whistles were lumped (right) to correspond in number to the author's. Whistles were drawn in frequency vs. time contours.

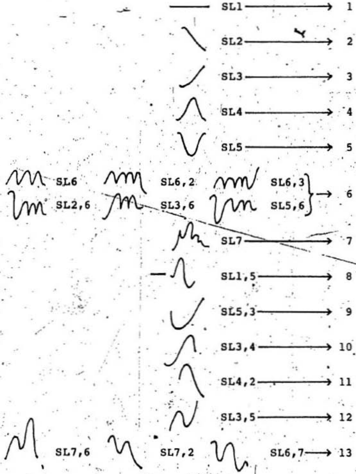

Fig. 18. Catalog of the author's whistle contours (left), and the categories into which whistles were lumped (right) to correspond in number to the observer's. Whistles were drawn in frequency vs. time contours.

faint.

Whistle categories were then lumped in the following way to make our categories correspond to each other 1:1. This resulted in our each having 13 categories (Figs. 17 and 18).

Results

Using a Likelihood Ratio Test (Silvey 1970), I tested whether there was a significant difference in how the observer and I counted the sounds (which depended on how we "categorized" or heard them), for each session and sound category. I assumed the counts for sound $\underline{i}$ in session $\underline{j}$ were Poisson distributed with parameter λ_{ij} for LSW, and μ_{ij} for the observer. The Likelihood Ratio Test tested:

$$H_0 : \lambda_{ij} = \mu_{ij}$$

$$\text{vs.} \quad H_1 : \lambda_{ij} \neq \mu_{ij}$$

The test statistic was:

$$F = \sum_{i} 2[L_{ij}.\ln(L_{ij}) + O_{ij}.\ln(O_{ij}) - (L_{ij}+O_{ij}).\ln((L_{ij}+O_{ij})/2)],$$

(when $L_{ij}>0$ and $O_{ij}>0$), where L_{ij} is the sounds I hear of type $\underline{j}$ in session $\underline{i}$, and O_{ij} is the sounds the observer hears of type $\underline{j}$ in session $\underline{i}$.

Under H_0, F should be asymptotically distributed as χ^2 with k d.f. In this case k is the number of sessions for which both the observer and I had non-zero counts. Significantly high values of F indicated that the observer and I had different rates of counting the sounds; and significantly low values, that there was more agreement between the two counts than would be expected from two independent Poisson processes with the same mean.

The tests were performed on each sound category separately, and on all sounds combined just using Grade 0 sessions. Counts of whistle categories 4, 5, 7, 9, and 11 were significantly different to at least a .10 level (Fig. 19). The categories then were manipulated to reduce the values of F as indicated on Fig. 19. At the "optimal" categorization, there were no values of F significant at the .10 level, i.e. there was no significant difference between the observer's counts and mine when sounds were categorized like this. This "optimal" categorization turned out to be the one I had used in my original analysis (Taruski's (1976) categories). Next, sessions with problems were used, in order to investigate the deleterious effects of poor sound quality (Table 12). These sessions were analyzed alone or in various combinations. Only "background noise" (4) produced a significant difference between the observer's counts and mine at the .05 level over all whistle types.

Fig. 19. Examination of reliability between observer and author for whistle categories 1-13 (boxed numbers). Values of the statistic F (defined in text) under the H_0 should be distributed as chi-squared and are presented with degrees of freedom in parentheses. Significantly high values ($p<.10$) indicate counts between observer and author were different. Significantly low values ($p>.90$) suggest the two counts agreed more closely than would be expected from the model. Categories were then collapsed in the manner shown to reduce F-values until whistle categories T1-T7 were obtained in which there were no significant differences ($p>.10$). Overall F-values are given before and after categories were lumped.
= $p>.995$, + = $p<.10$, * = $p<.05$, ** = $p<.01$.

