VOCALIZATIONS OF THE PILOT WHALE
(GLOBICEPHALA MELAENA, TRAILL)

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Vocalizations of the pilot whale

(Globicephala melaena, Traill)

by

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Abstract

Vocalizations produced by pods of pilot whales were recorded in the inshore waters of Newfoundland. Phonations from a stranded individual were also recorded. Samples of from 6.5 to 43 minutes duration were analyzed with a continuous real-time spectrum analyzer. All audible phonations were categorized on the basis of acoustic properties and temporal associations to create a catalog of the species' vocal repertoire (total coded phonations = 2449).

Phonations were found to be highly variable across pods but quite constant within pods. Variations associated with successive repetitions and different temporal clustering tendancies were also found. Occasionally, temporal patterns allowed between and within individual variability to be distinguished. The importance of measuring variability in the vocalizations of social delphinids and the possible sources of variance are discussed.

Underwater broadcasts of sounds to pilot whales were conducted. After the broadcast of killer whale phonations to one pod, consistent changes in the relative frequency of three phonation categories occurred but results are inconclusive. Playback of phonations to the same stranded animal that produced the sounds resulted in a general increase in vocalization rate. This individual also responded to each playback phonation with an immediate emitance of a phonation of the same category.

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Introduction

The purpose of this study was to investigate the vocalizations of the pilot whale, Globicephala melaena, a dolphin species common to the North Atlantic. As any attempt to understand animal communication "must necessarily begin at the place where the system is complete in all its parts, in nature" (Marler, 1965, p. 544), auditory signals of free-ranging pilot whales, recorded in the inshore waters of Newfoundland, were used.

Vocalizations recorded from a stranded pilot whale were analyzed to assess within individual variability in the vocal emissions of this species. Sequential patterning of some vocalizations were studied for "clues" to between individual signal variation in recordings of pods (groups) at sea and recordings of different pods of pilot whales were compared to examine between pod variability. Underwater sound broadcasts were employed in an attempt to find consistent vocal responses from different pods. These data were also used to create a catelog of the species' vocal repertoire. Temporal patterning of vocal signals and temporal associations among signals were also examined, the latter by means of cluster analysis.

To the best of my knowledge, this is the first time an odontocete species' vocal repertoire has been documented with any attention being paid to the essential question of sources of signal variability. This study also represents the first attempt at examining temporal patterning in vocalizations recorded from groups of non-captive odontocetes and is the first report of vocalizations recorded from a stranded animal of this species.

Delphinid vocalizations are widely accepted as being used for intraspecific communication (e.g., Caldwell & Caldwell, 1977; Dreher, 1961; Herman & Tavolga, 1980; Lang & Smith, 1965; Lilly, 1963; Lilly & Miller, 1961b), at some unknown level of complexity. Regardless of the complexity in the semantics, syntactics, and pragmatics of delphinid phonations, there are certain prerequesites of communication that are expected to be met. One expectation of intraspecific communication is that all members of the species share a common repertoire of communication signals, or at least have some signals in common. There are, however, many possible sources of signal variability that must be considered.

Individual variation in vocal signals

The existence of individual variation in vocal signals has been reported in many animal groups, including birds.

(e.g., Beer, 1970; Brooks & Falls, 1975; Lemmon, 1977; Thorpe, 1972; White & White, 1970), gorillas (Fossey, 1972), wolves (Harrington & Mech, 1978; Theberge & Falls, 1967), humpback whales (Hafner, Hamilton, Steiner, Thompson, & Winn, 1979; Payne & McVay, 1971), sperm whales (Backus & Schevill, 1966), and dolphins (M. Caldwell & Caldwell, 1965, 1971; Caldwell, Caldwell, & Hall, 1973; Caldwell, Caldwell, & Miller, 1973; Hickman & Grigsby, 1978).

Individual variability, within or between individuals, cannot be reliably measured from recordings of wild groups of pilot whales as there is no available method to identify which individual (or individuals) is vocalizing. The use of a hydrophone array has allowed researchers to determine the identity of vocalizing right whales (Clark & Clark, 1980), and sperm whales (Watkins & Schevill, 1975, 1977) when there are a few widely spaced animals in an area. With smaller, more gregarious dolphins, the use of a hydrophone array has met with more limited success (e.g., Watkins & Schevill, 1974).

Under rare conditions, individual pilot whales do become isolated and vocalizations from a single animal can be recorded. Strandings and entanglements with fishing gear are two such situations where within individual variability could be measured. In the present study individual pilot whales were recorded on four occasions, although vocalizations were emitted in only one case. As other members of this individual's pod were recorded as a group at sea, a comparison could be made between the observed within individual variability and the within group variability.

<u>Regional or dialectic signal variation</u>

In addition to individual variations in vocal signals, regional variations and/or dialects have also been found in the vocalizations of birds (e.g., Lemmon, 1977; Marler & Tamura, 1964; Pitocchelli, 1981), monkeys (Green, 1975), picas (Sommers, 1973), male elephant seals (LeBoeuf & Peterson, 1969), killer whales (Ford & Ford, 1981), and have been postulated in belugas (Morgan, 1979) and pilot whales (Taruski, 1976). (See Conner, 1982, for a discussion of the distinction between geographic variations and dialects in mammalian vocalizations.) Dialectic differences are generally thought to arise through ontogenetic factors (e.g., Bremond, 1963; Busnel, 1977; Green, 1975; Lemmon, 1977; Treisman, 1978) and might therefore exist between pods of pilot whales found in the same area if individual exchanges among pods, through immigration/emmigration, occurred infrequently. The possibility of dialectic differences among pods of pilot whales was examined by comparing vocalizations from different pods recorded in the same area, at approximately the same time of year.

Graded vocal signals

In his study of the vocal repertoire of the pilot whale, Taruski (1976) found "no clear mutually exclusive categories" (p. i) of auditory signals. Communicative signals, however, need not be discrete (i.e., are not always stereotyped or delivered in an all-or-nothing way). Extensive intergradations of signal types can occur in some species (Marler, 1967). "Grading may occur in several acoustical dimensions independently, such as frequency, tonal structure, and duration, each varying continuously, making it unrealistic to subject the sounds to strict categorical classification" (Marler, 1977, p. 56). Primates, for example, have exceedingly variable signals (Fossey, 1972; Gautier, 1974; Green, 1973; Rowell & Hinde, 1962), some species exhibiting "an almost infinite series of intermediates between the main sounds" (Rowell & Hinde, 1962, p. 294). Rodents and lagomorphs also exhibit gradations in their vocalizations (Eisenberg & Kleiman, 1977). The point has been made by Lieberman (1977) that the spectrographic techniques typically used to analyze animal sounds would also indicate gradations in the physical properties of certain discrete phonetic elements in human speech. Presumably, animals that exhibit little stereotypy of signals will be less sensitive to within-category variations than to variations between categories (Marler, 1977).

Pilot whales are very social animals. In some social species individuals may become familiar with all other group members. In these circumstances effective communication can be "achieved by experienced interactants with signals that are uncompleted and undramatized, including subtly changing points along graded signal continua," (Green & Marler, 1979, p. 137). Green and Marler (1979) go on to point out that "porpoises and whales", in addition to primates, might exhibit these characteristics. Not surprisingly then, Taruski's (1976) examination of the vocal repertoire of pilot whales suggests that this species does have a graded repertoire of whistle contours.

Classification of vocal signals

As it is futile to treat all phonations as unique, the crucial problem of classifying graded signals arises. All subsequent analysis and conclusions made from categorical data will be dependent upon the classification system and may reflect the coding method used more than the actual raw data (Machlis, 1977). Fossey (1972), in reference to classifying the graded signals of gorillas, states that "these calls could be grouped together on the basis of similarities in their physical structure, my subjective impression of these sounds, the context in which they occurred and the responses which they elicited", (p. 51). Another method of classifying graded phonations, one that has been proposed to have special importance in human speech perception (e.g., Liberman, 1980), is by the sound production mechanism (Marler, 1965).

Production mechanism

With pilot whale vocalizations, the possible coding methods are more limited. Only recently has strong evidence been presented on the location of sound production in delphinids (Dormer, 1979; see also review by Popper, 1980). Present knowledge about sound production mechanisms is insufficient to be used in classifying dolphin phonations.

Context and elicited response

"The communicative act cannot be isolated from the circumstances in which the signaler and recipient find themselves at the time they are participating in the exchange" (Marler, 1965, p. 544). The context of a signal includes everything that accompanies and preceeds the signal as well as the states of the signalling and receiving animals (Smith, 1977; Shalter, Fentress & Young, 1977). A major difficulty in cetacean research is that surface observations are so drastically limited in that only a very minute, perhaps even trivial component of the animals' behavioral repertoire can be sampled. The lack of a good behavioral and environmental contextual framework, within which vocal behavior must be considered, could account for qualitative and/or quantitative variations in the emitted signal or in the message it might encode (Bremond, 1963; Cullen, 1972; Green, 1973; Hailman, 1977; Marler, 1967; Smith, 1965, 1977; Shalter, Fentress, & Young, 1977).

When recording pilot whales at sea, the identity of the vocalizing individual is unknown. Successive phonations, therefore, cannot be determined to have emanated from a single animal or a vocal exchange between two (or more) individuals. Even if the identities of the signaling and receiving individuals were known, their behavior at the time of the exchange would not be. This makes grouping pilot whale phonations solely on the basis of the contexts in which the sound is emitted and the responses elicited by the sound impossible. Grouping pilot whale phonations must therefore be done on the basis of acoustic properties and what little contextual data is available.

With the social cetacea, the non-vocal behavioral categories that can be used as contextual data for vocal studies usually refer to group movements and behavior (e.g., feeding, transiting, lolling at surface). The relative importance of these observable events and events occurring beneath the surface, including undetectable individual interactions, is unknown. Mass strandings of pilot whales (G. macrorhyncha) have led observers to state that "survival is so closely integrated with the structure of the social organization that the individual cannot act for itself" (Kritzler, 1952, p. 329), and "even under duress the closely knit social behavior of this species precludes individualized responses" (Fehring & Wells, 1976, p. 193). These statements suggest that during a stranding there is very little individual behavioral variability. If so, group behavior might accurately reflect the behavior of vocalizing individuals. Group movements and behavior, however, account for only a very small amount of the variability observed in recordings of pilot whale vocalizations made at sea (Taruski, 1976).

One would assume that the unobservable behavior of vocalizing individual pilot whales is contextually more relevant to the emitted vocalizations than the observable group movements. Some evidence for this in groups of Hawaiian spinner porpoises (Stenella langirostis) has been reported by Watkins and Schevill (1974). Many recorded acoustical exchanges in their sample occurred from animals within 10 to 15 meters of each other, indicating that these vocalizations were part of interactions involving individuals in relatively close spatial proximity.

Vocalizations that tend to occur in close temporal proximity might be in response to a common or related "state" (internal or external) that the vocalizing animals (or, animal) are in at that moment. In this study, temporal associations among vocalizations were used as measures of vocal context to aid in the classification of some signals.

Controlling context

One possible way to circumvent the uncertainty of the context animals are acting within is to study extreme situations where one factor is expected to override all others. Such cases may involve harpooning animals (Bushnel & Dziedzic, 1966), driving herds of whales onshore (Taruski, 1976), or natural strandings of animals (D. Caldwell & Caldwell, 1971). Recordings made in these situations may not, however, be representative of vocalizations under more normal circumstances.

A less drastic way in which behavior and vocalizations can be directed to a particular aspect of the animals surroundings is by broadcasting sounds to the animals in their natural environment. This technique has been used to influence movement patterns of cetacea (Cummings & Thompson, 1971; Fish & Vania, 1971), to demonstrate recognition of conspecific sounds (Clark & Clark, 1980), to influence sound production (Evans & Dreher, 1962), and in attempts to elucidate the meaning of specific sounds played back to captive (Dreher, 1966), and free-ranging dolphin species (Morgan, 1979; Taruski, 1976). Although the vocalizations emitted under these conditions might be abnormal, recording different animals under the same known context could reduce variability related to undetectable environmental factors and thereby facilitate comparisons between groups.

In the present study, underwater sound broadcasts were employed in samples recorded from different pods of pilot whales. Killer whale phonations, recorded within the study area, were used as playback stimuli (3 trials). Three samples from other pods incorporating (1) white noise, (2) constant tone, and (3) variable tone broadcasts were used as controls. Killer whale sounds were choosen as a broadcast stimuli because they had previously been used in playbacks to pilot whales (Taruski, 1976) as well as to many other cetacean species. Killer whales and pilot whales have overlapping geographic ranges in the study area, however there have been no reports of interactions between these two Delphinid species in the wild.

Pilot whales may have perceived the broadcast of killer whale phonations as "novel sounds" either because of distortion, as a result of the quality of the killer whale recording used for the playback and/or limitations of the broadcasting apparatus, or the animals may never have been exposed to killer whales. If this was the case, broadcast of the synthesized variable tone, which was acoustically more similar to the killer whale phonations than the pure tone, was expected to have elicited similar responses to broadcasts of killer whale sounds. The constant tone broadcast was also expected to be perceived as a novel sound although perhaps a less "interesting" one than the variable tone. It was thought that the noise broadcast, if perceived above the existing noise from distant boats and surf, probably would be ignored, but would control for the experimental procedure of placing the loudspeaker over the side of the boat and the presence of the loudspeaker in the water.

Temporal patterning of vocal signals

With a classification system for pilot whale phonations it would be possible to examine the communicative role that sequential patterning of signals plays in this species. Herman and Tavolga (1980) have stated that "given their short life [acoustic signals] may be patterned sequentially in many ways to greatly increase their information content" (p. 152). Narwhal pulsed tones have been shown to be repeated with regular repetition rates (Ford & Fisher, 1978; Watkins, Schevill, & Ray, 1971) and the temporal patterning of sperm whale clicks has been proposed to have a communicative function (Watkins & Schevill, 1977). Sequential ordering of "themes" in humpback whale "song" has been found to be very structured (Payne & McVay, 1971). The role of sequential patterning of dolphin whistles has, however, been largely ignored.

<u>Previous pilot whale vocal repertoire studies</u>

In the summary of his study of pilot whale vocalizations recorded at sea, Taruski (1979) states, "The whistle repertoire of the North Atlantic pilot whale (<u>Globicephala melaena</u>) is shown to be a continuum or matrix in which no mutually exclusive contour categories can be defined" (p. 367). Taruski's (1976) inabilty to find natural occurring categories of whistles could have been a function of the whistles themselves, the attempted classification scheme, or his sampling methodology. The whistles analyzed by Taruski (1976) were random samples, recorded on three cruises that covered the area from Newfoundland south to Hudson Canyon, from different behavioral and environmental contexts. Pod membership was not considered a variable in his study nor was any apparent attempt made to assess within or between individual variability in contour use.

Busnel and Dziedzic (1966) were able to identify five basic signal types from their small sample of pilot whale phonations (423 signals identified, 185 of these analyzed sonographically) recorded from one school of eleven animals, one of which had been harpooned. They reported some variability within these categories and other less frequent signals were recorded that did not fit into these categories.

The present study

The purpose of this study was to create a catalog of the phonations produced by free-ranging pilot whales. The classification system developed was used to look for variations in the phonations used by different groups. Variability in the phonations recorded from a single group was also documented and where possible, clues to the probable sources of variability were presented. The catalog of pilot whale phonations also allowed a preliminary examination of ways in which phonations were repeated in time, and temporal associations among different signals.

Material and Methods

Study area

Pilot whale vocalizations were recorded in Newfoundland's inshore waters from July to September 1979 and July to November 1980. Recordings were made in Lamaline Bay, Conception Bay, and Trinity Bay. Vocalizations of a stranded individual were recorded after the natural mass stranding of 135 pilot whales near Point au Gaul, Lamaline Bay (46°52'N 55°46'W), and recordings were made during the stranding of a single animal near Point Leamington (49°20'N 55°24'W), New Bay. An individual pilot whale entrapped in a gill net at Fredrickton, in Charles Hamilton Sound (49°40'N 54°80'W), and a single beached animal near Charleston, Bonavista Bay (47°40'N 53°75'W; see Figure 1) were also recorded.

Recording apparatus

All recordings, except those of stranded or entrapped animals, were made from a 4.3 m inflatable boat. The recordings were made on one channel of a Uher 4400 Report Stereo tape recorder at a tape speed of 19 c.p.s. (flat frequency 20 Hz - 20 kHz) with the exception of tape PaGT4 which was recorded at 9.5 c.p.s. A Gould CH-17 UT

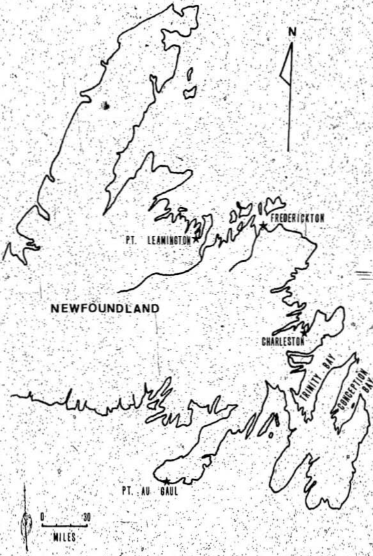


Figure 1. Map of study area showing recording locations.

hydrophone was used for all recordings (flat frequency 20 Hz - 18 kHz) made at sea while a Uher microphone was used to record the Point au Gaul stranded animal. The other channel of the stereo was used to record behavioral observations and when at sea, descriptions of group movements, weather conditions and contextual information such as the presence of other boats, whales, sea birds etc., were also recorded.

Recording methods - at sea

Once contact with a pod of pilot whales was made, the boat was moved from 50 - 150 m ahead of the pod, depending on the rate at which they were transiting. The motor was stopped and the hydrophone lowered. The animals were recorded as they passed by the boat until they were no longer within good acoustic range. The boat was moved in front of the animals again and the process repeated. Pods of pilot whales that were lolling (floating at the surface with no apparent direction of movement) were approached to within 100 m before the motor was stopped and recording commenced. If the lolling pod showed a preferential orientation, the recording was made from that direction so that a maximum number of animals was facing the hydrophone. If the animals were randomly oriented, the boat was moved to the windward side of the pod so that any drifting of the boat was in the direction of the whales.

Using these methods, most recordings were made from a distance of 20 - 150 m and for durations of up to 20 minutes without interruption. Most continuous recordings were from 5 - 15 minutes in duration.

In total over 33 hours of recordings were made across more than 20 sampling days. Contact with pilot whales was maintained for up to 10 hours per day, resulting in as much as five or more hours of recordings. The duration of a recording session depended primarily on the visibility of the animals and the clarity of the phonations. These in turn were dependent on the weather conditions and sea state. With the exception of three sessions, all recording was limited to daylight hours.

