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Vocalizations of the Sperm Whale (Physeter macrocephalus) off the Galápagos Islands as Related to Behavioral and Circumstantial Variables

by

Linda S. Weilgart

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
at
Dalhousie University
Halifax, Nova Scotia
June, 1990

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by Linda Susan Weilgart

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

The purpose of this study was to gain insight into the significance of sperm whale (Physeter macrocephalus) sounds by examining their relationship to behavioral and circumstantial variables. Whales were tracked continuously for periods totalling months, off the Galápagos Islands, Ecuador, and sperm whale vocalizations were recorded systematically. In addition to the usual clicks (long series with interclick intervals of about 0.5 s), creaks (clicks at high repetition rates), and codas (short, repetitive click patterns) previously reported in the literature, a new vocalization type was discovered--"slow clicks." These were found to be produced by mature males and were distinctively different from the females' usual clicks. There was a strong correlation between behavior visible at the surface and rates at which different types of vocalizations were heard. Codas were given in social situations of large "clusters" (whales swimming together within 100 m of another), whereas usual clicks were associated with feeding behavior, when whales were diving deeply and dispersed in smaller clusters. Codas were relatively rare, and could be categorized into 23 discrete, almost non-overlapping types according to number of clicks and proportional lengths of interclick intervals. Codas overlapped or followed one another according to type in a non-random way, and coda type "5" tended to initiate coda exchanges. The rate of production of different coda types varied with behavioral and circumstantial variables such as identified group, month, maximum cluster size, presence of male, but the specific details of these relationships were not clear. It is hypothesized that usual clicks function as echolocation, slow clicks as a sign of male maturity and competitive ability, creaks as echolocation and communication, and codas as a means of social communication which serves to maintain social cohesion within stable groups of females following periods of dispersion during foraging.

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Parts of this thesis are published as scientific papers, especially: "Distinctive vocalizations from mature male sperm whales (Physeter macrocephalus)", by L.S. Weilgart and H. Whitehead, 1988, Can. J. Zool. 66: 1931-1937.

CHAPTER 1. INTRODUCTION

The purpose of this study was to determine the role of sound in the life of the sperm whale (Physeter macrocephalus). Of particular interest was the means by which sperm whales use their vocalizations for social communication. Such investigations can aid in understanding the relationship between sound and behavior in social odontocetes, and can shed light on the evolution of diverse systems of acoustic communication in animals generally.

1.1 Natural history

Sperm whales are among the largest of all whales--the only odontocete member of the great whale species. They are distributed worldwide, and generally inhabit deep waters off continental shelves (Caldwell et al. 1966). Sperm whales are deep-diving, feeding at depths of around 400 m when off the Galápagos Islands (Papastavrou et al. 1989), although they have been caught in submarine cables at depths of up to 1100 m (Heezen 1957). Bathypelagic and mesopelagic squid account for most of the sperm whale's diet, especially at lower latitudes (Clarke 1980).

Females mature sexually at 7-12 years of age (9 years on average); males reach sexual maturity much later (around 18-19 years) and are not sociologically mature (able to gain access to groups of females) until about 25 years of age (Best 1979; Best et al. 1984). Females calve once every 5 years, on average (Best et al. 1984). Lactation lasts about 2 years, but calves may continue to suckle for as long as 13 years (Best 1979). Sharks (Gambell et al. 1973; Arnbom and Whitehead 1989) and particularly killer whales, Orcinus orca (Best et al. 1984; Arnbom et al. 1987) are known to be predators of sperm whales, especially the calves.

Sperm whales exhibit extreme sexual dimorphism in size. Mature males are 3.2 times the mass and, at a maximum of 18 m, 1.4 times the length of mature females, which can reach up to 12 m in length (Best 1979). Mature bulls also feed on larger squid than females and immatures (Clarke 1980), and are probably able to dive deeper (Best 1979).

Sperm whales are long-lived, with a life span of 60-70 years (Lockyer 1984). They possess the largest brain in the animal kingdom. At birth, their brain size is about 40% that of the adult brain weight (Best et al. 1984).

Sperm whale females and their young invariably form long-lasting associations (Best 1979), which are stable in composition over periods of years (Ohsumi 1971; Whitehead and Waters, in press). These "nursery groups" contain from 10-30 members (Best 1979; Whitehead and Waters, in press), which may be genetically related (Arnbom and Whitehead 1989). As males, and possibly also females, mature (at about 4-15 years of age), they gradually leave their natal group and form "juvenile" or "bachelor" schools (Best 1979). Nursery groups, which have been classified as "extended matricentral families", exhibit tight schooling behavior and strong social cohesion (Best 1979). Adult females have been observed to behave altruistically toward injured group members (Caldwell and Caldwell 1966), and communal caring for calves appears to take place within groups (Gordon 1987).

The social system of the sperm whale is unique in that the sexes are widely segregated geographically for most of the year. Males generally form smaller and smaller aggregations as they mature (Gaskin 1970), and are found at higher and higher latitudes, with very large solitary males frequenting polar regions (Best 1979). Nursery groups, in contrast, inhabit tropical and subtropical waters to latitudes of about 40°(Best 1979). Mature males only migrate to the lower latitudes during the breeding season (Best 1979), during which time they accompany groups of females for periods of only a few hours (Whitehead and Arnbom 1987). Competitive fighting for access to females probably occurs among mature males, though observations of such battles in modern times have been rare (Best 1979).

1.2 Sperm whale sounds

a) **Clicks**

Sperm whale sounds were first described by Worthington and Schevill (1957), who heard impulsive "clicks" about half a second apart. Later, a much more detailed analysis of these sounds was given by Backus and Schevill (1966). They noted that the clicks which were often made up of a series of pulses, were broadband from about 200 Hz to 32 kHz, with the dominant frequency around 5 kHz; that the interval between clicks generally varied from about 0.025 to 1.250 s, and that the whole click lasted about 2-24 ms.

Watkins (1980) also reported that clicks were sharp onset, broadband pulses, but that the higher frequency content of the clicks could only be heard within 20 m of the whales. At 2 km, most of the audible energy was below 5-6 kHz. This observation agrees reasonably well with Levenson (1974), who found that the maximum energy in a sperm whale click occurred from 2-8 kHz. Watkins (1980) noted that clicks displayed little directionality, showed no change in character with depth, and though sound levels were highly variable, could be heard at distances of over 10 km under good conditions. Mean broadband (250 Hz-16 kHz) source levels were measured by Levenson (1974) to be 171.2 dB *re* 1 µPa with a standard deviation of 2.9 dB.

Clicks were characteristically repeated in long sequences with very regular intervals (Backus and Schevill 1966). Watkins (1980) presented repetition rates of about 1.5 to 3 clicks/s (i.e., clicks heard every 0.3 to 0.6 s), while Mullins et al. (1988) gave interclick intervals of 0.96 and 0.69 s, respectively, for two maturing males off Nova Scotia. These click series could continue without interruption or appreciable change in interclick interval for 20 min or more (Watkins 1980). Approximately two thirds of each hour of acoustic recording consisted of these "usual clicks" (Mullins et al. 1988).

b) Creaks

"Creaks", sounding like a rusty hinge, were also heard by Worthington and Schevill (1957). Since the human auditory system cannot resolve auditory events that occur at a rate of over 20/s (Lieberman 1977), clicks given at high repetition rates are perceived as "creaks". Higher rates of clicking, at 60-80 or more clicks/s, were also encountered by Watkins (1980) and Norris and Harvey (1972). Backus and Schevill (1966) presented a maximum repetition rate of 50 clicks/s.

Creaks may be quite prolonged, lasting a minute or more (Norris and Harvey 1972). Mullins et al. (1988) reported mean (and standard deviation) creak durations of 26.8 s (15.7) for one whale, and 61.0 s (71.0) for another.

c) Codas

Backus and Schevill (1966, p. 517) alluded to "short, irregularly spaced sequences of clicks which are repeated several times within the space of a few tens of seconds". These "codas" were later characterized by Watkins and Schevill (1977a) as being stereotyped, repetitive patterns, composed of short series of 3 to 40 or more clicks. Though these sounds were only heard occasionally, Watkins and Schevill (1977a) described them as distinctive and prominently recognizable against the background of usual click sounds from sperm whales. Codas were usually about 0.5 to 1.5 s in duration and could be precisely repeated from 2 to 60 or more times, according to Watkins and Schevill (1977a).

d) **Summary**

Despite one report to the contrary (Perkins et al. 1966), which attributed a wide variety of sounds to sperm whales (including "chirps", "squawks", "yelps"), it is generally agreed that sperm whales produce only clicks (Backus and Schevill 1966). These clicks, however, can be used in different ways to produce at least three different vocalization types: a) regular, "usual clicks", by far the most common type of vocalization; b) creaks; and c) codas. Finally, an additional, previously unidentified, vocalization type, called the "slow click", is described in this study. It is thought to be produced by mature males.

1.3 Possible functions of sperm whale sounds

a) **Clicks**

Backus and Schevill (1966) proposed echolocation as a probable function of the usual clicks. Their "burst-pulse" structure (each click composed of a series of pulses) would be useful in distinguishing echoes in a high noise field, they reasoned. As well, they noted "signature" information in the clicks, i.e. considerable variation from one whale's click series to another's, but great similarity among successive clicks of one whale. Such signatures, they argued, would be necessary in echolocation to distinguish echoes from one whale's clicks from echoes of another's. Like Backus and Schevill (1966), Norris and Harvey (1972) hypothesized that usual clicks are "search mode" echolocation, used to scan long distances of open ocean.

Watkins (1980), however, disagreed since sperm whale clicks exhibit different characteristics from clicks of other odontocetes. He believed that sperm whale clicks were not directional enough, too regular in interclick interval, not given often enough, too loud, and too long in duration to be primarily used for echolocation. Instead, he proposed that usual clicks were mainly social signals (Watkins 1980), since whales seemed to coordinate their movements underwater (Watkins and Schevill 1977b). These authors noted that sperm whales which were at the surface together were relatively silent, but upon diving together, began clicking at depths of 5 to 25 m while spreading out, maintaining separations of several hundred meters (Watkins and Schevill 1977b). Though widely separated underwater, the whales surfaced usually within 50 m of each other (Watkins and Schevill 1977b). Watkins et al. (1985) also referred to these long series of regular, usual clicks as "contact calls" with no indication of use as echolocation. Papastavrou et al. (1989) found that sperm whales started to produce clicks later in their dives, at depths of 150 to 300 m, before leveling off at around 400 m.

Recent evidence (Mullins et al. 1988), however, strongly suggests that usual click sequences are not related to the presence or absence of nearby whales, and thus they are not likely to function primarily in social communication. Gordon (1987) has correlated acoustic output with fine-scale movements of sperm whales, which also indicated that echolocation is probably the primary function of usual clicks.

b) **Creaks**

Creaks are probably produced when the whale is examining a close target. Norris and Harvey (1972) heard these high repetition rate clicks when a phonating whale approached and collided with their hydrophone. Mullins et al. (1988) found creaks to be emitted very infrequently (about once per h per whale). Changes in a whale's orientation underwater were accompanied by creaks suggesting that creaks, in particular, may assist in locating prey through echolocation just prior to ingestion (Gordon 1987).

Watkins et al. (1985) reported that variable click sequences emitted at relatively rapid rates (to 90/s) were heard in conjunction with codas during "social activities." These creaks were sometimes longer than 30 s in duration (Watkins et al. 1985).

c) **Codas**

Backus and Schevill (1966) hypothesized that the short, repetitive click sequences, later termed "codas" by Watkins and Schevill (1977a), represent communication as they did not seem suited as echolocation signals. These sounds were heard from groups of whales lying immobile at the surface for longer periods of time when Backus and Schevill (1966) saw no need for whales to echolocate. Watkins and Schevill (1977a) and Watkins et al. (1985) believed that codas served as a means of individual identification, though Watkins et al. (1985) also noted the occurrence of "general-use codas" which were the same coda sequences produced by different whales. One apparent exchange of codas between two whales was related to changes in underwater movement (Watkins and Schevill 1977a). Coda exchanges also seemed to occur only between whales that were close together (Watkins and Schevill 1977a). Watkins and Schevill (1977a) reported that codas were heard only when whales were underwater, in contrast to Backus and Schevill (1966). Codas (Watkins and Schevill 1977a), as well as similar-sounding array calibration pingers (Watkins and Schevill 1975), elicited silence in other sperm whales, suggesting that whales may have interrupted their own sound production to listen.

1.4 How sounds are produced

The large forehead of the sperm whale, particularly the huge, oil-filled sack, the spermaceti organ, which lies within it, is strongly implicated in sound emission (Norris and Harvey 1972). It is proportionally larger in males than in females, comprising 20% of the total length in an 11 m female, 23% of the total length in an 11 m male, but 26% in a sociologically mature male of 16 m (Nishiwaki et al. 1963). Norris and Harvey (1972) proposed that the function of the spermaceti organ is to act as a sound reverberation chamber. The pulse is produced at the cornified valvular lips, or *museau du singe*, at the anterior end of the spermaceti organ. While most of the sound energy travels forward, some of the signal is reflected back between two vertically oriented air sacs that bound the anterior and posterior ends of the spermaceti organ and seem to function as sound mirrors. This complex anatomical system, using air recycled between a network of nasal passages to actuate the *museau du singe*, is suggested as a means of producing the burst-pulse clicks useful to the sperm whale in echolocating at depth (Norris and Harvey 1972).

1.5 Contextual studies

In order to broadly ascertain the communicative functions of vocalizations, it is necessary to study the contexts in which such sounds are produced and responded to (Smith 1977a). This has been done only relatively recently with wild cetaceans since often only a limited fraction of the animal's behavioral repertoire can be sampled. Nevertheless, among the social odontocetes, broad relationships between behavior and vocalizations have been found for killer whales, Orcinus orca (Ford 1989), pilot whales, Globicephala melas (Taruski 1979; Weilgart and Whitehead, in press), and beluga whales, Delphinapterus leucas (Sjare and Smith 1986; Faucher 1989), although usually these relationships were not definitive in that no call type could be correlated exclusively with any behavior or circumstance (i.e., vocalizations usually could not be predicted based on behavior visible at the surface.).

The objective of this study was to examine the behavioral, circumstantial, and environmental correlates of sperm whale sounds in order to gain insight into the functions and meanings of their vocalizations. To study the relationship between sounds and behavior, systematic visual and acoustical recordings were made in a variety of behavioral contexts over periods of months while in almost continuous contact with sperm whales. Though Watkins and Schevill (1977a) were roughly able to determine the relative positions of phonating whales underwater by means of hydrophone arrays, their total observations were limited to periods of at most 3-4 h. The long-term nature of this study should give a more accurate representation of the types of vocalizations produced by sperm whales and the circumstances in which they are heard.

CHAPTER 2. METHODS

2.1 Collection of data at sea

Using a 10-m auxiliary sloop, Elendil, with a crew of 5-6, sperm whales were tracked in the waters around the Galápagos Islands, Ecuador (0°N, 90°W). These volcanic islands are located about 600 nautical miles from mainland Ecuador (Fig. 1). Tracks of the research vessel while following sperm whales are shown in Fig. 1. Research was carried out between 23 February and 20 April 1985 (a total of 30 24-h days spent tracking sperm whales), and between 3 January and 28 June 1987 (57 days spent tracking sperm whales). The peak mating season for females off the Galápagos is most likely during April and May (Whitehead et al. 1989b; see also Sec. 3.2f). Typically, 10-14 days were spent at sea before returning to port for 4-5 days for resupplying.

Groups of sperm whales were tracked acoustically using a custom-made directional hydrophone to obtain bearings on the clicks made by the whales. This allowed us to stay within about 2 km of groups of sperm whales during most of the tracking time. Groups principally consisted of female sperm whales and their young, but these were sometimes accompanied by large, mature males (Whitehead and Arnbom 1987; Whitehead and Waters, in press). Sperm whale vocalizations were recorded regularly for 5 min/h on the hour around the clock

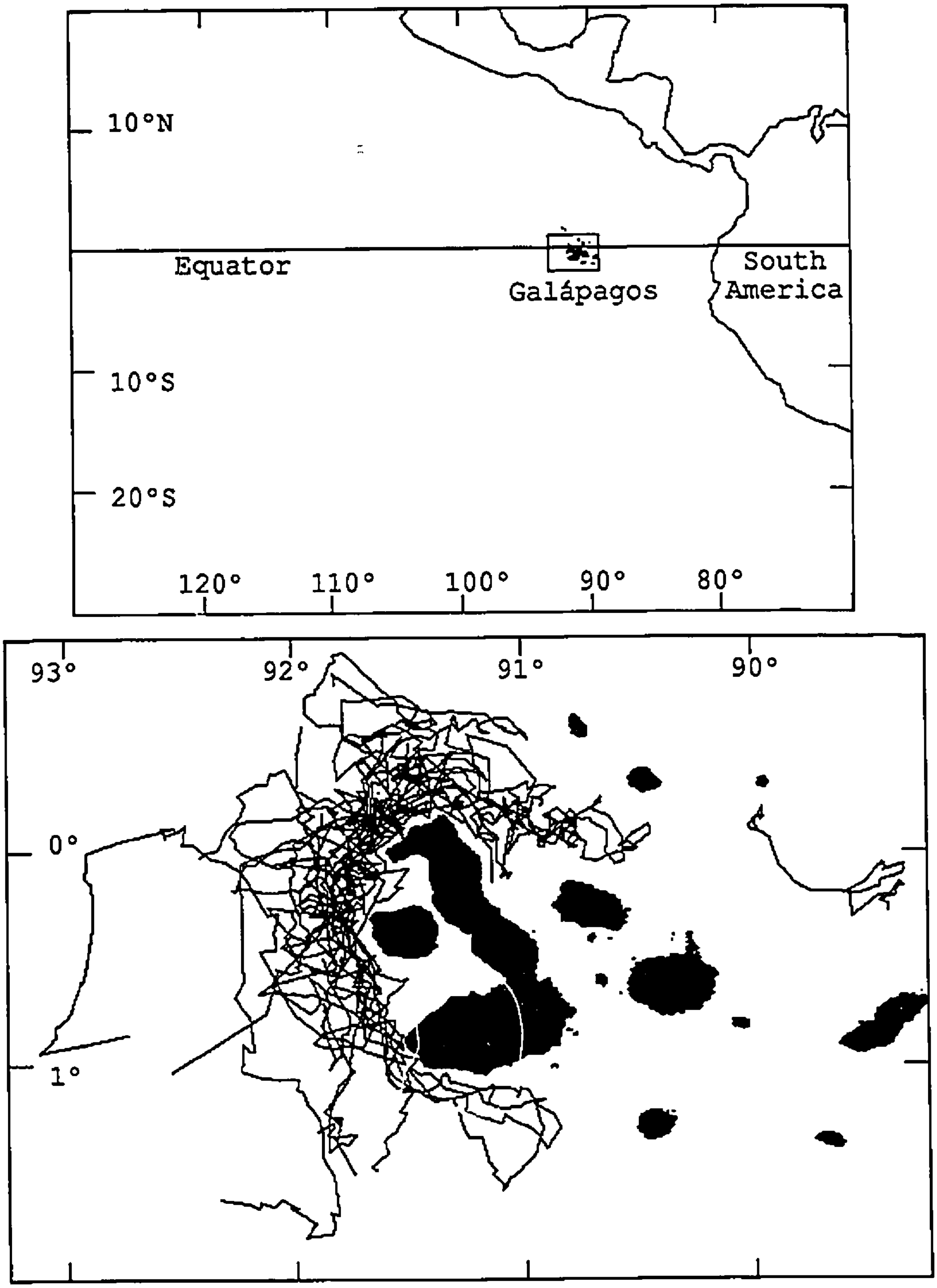

Fig. 1. Galápagos Islands, study area (above) and routes taken by research vessel while tracking sperm whale groups in 1985 and 1987 (beneath).

on Uher 4000, Sony TC770, or Nagra IV-SJ tape recorders through a Benthos AQ17 omnidirectional hydrophone (10-m cable) and Barcus-Berry "Standard" or Ithaco 453 preamplifier. The system was flat from 150 Hz to 10 kHz (± 3.5 dB) but high-pass roll-off filters in the preamplifiers were used to minimize wave noise. Recordings were made at 19 cm/s. A total of 56 h of acoustical recordings were made in 1985; 86 h in 1987. In addition, one 5-min session of sperm whales recorded off the West Indies (15°N, 62°W), on 16 December 1984, with a similar recording system, was used in the analysis of "slow clicks" (see Sec. 3.2). Each 5-min recording on the hour will be subsequently referred to as a "session".

During daylight, the composition and surface behavior of all visible whale clusters (whales swimming at about the same speed in the same direction and within 100 m of one another--Whitehead and Arnbom 1987) were recorded every 5 min over the 5-min interval. Specifically, cluster size, number of clusters, number of mature males, number of calves, estimated speed of the whales, number of breaches (leaps from the water), number of lobtails (tail flukes thrashed onto the water surface), number of fluke-ups (flukes raised before deep diving), number of sideflukes (half of flukes visible above the water surface, seen when whale was on its side or turning), and the number of spyhops (head lifted above water) were all recorded (Fig. 2). Environmental data such as the presence of fog were collected every 3 h.

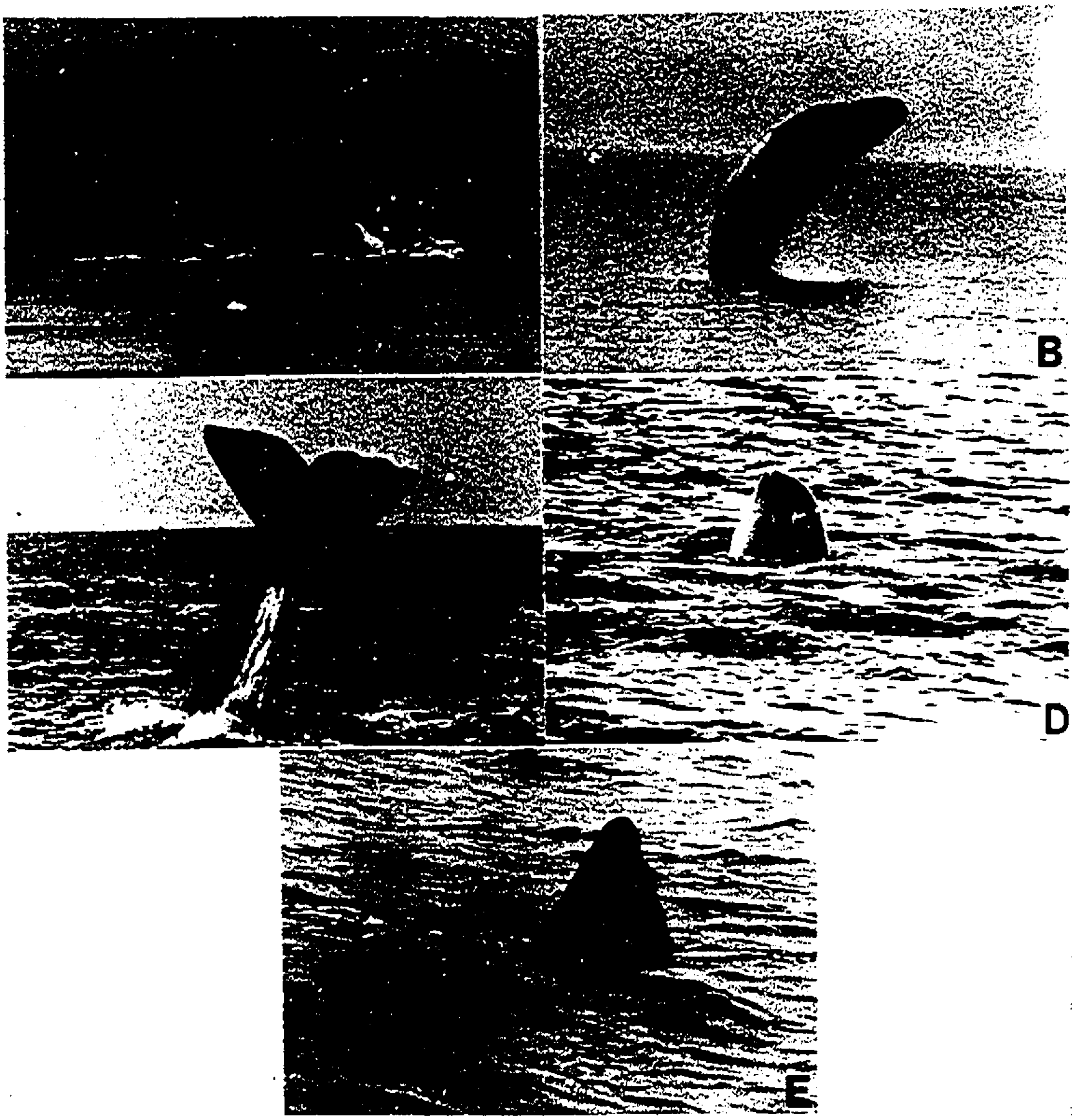

Fig. 2. Behavior types: A) fluke-up; B) breach; C) lobtail; D) spyhop; E) sidefluke.

Photographs of flukes and dorsal fins were taken during daylight for the individual identification of the whales (Arnbom 1987). During the 1985 and 1987 studies, 583 individuals were identified from fluke photographs (Whitehead and Waters, in press). The identifications were used to allocate whales into "groups" with virtually closed membership over periods of months, and to estimate the sizes of these groups (Whitehead and Arnbom 1987; Whitehead and Waters, in press). A few "transient" whales appeared to move between groups (Whitehead and Waters, in press). For the analysis of the relationships between coda type and behavioral and circumstantial variables, groups were assigned to a particular recording session with certainty if two or more members of a group were identified within 120 min of the session (or if the session occurred at night, two or more members were identified both the previous evening and following morning). In addition, no individuals from other groups or transients could be identified within 120 min of the session for this definite assignment of group to session to hold.

The four mature males identified during 1985 which were used in this study, were given identification numbers 500, 502, 503, and 504; the two mature males from 1987 were identified as 511 and 513 (Whitehead and Arnbom 1987; Whitehead and Waters, in press). The one mature male recorded in the West Indies was numbered 555. Males ranged in total body length from 12.8 to 16.4 m (Whitehead and Waters, in press).

2.2 Aural analysis

The 142 h (1,696 sessions) of acoustical recordings from both 1985 and 1987 were first analyzed aurally by signalling to a computer when particular sounds were heard. Codas, creaks, usual clicks, and "slow clicks" were entered into the computer together with the times at which they occurred. "Slow clicks" or SCs are sperm whale vocalizations different from those mentioned previously. They can be recognized by their distinctive tonal characteristics and may sound "clanky", "whamming", "metallic", or like the cracking of a stick. Principally, however, they are distinguished from the usual clicks described by Backus and Schevill (1966) by their slow repetition rates. These vocalizations seem to be made by mature males (see Sec. 3.2a), in contrast to the usual clicks heard from groups of females and immatures.

Since recordings were often not the full 5 min in length, only the first 4 min of each session was used. This gave the following acoustical variables for use in statistical analysis:

1) the number of codas;

2) the number of creaks and, whenever possible, their durations;

3) the interclick intervals of slow clicks and whether more than one particular individual producing slow clicks could be distinguished based on interclick interval and tonal quality;

4) the interclick intervals of usual clicks whenever possible.

Recording sessions which consisted completely of silence, even though whales were close, were also noted. During analysis tapes were played at 19 cm/s (real time). Poor quality sessions or sessions that were under 4 min in length were eliminated from the statistical analysis (124 sessions eliminated).

2.3 Usual clicks

a) **Interclick intervals (ICIs)**

Because of the large quantity of usual click (UC) sequences heard simultaneously in 1985, clicks from a single individual were impossible to pick out on all but a few occasions. Therefore, interclick intervals (ICIs) of UCs were measured from only 9 recording sessions, with a total of 1,397 ICIs measured. It is probable that each of the sequences selected represents clicks from a different individual because of the large number of whales present (ca. 400 sperm whales in the study area at any time -- Whitehead and Waters, in press) during the recordings, even though one cannot be sure of the identity of the vocalizing whale. In 1987, because of the generally lower click rates of that year (see Sec. 3.3c), many more individual usual click sequences could be distinguished than in 1985. Since mature males comprised only 2-3% of the population, even during the height of the mating season (Whitehead et al. 1989b), it is unlikely that these usual click sequences were produced by mature males.

b) **Frequency structure**

Thirty-eight UCs from 6 recording sessions in 1985 (all on different days) and 11 sonagrams (each 1.28 s in duration) were examined with respect to frequency structure. They were divided into 12 series. Because of the regular repetition rate of clicks within a series, I believe that each series represents the clicks of a single individual. Different series from the same sonagram had independent and different ICIs and were almost certainly from different individuals. Thus, clicks from the same sonagram were not necessarily from the same individual, yet clicks from more than one sonagram were attributed to the same individual if belonging to the same uninterrupted series. Again, given the number of individuals in the population, and assuming the majority of animals vocalize, it is likely that all or most of the 12 series are from different animals.

Sonagrams were produced on a Kay Digital Sona-Graph, Model 7800. The frequency range sampled was 0-16 kHz, with a 1.28 s sampling time, and 300 Hz analysis filter. The shading contour option was used, which produced contour lines connecting points of equal sound intensity. Eight shades of grey distinguished each intensity level, with a 6 dB increment from one shade to the next. These contours allowed intensity peaks within clicks to be recognized (Fig. 3). One to three calibration lines produced by the sonograph were printed on each sonagram.

A transparent overlay of calibration lines spaced at 500 Hz intervals was used to determine at which frequencies (to the nearest 100 Hz) the intensity peaks of each click were located. For each click, the frequencies of 2-7 peaks were recorded (depending on how many were evident), in order of decreasing intensity. If there were several peaks of the same level of intensity (same contour), all were noted. The duration of the longest portion of each click was also measured.

c) **Click rate analysis**

A section of each of the hourly 5-min recording sessions was chosen so that it did not contain obvious extraneous sounds, such as the banging of the boat's rudder, or vocalizations of other cetaceans, or codas, slow clicks, or creaks. This meant that counts were almost entirely of usual clicks. Sixteen seconds from each session were input to a Tectronix 2220 Digital Oscilloscope (sampling at 0.25 kHz)

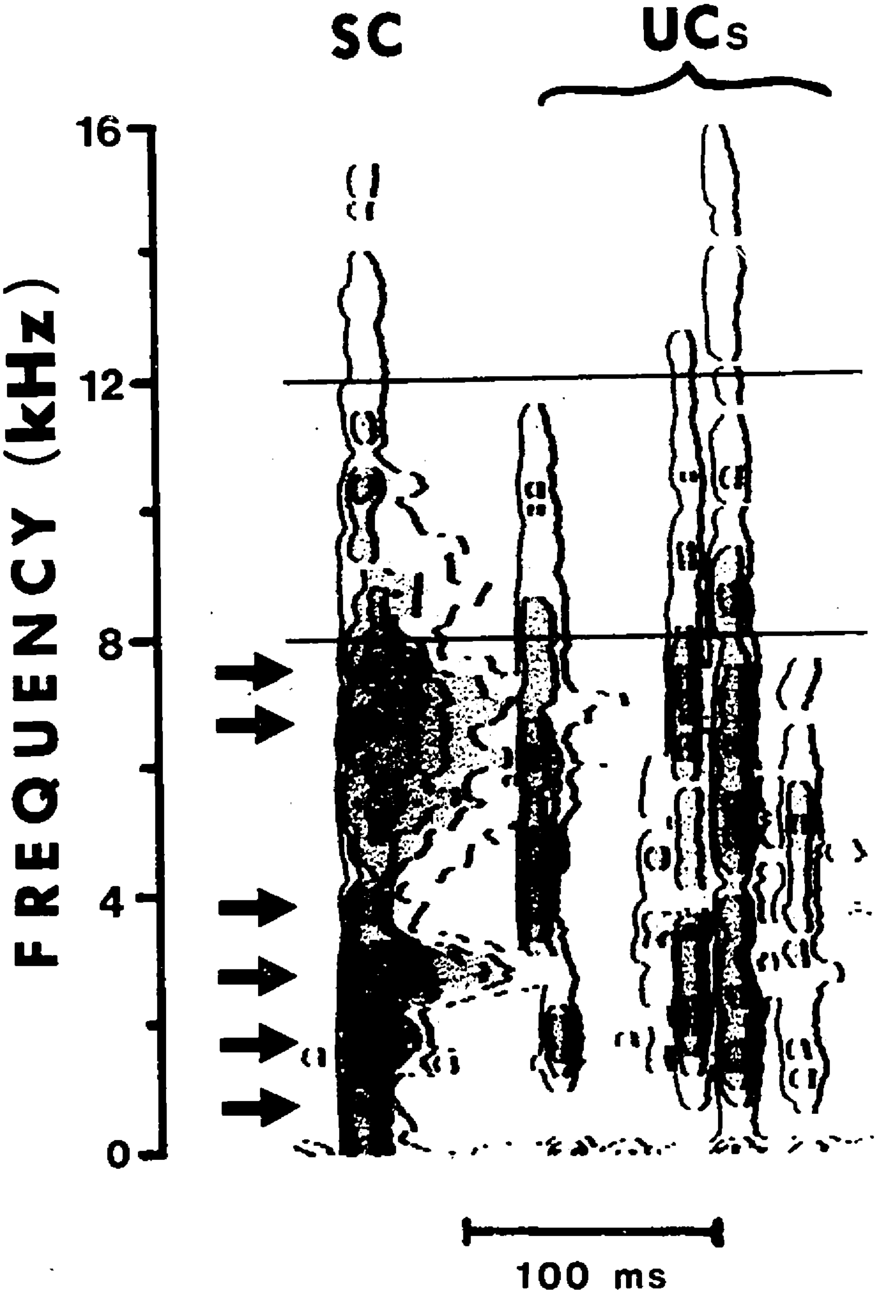

Fig. 3. Contour spectrogram (frequency vs. time) of slow click (SC) and several usual clicks (UCs). Arrows denote peaks in intensity at 0.8, 1.8, 2.8 ("ringing"), 3.8, 6.7, and 7.5 kHz. (Reprinted courtesy of the Canadian Journal of Zoology.)

through a Krohn-Hite 330N band-pass filter (set to a high pass roll-off of 10 kHz to maximize the signal-to-noise ratio). The vertical gain of the oscilloscope was adjusted so that the background noise formed a band 0.6 major divisions on either side of the x-axis (time). Sessions in which the clicks did not then rise above, or below, 1.0 divisions from the x-axis were discarded. This left a total of 1,322 sessions analyzed. The digitized sequence was then sent through an RS-232 port to a microcomputer, where a BASIC program written by H. Whitehead, Dalhousie University, counted the times that the trace moved 1.0 major units from the x-axis. After each counted click, the program did not count any more clicks for the next 78 ms, in order that each would only be counted once. The click rate, c', for each session was then estimated from the number of clicks counted, β, by:

$$c' = \beta/(16.0 - 0.078\times\beta) \quad \text{clicks/s}$$

Tests showed that the routine did count the actual number of clicks in a sequence with a low click rate (clicks were also counted by eye on the oscilloscope), and that its results were repeatable. Click rates from the same session were compared and found to differ little. An adjustment was made to compensate for biases introduced at high click rates (>100 clicks/s) due to digitization (Whitehead and Weilgart 1990).