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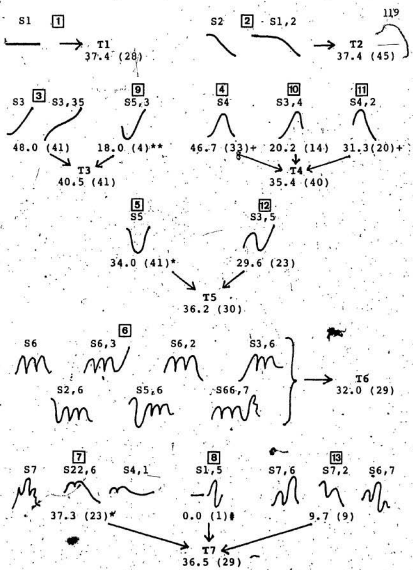
119



OVERALL BEFORE

381.6 (291)**

OVERALL AFTER

255.4 (242)

Table 12. Examination of reliability between observer and author using different quality codes. The similarity between the observer's and author's counts of whistle types T1-T7 over 109 sessions was tested. If the two counts were from Poisson distributions with the same mean, then the statistic given here should be distributed as chi-squared. The degrees of freedom are given beneath each value of the statistic. Significantly high values (* = P<0.05, + = P<0.10) suggest that the two Poisson distributions had different means. Significantly low values (# = P>0.90) suggest that the two counts agreed more closely than would be expected from two Poisson distributions with the same mean. Tests were carried out for different subsets of the data, based upon the sessions' quality codes. The number of sessions with each combination of quality codes is given under N. Quality codes: 0 - sessions without problems, 1 - slightly faint, 2 - faint, 3 - very faint, 4 - background noise, 5 - very noisy, 6 - many whistles, 7 - noisy and distant, 8 - many sounds and faint.

Table 12. (see facing page).

Qual. Codes	N	Whistle Types T1	T2	T3	T4	T5	T6	T7	All
0	47	37.4 (28)	37.4 (45)	40.5 (41)	35.4 (40)	36.2 (30)	32.0 (29)	36.5 (29)	255.4 (242)
1	11	6.4 (9)	6.6 (11)	6.5 (8)	7.9 (9)	4.6 (5)	10.3 (6)	10.4 (8)	52.8 (56)
2	17	7.6 (11)	8.6 (16)	10.8 (15)	19.9 (14)	9.3 (11)	16.3 (12)	5.9 (6)	78.3 (85)
3	12	5.9 (7)	12.5 (11)	13.7 (11)	9.2 (9)	9.0 (8)	5.5 (6)	5.2 (5)	61.0 (57)
4	5	1.6 (3)	9.2 (5)	3.7 (3)	4.3 (4)	4.7 (3)	4.2 (3)	8.9* (3)	36.6* (24)
6	11	8.0 (7)	11.6 (11)	8.5 (11)	3.3 (7)	7.7 (10)	5.5 (9)	3.3 (5)	47.9 (60)
8	3	1.4 (1)	0.3 (2)	0.3# (3)	1.5 (2)	1.7 (3)	2.9 (3)	1.9 (2)	10.1 (16)
2,4	22	9.1 (14)	17.8 (21)	14.5 (18)	24.2 (18)	14.0 (14)	20.6 (15)	14.7+ (9)	114.9 (109)
3,5, 7	15	7.3 (9)	20.5 (14)	15.8 (14)	13.4 (12)	10.4 (9)	11.2 (9)	8.0 (6)	86.5 (73)
6,8	14	9.3 (8)	11.9 (13)	8.8 (14)	4.8 (9)	9.4 (13)	8.5 (12)	5.2 (7)	58.0# (76)
0,1	58	43.8 (37)	45.5 (55)	46.7 (50)	42.0 (50)	40.5 (40)	33.2 (35)	42.2 (34)	293.8 (301)
0,6	58	45.4 (35)	50.2 (54)	44.2 (53)	38.4 (49)	44.6 (44)	28.4 (37)	39.5 (34)	290.7 (306)
0,8	50	38.8 (29)	37.7 (47)	40.8 (44)	36.9 (42)	37.9 (33)	34.9 (32)	38.4 (31)	265.5 (258)
0,2, 4	69	46.5 (42)	55.6 (61)	43.7 (63)	61.8 (61)	52.1 (53)	42.4 (45)	51.5+ (39)	353.5 (364)
0,3, 5,7	62	44.7 (37)	57.2 (55)	46.6 (56)	48.2 (54)	49.4 (47)	32.4 (39)	38.3 (34)	316.8 (322)
All	109	70.6 (69)	65.1 (83)	80.2 (97)	84.0 (97)	72.5 (86)	72.9 (76)	63.5 (66)	508.7# (574)

