

Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands

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To gain insight into the function of sperm whale vocalizations known as codas (short, patterned series of clicks), sperm whales (*Physeter macrocephalus*) were tracked continuously for periods of days totalling months off the Galápagos Islands, Ecuador, and vocalizations were tape recorded systematically. In total, 1333 codas were classified according to their temporal pattern and the number of clicks they contained. Codas were found to be temporally very clustered, and could be categorized into 23 fairly discrete types. Sequential analysis of codas revealed that they overlapped one another according to type in a nonrandom way, and that type 5 tended to initiate coda exchanges. "Regular" coda types (with evenly spaced clicks) tended to occur with other regular coda types and "irregular" coda types (with one or two delayed final clicks) were heard with other irregular coda types. Codas may function principally as a means of communication, to maintain social cohesion within stable groups of females following periods of dispersion during foraging.

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Des cachalots macrocéphales (*Physeter macrocephalus*) au large des îles Galápagos, en Équateur, ont été suivis pendant des jours entiers sur des périodes de plusieurs mois et leurs vocalisations enregistrées dans le but de comprendre le sens des vocalisations connues sous le nom de « codas » (séries de cliquetis courts et modulés). En tout, 1333 codas ont été classifiées d'après leur structure temporelle et le nombre de cliquetis qu'elles contenaient. Les codas étaient très regroupées dans le temps et pouvaient se répartir en 23 types assez distincts. Une analyse séquentielle des codas a montré que, d'après leur type, les codas se chevauchaient de façon non-aléatoire et que le type 5 avait tendance à susciter des échanges de codas. Les types réguliers de codas (avec cliquetis échelonnés de façon régulière dans le temps) se retrouvaient généralement en même temps que d'autres types réguliers; de même, les types irréguliers (avec un ou deux cliquetis finaux différés) s'entendaient avec d'autres types irréguliers. Les codas semblent servir principalement de moyens de communication pour maintenir la cohésion sociale dans un groupe stable de femelles après les périodes de dispersion pour la recherche de nourriture.

[Traduit par la rédaction]

Introduction

Generally, those odontocete species that are very gregarious, forage communally, and exhibit highly developed social systems (such as the oceanic dolphins of the family Delphinidae, pilot whales (*Globicephala melas*), and belugas (*Delphinapterus leucas*)) produce whistles, along with pulsed sounds and clicks (Herman and Tavolga 1980). The most notable exception is the sperm whale (*Physeter macrocephalus*), which is the only social cetacean that does not whistle, appearing to use patterns of broadband pulses or "clicks" for social communication (Herman and Tavolga 1980).

Sperm whales are long-lived, with a life-span of 60–70 years (Lockyer 1984). About 10–20 females and their young form long-lasting associations, which are stable in composition over periods of years (Ohsumi 1971; Best 1979; Whitehead et al. 1991). These "nursery groups" may be genetically related (Arnbom and Whitehead 1989) and exhibit tight schooling behaviour 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).

"Usual clicks," long series of regularly spaced clicks given for periods of about 20 min or more at a time, are the most common sounds heard from sperm whales. Sperm whales also produce distinctive, short, patterned series of clicks, termed codas by Watkins and Schevill (1977).

Backus and Schevill (1966) hypothesized that codas represented communication, as they did not seem suited for use as echolocation signals because of their pattern and repetition rate. Watkins and Schevill (1977) 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. Codas are often exchanged between whales, and one apparent exchange of codas between two whales was related to changes in their underwater movement (Watkins and Schevill 1977). Coda exchanges seemed to occur only between whales that were close together (Watkins and Schevill 1977). Codas (Watkins and Schevill 1977), as well as similar-sounding pingers used to calibrate a hydrophone array (Watkins and Schevill 1975), elicited silence in other sperm whales, suggesting that whales may interrupt their own sound production to listen.