Recording methods - strandings and entrapments

At Point au Gaul, stranded individuals were recorded by holding a microphone approximately 15 cm from the animals blowhole.

The stranded animal at Charleston was recorded with a hydrophone (see specifications above) moored about 2 m away in approximately 1 m of water. All sounds were monitered from shore at a distance of about 10 m from the whale.

The entraped animal at Fredrickton was also recorded with a hydrophone and monitered from a trap skiff held in position by rowing.

Playback experiments - pods at sea

Playbacks for underwater broadcast were made with a Uher 4400 Report Stereo through a M.U.N. Technical Services 20 watt amplifier (flat 200 Hz - 4 kHz + 2 db) and a Lubell (Model 98) underwater loudspeaker (flat 200 Hz - 5 kHz). The duration of all broadcasts was 60 seconds.

The playback samples were usually 5 minutes in duration (2.5 minutes before and after the broadcast), plus the one minute broadcast duration. It was felt that any reaction to the broadcast of sounds would be quite immediate and most noticable during the playback or within the first 60 seconds after the playback. The 2.5 minute pre-playback duration also seemed sufficient to obtain a good "baseline" vocal and behavioral record. By limiting the durations of these later samples to 5 minutes, it was possible to sample recordings from more groups of whales. As it took up to several days to code 60 seconds of recording, depending on the number of phonations, larger samples were also not practical. Additional problems arise in that pods often do not remain close enough to the boat to get good recordings for durations of over 6 minutes.

The following four types of sounds were used in the playbacks:

1. Killer whale (Orcinus orca) phonations recorded in the presence of feeding killer whales off the coast of Newfoundland. (See Steiner, Hain, Winn, & Perkins, 1979, for a description of the recordings.)
2. White noise, emitted through the broadcasting equiptment as pink noise (energy concentrated between 2 - 6 kHz) due to tape recorder noise.
3. Constant tone, fundamental frequency of 27 kHz, no amplitude modulation (AM).
4. Variable tone, fundamental frequency ranging from 500 Hz - 6 kHz with variable frequency modulation (FM) rates and AM rates.

Playback intensities measured 30 - 35 dbs above ambient 6 m from source.

Vocalizations recorded before the onset and after the cessation of the broadcast were analyzed for comparison of phonation types and rates.

The behavior of the pods (transiting or lolling) and their distance from the loudspeaker at the onset of the playbacks varied.

Playbacks to stranded individuals

Vocalizations recorded from a stranded immature female pilot whale (field #19) at Point au Gaul were played back to other individuals of the stranded pod through a Uher 4400 Report Stereo. This recording was also played back to the same individual that produced the recorded vocalizations (i.e. animal 19).

The animal's vocal behavior and a description of it's actions during the playback were recorded on one track of another Uher 4400 Report Stereo with a Uher microphone held near the animal's blowhole.

Recording analysis

All recordings were listened to at least once in their entirety. Notes were made on the clarity of the recording, the presence of rare or unusual surface behavior, vocalizations or contexts, and the quality of the behavioral observations which varied due to observer fatigue and visibility of the animals. From these notes, over 12 hours of recordings were selected for continuous sound analysis based on their clarity and the recording context. Selected tapes were played into a Saicor SAI-53B real time spectrum analyzer, with a Honeywell 1856 Visicorder printout. Tapes were played on a Uher 4400 Report Stereo at 1/4 speed (4.7 c.p.s.) and the 0 - 5.0 c.p.s. scale of the analyzer was used. This gave a continuous real-time printout of 0 - 20 kHz (effective bandwidth 100 Hz) at a time scale of 2 c.p.s.

From those tapes processed by the real time spectrum analyzer, eight samples were taken and analyzed in detail.

1. Point au Gaul - Recordings were made from a pod of approximately 30 pilot whales in Lamaline Bay (Figure 1) on 15 July, 1979, one day after the stranding in the bay of 135 animals on a beach near Point au Gaul. Some members of this pod had been stranded and towed off the beach by fishermen, as evidenced by rope tied around their tail flukes. The sample duration was 43 minutes.
2. Killer whale/pink noise playback - Recording was made on 1 October, 1980, in Trinity Bay. Killer whale phonations were broadcast to a pod of approximately 70 pilot whales for a duration of 60 seconds. The two and one-half minute post playback sample was taken after approximately 60 additional seconds of noise from the broadcast apparatus. Total sample duration was five minutes.
3. Killer whale playback, trial#1 - Recording was made on 18 October, 1980, in Trinity Bay. Killer whale phonations were broadcast to a pod of approximately 25

pilot whales for a duration of 60 seconds. Sample duration was five minutes.

4. Killer whale playback, trial#2 - Recording was made approximately 30 minutes after sample 3 (18 October, 1980) to the same group of whales. Sample duration was five minutes.
5. Noise playback - Recording made about 10 minutes after sample 4 (18 October, 1980), before and after the broadcast of noise to a different group of about 30 whales. Sample duration was five minutes.
6. Constant Tone playback - recording was made on 15 October, 1980, in Trinity Bay. Sample of 1.25 minutes before and 2.5 minutes after the broadcast of a tone to several groups of pilot whales totalling almost 200 animals.
7. Variable tone playbacks - Recorded approximately 30 minutes after sample 5 (15 October, 1980). A variable tone was broadcast to a different group of approximately 30 animals and two and one-half minute samples were taken before and after the playback. Five minutes after the playback, another 60 second variable tone playback was broadcast and a further one and one-half minute sample taken. Total sample duration was 6.5 minutes.
8. Stranded individual - Recorded in air from the blowhole

of an immature 221 cm female pilot whale stranded at Point au Gaul on July 14, 1979. Vocalizations recorded from this animal were later played back to stimulate further vocalizing from the same animal. Total sample duration was 26.5 minutes.

Phonation coding

Both pulsed and non-pulsed phonations were analyzed as both might serve a function in communication (Busnel & Dziedzic, 1966; Caldwell & Caldwell, 1977; Herman & Tavolga, 1980; Lilly & Miller, 1961a). For this reason the term "phonation" was used to refer to an emitted "whistle" or "pulsed tone" and the term "form" to describe the resulting frequency contour.

Phonations were grouped into categories on the basis of similar acoustic properties, determined by form traces and aural impressions. In categorizing the pilot whale sounds, emphasis was placed on frequency changes over the duration of sounds (i.e., the "shape" of the form) although absolute frequency and duration were also taken into consideration. This decision was in part based on the relative ease with which frequency modulations (FM) and frequency inflections could be detected compared with absolute frequencies and durations. It was also noted that in repetitions of phonations, frequency and duration were often more variable than the overall shape of the form. Frequency contours from spectrographic analysis have also been used in most other studies of dolphin vocalizations (M. Caldwell & Caldwell, 1965, 1973, 1979; Caldwell, Caldwell & Hall, 1973; Caldwell, Caldwell & Miller, 1973; Dreher, 1961, 1966; Evans & Dreher, 1962; Lilly, 1963; Lilly & Miller, 1961a, 1961b, Steiner, Hain, Winn & Perkins, 1979; Taruski, 1976; Watkins & Schevill, 1974; Watkins, Schevill & Best, 1977; Watkins, Schevill & Ray, 1971) although the method is open to the criticism that important properties of the sounds may be overlooked (e.g., Busnel, 1966).

Tapes were listened to at speeds of 1/2 - 1/8 real-time concurrently with visual examination of the real time spectrum printout. In this way, phonations that were unclear on the spectrum printout, due to several contours being superimposed, could often be discerned. Occasionally, phonations that were not intense enough to show up clearly on the spectrum printout could also be classified. Some sections of a tape were listened to as many as 30 times at various speeds to aid in classifying weak or superimposed phonations.

Sample 1, recorded at Point au Gaul, was the first sample from which phonations were categorized. Every form visible on the spectrum printout was categorized. As new forms were found, they were assigned a code and traced for future reference. Variations within categories were also documented. If a sound could not be identified aurally or visually, it was coded as an unknown phonation. As the number and type of phonations varied unpredictably over relatively short periods of time, this sample was increased several times to a final duration of 43 minutes (1410 coded phonations) to try and clarify any patterns in this variability that may have existed.

Sounds from the playback samples were initially coded without reference to the categories developed from the Point au Gaul sample. Tracings were made to document all new categories and variability within the created categories.

Temporal analysis of coded phonations

As several animals may have been vocalizing at one time, a first order Markov chain analysis could not be used to measure vocal responses to phonations. A rough measure of the temporal associations among phonations could be obtained by dividing recording sessions into successive intervals and counting the frequency of each form type in these intervals (see Appendix B).

Cluster analysis, an analytic technique used for discovery rather than to support specific hypothesis (DeGhett, 1978), was then performed using correlation coefficients and average linkage (Wishart, 1978) on the frequency of each form per sucessive 15 second interval. The formulae used are presented in Appendix A. Phonations were most likely to be clustered together if they tended to occur in proportional frequencies in the same 15 second intervals. The index of similarity was, therefore, a measure of temporal association or vocal context.

The choice of 15 second duration time units was somewhat arbitrary although it was felt that this was short enough to pick up any possible first order relationships yet long enough to result in a minimal number of units with one or no phonations. At the same time, the inherent assumptions of a first order model were avoided. To check the effects of varying the time unit, sample 1 was reclustered using 30 second time units. Clustering was also redone using binary data (the presence or absence of forms in intervals).

The initial form categories for each playback sample were also clustered using average linkage on the frequency of each form type per 15 second interval.

Phonation recoding

The number of categories within each sample was abridged by pooling categories with high similarity indexes and/or similar acoustic properties. Rare categories with two or fewer cases were omitted.

The same forms were rarely found in samples taken from different pods. A new broader "common coding" scheme was used to amalgamate forms from different samples that had common physical characteristics. These more general categories also reduced the number of different form classes within each sample.

Results

Coding of phonation categories

Forms from each sample were initially coded separately in a highly discriminating manner, allowing very little variability within classes. The resulting classes were then abridged by pooling acoustically similar classes and omitting rare classes (containing two or fewer cases). A broader common coding scheme was also used to amalgamate forms from different pods. The number of resulting groups from each of these three coding trials and the total number of forms included were given in Table 1. Figure 2 compares the cumulative number of different form groupings obtained using the different coding trials for sample 1.

To distinguish between these coding systems, the term "class" will be used to describe forms grouped together in the initial coding scheme and "category" will be used for the common coding groups.

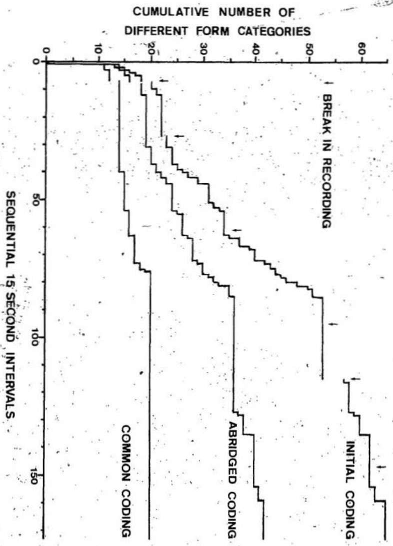
Two sets of characters were used to code each form at different levels of discrimination. The first digit in the code series corresponds to one of the seven whistle categories defined by Taruski (1976). These very broad categories were:

1. Level frequency - very little change in frequency

Table 1. Number of different form groups (Nd) and the total number of coded forms (Nt) obtained in the different samples using the different coding methods.

Sample	Sample duration (min.)	Coding Method initial Nd	initial Nt	abridged Nd	abridged Nt	common Nd	common Nt
1. Point au Gaul	43	65	1410	42	1406	20	1406
2. Killer whale – noise	5	22	163	12	153	15	163
3. Killer whale #1	5	17	128	12	123	8	123
4. Killer whale #2	5	11	97	8	95	8	97
5. Noise	5	12	162	11	161	8	161
6. Constant tone	4.2	8	81	8	81	7	81
7. Variable tone	6.5	21	191	12	177	10	187
8. Stranded individual	26.5	23	217	13	217	12	217
Pooled	100.2	120	2449	60	2413	25	2435

Figure 2. Cummulative number of different form groups for each of the three coding methods from sample 1. Arrows denote breaks in the recording.


CUMULATIVE NUMBER OF DIFFERENT FORM CATEGORIES
0
10
20
30
40
50
60
SEQUENTIAL 15 SECOND INTERVALS
0
50
100
150
BREAK IN RECORDING
INITIAL CODING
ABRIDGED CODING
COMMON CODING

throughout the duration of the whistle

2. Falling frequency - a noticeable decrease in the frequency throughout all or most of the duration of the whistle
3. Rising frequency - a noticeable increase in frequency throughout all or most of the whistle
4. Up-down - a whistle in which frequency first rises then falls: a hump-shaped or inverted U or V shaped form
5. Down-up - a whistle in which frequency first falls then rises: a U or V shaped form
6. Multihump - a whistle in which there were at least two frequency inflections
7. Wavers - no whistles were coded as wavers

If the form was amalgamated with other forms belonging to a different Taruski (1976) category using the common codes, a second digit followed, indicating the category in which most of the pooled forms belonged (e.g., a rising frequency form that was pooled with multihump forms would be coded 3-6). The digit (or digits) were then followed by a letter. The digit (or second of two digits) and letter taken together identified the common category.

Forms from different samples were pooled on the basis of physical (acoustic) properties, while forms from a single sample were pooled on the basis of both physical properties and temporal associations. In some instances forms remained coded separately from all others (i.e., a class created in the initial coding trial may have remained separate in the common coding trial). If the form was omitted from the common coding, "00" followed the Taruski (1976) category code.

The second set of characters was comprised of the recording sample number (see pp. 21 - 23) followed by two digits which identified the initial, uncombined classes (e.g., 3-6A/130 was form class 30 from sample 1, recorded at Point au Gaul).

<u>Phonation form catalog</u>

1. Constant frequency forms:

1A - level frequency, 2kHz or less. These forms all had some energy 2 kHz or less in frequency and durations of 0.25 - 1.00 s. The maximum change in frequency was approximately 300 Hz per s. Variations included the presence of an abrupt, stepwise change in frequency, (e.g., 1A/116), or a slightly curved contour (e.g., 5-1A/155). Usually 1A forms had numerous regular harmonics but some appeared pulsed, with numerous irregular harmonics (e.g., 3-1A/136). This category was comprised of form classes 110, 112, 113, 114, 116, 136, 198, and 413 (see Figure 3).

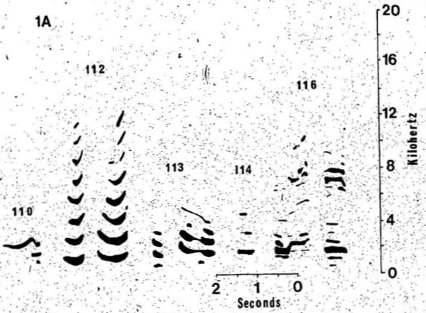
1B - level frequency, 2 - 6 kHz. The frequency range for 1B forms was from 2 - 6 kHz with durations less than 1.2 s, usually about 0.5 s. Very little change in frequency was observed but some forms had abrupt increases in frequency at the end (e.g., 118) or decreases in frequency at the start (e.g., 514). This category was comprised of form classes 111, 118, 222, 217, 311, 411, 415, 422, 511, 513, 514, and 613 (see Figure 4).

1C - very short, variable frequency. These forms were grouped on the basis of their very short durations, typically less than 0.25 s. Frequency was highly variable, but always less than 8 kHz. No harmonics were present unless the phonation was pulsed, with the exception of one 216 form. This category was comprised of form classes 115, 216 (see Figure 3), and 815 (see Figure 5).

2. Falling frequency forms:

2A - frequency decreases 2 kHz or less. The change in frequency was less than 2 kHz for the 2A forms, in most cases proportional to the initial frequency. The rate of change was approximately 1/2 of the initial frequency

Figure 3. Component form classes of common form categories 1A and 1C. Note that time proceeds from left to right.


1A
112
116
113
114
110
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

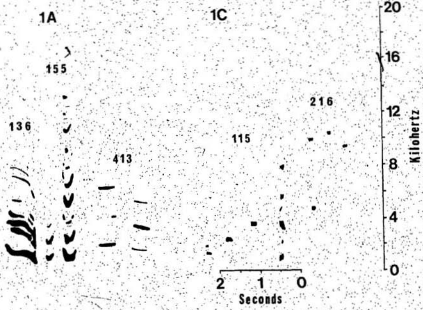

1A
1C
155
216
136
115
413
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

Figure 4. Component form classes of common form category 1B

1B

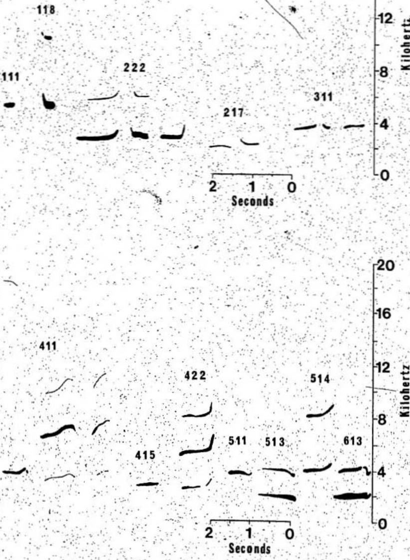
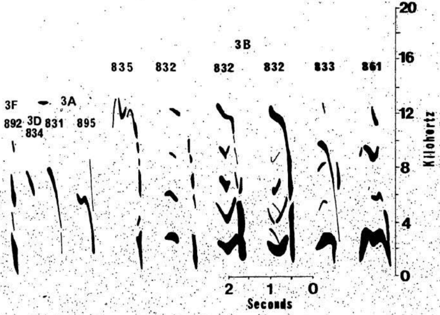
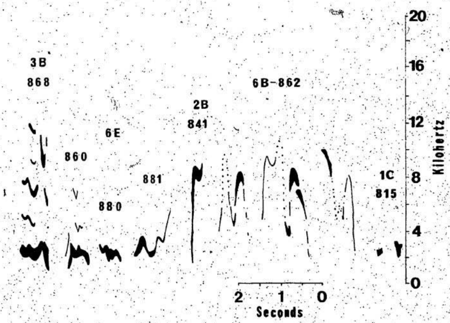

118
111
222
217
311
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds
411
422
514
415
511
513
613
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

Figure 5. Forms recorded from a stranded individual (sample 8).