Counts of whistle T7 were significantly different in "background noise", "background noise and faint", and "background noise and faint with O.K. sessions". For all 109 sessions, the overall significance was at the .975 level, meaning my counts and the observer's were significantly better correlated than would be expected if they were from Poisson distributions with the same mean. This showed that the sounds the observer heard and categorized corresponded to mine in a 1:1 fashion.

TEST 3: RELIABILITY BETWEEN MYSELF AND SPECTROGRAMS

Test 3a: Examination of the 7 Whistle Types

After categorizing pilot whale whistles into 7 categories by aural impression, it was felt necessary to define these categorized sounds more objectively by unambiguous measurements from the spectrograms produced during Test 2.

Methods

For each whistle type, S1 - S7, 10 whistles were sampled from the 110 spectrograms ("filmed" sessions), and the following measurements were performed: maximum frequency, minimum frequency, beginning frequency, end frequency, maximum frequency change, rate of maximum frequency change, duration, number of maxima inflection points, number of minima inflection points, and number of harmonics. A drawing of the whistle's appearance on the spectrogram was also made (see Fig. 5, p. 21, for spectrogram tracings of some of these whistles).

The maximum frequency change of a whistle was defined as the greatest adjacent change in frequency until a level or reversal in slope or the end of the whistle was encountered. The rate of maximum frequency change was defined as the duration (length) of the maximum frequency change, in seconds. (Since tape speed was 1/2 full speed, these numbers were halved for actual rates and durations). The number of maxima inflection points was defined was the number of times the frequency contour went up (positive slope) and then down (negative slope), to produce a peak. These increases and/or decreases had to be greater than .25 kHz to be counted as maxima or minima. If the whistle rose in frequency, then levelled off and never decreased in frequency, it was not counted as having a maximum inflection point. The number of minima was defined similarly, except the slopes were reversed, i.e. to form a trough. The number of harmonics counted included those that showed up at least partially within the range of frequencies displayed. Whistles of higher frequency will obviously have fewer harmonics appearing on the spectrogram, as many of these harmonics will occur beyond the range of frequencies displayed. When only a portion of the whistle had harmonics, this was specified. All frequencies were measured to the nearest 250 Hz (.75 mm); all time measurements, to the nearest .5 sec. (1.25 mm), (which is .25 sec. in actual time).

The first clear whistle of good quality and unambiguous category on a randomly sampled spectrogram was measured. This meant that the whistle type as seen on the spectrogram had to correspond and agree with my and (preferably)/or the observer's aural interpretation of that whistle type. In order to avoid taking measurements from identical or very similar stereotyped whistles (possibly "signature" whistles), not more than one whistle of the same category was measured from each spectrogram. The chosen whistles were measured and placed under their respective whistle types until 10 whistles were measured for each of the 7 types. Pulsed sounds were not measured since their portrayal on a spectrogram was unclear and difficult to measure. Besides, aural impressions from pulsed sounds were comparatively unambiguous, thereby making objective measurement not so necessary as with the whistles.

A stepwise discriminant analysis was performed on whistle types S1-S7 using 10 variables~~:~~ maximum frequency, minimum frequency, beginning frequency, end frequency, maximum frequency change, rate of maximum frequency change, duration, number of maxima, number of minima, and number of harmonics. The Wilks method in the SPSS procedure DISCRIMINANT was used. As previously mentioned, 10 whistles of each type (1-7) were selected to yield a total sample size of 70 whistles. This representative cross-section of all the whistle types gave a measure of the variability within and between whistle types.