In data collected off the Galápagos Islands, Whitehead and Weilgart (1991) found a strong and significant correlation (canonical correlation of 0.723) between sperm whale vocalizations and visually observable activities. Canonical loadings related large groupings, few fluke-ups (tail flukes raised before deep dives), little consistency of heading, low whale speeds, and many lobtails (tail flukes thrashed onto the water surface), sideflukes (half of flukes visible above the water surface, as when the whale is turning), spyhops (head raised above water), and breaches (leaps from the water) to large numbers of codas but few usual clicks. Canonical loadings thus contrast foraging behaviour, during which animals are spread out in small groupings, travelling fast, and diving deeply with aggregative behaviour, when whales are tightly grouped at the surface, moving slowly and manoeuvring beside one another (as reflected by the sideflukes and spyhops). Usual clicks were heard most frequently while whales were diving deeply and apparently

foraging, and codas were heard most commonly during aggregation (Whitehead and Weilgart 1991). More codas were also heard in the presence of mature males and first-year calves (Weilgart 1990). The above results strongly indicate that codas are used in communication.

While codas are believed to play a communicative role, there has been little attempt to understand more about their biological significance. This report is the first effort to characterize the coda repertoire of a population of sperm whales. In this study, codas were classified according to their temporal pattern and the number of clicks they contained, in an attempt to gain insight into their function.

Methods

Collection of data at sea

Using a 10-m auxiliary sloop, *Elendil*, with a crew of 5 or 6, sperm whales were tracked in the waters around the Galápagos Islands, Ecuador (0°N, 90°W). Research was carried out between 23 February and 20 April 1985 (a total of thirty 24-h tracking days) and between 3 January and 28 June 1987 (57 tracking days). These periods included parts of the mating season for females off the Galápagos Islands, the peak of which is most likely during April and May (Whitehead et al. 1989). Typically, 10–14 days were spent at sea before returning to port for 4–5 days for resupplying.

Groups of sperm whales were tracked visually, and also acoustically using a custom-made directional hydrophone to obtain bearings on the clicks made by the whales (cf. Whitehead and Gordon 1986). This allowed us to stay within about 2 km of groups of sperm whales during most of the tracking time; while recording codas we were usually within 300 m. Groups consisted principally of female sperm whales and their young, but they were sometimes accompanied by large, mature males (Whitehead and Arnborn 1987; Whitehead and Waters 1990). Sperm whale vocalizations were recorded regularly for 5 min/h on the hour around the clock by means of 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 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 recordings was made in 1985 and 86 h in 1987. Each 5-min recording will be subsequently referred to as a session.

Acoustic analysis of codas

Initially, all 142 h (1696 sessions) of acoustical recordings were analyzed aurally to count the codas. Tapes were played at 19 cm/s (real time). The first 4 min of each 5-min session was used, since recordings often did not last the full 5 min. Poor-quality sessions or sessions less than 4 min in length were eliminated from the statistical analysis (124 sessions were eliminated).

As coda analysis was extremely time-consuming, only the best 15 out of 655 sessions in 1985 and 36 out of 1041 sessions in 1987 that had the fewest background clicks or noise and the most clearly distinguishable codas were then used for detailed coda analysis. There were 315 sessions containing at least 5 codas (thus warranting analysis), so the 51-session sample from both years comprised 16% of all sessions available for coda analysis. In total, 1333 codas were 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. To examine the temporal pattern of clicks within codas, sounds were filtered with 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 s scroll speed (time taken for the trace to travel across the screen)). As an approximate measure of time periods between different codas, for each coda encountered, the tape recorder counter number was noted (this can be estimated to within 3–4 units, or about 3–5 s)

and the clicks in the coda were counted. The intervals between the clicks in the coda, from the beginning of one click to the beginning of the next, were measured in seconds (accurate to ± 0.01 s in recording time) from the oscilloscope screen or, very rarely, from the spectrograph.

Codas were categorized on the basis of these interclick intervals. The clicks in a coda could be very regularly spaced, with all interclick intervals nearly the same length, or one or two clicks could be separated from the remainder by longer intervals. If these longer intervals were at least 50% greater than the mean interval distances between the other, regular clicks in that coda, the coda was classified differently. Whereas a regular 7-click coda would simply be referred to as 7, a 7-click coda with a delayed click at the end would be 6+1. Coda types 5 and 4+1 (Fig. 1) could thus be distinguished from one another. Usually these longer intervals occurred at the end of the coda. If there was little similarity in spacing between any of the clicks of a coda, that coda was simply classified according to the number of clicks and "variable" was added (e.g., 8var), but such coda types were quite rare.