3B
835
832
832
832
833
861
3F
3A
892
3D
834
831
895
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

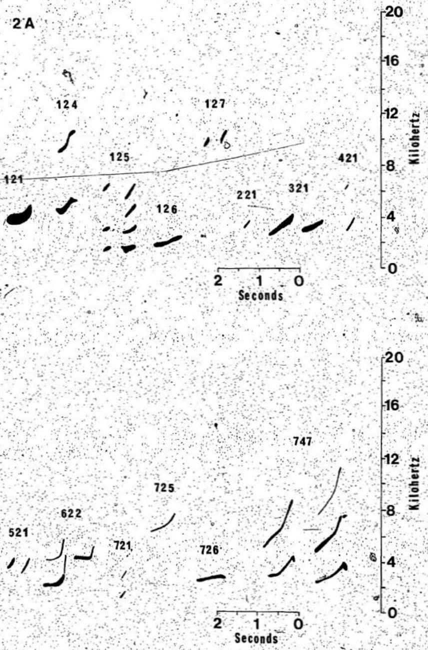

3B
868
6E
860
880
881
2B
841
6B-862
1C
815
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

per s (exceptions were 747, 725, & 721). The decrease in frequency was constant (except 622) throughout the duration of the form. This category was comprised of form classes 121, 124, 125, 126, 127, 221, 321, 421, 521, 622, 721, 725, 726, and 747 (see Figure 6).

2B - large, rapid decrease in frequency. The basic component of these forms was a very rapid decrease in frequency over durations of less than 0.25 s. These changes in frequency were as much as 14 kHz, at rates of approximately 200 kHz per s. The sudden decrease in frequency often resulted in incomplete form traces (a result of the spectral analysis sampling rate). The frequency at the start of the rapid decrease was in or near the ultrasonic range (from 16 - 20+ kHz). These forms decreased in frequency continually (e.g., 224 and 623), or had inflections. The overall trend was always to lower frequencies. Later increases in frequency never were as high as the initial frequency. The 255 forms had one inflection, following a down-up contour over 0.5 - 0.7 s. The 265, 765 and 841 (N=1) forms had two inflections (down-up-down) over 0.4 - 1.2 s. The 841 form occurred less than 4 s before the 862 variant with extra inflections and is almost identical to the end of this 862 form (see Figure 5, p. 37). It is therefore possible that the 841 form is related to the

Figure 6. Component form classes of common form category 2A

2 A

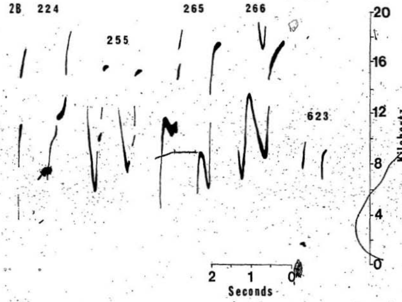

124
127
125
121
126
221
321
421
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds
747
725
622
521
721
726
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

6B/862 forms, the usual first component having been too faint for detection or omitted. Forms 265 and 724 sometimes had initial increases in frequency before the rapid decrease in pitch. This category was comprised of form classes 224, 255, 265, 266, 623, 724, 765 (see Figure 7), and 841 (see Figure 5, p. 37).

3. Rising frequency forms:

3A - short, rapid increase in frequency. All 3A forms had a rapid increase in frequency of 3 - 14 kHz, and durations usually were less than 0.50 s, but occasionally as long as 1.3 s (e.g., 338). Initial frequencies often were less than 1 kHz but ranged as high as 5 - 6 kHz (e.g., 190, 732). Sudden increments in frequency also occurred (e.g., 338) that were occasionally melodic (e.g., 190, 290). Frequency sometimes leveled off near the end of the contour (e.g., 196) or even had an inflection (e.g., 195, 895). Harmonic relationships were sometimes seen between 3A forms within a sample (e.g., 732, 731). A discernible pause of less than 0.2 sec in duration was present within the 137 forms. This category was comprised of classes 131, 137, 138, 190, 195, 196, 231, 290, 331, 332, 338, 631, 632, 732, 731, 831, and 895 (see Figures 8, 9, & 5, p. 37).

Figure 7. Component form classes of common form categories 2B and 3E


2B
224
255
265
266
623
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

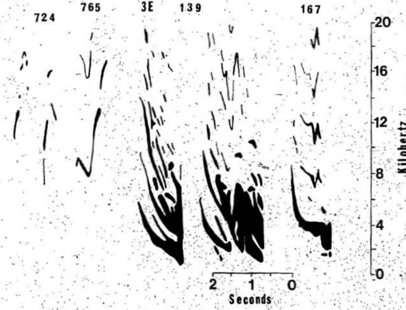

724
765
3E
139
167
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

Figure 8. Component form classes of common form category 3A

3 A

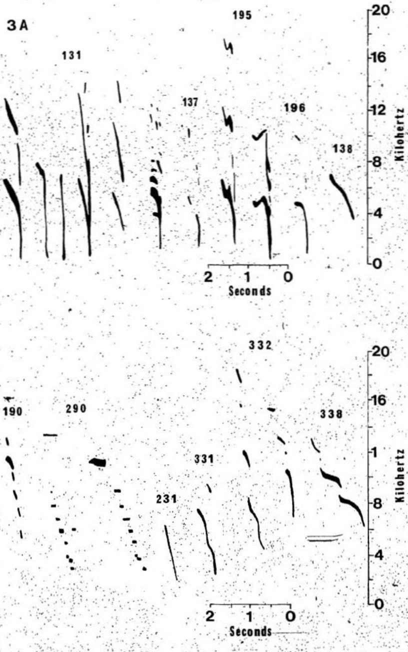
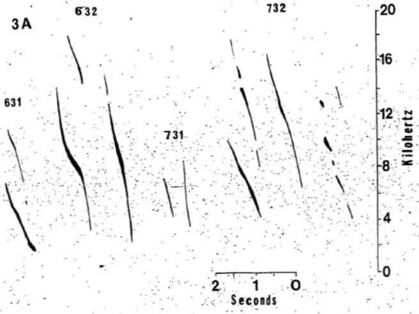
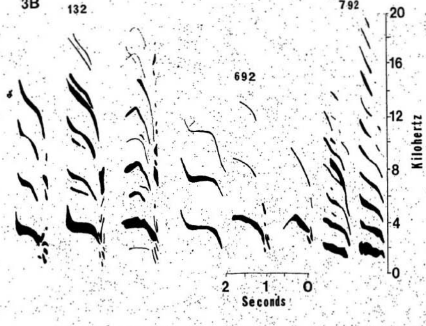

195
131
137
196
138
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds
332
190
290
338
331
231
20
16
1
8
4
0
Kilohertz
2
1
0
Seconds

Figure 9. Component form classes of common form categories 3A (cont.) and 3B

3A


632
732
631
731
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

3B

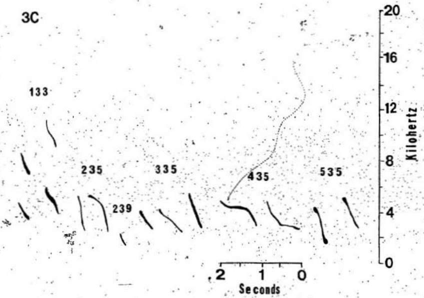

132
792
692
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

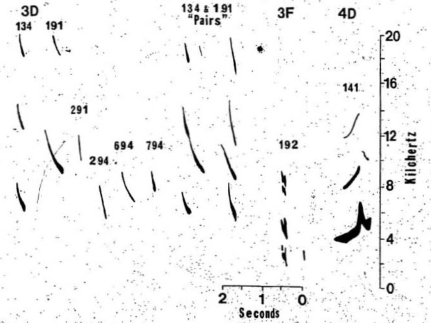
3B - sigmoidal increase in frequency to less than 5 kHz. These forms were usually sigmoidal in shape. The initial increase in frequency leveled off then the phonation terminated with another increase in frequency. The initial frequency was between 1 - 2 kHz while the terminal frequency ranged from 2 - 5 kHz. The durations of 3B forms was from 0.50 - 1.25 s. "Double whistle" variations were present in three of the four samples containing 3B forms (samples 1, 7, and 8 but not 6). Sample 7 variations were generally lower in frequency, did not have an initial broad-band component, and exhibited less terminal inflection than 132 forms. The most numerous sample 8 3B forms (832, N=125) were shorter in duration and lower in frequency than the 132 forms recorded from the Point au Gaul pod. This individual produced many variations including forms with no formants below 11 kHz after the initial attack (form 835, N=4), forms with a pause (N=2) and forms with terminal decreases in frequency (833, N=16; 861, N=1). One case with a terminal decrease in frequency was also found in each of samples 1 and 6. This category was comprised of classes 132, 692, 792 (see Figure 9, p. 44), 832, 835, 861, 833 and 868 (see Figure 5, p. 37).

3C - short increase in frequency below 6 kHz. The 3C forms were lower in frequency and had a smaller increase in frequency than the 3A forms. The initial frequency was usually greater than 2 kHz, with the exception of 535 (initial frequency around 1.8 kHz). Terminal frequencies were sometimes as high as 6.2 kHz (e.g., 535) but were typically less than 6 kHz. The duration of 3C forms was less than 0.5 s (except 335 and 435) and occasionally as short as 0.25 s (e.g., 239). Some 435 forms were slightly sigmoidal in shape. The 3C forms showed considerable variability and could be considered abbreviated 3A forms. Harmonics were seldom present except in 133 forms. This category was comprised of form classes 133, 235, 239, 335, 435, and 535 (see Figure 10).

3D - short increase in frequency between 6 - 10 kHz. These forms exhiibited short durations (less than 0.5 s) and higher initial frequencies (6 - 10 kHz) than 3A and 3C forms. The increase in frequency was quite constant throughout the form duration. Harmonics were ocassionally present but were often too faint to be detected. Form categories 134 and 191 may have been harmonically related, indicating the possibility of a similar production mechanism. These two forms had been recorded simultaneously and coterminously (Figure 10). This category was comprised of form classes 134, 191,

Figure 10. Component form classes of common form categories 3C, 3D, 3F, and 4D


3C
133
235
239
335
435
535
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds


3D
134
191
291
294
694
794
134 & 191
"Pairs"
3F
192
4D
141
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

291, 294, 694, 794 (see Figure 10, p. 46), and 834 (see Figure 5, p. 37).

3E - long, "noisy" increasing frequency. These noisy sounds were characterized by a broad band attack with some initial energy between 1 - 6 kHz (in the case of 139) or between 2 - 4 kHz (for 167 & 839 forms). The frequency increased to from 4 - 8 kHz over 1.0 - 1.5 s. The 167 forms may have been less intense traces of 139 forms as these differed mainly in their timbre. Note that the 6C/168 forms were composed of 139 forms with additional terminal inflections, but were coded with 117 and 119 forms (similar to the 6C/168 terminal component). The 6C/168 forms had a stronger temporal association with the 117 and 119 forms due to the smaller number of intervals in which they were found. This category was comprised of form classes 139 167 and 839 (see Figure 7, p. 41).

3F - very short noisy. These were very short duration (less than 0.2 s), low frequency, broad band sounds. The 3F forms were very similar to the start of many 3A and 3B forms and were probably terminated or truncated phonations. It is also possible that these forms might have served as phonemes. These sounds were only recorded from Point au Gaul animals, samples 1 and 8 (form classes 192, and 892 see Figures 10, p. 46 and 5, p. 37).

4. Up-down forms:

4A - rapid up-down, 4 - 8 kHz. The basic component of the 4A forms was an initial sharp increase in frequency of 4 to 8 kHz followed by an equally rapid decrease in frequency, usually of 1 - 2 kHz (e.g., 144, 844), but ranging to over 4 kHz (e.g., 145). This decrease in frequency was never below the initial frequency. The up-down component was sometimes followed by a short increase in frequency to a pitch slightly higher than the first inflection frequency (e.g., 188, 228, 337, 537, and 795) or slightly lower (e.g., 333). Other forms had a second up-down component with the second downward inflection always at a higher frequency than the first (e.g., 187). This may have also been followed by additional inflections (e.g., 108). Although these forms exhibited variable degrees of inflection and consequently a wide range of durations, they were coded together due to the presence of the same basic component in all and the close temporal association among the sample 1 forms in this category (see Figure 11). The 844 forms were also associated with multihump forms (864, N=2) resembling forms 189 and 108 (see Figure 12).

Figure 11. (A) Sequence of sample 1, 4A variants with similar 6B and 3A form variants (B) Sequentiial repetitions of 4B forms from sample 7

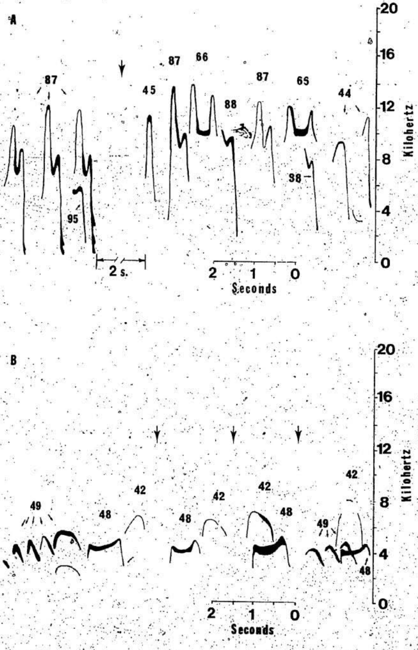
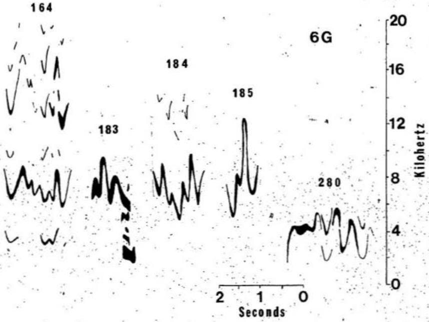
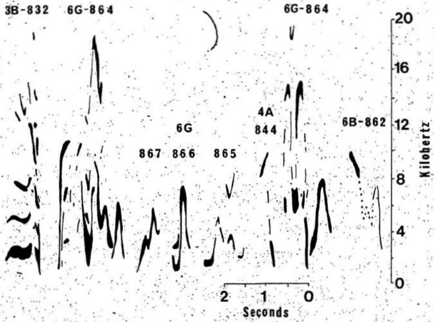

A
87
95
45
87
66
88
87
66
88
44
2 s.
2
1
0
Seconds
20
16
12
8
4
0
Kilohertz
B
49
48
42
48
42
42
48
49
42
48
2
1
0
Seconds
20
16
12
8
4
0
Kilohertz

Figure 12. Component form classes of common form category 6G and a sequence of forms from sample 8


164
6G
184
185
183
280
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

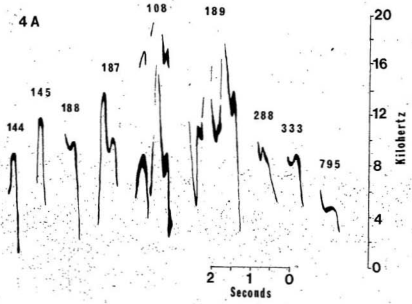

3B-832
6G-864
6G-864
4A
844
6G
867
866
865
6B-862
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

This category was comprised of form classes 144, 145, 187, 188, 189, 108, 288, 333, 337, 537, 795 (see Figure 13), and 844 (see Figure 5, p. 37).

4B - "smooth" up-down. The initial and terminal frequencies of these forms differed by less than 2 kHz. The frequency changes were usually less than 4 - 5 kHz although 542 variants covered frequency ranges of up to 10 kHz. Forms in this class often had a detectable harmonic structure. Changes in frequency were usually continuous but stepwise increments, especially during the initial increase in frequency, also occurred (e.g., 543 and 748). Forms were often very asymmetrical (e.g., 542, 445, and 742) but assymmetry was also observed (e.g., 744). Some of the observed variations within a sample seemed associated with sequential repetitions of a form (e.g., sample 7, see Figure 11, p. 49). Form 143 occurred in close temporal association with form 126 (see Figure 14). This category was comprised of form classes 143, 246, 444, 445, 542, 543, 742, 743, 744, 748, and 749 (see Figure 15).

4C - rapid up-down, 10 kHz or more. These forms were all characterized by very rapid increases in frequency of over 10 kHz, often reaching into the ultra-sonic range. In 242 forms the initial up-down component was followed

Figure 13. Component form classes of common form categories 4A and 6C


4 A
144
145
188
187
108
189
288
333
795
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

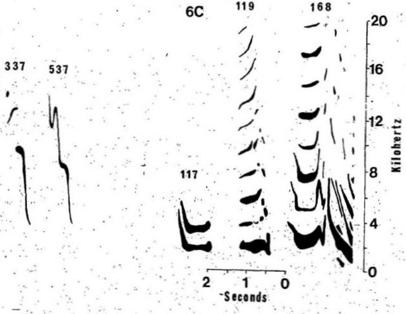

337
537
6C
119
168
117
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

Figure 14. The initial repetitions of two bouts of 4B/143 forms showing development of the 143 contour from 133 forms

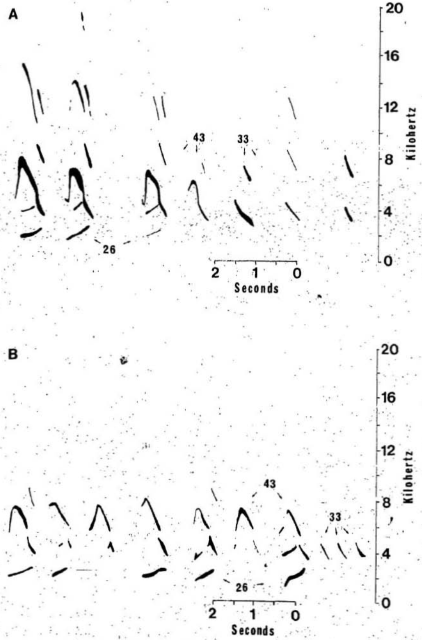
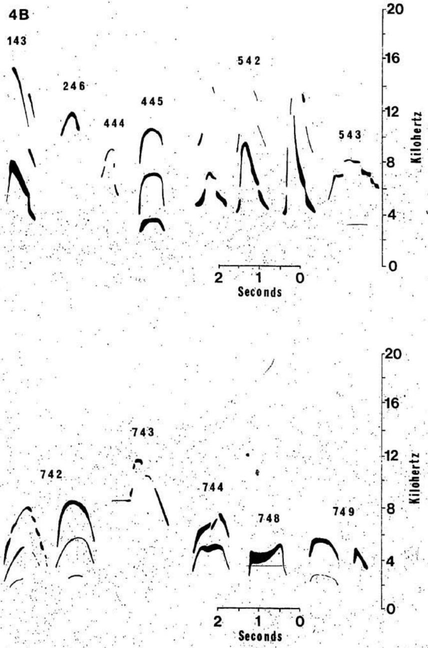

A
20
16
12
8
4
0
Kilohertz
43
33
26
2
1
0
Seconds
B
20
16
12
8
4
0
Kilohertz
43
33
26
2
1
0
Seconds

Figure 15. Component form classes of common form category 4B

4B

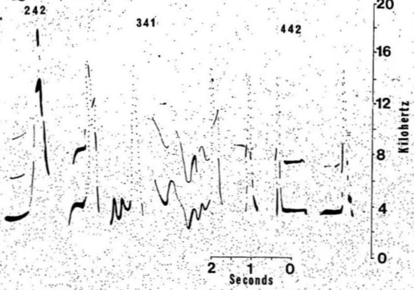

143
246
444
445
542
543
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds
742
743
744
748
749
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

by a constant frequency (2 - 3 kHz) of over 0.5 s duration, often with harmonics. The 341 forms also had a constant frequency component (approximately 4 kHz) after the initial up-down but ended with a sharp decrease in frequency of about 2 kHz. This was sometimes followed by extra inflections that were regular and sinusoidal or erratic. One variant has been recorded with each of four, seven, and nine inflections added to the basic 341 contour. Durations for these variants were 0.8, 1.7, and 1.5 s respectively. The initial rise of many 341 forms followed a 4A/337 contour. The 442 forms differed from the other 4C forms in that the sharp rise in frequency occurred without, before, or after a constant frequency component of about 0.5 s duration. Both the initial and terminal frequencies of 442 forms were near 4 kHz. This category was comprised of form classes 242, 341, and 442 (see Figure 16).