Results and Remarks

Some interesting tendencies were apparent from the means of each variable for each whistle type (Table 13). S1 and S4 tended to be fairly low frequency whistles overall. Those whistle types which ended with an upward slope (S3 and S5) had the highest mean maximum frequencies. They also had the greatest maximum frequency changes on average. S2 and S3, while only opposite in slope, were quite different from each other. S3 was generally higher, spanned a wider frequency band but had a shorter duration, i.e. was steeper, on average, than S2. S5 was similarly distinguished from S4. Whistles S2 and S4 and whistles S3 and S5, because of the way they ended, seemed to have more in common than if they were grouped according to number of frequency inflections (S2 with S3, and S4 with S5). S6, the waver, tended to be a fairly high whistle overall (had the highest mean minimum frequency). The beginning and end frequency

Table 13. Means (above) and standard deviations (beneath) of various whistle parameters for whistle types S1-S7, and overall. Measurements were made on 10 randomly selected sounds in each type. These can be compared with measurements by Steiner (1981) of N. Atlantic pilot whale whistles off Newfoundland and Nova Scotia, given in the column marked "WS". Steiner (1981) does not give separate numbers of maxima and minima, rather the total number of inflection points, marked *.

	Whistle Types:								
	S1	S2	S3	S4	S5	S6	S7	All	WS
Max. Freq.	2.9	4.4	6.3	4.1	5.7	5.6	4.6	4.8	4.7
(kHz)	1.1	1.8	2.3	1.5	2.0	2.4	0.6	2.0	1.9
Min. Freq.	2.9	2.7	3.4	2.3	3.5	3.6	2.3	3.0	2.8
(kHz)	1.1	1.2	1.4	0.9	1.4	1.3	0.8	1.2	1.2
Begin. Freq.	2.9	4.4	3.5	2.7	4.4	4.3	3.1	3.6	3.7
(kHz)	1.1	1.8	1.4	1.2	1.9	1.8	1.0	1.6	1.7
End Freq.	2.9	2.7	6.3	2.8	5.5	4.3	2.8	3.9	3.5
(kHz)	1.1	1.2	2.3	1.2	2.0	2.2	1.2	2.1	1.9
Max. Freq.	0.1	1.8	2.8	1.8	2.1	1.9	1.7	1.7	–
Change (kHz)	0.1	0.9	1.1	0.7	1.4	1.9	0.6	1.3	–
Rate of Freq.	1.1	1.0	0.8	0.5	0.5	0.3	0.3	0.6	–
Change (sec)	0.5	0.5	0.4	0.3	0.2	0.1	0.1	0.4	–
Duration	1.3	1.1	1.0	1.3	1.0	2.1	1.5	1.3	0.7
(sec)	0.4	0.4	0.5	0.5	0.2	1.2	0.7	0.7	0.7
No. of	0.0	0.0	0.0	1.0	0.4	4.4	3.3	1.3	
Maxima	0.0	0.0	0.0	0.0	0.5	2.5	1.6	2.0	
									*1.0
No. of	0.0	0.0	0.1	0.0	1.0	4.1	2.5	1.1	*1.3
Minima	0.0	0.0	0.3	0.0	0.0	2.3	1.6	1.8	
No. of	0.7	0.7	0.6	1.3	0.5	0.3	1.1	0.7	–
Harmonics	1.6	1.1	0.8	1.3	0.7	0.7	0.9	1.1	–

also tended to be the same in S6. More harmonics tended to be associated with S4, and to a lesser extent, S7, than with the other whistles.