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 more "clacky" and castanet-like than usual clicks, probably corresponding to clicks with a more pronounced multiple-pulse structure (cf. Backus and Schevill 1966). Only codas with 3–13 clicks inclusive were used, since distinguishing shorter or longer codas from usual click series was sometimes unreliable, owing to the absence of a clear beginning and end.

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 two or more codas overlapped one another. Aural impression (usually at 1/5 to 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 the oscilloscope or the spectrograph, usually because of interfering usual clicks or noise. To be classified as belonging to the same coda, clicks had to be separated by not more than 0.75 s (a time interval chosen arbitrarily and based on commonly observed time intervals between and within codas).

Results

Frequency of occurrence of codas

Codas were highly clustered temporally, with 65.3% of all sessions ($n = 1572$) completely lacking codas. The majority of the 6367 codas heard in total occurred in only 8% of the sessions. A mean of 4.05 codas was heard per 4-min session, with a standard deviation of 10.24. There was an average of very approximately 20–30 whales within range of the hydrophone at any time (Whitehead and Weilgart 1990). Each whale thus produced codas at a mean rate of very approximately 2.4 per hour.

Coda classification

Plots were made to determine not only whether the categories previously determined (by the $>50\%$ mean interclick-interval length rule (see Methods)) were valid, but also whether additional categories were present. Codas containing the same total number of clicks, regardless of their classification based on pattern (e.g., 8+1 would be grouped with 9-click codas), were displayed on the same plot. Two interclick intervals were plotted against one another for each coda type (based on total click number). These intervals were analyzed as relative proportions of the total coda length, since the relative timing pattern discriminated coda types better than the absolute lengths