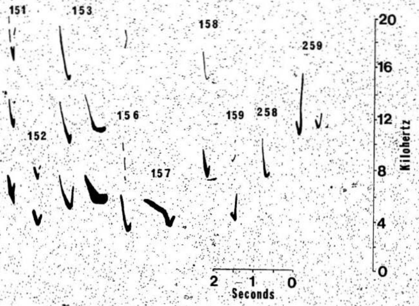
4D - falling up-down. The 141 forms that made up this category decreased in frequency from an initial value of about 5 kHz to a terminal frequency of 4 kHz. Durations ranged from 0.5 - 1.0 s. The steady decrease in frequency was interrupted by a short up-down component spanning about 1 kHz. These sounds were similar in slope, duration, and frequency to 2A/747 forms but with

Figure 16. Component form classes of common form categories 4C and 5A. Dotted sections of the forms were not intense enough to show up on the spectrum printout but were drawn in on the basis of auditory analysis at reduced speeds.

4C


242
341
442
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

5A


151
153
158
259
156
159
258
152
157
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

the up-down inflection. This category was comprised of form class 141 (see Figure 10, p. 46).

5. Down-up forms:

5A - short down-up. These were short duration (less than 0.5 s) down-up forms of variable frequency. The minimum frequency in these forms, however, was often 3, 5, or 7 - 8 kHz. Some forms appeared to be harmonically related. Usually the terminal frequency was higher than the initial frequency (except forms 159 and 259). The two 858 forms occurred immediately before and after a 3E/839 form. This category was comprised of form classes 151, 152, 153, 156, 157, 158, 159, 259, and 258 (see Figure 16, p. 56).

5B - long down-up. These were longer in duration than the 5A forms, and were characterized by a constant frequency (usually) component in the middle of the form. This middle component exhibited considerable variability including inflections or abrupt frequency changes in the 154 forms. Extra inflections may have also been present at the start of the form (e.g., the 654 forms always had an initial increase in frequency). The basic frequency typically decreased rapidly from 10 kHz to 4 kHz over about 0.5 s duration. The terminal increase in frequency was variable, but usually rose to near the initial frequency. The basic frequency was the first harmonic in the 154 forms. The fundamental frequency and even harmonics were usually only detectable during the middle part of the form and occasionally not at all. This category was comprised of form classes 154, 165 and 654 (see Figure 17).

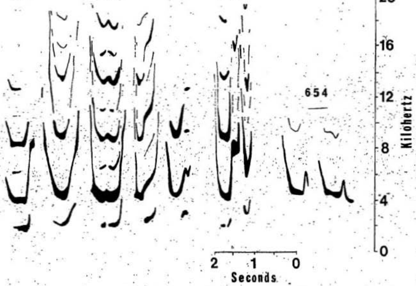
5C - level down-up. The 5C forms had an initial frequency of about 3 kHz which decreased very gradually at first, then fell to 2 kHz. This sharper decrease in frequency was immediately followed by an increase to the initial frequency. Form class 552 was the only component of this category (see Figure 17).

6. Multi-hump forms:

6A - sigmoidal increase to 7 kHz. All 6A forms ended with a relatively constant frequency (about 6 kHz) component of 0.5 s duration, followed by a rapid increase in frequency of about 1 kHz. The initial component of the form was either a rapid increase in frequency from an initial value of 2 - 4 kHz (e.g., 130 and 161) or a broad band attack from less than 1 kHz (e.g., 193). These three forms all had a sigmoidal contour. The initial component could also have been a decrease then increase in frequency over a range of about 1 kHz (e.g., 162). Forms 161 and 162 exhibited some decrease

Figure 17. Component form classes of common form categories 5B, 5C, and 6A

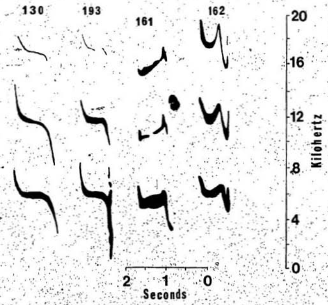
5B


154
165
654
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

5C


552

6 A


130
193
161
162
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

in frequency during the middle component. Durations ranged from about 0.8 s for 161 and 162 forms to 1.3 s for 130 and 193 forms. These phonations were temporally associated with each other and with 3E phonations. This category was comprised of form classes 130, 161, 162, and 193 (see Figure 17, p. 59).

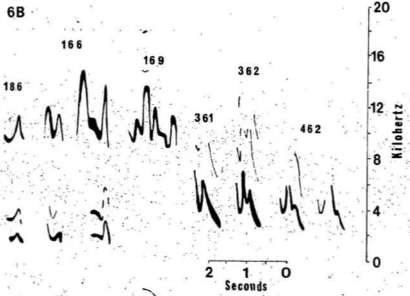
6B - double hump. These forms were characterized by an initial up-down-up contour that on occasion had additional inflections on the end. These "double peaked" contours differed between samples but showed little variability within a sample. In sample 1, the basic frequency started around 9 kHz, increased to approximately 11 kHz then decreased to 9 - 10 KHz, followed by another increase in frequency (e.g., 186). This second increase sometimes peaked near 13 kHz then decreased again to near 10 kHz (e.g., 166). Both the 186 and 166 forms had detectable fundamental and first harmonic formants at about 2 and 4 kHz but no other energy was detectable below the fifth harmonic. The fifth harmonic was the basic frequency. Form 166 exhibited variability in the middle component; between the peaks in frequency and also in the peak frequencies themselves. The second peak, however, was never lower in frequency than the first. Forms coded 169 (N=2) were modified 166 forms, having additional terminal inflections. Both 169 forms occurred during an interval within a bout of 6B forms. The 186 forms could have been considered truncated 166 forms whereas the 169 forms were "elongated" 166 forms. In samples 3 and 4, 6B forms started near 3 kHz and inflected at approximately 6, 5, and 7 kHz. Again the second peak was never lower in frequency than the first. The longer forms in samples 3, 4, and 5 (e.g., 362, 462, and 562) typically had two more inflections than the shorter versions (e.g., 361 and 561). Variants of 6B in sample 5 included one case where the second peak was lower in frequency than the first. Some forms were also shifted upward by about 1 kHz and the 563 forms (N=5) consisted of 562 forms with extra inflections on the end. Sample 8 variations differed from the sample 1 forms though the stranded animal recorded in sample 8 was thought to be from the same pod as in sample 1. The 862 forms (N=6) started at a frequency of 2 - 4 kHz, increased to 8 kHz, decreased to about 4 kHz, increased to about 10 kHz then decreased to 4 - 6 kHz over a 0.7 - 1.0 s duration. One form did not have a terminal decrease in frequency while another variant had two extra terminal inflections. The sample 8 animal also produced two different forms that were basically double-humped contours but were coded with other multihumped forms with which they were temporally associated (see Figure 12, p. 50). This category was comprised of form classes 166, 169, 186, 361, 362, 462, 561, 562, and 563 (see Figure 18), and 862 (see Figure 5, p. 37).

6C - miscellaneous 4 kHz or less. These form classes were temporally associated and all were relatively rare (117, N=2; 119, N=2; 168, N=4). All cases occurred within a two minute segment of sample 1. The common feature of these forms was a fairly constant frequency component of about 0.5 s duration that ended with an increase in frequency. This basic component may have occurred alone (e.g., 117), may have been preceeded by a short period of frequency modulation (e.g., 119), or may have been preceeded by a 3E/139 form (e.g., 168). These forms were also temporally associated with 3E/139 forms and might have represented variants of the 3E category. The 3C forms always occurred close in time to 3E forms but 3E forms frequently occurred without 6C forms. This category was comprised of form classes 117, 119, 168 (see Figure 13, p. 52).

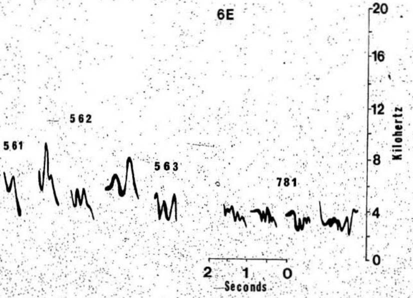
6D - "W" shaped. The 6D contours were all basically shaped like the letter "W" with variations in the center peak height, the slope, and the amount of frequency modulation. All forms tended to increase in frequency

Figure 18. Component form classes of common form categories 6B and 6E

6B


166
169
186
362
361
462
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

6E


562
561
563
781
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

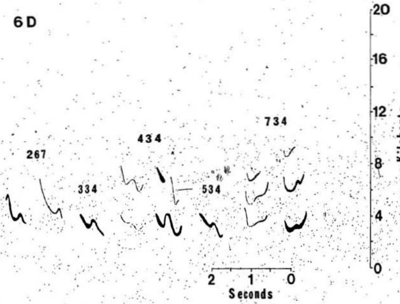
except 734 which exhibited a decreasing trend in frequency. The initial frequency was between 3 and 4 kHz. Total duration for these forms was from 0.5 to 0.7 s. Some 267 variants did not have the initial frequency inflection. This category was comprised of form classes 267, 334, 434, 534, and 734 (see Figure 19).

6E - multiple inflections 2 - 4 kHz. The 781 forms had energy in the range of 2 - 4 kHz and durations of 0.5 to 1.0 s. Inflections numbered 6 to 10 and arose from rapid frequency modulations around a central frequency of about 3 kHz. The sample 8 forms (860, N=4; 880, N=3; and 881, N=1) had 4 (881), 5 (860) or 6 (880) inflections. This category was comprised of form classes 781 (see Figure 18, p. 63), 860, 880 and 881 (see Figure 5, p. 37)

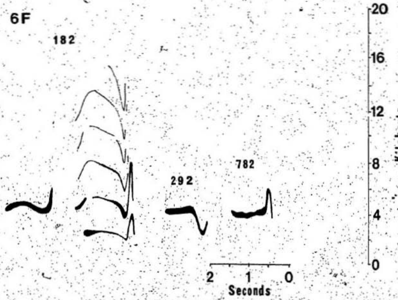
6F - FM around 4 kHz. These forms were characterized by an initial short (0.2 - 0.3 s duration) up-down (e.g., 182 and 782) or down-up (e.g., 292) component followed by a longer (0.5 to 1.0 s duration) more constant frequency component with energy concentrated around 4 kHz. Harmonically related formats were sometimes present. Frequency ranged between 2 and 6 kHz while durations varied around 1.0 s. Some frequency modulation occurred during the last part of some forms. This category was

Figure 19. Component form classes of common form categories 6D and 6F

6D


267
334
434
534
734
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

6F


182
292
782
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

comprised of form classes 182, 292, and 782 (see Figure 19, p. 65).

6G - miscellaneous multi-humps. These were miscellaneous multi-hump forms, generally long in duration with many frequency inflections. Form 164 inflected 11 times over a duration of 1.7 s. The basic frequency was between 6 and 9 kHz and harmonics were present in this form. Forms 184 was fairly similar to 164 with 9 inflections within a frequency range of 5 - 10 kHz. The duration of form 168 was 1.2 s and one faint harmonic was present. Forms 164 and 184 were not temporally related. Form 184 and 185 occurred about 15 s apart and both had energy concentrated in the same range. Form 185 had five frequency inflections during it's 0.8 s duration. This form (185) had no harmonics and showed some resemblance to 4A forms. Form 181 inflected only three times and had a basic frequency of between 4 and 7 kHz. This form (181) is similar to the 6A/162 forms although there was no temporal association between them. Form 183 inflected 5 times between 6 and 10 kHz over 1.0 s. There were no harmonics present in form 183 which started out with broad band energy from 2 to 8 kHz. Form 280 was lower in frequency (between 2 and 6 kHz) and inflected 9 times over about 2 s. The two 864 forms inflected 5 and 9 times over durations of 1.2 and 1.8 s.

Both 864 forms ranged in frequency from 2 to ~10 kHz, had harmonics, and started with similar up-down components. The unique 865, 866 and 867 forms were temporally associated with the two 864 forms, all of the sample 8 variants occurring within 11 seconds (see Figure 12, p. 50). These forms (865, 866 and 867) had only 5, 2 and 4 inflections respectively within a frequency range of 1 - 8 kHz. This category was comprised of form classes 164, 181, 183, 185, 280 864, 865, 866 and 867 (see Figure 12, p. 50).

Variability within categories

Twelve main types of variation were observed among phonations, within samples, that were classified in the same form category on the basis of temporal association and/or overall acoustic similarities. These main types of variation were:

1. truncation - These phonation variants started like other phonations then ended abruptly (e.g., 3F, 6B/186).
2. abbreviation - Some forms were distinguishable by shorter durations and frequency ranges although rate of frequency change and shape were the same (e.g., 3A, 3C, and 3D).
3. melodic, stepwise frequency changes - Stepwise frequency increments were sometimes observed instead of a smooth

"glissando" (e.g., 3A/137, 3B/832).

4. reversals - Some 4C forms had the characteristic up-down component preceeded by a constant frequency component while other variants started with the up-down component and terminated with a constant frequency component.
5. pauses - Forms occurred with characteristic shapes and durations but containing discernible pauses (e.g., 3A/137, 3B/832).
6. frequency - Form frequencies were quite constant within categories recorded from a single pod but the shorter duration forms, most notable 5A and 1C forms, varied considerably in frequency.
7. initial attack and first inflection - The 6A forms started with broad-band attacks, a smooth increase in frequency, or a short down-up frequency inflection.
8. terminal inflection - Variations of 3B forms included some that followed the usual contour shape until the terminal inflection which would be a decrease in frequency instead of the usual increase in frequency.
9. slope or overall frequency trend - The 6D forms had a characteristic "W" shape but some tended to increase in frequency while others decreased in frequency.
10. double whistles - The simultaneous emitance of two narrow-band sounds (first reported by Caldwell & Caldwell, 1969) was observed in 3B variants from 3

samples.

11. additional frequency inflections - Additional frequency inflections were sometimes observed at the start (e.g., 5B/654) but were usually added to the end of the more common variant (e.g., 4A, 4C, and 6B).
12. harmonic structure - Variation in the number and relative strengths of the harmonics of some forms were not attributable to overall signal strength (e.g., 3B/832, 6B).

The sample 8 3B variants recorded from a single animal included double whistle forms, pauses, terminal inflection variants and variability in the number and relative strengths of the harmonics.

Component sample contexts, surface behavior and vocalization

As the different samples analyzed differed with respect to size, recording context, date, and the pod being recorded, they will be treated separately. Comparisons will then be made among the different samples.

(i) Point au Gaul - These recordings were made on 15 July 1979, the day after the mass stranding of 135 pilot whales near Point au Gaul (McLeod & Lien, in press).

Behaviorally the animals seemed "normal" although some had definately been removed from the beach (as evidenced by the presence of short pieces of rope tied around their caudal peduncles). The data obtained from this sample may, therefore, have been pathological (see Appendix B).

The frequency of occurrence of the phonations recorded in sample 1 was highly variable. Of the 1410 forms coded, twelve form categories in the original coding trial occurred only once while one (131) occurred 431 times. Common coding resulted in the form categories, present in sample 1, having frequencies, of from 5 to 559 (see Table 2).

The relationship between log frequency of form type and rank, according to frequency of occurrence, fit a negative exponential function (r=-0.94, Figure 20; see Schleidt, 1973). Over one third of all recorded vocalizations were of one type (common code 3A). The top three ranking forms (3A, 3B and 3D) accounted for over 50% of all vocalizations recorded.

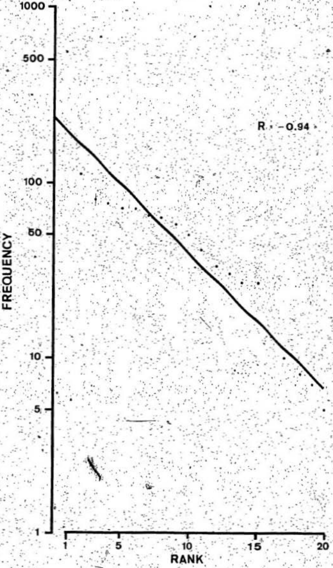
As this sample (43 minutes) was larger than the other samples taken together, any temporal patterns regarding vocalizations should be more apparent in these data.

It was apparent from looking at the number of each form type in successive intervals (see Appendix B) that many sounds were not randomly distributed in time, exhibiting

Table 2. Frequency and rank order of common form categories per sample.

	Sample number															
Common	1		2		3		4		5		6		7		8	
code	N	R	N	R	N	R	N	R	N	R	N	R	N	R	N	R
1A	65	7					5	6								
B	13	16	24	3	14	4	28	1	17	5	4	6				
C	33	12	3	12											37	2
2A	71	5	4	10	7	6	4	7	2	7	18	1	32	2		
B			30	1							8	4			1	12
3A	559	1	8	8	9	5					16	2	37	1	11	3
B	109	2									13	3	16	5	132	1
C	51	10	12	5	3	8	14	3	18	4						
D	79	3	25	2							6	5	23	3	6	5
E	27	14													2	10
F	30	13													4	8
4A	77	4	3	11	32	1			20	3			11	6	3	9
B	27	14	2	13			7	5	46	1			22	4		
C			9	5	30	2	25	2								
D	7	19														
5A	63	8	9	5											2	10
B	58	9									2	7				
C									3	8						
6A	41	11														
B	73	5			23	3	3	8	43	2					6	5
C	8	18														
D			4	9	5	7	11	4	10	6			4	8		
E													9	7	8	4
F	10	17	7	8									2	10		
G	5	20	2	13											5	7

Figure 20. Log frequency of common code forms versus rank according to frequency of occurance for sample 1


1000
500
100
50
10
5
1
FREQUENCY
R = -0.94
1
5
10
15
20
RANK

temporal clustering or bouting. Objectively defining a bout can be very problematic (see Machlis, 1977, for a discussion of this issue). From the matrix of form frequencies in successive intervals, two separate definitions seem appropriate (keeping in mind the limitations imposed by group or pooled data). These definitions of a bout are: 1) two or more successive intervals in which a given form was present, 2) the presence of two or more forms in one or successive intervals.