Variables were entered by the stepwise discriminant analysis procedure, in the following step order (Wilks' Lambda in parentheses, indicating their usefulness in discriminating categories): 1) No. of maxima (.2975), 2) No. of minima (.1213), 3) Maximum frequency change (.0590), 4) End frequency (.0408), 5) Beginning frequency (.0239), 6) Rate of maximum frequency change (.0174), 7) Maximum frequency (.0137), 8) Minimum frequency (.0120). Variables "Duration" and "No. of harmonics" were not used in the analysis by the procedure. Presumably, the discriminations which could be performed using these 2 variables were already covered by the other variables (e.g. "Duration" was possibly covered by "No. of maxima").

Variables "No. of maxima" and "No. of minima" were clearly the most useful in separating the whistle types. These variables defined the whistles' complexity in terms of the number of inflection points. These parameters were also the ones most easily distinguishable by ear and thus, were used as a basis for setting up the 7 categories, defined by contour.

89% of the variance was accounted for by Discriminant Functions 1-3, and with the addition of Function 4, this was increased to 97%. (Table 14). Function 1 completely

Table 14. Results of discriminant function analysis of various parameters of whistle types. Each function is a linear combination of the different characteristics of the sounds (the coefficients are given in the lower part of the table). The functions, which are orthogonal, are calculated in turn to account for the maximum residual variance.

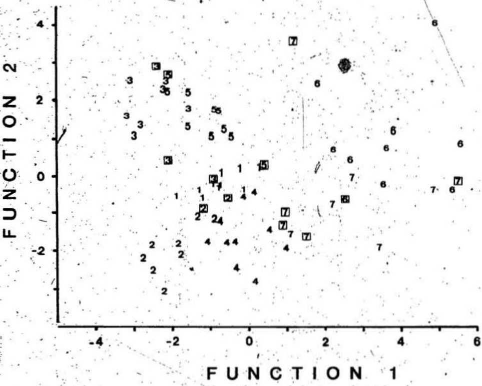
	Functions			
	1	2	3	4
Percent of Variance Accounted For	52.40	21.02	15.68	7.89
Significance	<0.0001	<0.0001	<0.0001	<0.0001

Standardized Canonical Discriminant Function Coefficients:	1	2	3	4
Max. Freq.	-0.66	0.92	-2.98	-0.43
Min. Freq.	-0.24	-0.11	0.44	-0.90
Beginning Freq.	0.62	-1.17	2.00	0.97
End Freq.	0.53	0.99	-0.23	0.16
Max. Freq. Change	-0.70	-0.66	1.56	0.94
Rate of Max. Change	-0.38	-0.09	0.06	-0.50
No. of Maxima	1.76	-1.45	-1.39	0.08
No. of Minima	-0.52	1.70	1.64	-0.27

separated the complex whistles (S6 and S7) from the rest, as "No. of maxima" was overwhelmingly the most important variable. Function 2 compared the number of minima with the number of maxima. Whistle type S5 (⋁) which usually had 1 more minimum than maximum was separated from type S4 (⋀) which had 1 more maximum than minimum. In other words, the peaks were distinguished from the troughs. The function also used a combination of beginning frequency and end frequency to separate S2 (╲ - high beginning, low end) from S3 (╱ - low beginning, high end). This discrimination was less complete than the separation between S4 and S5, though. Function 3 separated whistles S2 from S4, and S3 from S5 on the basis of differing maximum frequency and beginning frequency. Function 4 quite clearly separated S1 (——) from the rest of the whistles by S1's characteristics of low maximum frequency change and low beginning frequency. (S1 was distinguished from S4 which also shared the above characteristics, by S1's relatively high minimum frequency). Whistles S6 and S7 were separated in Functions 2 and 3.

When Functions 1 and 2 were plotted against each other (Fig. 20), distinct ranges emerged for the 7 whistle types, although these merged into one another. It is clear that pilot whale whistles are very graded signals. Points were fairly evenly distributed across each whistle type, except in complex whistles S6 and S7, where the coverage was more

Fig. 20. Categorization of whistles by discriminant functions. Discriminant functions 1 and 2 categorized 10 randomly chosen whistles of each of the 7 whistle types based on various whistle parameters. Boxed numbers indicate whistles which were incorrectly classified by the discriminant analysis. Numbers represent their respective whistle category, S1-S7.