2.4 Slow clicks (SCs)

a) Interclick intervals (ICIs)

For the examination of ICIs of SCs, 84 recording sessions were used in 1985, containing a total of 1,663 ICIs. In 1987, 133 sessions were used with a total of 2,575 ICIs.

In comparing the ICIs of different males, SCs were attributed to a particular male if he was identified (from a photograph of his flukes) within about 1 h of the recording session (Table 1), and if no other male was seen or heard (judged by two SC series being heard simultaneously) on the same day. The recording session of Male 555 from the West Indies was also used because, while not identified, he was nevertheless assumed to be different from the Galápagos males. Thus, there were 24 sessions which could be ascribed to one of the 7 known males. Over half of the recording sessions used took place within 15 min of the identifying fluke-up (Table 1). While it is unlikely that an unidentified second male was heard singly but never seen the whole day, the association of a particular SC series to an identified male is imperfect, and does not prove the identity of the emitter with absolute certainty.

b) Frequency structure

For the examination of the frequency structure of SCs, 43 sonagrams were used, each depicting one SC (Table 1). A

Table 1. The number of 5-min recording sessions and sonagrams used for the analysis of slow clicks of each known male (one slow click per sonagram). The time (in minutes) between the identifying fluke photograph of a male and the acoustical recording of his slow click is given. The attribution of a slow click recording to a particular male is more definite if the recording is made after the fluke photograph (A), than if the recording is before the identifying fluke-up (B). Male 555 from the West Indies was not identified, but was nevertheless assumed to be different from the other Galápagos males.

Male ID No.	Date	Time recorded	Min. between recorded and ID'd	No. of sonagrams per session
555	16/12/84	09.42	--	2
502	31/ 3/85	08.02	48 (B)	2
502	31/ 3/85	09.04	14 (A)	1
502	31/ 3/85	10.58	23 (A)	1
502	31/ 3/85	12.09	34 (A)	2
502	31/ 3/85	12.58	23 (A)	2
502	31/ 3/85	16.08	12 (B)	1
503	14/ 4/85	09.06	21 (A)	2
503	14/ 4/85	16.00	5 (A)	2
503	14/ 4/85	17.05	5 (A)	2
503	15/ 4/85	07.58	8 (A)	1
503	15/ 4/85	10.05	5 (A)	1
500	17/ 4/85	10.05	10 (A)	2
500	17/ 4/85	11.08	7 (A)	2
500	17/ 4/85	14.08	65 (A)	2
500	19/ 4/85	10.04	4 (A)	2
500	19/ 4/85	11.11	8 (A)	2
504	19/ 4/85	16.00	10 (A)	2
513	18/ 4/87	07.07	7 (A)	2
513	19/ 4/87	06.58	22 (B)	2
513	19/ 4/87	08.08	48 (A)	2
513	19/ 4/87	17.02	13 (B)	2
511	3/ 6/87	08.10	45 (B)	2
511	3/ 6/87	09.01	6 (A)	2
	sessions:	24	sonagrams:	43

maximum of two SCs were analyzed per session, and an attempt was made to choose SCs as widely separated in time as possible (e.g. from the beginning and end of the session). The 7 known males were represented. The 24 sessions given in Table 1, which related a particular male to a SC series, were used to compare the frequency structure of different males' SCs. Sonagrams were produced, intensity peaks were located, and durations were measured as for the UCs (Sec. 2.3).

2.5 Coda and creak type visual analysis

a) **Codas**

Sessions with clear codas were analyzed further using spectrograph and oscilloscope. Only the best 15 out of 655 sessions in 1985 and 36 out of 1041 sessions in 1987 which had the fewest background clicks or noise and the most clearly distinguishable codas were used for detailed coda analysis. There were 315 sessions containing at least 5 codas, so the 51-session sample from both years comprised 16% of all sessions available for coda analysis. A total of 1,305 codas was examined in detail. Tapes were played back at half speed (9.5 cm/s) on either a Uher 4200 or a Nagra IV-SJ tape recorder.

Sounds were passed through a Krohn-Hite 330N band pass filter set to a high pass roll-off of 6 kHz and displayed on a Tectronix 2220 digital storage oscilloscope (sampling at 410

Hz) and/or a Uniscan II real-time spectral analyzer (0-5 kHz, 3.2 scroll speed -- time taken for the trace to travel across the screen). For each coda encountered, the tape recorder counter number was noted (accurate to ± 2 units or perhaps 2-4 s) and the number of clicks in the coda was counted. Intervals between the clicks of the coda were measured in seconds (accurate to ± 0.01 s in record time) from the oscilloscope screen, or very rarely, from the spectrograph.

Codas were categorized based on these interclick interval measurements. Usually the clicks in a coda were very regularly spaced, with all interclick intervals more or less the same length. Sometimes, however, one or two clicks were separated by longer intervals from the rest of the clicks. If these intervals were at least 50% greater than the mean interval distances of the other clicks in that coda, the coda was classified differently. Whereas a regular 7-click coda would simply be called "7", a 7-click coda with a delayed click at the end would be called "6+1". Coda types "5" (Fig. 4) and "4+1" (Fig. 5) could thus be distinguished. Usually these longer intervals would occur at the end of the coda. If there was little similarity in spacing between any of the clicks of a coda, that coda was called irregular and simply classified by the number of clicks and the term "variable", e.g. "8var".

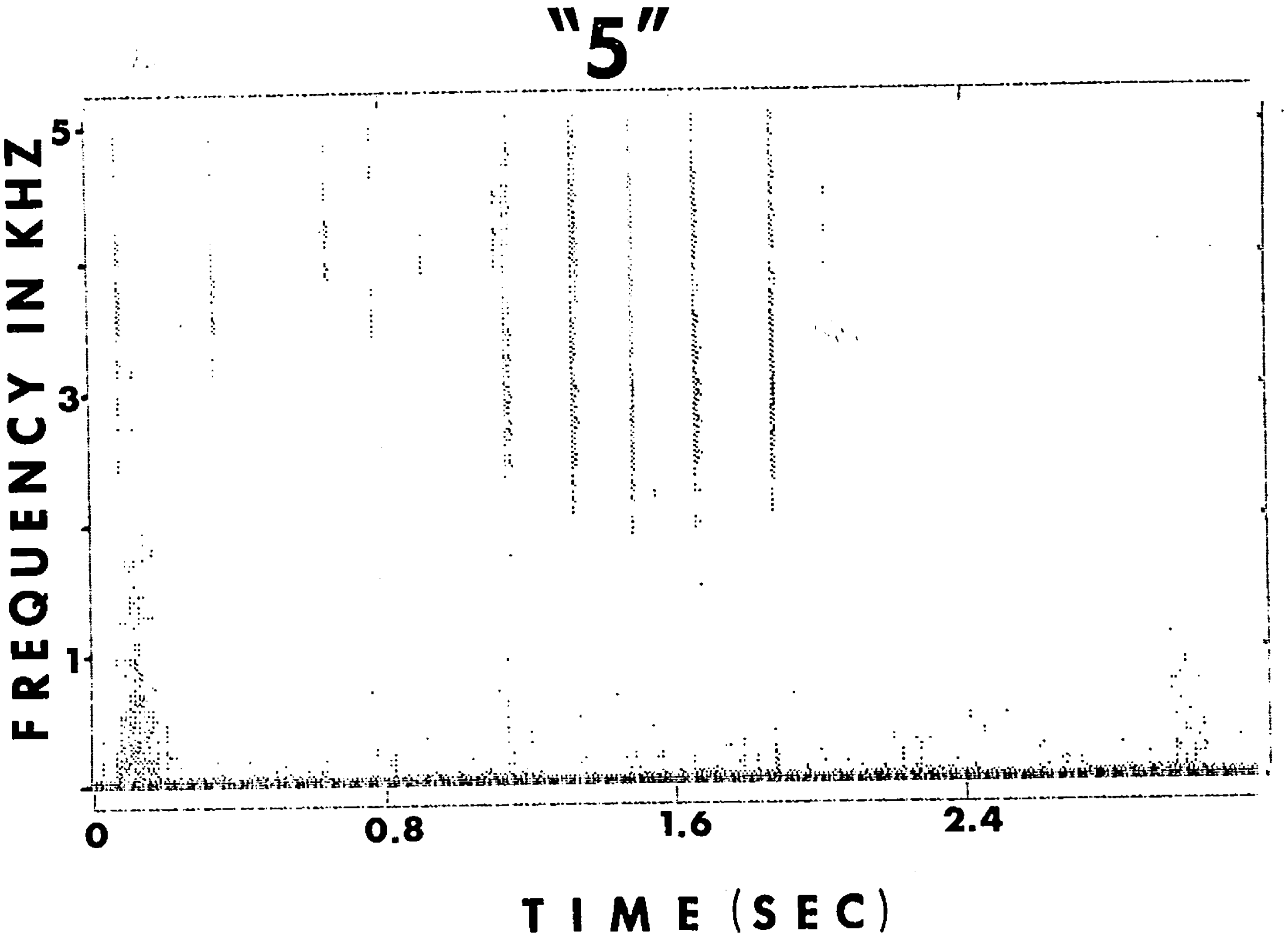

Fig. 4. Spectrogram (frequency vs. time) of coda type "5".

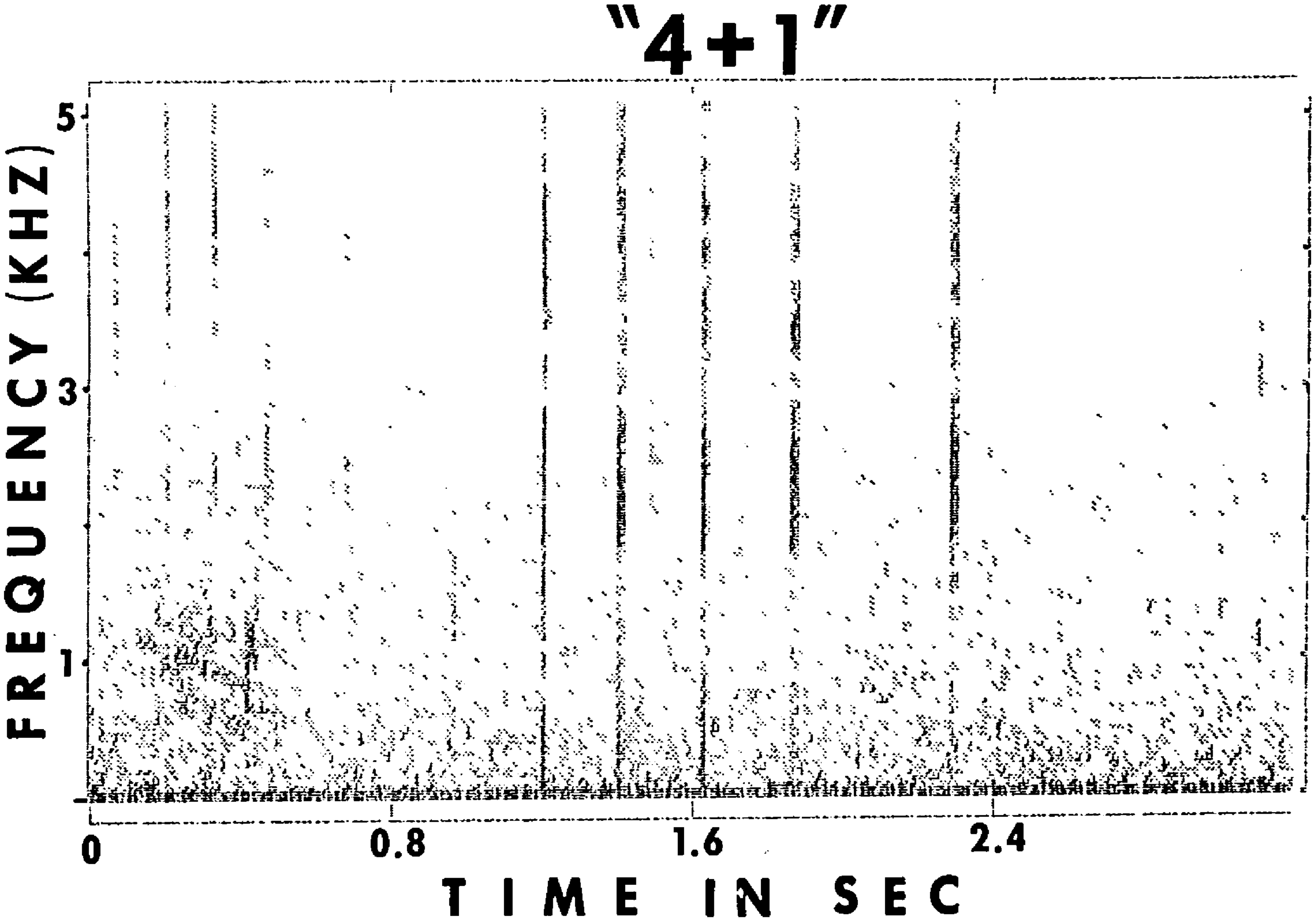

Fig. 5. Spectrogram (frequency vs. time) of coda type "4+1".

Codas were distinguishable from usual clicks mainly by their pattern and because they usually occurred in short series. In addition, the tonal characteristics of their individual clicks were often distinctive, sounding "clacky" or castanet-like. Thus, a single click could sometimes sound like a coda click. But while codas of 1 or 2 clicks may exist for sperm whales, only codas of at least 3 clicks were easily noticeable and distinct enough from single usual clicks. Similarly, sometimes a series of 20 or more clicks which had a coda-type tone to them (without being creaks -- Sec. 2.5b), would be heard. It could be difficult to note a clear beginning and end to these "codas". If, in addition, they had interclick intervals similar to those of usual clicks, distinguishing them became unreliable. Therefore, only codas with between 3 and 13 clicks, inclusive, were used. Codas over 13 clicks in length were considered creaks since their interclick intervals were, with few exceptions, also less than 0.1 s long (see "Creaks", Sec. 2.5b, below).

Codas were generally displayed and stored on the oscilloscope screen and then replayed at 1/5 to 1/8 speed to confirm that all clicks sounded similar and belonged to the same coda. Special note was taken if codas overlapped each other. Aural impression (usually at 1/5-1/8 tape speed), spectrographic appearance, interclick interval length, and intensity differences were used to determine which clicks belonged to which coda. Rarely, codas were classified strictly on aural impression if they could not be detected visually on either oscilloscope or spectrograph, usually because of interfering usual clicks or noise. For clicks to be classified as belonging to the same coda, they could not be separated by more than 0.75 s; otherwise they were called a new coda. Two clicks less than 0.05 s apart were described as a double click but were treated as a single click in coda classification and measurement (the second click was used in measuring). These double clicks almost invariably occurred as the first clicks of a coda.

b) **Creaks**

Creaks were also recorded along with their counter number position, approximate number of clicks, and estimated average interclick interval. Creaks were distinguished from codas in that more than two interclick intervals had to be less than 0.1 s long to be classified as creaks. This was an arbitrary distinction but usually coincided with the perception of a "creak" sound at full tape speed. Also, codas with more than 13 clicks were classified as creaks, though these usually fulfilled the previous (<0.1 s interclick interval) condition as well, as previously mentioned.

2.6 Statistical analysis

Statistical analysis was generally carried out using SYSTAT routines (Wilkinson 1987). Correlation matrices were used as input for multivariate analyses. Varimax rotations were undertaken for the principal components analyses. However, the interpretation of factors was thereby not substantially improved. Results of these rotations are therefore not presented.

a) Relationships between acoustical and behavioral/circumstantial variables (for Results Sec. 3.3)

i) Continuous variables

Correlations between acoustical and behavioral variables were calculated among the following acoustical variables:

1) Number of codas heard per 4-min session

2) Number of creaks heard per 4-min session (both those heard in conjunction with codas and those not)

3) Number of different slow click series heard, presumably from different individuals, per 4-min session. This was based not solely on aural impression but also on staggered interclick intervals. The maximum number of different slow clicks heard was two; the minimum, of course, was zero.

4) Whether or not a 4-min recording session was silent, though whales were close

5) Click rate in clicks/s, as determined by computer, using only "good" sessions (see Section 2.3c)

6) Whether (or not) click rates were under 20/s (low click rate) -- an indication that whales were behaving socially (Whitehead and Weilgart 1990; see Sec. 3.3),

and

7) Whether (or not) click rates were over 60/s (high click rate) -- an indication that more than one identified group was present (Whitehead and Weilgart 1990; see Sec. 3.3).

Behavioral or circumstantial variables consisted of:

1) Total number of clusters (including calves and males) counted (sum of all 5-min interval counts 0.5 h before and after the hourly acoustical recording session);

2) Total number of clusters seen at or within 500 m from the boat;

3) Total number of individuals (excluding calves and males) seen (sum of all 5-min interval counts 0.5 h before and after the recording session);

4) Total number of individuals seen at or within 500 m from the boat;

5) Total number of individuals seen more than 500 m from the boat;

6) Mean cluster size (non-calves and non-males) within 500 m of the boat (number of individuals/number of clusters within 500 m);

7) Maximum cluster size (non-calves and non-males) in the 0.5 h before and after the hourly acoustical recording session;

8) Maximum number of males seen together in the hour (as above);

9) Total number of calves seen (sum of all 5-min counts) in the hour;

10) Mean estimated speed of whales in knots;

11) Proportion of whales heading the same direction, formally the mean vector speed standardizing all speeds at 1.0 (when >5 speeds and headings were recorded);

12) Number of breaches, lobtails, fluke-ups, sideflukes, and spyhops seen during the hour;

13) Number of breaches, lobtails, fluke-ups, sideflukes, and spyhops seen at or within 500 m of the boat, during the hour;

14) Number of breaches seen more than 500 m from the boat.

Pearson correlation coefficients were computed among these variables from the complete data set for both 1985 and 1987 field seasons, only excluding sessions with fog or poor visibility for other reasons. Sample sizes were usually around 800, but reached a maximum of 1,572 when comparing acoustical variables with each other. To highlight only the most major relationships between vocalizations and behavior, only those correlation coefficients which were greater than an arbitrarily chosen value of 0.3 were used. Because of the large sample sizes, much lower correlations would also have been very highly significant ($p<0.001$ for $r \approx 0.10$).

It was determined that the data for all variables were not normally distributed even when square-root and log (+1) transformations were employed, and that most variables were usually significantly ($p<0.05$) autocorrelated for lags of less than 8 h. Nevertheless, Pearson correlation coefficients were used because non-parametric correlations could not easily be performed on such a large data set. However, Spearman correlation coefficients were calculated on a reduced data set which practically eliminated autocorrelation by using only the sessions from 08:00 h and 16:00 h. Sessions with fog were also excluded. The relationships given in Sec. 3.3 with Pearson correlation coefficients greater than 0.3, also had highly significant ($p<0.01$) Spearman correlation coefficients on the reduced data set, except where noted.

ii) Discontinuous circumstantial variables

Discontinuous circumstantial variables (year: 1985, 1987; month: Jan.-June; maximum number of males seen together in the hour: 0, 1, 2; whether or not a calf was present: 0, 1; time of day: 1-24; and group identity) were related to discontinuous acoustical variables (minimum number of individuals producing slow clicks: 0, 1, 2; whether or not a recording sessions was silent; whether or not click rates were under 20/s (low click rate), and whether or not click rates were over 60/s (high click rate)). Likelihood ratio G tests were performed to determine which relationships were significant.

The above discontinuous circumstantial variables were also related to continuous acoustical variables (number of codas, number of creaks, and click rate in clicks/s) using a Kruskal-Wallis one-way analysis of variance. All tests were done using the reduced data set which excluded sessions with fog and autocorrelation, except when time of day was examined. Since the reduced data set was comprised only of sessions from 08.00 h and 16.00 h, the total data set needed to be used in the analysis of diurnal effects. Only significant results ($p<0.05$) are presented below.

b) **Correlations between coda types, creak types, and behavioral/circumstantial variables** (for Results Sec. 3.7 and 3.8)

i) Coda types

The acoustical variables used were the total numbers of each of the 23 coda types (from Table 2; see Sec. 3.5b for categorization) for each session, various groupings of these 23 coda types, and creak variables. The variable "regular codas" included the total numbers of all regular coda types for each session, i.e. summed numbers of coda types "3", "4", "5", "6", "7reg", "8reg", "9", "10", "11", and "12". The variable "irregular codas" consisted of all of the remaining coda types (those with "var", "+1"s, "+1+1"s, "7L", "8L", etc.). In addition, coda types were divided up into "short codas" (those with a total click number of 6 or less), "medium codas" (total click number of 7-8), and "long codas" (total click number of 9-12). "Total coda number" represented a total of all codas for each session, even those which did not belong to one of the 23 coda types (i.e. usually rare types too uncommon for the above categorization).

hour: 0, 1, 2; whether or not a calf was present: 0, 1; time of day: 1-24; and group identity) were related to discontinuous acoustical variables (minimum number of individuals producing slow clicks: 0, 1, 2; whether or not a recording sessions was silent; whether or not click rates were under 20/s (low click rate), and whether or not click rates were over 60/s (high click rate)). Likelihood ratio G tests were performed to determine which relationships were significant.

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Table 2. Acoustical variables, number of occurrences, and (for coda types only) mean total length (s), standard deviation, and coefficient of variation.

Sound type	Number counted	Mean total length	S.D.	C.V.
"3"	11	0.49	0.20	0.41
"3var"	9	0.60	0.07	0.12
"3+1"	31	0.83	0.11	0.13
"4"	30	0.75	0.23	0.31
"2+1+1"	7	1.47	0.08	0.05
"4+1"	152	1.18	0.11	0.09
"5"	232	0.77	0.23	0.30
"5+1"	107	1.24	0.13	0.10
"6"	83	1.18	0.35	0.30
"6+1"	16	1.60	0.30	0.19
"7L"	31	0.84	0.14	0.17
"7reg"	103	1.38	0.29	0.21
"5+1+1"	12	1.78	0.13	0.07
"8L"	50	0.97	0.15	0.15
"8reg"	101	1.51	0.31	0.21
"7+1"	23	1.25	0.28	0.22
"6+1+1"	7	1.97	0.29	0.14
"8+1"	9	1.44	0.57	0.40
"9"	41	1.70	0.38	0.22
"10"	24	1.96	0.90	0.46
"9+1"	10	1.43	0.42	0.29
"11"	13	2.43	0.48	0.20
"12"	6	2.52	0.33	0.13
regular codas	644			
irregular codas	464			
short codas	662	Mean = 1.36		
medium codas	343			
long codas	103			
total coda no.	1333			
total creak no.	306			
creak int. <25ms	67			
creak int. <75ms	140			
creak int. >75ms	73			
<11 clicks/creak	94			
<16 clicks/creak	75			
<21 clicks/creak	46			
<31 clicks/creak	39			
>30 clicks/creak	24			

ii) Creak types

Creaks were divided up into categories according to the number of clicks they contained and categories based on the estimated average interclick intervals of the creaks. Mean interclick intervals of 25 ms or less were called "short interval creaks", mean interclick intervals of between 25 ms and 75 ms were termed "medium interval creaks", and "long interval creaks" had interclick intervals of greater than 75 ms, on average. Creaks were divided into 5 categories based on the number of clicks they contained: 1) fewer than 11 clicks; 2) between 11 and 15 clicks, inclusive; 3) between 16 and 20 clicks, inclusive; 4) between 21 and 30 clicks, inclusive; and 5) more than 30 clicks. The variable "total creak number" tallied the total number of all creaks for each session. Since interclick intervals and number of clicks per creak were not specified for all creaks, this total would be slightly higher than that obtained by summing the five clicks per creak categories or the three interclick interval categories together.

In summary, the 38 acoustical variables were: coda types 1-23, regular codas, irregular codas, short, medium, and long codas, total coda number, short interval creaks, medium interval creaks, long interval creaks, number of clicks per creak (categories 1-5), and total number of creaks.

iii) Unstandardized and standardized data sets

Acoustical variables were subjected to statistical analysis in two different forms: unstandardized and standardized. In the unstandardized form, raw total counts of each of the variables for each session were used. In the standardized form, coda types 1-23, regular, irregular, short, medium, and long codas were divided by the total number of codas of the 23 types for each session, to give relative numbers of each particular variable. This denominator was not the same as the variable "total coda number" since the latter included codas other than those categorized into the 23 types. Similarly, the short, medium, and long interval creaks, and the 5 categories of numbers of clicks per creak were each divided by the variable "total creak number". Obviously, variables "total coda number" and "total creak number" were absent from the standardized data set.

iv) Circumstantial/behavioral variables

There were 14 circumstantial and behavioral variables used in the examination of the contexts of different coda types. The month (January-June) and year (1985 and 1987) of the session were used, and time of day was divided up into 5 blocks of 4 h each: 1) 02.00-06.00; 2) 06.00-10.00; 3) 10.00-14.00; 4) 14.00-18.00; 5) 18.00-22.00. No sessions analyzed for coda types occurred in the 22.00-02.00 time period. The presence or absence of males, the presence or absence of calves, and the occurrence or not of clusters joining were discontinuous variables. Other variables included: the estimated speed of the whales, the maximum cluster size, the number of clusters, and the number of breaches, lobtails, flukes, sideflukes, and spyhops seen within 500 m of the boat.

Since the 5-min acoustical recordings were often not done exactly simultaneously with the 5-min behavioral intervals (acoustical recordings were done once for 5 min every h, whereas behavioral data were collected every 5 min), the two adjacent 5-min behavioral intervals which included the acoustical recording were used. Some variables (speed of whales and number of clusters) were averaged over the two intervals, whereas for maximum cluster size, the maximum was taken of the two intervals. The number of breaches, lobtails, flukes, sideflukes, and spyhops was obtained by adding together the values of each variable for the two intervals.

In summary, the 14 circumstantial and behavioral variables were: month, year, time of day, presence of males, presence of calves, occurrence of joins, speed of whales, maximum cluster size, mean number of clusters, number of breaches, lobtails, flukes, sideflukes, and spyhops. The last variable was the identity of group seen during the 5-min acoustical recording session, when it could be reliably determined (Whitehead and Waters, in press). Groups from 1985 included: G3, G6, G11, G12, G18, and G19. Groups from 1987 were: H2, H3, H5, H7, H12, H13, H21, H36. Groups that were reidentified in 1987 as being the same as in 1985 were combined. Thus group G2 was lumped with H5, and group G9 was combined with H21 (Whitehead and Waters, in press).

c) **Graphical displays of data**

Box plots are given in Fig. 10 (unnotched) and Figs. 13, 14, 15, 16, and 17 (notched). The center vertical line marks the median, and the box represents the interquartile range. Horizontal lines denote the range of most of the values. Outside values are represented by stars, and extreme outside values by circles. This is the same for notched box plots, except that the medians are depicted by center horizontal lines and are notched, and vertical lines denote the range of most of the values. Boxes return to full width at the lower and upper confidence interval values. If the intervals around two medians do not overlap, one can be confident at about the 95% level that the two population medians are different (Wilkinson 1988). However, some box plots are done on the full data set (without restrictions to remove autocorrelation), and thus confidence intervals suggested by notches are not strictly accurate.

The "jitter" option was used to produce Figs. 25 and 26. Since interclick intervals of creaks were usually estimated by numbers of clicks per 0.05 s, and since these intervals generally assumed only about 5 possible values (2 to 5 clicks/0.05 s), points in these plots would often overlap. To prevent points from lying on top of one another in scatterplots, the jitter option adds a small amount of uniform random error to the location of each point (Wilkinson 1988). In Fig. 26 especially, points appear to be clustered along three horizontal lines, but this, again, is an artifact of the way intervals were estimated, with few possible values.

CHAPTER 3. RESULTS

3.1 Usual clicks

a) **Interclick intervals (ICIs)**

The distributions of median interclick intervals for series of usual clicks (UCs) had similar shapes and similar medians for both 1985 and 1987 (Fig. 6). The median for all UC interclick intervals was 0.51 s in 1985, and 0.55 s in 1987. These medians are similar to the middle of the range of ICIs given by Backus and Schevill (1966), namely 0.64 s.

b) **Frequency structure**

To examine each click's pattern of intensity peaks over the range of frequencies studied, the peaks of all 38 UCs from 1985 were displayed (Fig. 7). Clicks were grouped according to the probable identity of the emitter. Individual variation in emphasized frequencies was apparent, though probably not sufficient to definitely identify individuals within a reasonably large sample.

c) **Duration**

Backus and Schevill (1966) presented the range of usual click durations as 2-24 ms. UC durations measured in 1985 by

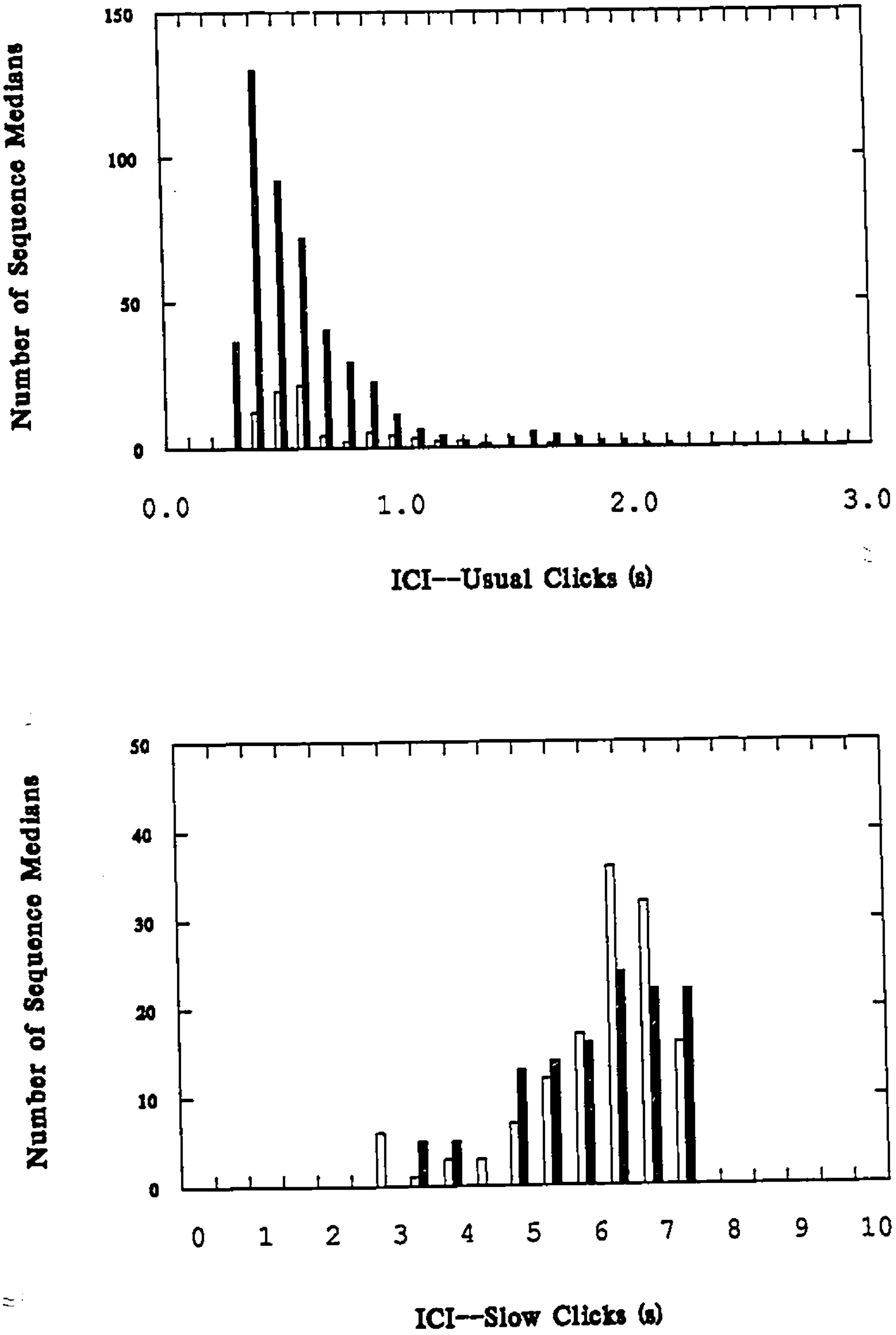


Fig. 6. Distribution of interclick intervals (sequence medians in s) for usual clicks and slow clicks (1985=white; 1987=black).

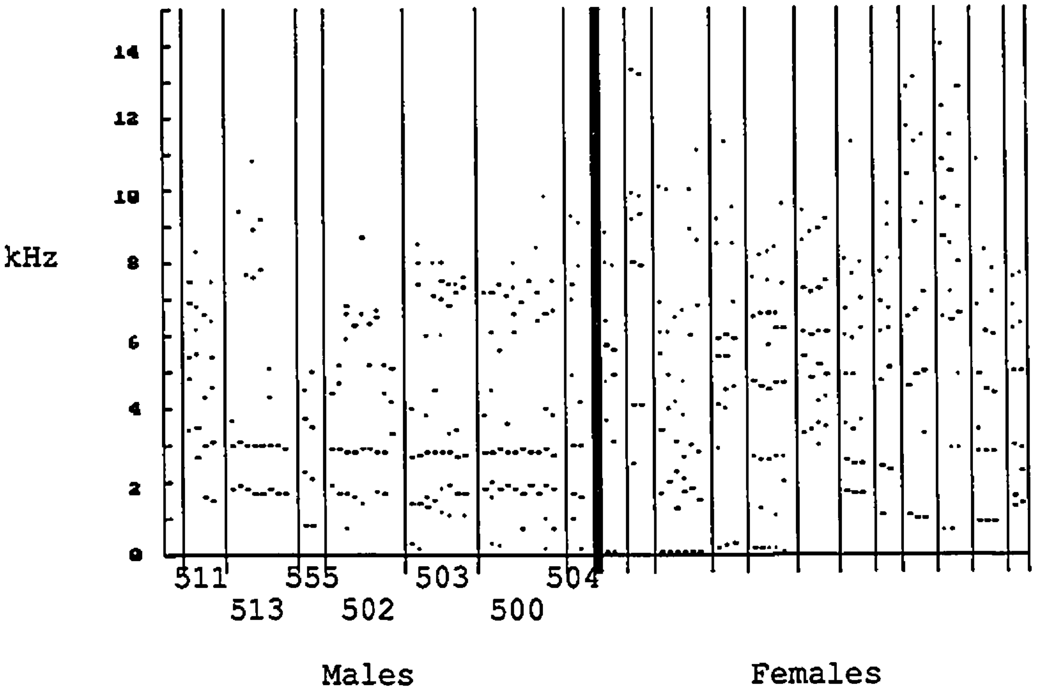


Fig. 7. Frequency plots of intensity peaks for slow clicks of different males (left) and usual clicks from females (right). Each vertical series of points represents intensity peaks of one click. Vertical lines separate individuals.

sonagram were not very accurate, particularly at durations of under, very approximately, 10 ms, but results were of a similar magnitude as those of Backus and Schevill (1966). A waveform of a UC is presented in Fig. 8.