The frequency per interval plots for the different form categories (Figure 21) give some indication of the "density" with which forms occurred but, due to the limits imposed by the 15 second interval durations, do not allow an assessment of bouting tendencies.

By looking at "sessions" (defined as sequences of one or more intervals, all of which had at least one occurrence of a given form) the arbitrariness imposed by the 15 s duration time units can be circumvented in part. Figure 22 shows the number of forms and intervals per session for each common category recorded in the Point au Gaul sample. From these histograms a basic assessment of temporal clustering of the different form classes can be made. Both 4B and 6A forms never occurred singly while 3E and 4D forms occurred singly only once. Only three single occurrence sessions of 3A were

Figure 21. Histograms showing form frequencies per 15 s interval for each category recorded in sample 1

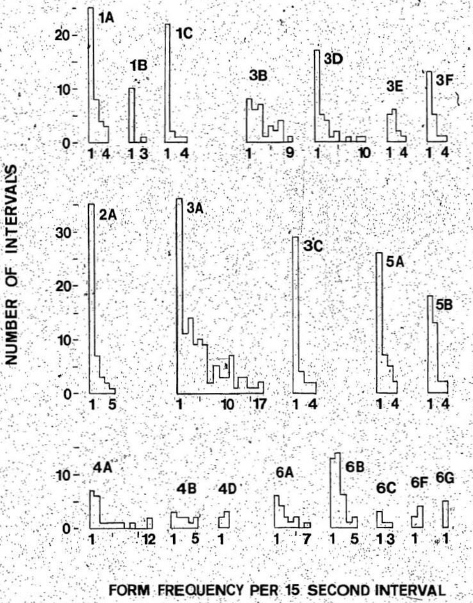
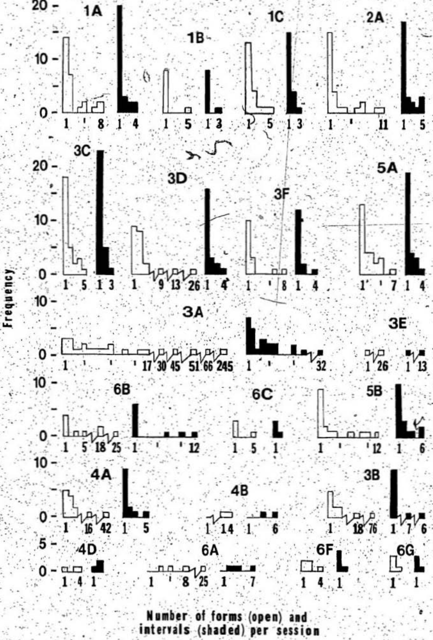

NUMBER OF INTERVALS
FORM FREQUENCY PER 15 SECOND INTERVAL
1A
1B
1C
3B
3D
3E
3F
0
10
20
1 4
1 3
1 4
1 9
1 10
1 4
1 4
2A
3A
3C
5A
5B
0
10
20
30
1 5
1 10 17
1 4
1 4
1 4
4A
4B
4D
6A
6B
6C
6F
6G
0
10
1 12
1 5
1
1 7
1 5
1 3
1
1

Figure 22. - Histograms showing the frequency and interval distributions per session for each category recorded in sample 1


Frequency
20
10
0
1A
1
8
1
4
1B
1
5
1
3
1C
1
5
1
3
2A
1
11
1
5
3C
1
5
1
3
3D
1
9
13
26
1
4
3F
1
8
1
4
5A
1
7
1
4
3A
1
17
30
45
51
66
245
1
32
3E
1
26
1
13
6B
1
5
18
25
1
12
6C
1
5
1
5B
1
12
1
6
4A
1
16
42
1
5
4B
1
14
1
6
3B
1
18
76
1
7
6
5
4D
1
4
1
6A
1
8
25
1
7
6F
1
4
1
6G
1
1
Number of forms (open) and
intervals (shaded) per session

observed. One session of 32 intervals duration (8 minutes) consisted of 245 repetitions of 3A forms. In contrast to these, 1B and 6C forms always occurred singly except for one bout of 5 repititions over 3 intervals for 1B and one bout of 5 repetitions over 2 intervals for 6C. Most form types occurred both singly and in bouts.

Differences among the forms in the distributions of intervals per session and number per session do not seem to be simply functions of their overall frequencies. Some forms seem to have a higher tendency to occur in bouts than others. A statistical analysis of the distributions shown in Figure 19 (p. 65) cannot be done as there is no measure of within or between individual variability.

(2) Killer whale - noise playback. The pilot whales had transited past the boat in a tight group. During the pre-playback period the group was approximately 70 m away with some animals moving toward the boat again. During the first 30 s of the killer whale broadcast, surface activity increased and by the end of the 60 s playback the whole group had turned and was heading toward the boat. During the noise broadcast, the whales turned back to their original heading. The pod continued lolling until the end of the post playback period. One spyhop (vertical raising of the head out of the water) was observed while the animals

were lolling. White-sided dolphins were also in the area during the playback (one was observed to leap completely out of the water shortly after the noise ended).

Vocally, the only apparent differences in the phonations recorded before and after the playback were that 1C, 6G, 4C and 6F forms only occurred after the playback (Table 3). The median number of phonations per 15 s interval increased from 7 (range 3 – 10) to 9 (range 5 – 15) after the playback.

(3) Killer whale playback (Trial #1). During the pre-playback period, the group of approximately 25 pilot whales travelled to a position about 100 - 150 m away from the boat. During the playback, no change in the pods behavior was observed. As soon as the playback ended, three or four whales surfaced less than 50 m away from, and facing the boat and loudspeaker. This type of "scouting" behavior has also been reported by M. Caldwell and Caldwell (1964), Evans and Dreher (1962), and Morgan (1979), for other delphinid species. Herman and Tavolga (1980) have suggested that scouting behavior is typical of dominant individuals in a hierarchial social group. In this instance, the animals involved were not noted to have been larger animals as reported by Morgan (1979).

Clicks, probably echolocation, were recorded during all

Table 3. Frequency of common forms per 15 s interval recorded before and after the broadcast of killer whale phonations and noise (sample 2).

Common	15 second interval																				
Code	10	9	8	7	6	5	4	3	2	1	PB	1	2	3	4	5	6	7	8	9	10
5A	1			1		1	2		1			1			1	1					
2B	1		3	3	2	4	4	3	2	2		2		2	3	2	4	2	4	1	7
1B	3	2							1			4	2	1	1		4	1	3		2
4A	1					1							1								
3D		1	2	1	1	1	1	2	3	2			1	1	1	1			1	2	4
3C			2	1	1	1		2					1	1		2	1				
6D					1		1	1													1
3A						1				3						2	1	1			
2A						1							1						1		1
4B										1										1	
1C												1	1							1	
6G												1						1			
4C															2		2	2	1	2	
6F																2	1	2	1	1	

pre- and post-playback intervals. After the 2.5 minute post-playback period, more animals were observed within 50 - 60 m of the boat.

Phonations recorded after the playback were primarily of types 6B and 2A, neither of which were recorded prior to the broadcast (Table 4). There was also an increase in the number of 4A forms recorded after the playback. The median number of phonations per 15 s interval increased from 1 (range 0 - 6) to 10 (range 1 - 19) after the broadcast. Some increase in the number of recorded phonations might have been expected to result from the movement and orientation of some animals toward the boat.

(4) Killer whale playback (Trial #2). Before the broadcast, the same pod of whales moved toward the boat to a position about 100 m away, from a position 200 m away, and started lolling. No observable change in behavior occurred during the playback or post-playback periods.

There was no obvious vocal reaction to the playback. Some forms, 2A and 4B, were only recorded after the playback but not until after 45 and 30 s respectively (Table 5). Median vocal rates before and after the playback were 3.5 (range 0 - 13) and 4.5 (range 2 - 9) phonations per 15 s interval respectively.

Table 4. Frequency of common forms per 15 s interval recorded before and after the broadcast of killer whale phonations (sample 3).

Common	15 second interval																				
Code	10	9	8	7	6	5	4	3	2	1	PB	1	2	3	4	5	6	7	8	9	10
3A	3	1	1									1		1	2						
1B	2	2	1									1						1	3	4	
4A	1	2										2	3			3	10	3	5	3	
6D							4	1													
3C								2				1									
4C												6	7	6	7	2		2			
6B												3	4	4	3	1	4	1		2	1
2A																	5	2			

Table 5. Frequency of common forms per 15 s interval recorded before and after the playback of killer whale phonations (sample 4).

Common										15 second interval											
Code	10	9	8	7	6	5	4	3	2	1	PB	1	2	3	4	5	6	7	8	9	10
1B	3			1	1			5	9	6		1	1								1
3C	3							6	4	1											
4C		2		3													4	6	2	4	4
6D			1		1		1	1		1		1	1	2	1	1					
1A			1											1	2		1				
6B				1											1	1					
2A																	2	1	1		
4B														6						1	

(5) Noise playback. A different group of whales (i.e. spatially separate) moved past the boat, within approximately 50 m of the loudspeaker. As they passed nearest the boat, the noise was broadcast. During the playback, no observable changes in the direction or the rate at which the animals were travelling was noticed. There was no observable reaction to the noise by the whales.

Vocally, 4B forms accounted for 62% of all vocalizations after the playback yet these phonations had not been recorded prior to the broadcast (Table 6). The median number of phonations per interval was 9 (range 3 - 13) before and 7 (range 3 - 15) after the playback.

(6) Constant tone playback. Several groups of whales were near the boat during the pre-playback period. The group closest to the loudspeaker was about 100 m away. During the playback, some of these animals oriented towards the boat but did not approach until after the broadcast had ended. During the post-playback period, some lunging was observed for approximately 15 - 30 s. The presence and behavior of large numbers of gulls indicated that the whales were probably feeding at that time. The animals then moved away near the end of the post-playback period.

No vocal reaction to the playback was apparent although form type 2A only occurred after the playback (Table 7).

Table 6. Frequency of common forms per 15 s interval recorded before and after the broadcast of noise (sample 5).

Common	15 second intervals																				
Code	10	9	8	7	6	5	4	3	2	1	PB	1	2	3	4	5	6	7	8	9	10
6D	2							1	2	2		2	1								
3C	1	2	2	2		3		2	1	3							2				
6B		3	5	5	3	3	3	2	2	1		8	3	1	4						
4A		4	3		1		1	3	2	2		4									
1B			1	6	2	1	1	2	2				1						1		
5C						2	1														
2A									3								1				
4B												1		4	4	3	8	7	6	8	5

Table 7. Frequency of common forms per 15 sec interval recorded before and after the broadcast of a constant tone (sample #6).

Common	15 second interval												
Code	5	4	3	2	1	PB	1	2	3	4	5	6	7
2A	5	3								1		6	3
3D	1			1			2			1	1		
5B	1	1											
1B	1	1	1		1								
3A			2	2			3			1	1	4	3
3B					1		3	3	1	4	1		
2B							1	5	1		1		

The median number of phonations per interval was 3 (range 2 - 8) before and 7 (range 2 - 10) after the playback.

(7) Variable tone playback. Several groups of pilot whales, totalling about 200 animals, were in the area during this sample. One group of about 30 animals, composed of proportionally more large animals than were usually observed, travelled toward the boat and were lolling on all sides of the boat during the pre-playback period. Just as the whales began moving away from the boat at a distance of approximately 40 m, the playback began. All animals submerged during the playback and did not resurface until half way through the post-playback period. By the end of the playback, more groups were heading in the general direction of the boat and the original group was again on all sides of the boat. At that time these animals were not vocalizing (Table 8). The only change in the types of vocalizations was the presence of 4A forms shortly after the playback. These phonations were not recorded during the pre-playback period. The median number of phonations per interval was 9 (range 0 - 25) before and 4.5 (range 3 - 19) after the playback.

After the post playback period, there were an estimated 100 pilot whales within a 70 m radius of the boat, yet no sounds were recorded. Two minutes and 30 seconds after the

Table 8. Frequency of common forms per 15 second interval recorded before and after the broadcast of a variable tone (sample #7).

Common	15 second interval																				
Code	10	9	8	7	6	5	4	3	2	1	PB	1	2	3	4	5	6	7	8	9	10
3B	1	5	6	3				1													
2A		7					1	3	3	1			1	8	4	3	1				
3D				1			1	1	1	1		1	2	3	4	8					
4B						1	7	9	4	1											
3A							5	3	2	7		8	3	6	1	2					
6I							1	5	1	2											
6D								2	1	1											
6F								1	1												
2B									3												
4A														2	6	1	2				

post-playback period, a second 60 s variable tone was broadcast to the whales that had by that time moved to a distance of approximately 100 m. During this second post-playback period, the whales again approached the boat to within 40 m then turned around and swam off in the opposite direction. At the same time, another group was approaching from the other direction. As these animals got closer, "typical" vocalization rates were again recorded.

The vocalizations recorded after the second playback were classified as 2A (N=7), 3D (N=2), 4B (N=18) and 3A (N=1).

(8) Stranded individual. These recordings were made on 14 July 1979, approximately 8 hours after the mass stranding of 135 Pilot whales at Point au Gaul. Of these animals only two were vocalizing by this time although others were said to have been vocalizing on the beach earlier. The vocalizations of these stranded individuals may have been distorted due to the physical and emotional stress of having their bodies out of the water.

The two vocalizing animals were immature females lying next to each other on the beach. Both were part of a group of 28 animals that had refloated themselves and/or been successfully towed off the beach but came ashore about 0.5

km from the original stranding location. One of these (field #18, 267 cm long) vocalized very rarely and only four very faint phonations were recorded from this animal. Two of these were too faint for classification while one sounded like a 3A form (similar to 3A/831) and another was very similar to the 3B/832 forms.

The other vocal individual (field #19, 221 cm long) vocalized fairly frequently, emitting 47 vocalizations in 14.3 minutes (median onset-onset interval = 8.3 s, inter-quartile range 3.90 - 25.6). Twenty-nine (62%) of these vocalizations were initially coded as one type (832) and six forms were of a similar category (833). Eleven other initial form categories were recorded once or twice in this sample (Table 9). When these forms were recoded using common code categories, the two most frequent form types were pooled resulting in 38 3B forms (81%).

Parts of this recording (Tape PaG-T4) were broadcast to several of the more active animals at the original stranding site but no vocal or physical responses were observed.

A 1.5 minute section of tape PaG-T4, containing four 3B/832 phonations, was played back to the same animal that originally produced the vocalizations (i.e. animal #19). The recording of the playbacks and animal 19's vocalizations during and between playback trials (Tape PaG-TA) has 170

Table 9. Frequency of form categories recorded from a stranded animal (sample 8).

	Recording Tape			
	PaG-T4		PaG-TA	
Form Code	N	%	N	%
1C/815	2	4	35	21
3A/831	1	2	8	5
3B/832	29	62	74	44
3B/833	6	13	9	5
3D/834	1	2	5	3
3B/835	1	2	4	2
3E/839	2	4		
2B/841			1	1
4A/844	1	2	2	1
5A/858	2	4		
6E/860			4	2
3B/861			1	1
6B/862			5	3
6B/863			1	1
6G/865			1	1
6G/866			1	1
6G/867			1	1
3B/868	2	4	6	4
6E/880			3	2
6E/881			1	1
3F/892			4	2
3A/895			2	1
Totals	47	100	170	100

codable phonations (plus the 15 playback phonations) over a duration of 12.2 minutes (median = 3.05 inter-quartile range 1.10 - 5.45). As vocalizations increased from 42 in the first 12 minutes of PaG-T4 to 168 in the first 12 minutes of PaG-TA, the playback of 25 phonations had an obvious general faciliatory effect on the vocalization rate of this individual ($p < 0.0001$, Mann-Whitney U test).

In addition to this general effect, most of the playback phonations were immediately followed by vocalizations from animal 19 (median onset-onset interval between playbacks and next "live" vocalization = 0.70 s, inter-quartile range 0.60 - 2.00). Superimposing two sequences of events will result in shorter between event intervals than either sequence taken separately. To test that the playback phonations were not randomly superimposed on the animals vocalization sequence, the intervals between the onsets of playback phonations and succeeding live phonations were compared with the intervals between the onset of playbacks and preceeding live phonations (median = 3.70, inter-quartile range 1.50 - 6.90). Intervals between playbacks and succeeding phonations were significantly shorter than between playbacks and preceeding phonations ($p < 0.02$, Mann-Whitney U test). In addition to the overall increase in vocalization rate, vocalizing occurred in response to each playback phonation.

Seventy-four of the vocalizations recorded during the playback sample were 832 forms. Ninety-four (55%) of the 170 phonations were coded as common form category 3B. The second most frequent form type in this sample was 1C/815, accounting for 35 (21%) of all phonations coded. In total, 21 different initial form categories and 10 common form categories were recorded in this sample.

Of the vocalizations immediately following the 15 3B/832 playbacks, thirteen were 3B/832 forms while one was a 3B/831 form and one a 3A/831 form. Using the percent frequency of 832 forms during the playback trial, the probability of randomly selecting 13 or more 3B/832 vocalizations in 15 trials can be calculated to be $p = 0.0008$ ($p < 0.01$, Sign test for matched pairs). The broadcast seems to have stimulated the animal to emit acoustically similar 3B/832 vocal signals to the playback stimuli.

Comparison of vocalizations from the stranded individual and Point au Gaul pod.

After the initial mass stranding at Point au Gaul, an estimated 65 animals were either towed off the beach or swam off on the next high tide. Of these, 65 animals, 28 restranded, including the sample 8 individual. The Point au Gaul pod (sample 1) was estimated to consist of about 30 individuals, some with rope around their tail flukes from being towed off the beach earlier. This evidence strongly suggests that the stranded individual (sample 8) was a member of the same large herd as the pod recorded in sample 1.

Not all of the vocalizations recorded from the stranded individual, however, can be classified into the categories created from the sample 1 pod. Eight of the 23 different initial form categories (815, 831, 834, 839, 844, 858, 892, & 895) are virtually identical to forms recorded in sample 1. The 5 3B variants (832, 833, 835, 861, & 868) accounted for 61% of the stranded animals vocalizations and though not identical, are similar to the sample 1 3B forms and exhibit the same variations. The unique 841 form recorded during the playback was different from all sample 1 forms. The other 9 samples 8 forms were all multihump contours (6B/862, 6B/863, 6G/864, 6G/865, 6G/866, 6G/867, 6E/860, 6G/880, & 6G/881). These multihump forms were also recorded during the playbacks and accounted for less than 9% of the total number of codable phonations recorded from this animal.