FUNCTION 2
4
2
0
-2
-4
-2
0
2
4
6
FUNCTION 1

erratic and dispersed. This was not remarkable in S7, as this whistle type showed great variability. McLeod (1982) also found that more complex phonations were more variable in pilot whales. Whistle types were roughly arranged on the plot in a horizontal continuum of increasing complexity from left to right. Whistle type S1, although it appeared to be overlapping with groups around it, was actually quite distinct, thanks to Function 4. This was not visible on the 2-dimensional plot which deprived us of the added information supplied by Functions 3 and 4. Groups S1, S2, S3, S4, and S5 were vertically arranged in terms of final slope. S1 was situated between whistle types ending in a positive slope (S3 and S5), and those with downward sloping endings (S2 and S4). It is interesting to note that only one whistle in group S7 ended with an upward (positive) slope. Moreover, there seemed to be a gap between S5 and S6/S7 -no merging took place here at all. This could mean that sounds of moderate complexity (perhaps 2-3 inflection points) and having upward sloping endings, do not exist in the "vocabulary" of those pilot whales which were recorded.

Based on the discriminant functions, the computer attempted to classify the 70 whistles into their correct categories (Table 15). It was quite successful with all groups, notably with S1 and S4, but was only 50% correct in group S7. This can again be explained by the highly variable nature of S7. On the other hand, S1 and S4 seemed

Table 15. Classification of whistle types using discriminant function analysis. The classification by the author (using aural impression and the whistles' appearance on a spectrogram) of 10 whistles in each sound category is compared with classification using the discriminant functions shown in Table 14, based upon various whistle parameters (e.g. maximum frequency, no. of maxima, etc.). The numbers of sounds correctly classified by the discriminant functions are underlined.

No. of Whistles:

		Predicted Group Membership by Discriminant Functions:						
		S1	S2	S3	S4	S5	S6	S7
Actual Group	S1	10	0	0	0	0	0	0
	S2	2	8	0	0	0	0	0
	S3	2	0	7	0	1	0	0
	S4	0	0	0	10	0	0	0
	S5	1	0	1	0	8	0	0
	S6	0	0	0	0	0	9	1
	S7	0	0	0	3	1	1	5

to be fairly distinctive whistles. Most of the errors were a result of the computer being supplied with incomplete information about the whistle, causing it to simplify the whistle. 11 out of 13 errors could be blamed on oversimplification. This is quite understandable since the 10 variables I chose by which to characterize the whistles clearly did not create a full and complete "visual picture" of the whistle to the computer. Errors seemed to be mainly a result of an inability to adequately define a whistle's contour given only a few physical characteristics. Some of the errors it made, though, could well have also been made by myself during the aural analysis. Small frequency changes, in particular, are not well distinguished by ear. Altogether, 13/70 whistles (18.6%) were placed in the wrong group, but in 10 of these 13 errors, the second highest probability group was correct.

Test 3b: Relative Frequencies of Whistle Types

While the above analysis gave a representative cross-section of the 7 different whistle types, it did not give a measure of which whistle types were most frequently heard. This was attempted in the following.

Methods

50 "filmed" sessions were randomly selected, and the first clear sound encountered, regardless of type, was chosen to be measured. Only one whistle of each session was used. (Sometimes (13 out of 50 times), these whistles were the same ones as chosen for the above analysis).

Results and Remarks

The results are shown in Fig. 21, where Function 1 is plotted against Function 2. Clearly S6 and S7 are relatively rare whistles. One tends to hear mostly simple whistles--S1, S2, and S3, with S3 more frequent than S2. In the whistles of intermediate complexity, S4 is about twice as common as S5. According to my judgement about the contour appearing on the spectrogram, 9 of these 50 whistles (18%) were categorized incorrectly. However, the second highest probability group was correct in 7 of the 9 errors.