3.2 Slow clicks (SCs)

a) **Correlation with presence of mature males**

There was a close correspondence between occasions when males were seen and when SCs were heard: if SCs were heard during daylight, a mature male was usually seen (Fig. 9). The relationship between seeing mature males and hearing slow clicks was also highly statistically significant ($p<0.001$; G test, $n=121$; Table 3). The vast majority of time (77.6%) that one male was seen, at least one slow-clicking individual was also heard (Table 3). Only 2.8% of the time that no slow click was heard, at least one male was nevertheless seen.

Higher numbers of different slow clicks were heard when males were seen together (Pearson $r=0.562$, $p<0.001$, $n=821$). Forty-four percent of the time that two males were sighted together, two different slow click series were also heard (Table 3). An additional 33.3% of the time two males were seen, one slow clicker was heard, giving a total of 77.7% of the time that at least one slow clicker was heard when two males were seen as present.

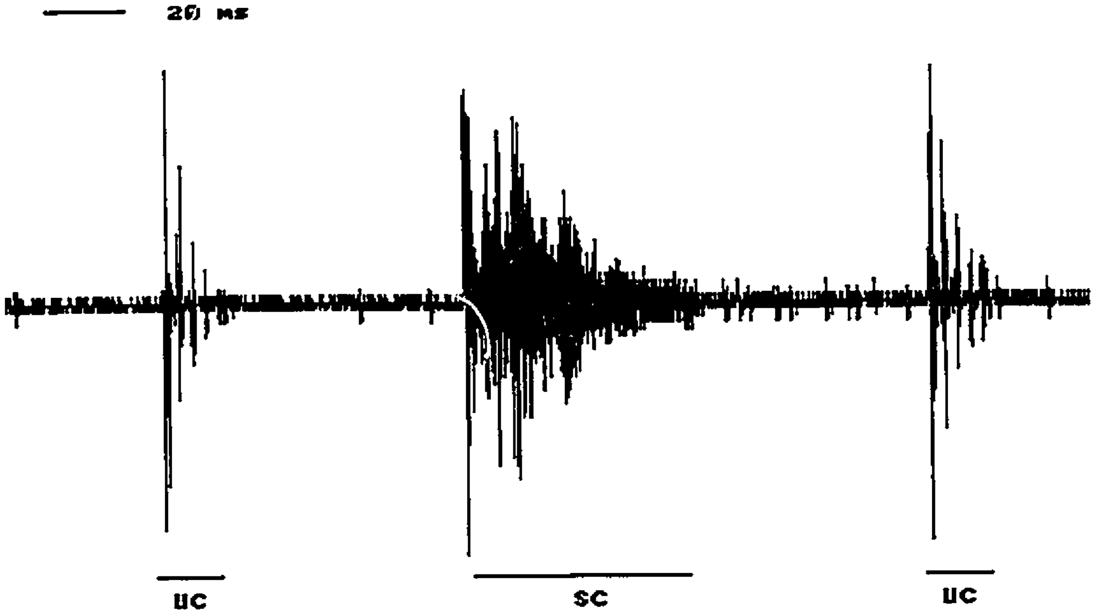


Fig. 8. Sample waveforms (amplitude vs. time) for usual clicks (UCs) and a slow click (SC). These UCs show the multiple pulse structure of clicks unusually clearly.

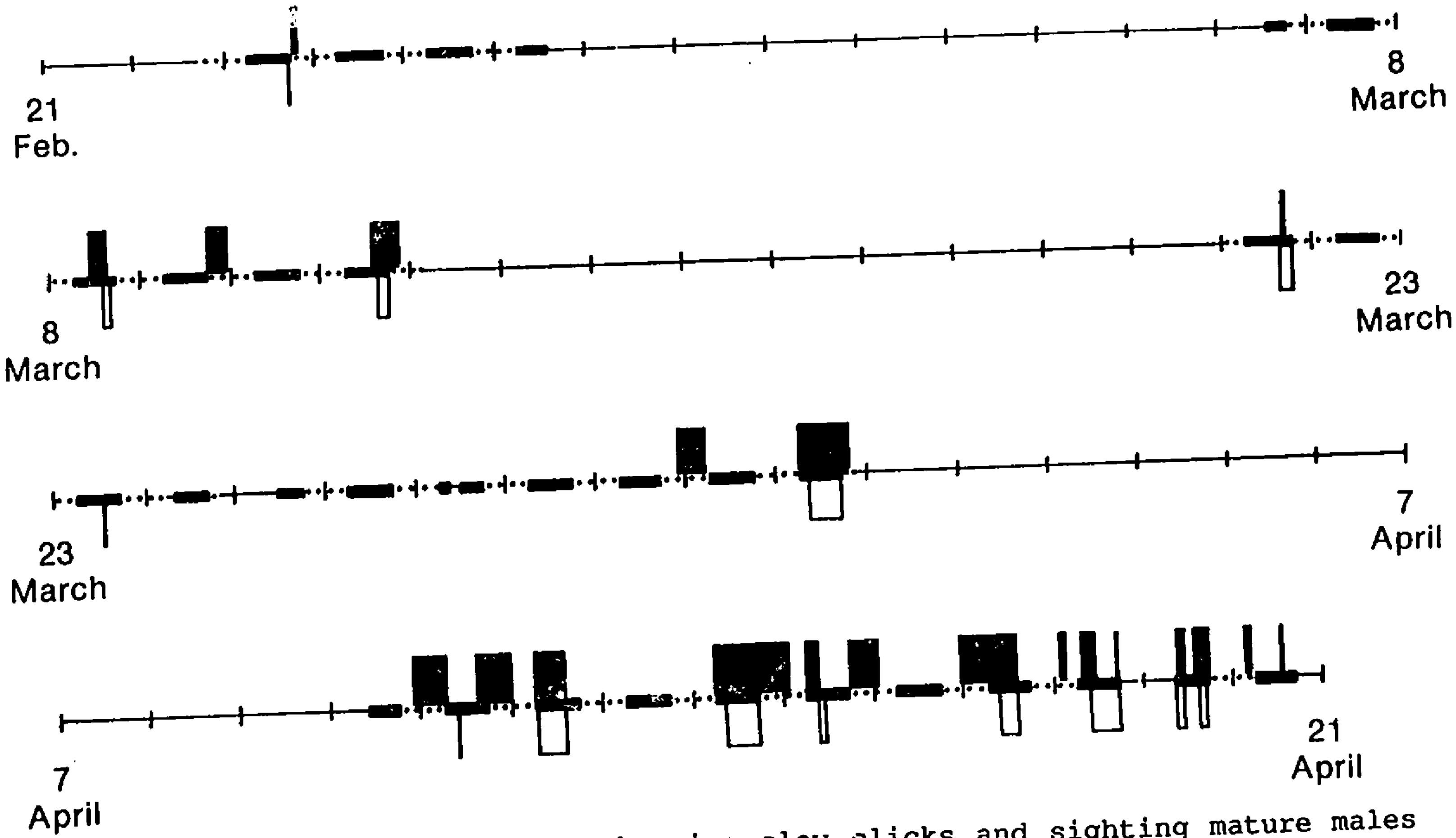


Fig. 9. The association between hearing slow clicks and sighting mature males (1985 only). Times of visual or acoustic contact: darkened time scale (day); dotted lines (night). Solid blocks above time line: slow clicks heard; open blocks below: male seen. (Reprinted courtesy of Canadian Journal of Zoology.)

Table 3. The relationship between hearing slow clicks and seeing mature males.

		No. of mature males seen			
		0	1	2	Total
No. of diff. slow click series heard	0	659	17	2	678
	1	75	53	3	131
	2	2	6	4	12
Total		736	76	9	821

While slow clicks were almost always heard once males had been sighted, the converse was not true. Even though only daylight sessions were used in this test, only 46.2% of the time that at least one slow-clicking individual was heard, at least one male was also sighted, i.e. 53.8% of the time slow clicks from at least one individual were heard but no male was seen (Table 3). Slow clicks apparently carry over long distances, whereas males can usually only be visually identified with certainty within 500 m.

Thus, there can be little doubt that slow clicks are produced by mature males off the Galápagos Islands. The following is the first description of this sperm whale vocalization.

b) Interclick intervals (ICIs)

The distributions of median ICIs for SCs were again quite comparable between years, both in shape and in median (Fig. 6). The median ICI of all slow clicks was 6.03 s for 1985 and 6.06 s for 1987. The distributions of median ICIs for UCs and SCs were almost totally discrete, with the exception of one median UC outlier. The median ICI for SCs was longer than that for UCs by more than a factor of 10.

Differences among ICIs of identified males were apparent in box plots, which present ICIs of 6 of the 7 known males (Fig. 10). These differences, however, were not sufficiently

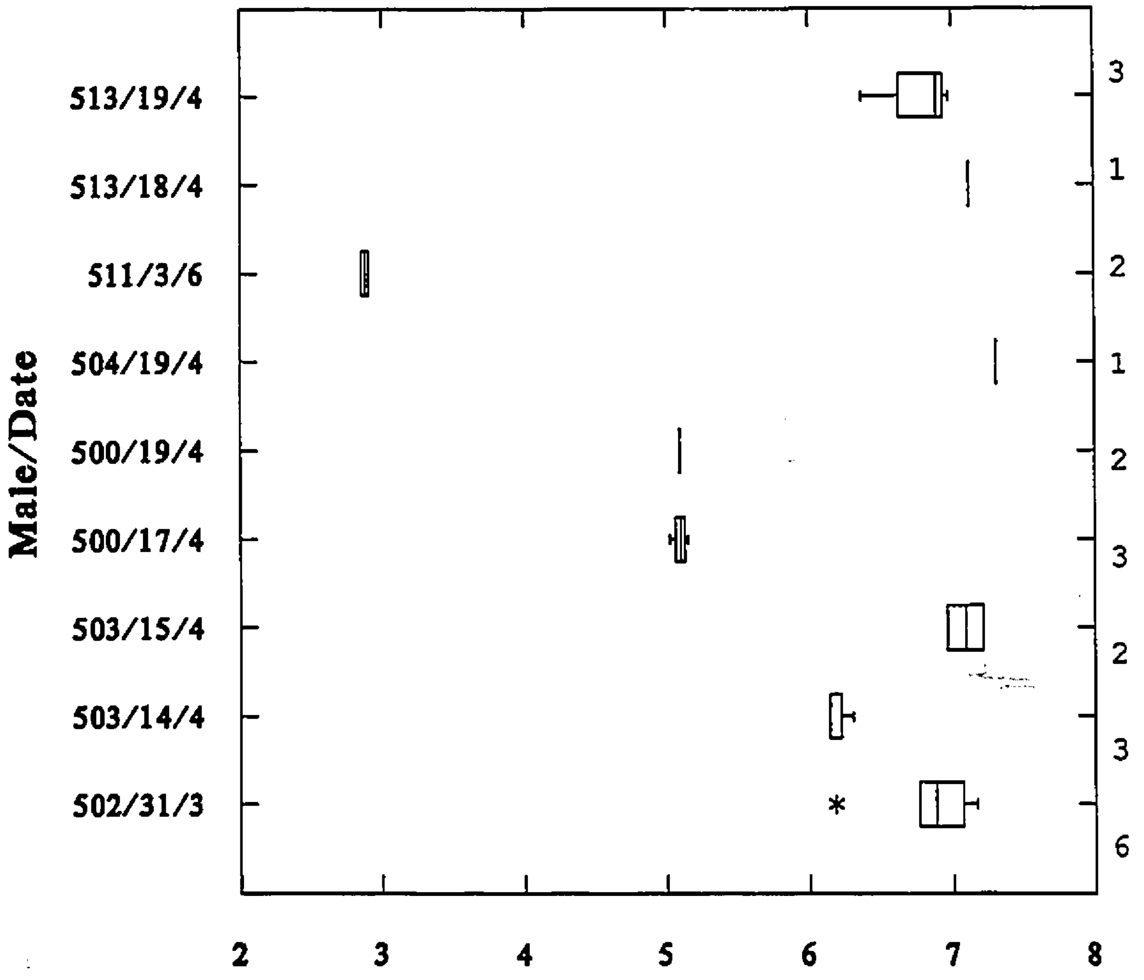


Fig. 10. Box plots of session median interclick intervals of known males on different days. Sample sizes are given on the right. Medians are denoted by vertical lines, interquartile ranges by boxes (see Sec. 2.6c).

distinct to allow positive identification of these 6 males by their ICIs alone. Moreover, the individual differences in ICI were probably not reliable identity cues, since there was some indication that males altered the length of their ICI between days. On three occasions, the same identified males were recorded on two different days: Male 503 altered his ICI significantly from 14 to 15 April, Male 513 shifted the length of his ICI somewhat from 18 to 19 April, while Male 500 showed no difference in ICIs between 17 and 19 April.

c) **Frequency structure**

As with the UCs above, the peaks of all 43 SCs were displayed to examine each click's pattern of intensity peaks over the range of frequencies studied (Fig. 7). Clicks were again grouped according to the identity of the emitter. Since only 2 SCs of Males 555 and 504 were represented by sonagram, and both came from the same sessions, sample sizes are small and results should be viewed with caution. Two consistent bands of peaks at about 1.8 kHz and 2.8 kHz are discernable in the display of the SCs. The bands were somewhat different in the SCs of the West Indies male (555). There were no similarly obvious bands of peaks running through the UCs. Though this is not evident from Fig. 7, the intensities of these two peaks in slow clicks were usually greater than those of usual click peaks.

Again, while there may have been some individual differences among males in the frequencies emphasized, no immediately obvious patterns of peaks were peculiar to particular individuals. The UCs, in general, showed more variation between individuals, and contained relatively more intense peaks at higher frequencies than the SCs.

Peaks of each click were compared with those of every other click to estimate whether there was more variation between individuals than within them in the pattern of emphasized frequencies. If the two clicks being compared shared peaks within 300 Hz of each other, a match was tallied. The greater the number of matches present between two clicks, the more similar they were thought to be. The number of matches was then examined in relation to the association the two compared clicks had to each other, i.e. each produced by a different male, both produced by the same male but from different sessions, or a SC being compared to a UC, etc. (Fig. 11). The same 38 UCs and 43 SCs depicted in Fig. 7 were used in this comparison.

The greatest similarity (highest mean number of matches) in the pattern of emphasized frequencies was present between clicks from the same male but recorded on two different dates. This was followed in mean number of matches by clicks from the same male and same session, and then clicks from the same male but from different sessions of the same day. The grand mean from these three within-individual associations was 2.92

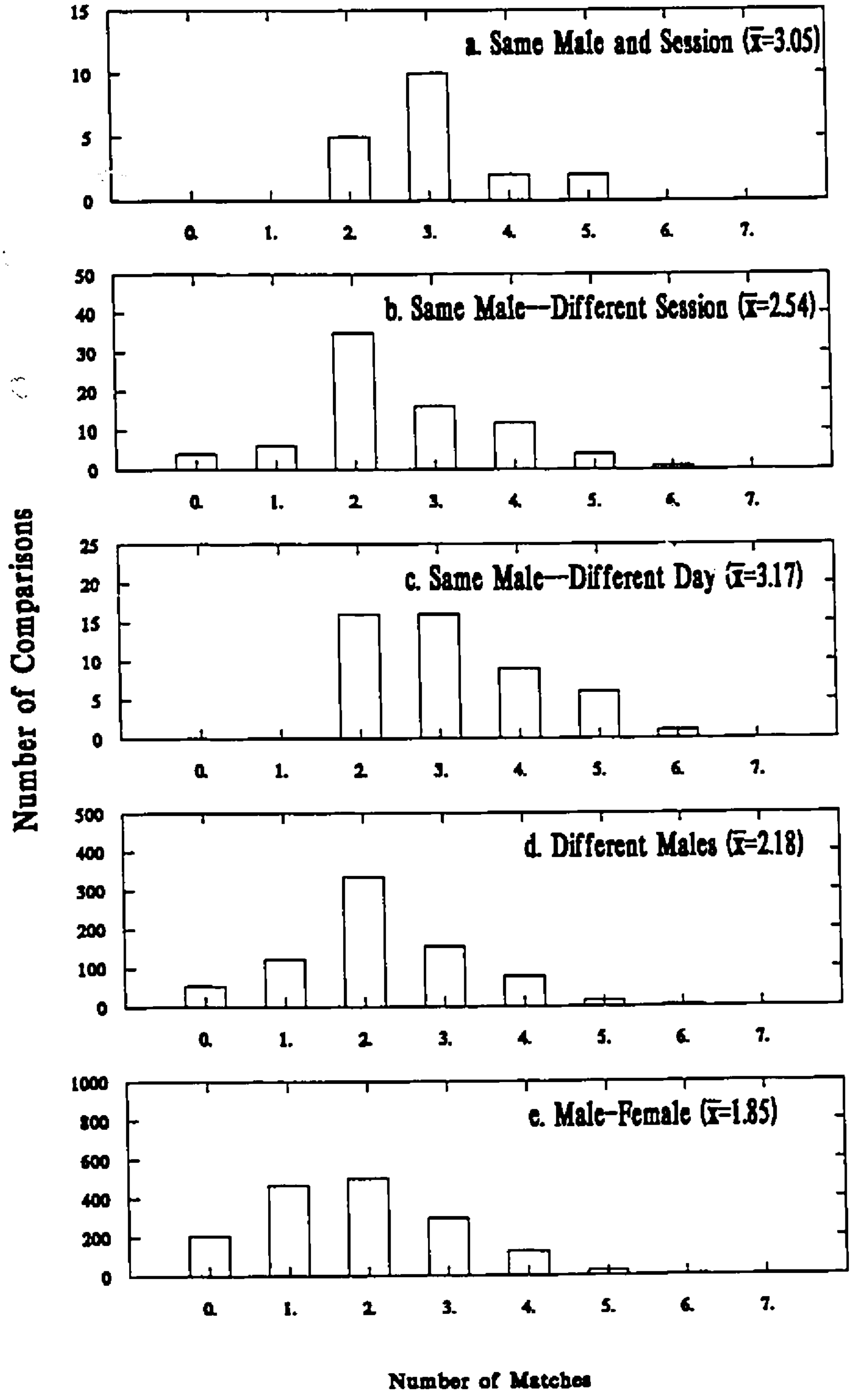


Fig. 11. Number of matches (times intensity peaks were within 300 kHz of one another) for clicks from same male (same session, a.; same day, b.; different days, c.), different males (d.) and individuals of different sex (e.).

matches. This can be compared to a mean of 2.18 matches between clicks from different males, and 1.85 matches between UCs and SCs. This analysis, though very insensitive and not a formal test, revealed a greater similarity in the frequencies emphasized in clicks from the same individual as opposed to clicks from different individuals. However, the greatest differences in frequency structure occurred between UCs and SCs. The results of this analysis were similar when different criteria for a match were used (e.g. peaks within 200 Hz of each other).

d) **Duration**

SCs had a median duration of 68 ms, and a range of from 28 to 124 ms in 1985. In 1987, the median SC duration was 80 ms, with a range of from 24 to 160 ms. The overall median duration for both years combined was 68 ms. Thus, SCs were generally longer in duration than UCs. Durations were measured by sonagram and therefore, were not very accurate, perhaps overestimating durations by roughly 5-6 ms. A comparison of the waveforms of a UC and a SC (Fig. 8) shows that the SC has approximately 3.5 times the duration of the UC.

The longer durations of SCs were mostly a result of the "ringing" quality (slow damping) which occurred at peaks of intensity, located at usually only fairly low (<4.0 kHz) frequencies. The 2.8 kHz band common to all males often showed ringing, whereas the 1.8 kHz band practically never did. This "ringing" quality is displayed clearly in both the SC sonagram (Fig. 3) and waveform (Fig. 8).

e) **Relationship to male's length**

The exact location of the two intensity peaks (at roughly 1.8 and 2.8 kHz) varied from about 1.6 to 1.9 kHz for the lower band, and about 2.7 to 3.2 kHz for the upper band in 8 identified mature males for which body length information exists. Total body length was measured photographically (Gordon, in press), and males from both years were used in this analysis.

There was no significant relationship between either the frequency location of the lower (Pearson, $r=0.567$, $p>0.10$, $n=8$) or upper (Pearson, $r=-0.537$, $p>0.10$, $n=8$) band of intensity peaks and the males' total body length. These two correlation coefficients were of similar magnitude but opposite in sign.

A correlation coefficient was also calculated between the males' total body length and their median ICI, but this negative correlation was also not significant (Pearson, $r=-0.494$, $p>0.10$, $n=8$).

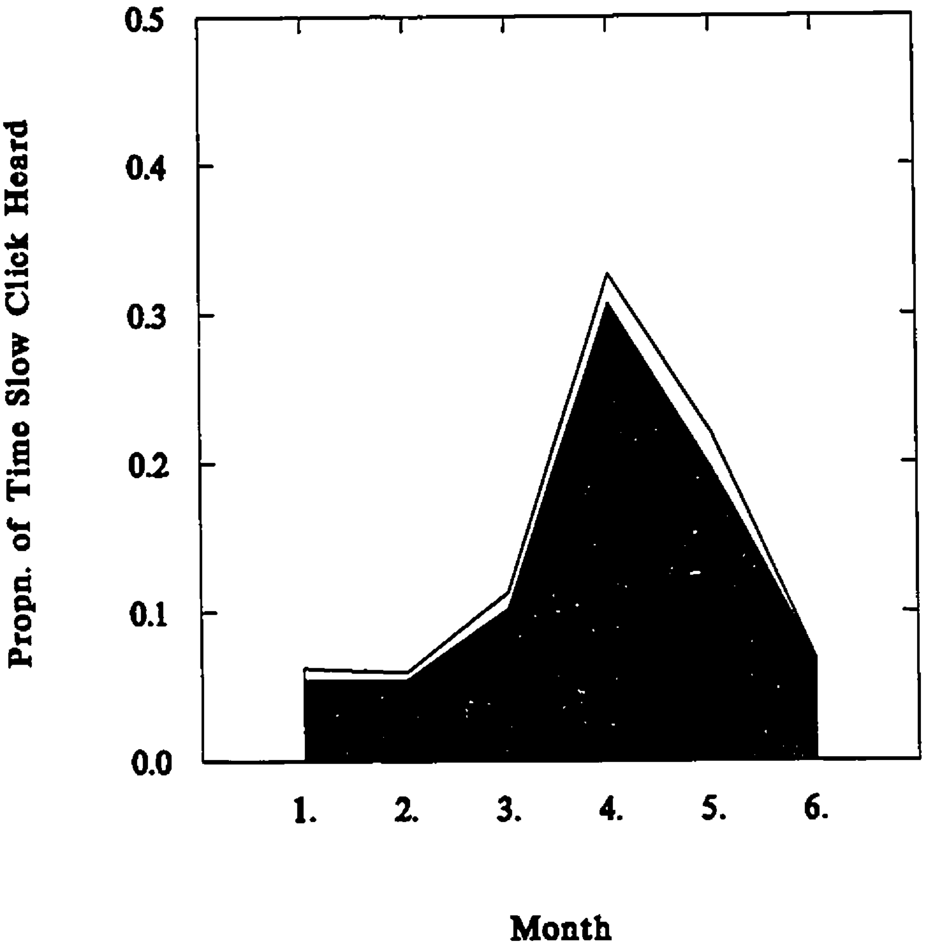


Fig. 12. Monthly variation in the incidence of slow clicks (proportion of sessions in which slow clicks were heard). The proportion of sessions in which slow clicks were heard from two individuals simultaneously is shown in white.

f) **Monthly variation in slow clicks**

Slow clicks showed a distinct trend with respect to month (G test, $p<0.05$, $n=127$). Most slow clicks were heard in April, when 32.7% of the time at least one slow clicking individual was heard (Fig. 12). This is in comparison with January, February, and June, when only 6.2%, 6.9%, and 6.9%, respectively, of the time at least one individual producing slow clicks was heard. March, and especially May, also showed higher incidences of slow clicks (March-11.3%, May-21.9%). Two individuals simultaneously producing slow clicks were heard most often in April and May. This seems to indicate that April-May is the season of peak mating off the Galápagos, but that some mating probably occurs in March and at other times of the year as well.

g) **Summary**

There is little doubt that slow clicks are produced by mature males off the Galápagos, since their occurrence was strongly correlated with the presence of males, two different slow click series were often heard when two males were seen, and there were some consistent individual differences in frequency emphasis and interclick interval between different males. These differences were not distinct enough to allow me to identify individuals. The usual clicks heard from groups of females and immatures showed somewhat more variation in frequency emphasis between individuals. Slow clicks could be distinguished from usual clicks primarily by their longer interclick intervals, but also by their peaks of stronger intensity at lower frequencies, especially those at 1.8 and 2.8 kHz, and their longer durations. There was no significant relationship between male body length and frequency location of the two main peaks in intensity, or between body length and interclick interval of their slow clicks. Slow clicks were heard more often in April and May.

3.3 Correlations between acoustical and behavioral/circumstantial variables (See Methods Sec. 2.6a)

a) **Behavioral**

Both codas and creaks were very significantly correlated with the number of sideflukes and spyhops seen (and those within 500 m) (Table 4). Higher click rates were heard when more fluke-ups were seen (r=0.429), and when more fluke-ups were seen within 500 m (r=0.323). High click rates (over 60/s) were also positively correlated with fluking (r=0.340).

b) **Social**

The number of codas heard was highly correlated with the number of clusters within 500 m, the total number of individuals, and the total number of individuals within 500 m (Table 4). Greater numbers of codas were also heard from larger clusters as indicated by mean cluster size and maximum

Table 4. Pearson correlation coefficients between sounds and behavior for the complete 1985 and 1987 data set (excluding sessions with fog). Sample sizes were around 800. Spearman correlation coefficients, computed on these same relationships but using only a subset of these data, were highly significant ($p<0.01$). The one exception was the relationship of number of codas with maximum number of males seen together, which was only significant at the 0.05 level. Sample sizes of the reduced data set used for Spearman correlations were around 120.

	No. of codas	No. of creaks
No. of clusters within 500m	0.313	--
No. of individuals	0.567	0.502
No. of individuals within 500m	0.583	0.519
Mean cluster size	0.449	0.380
Maximum cluster size	0.548	0.496
Maximum no. of males together	0.301	--
No. of sideflukes	0.428	0.397
No. of sideflukes within 500m	0.425	0.397
No. of spyhops	0.385	0.334
No. of spyhops within 500m	0.383	0.333
No. of creaks	0.640	

cluster size. Creaks, which were themselves highly correlated with codas, showed similar relationships with number of individuals, number of individuals within 500 m, mean cluster size, and maximum cluster size. Incidentally, correlations between mean cluster size and number of clusters or number of clusters within 500 m, were low, not significant, and slightly negative.

Click rates, which are affected not only by the number of individuals present underwater but also by their sociality (Whitehead and Weilgart 1990), tend to be higher when whales are spread out in many clusters rather than grouped in large clusters. Indeed, click rates were positively correlated with numbers of clusters (r=0.446) and numbers of individuals seen more than 500 m away (r=0.412), which is also an indication of numbers of clusters present. High click rates (over 60/s) were similarly correlated with number of clusters seen (r=0.339). Click rates were <u>not</u> correlated, or slightly negatively correlated, with mean cluster size (r=-0.140) and maximum cluster size (r=-0.005). Repeating this association, low click rates (under 20/s) were related to mean cluster size (r=0.425). Indeed, whales tended to be silent in situations of large mean cluster size (r=0.399). This relationship was not significant using Spearman correlation coefficients, but because this variable only had two possible values (silence or lack of it), the Spearman correlation was not appropriate and could not give meaningful results. Click rates were also not strongly correlated with the total number of individuals seen ($r=0.189$), since click rates reflect the number of whales present <u>underwater</u>. Usual clicks are not generally heard from whales at the surface (Watkins 1980; Mullins et al. 1988; Papastavrou et al. 1989).

Codas were heard more often when more males were seen together (Table 4). Again, this correlation ($r=0.301$) was only significant at the 0.05 level using the Spearman correlation, since this test is not very appropriate for variables which assume only a few possible values. When the number of codas was compared with the discontinuous variable of presence or absence of males, significantly more (Kruskal-Wallis, $p<0.05$; $n=121$) codas were heard when males were present than when not (Fig. 13). Fig. 13, which represents the full data set, shows that the highest three or four coda totals were heard when one or two males were present, even though mature males were rather scarce. Clearly, however, high numbers of codas were still produced in the absence of males.

Significantly more codas (Kruskal-Wallis, $p<0.001$; $n=113$) and, to a lesser degree, creaks (Kruskal-Wallis, $p<0.05$; $n=113$) were heard when a calf was present than when absent. Maximum numbers of codas (Fig. 14) and creaks (Fig. 15) were heard in the presence of a calf, as opposed to its absence.

Click rates differed significantly among different identified groups (Kruskal-Wallis, $p<0.05$; $n=63$). Click rates

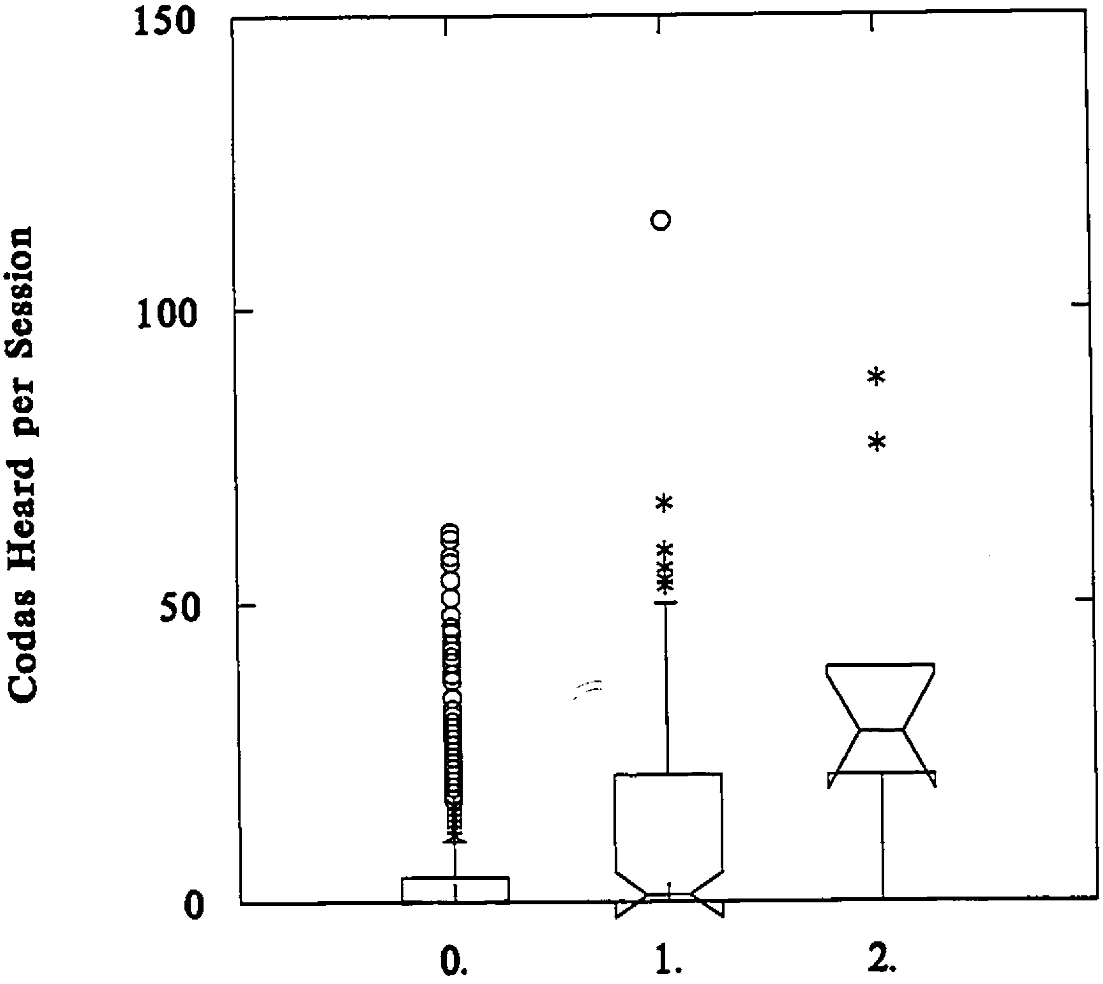


Fig. 13. Codas heard per session when no large males, one large male, and two large males were sighted together. Boxes are notched at median. See Sec 2.6c for explanation of symbols.