Comparison of playback samples

The sample 3, 4, and 5 phonations, all recorded within two hours on 18 October, 1980, exhibit the most similarities. That samples 3 and 4 are similar is not surprising as they were recorded from the same pod and the same broadcast stimuli was used. Sample 5, however, was recorded from a different group that was less than 1 km away and was heading in the same direction as the sample 3 and 4 pod. The greater similarity between the phonations from these two groups suggests that they may have both been part of a larger herd that had dispersed to feed, as has been observed for Pacific pilot whales (Brown & Norris, 1956) and other herds of pilot whales in the same bay of Newfoundland (Sergeant, 1962; and personal observations).

Pre and post-playback samples were compared on the basis of: 1) percent simple versus complex phonations, 2) percent by Taruski's (1976) categories (level, falling, rising, up-down, down-up, and multihump contours), 3) percent by common form categories, and 4) percent with rising, falling or level frequency attacks.

The most appropriate samples for comparison of playback effects were 3 and 4 as these were recorded from the same animals and the same playback stimulus (killer whale vocalizations) was used.

On the basis of Taruski's (1976) finding that "high arousal was associated with a high proportion of complex whistles" (p. 367), the common categories were collapsed into the same simple (level, falling and rising) and complex (up-down, down-up, and multi-hump) whistle categories used by Taruski (Figure 23). In both the killer whale playbacks to the same pod, (samples 3 and 4) the percent simple whistles decreased by at least two-thirds after the broadcast.

To determine if this consistency could be related to any of the six component Taruski (1976) categories, the common codes were collapsed again (Figure 24). Each of the six categories showed the same trends after the two killer whale broadcasts (i.e. categories 1 and 3 decreased, and categories 2, 4 and 6 increased after the killer whale broadcasts while no category 5 forms were recorded before or after the broadcast in either trial).

In an attempt to relate these trends to the common category codes developed independently of Taruski (1976), the samples were compared on the basis of the percent of the total number of phonations attributable to each of the common codes. In both the killer whale playback samples to the same pod, 1B forms decreased in relative frequency (from 25% to 9% and 49% to 7%) as did 3C forms (10% to 1% and 27% to 0%) while the 2A forms were only present after the broadcasts (0% to 7% and 0% to 9%) and the 4C forms increased in relative frequency (0% to 29% and 10% to 43%).

Figure 23. Percent simple (open) and complex (hatched) phonations recorded before and after each of the seven playbacks to pods at sea.

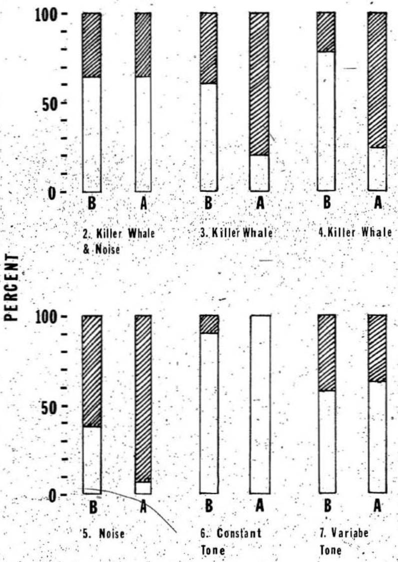
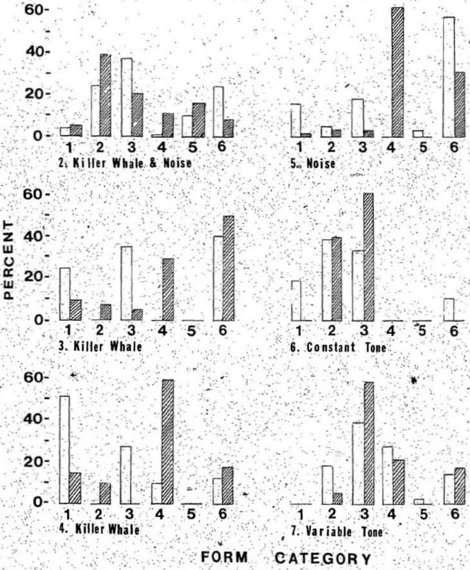

100
50
0
B
A
B
A
B
A
2. Killer Whale & Noise
3. Killer Whale
4. Killer Whale
PERCENT
100
50
0
B
A
B
A
B
A
5. Noise
6. Constant Tone
7. Variabe Tone

Figure 24. Percent of phonations recorded before (open) and after (hatched) broadcasts to pods at sea of the seven playback stimuli. Phonations divided into Taruski's (1976) categories.


60-
40-
20-
0-
1 2 3 4 5 6
2. Killer Whale & Noise
1 2 3 4 5 6
5. Noise
PERCENT
1 2 3 4 5 6
3. Killer Whale
1 2 3 4 5 6
6. Constant Tone
1 2 3 4 5 6
4. Killer Whale
1 2 3 4 5 6
7. Variable Tone
FORM CATEGORY

Sample 2 (killer whale-noise playback recorded 10 days prior to samples 3 and 4) also exhibited a decrease in 3C forms (from 10% to 5%) and an increase in 2A (from 1% to 3%) and 4C forms (from 0% to 9%). In this case, however, 1B forms increased from 9% to 19% after the broadcast (see Table 10).

The consistent changes in the phonations after the broadcast of killer whale phonations to pilot whales were a result of the changes in the relative frequencies of the common form codes, 1B, 3C, 2A and 4C. Changes in the relative frequencies of the first four Taruski (1976) categories are consistent with changes in the component common code forms. Changes in the level frequency forms (category 1) were totally due to changes in 1B form frequencies and changes in falling frequency forms (category 2) were totally due to changes in the frequency of 2A forms. Decreasing frequency forms (category 3) decreased in frequency in both samples 3 and 4 due to decreases in the relative frequency of 3C forms, this decrease being augmented in sample 3 by decreases in the frequency of 3A forms. Up-down forms (category 4) increased in relative frequency in sample 3 due to increases in both 4A and 4C form frequencies and in sample 4 due to increases in the frequencies of both 4B and 4C forms.

The increase in complex phonations after the playback of

Table 10. Common form code frequencies as percent of total phonations recorded before (B) and after (A) the playbacks to pods at sea (samples 2 to 7).

Common	Sample Number											
	2		3		4		5		6		7	
Code	%B	%A	%B	%A	%B	%A	%B	%A	%B	%A	%B	%A
1A					2	9						
B	9	19	25	9	49	7	17	3	19	0		
C	0	3										
2A	1	3	0	7	0	9	3	1	38	22	16	26
B	36	28							0	17	3	0
3A	6	4	25	4					19	26	18	30
B									5	26	17	0
C	10	5	10	1	27	0	18	3				
D	21	12							10	9	5	27
4A	3	1	15	28			18	5			0	17
B	1	1			0	15	0	62			24	0
C	0	9	0	29	10	43						
5A	9	3										
B									10	0		
C							3	0				
6B			0	22	2	4	31	22				
D	4	1	25	0	10	13	8	4			4	0
E											10	0
F	0	7									2	0
G	0	2									3	0

killer whale sounds was accountable by the increase in the frequency of 4C (complex) forms and the decrease in the frequency of 1B (simple) and 3C (simple) forms, which in both samples 3 and 4 was greater than the increases in the frequencies of 2A (simple) forms.

A comparison of pre- and post-playback phonations recorded in sample 5 (noise playback) also reveals an increase in complex phonations after the playback. As in samples 3 and 4, form categories 1 and 3 decreased in relative frequency but unlike the killer whale playbacks, so did category 6. The increase in complex whistles after the noise playback was almost entirely due to a sharp increase in category 4 forms (0% before, 62% after). The increase in type 4 forms was completely due to an increase in 4B forms (0% to 62%). In this sample 4C forms were not present and 4A form decreased from 18% to 5%. As observed after the killer whale broadcasts (samples 3 and 4), 1B forms decreased (17% to 3%) as did 3C forms (20% to 3%) after the noise playback. In sample 6 (constant tone playback), no obvious change in vocalization was observed except for a slight increase in 3A, 3B, and 3D forms. In sample 7 (variable tone playback) category 6 forms (6D, 6F, 6I, and 6H) were not heard after the broadcast.

The temporal clustering of phonations and the rapid changes in the type and number of phonations recorded in sample 1 suggests that some of the pre/post playback differences in phonations could be simply due to the 60 s break in the samples during the broadcast of the playback stimuli.

The consistent changes in relative frequency of 1B, 3C, and 4C forms after the two killer whale playbacks may have been responses to the killer whale broadcast, however, phonations recorded after the broadcast of noise to another pod showed some similar changes.

Clustering of common categories

Very little similarity is observed among the dendograms showing clustering of the common form categories for the different recording samples.

In sample 1, the highest temporal association was between form categories 2A and 4B (r=0.618, Figure 25). Components of these categories, 126 and 143 forms, were clustered using the original form codes with a similarity index of 0.953.

Even when the two killer whale playback samples to the same group of whales (samples 3 and 4) was compared, no similar clusters were observed.

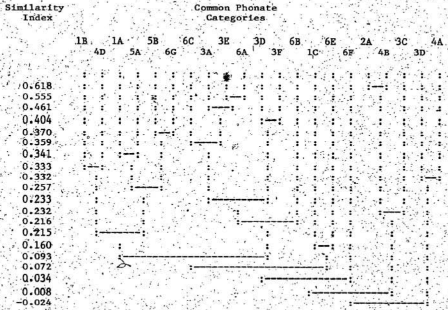


Figure 25. Dendogram showing average linkage clustering of common forms recorded at Point au Gaul (sample 1). The similarity index is a relative measure of temporal association among forms. (see page 27 of text).

When clustering was done on the phonations recorded before and after the broadcasts separately, differences were observed within some samples but again there was no similar clustering when the before broadcast or after broadcast clusters were compared among samples.

Temporal relationships

Examples will be used to illustrate the way in which some form categories were associated and the way in which some phonations changed with successive repetitions.

6B forms - All twelve of the shorter 186 forms occurred close to 166 forms, usually at the start or end of a 166 bout.

INTERVAL	127											138
FORM 186	2	1										1
FORM 166	1	2	3	2	2	3	2	1	2	2	1	

INTERVAL	163									172
FORM 186	2		2			1		1	2	
FORM 166		1		2	2	1	1			3

Prior to interval 127, no 186 forms were observed.

Both of the longer 169 forms occurred in the middle of a 166 bout.

INTERVAL	79							86
FORM 169		2						
FORM 166	5	2	2	2	1	2	1	1

Similarly in sample 3 (Killer whale playback), the shorter 361 forms occurred at the start and end of a 362 bout.

INTERVAL	1								10
FORM 361	2							1	1
FORM 362	1	4	4	3	1	4	1	1	

In sample 5 (Noise playback) where there were three 6B variants (561, 562 and 563). The ordering was as follows:

INTERVAL	9								1	PB	1			4
FORM 561	2	1												
FORM 562	1	4	5	3	2	3			1		8	3	1	4
FORM 563					1		2	2						

Again the shorter variant, 561, occurred near the start of a bout and the longer version, with the most inflections, occurred sometime during the bout. As the playback started before a 15 second bout occurred without a 6B form, it is not known if the bout continued through the playback until post-playback interval 4, or if it stopped before the broadcast and resumed again after the playback ended.

Five of the six sample 8 6B forms occurred within 43.8 s, again indicating a tendency for these signals to occur in bouts, however, the only 6B form with an extra inflection occurred at the start of this sequence. The two complex 6G/864 forms did occur within the duration of this bout and show some similarity to the sample 8 6B variants. The 6G/864 forms could be more complex variants of the 6B forms.

In the other sample with 6B forms, sample 4, there was only one variation present (462).

From these samples, recorded from different pods of whales, it appears that these forms (6B) usually have two or three versions. The shorter versions occur at the start of some bouts and occasionally at the end of a bout while the longer, more complex variants occur during the middle of bouts.

4B/143 - In both sessions of 143, the bout was initiated by three 3C/133 forms (Figure 14, p. 53). In the later 143 forms, the 133 form is preserved as the initial component. An intermediate form is present in the second bout (first 143 form, Figure 14-A, p. 53) but not in the first session (Figure 14-B, p. 53).

4A forms - Figure 11-A (p. 49) shows the way in which 4A forms and "similar" 3A/195 and 6B/166 forms occurred in a sequence. The first two of the 4A/187 forms seem intermediate in frequency between 6B/166 forms and the more "typical" lower frequency 187 forms that occurred later in the sequence.

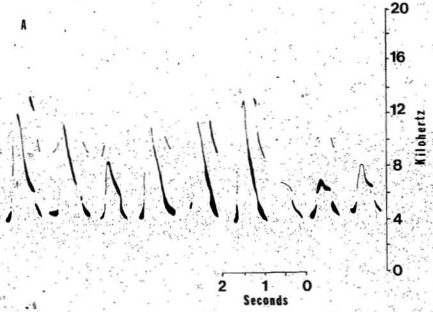
4B forms - Figure 11-B (p. 49) shows the last of a sequence of 4B forms as they occurred after the second variable tone broadcast. Three variations are present in this sequence. All three occur simultaneously at the start of the sequence, indicating that they are produced by three different individuals. With the exception of the first form coded 747 in the final sequence of 747 forms, the three categories are very distinct. The 748 and 742 forms occurred at fairly regular intervals and were perhaps simultaneous bouts by two individuals.

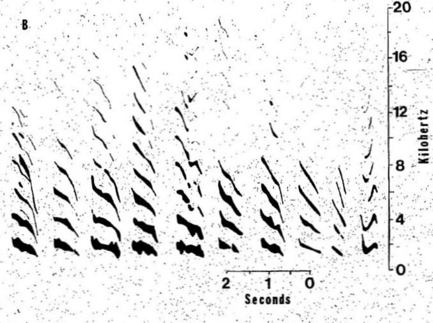
The overall similarities among the three categories and their occurrence in the same interval and probably the same context, suggests that they are the same basic signal (i.e., have the same semantic value to the whales). The last series of 749 forms shows a "tapering off" of this form at the end of the bout.

Figure 26-A shows a series of 4B/542 forms. Each repetition is slightly different than the adjacent ones. Differences include the extent of the frequency sweep, and the "smoothness" of the form. In this case, the initial and terminal frequencies as well as the durations were quite constant.

Figure 26-B shows a sequence of 3B/792 forms. Again no two sounds are exactly alike. The first in the series has more frequency modulation than the successive repetitions. The final 792 form in this session was the only "double whistle".

Figure 26. Sequential repetitions of 4B/542 forms (A) and 3B/792 forms (B).


A
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

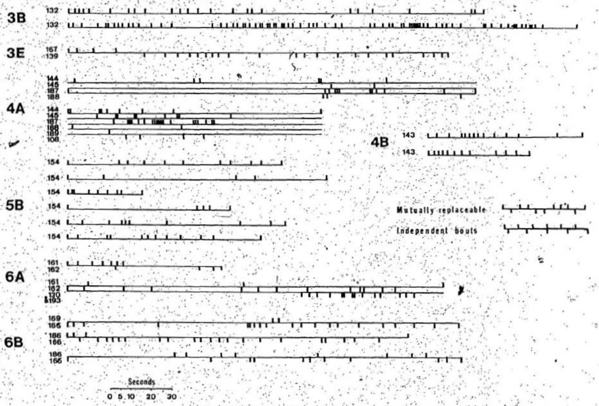

B
20
16
12
8
4
0
Kilohertz
2
1
0
Seconds

Some bouts were looked at in more detail by plotting the different categories of signal events along a time dimension (Figure 27). Figure 27 shows the actual temporal arrangements of several common category bouts. It was felt that these graphs might indicate if variants within categories were produced by a single animal or two or more animals. If variations were mutually replaceable in sequences (i.e., there was a regular pattern of repetitions when all variations where taken together) it could be argued that they were emitted by a single animal (or an antiphonal duet). Alternatively, variations exhibiting regular independent repetition rates could be considered to have emanated from more than one individual (see Figure 27).

None of the bouts plotted exhibit very regular repetition rates either when the variants are considered separately or together. The 3B, 5B, and 4B bouts, all involving only a single variation, illustrate the irregularity of interval lengths between repetitions. Rather than occurring at regular intervals, 3B/132 and 4B/143 forms seem to follow "burst patterns" in which repetition rates peak and then fall off. The 5B/154 forms do not conform to this pattern.

Within the multi-variant categories, there also seem to be some bursts. The 4A forms show very tight clusters,

Figure 27. Sequential repetitions of several common form categories (from sample 1) showing the temporal relationships among the component form class(es). Vertical bars indicate the time of each occurrence for the form class identified on the left (all forms are treated as though they had a duration of one bar width). Idealized schemata of mutually replaceable and independently bouted variants is represented on the right.


3B
132
132
3E
167
139
4A
144
145
187
188
144
145
187
188
189
108
4B
143
143
5B
154
154
154
154
154
154
Mutually replaceable
Independent bouts
6A
161
162
161
162
130
&193
6B
169
166
186
166
186
166
Seconds
0 5 10 20 30

however, it is impossible to determine how many individuals were involved in producing these sounds.

The 6A forms show some bursting when considered together whereas the 3E forms seem to simply shift from one form to another.

The 6B variants exhibited the closest pattern to that expected from mutually replaceable events. For these signals, perhaps the emittance of longer, more complex variations (e.g., 169), rather than increasing repetition rates, conveys increased arousal or intensity.

Discussion

Repertoire size

From his review of studies of the signal repertoires for various species, Wilson (1972) concludes that "even the most highly social vertebrates rarely have more than 30 - 35 separate displays in their repertoire" (p. 56). Hailman (1977) has suggested that most repertoire size estimates "probably underestimate the actual repertoires of information-transmitting behavioral patterns", (p. 263) also pointing out that "objectively defining the repertoire is difficult if not impossible" (p. 263).

Efforts to estimate the whistle repertoires of small numbers of captive and wild delphinids have resulted in species estimates of from 5 - 23 different contours, at times producing "widely varying results between and even within species" (Herman & Tavolga, 1980, p. 174). Studies of sounds recorded from short encounters with animals at sea are not likely to include the full complement of the species' vocal repertoire (Watkins, 1974). Busnel (1977) estimated that the number of signals in a delphinid species' repertoire would be roughly 30 - 40.

Of the 25 total common code categories, 17 were recorded from at least two different pilot whale pods. Only one category (2A) was found in all seven group samples. Twenty common code categories were obtained from one sample of 1410 phonations (Point au Gaul, sample 1) while 12 were recorded from a single individual (total sample size 217, sample 8).

The apparent asymptotic nature of Figure 2 indicates that even with an increased sample size most, if not all, of the sounds produced by this one group of pilot whales (Point au Gaul, sample 1) would fit into the existing common coding scheme, making it complete with 20, or slightly more, different signal types.