These results of the frequency with which one hears the different whistle types were compared with my original aural analysis (Table 16). These analyses agree fairly closely except in the cases of S1 and S6. Many fewer of the S1 whistles were heard than were seen on the spectrogram. Clearly, this monotonal, relatively low sound is very easily

Fig. 21. Categorization by discriminant functions, representing relative frequencies of occurrence of whistle types. Discriminant functions 1 and 2 categorized 50 randomly chosen whistles, regardless of type. Whistles S1-S7 (represented by their respective numbers) were categorized based on various whistle parameters. Boxed numbers indicate whistles which were incorrectly classified by the discriminant analysis.

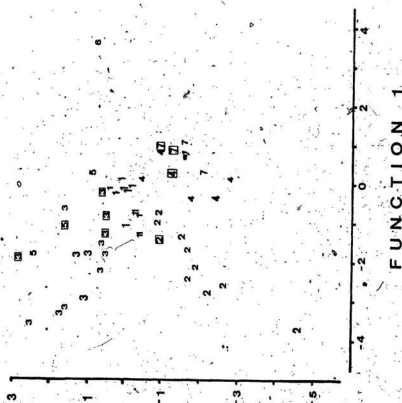

FUNCTION 1
-4
-2
0
2
4
FUNCTION 2
3
1
-1
-3
-5

Table 16. Relative frequencies of occurrence of whistle types S1-S7. Frequencies are given for the aurally analyzed whistles (selected data), and those categorized by spectrographic appearance using either the discriminant functions given in Table 14, or the author's classification of the full spectrogram of the whistle.

	Aural Analysis:		Spectrographic Analysis:			
			Discriminant Classification:		Visual Classification:	
	n	%	n	%	n	%
S1	908	7.6	16	32.0	12	24.0
S2	2,425	20.4	10	20.0	10	20.0
S3	2,520	21.2	11	22.0	14	28.0
S4	1,773	14.9	7	14.0	6	12.0
S5	1,268	10.7	3	6.0	3	6.0
S6	2,116	17.8	1	2.0	1	2.0
S7	875	7.4	2	4.0	4	8.0
Total	11,885		50		50	

tuned out in favor of the more "aurally interesting" whistles which are rapidly changing in frequency. Alternatively, S6 is much more frequently heard than seen. Since these wavers often fluctuate very rapidly in frequency, high resolution is needed to discern these on the spectrogram. For a waver to appear clearly on a spectrogram, the tape speed would have had to have been reduced to 1/4 or 1/8 normal speed. As these were done at 1/2 speed, at best, only fragments of the waver could be detected. The human ear, however, has no trouble picking up these rapid changes in frequency, making aural analysis desirable in some respects. Another problem with wavers is that they tend not to be produced in discrete "units"--it is difficult to determine when one waver has stopped and the next has started. If the change in frequency is slight, they could also, conceivably, be confused with S1 whistles.

SUMMARY AND CONCLUSION OF ALL RELIABILITY TESTS

The self-reliability test showed that there was a very significant correlation (in all categories except S1, where correlations were marginally significant, $p \approx .05$), between a subset of my original aural analysis and a re-analysis.

Test 2, which examined the reliability between myself and another observer, determined that our counts were significantly better correlated with each other than would be expected were they taken from Poisson processes with the same mean. This meant that our categorizations of sounds showed a 1:1 correspondence with one another. The whistle classification scheme used in the original aural analysis (Taruski's (1976) categories) was also statistically justified.

Test 3 examined the reliability between myself and spectrograms. In Test 3a, discriminant functions using whistle parameters such as beginning frequency, number of maxima, etc., classified most whistle types quite successfully into their correct categories. Only with whistle S7 was categorization less good. In Test 3b, 18% of randomly chosen whistles were incorrectly categorized, based on my judgement about their spectrogram appearance. Considering the limited information that was given about each whistle (with which to determine contour category), these results were deemed good.

In conclusion, while there were problems with certain whistle types in some of the reliability tests, overall, aural analysis showed itself to be reliable.