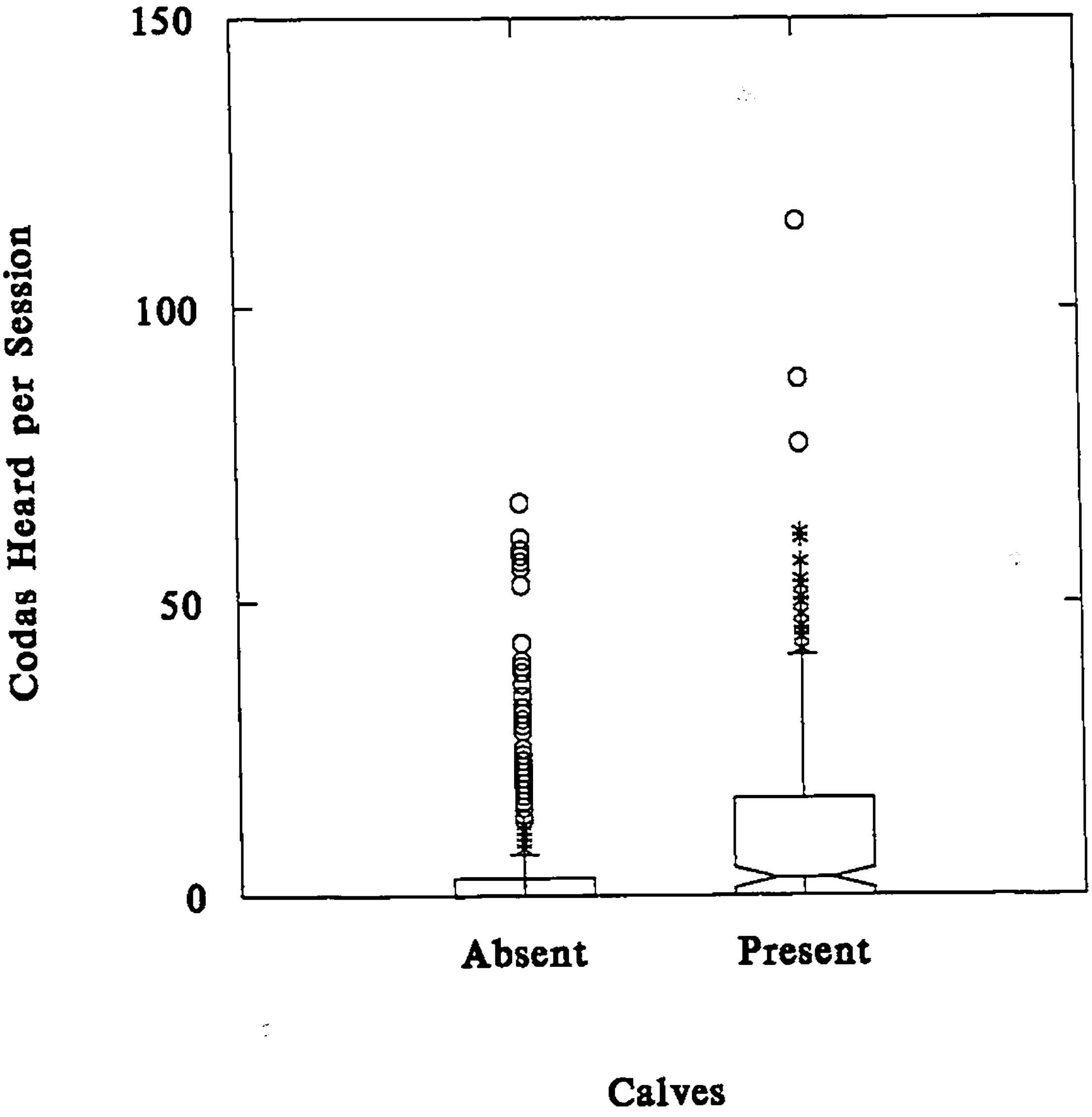


Fig. 14. Codas heard per session when calves were and were not sighted. Boxes are notched at median. See Section 2.6c for explanation of symbols.

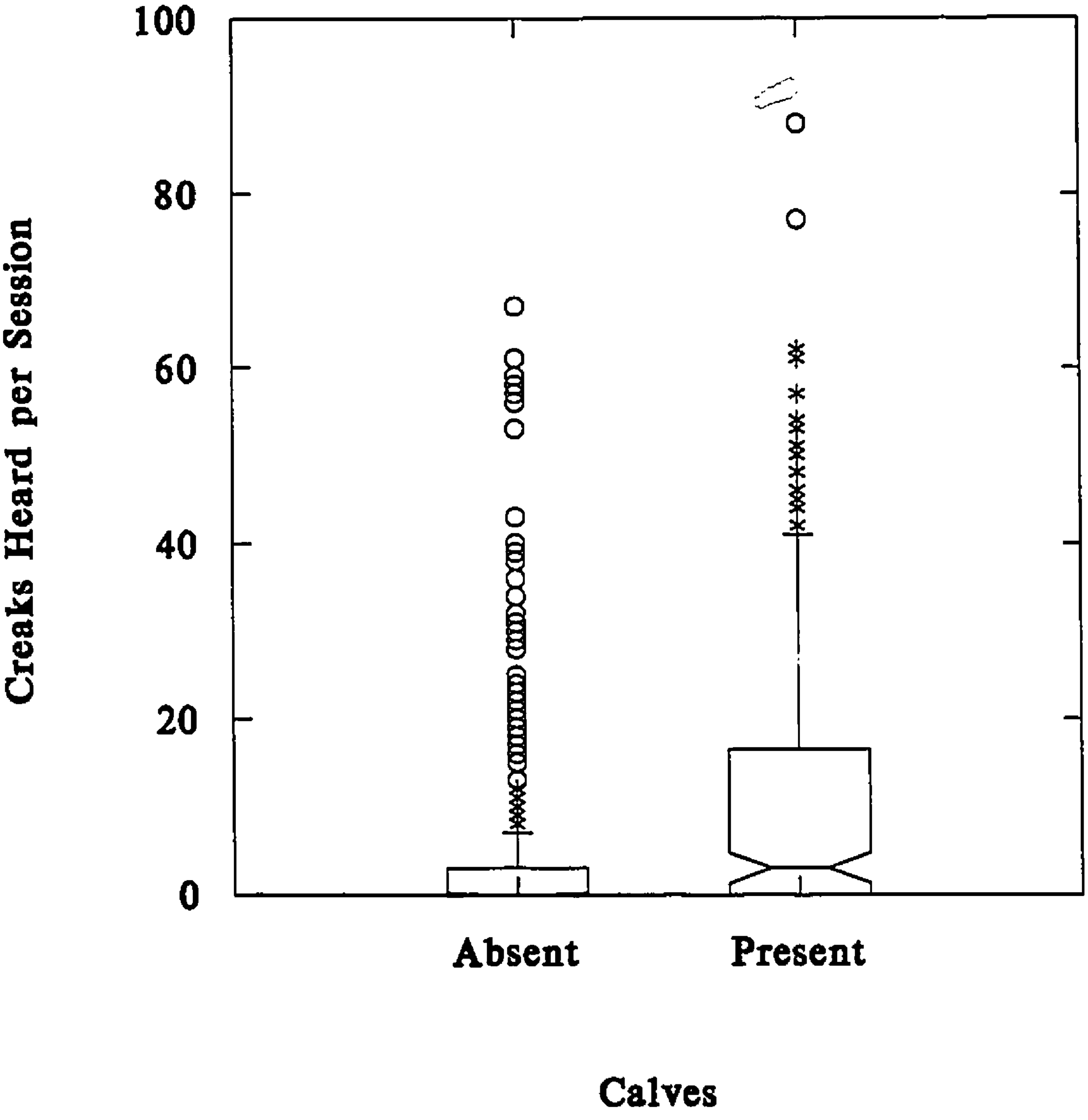


Fig. 15. Creaks heard per session when calves were present and absent. Boxes are notched at median. See Section 2.6c for explanation of symbols.

seemed related to the number of individuals present in the group and thus have potential for use in acoustic censusing (Whitehead and Weilgart 1990).

c) **Temporal**

Click rates were significantly higher (Kruskal-Wallis, $p<0.001$; $n=118$) in 1985 than in 1987 (Fig. 16). In 1987, there were also significantly more (G test, $p<0.05$; $n=125$) sessions containing low click rates than in 1985. In 1985, only 10% of all sessions contained click rates of under 20/s, whereas in 1987, 26% of all sessions contained very few clicks. This seems to signify that groups met less often in 1987 (Whitehead and Weilgart 1990), which was a year in which a small-scale El Niño oceanographic event occurred and in which the feeding success of sperm whales appeared to be reduced, in comparison with 1985 (Whitehead et al. 1989a).

An examination of high click rates revealed a similar trend to that above. In 1985, 57.6% of all sessions contained high click rates, compared with only 23.9% in 1987 ($p<0.001$; G test, $n=125$). No significant ($p<0.05$) seasonal effects in click rate could be discerned within years.

Creaks were also heard significantly more often ($p<0.001$; Kruskal-Wallis, $n=118$) in 1985 than in 1987 (Fig. 17).

Times of silence (when no clicks were heard despite whales being close) showed a diurnal effect ($p<0.001$; G test, $n=1572$), as did times of low click rates ($p<0.05$; G test,

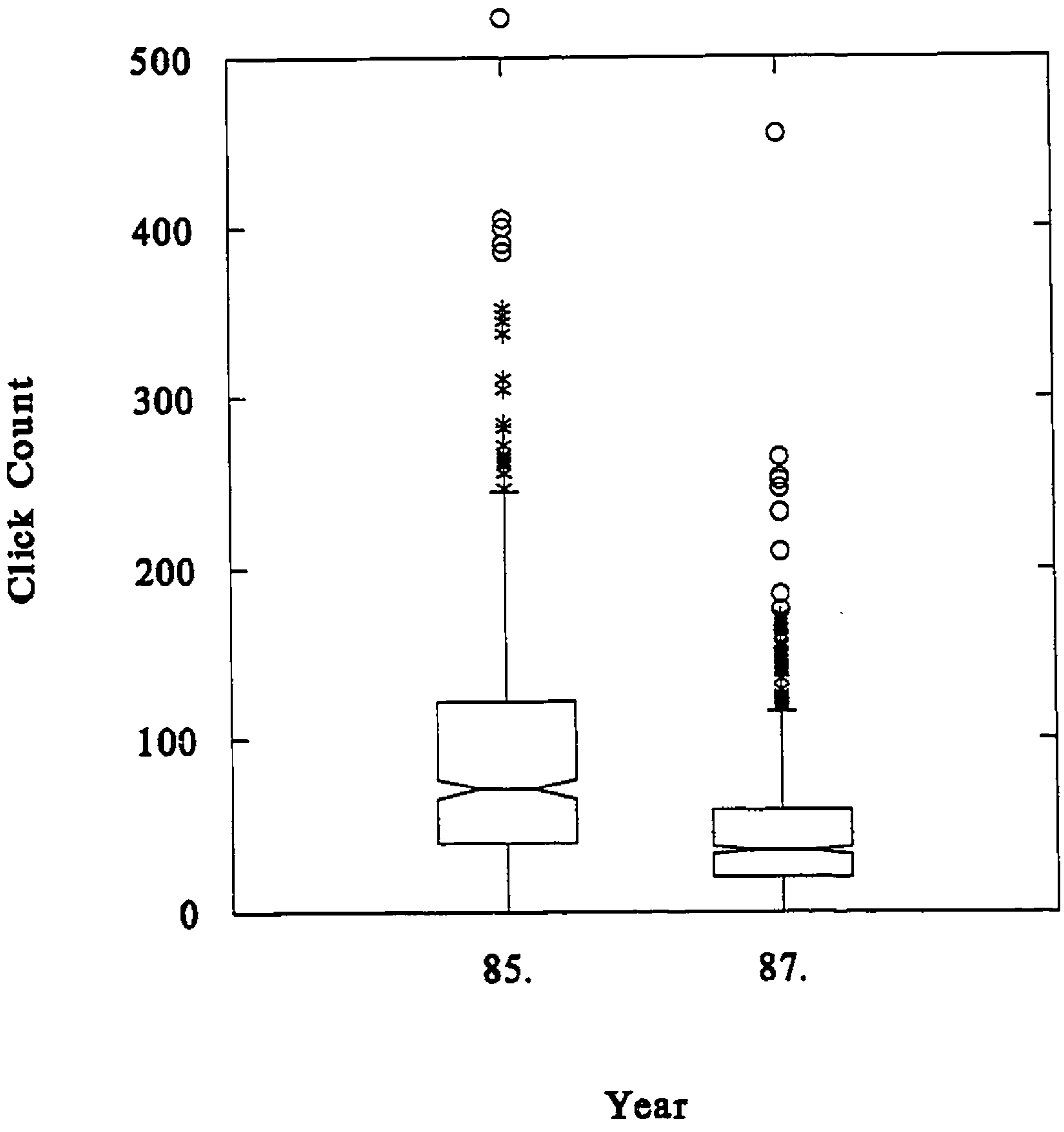


Fig. 16. Click counts (clicks/s) during 1985 and 1987. Boxes are notched at median. See Section 2.6c for explanation of symbols.

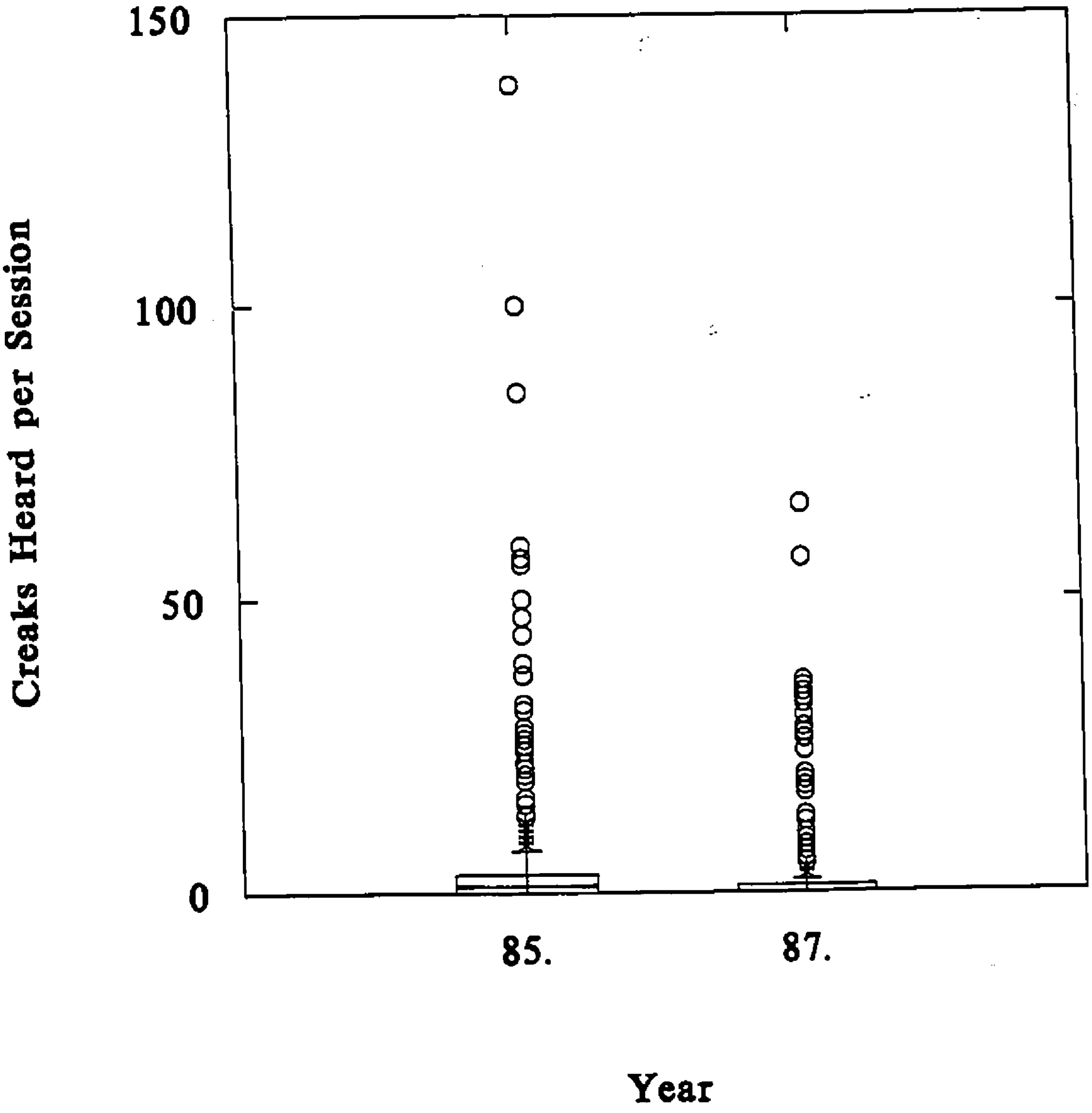


Fig. 17. Creaks heard per session in 1985 and 1987. Boxes are notched at median. See Section 2.6c for explanation of symbols.

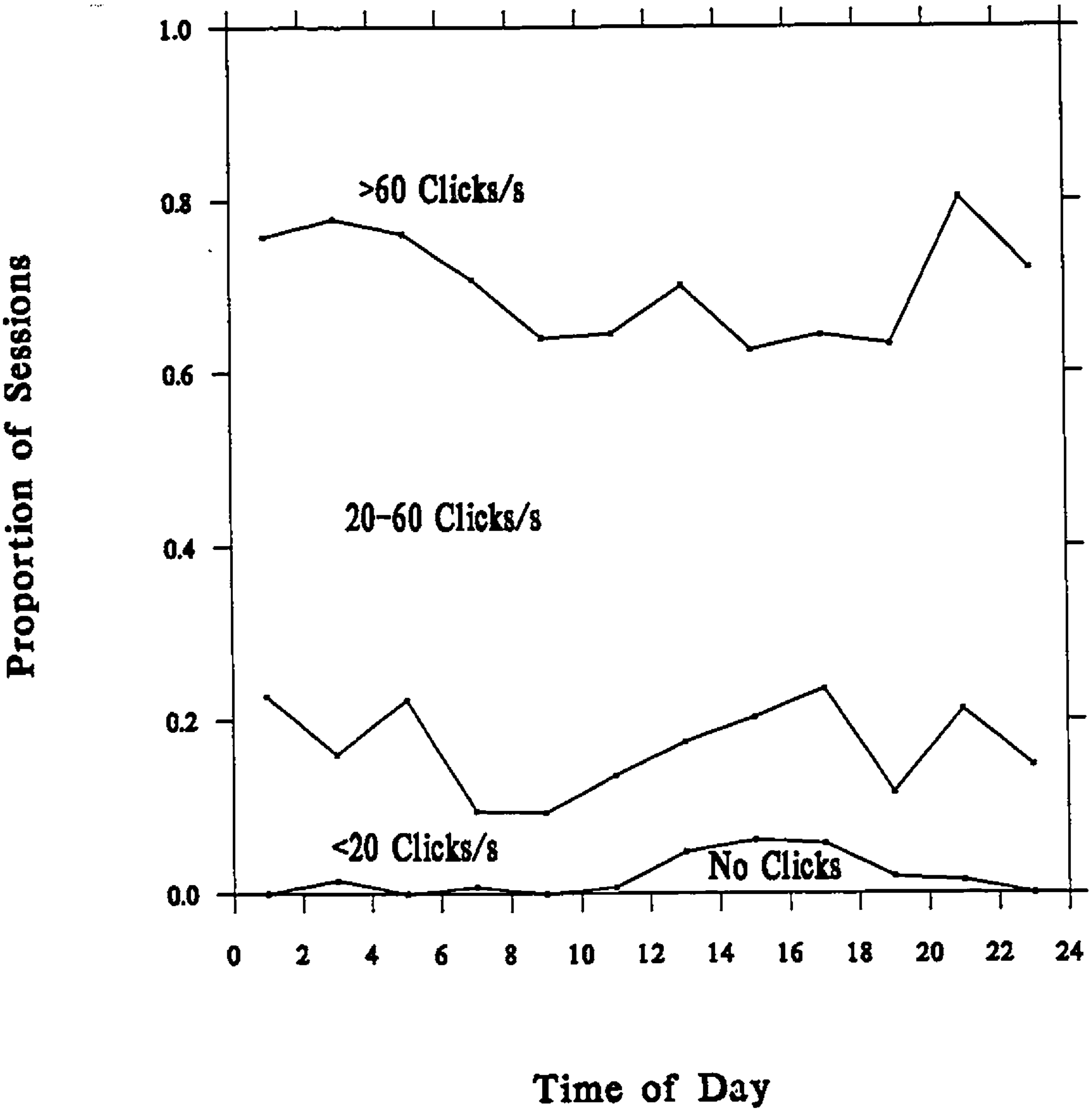


Fig. 18. Proportion of sessions with high click rates (>60 clicks/s), and low click rates (<20 clicks/s) and silent sessions with time of day.

n=1452). Silent times or times of low click rates were more common during the afternoon (Fig. 18).

Diurnal differences were significant for high click rates ($p<0.05$, G test, n=1452). Click rates over 60/s occurred most commonly during the daytime (Fig. 18). The times of overlap between low and high click rates (the afternoon), seemed to show that whales were either socializing or more than one group was present, and less frequently was there an intermediate between these two cases. Because high click rates occurred more often during the day, groups may have been meeting with other groups more often in the daytime than in the nighttime. Socializing seemed to occur mostly in the afternoon, as evident from both the no click and low click rate relationships.

Due to the large data set, the following significance tests could only be done on each year separately. Click rates varied significantly with time of day ($p<0.05$ for both 1985 and 1987; Kruskal-Wallis, n=477 (1985), n=892 (1987)). Click rates were highest, in general, in the daytime (Fig. 19), just as was shown above for the high click rate diurnal relationship.

Codas showed a very clear diurnal trend, especially in 1985 ($p<0.001$; Kruskal-Wallis, n=477), rising in number abruptly at 09.00 h and falling very sharply after 17.00 h (Fig. 20). In 1987, the diurnal relationship was not quite as

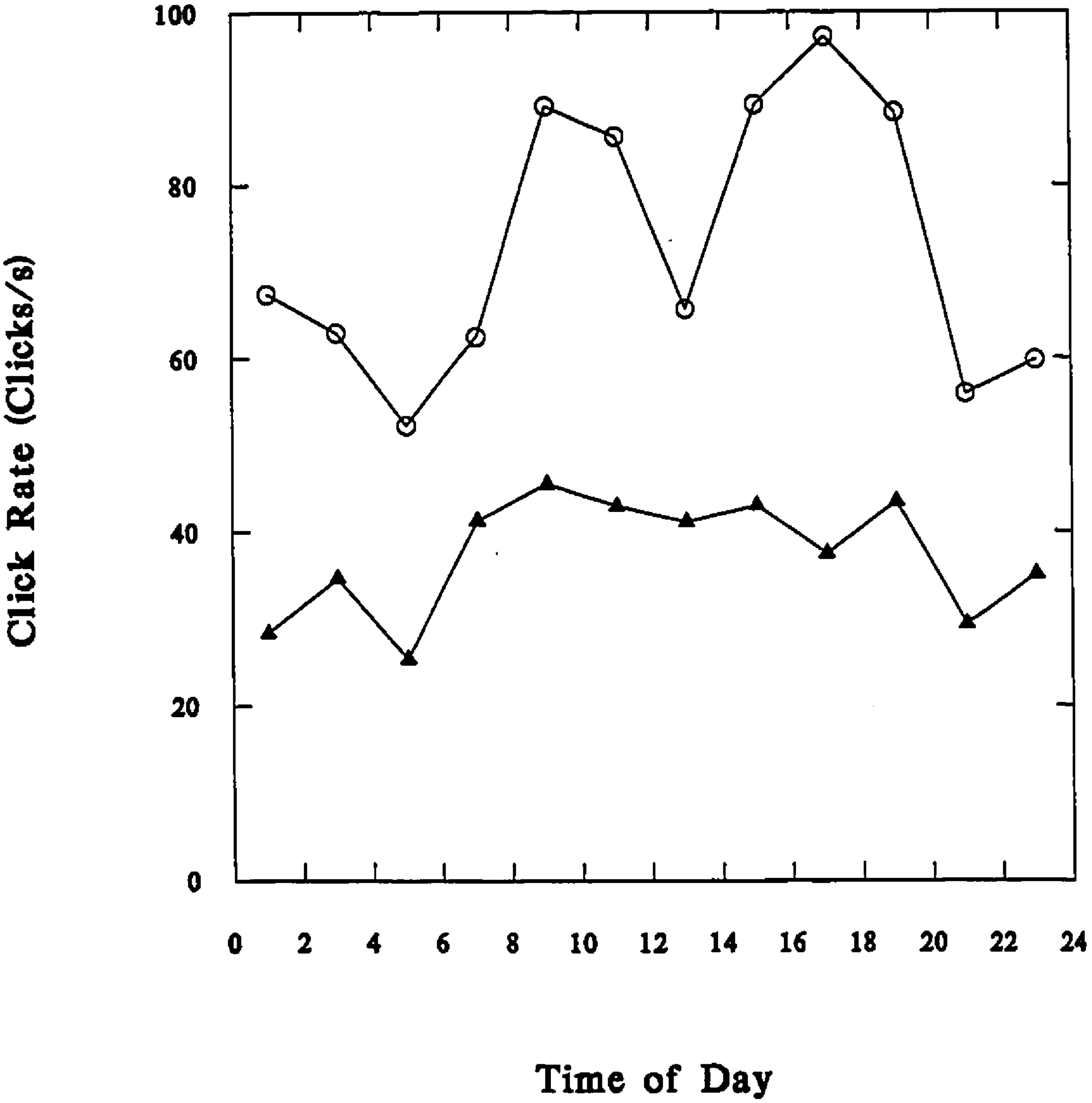


Fig. 19. Mean click rate for 1985 (circles) and 1987 (triangles) with time of day.

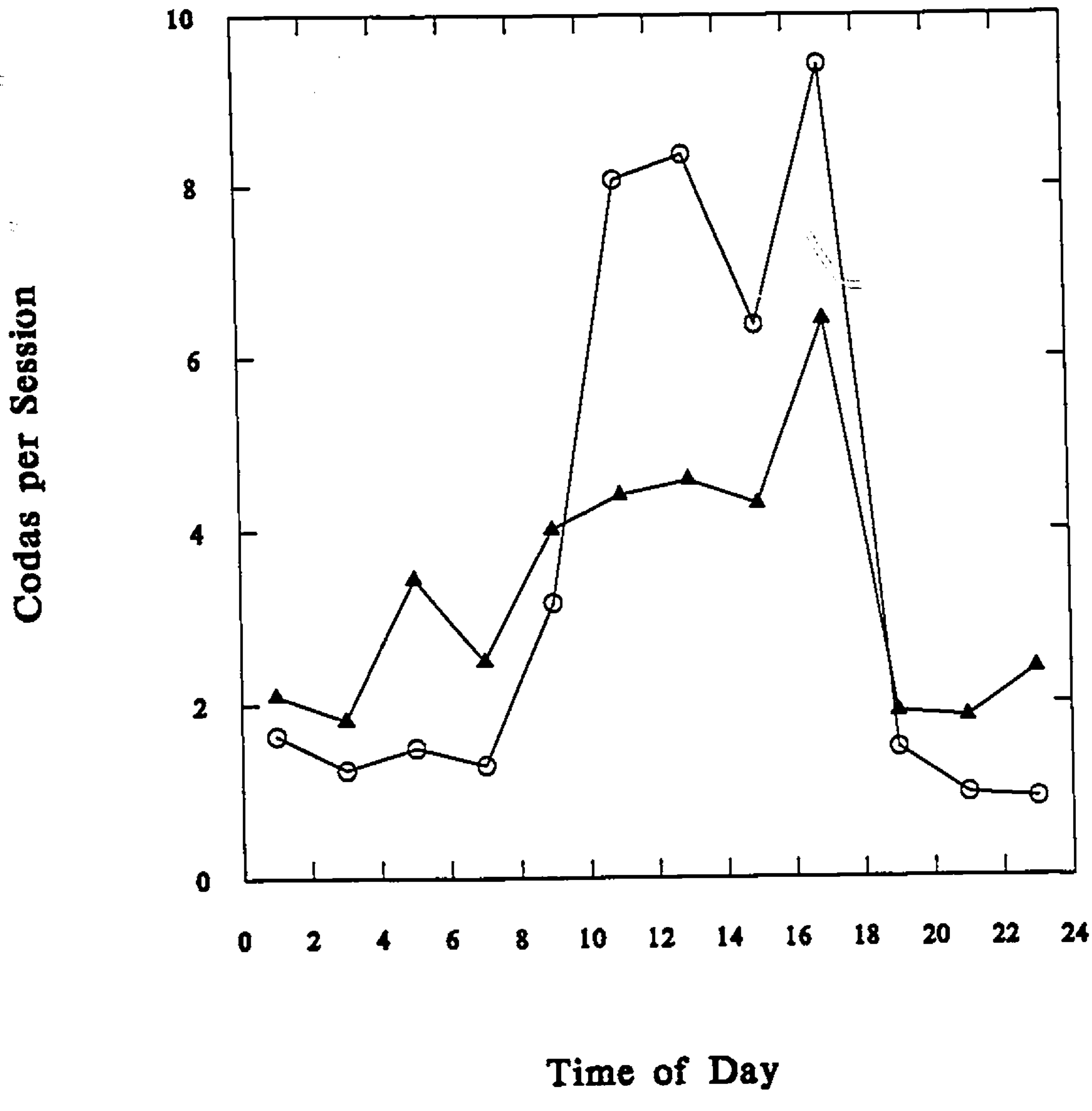


Fig. 20. Mean number of codas per session for 1985 (circles) and 1987 triangles) with time of day.

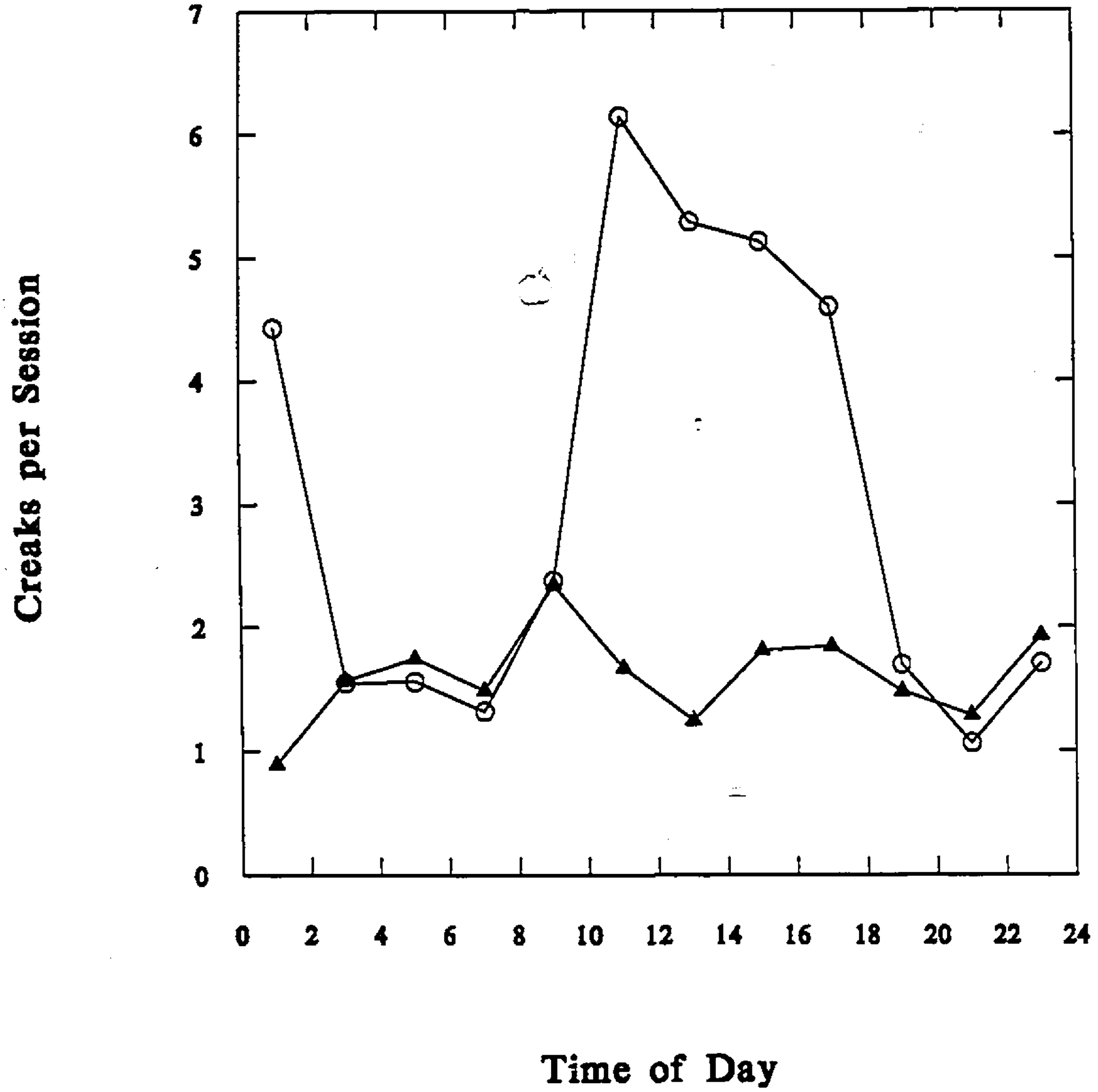


Fig. 21. Mean number of creaks per session for 1985 (circles) and 1987 (triangles) with time of day.

obvious nor significant ($p>0.05$; Kruskal-Wallis, $n=892$), but showed a similar trend to that of 1985.

The number of creaks heard paralleled the relationship for codas but was not as distinct (Fig. 21). Creaks varied significantly with time of day in 1985 ($p<0.001$; Kruskal-Wallis, $n=477$), also highest from 09.00-17.00 h. Unlike codas, there was a peak at midnight in creaks heard in 1985. In 1987, however, no clear diurnal pattern could be discerned, and creaks were not significantly related to time of day (Kruskal-Wallis, $p>0.05$; $n=892$).

d) **Principal components and canonical correlation analyses (sounds and behavior)**

In order to summarize the relationships between many variables, a principal components analysis and a canonical correlation analysis were carried out. For the principal components analysis, the following variables were used, chosen to reduce confounding effects of "numbers of individuals": whale speed, proportion of whales heading the same direction, number of breaches per individual seen at the surface, number of lobtails per individual, number of fluke-ups per individual, number of sideflukes per individual, number of spyhops per individual, number of distant (>500 m away) breaches per individual, mean cluster size, maximum cluster size, number of codas, number of creaks, and whether or not click rates were low (under 20/s). The total data set (including autocorrelated data and sessions with fog) was used, since no tests of significance were performed, which may have been rendered meaningless by autocorrelation.

Only the first four principal components had eigenvalues greater than one. These accounted for 61% of the total variance (25.9%, 13.4%, 11.9%, and 9.9%, respectively). The first, and by far the most important, component (Table 5) seemed to represent an index of sociality, with large cluster sizes, high numbers of codas, and to a lesser degree, creaks heard, lack of directional coordination (low proportion of whales heading the same direction), few fluke-ups, many sideflukes and spyhops, slow speed, low click rates, and slightly more than average lobtails and breaches seen. The second component was dominated by high numbers of especially breaches (both all breaches and just those distant), but also lobtails. The third component reflected high numbers of sideflukes and spyhops, low speed, little directional coordination, somewhat larger cluster sizes, somewhat more breaches, and fewer clicks. The fourth component represented medium and high click rates and high numbers of creaks heard. The number of codas was somewhat higher with positive values of this component, as was the number of fluke-ups and the whales' speed. Mean cluster size was slightly smaller.