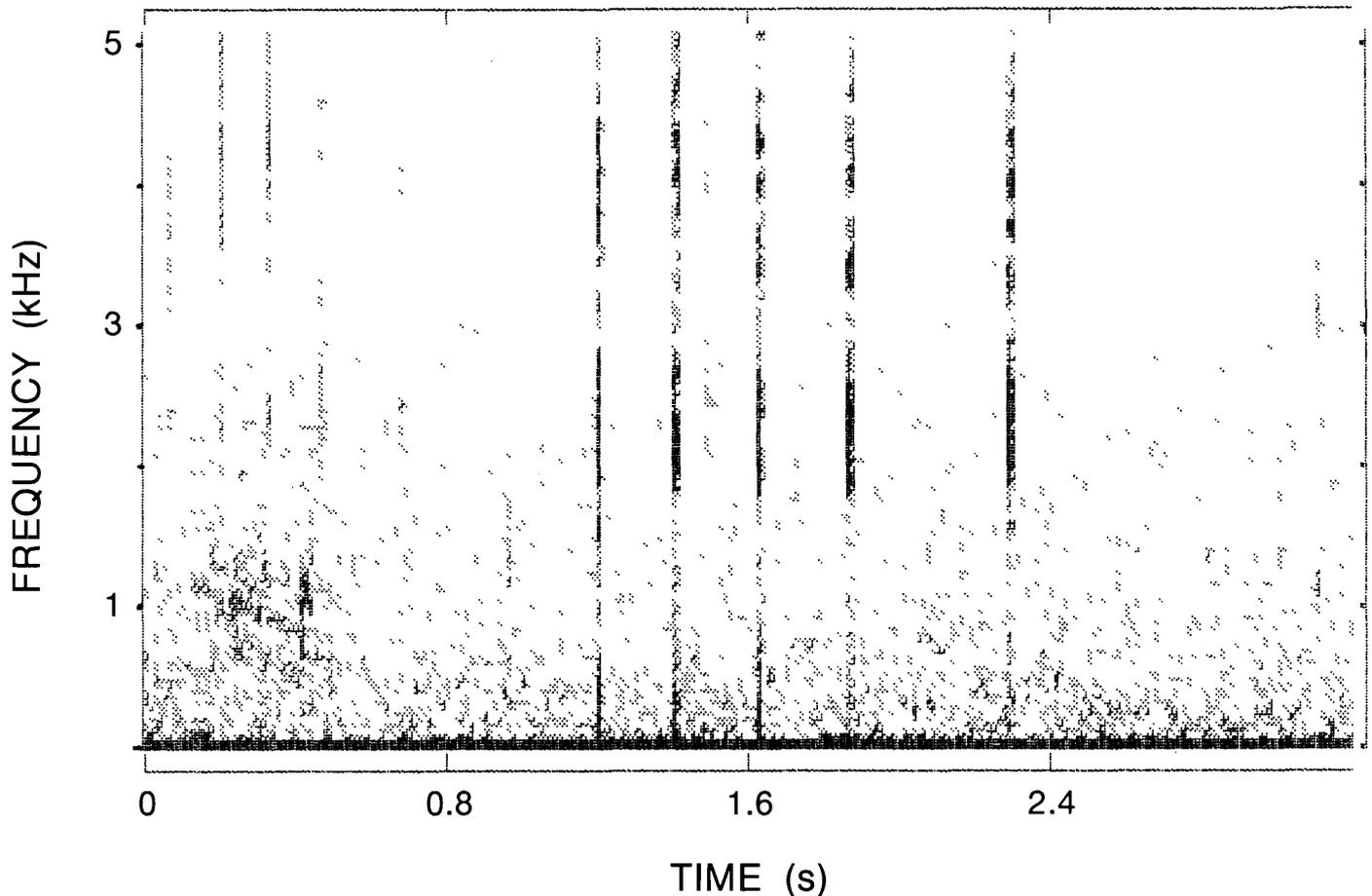


FIG. 1. Spectrogram (frequency versus time) of coda type 4+1.

of intervals. Moore et al. (1989) also found that relative timing patterns were more conservative for coda types than was tempo (absolute timing). For codas containing 4 or more clicks in total, the first and last intervals were usually chosen to be plotted. Other 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 for further analysis.

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 category or even the 4, 3+1, or 2+1+1 category (Fig. 2a). All categories previously defined (like +1) were found to be valid (non-overlapping), e.g., 4+1 and 5 (Fig. 2b) or 5+1 and 6 (Fig. 2c).

Two new categories in addition to those previously defined became apparent. By plotting 7-click codas we discovered that not only did they fall into groups 6+1, 5+1+1, and 7, but category 7 could be further separated into two almost discrete groups: those whose first interval made up more than 0.178 of the total length, and those whose first interval made up less than 0.178 of the total coda length (Fig. 2d). The 7's with shorter first intervals were found to have more regularly and evenly spaced clicks and were therefore referred to as 7reg, as opposed to 7L, the codas with longer first intervals. Similarly, 8-click codas could be separated into 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 of the total length and where, furthermore, the clicks were more regularly spaced.

Using these plots, 23 fairly discrete, almost non-overlapping coda types were established (Table 1). 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, 8L, and those types with the suffixes +1 or +1+1, which will be collectively referred to as irregular codas.

Relative abundances of coda types

The most common coda type heard was 5 (19% of all codas; Table 1), followed by 4+1 (13%), 7reg (10%), 8reg (10%), 5+1 (10%), and 6 (8%). Conceivable coda categories such as 3+1+1, 4+1+1, or 7+1+1 were either totally absent or occurred only once. While it is possible that coda types containing more than 12 clicks exist in the sperm whale's repertoire (see Methods), they may not be very prevalent, considering the rarity of coda type 12 (Table 1). Further evidence that most codas probably consist of 3–10 clicks is provided by Watkins (1979), who found that whales ignored one or two coda-like underwater pinger pulses produced by the scientific equipment but short series of 6–10 pinger pulses caused the whales to fall silent as if to listen.