The number of abridged code categories was still increasing at 42 after 1406 sounds were coded, as was the number of original, initial code categories at 65 after 1410 phonations were coded. Including the playback samples recorded from five other pods, the total number of different signals increases to about 25, 60 and 120 for the common, abridged and initial coding methods respectively.

In addition to lumping and splitting decisions, there are two potential methodological causes for under or over estimating a species' repertoire size when categorizing animal signals primarily on the basis of an analysis of their acoustic properties. The use of very discriminating techniques can show "significant" differences between signals that are identical to the receiving animal. As

Green and Marler (1979) state:

> Every signal can vary along the dimensions that physically describe it. Variations in some, however, may fail to be perceived. Thus, not every bit of the signal-pattern information theoretically available is necessarily assessed or utilized by the receiver. (pp. 92-93).

In pooling distinguishable forms into the common form categories, it was felt that the differences in the component form classes might be "subtle" variations of the same signal that: a) conveyed information about the signaling animal's identity, b) were ignored by the receiving animals, or c) were not perceived by the receiving animals.

There also exists the danger of ignoring physical dimensions that are utilized by the receiving animals. Given that the Point au Gaul phonations were initially categorized into over 60 categories, it could be postulated that these variations are in fact different signals (i.e., have different "meanings" to the whales) and the repertoire of the pilot whale would number well over 100 (including the other samples). What must be considered before such a position is taken is the role of other factors; such as acoustic properties (e.g., amplitude contours, harmonic structure, etc.), production mechanism, perceptual mechanism, and context, in determining whether two sounds are the same or different. Frequency contours that seem quite different may have very similar amplitude contours. Alternatively, very similar frequency contours may have very different amplitude contours that allow the animals to perceive the sounds as discrete and interpret them properly (e.g., individual characteristics of amplitude variations in gannet calls, White & White, 1970).

The highly discriminating initial coding method was used only because it is easier to pool than to split previously coded categories. Undoubtedly the resulting number of signal types from this coding method is highly inflated. Theberge and Falls (1967) state:

> Communication can take place on two levels: universal and individual. Communication that is universal (occurring within the species in general) requires a symbolism that is the same throughout the species . . . Communication on the individual level may occur between animals that have learned to recognize individual traits in animals with which they are associated." (p. 335).

The abridged codes seem to reflect the natural groupings of the Point au Gaul sounds quite well but few sounds from the playback samples fit these categories. Although the observed between pod variability could reflect dialect differences, other possible explainations have not been ruled out. It could be that the common codes more closely represent this species' "universal" communication signals. Variations within these categories, perhaps as represented by the abridged or initial form codes, could encode information about the signalling animal's identity and correspond to nuances associated with communication at the "individual level". As the recordings analyzed in this study are from different contexts (post-stranding, playbacks of different acoustic signals, and stranding), it is also possible that the observed differences between pods were context related.

Although objectively defining the repertoire size is impossible, by presenting different categorization schemes and documenting the variability within categories, the subjectiveness of the classifications can be assessed.

Signal variablity

Three possible sources of variability exist for animal signals. These three types of variation are: 1) within individual variation 2) between individuals variation 3) between groups, or populations, variation.

Every emittance of a given signal by an individual need not be identical. Phonations from an individual may exhibit intrinsic variability, transitional variability (changes to a phonation with repetitions), ontogenetic variability and variation associated with dominance changes. Variability could also exist among signals, of the same type, emitted by an individual under different behavioral or environmental contexts.

Intrinsic variations have been found in the phonations of individual dolphins (Lang & Smith, 1965; Lilly, 1963) as have ontogenetic differences (M. Caldwell & Caldwell, 1972; 1979), and contextural differences (Lilly & Miller, 1961a, 1961b). In this study intrinsic variations were found in the vocalizations of a stranded individual and temporal or transitional variations were found in sequences of signals recorded from pods at sea.

Within a pod of whales, individuals' phonations might differ because of signature information in the signals (op cit), social context differences, or differences in the animals age (Caldwell & Caldwell, 1979). Sex or dominance class of the individuals may also underlie individual variation. Sex and social status related differences in dolphin phonations have not been studied, although reports of dominance systems in captive and wild bottlenosed dolphin groups are common (Herman & Tavolga, 1980). Differences in the vocalizations of gorillas (Fossey, 1972) and chimpanzees (Marler, 1976) have been correlated with social rank. In wolves, the vocalizations of adult males, adult females, and pups can be distinguished (Field, 1979). Gould (in press) states that sexually dimorphic vocalizations are most likely when the sexes differ in size, as they do in pilot whales.

Defense of females is also a likely correlate of sexually dimorphic vocalizations (Gould, in press) and pilot whales are thought to be polygynous (Sergeant, 1962).

Eight of the 23 different initial categories emitted by an immature stranded individual in this study were virtually identical to sounds recorded from other members of this animal's pod, despite the differences in recording contexts (i.e. stranded as opposed to free swimming). The majority of the signals emitted by this animal, however, were distinguishable from all sounds recorded from the pod at sea. As this was the only stranded individual to be recorded, it is impossible to know whether to attribute these differences to signature information, contextual differences or the age/sex class of this individual.

The observed between pod variability in recorded acoustic signals could be due to differences in the sample contexts, or dialect differences. If the differences were context related, they would have different meanings that reflect the different contexts in which they are emitted and could therefore be considered different signals. If over 90% of a pilot whales vocalizations are signature whistles, as reported by Caldwell and Caldwell (1965) for a group of five captive bottlenosed dolphins, then differences in the vocalizations recorded from different groups could also be due to individual signature whistle differences. In this study, 61% of the vocalizations produced by a stranded animal were of one type that was similar to, but not identical to phonations recorded from other members of the same pod at sea. As this stranded individual emitted a total of 23 distinguishable phonations representing 12 of the 25 total common code categories in a 26.5 minute sample, it is extremely unlikely that all of the different forms recorded from pods at sea were emitted by different individuals. Signature vocalizations may account for some unknown portion of the observed between pod differences but not all.

The differences observed in the vocalizations recorded from different pods could also be dialectic variations. Dialect differences in contour use by pods of killer whales have been reported by Ford and Ford (1981). Although Taruski (1976) found no regional differences between samples taken from two species of pilot whales in the frequency with which his seven contour categories occurred, regional variation and dialect differences could exist within the contour categories he used. In the recordings presented here, contextual differences related to the playbacks would be expected to be limited to the post-playback recordings. As comparisons of only pre-playback samples would show much of the total signal variance observed among these samples, the existence of dialects is suggested. The small sample sizes from these different pods and consequently the lack of within pod variability measures makes it impossible to test for the existence of dialects in this data.

The ability of bottlenosed dolphins to mimic (Caldwell & Caldwell, 1972, 1979) indicates that the mechanism for dialect development exists in at least this delphind species.

The common form categories devised exhibit considerable internal variability. Some of the differences within categories seem to be gradations while other within category variations are more discrete. In general, the more complex phonations (i.e. those with more frequency inflections and longer durations) exhibited more variability. Most forms with more than three inflections were unique (6G forms) or were variants of forms that usually had three or fewer inflections (e.g., 4A/189, 5B/165, 6B/169). The one category made up of similar forms with more than three inflections (6E) exhibited a lot of variation in the number of inflections but could be classified as similar on the basis of the relatively small frequency range of the component forms. Twelve types of signal variation were observed within form categories from a single pod. These include variation in, or the presence of: truncation, abbreviation, melodic frequency increments, pauses, reversals, frequency, initial inflection, terminal inflection, slope, double whistles, additional inflections, and harmonics. Five variants of one form class were recorded from the stranded individual (sample 8). These variants are not, therefore, necessarily individual variations and might encode contextual information.

For a given species, the perceived differences among signals with different "meanings" should be greater than the perceived differences amoung signal events with the same meaning (Marler, 1965). There is a tendency in studying animal communication to draw negative conclusions concerning the linguistic capabilities of non-humans based on findings of graded rather than discrete signals (Lieberman, 1977). Vocalizations that are acoustically graded need not be perceived as such. Discrete perception of acoustically graded signals has been found for human speech sounds (Eimas & Corbit, 1973; Eimas, Siqueland, Jusczyk, & Vigorito, 1971). Innate auditory templates have been postulated for some songbird species (Marler, 1970) but no evidence has been found that such specialized sensory mechanisms are operative in categorical speech perception (Studdert-Kennedy, 1981). Regardless of the mechanisms involved, catalogs of a species' graded signal repertoire must be subjected to perceptual experiments to determine their discreteness as signalling units.

It is common for publications on cetacean vocalizations to present "representative" sonograms of categorized signals (notable exceptions are Busnel & Dziedzic, 1966; Lang & Smith, 1965), implying stereotyped, discrete signals. Measures of variability are necessary for any comparisons between individuals, between age/sex classes, between groups, between populations, and between species. Such comparisons are essential if we are to understand the full significance of communicative signals.

Signal frequency

Schleidt (1973) points out that there are at least three possible different functions for high repetition rates for signals: (1) to make the signal more conspicuous (2) to exceed the noise in the channel, and (3) to achieve a cumulative effect over time which builds up until some critical threshold is reached in the receiver. The signals that occur with the highest frequency are expected to have a "tonic" effect and usually function in establishing social relations between communicants or to maintain such relationships.

Whistling rates in delphinids are reported to increase during stressful situations or when animals are excited.

These situations include being separated from familiar individuals, stranding or being injured (Herman & Tavolga, 1980). The Point au ~~Gaul~~ recording context might therefore be expected to have higher whistling rates than average. The Point au Gaul pod was estimated to be no larger than the other pods sampled although the number of animals recorded in each sample is not accurately known. The number of vocalizations per interval varied considerably in a non-normal fashion (Appendix C), in part due to the recording distance and direction. While these factors make statistical comparisons unjustified, the average number of phonations per minute was slightly higher for the Point au Gaul sample than any of the others. Any real difference in the mean phonation rate would probably be due to the high frequency of 3A forms which accounted for over 50% of the phonations recorded at Point au Gaul. The high frequency of these forms suggests that they may serve an analogous function to the contact calls of non-human primates.

Temporal clustering of phonations

Bouting in delphinids has received little attention. Lilly (1963) reported that calls were repeated many times "until an appropriate response was elicited" (p. 116). Pulsed sounds produced by narwhals have been found to occur with regular repetition rates (Ford & Fisher, 1978; Watkins, Schevill, & Ray, 1971). Ford and Fisher (1978) were able to identify 48 bouts of pulsed tones from their sample.

Repetition rates have been associated with quantitative information (Marler, 1965) possibly indicating motivational changes (Lemmon, 1977). Variation with successive repetitions of sounds, as was observed with some bouts by pilot whales, have been proposed to function in preventing habituation (Marler, 1969), but may also indicate qualitative changes. Specifically, the presence of more complex variants (usually with extra terminal inflections) within a sequence of phonations and simpler variations (i.e. fewer inflections) at the start and end of sequences, as found in this study, may indicate changing levels of arousal and/or changing signal intensity. Taruski (1976) found a correlation between complex whistles and high arousal. In this study complex whistles increased after the broadcast of killer whale phonations (sample 3 and 4).

Different bouting tendencies do seem to exist among the phonation categories and some forms occurred in burst patterns (repetition rate increased then tapered off). With few exceptions in the present study, sounds that are sometimes bouted may also occur as single events. The distinction between single events and slow bouts or between two short bouts and one long bout is, however, somewhat arbitrary (Machlis, 1977). Analysis of bouting in the vocalizations of pods of pilot whales is further complicated by the uncertainty of whether one or more animals are emitting the phonations.

Within samples, different forms were clustered together indicating temporal association, however, no consistent association between categories was found among samples.

Implications for future research

"The more variable the response or behavioral system under investigation, the more careful one must obviously be in making generalizations" (Fentress, 1967, p. 339). With respect to the present study, the high degree of variability in the signals recorded from pilot whales makes it very difficult to generalize to the species as a whole.

It is suggested that procedures employed in future field studies of a delphinid species' vocalizations should include time sampling proceedures that can detect bouting of signals. Variability of signals within and between groups of animals must be documented. The differences found among pods recorded in the same area indicate that taking small or random samples from many groups might result in an inability to categorize the recorded phonations (as found by Taruski, 1976) even when separate categories of sounds exist within groups. Analyzing sequences of signals provides important information on temporal associations among signals, temporal variability within signals, and evidence for individual variability within signals.

The sources of variability in the vocalizations recorded from different pods, as found in this study, must be determined. Although this study presents the largest sample of an odontocete species' vocalizations to date, in order to determine whether these differences are true dialects even larger samples from pods under natural conditions are needed. By recording pods for long periods, within pod variability, including contextual variability, can be assessed. Measurements of between and within individual variability are also essential. Analyzing sequential repetitions of phonations and temporally associated phonations that are acoustically similar can give valuable clues to within individual variability and between individual variability. More concrete measures of between and within individual variability are also needed, however, and must come from captive pilot whale studies.

References

Backus, R. H., & Schevill, W. E. Physter clicks, in: Whales, dolphins and porpoises. (Norris, K. S., Ed.). Berkeley: University of California Press, 1966.

Beer, C. G. Individual recognition of voice in the social behavior of birds, in: Advances in the study of behavior (Vol. 3, Lehrman, D. S., Hinde, R. A., & Shaw, E., Eds.). New York: Academic Press, 1970.

Bremond, J. C. Acoustic behavior of birds. in: Acoustic behavior of animals (Busnel, R. G., Ed.). Amsterdam: Elsivier, 1963.

Brooks, R. J., & Falls, J. B. Individual recognition by song in white-throated sparrows, I. Discrimination of songs by neighbours and strangers. Canadian Journal of Zoology, 1975, 53, 879-888.

Brown, D. H. and Norris, K. S. Observations of captive and wild cetaceans. Journal of Mammalogy, 1956, 37, 311-326.

Busnel, R.-G. Acoustic communication, in: How animals communicate (Sebeok, T. A., Ed.). Bloomington: Indiana University Press, 1977.

Busnel, R.-G., & Dziedzic, A. Acoustic signals of the pilot whale Globicephala melaena and of the porpoises Delphinus delphis and Phocoena phocoena. Whales, dolphins, and porpoises (Norris, K. S., Ed.), Berkeley: University of California Press. 1966.

Caldwell, D. K., & Caldwell, M. C. Sounds produced by two rare cetaceans stranded in Florida. Cetology, 1971, 4, 1-7.

Caldwell, D. K., & Caldwell, M. C. Cetaceans. in: How animals communicate (Sebeok, T.A., Ed.). Bloomington: Indiana University Press. 1977.

Caldwell, M. C., & Caldwell, D.C. Experimental studies on factors involved in care-giving behavior in three species of the cetacean family Delphinidae. Bulletin of the Southern California Academy of Science, 1964, 63, 1-20.

Caldwell, M. C., & Caldwell, D. K. Individual whistles contours in bottlenosed dolphins (Tursiops truncatus). Nature, 1965, 207, 434-435.

Caldwell, M. C., & Caldwell, D. K. Simultaneous but different narrow-band sound emissions by a captive eastern Pacific pilot whale Globicephala scammoni. Mammalia, 1969, 33, 505-510.

Caldwell, M. C., & Caldwell. D. K. Statistical evidence for individual signature whistles in Pacific whitesided dolphins, Lagenorhynchus obliquidens. Cetology, 1971, 3, 1-9.

Caldwell, M. C., & Caldwell, D. K. Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. Cetology, 1972, 9, 1-8.

Caldwell, M. C., & Caldwell, D. K. The whistle of the Atlantic bottlenosed dolphin (Tursiops truncatus) - Ontogeny. in: The behavior of marine animals Vol. 3, Cetaceans (Winn, H.E., & Olla, B.L., Eds.). New York: Plennum Press. 1979.

Caldwell, M. C., Caldwell, D. K., & Hall, N. R. Ability of an Atlantic bottlenosed dolphin (Tursiops truncatus) to discriminate between, and potentially identify to individual, the whistle of another species, the common dolphin (Delphinus delphis). Cetology, 1973, 14, 1-7.

Caldwell, M. C., Caldwell, D. K., & Miller, J. F. Statistical evidence for individual signature whistles in the spotted dolphin, Stenella plagiodon. Cetology, 1973, 16, 1-21.

Clark, C. W., & Clark, J. M. Sound playback experiments with southern right whales (Eubalaena australis). Science, 1980, 207, 663-665.

Conner, D. A. Dialect versus geographic variation in mammalian vocalizations. Animal Behaviour, 1982, 30, 297-298.

Cullen, J. M. Some principles of animal communication, in: Non-verbal Communication (Hinde, R. A., Ed.). Cambridge: Cambridge University Press, 1972.

Cummings, W. C., & Thompson, P. O. Grey whales avoid the underwater sounds of killer whales, Orcinus orca. U.S. Fish and Wildlife Service Fishery Bulletin, 1971, 63, 525-530.

DeGhett, V. J. Hierarchical cluster analysis, in: Quantitative ethology (Colgan, P. W., Ed.). New York: John Wiley and Sons, 1978.

Dormer, K.J. Mechanism of sound production and air recycling in Delphinids: Cineradiographic evidence. Journal of the Acoustical Society of America, 1979, 65, 229-239.

Dreher, J. J. Linguistic considerations of porpoise sounds. Journal of the Acoustial Society of America, 1961, 1799-1800.

Dreher, J. J. Cetacean communication: Small-group experiment. in: Whales, dolphins, and porpoises (Norris, K.S., Ed.) Berkely: Universith of California Press, 1966.

Eimas, P. D., & Corbit, J. D. Selective adaptation of linguistic feature detectors. Cognitive Psychology, 1973, 4, 99-109.

Eimas, P. D., Siqueland, E. R., Jusczyk, P., & Vigorito, J. Speech perception in infants. Science, 1971, 171, 303-306.

Eisenberg, J. F., & Kleinman, D. Communication in lagomorphs and rodents. in: How animals communicate (Sebeok, T. A., Ed.) Bloomington: Indiana University Press, 1977.

Evans, W. E., & Dreher, J. J. Observations on scouting behavior and associated sound production by the Pacific bottlenosed porpoise (Tursiops gilli, Dall). Bulletin of the Southern California Academy of Science, 1962, 61, 217-226.

Fehring, W. K., & Wells, R. S. A series of strandings by a single herd of pilot whales on the west coast of Florida. Journal of Mammalogy, 1976, 57, 191-194.

Fentress, J. C. Observations on the behavioral development of a hand-reared male timber wolf. American Zoologist, 1967, 7, 339-351.

Field, R. A perspective on syntactics of wolf vocalizations, in: The behavior and ecology of wolves (Klinghammer, E., Ed.). New York: Garland STPM Press, 1979.

Fish, J. F., & Vania, J. S. Killer whale, *Orcinus orca*, sounds repel white whales, *Delphinapterus leucas*. *U.S. Fish and Wildlife Service Bulletin*, 1971, *69*, 531-535.