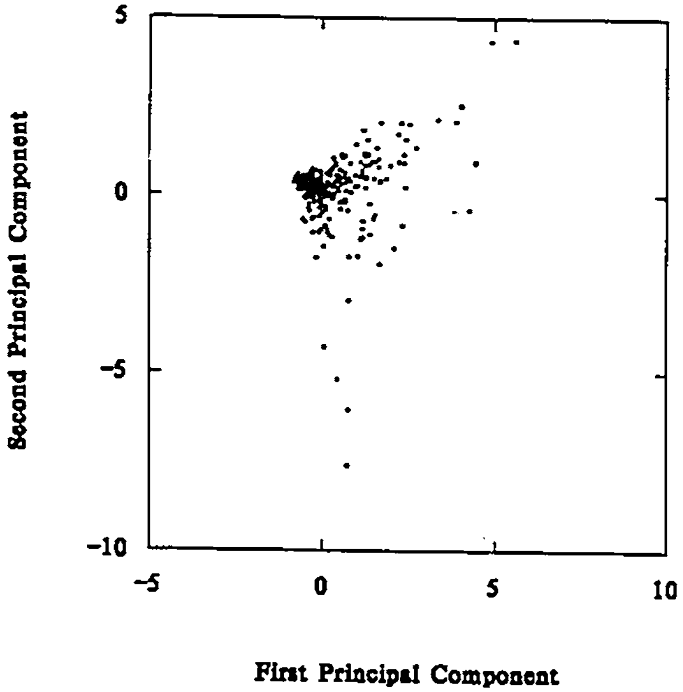
A plot of Factor 1 (sociality) vs. Factor 2

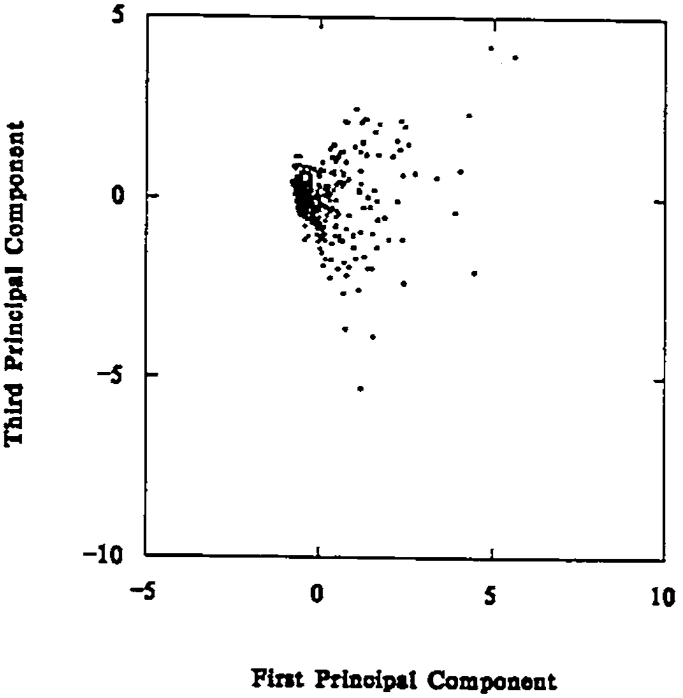
Table 5. Component loadings for the first four principal components from a principal components analysis on various behavioral and acoustical variables. The first four principal components accounted for 61% of the total variance. "Proportion" means the proportion of whales heading the same direction (directional coordination).

	1	2	3	4
Mean cluster size	0.794	0.182	0.303	-0.215
Maximum cluster size	0.818	0.246	0.285	-0.030
Whale speed	-0.305	0.123	0.522	0.272
Proportion	-0.518	0.160	0.477	0.104
No. of breaches/ind.	0.192	-0.830	0.278	0.130
No. of distant breaches/ind.	0.136	-0.812	0.186	0.151
No. of lobtails/ind.	0.215	-0.403	0.140	-0.108
No. of sideflukes/ind.	0.442	-0.108	-0.567	0.132
No. of spyhops/ind.	0.420	-0.092	-0.561	0.170
No. of fluke-ups/ind.	-0.453	0.068	-0.023	0.340
No. of codas	0.714	0.185	0.151	0.363
No. of creaks	0.618	0.199	0.187	0.549
Low click rate	0.370	-0.019	0.206	-0.713
Eigenvalue	3.37	1.74	1.54	1.29

(breach-lobtail) (Fig. 22) showed that there was little scatter in the points in situations of low sociality (i.e. feeding behavior). High numbers of breaches and lobtails were invariably seen only in cases of high sociality. When Factor 1 (sociality) was plotted against Factor 3 (high numbers of sideflukes and spyhops, low speed and directionality) (Fig. 23), it was again evident that at low levels of sociality, variation in behavior was less.

A canonical correlation analysis was performed between the acoustical and behavioral variables. The reduced data set (excluding autocorrelation and sessions with fog) was used with 47 cases. Because of non-normality of the data, significance levels of the correlations may not be quite correct. Variables were chosen so as not to be confounded by the effect of numbers of individuals, as before. Acoustical variables were: numbers of codas, numbers of creaks, and low click rates (under 20/s). Behavioral variables were: mean cluster size, maximum cluster size, speed of whales, proportion of whales heading the same direction, breaches per individual, lobtails per individual, fluke-ups per individual, sideflukes per individual, spyhops per individual, and distant breaches (>500 m away) per individual. The first canonical correlation (0.756, p<0.001) related high numbers of codas, high numbers of creaks, and low click rates with large clusters, few fluke-ups, but many sideflukes, spyhops and breaches, i.e. high sociality (Table 6). This was similar to





Figs. 22 and 23. Second and third principal components plotted against first principal component of behavioral and acoustical variables.

Table 6. Canonical loadings (correlations between dependent variables and dependent canonical factors) between acoustical and behavioral variables. A reduced data set, excluding autocorrelation and sessions with fog, was used (47 cases). The first ($r=0.756$, $p<0.001$) and second ($r=0.671$, $p<0.05$) canonical correlations are shown. "Proportion" means the proportion of whales heading the same direction (directional coordination).

1st Canonical Correlation (Canonical Loadings)

No. of codas	0.905	Mean cluster size	0.693
No. of creaks	0.651	Maximum cluster size	0.795
Low click rate	0.646	Whale speed	-0.160
		Proportion	-0.256
		No. of breaches/ind.	0.379
		No. of distant breaches/ind.	0.415
		No. of lobtails/ind.	0.185
		No. of sideflukes/ind.	0.494
		No. of spyhops/ind.	0.476
		No. of fluke-ups/ind.	-0.728

2nd Canonical Correlation (Canonical Loadings)

No. of codas	0.346	Mean cluster size	0.344
No. of creaks	0.635	Maximum cluster size	-0.199
Low click rate	-0.690	Whale speed	0.076
		Proportion	-0.055
		No. of breaches/ind.	0.520
		No. of distant breaches/ind.	0.444
		No. of lobtails/ind.	0.404
		No. of sideflukes/ind.	-0.084
		No. of spyhops/ind.	-0.261
		No. of fluke-ups/ind.	-0.176

the results of the first principal component in the above principal components analysis. The second canonical correlation (0.671, $p<0.05$) related high creaks and medium and high click rates with high numbers of breaches (both all breaches and just those near) and lobtails.

e) **Summary**

Codas, and creaks to a lesser extent, were heard when many whales were present, especially when these formed large clusters; when mature males were present (codas only), when calves were present, and when sideflukes and spyhops were observed. Breaches and lobtails were not strongly correlated with the number of codas or creaks heard. Codas and creaks were highly correlated with each other. Click rates, on the other hand, were higher when whales were spread out in many (smaller) clusters rather than in (fewer) large clusters, in which case they sometimes would remain completely silent. High click rates were also heard in conjunction with fluking. Click rates were related to the number of group members in an identified group and thus could be useful for acoustic censusing. Higher click rates were heard in 1985--an indication that groups met more often than in 1987. Particularly the production of codas, but also click rate and creak production, varied diurnally, with all three vocalizations more common during the daytime, and especially the afternoon.

A principal components analysis on sounds and behavior revealed that most of the variance was accounted for by an index of "sociality", in which principally high numbers of codas were heard and large cluster sizes were seen. High numbers of creaks were also heard, and many sideflukes and spyhops were observed. On the other hand, there was little fluking, little directional coordination, and few clicks heard. The first canonical correlation of a canonical correlation analysis between acoustical and behavioral variables reinforced this general picture, with high numbers of codas, high numbers of creaks, and low click rates related to large cluster sizes, few fluke-ups, and many sideflukes and spyhops seen.

Other major factors represented in the next three principal components were, respectively: a) many breaches and lobtails b) high numbers of sideflukes and spyhops but low speed and directional coordination; and c) high numbers of clicks and creaks. The second canonical correlation seemed to relate the second ((a) above) and fourth (c) principal components together, with high numbers of breaches and lobtails seen together with high numbers of clicks and creaks. Plots of principal components against each other showed that there seemed to be little variation in situations of low sociality, whereas highly social situations varied greatly.

3.4 Creaks

The mean number of creaks heard per session was 2.52, with a standard deviation of 7.83 (n=1572 5-min sessions). The maximum number of creaks heard per session was 138.

a) **Creak lengths determined from aural and visual analyses**

Creak lengths or durations were measured in two ways: a) aural analysis, and b) coda and creak type visual analysis. In the aural analysis, a computer was signalled at the beginning and at the end of hearing a creak. This type of measurement of duration was thus not very accurate and probably was biased in favor of longer creaks. Creaks that were heard in the absence of codas were used. A total of 501 creaks were measured in this way for both years. A distribution of creak lengths shows most creaks to be under 8 s in duration (Fig. 24). Mean creak duration was 5.05 s with a standard deviation of 6.31 s, and a range of from 0.22 s to 52.9 s. Results were consistent between years (means and standard deviations): 5.01 ± 6.27, n=323 (1985); 5.11 ± 6.40, n=178 (1987).

In the visual creak type analysis, a total of 278 creaks were counted. While only the rough number of clicks and the estimated mean interclick interval was noted, a very approximate creak length could be determined by multiplying the number of clicks by the estimated mean interclick

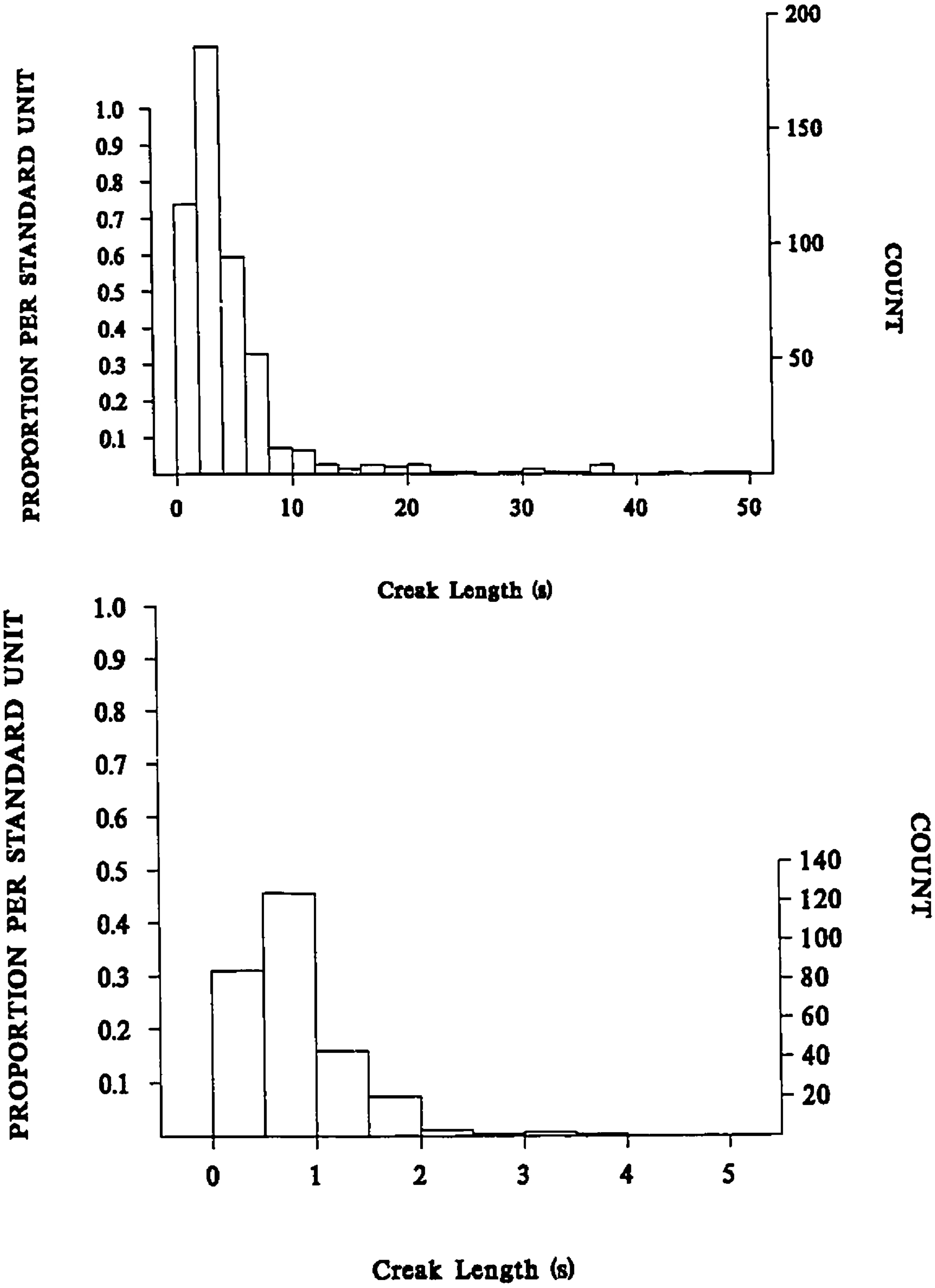


Fig. 24. Distribution of creak lengths from aural analysis (above) and visual coda type analysis (below). The scale at the left is standardized by the sample standard deviation.

interval. Here, a distribution of creak lengths revealed that most creaks were under 1 s in duration (Fig. 24). Mean total creak length was about 0.77 s, with a standard deviation of 0.51 s, and a range of from 0.10 to 3.9 s.

There was therefore quite a discrepancy between the two measures of creak length. While the different means of measurement may have accounted for some of these differences, I believe they represent two different types of creaks: a) lengthy (>2 s) series of clicks with ICIs of under about 0.02 s, heard in conjunction with many usual clicks; and b) shorter series with, in general, longer ICIs, frequently heard together with codas. These latter creaks, which I termed "coda-creaks", sometimes had the characteristic coda-like tonal quality (castanet-sounding) and were more numerous. Unfortunately, I could not find a reliable way of distinguishing these two creak types, as their characteristics often overlapped. In the following analyses, creaks (which generally represent "coda-creaks" because of their greater numbers) will be considered with coda types.

b) Creak length as related to number of clicks and ICI

The mean number of clicks determined from the visual analysis of creak types was 16.7 clicks/creak (with a range of from 3 to 100 clicks/creak), and the mean ICI was 0.05 s (with a range of from 0.01 to 0.27 s). In general, not surprisingly, the creak length was greater when the creak had more clicks (Pearson r=0.48, p<0.01; Fig. 25) and when interclick intervals were longer (Pearson r=0.56, p<0.01). The length of the estimated mean interclick interval, however, was negatively correlated with the number of clicks in the creak (Pearson r=-0.30, p<0.01; Fig. 26). Generally, interclick intervals appeared to be longest at the beginning and end of creaks, with shortest intervals in the middle.

c) **Summary**

Creak lengths measured aurally were almost an order of magnitude greater than those measured visually from the oscilloscope. While this discrepancy may reflect biases in the two types of measurement (aural and visual), they probably represent two different types of creaks: those with longer durations but shorter ICIs, heard together with many usual clicks; and those that were shorter in duration with longer ICIs, heard in conjunction with codas. The results of the analyses presented in this study generally pertain to these latter "coda-creaks", since they were more numerous. Generally, creaks with greater numbers of clicks had shorter ICIs as determined from the visual analysis.

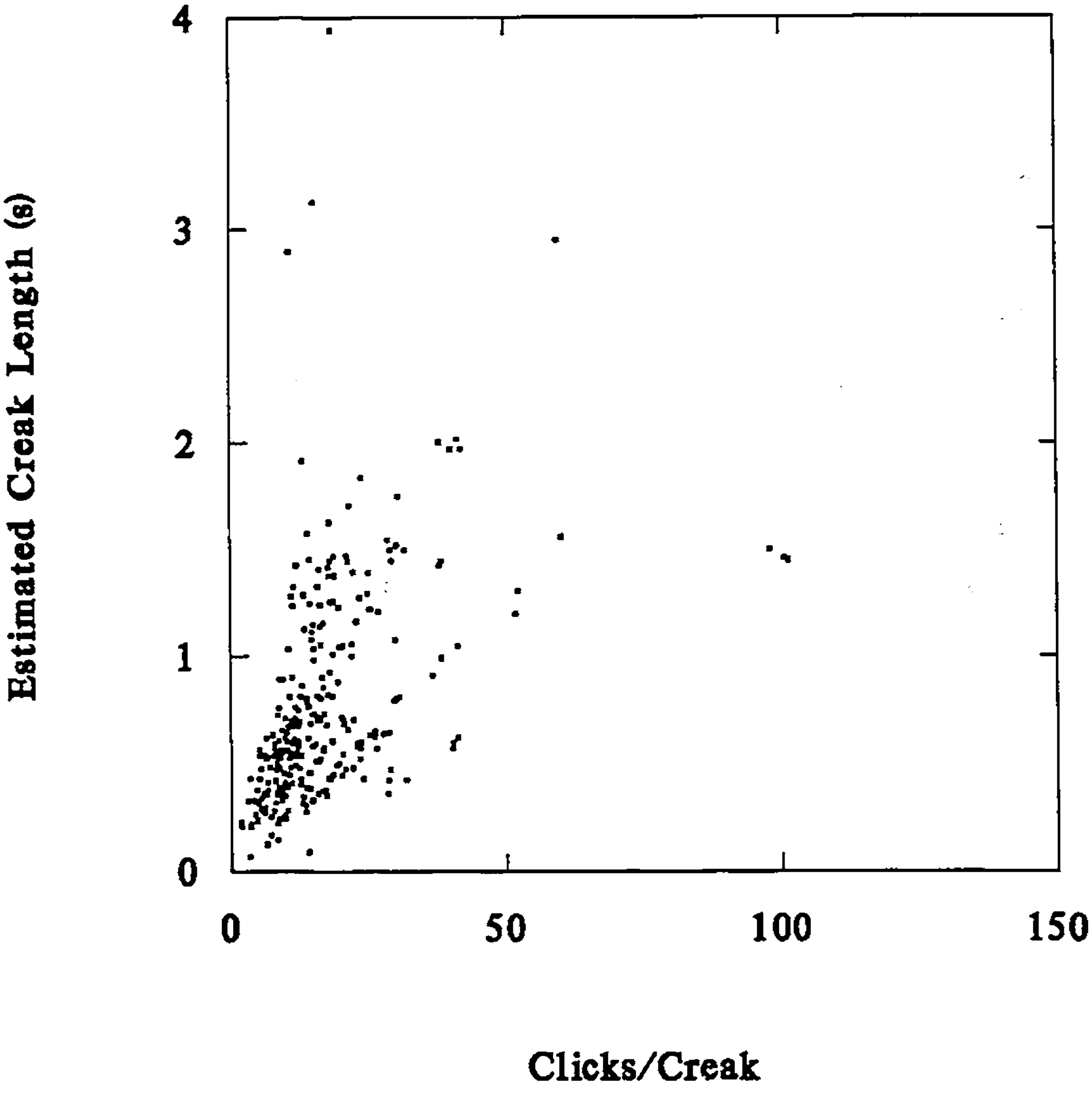


Fig. 25. Estimated creak length (no. of clicks - 1 x estimated mean interclick interval) plotted against the number of clicks per creak. See Section 2.6c for explanation of jitter in plot.

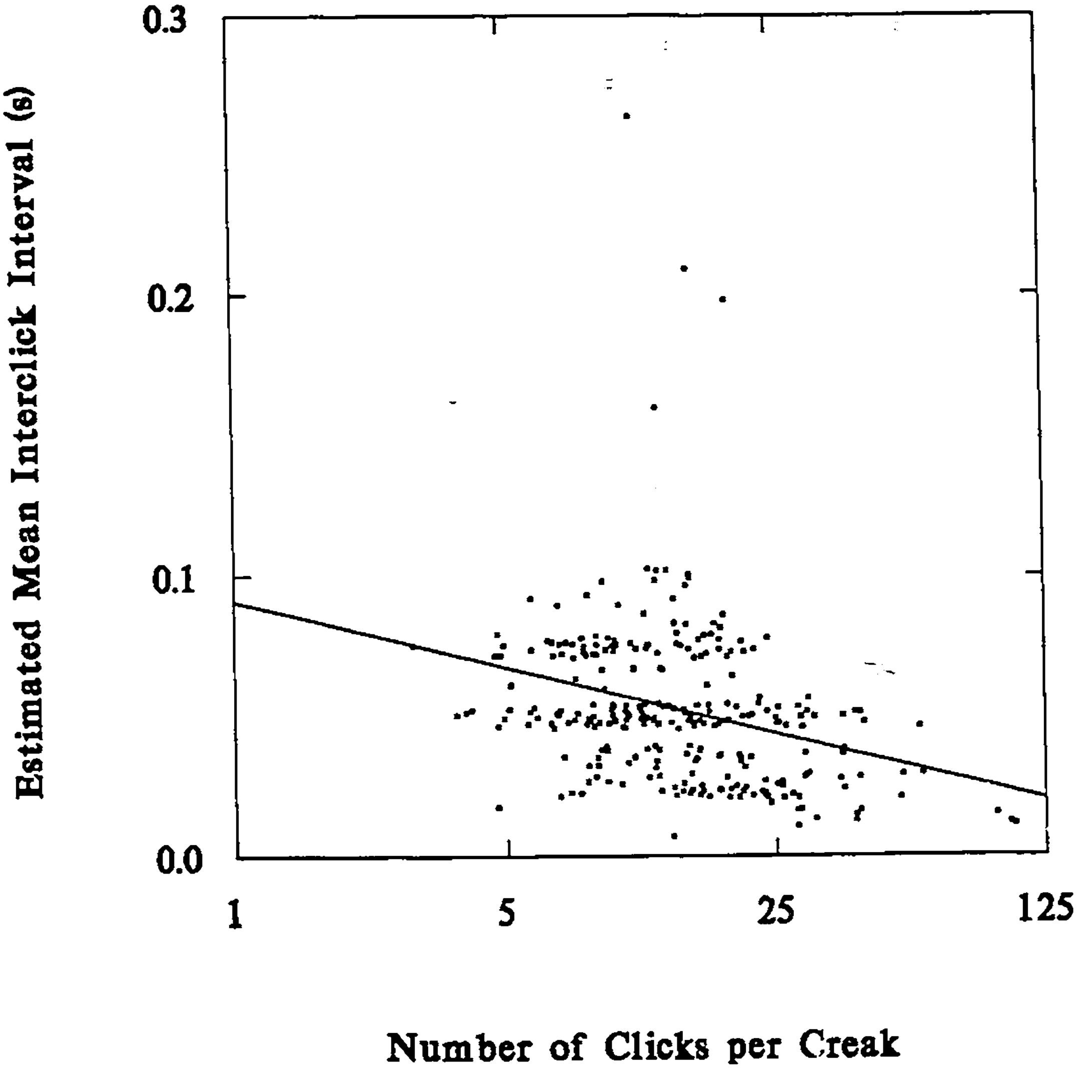


Fig. 26. Estimated mean interclick interval plotted against the number of clicks per creak (logarithmic scale). A linear regression line is shown. See Sec. 2.6c for explanation of jitter in plot.

3.5 Codas and coda types

a) Frequency of occurrence

A mean of 4.05 codas were heard per 5-min session, with a standard deviation of 10.24 (n=1572 sessions). The maximum number of codas heard in any one session was 115. Codas were a relatively rare occurrence, with 65.3% of all sessions completely lacking codas (Fig. 27). Eighty per cent of all sessions had fewer than 5 codas. The majority of the 6,367 codas heard in total occurred in only 8% of all sessions.

b) Coda classification

Plots were made to determine not only whether categories previously defined (by the >50% mean ICI length rule--see Sec. 2.5a) were valid but whether there were more categories present than were previously defined. Codas containing the same total number of clicks, regardless of their classification based on pattern (i.e. "8+1" would be grouped under 9-click codas) were displayed on the same plot. Two interclick intervals were plotted against each other for each coda type (based on total click number). These intervals were analyzed as relative proportions of the total coda length. For codas containing more than 4 clicks in total, usually the first and last intervals were chosen to be plotted. Other

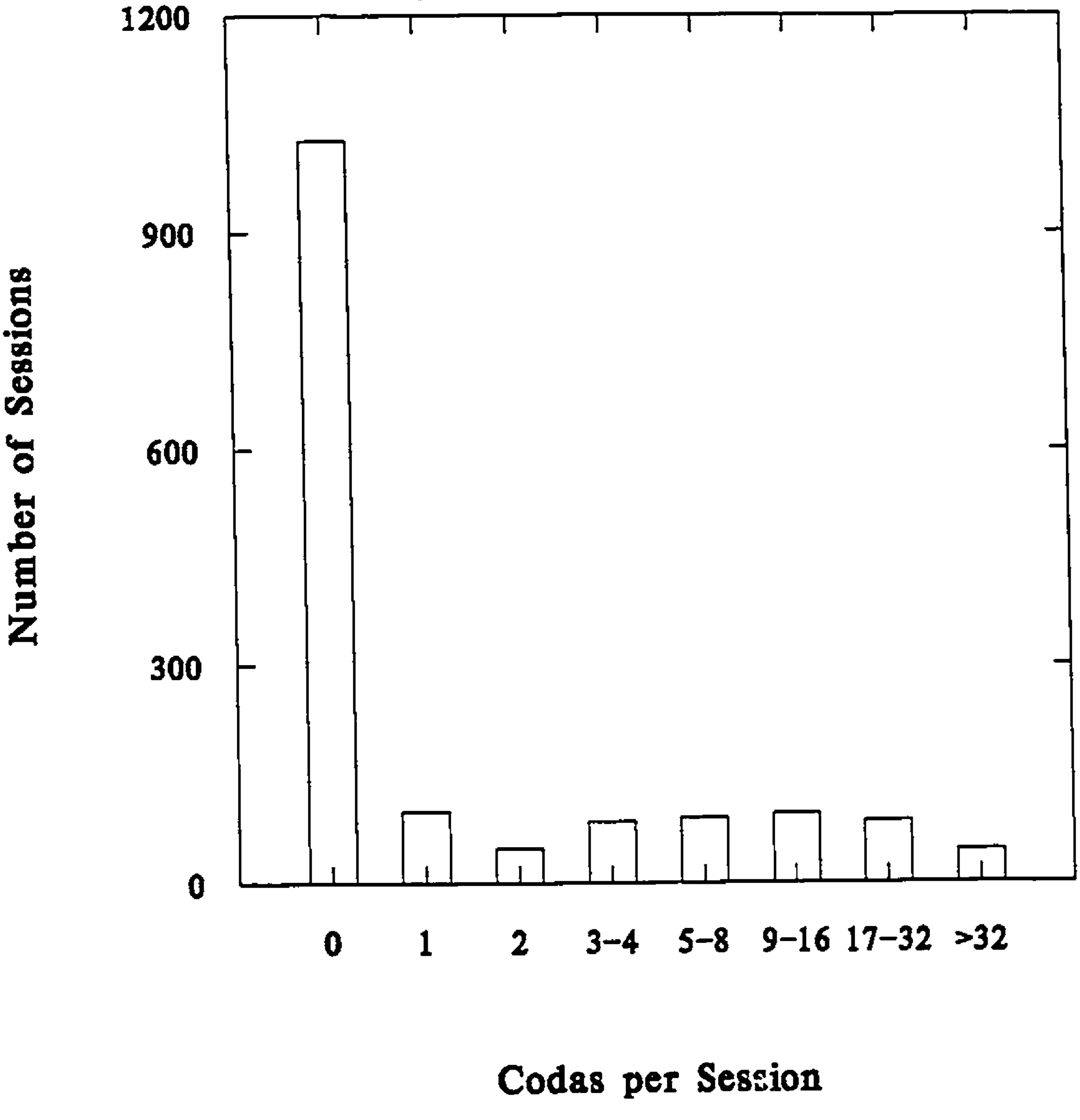


Fig. 27. Number of codas per session.

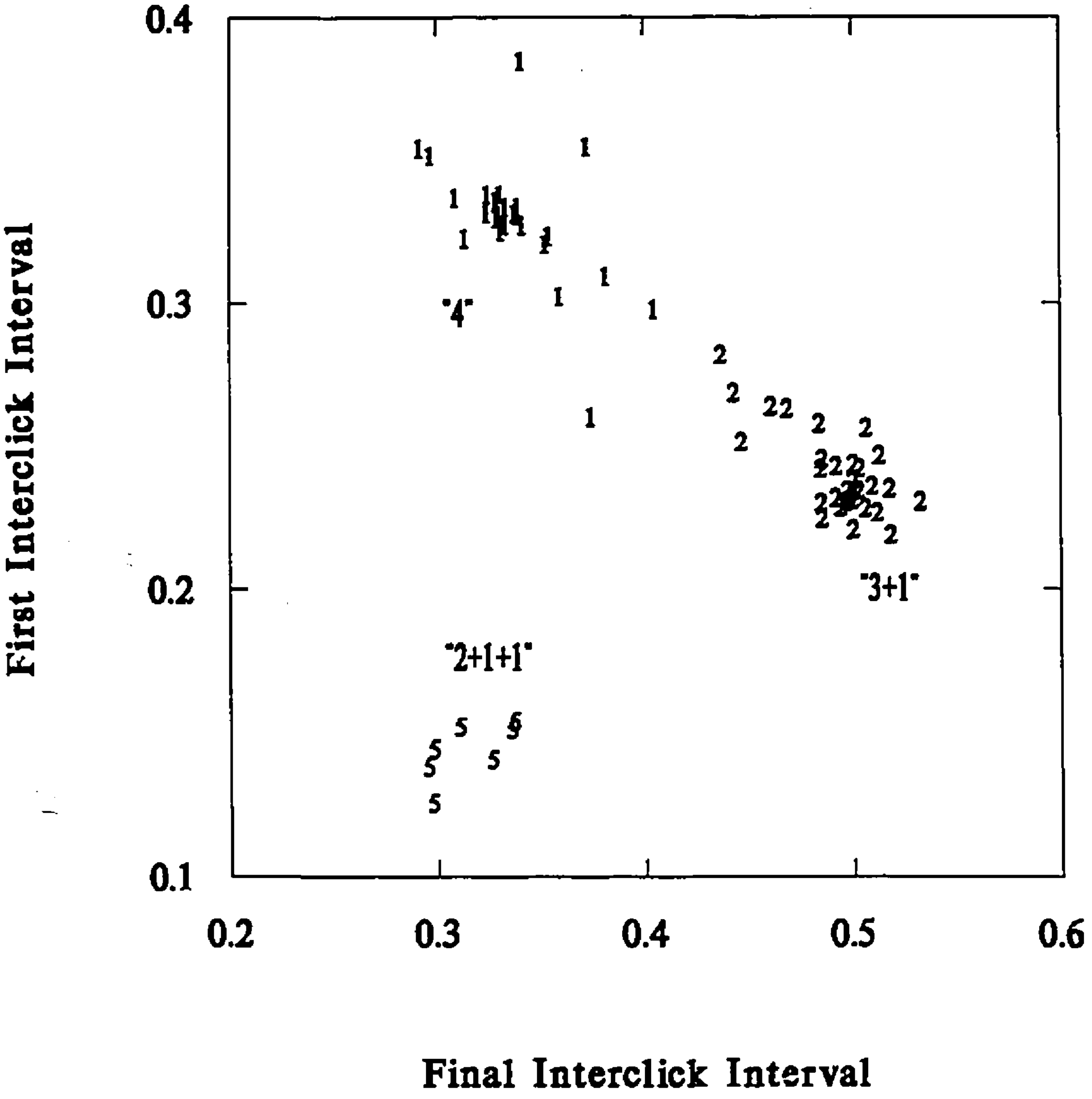


Fig. 28. Plot of the first against the final interclick interval (as proportions of total coda length) for codas containing four clicks.

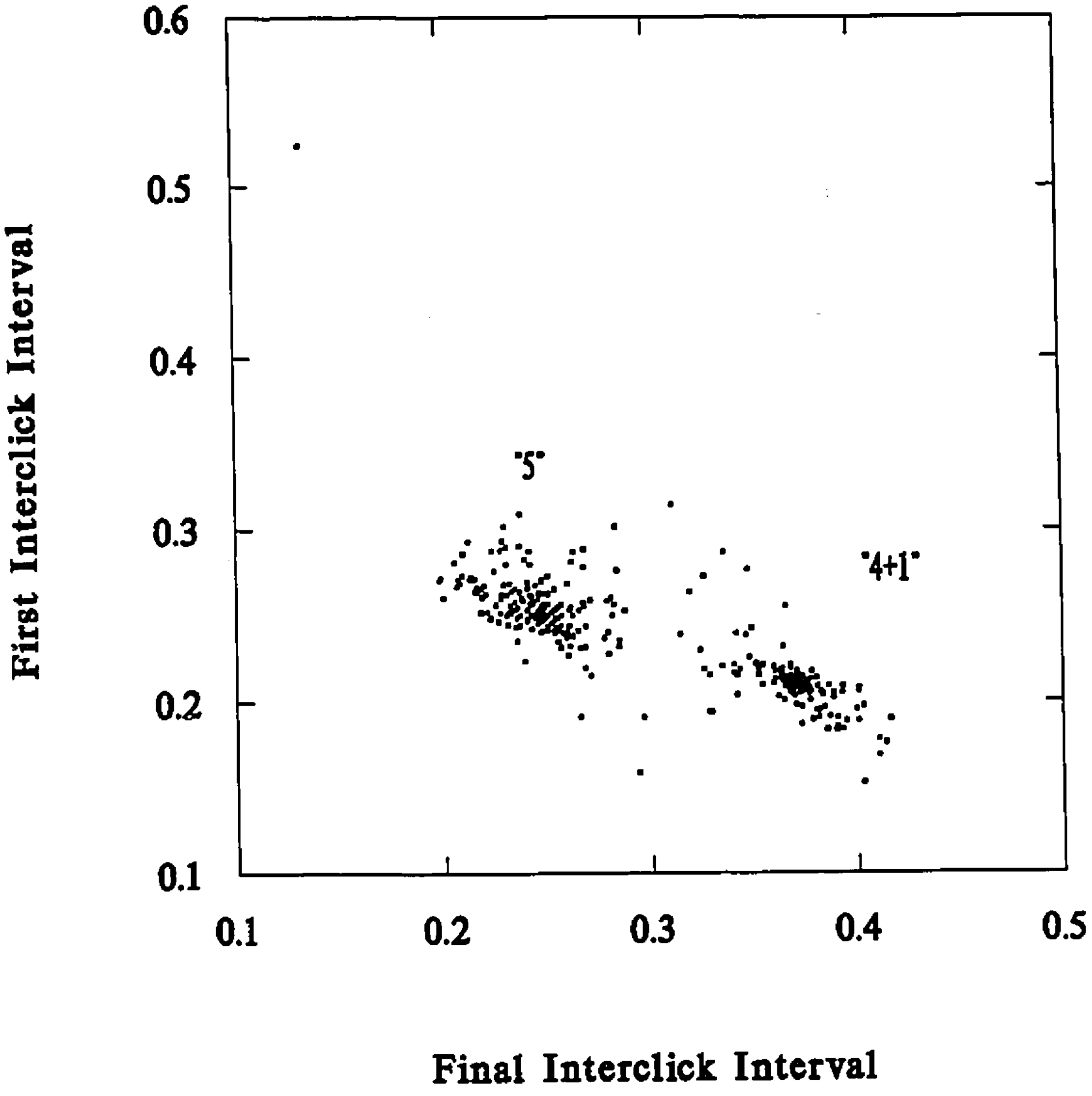


Fig. 29. Plot of the first against the final interclick interval (as a proportion of total coda length) for codas containing five clicks.