Interclick interval length of coda types

When mean interclick intervals were plotted for each coda type (Fig. 3), it was apparent that first intervals between coda

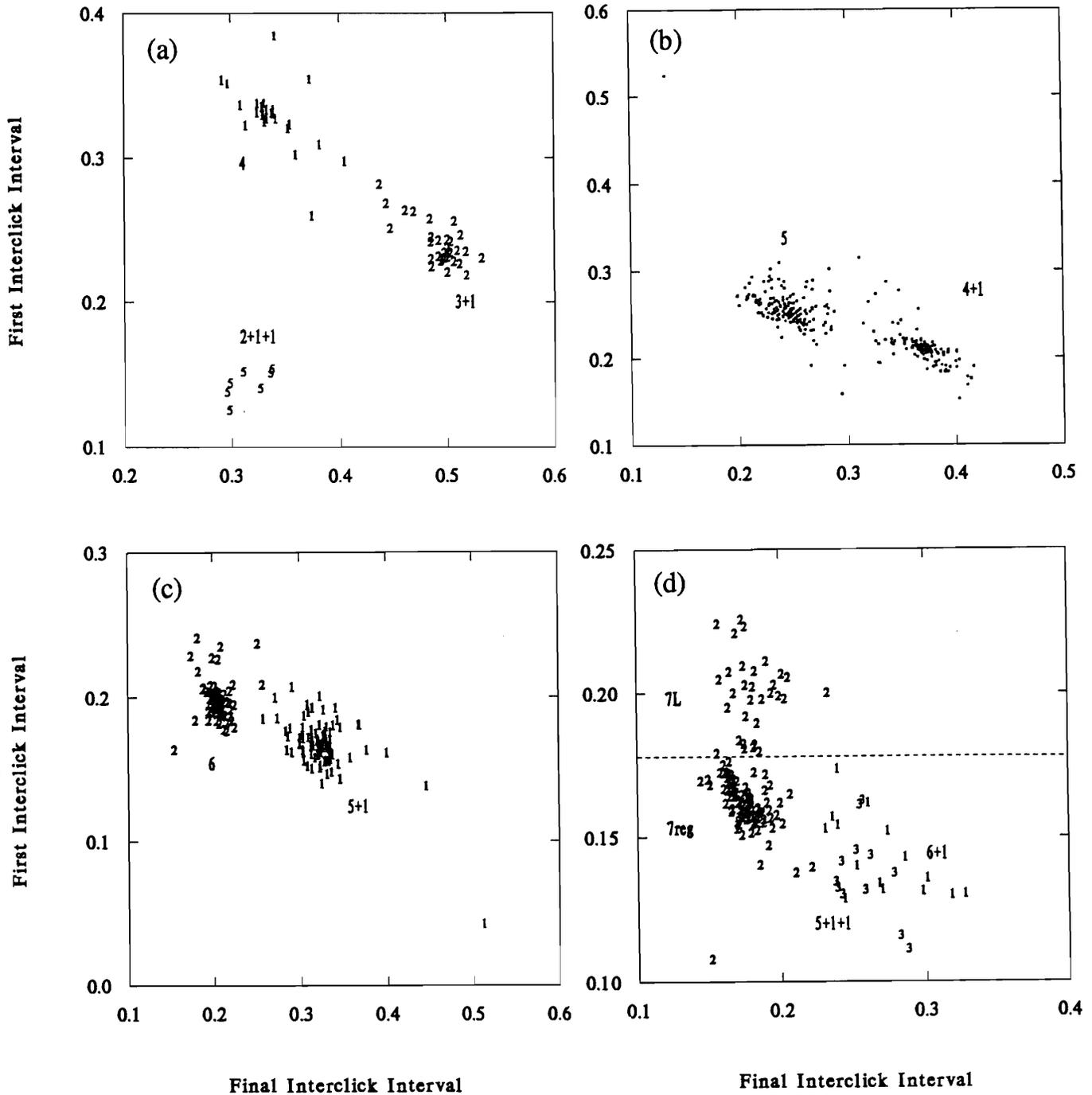


FIG. 2. Plots of the first against the final interclick intervals (as proportions of total coda length) for codas containing four clicks (a), five clicks (b), six clicks (c), and seven clicks (d). The broken line in *d* divides coda 7L from coda 7reg. Codas 5+1+1 (3) and 6+1 (1) were separated by the length of the fifth interval. The numbers in the plots are used only as symbols to distinguish the different coda types.

types were all fairly similar in length. Moreover, it appeared that the relationships 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 were simply additive. The delayed final one or two clicks were added onto a "root" coda of similar length and with similar interclick intervals to the regular coda. 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 coda, as if the click between the root coda and the final 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, irregular codas had shorter intervals than their regular root codas.