Ford, J., & Fisher, H.D. Underwater acoustic signals of the narwhal (*Monodon monoceros*). *Canadian Journal of Zoology*, 1978, *56*, 552-560.

Ford, J., & Ford, D. The killer whales of B. C. *Waters*, 1981, *5*, 1-33.

Fossey, D. Vocalizations of the mountain gorilla (*Gorilla gorilla beringei*). *Animal Behavior*, 1972, *20*, 36-53.

Gautier, J.-P. Field and laboratory studies of the vocalizations of the Talapoin monkeys (*Miopithecus talapoin*). *Behavior*, 1974, *51*, 209-273.

Gould, E. Mechanisms of mammalian auditory communication. in: *Recent advances in the study of mammalian behavior*, (Eisenberg, J. F. and Kleiman, D. G., eds.). Special publication no. 7, The American Society of Mammalogists, in press.

Green, S. Physiological control of vocalizations in the Japanese monkey: Inferences from a field study. *Journal of the Acoustical Society of America*, 1973, *53*, 310 (Abstract).

Green, S. Dialects in Japanese monkeys: Vocal learning and cultural transmission of local-specific behavior? *Z. Tierpsychology*, 1975, *38*, 304-314.

Green, S., & Marler, P. The analysis of animal communication. in: *Handbook of behavioral neurobiology, Vol. 3, Social behavior and communication* (Marler, P., & Vandenbergh, J., Eds.). New york: Plennum Press, 1979.

Hafner, G. W., Hamilton, C. L., Steiner, W. W., Thompson, T. J., & Winn, H. W. Signature information in the song of the humpback whale. *Journal of the Acoustical Society of America*, 1979, *66*, 1-6.

Hailman, J. *Optical Signals*. Bloomington: Indiana University Press, 1977, 362 pp.

Harrington, F. H., & Mech, L. D. Wolf Vocalization, in: *Wolf and Man: Evolution in parallel* (Hall, R. L., & Sharp. H. S., Eds.). New York: Academic Press, 1978.

Herman, L.M., & Tavolga, W.M. The communication Systems of cetaceans, in: Cetacean behavior (Herman, L.M., Ed.). New York: Wiley Interscience, 1980.

Hickman, D. L., & Grigsby, E. M. Comparison of signature whistles in Tursiops truncatus. Cetology, 1978, 31, 1-10.

Kritzler, H. Observations on the pilot whale in captivity. Journal of Mammalogy, 1952, 33, 321-324.

Lang, T. G., & Smith, H. A. P. Communication between dolphins in separate tanks by way of an electronic acoustic link. Science, 1965, 150, 1839-1844.

LeBoeuf, B. J., & Peterson, R. S. Dialects in elephant seals. Science, 1969, 166, 1654-1656.

Lemmon, R. E. Bird song: An acoustic flag. BioScience, 1977, 26, 402-408.

Liberman, A. M. An ethological approach to language through the study of speech perception, in: Human ethology (von Carnach, M., Foppa, K., Lepenies, W., & Ploog, D., Eds.). Cambridge: Cambridge Univsity Press, 1980.

Lieberman, P. The phylogeny of language, in: How animals communicate (Sebeok, T. A., Ed.). Bloomington: Indiana University Press, 1977.

Lilly, J. C. Distress call of the bottlenosed dolphin: Stimuli and evoked behavioral responses. Science, 1963, 139, 116-118.

Lilly, J. C., & Miller, A. M. Sounds emitted by the bottlenosed dolphin. Science, 1961a, 133, 1689-1693.

Lilly, J. C., & Miller, A. M. Vocal exchanges between dolphins. Science, 1961b, 134, 1873-1876.

Machlis, L. An analysis of the temporal patterning of pecking in chicks. Behavior, 1977, 63, 1-70.

Marler, P. Communication in monkeys and apes, in: Primate behavior (DeVore, I., Ed.). New York: Holt, Rinehart and Winston, 1965.

Marler, P. Animal communication signals. Science, 1967, 157, 769-774.

Marler, P. A comparitive approach to vocal learning: song development in white-crowned sparrows. Journal of Comparative and Physiological Psychology, 1970, 71, 1-25.

Marler, P. Social organization, communication and graded signals: The chimpanzee and the gorilla, in: Growing points in etholgy (Bateson, P. P. G., & Hinde, R. A., Eds.). Cambridge: Cambridge University Press, 1976.

Marler, P. The evolution of communication, in: How animals communicate (Sebeok, T. A., Ed.) Bloomington: Indiana University Press, 1977.

Marler, P., & Tamura, M. Culturally transmitted patterns of vocal behavior in sparrows. Science, 1964, 146, 1483-1486.

McLeod, P. J., & Lien, Q. J. Recent strandings of pilot whales (Globicephala melaena, Traill) in Newfoundland. in preparation.

Morgan, D. W. The vocal and behavioral reactions of the beluga, Delphinapterous leuca, to playback of its sounds, in: Behavior of marine aniamals Vol. 3, Cetaceans (Winn, H. E., & Olla, B. L., Eds.). New York: Plennum Press, 1979.

Payne, R. S. and McVay, S. Songs of humpback whales. Science, 1971, 173, 585-597.

Pitocchelli, J. Song dialects, and vocal development of savannah sparrows (Passerculus sandwichensis labradorius, Howe) breeding in Newfoundland and the St. Pierre et Miquelon Islands. Unpublished M. Sc. thesis, Memorial University of Newfoundland, 1981.

Popper, A. N. Sound emission and detection by delphinids, in: Cetacean behavior (Herman, L. M., Ed.). New York: Wiley Interscience, 1980.

Rowell, T. E., & Hinde, R. A. Vocal communication by the rhesus monkey (Macaca mulatta). Proceedings of the Zoological Society of London, 1962, 138, 279-294.

Schleidt, W. M. Tonic communication: Continual effects of discrete signs in animal communication systems. Journal of Theoretical Biology, 1973, 42, 359-386.

Sergeant, D. E. The biology of the pilot or pothead whale

Globicephala melaena (Traill) in Newfoundlan waters. Fisheries Research Board of Canada Bulletin, 1962, 132, 84 pp.

Shalter, M. D., Fentress, J. C., & Young, G. W. Determinants of response of wolf pups to auditory signals. Behaviour, 1977, 60, 98-114.

Smith, W. J. Message, meaning, and context in ethology. American Naturalist, 1965, 99, 405-409.

Smith, W. J. The behavior of communicating. Cambridge, Massachusetts: Harvard University Press, 1977.

Sommers, P. Dialects in southern Rocky Mountain picas, Ochotona princeps. Animal Behaviour, 1973, 21, 124-137.

Steiner, W. W., Hain, J. H., Winn, H. E., & Perkins, P. J. Vocalizations and feeding behavior of the killer whale (Orcinus orca). Journal of Mammalogy, 1979, 60, 823-827.

Studdard-Kennedy, M. The beginnings of speech. in:Behavioral development. (Immelmann, K., Barlow, G. W., Petrinovitch, l., & Main, M., Eds.). Cambridge: Cambridge University Press, 1981.

Taruski, A. G. Whistles of the pilot whale (Globicephala spp.): Variations in whistling related to behavioral/environmental context, broadcast of underwater sound, and geographic location. Unpublished Ph.D. thesis, University Rhode Island, 1976.

Taruski, A. G. The whistle repertoire of the north Atlantic pilot whale (Globicephala melaena) and its relationship to behavior and environment. in: Behavior of marine animals Vol. 3, Cetaceans (Winn, H. E., & Olla, B. L., Eds.). New York: Plennum Press, 1979.

Theberge, J. B., & Falls, J. B. Howling as a means of communication in timber wolves. American Zoologist, 1967, 7, 331-338.

Thorpe, W. H. Vocal communication in birds. In: Non-verbal communication, (Hinde, R. A., Ed.) Cambridge: Cambridge University Press, 1972.

Treisman, M. Bird song dialects, repertoire size, and kin association. Animal Behavior, 1978, 26, 814-817.

Watkins, W. A. Bandwidth limitations and analysis of cetacean sounds with comments on "delphinid sonar: measurement and analysis" [K. J. Diercks, R. J. Trochta, & W. E. Evans, J. Acoust. Soc. Am. 54, 200-204, 1973]. Journal of the Acoustical Society of America, 1974, 55, 849-853.

Watkins, W. A., & Schevill, W. E. Listening to Hawiian spinner porpoises Stenella cf. longirostris, with a three dimentional hydrophone array. Journal of Mammalogy, 1974, 55, 319-328.

Watkins, W. E., & Schevill, W. E. Sperm whales (Physeter catedon) react to pingers. Deep sea research, 1975, 22, 123-129.

Watkins, W. A., & Schevill, W. E. Sperm whale codas. Journal of the Acoustical Society of America, 1977, 62, 1485-1490.

Watkins, W. A., Schevill, W. E., & Best, P. Underwater sounds of the Cephalorhynchus heavisidii (Mammalia: Cetacea). Journal of Mammalogy, 1977, 58, 316-320.

Watkins, W. A., Schevill, W. E., & Ray, C. Underwater sounds of Monodon (narwhal). Journal of the Acoustical Society of America, 1971, 49, 595-599.

White, S. J., & White, R. E. C. Individual voice production in gannets. Behavior, 1970, 37, 40-54.

Wilson, E. O. Animal Communication, Scientific American, 1972, 227, 53-60.

Wishart, D. Clustans user's manual (3rd ed.). Edinburgh University: Program Library Unit, 1978.

Appendix A

Cluster analysis formulae

Similarity coefficient formula:

$$\frac{(AD - BC)\ (AD - BC)}{(A+B)(A+C)(B+D)(C+D)}$$

where: A= number of attributes common to cases i and k;
B= number of attributes present in case i and absent in case k
C= number of attributes present in case k and absent in case i
D= number of attributes absent in both cases i and k

Average linkage (unweighted pair-group method) fusion of clusters:

Let P and Q be fused, then the similarity S(R,P+Q) between any cluster R and the new cluster (P+Q) is obtained from the transformation:

$$S(R,P+Q) = \frac{NP}{(NP+NQ)} \times S(R,P) + \frac{NQ}{(NP+NQ)} \times S(R,Q)$$

where NP and NQ are cluster sizes.

Appendix B. Frequency of common code phonations per sequential 15 s intervals with concurrent behavioral observations. Miscelaneous behaviors (Misc.): SH-spyhop; TU-turn; CR-crowd; OS-animal on side; LT-lobtail & flippering; Distance from boat (Dist.) < 50 m, LO-lolling, El-echolocation; + indicates behavior observed.

Common Form	15 second interval																										
& Behavior	1	2	3	4	5	6	*	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Misc.				SH				SH	CR							TU					TU						
Dist.	+	+	+	+	+	+																					
LO																					+	+	+				
EL	+				+	+					+	+		+									+	+		+	+
1A	1													1													
B	3	1	1																								
C	1																										
2A	1			1	1			1		1	1	2															
3A	11	6			6	3		1		11	3	16	8	7	7	1	1	3	9		1			2		2	
B								1																			
C			1	2				1		1	1			1												1	
D								2										1							1		
E																											
F	1				1					1																	
4A	2																										
B																											
D	2	2			1																						
5A	1	1	1								1		1			1		1									
B																											
6A																											
B																											
C																											
F	1																										
G																											

* Denotes a break in the recording. Other breaks in the recording sample correspond to the start of a new page in the table.

Appendix B (cont.). Frequency of common code phonations per sequential 15 s intervals with concurrent behavioral observations. Miscelaneous behaviors (Misc.): SH-spyhop; TU-turn; CR-crowd; OS-animal on side; LT-lobtail & flippering; Distance from boat (Dist.) < 50 m, LO-lolling, El-echolocation; + indicates behavior observed.

Common Form											15 second interval																							
& Behavior	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Misc.										TU						CR	CR	TU	TU															
Dist.											+	+	+	+																				
LO						+	+	+																+	+	+								
EL		+	+					+	+	+	+	+						+	+	+				+		+					+			
1A										4	2	1	1		1	2	1	3		1					1							2		
B										1		1																						
C									4						1																			
2A		1			1			2				1	1	2	2	1											1	1	4	3	1		1	1
3A	1	2	1	1	1	1			4	6	8	3	6	1	3	5	1	3	6	5			1	3										
B	5	1	3	3	2	3	1			3		1		3																				
C							1					1		3	1	1											1	2		1				1
D		2									1				2																			
E																																		
F			1												1																			
4A																																		
B																												2	5	4	1	1	1	
D																																		
5A	1		2								4		2		3	1																		
B														1		1																		
6A																																		
B																																		
C																																		
F																																		
G																																		

Appendix B (cont.). Frequency of common code phonations per sequential 15 s intervals with concurrent behavioral observations. Miscelaneous behaviors (Misc.): SH-spyhop; TU-turn; CR-crowd; OS-animal on side; LT-lobtail & flippering; Distance from boat (Dist.) < 50 m, LO-lolling, El-echolocation; + indicates behavior observed.

Common Form	15 second interval																																	
& Behavior	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
Misc.									SH													SH								SH	SH	SH	SH	
Dist.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+		+
LO		+	+	+						+	+	+		+	+	+																		
EL	+					+	+	+			+	+	+	+	+	+					+	+	+	+	+	+	+			+	+	+		+
1A	1	1				1						3	4	1			2		1	4				1		2					1		1	
B					1							1													1		1							
C			1	1		2					1	3	1			1	1		1			1						1						
2A	1	1		1		1				1		1								1	1	1	2	1			1							
3A	3	2	1	10	10	1	11	11	1	2	5	5	8	14	13	17	6	4	11	12	10	4	8	17	15	13	11	11	6	1	1	1		3
B														1					1															
C	1			1	1								1				1			1					1		1	5	3			1		
D			2							4	1	3	5		1					9	7	10			1		1	5	3			1		
E															2	2	1	2	4	2	1	1	2	3	2	1	3							
F				1			2												1	2	2	3			1									
4A							1																		1		1							
B																																		
D																																		
5A				1	1	1	2				1	2	2			1				1														
B	1		2	2	1	1	2	2										1		1				1	1	1								
6A			2	5	1		2	1					1	2	1	1			3	1	4	5	7	3	2									
B													3			1			5	4	2	2	1	2	1	1								
C																		1			1		1		3	2								
F																							2											
G							1																		1									

Appendix B (cont.). Frequency of common code phonations per sequential 15 s intervals with concurrent behavioral observations. Miscelaneous behaviors (Misc.): SH-spyhop; TU-turn; CR-crowd; OS-animal on side; LT-lobtail, & flippering; Distance from boat (Dist.) < 50 m, LO-lolling, El-echolocation; + indicates behavior observed.

Common Form	15 second interval																			
& Behavior	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14
Misc.											SH									
Dist.							+	+	+											
LO												+	+	+						
EL		+	+		+	+						+	+			+	+	+		
1A				1								2			1					
B																				
C									1								1			
2A		2	4	2	3				1											
3A	2		1	4						1	4									
B																				
C		4		1							1			2			1			
D			1					1	1					1	1		1			
E																				
F	1		1																	
4A			1	2													2			
B		3	5	2	3															
D																				
5A	2						1	1							3	1	1			
B																				
6A																				
B																				
C																				
F																	2	2		
G																				

Appendix B (cont.). Frequency of common code phonations per sequential 15 s intervals with concurrent behavioral observations. Miscelaneous behaviors (Misc.): SH-spyhop; TU-turn; CR-crowd; OS-animal on side; LT-lobtail & flippering; Distance from boat (Dist.) < 50 m, LO-lolling, El-echolocation; + indicates behavior observed.

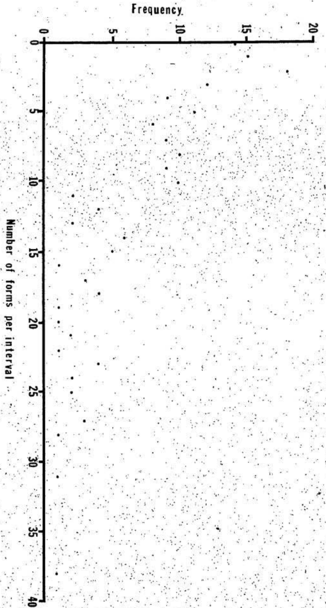
Common Form	15 second interval																														
& Behavior	115	16	17	18	19*	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Misc.																				OS												SH
Dist.																			+	+	+											
LO																																
EL	+	+	+								+	+	+	+	+		+	+	+	+	+	+	+					+	+	+	+	+
1A	3	1						1					1						1			1	3	1								
B																							1		1							
C	1							1				1			2	1			1			1	1						1			
2A		3			1			1					1									1			5	1	1					
3A	9	5	9	2	5	4	1	5	4	1		5	14	6	5		1	1	3	8		4	3	5	3	1		1	1	3	1	
B						2														2												
C		4		3	1	1	1					1				1										2						
D				1	1								1							3												
E		1																														
F													1	1									1		4	2						
4A		1												2			2				7	3	6		1	2						
B																																
D	2	1																														
5A	3	4		1									1					1	2				3			1						
B	4	4	1				1												1				1	3								
6A																																
B	1												3	3	3	2	2	3	2	1	2	2	1	1								
C																																
F						1																										
G																																

* Interval 119 is approx. 12 s in duration. There are 92 s silence (approx. 6 intervals) between intervals 119 and 120.

Appendix B (cont.). Frequency of common code phonations per sequential 15 s intervals with concurrent behavioral observations. Miscelaneous behaviors (Misc.): SH-spyhop; TU-turn; CR-crowd; OS-animal on side; LT-lobtail & flippering; Distance from boat (Dist.) < 50 m, LO-lolling, El-echolocation; + indicates behavior observed.

Common Form	15 second interval																									
& Behavior	147	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
Misc.							SH			SH									LT		[illegible]		SH			
Dist.								+	+	+	+	+	+	+	+	+	+	+								
LO		+	+	+	+	+	+	+	+	+	+	+	+													
EL		+	+			+			+			+														
1A					2												2			1						
B																										
C													1													
2A					1																					
3A	6	2	2		1	1	1	4	1		1	1	2	3	2	1					1					
B	3	7	3	2	1	7	7	6	4	2	5	9	6	2	5	7		1								
C		1																								
D					2					3																
E																										
F									2																	
4A												4	12	12	9	5			1							
B																										
D																										
5A	1								1					1						3						
B	2					2	1	3	1			1	2						2	2	2	2	2'	2		1
6A																										
B						5			1					1			2	1	2	2	2	2	1	1	2	3
C																										
F																			2							
G																										

Appendix C. Distribution of the number of forms coded per 15 s interval recorded at Point au Gaul (sample 1, 172 intervals, 1410 forms)


Frequency
0
5
10
15
20
Number of forms per interval
0
5
10
15
20
25
30
35
40