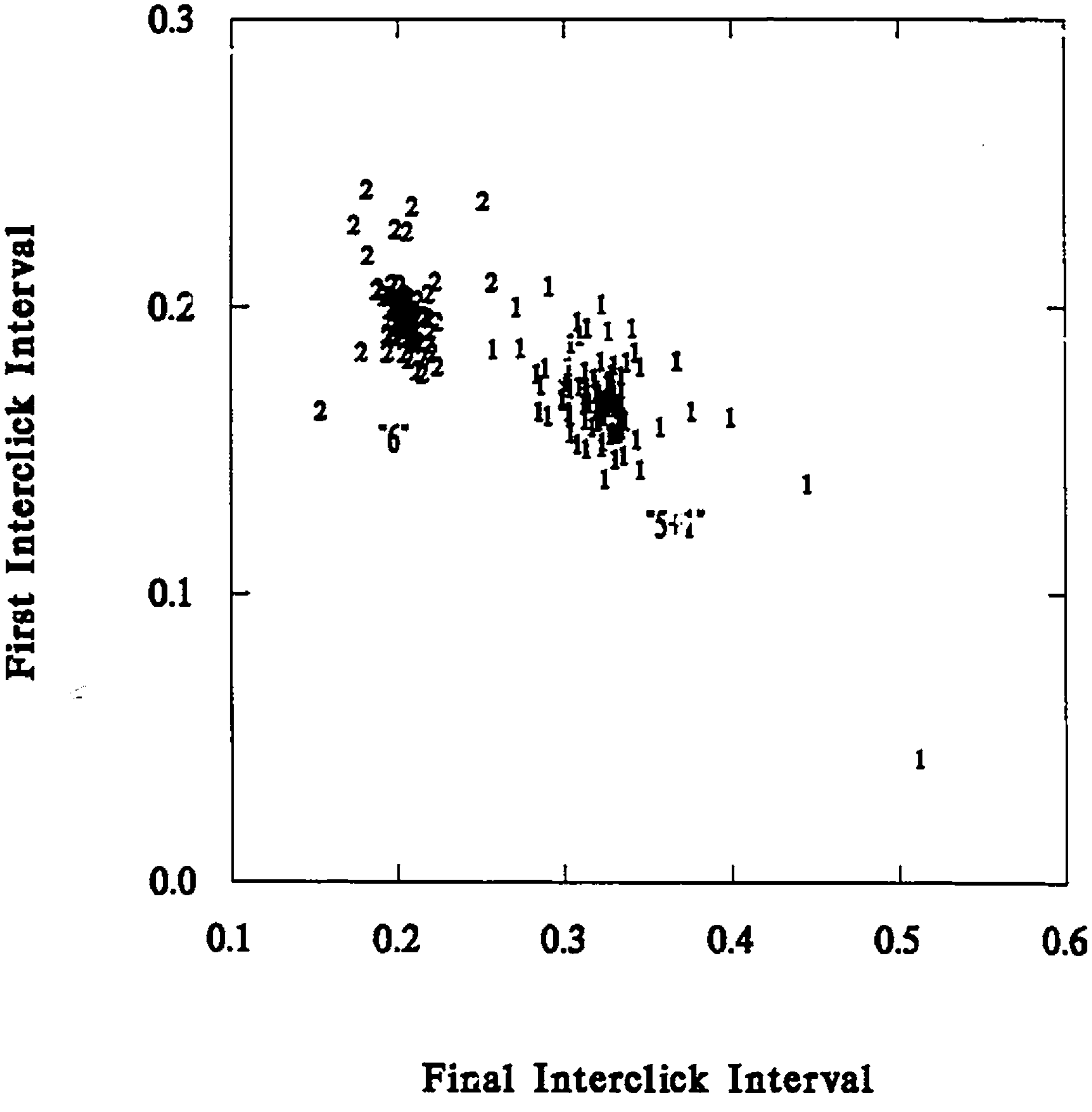


Fig. 30. Plot of first against final interclick interval (proportions of total coda length) for codas containing six clicks.

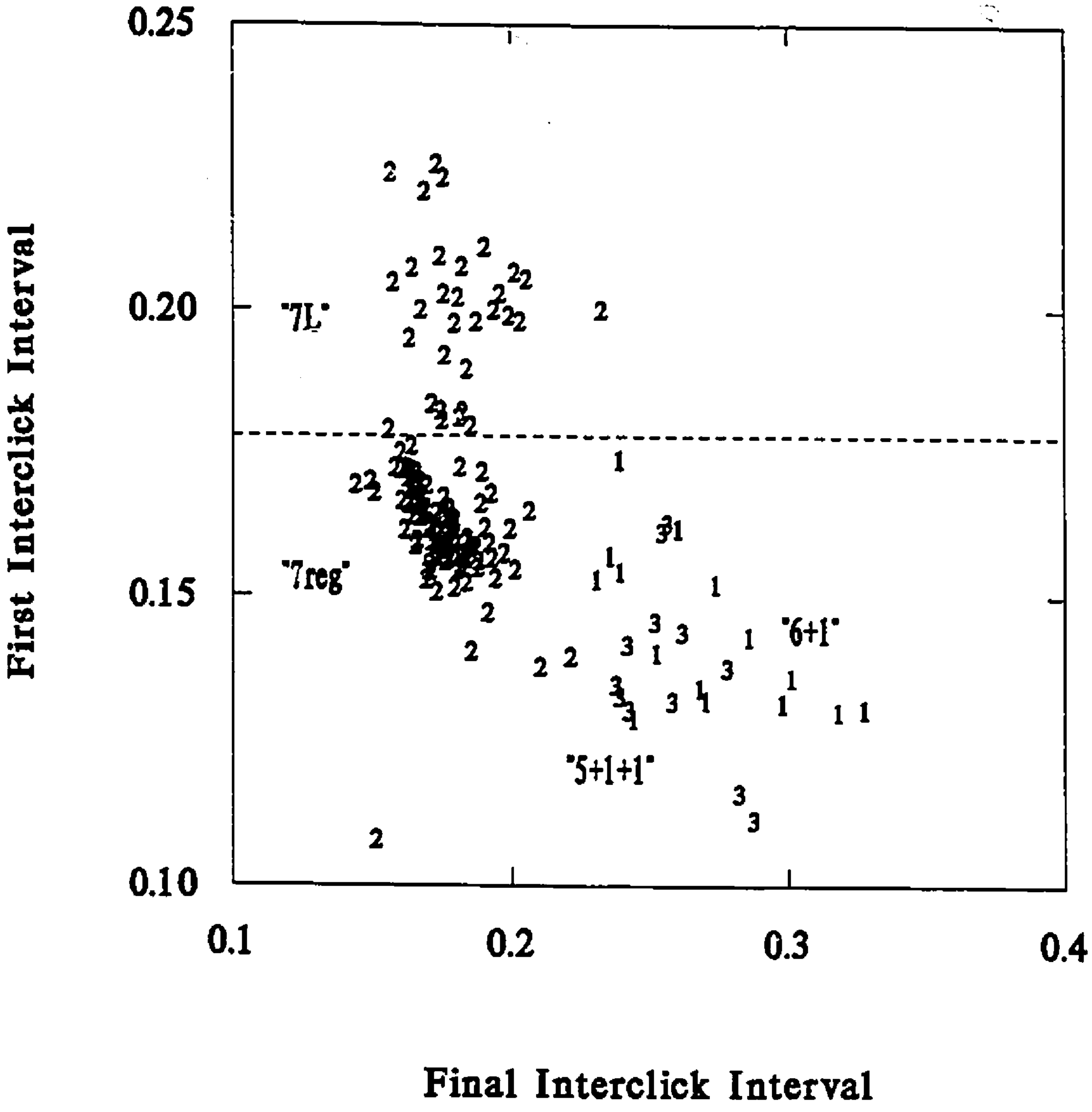


Fig. 31. Plot of first against final interclick interval (proportion of total coda length) for codas with seven clicks. A dashed line divides the "7L" from "7reg" codas. "5+1+1" (3) and "6+1" (1) were separated by the length of the 5th interval.

combinations of intervals were sometimes plotted if these plots were more instructive in separating categories. Final coda categories were determined by the extent of discreteness and non-overlap in their distributions on the plot and by their abundance. Only coda types that were heard 5 or more times were used.

Evenly spaced 3-click codas ("3") were separated from unevenly spaced 3-click codas ("3var"), while 4-click codas were easily grouped into the regular or even "4"s, the "3+1"s, and the "2+1+1"s (Fig. 28). All categories previously defined (as in the "+1"s) were found to be valid (non-overlapping), e.g. "4+1" and "5" (Fig. 29), or "5+1" and "6" (Fig. 30), but sometimes did not occur often enough (at least 5 occurrences) to warrant further analysis.

Two new categories beyond those previously defined were formed, however. It was discovered by plotting 7-click codas that not only did these fall into the groups "6+1", "5+1+1", and "7", but that the "7" category could be further separated into two almost discrete groups: those whose first interval comprised over 0.178 of the total length, and those whose first interval made up less than 0.178 of the total coda length (Fig. 31). The "7"s with shorter first intervals were found to have more regularly, evenly spaced clicks and were thus called "7reg" as opposed to "7L", the codas with longer first intervals. Similarly, 8-click codas could be separated into the types "7+1", "6+1+1", and "8", but the "8"s could be further subdivided into "8L", where the first interval was greater than 0.157 of the total coda length, and "8reg", where the first interval was less than 0.157 the total length and where furthermore the clicks were more regularly spaced.

Using these plots and eliminating those coda types heard fewer than 5 times in the whole analysis, 23 coda types were established. These are listed in Table 2. Coda types "3", "4", "5", "6", "7reg", "8reg", "9", "10", "11", and "12" will be referred to as "regular" codas; in contrast to "3var", "7L", and "8L", and those coda types containing "+1" or "+1+1", which will be known collectively as "irregular" codas.

c) **Relative abundances of coda types**

The most common coda type heard (and measured) was "5" (19% of all codas--Table 2). This was followed by "4+1" (13%), "7reg" (10%), "8reg" (10%), "5+1" (10%), and "6" (8%); i.e. 51% of all codas measured were one of these five types. Least common coda types were "12", "11", "2+1+1", "6+1+1", "3", "3var", and "8+1". These together comprised 5% of the total number of codas measured. Conceivable coda categories such as "3+1+1", "4+1+1", or "7+1+1" were either totally absent or occurred once. While it is possible that coda types containing more than 12 clicks exist in the sperm whale's repertoire (see Sec. 2.5a), if present, they may not be very prevalent, considering the rareness of coda type "12" (Table 2). Evidence that codas probably consist of between 3 and 10 clicks, for the most part, is provided by Watkins (1979). He found that whales ignored one or two coda-like underwater pinger pulses, but short series of about 6 to 10 pinger pulses caused the whales to fall silent (Watkins 1979).

The coda type "2+1+1" was only heard during one recording session, and based on aural impression, was most likely produced by a mature male, as its distinctive tonal characteristics resembled those of slow clicks. This was the only instance in which a coda sounded as though it was produced by a mature male.

d) **Coda type durations and their variability**

Codas had a mean duration of 1.36 s. Generally, codas containing greater numbers of clicks were longer in duration (Fig. 32). For the same total numbers of clicks per coda, however, there was much variation. Codas with "+1"s were longer than their regular coda counterparts with the same number of clicks. Codas with "+1+1"s were longer yet. So, "5+1+1" codas were longer than "6+1"s, which in turn were longer than the "7reg"s. This trend was reversed for codas with 8 or more clicks. "6+1+1"s were still the longest in duration of the 8-click codas, but "7+1"s, "8+1"s and "9+1"s were shorter than their regular counterparts. There was a parallel relationship between "7reg" and "8reg" codas and between "7L" and "8L" codas. In both cases, there was an

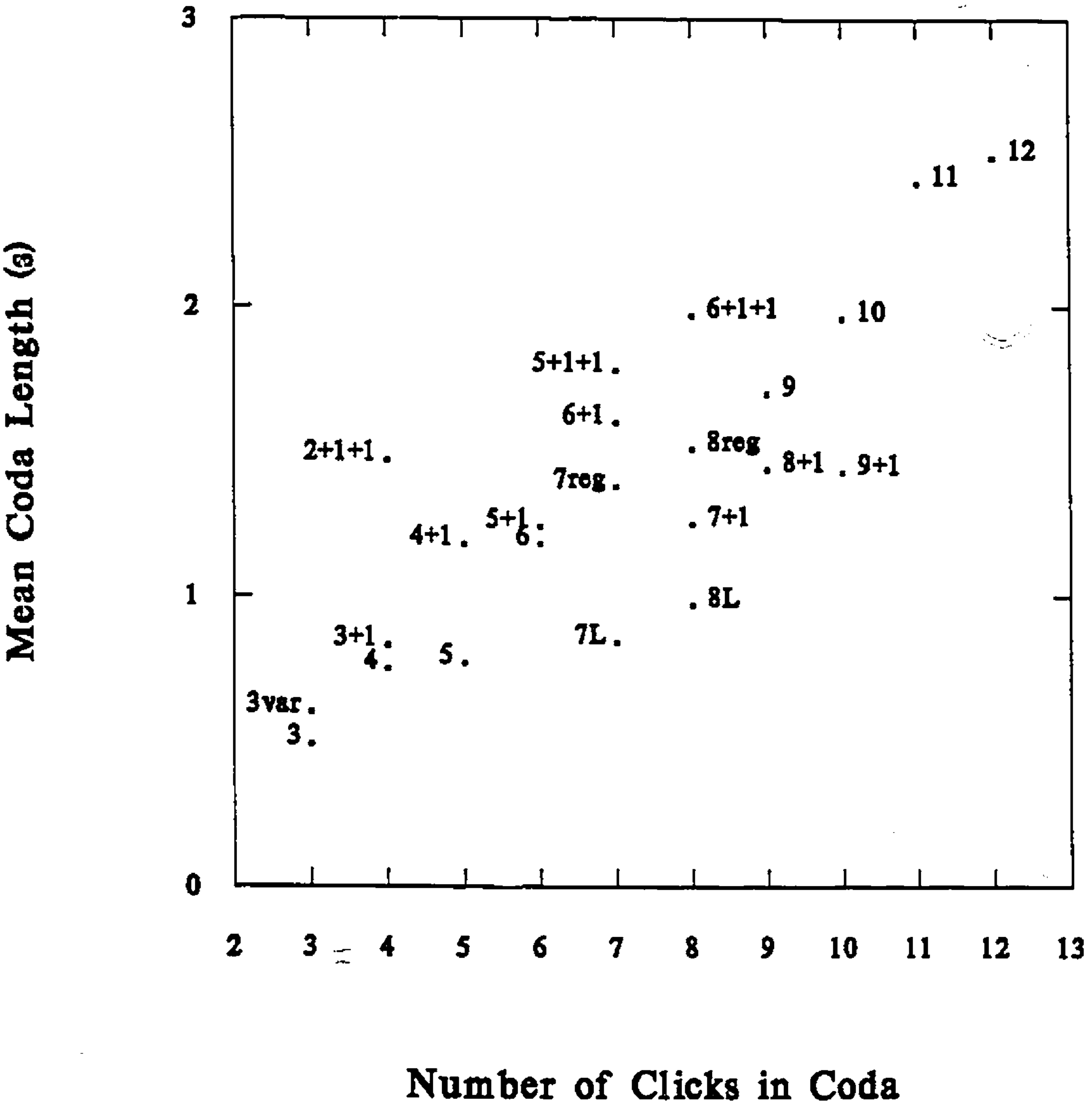


Fig. 32. Mean coda duration as a function of the total number of clicks per coda for different coda types.

increase of 0.13 s in length with the addition of the one click. The "2+1+1" coda thought to be produced by a mature male, was notably longer in duration than other 4-click codas; it was almost twice as long as the regular "4", on average. "5+1+1" and "6+1+1" were both only 1.3 times as long as "7reg" and "8reg", respectively.

Based on coefficients of variation (Table 2), coda types with least variability in length were "4+1", "5+1", and "5+1+1". "2+1+1" also had a low coefficient of variation, but as explained earlier (Sec. 3.5c), this could well be due to only one session being represented. Coda types "3", "8+1", and "10", in contrast, had high coefficients of variation for coda length. A trend could be discerned from comparing the variability in coda length between regular, "+1", and "+1+1" coda types with the same overall click number. Usually regular codas, with evenly spaced clicks, had the highest coefficient of variation, and the "+1+1"s, the lowest variability. The "+1"s were intermediate between these two in coda length variability. This trend holds for "2+1+1", "3+1", and "4"; "4+1" and "5"; "5+1" and "6"; "5+1+1", "6+1" and "7reg"; and "9+1" and "10"; but only partially for "6+1+1", "7+1", and "8reg". Coda types "8+1" and "9" were an exception to this rule: "8+1" was uncharacteristically variable in length, but sample size was small, as was also true for "6+1+1". Very similar values for coefficients of variation were found between "4+1" and "5+1", and between "4", "5", and

"6". "7L" and "8L" had almost identical coefficients of variation for length, as did "7reg" and "8reg", respectively.

e) Interclick interval length of coda types

Although codas generally became longer when greater numbers of clicks were present in the coda, mean intervals between clicks of a coda decreased slightly with increasing total click number (Fig. 33). There was a rough trend for interclick intervals to become increasingly shorter from "3"s to "9"s, becoming longer again for "11"s and "12"s. Only regular codas (with evenly spaced clicks) were used for this comparison. A notable exception was coda type "5" which had much shorter interclick intervals than the other codas, on average.

When mean interclick intervals were plotted for each coda type (Fig. 34), it was apparent that first intervals were all fairly similar in length between coda types. Moreover, it appeared that the relationship between "3" and "3+1"; between "4" and "4+1"; between "5", "5+1", and "5+1+1"; and between "6", "6+1", and "6+1+1" was simply additive. The delayed last one or two clicks were added onto a "root" coda of similar length and with similar interclick intervals as the regular coda had. Thus the first four clicks of a "4" and a "4+1" were nearly identical in spacing. The intervals between the last one or two delayed clicks were usually about twice the length of intervals between the initial clicks of the same

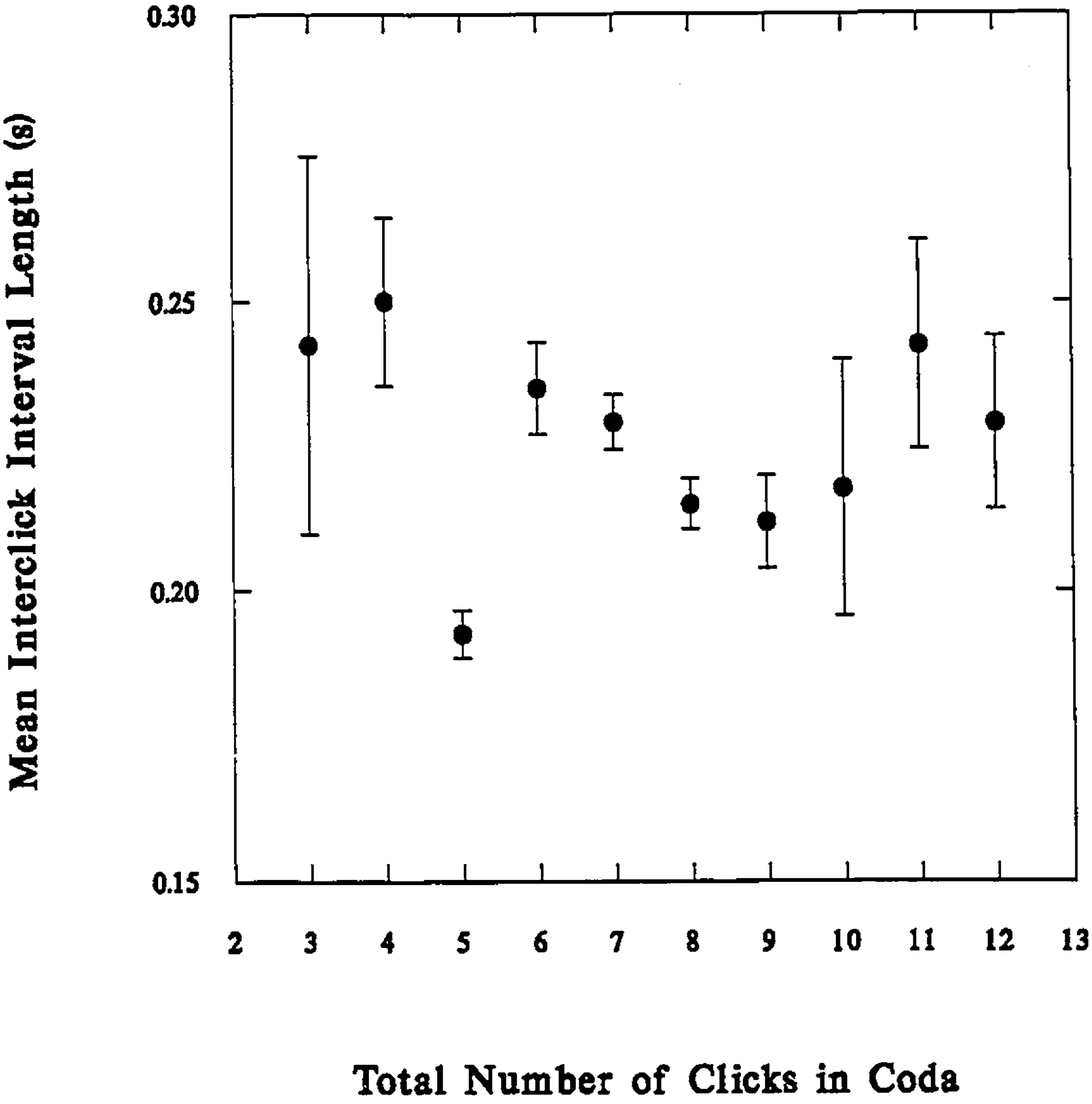


Fig. 33. Mean interclick interval length (with standard error bars) for regular codas with number of clicks per coda.

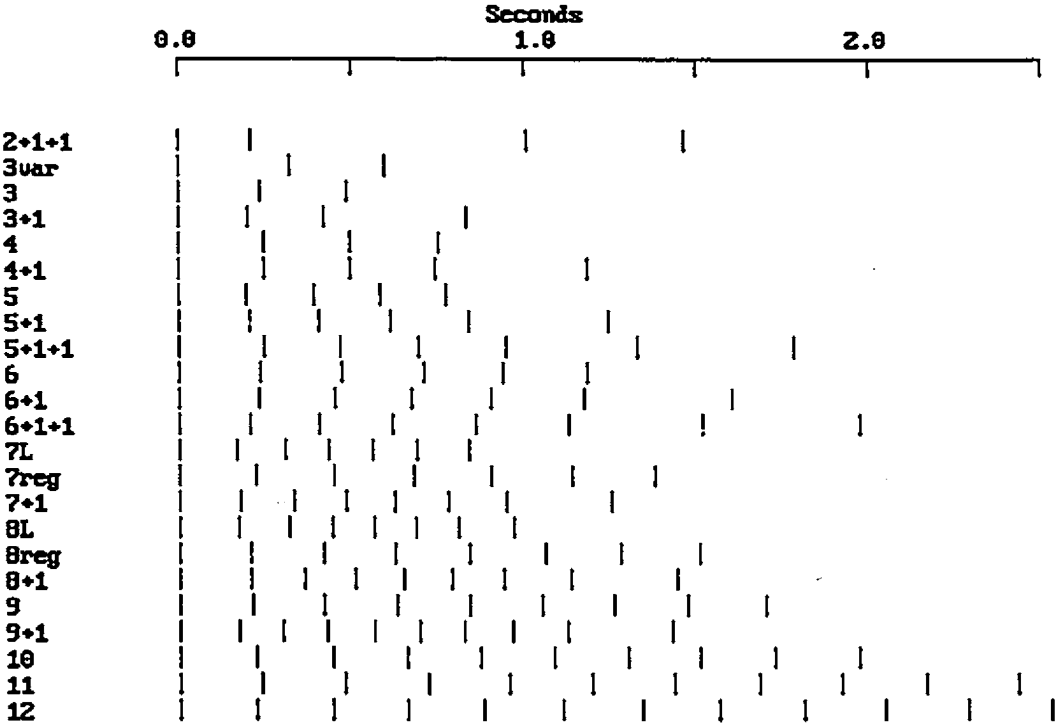


Fig. 34. Mean interclick intervals for each coda type.

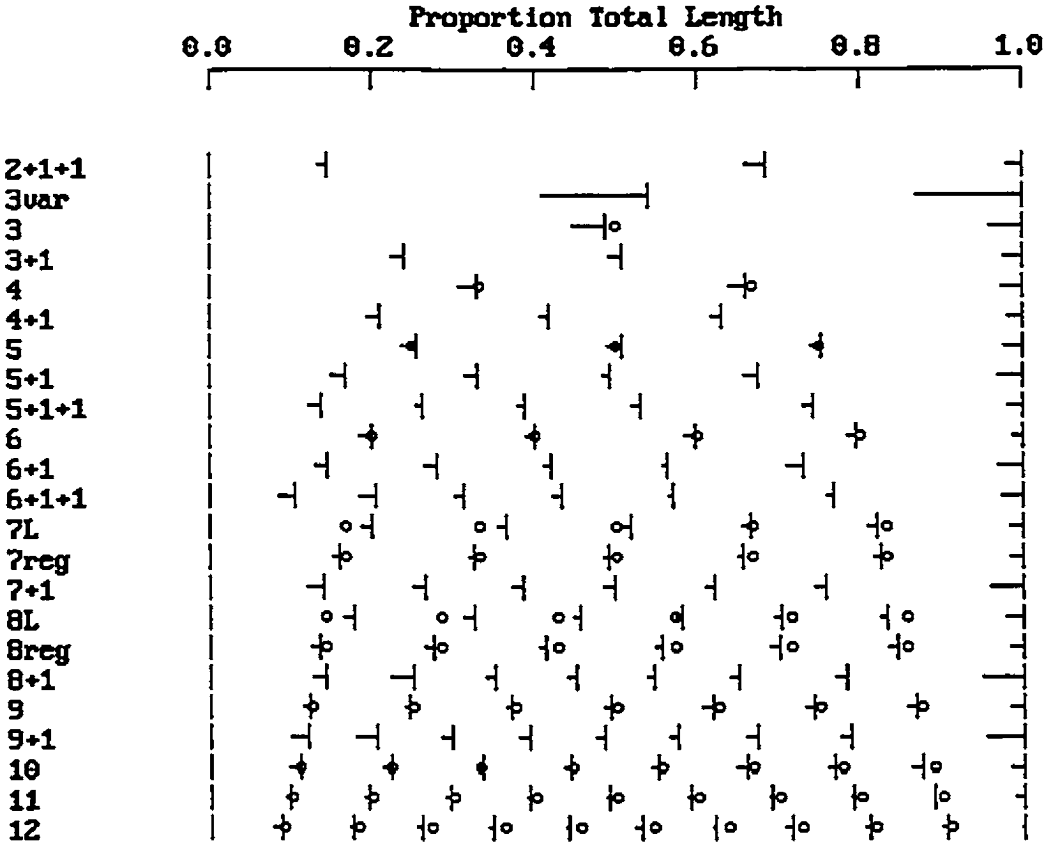


Fig. 35. Mean relative intervals (proportions of the total coda length) for each coda type. Circles denote expected positions of clicks for perfectly regularly spaced codas, and horizontal bars S.D.'s of previous interval.

coda or between clicks of the corresponding regular coda. It was as if a click had simply been skipped. This was not the case for "7reg" and "7+1" and codas with "roots" larger than 7. From "7+1" on, "+1" codas had shorter intervals than their regular "root" codas.

When lengths of all coda types were standardized and intervals were represented only as mean relative proportions of the total coda length (Fig. 35), several findings emerged. Standard deviations around interval lengths did not overlap between coda types such as "5", "5+1" and "6". This showed that these 3 types were fundamentally different in their relative interclick spacing and did not just vary by a matter of degree. This seemed to be the case for all 23 coda types (except perhaps "3var"). Also, there was a close correspondence between points showing expected interval lengths for perfectly evenly spaced clicks within a regular coda, and those of actual mean relative interclick intervals of regular codas. Regular codas ("3", "4", "5", "6", "7reg", "8reg", "9", "10", "11", and "12") had very evenly spaced clicks, with mean relative interval length equalling the total standardized coda length divided by the number of intervals. The intervals of coda type "5" were very close to the expected evenly spaced ones. All regular coda types, except "5", showed a slight but consistent trend towards longer than expected final intervals. First intervals showed no such consistent pattern.

f) Summary

Codas were a relatively rare occurrence, with about two-thirds of all sessions completely lacking codas. Coda types were found to be discrete and non-overlapping, and, using only those coda types heard five or more times in the analysis, could be categorized into 23 types. The most common of these was "5". Irregular coda types (those with much longer final interclick intervals (ICIs) -- the "+1"s or "+1+1"s) were longer in duration than their regular counterparts with the same number of clicks. For codas of 8 clicks and over, however, this trend was reversed. Generally, irregular codas showed less variability in length, based on coefficients of variation, compared to regular codas of the same number of clicks.

Although codas usually became longer with greater numbers of clicks per coda, among regular codas, mean ICIs decreased slightly with increasing click number. Coda type "5", though, had much shorter ICIs than the other regular codas, on average. Irregular codas were generally very similar to their regular coda counterparts in interclick spacing, except that the "+1" portion seemed to represent a skipped click (double the length of the previous, regular intervals). This did not hold for "roots" (portion of the coda before the longer "+1" interval) longer than 7 clicks. Standard deviations of the interval lengths did not overlap between coda types when these were standardized to represent the mean relative proportion of the total coda length. Regular coda types were very regular, corresponding closely to expected interval lengths for perfectly evenly-spaced clicks. All regular coda types (except "5", which was particularly evenly spaced) showed slightly longer than expected final intervals.

3.6 Sequential analysis of coda types

a) Overlapping codas

Overlaps, which were defined as instances in which one coda started before the other was finished, were examined in terms of which coda types overlapped or were overlapped by which other coda types. Coda types "3+1", "4", "4+1", "5", "5+1", "6", "7L", "7reg", "8L", "8reg", "9", >9, creaks, and other (any remaining coda types) were used as variables in this analysis, since large sample sizes were needed for each category. Table 7 gives for each coda type, which other coda type it most often overlapped (was the second coda in the overlap), and by which coda type it was most often overlapped (was the first coda in the overlap). Additionally, the observed and expected number of times each coda type was first or second in the overlap were compared. Expected values were corrected for the length of the coda by the following calculation. Let V = total number of overlaps; n_A = number of codas of type A; N = total number of codas; x_A = mean length of coda type A; and X = mean length of all codas, then:

Table 7. Most common overlaps between various coda types.

Coda Type	Most often overlaps (Coda type is second)	Most often overlapped by (Coda type is first)
"3+1"	"5+1"	"5+1"
"4"	"9", Other	Other
"4+1"	"4+1", "5+1", Other	"4+1"
"5"	"8reg", Creak	"6", "7reg"
"5+1"	Creak	"4+1", Other
"6"	"7reg"	"8reg"
"7L"	Other	Other
"7reg"	"8reg"	"6"
"8L"	Other	nothing
"8reg"	"6"	"7reg"
"9"	"8reg"	"8reg"
>9	"5+1"	Creak
Creak	Creak, Other, "8reg"	Creak, Other
Other	Other	Other

Expected no. of times coda A is first = $V \times n_A/N \times x_A/X$

Expected no. of times coda A is second = $V \times n_A/N$

Chi-squared values for all comparisons combined revealed significant differences between coda types in expected and observed numbers of first (χ^2=37.16, $p<0.005$, 13 df) and second (χ^2=50.21, $p<0.005$, 13 df) positions in an overlap. That is, coda types overlapped or were overlapped by other coda types in a non-random way. Individual coda types also differed significantly from the expected in their position in overlaps: coda type "4" was first more often than expected (χ^2=7.22, $p<0.01$, 1 df, n=7) and second more often than expected (χ^2=5.93, $p<0.05$, 1 df, n=9) in an overlap. Sample sizes were low, however. Type "5" was second less often than expected (χ^2=13.40, $p<0.005$, 1 df, n=11), but "6" was second more often than expected (χ^2=8.34, $p<0.005$, 1 df, n=21). Type "7L" was first more often than expected (χ^2=5.15, $p<0.05$, 1 df, n=7), though again sample size was low. Coda type "7reg" was second more often than expected (χ^2=18.23, $p<0.005$, 1 df, n=30), while "8reg" was first more often than expected (χ^2=8.25, $p<0.005$, 1 df, n=30). In summary, codas which "initiated" overlaps were "8reg", and perhaps "7L" and "4". Codas which tended to follow or be given in response were "6" and "7reg". Coda type "5" was not a response coda and rarely was second in an overlap.

Correlations were calculated to determine whether the number of overlaps per session and the overlap rate (overlaps/coda/session) were related to behavioral and circumstantial variables. The most significant correlations were between number of overlaps and maximum cluster size (Spearman r_s = 0.458, p<0.01, n=47) and between overlap rate and maximum cluster size (Spearman r_s = 0.493, p<0.01, n=47). More overlaps (r_s = -0.403, p<0.05, n=29) and higher overlap rates (r_s = -0.366, p<0.05, n=29) occurred when whales were moving slower.

b) "Echocodas"

A special type of overlap, which I called an "echocoda", occurred when one whale's coda clicks were heard in the interclick intervals of the first whale's coda, following the first whale's clicks by a fairly consistent delay in time (Fig. 36). These clicks were inserted so precisely that I first believed them to be echoes. Echocodas were heard on 41 occasions, and while many of these pairs of codas were of the same type, some varied by one or two clicks or more (as when the overlapping whale gave additional clicks after the first had finished, or when the overlapping whale began her coda after the second or third clicks of the first whale had

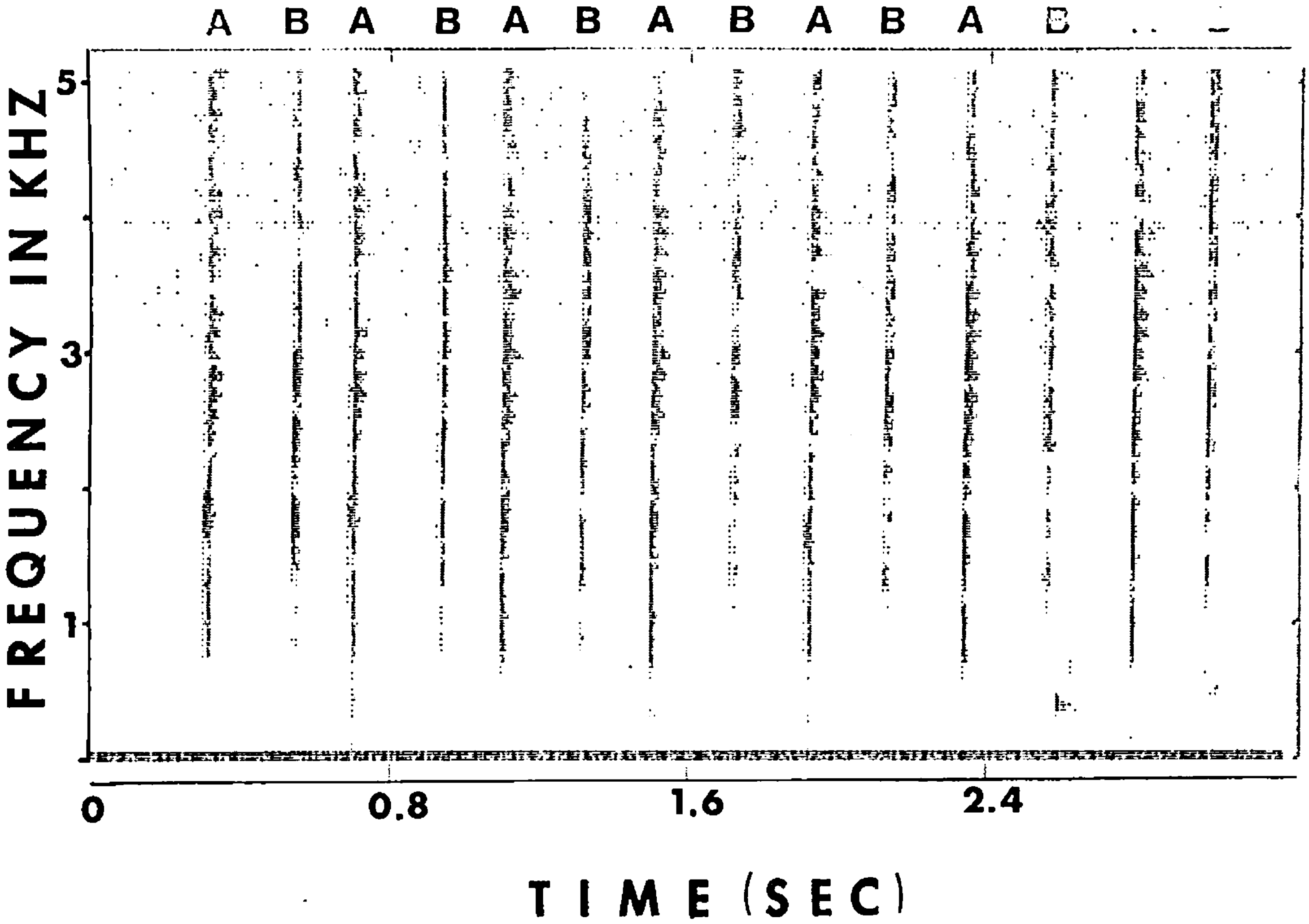


Fig. 36. Spectrogram of echocoda. Coda type "7reg" from individual A is overlapped by "7reg" from individual B. Tape is played at half speed.

already occurred) or by their pattern of the same number of clicks. The delays between the clicks of the two codas were usually around 0.10 s, but could range from 0.05 s to 0.20 s.

Upon investigation, these codas did not seem to be echoes, since: a) the delay in time between the clicks was too long to be a surface reflection (assuming whales were near the surface, as seemed usual during coda production), b) the intensity of the second coda was sometimes greater than that of the first, and c) the delays sometimes varied slightly from one pair of clicks to the next. These suspicions were confirmed by Dr. Michael Lamoureaux, Dalhousie University, who, using a cross-correlation program, found that the two sets of coda clicks were not sufficiently similar in waveform to be echoes.

c) **Transitions**

The sequence in which codas were heard was examined, whether codas actually overlapped or simply followed one another. This analysis was designed to answer the question: "Does one coda type follow another coda type more or less than would be expected if transitions were random?" The same coda type categories that were used in the overlap analysis were used for this transition analysis. There was a slight tendency for the same coda type to follow itself more often than any other coda type, but this only occurred in 6 of the 13 coda types, excluding "other" (Table 8). Moreover, the

Table 8. Transition matrices of actual and expected number of times that particular coda types follow particular other coda types.

ACTUAL NUMBERS

	Second:													
	3+1	4	4+1	5	5+1	6	7L	7reg	8L	8reg	9	>9	Creak	Other
First:														
3+1	0	0	2	1	7	1	0	0	0	0	0	0	4	16
4	1	2	3	4	1	1	0	1	2	2	1	1	4	7
4+1	1	4	87	2	13	0	1	1	2	0	0	0	14	22
5	0	4	3	100	4	16	1	26	1	13	7	2	19	22
5+1	3	1	16	2	26	1	3	0	3	1	1	3	12	34
6	0	3	0	18	2	10	0	7	1	13	4	3	9	11
7L	0	1	2	1	1	1	5	0	4	0	0	1	3	11
7reg	0	3	1	22	1	16	1	18	0	12	4	1	14	6
8L	2	1	3	2	6	0	5	0	11	0	0	1	5	12
8reg	0	2	0	12	0	10	0	19	0	16	4	1	25	10
9	0	2	0	7	1	4	1	5	0	4	3	1	8	4
>9	1	0	0	3	1	2	1	2	0	2	2	4	6	5
Creak	6	3	2	22	18	12	7	10	9	24	7	6	110	65
Other	15	3	31	23	23	9	6	11	15	7	8	5	67	106

EXPECTED NUMBERS

	Second:													
	3+1	4	4+1	5	5+1	6	7L	7reg	8L	8reg	9	>9	Creak	Other
First:														
3+1	1	1	3	4	2	1	1	2	1	2	1	1	5	6
4	1	1	3	4	2	1	1	2	1	2	1	1	5	6
4+1	3	3	13	20	10	7	3	9	4	9	4	3	28	30
5	4	4	20	29	14	11	4	13	6	13	5	4	40	44
5+1	2	2	9	14	7	5	2	6	3	6	3	2	19	21
6	2	2	7	11	5	4	2	5	2	5	2	1	15	17
7L	1	1	3	4	2	2	1	2	1	2	1	1	6	6
7reg	2	2	9	13	6	5	2	6	3	6	2	2	18	20
8L	1	1	4	6	3	2	1	3	1	3	1	1	9	10
8reg	2	2	8	13	6	5	2	6	3	6	2	2	17	19
9	1	1	4	5	3	2	1	2	1	2	1	1	8	8
>9	1	1	3	4	2	1	1	2	1	2	1	1	5	6
Creak	6	5	27	40	19	15	5	18	9	18	7	5	55	60
Other	6	6	30	44	21	16	6	20	10	20	8	6	61	66

Table 9. The difference between transitions from coda type A ⇒ coda type B and those from B ⇒ A (A ⇒ B - B ⇒ A). Positive values indicate that B tends to follow A (A ⇒ B); negative values, that A tends to follow B.

								B:						
	3+1	4	4+1	5	5+1	6	7L	7reg	8L	8reg	9	>9	Creak	Other
A:														
3+1	0													
4	1	0												
4+1	-1	1	0											
5	-1	0	1	0										
5+1	-4	0	3	-2	0									
6	-1	2	0	2	1	0								
7L	0	1	1	0	-2	1	0							
7reg	0	2	0	-4	1	9	1	0						
8L	2	-1	1	1	3	-1	1	0	0					
8reg	0	0	0	-1	-1	-3	0	7	0	0				
9	0	1	0	0	0	0	1	1	0	0	0			
>9	1	-1	0	1	-2	-1	0	1	-1	1	1	0		
Creak	2	-1	-12	3	6	3	4	-4	4	-1	-1	0	0	
Other	-1	-4	9	1	-11	-2	-5	5	3	-3	4	0	2	0

same coda type would be expected to follow itself if there were any correlations between coda types and circumstantial or behavioral data. To adjust for these circumstantial correlations, the difference between transitions from coda type A ⇒ coda type B and those from B ⇒ A was examined (Table 9). High negative values indicated that the B ⇒ A (or A follows B) transition was most common. High positive values indicated that the A ⇒ B transition was most common.

The analysis indicated that "6" tended to follow "7reg" more than vice versa. This is similar to the results from the overlap analysis which suggested that "6" most often overlapped "7reg". While "7reg" was found to be second more often than expected in an overlap, the same was also true for "6". Coda type "7reg" was found to follow "8reg" more than the other way around. This "8reg" ⇒ "7reg" sequence was reflected strongly in the overlap results. Not only did the overlap analysis suggest that "7reg" most often overlapped "8reg", but also that "8reg" was most often overlapped by "7reg". In addition, as noted above, "7reg" was more often second than expected, while "8reg" was more often first than expected in an overlap. "5+1" followed creaks more than the other way around, which was also in agreement with the overlap results, where "5+1" most often overlapped creaks. "Other" followed "5+1" more than vice versa which was reflected in the overlap results as well. "4+1" followed "other" more than the

Table 10. Comparisons between coda types of the number of times that a previous coda was not heard for the preceding 30 s or more. Only those coda types with sample sizes of >80 are given.

Coda Type	Total	No. w/ >30 s before coda-free	Propn. w/ >30 s before coda-free
"4+1"	150	4	0.027
"5"	219	12	0.055
"5+1"	104	3	0.029
"6"	83	3	0.036
"7reg"	100	2	0.020
"8reg"	94	3	0.032
"creak"	300	6	0.020
Total of all 23 coda types and creaks	1588	52	0.033

other way around. Again, overlap results showed a similar tendency, with "4+1" most often overlapping "other". Transition analysis revealed that creaks followed "4+1" more than vice versa, a result which was not paralleled in the overlap results.

d) **Initiating coda types**

To test whether certain coda types initiated coda exchanges, the time since the previous coda was heard was compared between coda types. Tape counter numbers were used to approximate time since last coda. Codas that were first in a session were eliminated from this analysis. When comparing coda types with a total sample size of greater than 80, coda type "5" stood out as being most frequently preceded by over 30 s of no codas, which was often silence (Table 10). The proportion of "5" codas with over 30 s of preceding coda-free time relative to the total number of "5" codas (excluding those first in the session) was also much higher than for other coda types with total sample sizes of over 80. This agreed with the overlap analysis which showed that "5" was second in an overlap less than expected.

e) **Summary**

Codas overlapped one another according to type in a non-random way, with the overlapping coda often containing one click more or less than the coda it overlapped. Coda types

"6" and "7reg" tended to be "followers" or responses (second in an overlap), while "5" was significantly less likely to be a "follower". Coda type "8reg" was first more often than expected--an "initiator". There were several indications that the overlap of "8reg" by "7reg" was a common occurrence. More overlaps were heard with larger clusters. Special types of overlaps, known as "echocodas", occurred when the overlapping whale's coda clicks were inserted very precisely into the interclick intervals of the first whale's coda, producing an echo-like sound.

There was generally a close correspondence between the results from the overlap and transition analyses, suggesting that whether a coda overlapped another or simply followed another was an unimportant distinction. Both analyses indicated that "7reg" was often followed by "6", creaks were often followed by "5+1", and again that "8reg" was often followed by "7reg". Only the transition analysis, though, found that "4+1" was followed by creaks more than the other way around. Coda type "5" may initiate coda exchanges, since it was the coda type most frequently preceded by periods of time not containing codas.

3.7 Correlations between coda types

a) **Spearman correlations**

Spearman correlation coefficients were first calculated between all acoustical variables, standardized and unstandardized, to examine overall relationships of occurrence within sessions. Results from the two data sets (standardized and unstandardized) were very similar. In general, all acoustical variables were very highly correlated with one another. Coda types "3+1", "4+1", and "5+1" were significantly correlated ($p<0.05$) with particularly many other coda types. As a rough rule, irregular coda types seemed to be significantly correlated with more coda types than were regular ones. In contrast, "3var" was not significantly correlated ($p>0.05$) with any other coda type, and "3", "2+1+1", and "4" were only significantly correlated with 0-1 other coda type (depending on the data set used). Coda types "7L", "7+1", "8+1", and "9+1" were significantly correlated with most creak variables and were also significantly correlated with creak total number.

b) **Principal components analysis and cluster analysis**

To describe more fully the overall interaction among the 23 coda types, a principal components analysis and average linkage cluster analysis were performed on counts of each coda type per session. Again, standardized and unstandardized data sets revealed similar results. I will address only the standardized one as it was marginally more clear. The first two principal components accounted for about 30% of the total variance (first-21.6%, second-10.1%) after which the percent of total variance explained dropped off to 15% for the third and fourth principal components (8% and 7%, respectively). The vector plot of component 1 vs. component 2 (Fig. 37) divided the 23 coda types into three fairly coherent, discrete groupings. The first principal component seemed to separate coda types on the basis of how regular or irregular they were. Thus, one grouping was comprised of regular codas "5", "6", "7reg", "8reg", "9", "10", "11", and "12", and the other major grouping contained irregular codas "3+1", "4+1", "5+1", "6+1", "7L", "8L", "7+1", "8+1", "9+1", "5+1+1", and "6+1+1". The third grouping was made up of "3", "3var", "4", and "2+1+1", which as determined from the correlation coefficients above, were significantly correlated with hardly any other coda types. The second principal component, although the separation was less perfect, seemed to distribute codas roughly by the number of clicks they contain, with fewer-click codas lower on the plot.

The average linkage cluster analysis on standardized (and unstandardized) data also separated regular codas from irregular ones (Fig. 38). The standardized tree diagram showed "3", "3var", and "4" forming one grouping (as in the principal components analysis), weakly connected to the

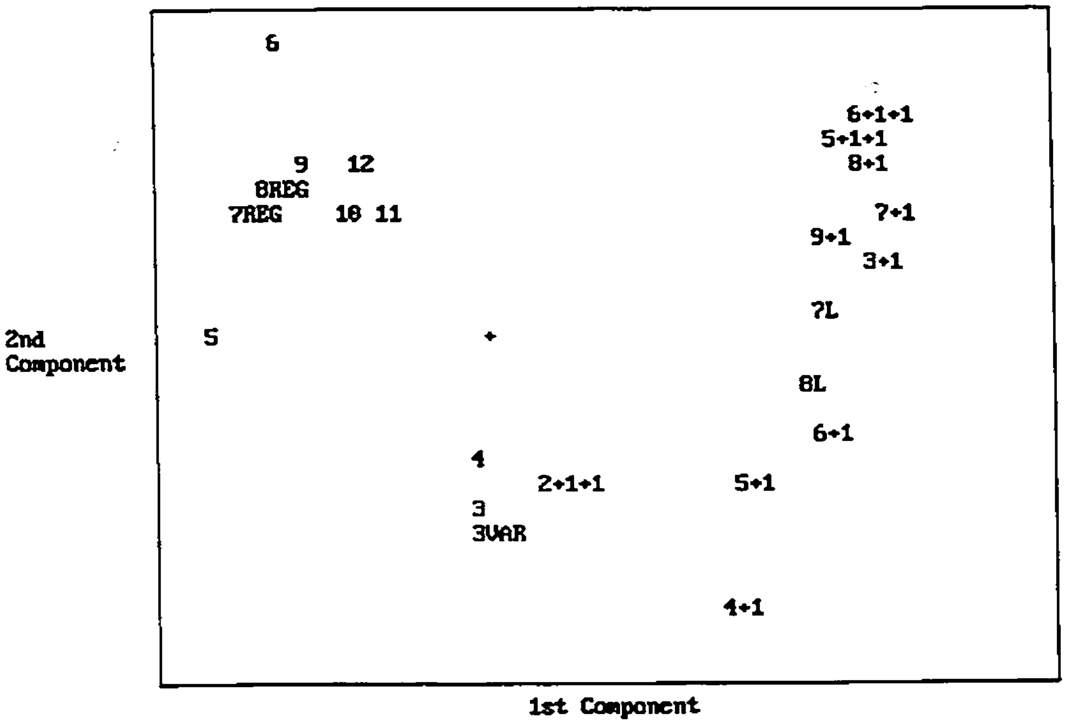


Fig. 37. Factor loading vector plot of first two principal components using standardized 23 coda types. Types plotted close together tended to occur in the same session. "+" denotes the origin.

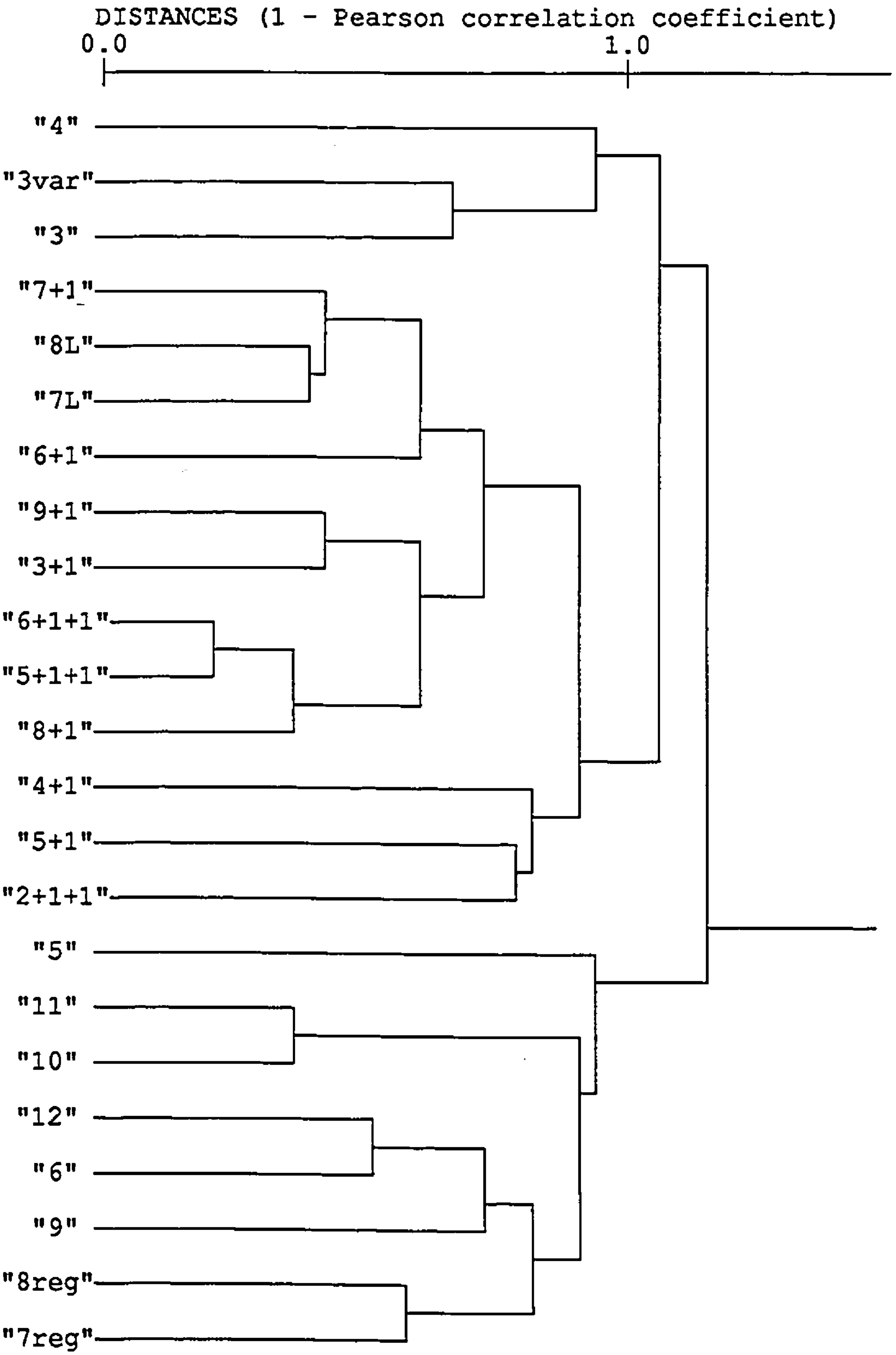


Fig. 38. Dendrogram showing results of average linkage cluster analysis on the standardized 23 coda types.

irregular codas, and finally these two groupings linked to the regular codas. Especially strongly linked were "5+1+1" and "6+1+1"; and "7L" and "8L"; as well as "10" and "11".

c) **Summary**

These analyses showed clear correlations among the rates at which almost all coda types were made. Regular coda types, in particular, tended to occur in the same 5-min recording session as other regular coda types, and irregular coda types tended to occur with other irregular coda types. Short codas also tended to occur with other short codas, and long codas with other long codas, but the relationship did not seem as strong. Creaks seemed most correlated with 4 coda types, all of them irregular ("7L", "7+1", "8+1", and "9+1"). In general, irregular coda types were correlated with more coda types than were regular coda types.

3.8 Correlations between coda types and behavioral/circumstantial variables

a) **Multivariate analyses**

Since significant correlation coefficients are often spurious when many correlations are carried out, and in order to clarify the overall relationship between acoustical variables and behavioral ones, a canonical correlation analysis and a multivariate analysis of variance were undertaken.

The canonical correlation analysis could only accommodate a few variables so the most common coda types ("4+1", "5", "5+1", "6", "7reg", "8reg", and long codas (of 9-12 clicks)) were chosen to be related to the behavioral variables of maximum cluster size, number of clusters, joining occurring or not, number of breaches, lobtails, flukes, sideflukes, and spyhops. Speed was omitted since sample sizes were lower than for the other variables. To eliminate possible effects of autocorrelation, a reduced data set was used, which contained only the last session of each day. This analysis was only done on unstandardized variables.

For the multivariate analysis of variance, acoustical variables "4+1", "5", "5+1", "6", "7reg", "8reg", long codas, and total creak number were related to the presence or absence of a male, the presence or absence of a calf, month, time of day categories 1-5, identified group, and year. Autocorrelations were removed from the data set except when comparisons were made between time of day and standardized and unstandardized acoustical variables. Only statistically significant results will be presented. Because these data are not normally distributed, significance tests of both the canonical correlations and the multivariate analysis of variance should be viewed with caution.

Table 11. First ($r=0.963$, $p<0.001$), second ($r=0.900$, $p<.001$), third ($r=0.819$, $p<0.05$), and fourth ($r=0.782$, $p<0.05$) canonical correlations of canonical correlation analysis of 7 coda types against 8 behavioral/circumstantial variables using unstandardized data with autocorrelation removed.

1st Canon. Corr. (Loadings)				2nd Canon. Corr. (Loadings)			
"4+1"	0.113	clst. size.	0.211	"4+1"	-0.070	clst. size	0.007
"5"	0.137	no. clst.	-0.577	"5"	0.442	no. clst.	0.388
"5+1"	0.129	joins	-0.592	"5+1"	-0.282	joins	-0.330
"6"	-0.286	breaches	0.229	"6"	-0.644	breaches	0.691
"7R"	-0.048	lobtails	0.011	"7R"	-0.213	lobtails	0.421
"8R"	0.525	flukes	0.256	"8R"	-0.128	flukes	0.697
long	-0.646	sideflukes	-0.292	long	-0.306	sideflukes	-0.132
		spyhops	-0.030			spyhops	0.262

3rd Canon. Corr. (Loadings)				4th Canon. Corr. (Loadings)			
"4+1"	-0.566	clst. size	-0.218	"4+1"	0.343	clst. size	0.132
"5"	0.262	no. clst.	-0.112	"5"	0.418	no. clst.	0.151
"5+1"	-0.052	joins	-0.418	"5+1"	-0.127	joins	-0.587
"6"	0.363	breaches	-0.266	"6"	0.332	breaches	-0.369
"7R"	0.313	lobtails	-0.407	"7R"	-0.344	lobtails	-0.654
"8R"	0.642	flukes	-0.100	"8R"	-0.112	flukes	-0.479
long	0.570	sdflukes	-0.113	long	0.230	sdflukes	0.326
		spyhops	-0.556			spyhops	0.471

i) Behavioral/social

The first four canonical correlations were significant (Table 11). There was a clear overall relationship between coda types and behavioral or circumstantial variables, but the specifics of this relationship were not obvious. However, coda type "5" seemed to have distinct associations with behavior types, as did perhaps "7reg" and "4+1". In contrast, "8reg" and long codas were associated with times when no behavior types were seen. Multivariate analysis of variance revealed that the relationship between the presence or absence of males and coda types was only significant using standardized data (Wilks' lambda, $p<0.05$). There was a significant (Wilks'lambda, $p<0.05$) relationship between identified groups and coda types, but again, only with the standardized data.

ii) Temporal

The multivariate analysis of variance showed that only unstandardized coda types were significantly related to month (Wilks' lambda, $p<0.05$). Similarly, only unstandardized acoustical variables were significantly related to time of day categories (Wilks' lambda, $p<0.01$). The fact that both time of day and month showed no significant relationship with the standardized data suggests that, though total coda numbers of the various types changed over time and from month to month, their relative proportions did not. There were no significant differences by year with coda types.

b) **Correlations**

While the above multivariate analyses showed broad overall associations between coda types and behavioral/circumstantial variables, Spearman correlation coefficients and the Kruskal-Wallis test were used to examine the specifics of these relationships. The relationships between the acoustical variables and the discontinuous variables like month, time of day (divided into categories), absence or presence of male, absence or presence of calf, occurrence or not of joining, and identified groups were examined using a nonparametric one-way analysis of variance, the Kruskal-Wallis test (a Mann-Whitney U-statistic was used when the grouping variable only had two categories, as in the absence or presence of male).

Since variables "3var", "3+1", "4+1", "5", "5+1", "6", regular codas, irregular codas, and <10 clicks/creak (length (1)) were shown to be autocorrelated, a reduced data set was used for these variables, which selected only the last session of each day. Both standardized and unstandardized data sets were used. Where both unstandardized and standardized data produced similar significant correlations, only the latter coefficients will be given. About 0.7 significant

Table 12. Spearman correlations between coda and creak types and behavioral/circumstantial variables. Correlations which were significantly positively ("+") or negatively ("-") correlated using both standardized (S) and unstandardized (U) data are unmarked (neither "S" nor "U"). The Kruskal-Wallis test was used for discontinuous variables. Correlations are often spurious: 0.7 significant correlations per coda type would be expected by chance.

		Variables:	
Coda type	Behavioral	Social	Temporal
"3"	+ breach	-	-
"4+1"	-	-	-
"5"	+ breach (S) + lobtail (U)	- speed (U)	month (U)
"5+1"	-	-	-
"6"	-	-	month
Short	- spyhop - sdfluke (S)	+ speed (S)	-
"6+1"	-	-	month
"5+1+1"	-	+ max. clst. size calf group	-
"6+1+1"	-	male group	-
"7+1"	-	joins group	-
"7reg"	+ sdfluke + spyhop (S)	-	month
"8reg"	-	-	month
"8L"	-	group (S)	-
Medium	+ sdfluke	- speed + max. clst. size	-
"8+1"	-	male calf group	-
"9"	+ breach + lobtail	-	month
"10"	-	-	time of day
"11"	-	group	-
"12"	-	- max. clst. size	-
Long	-	- speed (U)	-
Creaks:			
Med. ICI	+ lobtail (U) + spyhop (S)	+ max. clst. size (S)	-
Long ICI	-	joins (U)	-
21-30 clcks/ creak	-	joins (U)	-

correlations per coda or creak type would be expected to be spurious or random. Results are given in Table 12.

i) Behavioral

Spearman correlation coefficients revealed several strong, significant correlations between acoustical variables and behavioral ones (Table 12). Coda type "3" was related to breaches (Spearman $r_s = 0.294$, $p<0.05$, $n=47$) for both data sets, while "5" was only related to breaches in the standardized data set ($r_s = 0.296$, $p<0.05$, $n=47$). In the unstandardized data, "5" was positively correlated with lobtails ($r_s = 0.453$, $p<0.05$, $n=22$). Coda type "9" was associated with both breaches ($r_s = 0.353$, $p<0.05$, $n=47$) and lobtails ($r_s = 0.293$, $p<0.05$, $n=47$). Medium interclick interval creaks were heard together with lobtails ($r_s = 0.311$, $p<0.05$, $n=47$, unstandardized data), and spyhops ($r_s = 0.395$, $p<0.05$, $n=28$, standardized data).

Coda type "7reg" was heard very significantly more often in conjunction with sideflukes ($r_s = 0.397$, $p<0.01$, $n=47$), and in the standardized data, spyhops ($r_s = 0.329$, $p<0.05$, $n=47$). While medium codas (like "7reg") were very significantly positively correlated with sideflukes ($r_s = 0.389$, $p<0.01$, $n=47$), short codas showed the opposite trend ($r_s = -0.407$, $p<0.01$, $n=47$) with standardized data. Short codas were also negatively correlated with spyhops (r_s = -0.319, $p<0.05$, n=47).

ii) Social

Coda type "5" was very significantly negatively correlated with the whales' speed (r_s = -0.652, $p<0.01$, n=13) using unstandardized data. However, short codas, of which "5" is a part, were heard when speed was higher (r_s = 0.371, $p<0.05$, n=29, standardized data). Medium codas, in contrast, were negatively correlated with speed (r_s = -0.406, $p<0.05$, n=29). Since short codas and medium codas were negatively and positively, respectively, related to sideflukes (and spyhops, for short codas), there was internal consistency within the data because sideflukes and spyhops tended to occur at low speed. Long codas, like medium codas, were negatively correlated with speed, but only with the unstandardized data (r_s = -0.453, $p<0.05$, n=29).

Type "5+1+1", like medium codas (r_s = 0.323, $p<0.05$, n=47), to which group it belongs, was related to maximum cluster size (r_s = 0.323, $p<0.05$, n=47). Medium interclick interval creaks were also heard in association with maximum cluster size (r_s = 0.428, $p<0.05$, n=28) using standardized data. In contrast, coda type "12" was negatively correlated with maximum cluster size (r_s = -0.335, $p<0.05$, n=47). Joining of clusters was associated with "7+1" ($p<0.05$, 5 df, n=51), and in the unstandardized data, long interclick interval creaks ($p<0.01$, 1 df, n=47) and 21-30 clicks/creak (length (4)) ($p<0.05$, 1 df, n=47).

Coda types "6+1+1" ($p<0.05$, 1 df, n=47) and "8+1" ($p<0.05$, 1 df, n=47) were related to the presence of the mature male. Coda types "5+1+1" ($p<0.05$, 1 df, n=47) and again "8+1" ($p<0.01$, 1 df, n=47) were related to the presence of a calf. There were differences between identified groups in the number of coda types "5+1+1" ($p<0.05$, 13 df, n=41), "7+1" ($p<0.05$, 13 df, n=41, "6+1+1" ($p<0.01$, 13 df, n=41), "8+1" ($p<0.01$, 13 df, n=41), "11" ($p<0.01$, 13 df, n=41), and in the standardized data, "8L" ($p<0.05$, 13 df, n=41).

iii) Temporal

The following coda types varied by month: "5" (unstandardized data only; $p<0.05$, 5 df, n=25); "6" ($p<0.05$, 5 df, n=25), "6+1" ($p<0.05$, 5 df, n=51), "7reg" ($p<0.001$, 5 df, n=51), "8reg" ($p<0.05$, 5 df, n=51), and "9" ($p<0.01$, 5 df, n=51). Only coda type "10" varied with time of day ($p<0.05$, 4 df, n=51).

c) **Variations in coda length within coda type related to behavioral/circumstantial variables**

To examine whether variations in interclick interval lengths within the same coda type were important, coda lengths for coda types "4", "5", "5+1", "6", "7reg", and "8reg" (the most common coda types) were related to maximum cluster size, speed, number of clusters, breaches, lobtails, fluke-ups, sideflukes, spyhops, and identified groups. Sample sizes were usually too small to exhibit any major effects, but durations of coda type "5" varied with the number of fluke-ups seen ($r_s = -0.699$, $p<0.01$, $n=20$); i.e., greater numbers of fluke-ups were associated with shorter coda type "5"s. "8reg"s with shorter durations (and thus shorter ICIs) were also heard in conjunction with higher speed ($r_s = -0.676$, $p<0.05$, $n=9$) and more spyhops ($r_s = -0.591$, $p<0.05$, $n=12$), though sample sizes were small. There was no difference in a particular coda type's duration with group (Kruskal-Wallis, $p>0.10$), but again, sample sizes were only around 10.

d) **Summary**

There was a clear overall relationship between coda types and behavioral and circumstantial variables, but the specifics of this relationship were not obvious. Coda types "3", "5", "7reg", and "9" were correlated with various behavior types. In addition, "5" was heard when whales were moving slowly. "5+1+1" was associated with large cluster sizes, in contrast to "12", which showed the opposite trend. Short codas tended to occur when whales were moving faster (despite the strong reverse relationship with short coda "5") and when less surface behavior of certain types was observed. Medium codas were associated with slow speed, and, like medium interclick interval creaks, with large cluster sizes and certain behavior types. Long codas were also heard when whales were moving more slowly. Codas of type "5" which were shorter in duration were associated with more fluke-ups.

Coda type "8+1" was related to the presence or absence of both males and calves, as well as to groups. Type "6+1+1" was associated with the presence or absence of a male, while "5+1+1" was associated with the presence or absence of a calf. Both coda types, in addition to others, also varied with group. Several coda types varied with month, but there were also indications that while absolute coda numbers of various types changed over time and with month, their relative proportions did not. While there were relationships between coda types and month, presence or absence of a male, and identified groups, these variables were all related to each other since males were found only in particular months, as were certain identified groups. Coda types did not vary in frequency of occurrence over the two years. There was no difference in a particular coda type's duration with group.

3.9 Highlights of results

1. A new type of sperm whale vocalization, the "slow click", was described. It is almost definitely produced by mature males.

2. Slow clicks were distinguished from the usual clicks heard from groups of females and immatures primarily by their longer interclick intervals (6 s as compared to 0.5 s for females and immatures), but also by their tonal quality (peaks of intensity at 1.8 and 2.8 kHz), and their longer durations.

3. There were some individual differences in the frequencies emphasized, especially in usual clicks. Slow clicks also showed individual variation in interclick intervals but this was not reliable or distinct enough for individual identification.

4. There was a strong correlation between behavioral/circumstantial variables and rates at which different types of vocalizations were heard. An index of "sociality" emerged when examining relationships between behavioral and acoustical variables. High numbers of codas and creaks, but few usual clicks, were heard together with large cluster size, many sideflukes and spyhops, few fluke-ups, and little directional coordination.

5. There was little variation in acoustical and visually observable behavior in situations of low sociality, but more social situations showed much greater variability.

6. Particularly codas, but also clicks and creaks, varied diurnally, with all three vocalizations more common during the daytime.

7. Most of the codas heard occurred in only about 8% of all sessions.

8. Coda types were found to be discrete and non-overlapping, and could be categorized into 23 types.

9. Irregular coda types (the "+1" or "+1+1"s) were very similar to their regular coda counterparts (those with evenly spaced clicks) in interclick spacing, except that the "+1" portion represented a skipped click.

10. Regular coda types had very regularly spaced clicks.

11. Codas overlapped or followed one another according to type in a non-random way, with the overlapping or following coda often containing one click more or less than the coda it overlapped or followed.

12. Special types of overlaps, called "echocodas", occurred when the overlapping whale's coda clicks were inserted nearly precisely into the interclick intervals of the first whale's coda.

13. Coda type "5" was particularly evenly spaced, had much shorter interclick intervals than other regular coda types, was less likely to be second in an overlap, and was the coda type most frequently preceded by periods not containing codas ("5" was an initiator).

14. The distinction between regular and irregular coda types seemed important since codas were strongly associated with and occurred more often with their own category, i.e. regular coda types occurred with other regular coda types.

15. The rate of production of different coda types varied with behavioral and circumstantial variables such as identified group, month, maximum cluster size, presence of male, but the specifics of these relationships were not clear.

CHAPTER 4. DISCUSSION

4.1 Functions of sperm whale sounds

While sperm whale signals have been classified by form (acoustic structure) thus far in this thesis, they can also be categorized by their influence on the behavior of the receiving animal (Busnel 1977). Critical to the idea of communication is that the behavior of the recipients must be affected in some way (Wilson 1975). In animals, signals are usually related to: 1) mating, both in attracting mates and repelling competitors; 2) territorial behavior; 3) social status; 4) feeding behavior; 5) group movements; 6) avoidance of predators; or 7) social bonding. Those categories are, of course, often related and not mutually exclusive. With these guidelines in mind, I will investigate the possible functions of sperm whale vocalizations.

a) **Usual clicks**

Usual clicks were given about every half second and contained some individual variation in emphasized frequencies. Higher click rates were heard in conjunction with more fluking, and when whales were spread out in many, smaller clusters rather than grouped in few, large clusters. These results agree well with those of Gordon (1987). High click rates were also heard when whales showed directional coordination in movement, faster speed, and fewer sideflukes and spyhops. Click rates were positively related to the number of group members in an identified group and were highest in the daytime.

The above evidence, together with that from Backus and Schevill (1966) and Mullins et al. (1988) broadly supports echolocation as a primary function for usual clicks. Gordon (1987) convincingly argues for an echolocatory function as well. Papastavrou et al.'s (1989) observation that whales began clicking at depths of 150 to 300 m lends additional credence to this idea. With an interclick interval of 0.5 s, whales would be scanning at most the ca. 400 m stretch of ocean ahead of them [400 m = (0.5 s x 1520 m/s)/ 2, assuming that whales emit clicks only after receiving the previous click's echo]. Any signature information in the usual click would aid in distinguishing a whale's own echoes from those of her neighbors. Since sperm whales feed at depth, fluke-ups, which precede terminal dives, would be expected to be seen in conjunction with foraging. Using data from the same field study as this one, Whitehead (1989) found that foraging sperm whales formed ranks of about 550 m in length aligned perpendicular to the direction of travel. When whales surfaced, clusters containing a mean of 1.7 whales could be seen spread out along the rank. These ranks travelled at 2 knots (3.7 km/h) and maintained their headings over several hours (Whitehead 1989). All animals appeared to emit clicks, since click rates were related to the number of individuals in a group.

Whether sperm whale feeding shows a diel pattern is still not clear from the literature (Clarke 1980). The diel variation in click rate was related to the frequency of groups meeting (but not socializing), so the magnitudes of click rates do not simply reflect feeding activity. Click rates were higher in 1985 than 1987, suggesting that groups met less often in 1987. This may have been due to the 1987 "El Niño" oceanographic event which appeared to lower the feeding success of Galápagos sperm whales (Whitehead et al. 1989a).

Mullins et al. (1988) found that during the dive phase, sperm whales, even when solitary, produced clicks almost continuously, in contrast to Watkins (1980), who claimed sperm whales were silent for long periods, especially when alone. Watkins (1980) felt sperm whale clicks did not conform to an echolocation hypothesis, partially because their intensity level was greater than required. He therefore argued that usual clicks serve as contact calls (Watkins 1980; Watkins et al. 1985). However, sperm whales might need louder clicks than other odontocetes for ecological reasons. They feed on more dispersed and less acoustically reflective prey (squid lack swim bladders) than most oceanic delphinids, and do not travel in the large schools of hundreds to thousands of dolphins, which can sweep and search great expanses of ocean. Instead, they must scan longer distances for weak sound scatterers. Because they inhabit deeper waters, their clicks would have to be of higher amplitude if they orient themselves according to bottom contours. Group members foraged only a maximum of 550 m apart (Whitehead 1989), yet their clicks can be heard for 5 km or so. Cooperative signals such as contact calls should theoretically only be loud enough to travel to the intended receiver, and no louder, since this could attract predators (Krebs and Davies 1987). Unless sperm whales are coordinating their movements over ranges of 5 km, which does not seem to be the case (Whitehead and Weilgart 1990), it is unlikely that usual clicks are primarily intended as contact calls. This may well be a secondary function of usual clicks, though.

Norris and Harvey (1972) and Backus and Schevill (1966) presented reasons why the multiple-pulse structure of sperm whale clicks ("burst-pulsing") seemed optimum for long distance echolocation. More refined information about a target can be carried within a burst-pulse echo, as compared with an echo from a single click. In addition, greater size discrimination would be possible, and the burst pulse could be picked out from background noise at lower intensity levels due to neural summation effects (Norris and Harvey 1972).

b) **Slow clicks**

Slow clicks were produced by mature males, had much longer interclick intervals than usual clicks (a mean of about

6 s), displayed two consistent bands of intensity peaks at about 1.8 and 2.8 kHz, and were longer in duration than usual clicks, mainly because of their "ringing" quality. Neither the frequency location of the two intensity peaks, nor the interclick interval was significantly related to male body length. While usual clicks were heard from the much more common groups of females and immatures (mature males comprised only 2-3% of the population in the Galápagos and accompanied groups of females and immatures only 16% of the time--Whitehead and Arnbom 1987), this does not mean that mature males may not also produce usual clicks.

But how and why do mature males produce a click different from that of females and immatures? The forehead of the sperm whale (especially the spermaceti organ) is strongly implicated in sound emission (Norris and Harvey 1972). It is also proportionally larger in males than in females (Nishiwaki et al. 1963). This may alter the acoustical properties of the head, and thus change the sound of the click. The two intensity peaks at 1.8 and 2.8 kHz, for instance, may result from the almost ellipsoid spermaceti organ acting as a resonator in males. This would produce two resonance frequencies, one with greater effect on the vibration than the other (J. Meng, pers. comm.). The frequency location of these two intensity peaks may depend more on the proportions of the spermaceti organ than on just its length, hence the nonsignificant correlation between the two.

There was an indication that males from different breeding areas show greater differences in emphasized frequencies in their slow clicks than would slow clicks from males of the same area. The sample size (only Male 555) from the West Indies was small, but additional sonagrams from male slow clicks recorded in the West Indies (Karen E. Moore, pers. comm.) tentatively support this speculation.

Mature males, probably in order to sustain their larger size, generally inhabit a different ecosystem from the females and immatures. They mainly reside in colder waters (Best 1979), and usually feed on larger prey than do the females (Clarke 1980). As a consequence, a different kind of click may have evolved in mature males (if indeed clicks function in echolocation). Perhaps their larger head enables them to produce clicks of greater intensity. This, in turn, may allow them to increase their detection range for prey. This would be especially important when feeding on larger, and therefore generally more dispersed, prey. The longer ICIs of the males would also support the idea that males were scanning greater distances ahead. However, whether males could detect anything at ranges of 4-5 km (which corresponds to the maximum range of an average to long ICI of a SC) is unknown. Perhaps males could detect groups of females, though. The longer ICIs of SCs may also suggest that this click is either a physically strenuous sound to produce, or that it takes a period of time to generate (Walton 1990), and that the long interval represents a charging process to store energy before each click (Peter Tyack, pers. comm.).

Slow clicks, unlike usual clicks, were produced at the surface as well as underwater (Mullins et al. 1988). Mullins et al. (1988) reported that an 11-13 m maturing male from temperate waters (the Scotian Shelf) produced slow clicks when neither feeding (since he was at the surface) nor breeding (since he was far from the breeding grounds). Moreover, they found that the male could alternate between using usual clicks and slow clicks, and that these two vocalization types remained discrete, with no gradual change in interclick interval. This strongly suggests that the function of the slow click is different from that of the usual click, and that the slow click is not merely the inevitable acoustical result of larger head size in males. It may be noteworthy that the two subadult Scotian Shelf males' interclick intervals for usual clicks were slightly longer than the median calculated for the Galápagos usual clicks (0.69 s and 0.96 s, compared to about 0.53 s), but that the mean interclick interval for slow clicks was shorter than the median interclick interval for Galápagos slow clicks (4.57 s compared to 6.05 s). Maturing males may thus use interclick intervals that are intermediate between those from fully mature males and those from females.

Vocal characteristics, like the male's slow click, are often a good indicator of sex (Busnel 1977). In addition, these vocal characteristics may become more striking or appear for the first time when puberty arrives (Alcock 1975). Thus, the slow click may be a sign of a mature or maturing male. If this signal informs other sperm whales of the vocalizer's state of maturity, competitive ability, or physical fitness, it may function in repelling other males, as in toads (Davies and Halliday 1978) and red deer, Cervus elaphus, (Clutton-Brock and Albon 1979), and in attracting females. Some attributes of slow clicks (although probably not interclick interval or ringing frequency) may be reliable indications of male size (especially since the size of the spermaceti organ is related to overall body length -- Nishiwaki et al. 1963) or strength (since slow clicks may require effort to produce). Practicing these signals before entering the breeding grounds may then result in greater reproductive success. Indeed, Hall et al. (1988) believe that male Chillingham cattle have more complex calls than other Bovini, which are relatively silent, because juveniles have more opportunities to practice their vocalizations without fear of aggression from mature males or predation pressure. Subadult sperm whale males would also not have to fear aggression from more mature males, since the latter generally occupy higher latitudes when not on the breeding grounds (Best 1979).

c) **Creaks**

Creaks were strongly correlated with codas and appeared to be used in similar circumstances to codas. Creaks were significantly correlated with measures of aggregation (number of individuals present, mean and maximum cluster size) and with behavior types (sideflukes and spyhops), but not as strongly associated with these as were codas. Moreover, they showed some relationship to click rate as well (Sec. 3.3d). Like click rate, the number of creaks heard was higher in 1985 than 1987. Unlike codas, creaks were not significantly related to the presence of mature males.

There may have been two types of creaks -- one of shorter duration (about 0.77 s, on average) heard together with codas, and which dominated the analysis since it was more prevalent ("coda-creaks"); and the other of longer duration which occurred with usual clicks. Mullins et al. (1988) would have measured creaks of the latter type, and presented a mean creak duration from two males off Nova Scotia of 44 s. Gordon (1987) found that creaks lasted from 10 to 25 s for sperm whales off Sri Lanka. These values are both longer than the aurally measured long creaks of this study (mean of 5.05 s), but there was much variation in length, and some coda-creaks may have been included in my aural analysis. In any case, the existence of two types of creaks might explain why they shared similarities with both codas and clicks.

Gordon (1987) also distinguished between these two types of creaks. "Creaks" he believed were close-range echolocation signals, whereas what he calls "chirrups" (equivalent to my "coda-creaks"), he suggested as having a communicatory function. He found chirrups, unlike creaks, to have a very marked and regular pulsed structure (Gordon 1987).

On the one hand, creaks may be considered a form of communication because of their correlation with large aggregations of whales. Watkins et al. (1985) also heard creaks during "social activities". On the other hand, Mullins et al. (1988) and Gordon (1987) present evidence which suggests that creaks may be used by sperm whales as echolocation during feeding. Coda-creaks could also function as echolocation, but of a type only used in social circumstances perhaps (e.g. determining positions of group members as opposed to locating prey). Alternatively, they may be strictly a form of communication.

d) **Codas**

Codas were most strongly correlated with large aggregations of whales [number of close (within 500 m) clusters, number of individuals, number of close individuals, mean and maximum cluster size]. These measures (particularly number of individuals seen) indicated that most whales were at the surface when codas were heard, and that whales were grouped into one or a few large clusters, instead of many, very scattered, smaller clusters. Codas were also heard in conjunction with sideflukes and spyhops, behavior types which usually indicated that whales were twisting and turning about one another in tight clusters. Other variables associated with high coda numbers were lack of directional coordination, slow speed, low click rates, and few fluke-ups. Codas were slightly correlated with lobtails and breaches, and more codas were heard in the presence of mature males or calves. Codas were usually heard in the daytime, from 09.00 to 17.00 h.

These results support previously held opinions that codas are used for communication (Backus and Schevill 1966; Watkins and Schevill 1977a). Since whales were usually at the surface when codas were heard, a finding also confirmed by Gordon (1987); it can safely be assumed that they were not feeding. Watkins and Schevill (1977a), however, believe codas are produced at depth, but their observations were limited to at most a few hours. Codas emitted at the surface may have different tonal qualities from usual clicks because nasal passages and air sacs in the whale's forehead are not compressed at the surface as they may be under pressure of depth. This could alter the acoustic reflectivity of structures in the forehead, and might account for the "clacky" sound of codas.

Mullins et al. (1988) heard no codas while tracking single whales, but noted their occurrence when more than one sperm whale was present. Codas were often heard as exchanges between whales (Watkins and Schevill 1977a), and whales became quiet, as if listening, when codas, as well as coda-like pingers from a hydrophone array calibration system, were produced (Watkins and Schevill 1975). These findings also point to codas having a communicative function.

4.2 Coda communication compared with social communication in other species

For female and immature sperm whales, there is a strong correlation between behavioral/circumstantial variables and rates at which different types of vocalizations were heard (canonical correlation of 0.756; Table 6). This strong relationship between behavior and vocalizations is in contrast to results from studies of other social odontocetes (killer whales, Orcinus orca: Ford 1989; pilot whales, Globicephala melas: Taruski 1979, Weilgart and Whitehead, in press; and beluga whales, Delphinapterus leucas: Sjare and Smith 1986, Faucher 1989), which found that vocalization types could not be correlated exclusively with any behavior or circumstance. While codas as a group are heard in very recognizable circumstances and while vocalization types (codas vs. clicks) could usually be predicted based on visually observable behavior, specific coda types were just as difficult to correlate with behavioral/circumstantial variables as in the other odontocete studies mentioned above.

Codas clearly seem a form of social communication, but their precise significance warrants further investigation. Codas are a relatively rare vocalization type, with large numbers of codas occurring only occasionally. They thus appear to be reserved for highly specific functions. It may be illuminating to review the purposes or functions of social communication in other species to gain insight into the significance of sperm whale codas.

a) Individual identity

Several cetacean species, especially delphinids, are thought to possess acoustic "signatures" unique to individuals (Caldwell and Caldwell 1965; Caldwell and Caldwell 1977; Tyack 1986). Watkins and Schevill (1977a) also proposed this to be the case for sperm whale codas. However, I strongly believe that codas are not used primarily as a means of individual identification, since only 23 main coda types were discovered in a population of ca. 400 whales belonging to about 20 different identified groups (Whitehead and Waters, in press). Gordon (1987) also concluded that the evidence for individual identity codas was unconvincing. Again, it is not surprising that my results differ from those of Watkins and Schevill (1977a), as their observations were so limited. Still, it is possible that "signature" codas exist. The lengths of the interclick intervals within a particular coda type could vary from one individual to the next, or perhaps the rare, variable spaced coda types ("var"s) carry individual identity information. It is equally likely, however, that other cues, for instance the patterns of emphasized frequencies within clicks, could supply sufficient information for sperm whales to recognize the identity of the emitter.

b) **Group identity**

Ford (1989) found that in killer whales, certain types of social calls occurred in greater proportions during particular activities, but that most of the acoustical repertoire was devoted to group-specific information (group dialects). These dialects, he hypothesized, aid in intrapod communication and help to maintain the integrity of the social unit. Killer whale pods often associate with other pods in the area, so communicating pod affiliation by means of group-specific calls may be important (Ford 1989).

In sperm whales, there were indeed differences between groups in the numbers and proportions used of certain coda types. Codas may also function as indicators of group identity, since sperm whales, like killer whales, form stable maternal groups. While my data were not sufficiently large or complete to fully determine the presence or absence of group-specific codas, group dialects do not seem as clear in sperm whales as they do in killer whales. In killer whales, each of the 16 pods had a group-specific repertoire of 7-17 call types, while in sperm whales, only 23 coda types existed in total for about 20 groups. Group-specific coda type usage in sperm whales could also simply reflect a different "focus of interest" for that group. For instance, groups with calves or a certain age-structure may use different coda types. Their repertoire would be different but this would not be exclusively a result of group identity. It must be remembered, however, that my coda type categories may not conform to the categories used by sperm whales. Codas of a particular type but with different durations may be considered different categories by sperm whales. In killer whales, call duration seemed related to "emotional" state. Killer whales emitted calls of shorter duration than normal in situations of high arousal, such as when particular pods met (Ford 1989).

c) **Mating and territorial defense**

Much of animal communication is devoted to mating and territorial advertisement or defense. This is the primary function of bird song (Thorpe 1961), and in cetaceans, humpback whales (Megaptera novaeangliae) sing to attract mates and repel other male competitors (Tyack 1981). In sperm whales, greater numbers of codas are heard in the presence of males, but it is clear that many codas are heard when males are absent, at times other than the peak mating season, and even far from the breeding grounds, as in the Scotian Shelf males (Mullins et al. 1988). Calves also produce codas, which become more prevalent, complex, and stereotyped with age

(Watkins et al. 1988). Codas, then, do not function primarily in courtship or mating, and since sperm whale groups do not seem to be territorial (Whitehead and Arnbom 1987), in territorial defense.

Sperm whale codas may have similarities to the duetting found in birds (Smith 1977a; 1977b), some primates (Marshall and Marshall 1976; Gould 1983) and some species of bats (Matsumura 1981). Duetting pairs overlap one another's call with the precise timing seen also in the echocodas of sperm whales. Duetting is thought to have two main functions: defense of territory and pair bonding (Farabaugh 1982). Duets may reaffirm and maintain pair bonds or family cohesion (Farabaugh 1982). It has not definitely been proven that echocodas are a real response of one sperm whale to another and not simply a chance occurrence, but given that interclick intervals vary in length between and within coda types, it seems unlikely that such exact overlaps would occur accidentally. More research is needed on the functions of echocodas, but they could, as in bats, occur when mothers reunite with infants (Matsumura 1981). Sperm whale mothers probably leave their calves at the surface in the care of other females or immatures while they descend to feed at depths to which the calves cannot follow (Gordon 1987).

African elephants (Loxodonta africana), which resemble sperm whales most closely in social system (Best 1979), use vocalizations to search for mates (Poole et al. 1988). Mature males and groups of females call to each other over long distances and may advertise their sexual state. Both mature male elephants and sperm whales must go from group to group, searching for the few females which are in estrus for probably only a few days. Since both elephants and sperm whale bulls use this "roving male" mating strategy (Whitehead and Arnbom 1987), and because in both species males must travel long distances between dispersed groups of females, it is possible that their vocalizations may have similar functions. Sperm whale males do not seem to emit many codas (or else these do not sound distinct from those of females), but presumably females can hear and recognize their slow clicks. Females may advertise their reproductive state through codas, but codas do not seem to travel very far, perhaps only 500 m to 1 km (pers. obs.). Codas, then, probably are not a long-distance means by which males and groups with estrous females find each other. Sperm whale bulls, however, may have an advantage over elephant bulls in their ability to echolocate. The slow click may indeed be used to search the 5-6 km distance, corresponding to the slow click interclick interval, for groups of females. This probably cannot be its sole function, however, since males emit slow clicks even while with a group of females.

d) **Group movements**

Elephants also use their vocalizations in the spatial coordination of groups (Poole et al. 1988). They exchange contact calls between group members which may coordinate group movement over distances of several km. Sperm whale group members seem to coordinate their dive cycles as well (Whitehead 1989), distributing themselves over a large area, but resurfacing together at the end of dives (Watkins and Schevill 1977b). They do not, however, seem to use codas for this coordination, as usually none are heard until after whales have surfaced. Again, codas could probably not be used for long-range contact call because they do not appear to carry very far. Additional observations also indicate that codas produced at closer ranges are more "interesting" to sperm whales. Even though coda-like pinger sounds from an underwater array calibration system were audible for an estimated 1 km, only nearby whales (200 m or less) remained silent for at least 2 min, in contrast to distant whales which quieted for only a few seconds. Whales at intermediate ranges of about 500 m stopped clicking for 45-60 s (Watkins and Schevill 1975, 1977a; Watkins 1979). Still, codas could transmit information pertaining to those coordinated group movements or feeding formations which would occur <u>subsequent</u> to the time spent at the surface. There could also be, for instance, the sperm whale equivalent of the elephant's "Let's go" rumble (Poole et al. 1988), which would signal to group members when to restart feeding.

e) **Social bonding**

Finally, in primates, certain call types occur during periods of quiet resting, affiliating, and care giving (e.g. Smith et al. 1982; Gautier and Gautier 1977). In squirrel monkeys (Saimiri spp.), pairs, or more rarely triads, spend most of their resting time close to or huddling with each other (Symmes and Biben 1988). This behavior is most pronounced in adult females, and is accompanied by extensive vocalizing. Around 80% of the vocalizations are all of the same type--primarily tonal "chucks". Females were more likely to vocalize in response to chucks of more preferred partners, and did so with less delay (Symmes and Biben 1988). Vocal exchanges which are associated with affiliative interactions may function in social cohesion, reaffirming bonds within stable groups following dispersion or separation (Gautier and Gautier 1977; Smith et al. 1982).

The social system of squirrel monkeys is somewhat comparable to that of sperm whales. Group sizes are around 30, with 2-3 males per group (Robinson and Janson 1987). The genus is polygynous, and males compete vigorously for access to females. Females form strong affiliative relationships, exhibit no hierarchy, and exercise much control over group life. Groups are sexually segregated, with females spatially grouped together because of strong bonds between females and aggression they direct towards males. Alloparenting is common, as well as some allosuckling (Robinson and Janson 1987).

Though mature males are not a part of the stable female groups in sperm whales, sperm whales are similar to squirrel monkeys in the strong social cohesion displayed among females. Codas, like the "chucks", occur during social resting periods while whales are in tight clusters. Especially since group members have been dispersed during foraging, these periods may be important in maintaining social relationships. This seems to be the most likely function of sperm whale codas.

4.3 Discrete (digital) vs. graded (analog) communication

Signal structures with only two stereotyped signals or states possible, for instance the presence or absence of a signal, can be described as digital, while signals in which continuous variation is possible along a given dimension would be of an analog type (Green and Marler 1979). Discrete or digital signals are favored when auditory signals must function without support from other sensory modalities, such as vision. Long distance calls, calls which occur at night, or in dense vegetation all would be expected to be discrete. In contrast, graded signals are more common in close-range signalling, usually within groups, where backup visual cues could be provided to decrease ambiguity and misinterpretation (Green and Marler 1979). Graded signals have the potential for communication of more refined information (Marler 1976). Green and Marler (1979) propose that graded signals would be more prevalent in species with complex social interrelationships in which communicants are completely familiar with one another. Such species would tend to be long-lived, living in stable groups with overlapping generations. They suggest, however, that most animals use a mixture of discrete and graded signals, with only the very simplest organisms having a fully discrete or completely graded repertoire (Green and Marler 1979).

a) **Cetaceans**

In cetaceans, this rule generally seems to hold. Whistles, which are usually quite graded (e.g. Taruski 1979; Faucher 1989), except perhaps in the case of signature whistles (Caldwell and Caldwell 1965), do seem to be used by very gregarious species which forage communally and have the complex social systems mentioned above (Herman and Tavolga 1980). The most notable exception to this rule is the sperm whale. It is the only social cetacean which uses clicks for communication. Clicks, since they contain no frequency modulation, seem less able to be varied than whistles, except in interclick spacing. Even interclick intervals show little gradation from one type to another when the 23 coda types are standardized for length. Coda types, then, genuinely seem to be discrete, and appear to be very close to completely digital communication.

Because of bodily limitations, in cetaceans, vocalizations have to serve the communicative functions that most other animals perform by kinesics (facial expressions, clenched fists, raised epaulets, flared nostrils, etc.) (Bateson 1966). Sperm whale communication may be discrete, even though given over relatively close ranges, since visual cues are restricted by the medium (water visibility was often less than 10 m around the Galápagos), and because sperm whales are limited to using only body orientation or posture to provide supplementary visual cues for reducing ambiguity. Other channels of communication, such as olfaction, may provide supplementary cues. This does not, however, explain why other cetaceans use graded vocalizations.

b) **Other species**

Digital communication is prevalent in the animal kingdom, but usually occurs in less socially complex species. Cricket and grasshopper species, for instance, show characteristic songs, made up of pulses (Prosser 1986), and fish use temporally patterned pulses during the mating season (Fine et al. 1977). Among the socially more advanced species, bats are similar to sperm whales in that echolocation calls simultaneously can serve both communication and orientation functions (Fenton 1986; Matsumura 1981). Bat communication calls are used in species recognition, collision avoidance, and mother-young relationships, among other functions (Fenton 1986). Walruses (Odobenus rosmarus) exhibit discrete classes of airborne sounds (Miller 1985), in addition to underwater "codas" (Stirling et al. 1987). These underwater codas are made by males and consist of pulses typically grouped into a pattern. Differences in coda patterns are chiefly due to individual variations and seem to be used as a vocal display by males during courtship (Stirling et al. 1987). Thus, while these patterns bear much resemblance to sperm whale codas, their functions appear to be different. Higher primates (or higher animals in general) are expected to exhibit an unusual emphasis upon graded signals in their vocal repertoires. Squirrel monkeys, like sperm whales, do not fit this prediction. Their vocalizations are, for the most part, discrete, though there is some variation within certain acoustical categories (Marler 1976).

c) **Environmental constraints**

It is possible that sperm whales use discrete clicks because of physical constraints on acoustic communication in the environment. Clicks, because they are easy to hear and locate, may be the most widespread sounds among mammalian species (Gould 1983). Temporal aspects of signals, such as those used to define codas, are critical for information transfer since pulse timing is less subject to environmental distortion (Morton 1975). Larger animals, in particular, are also better at detecting brief sounds from a longer distance than are small mammals (Gould 1983). But while digital signals like codas are well designed for transmitting information with least danger of misinterpretation in high noise environments, it is questionable whether codas need to carry for such long distances. Codas seem to be close-range calls (Watkins and Schevill 1975, 1977a). Still, in conditions of high wind speed, ambient noise levels may be considerable. Mackay (1980) speculates that sperm whales only emit clicks because whistling is difficult at elevated pressure, but since codas are produced principally at the surface, this explanation cannot be complete. Bottlenosed whales (Hyperoodon ampullatus) are also deep divers and yet they produce low level whistles as well as clicks (Winn et al. 1970).

d) **Perceptual processing**

While many linguists believe that digital communication is one of the distinguishing features of human language (Sebeok 1972), dividing animal signals into graded and discrete classes may be misleading since the receiving animal may perceive signals in a digital or analog fashion, regardless of the digital or analogic nature of the signals themselves (Green and Marler 1979). A continuum of signal types may be perceived categorically, as is the case in human speech (Liberman et al. 1961) and in certain primate vocalizations (Marler 1983). On the other hand, digital signals may be assessed by summing them over time so that an analogic rate is obtained (Green and Marler 1979). Until the perceptual processing of digital or analog signals is known, these terms are of limited usefulness.

4.4 Conversational vocal exchanges

Symmes and Biben (1988) speculate that vocal exchanges in the contexts of mating, care giving, and affiliation could shed light on the roots of human conversation. Sounds of vocal exchanges are of relatively low intensity, and are directed to a small, but significant, often closely related, audience. Symmes and Biben (1988) suggest three criteria which might indicate a primitive form of conversation: a) turn taking, or ordered, nonrandom vocalizing which implies that interactants listen to each other and share rules about vocal behavior; b) "directionality", i.e. conversations are not reversible--order matters; and c) change in vocal pattern from the first speaker as a reaction to the vocal response given by the listener, i.e. B vocalizes following A, but A must additionally alter its vocal behavior as a result of B's response (Symmes and Biben 1988). Squirrel monkeys showed evidence that the above three conditions were fulfilled. "Chuck" calls could be identified as approximating "questions" and "answers", with answer calls 300 Hz higher than question calls. Terminating chucks always had higher frequencies (Symmes and Biben 1988).

Sperm whales also seem to exhibit turn taking, and clear exchanges of codas often take place. Their order of vocalizing is also nonrandom and nonreversible. Certain coda types tend to follow or overlap other coda types, and coda type "5" tends to initiate exchanges. The fact that regular coda types had longer than expected final interclick intervals relative to total length may signify to conversational interactants that the coda will soon end. An analogous phenomenon occurs in human conversation, when speakers lower their voices at the end of a sentence.

Since some coda types seem to be used in response whereas others tend to be first in an exchange, a "question and answer" dialog of the type described above for squirrel monkeys may be present in sperm whales. Overlaps, though, present somewhat of a puzzle since the respondent answers before she knows the type of the coda to which she is presumably responding. It is possible that sperm whales can determine the coda type of a coda from the first few interclick intervals. First intervals are all roughly the same length from one coda type to the next, but by the second and third intervals, there is somewhat more variation in duration between coda types (Fig. 34). It seems more likely, though, that whales are responding to codas previous to the one which is overlapped. Results were very similar between analyses of overlaps and transitions, suggesting that whether a coda overlapped another or simply followed another was an unimportant distinction. What has not been examined thus far is whether the first whale's coda changes as a result of the second whale's response. Transitions over longer sequences of codas clearly need to be studied, preferably with the ability to distinguish coda by individual.

4.5 Function and evolution of codas

Sperm whale behavior exhibited considerable variation in conditions of high sociality (Figs. 22 and 23). This variability may reflect flexible behavior patterns and indicate the need for more complex communication. Communication is of greatest importance when achieving and mediating cooperative relationships (Marler 1977). "The most advanced accomplishments [in communication] should evolve in animals whose societies are so constructed that groups of very close genetic relatives live together in social contact" (Marler 1977, p.48). The fact that particular coda types could not be specifically and simply related to particular types of behavioral and circumstantial variables may also point to a more highly developed communication system. Codas seem to have a function most like that of affiliative close-range signalling in squirrel monkeys, namely social bonding. For sperm whales that disperse to feed, periods during which social ties are reaffirmed through codas may be necessary.

Such social bonding may be particularly important in groups with calves, since calves appear to be left at the surface with other group members while mothers dive to depths which calves cannot attain (Gordon 1987). Higher rates of codas may also be associated with the presence of calves because females must determine which adults dive and which remain at the surface to "babysit". More codas may be heard in the presence of mature males because females may communicate their reproductive state and readiness to mate to both males and other group members. It is surprising that mature males do not seem to commonly exchange codas with females, though perhaps such situations have not been fully recognized or observed. It would seem that coda exchange would be important in mating and courtship to coordinate actions.

It is interesting to speculate how sperm whales may have evolved this peculiar means of communication by codas, in contrast to all other social cetaceans. As K-selected animals (members of populations usually at or near environmental carrying capacity), sperm whale populations are probably food-limited, and this indeed seems to be the case for whales off the Galápagos (Whitehead, in press). Thus, food-finding techniques which would allow individual whales to increase their feeding efficiency or success or even exploit new niches would be selected for. The highly specialized spermaceti organ and surrounding structures may have evolved to produce the distinctively loud clicks heard only from sperm whales (Norris and Harvey 1972). This, in turn, along with other adaptations for deep diving, could have enabled sperm whales to exploit the deep water habitat more efficiently and the species of squid which inhabit it. Clicks probably would have to be particularly loud to locate weak sound scatterers like squid over long distances and great depths, especially if these prey species were quite dispersed. Conversely, in order for clicks to function over long distances, they must be produced at depth to avoid acoustical interference from the water surface. Therefore, the ability to produce loud clicks and dive deeply may have evolved simultaneously. Broadband clicks are well suited as echolocation signals (e.g. Watkins 1980) and to overcome background noise. They can also be produced easily at depth, unlike whistles (Mackay 1980).

As deep divers, sperm whales may require periods of about an hour at the surface to reduce lactate concentrations in the blood (Kooyman 1989), or simply to rest. It is probably adaptive to rest together as a group to reduce predation, since it is clear that sperm whales are vulnerable to attack by killer whales (Arnbom et al. 1987). Once such large surface aggregations formed, those groups that were able to communicate information which allowed them to coordinate feeding formations or communal care of young, may have enjoyed greater survival rates and reproductive success. Since the spermaceti organ and whole sperm whale forehead were so highly specialized and evolved for click production, the ability to produce whistles may have been lost, if ever it was present in sperm whales. Thus, sperm whales may have used the already existing means of sound production for social communication as well. Clicks served both in food-finding (as usual clicks) and in communication (as codas), as is the case for bats (Fenton 1986). Codas could have assisted in the formation and maintenance of social bonds, and may have facilitated the evolution of the cooperative relationships seen in sperm whales today.

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