When the lengths of all coda types were standardized and intervals were represented only as mean relative proportions of the total coda length (Fig. 4), several findings emerged. Standard deviations around interval lengths did not overlap between coda types such as 5, 5+1, and 6, showing that these 3 types were fundamentally different in their relative interclick spacing and did not vary only in degree. This was the case for all 23 coda types (except perhaps 3var). Also, there was close

TABLE 1. Types, numbers of occurrences, and total lengths of codas

Coda type	Number counted	Total length (s)	
		Mean	SD
3	11	0.49	0.20
3var	9	0.60	0.07
3+1	31	0.83	0.11
4	30	0.75	0.23
2+1+1	7	1.47	0.08
4+1	152	1.18	0.11
5	232	0.77	0.23
5+1	107	1.24	0.13
6	83	1.18	0.35
6+1	16	1.60	0.30
7L	31	0.84	0.14
7reg	103	1.38	0.29
5+1+1	12	1.78	0.13
8L	50	0.97	0.15
8reg	101	1.51	0.31
7+1	23	1.25	0.28
6+1+1	7	1.97	0.29
8+1	9	1.44	0.57
9	41	1.70	0.38
10	24	1.96	0.90
9+1	10	1.43	0.42
11	13	2.43	0.48
12	6	2.52	0.33
No. of regular codas	644		
No. of irregular codas	464		
Total no. of codas	1333		
Mean		1.36	

correspondence between points showing expected interval lengths for perfectly evenly spaced clicks within a regular coda and those showing actual mean relative interclick intervals of regular codas. Regular codas had very evenly spaced clicks, with the mean relative interval length equalling the total standardized coda length divided by the number of intervals. All regular coda types except 5 showed a slight but consistent trend toward longer than expected final intervals. First intervals showed no such consistent pattern.

Sequential relationships between overlapping coda types

Overlapping codas, which were defined as instances in which one coda started before the other was finished, were examined to determine if particular coda types overlapped or were overlapped by other coda types. We chose overlaps because each coda in an overlapping "pair" could, we think, be reasonably assumed to have been produced by a different individual. The observed and expected numbers of times each coda type was first or second in the overlap were compared. Only the 14 most common coda types were used in this analysis. Expected values were corrected for the length of the coda by the following calculation. Let V be total number of overlaps, n_A the number of codas of type A, N the total number of codas, x_A the mean length of coda type A, and X the mean length of all codas, then

$$\text{expected number of times coda A is first} = V \times (n_A/N) \times (X_A/X)$$

$$\text{expected number of times coda A is second} = V \times (n_A/N)$$

χ^2 values for all comparisons combined revealed significant differences between coda types in expected and observed numbers of first ($\chi^2 = 37.16$, $p < 0.005$, 13 df) and second ($\chi^2 = 50.21$, $p < 0.005$, 13 df) positions in an overlap. That is, codas of different types overlapped one another in a non-random way. Individual coda types also differed significantly from the expected in their position in overlaps: coda type 8reg tended to "initiate" overlaps (was first more often than expected; $\chi^2 = 8.25$, $p < 0.005$, 1 df, $n = 30$), whereas coda types 6 ($\chi^2 = 8.34$, $p < 0.005$, 1 df, $n = 21$) and 7reg ($\chi^2 = 18.23$, $p < 0.005$, 1 df, $n = 30$) tended to follow or be given in response (second more often than expected). Coda type 5 was not a response coda, rarely being heard second in an overlap (second less often than expected; $\chi^2 = 13.40$, $p < 0.005$, 1 df, $n = 11$).

Initiating coda types

To test whether certain coda types initiated coda exchanges, the length of time since the previous coda was heard was compared among coda types. Tape counter numbers were used to approximate the length of time since the last coda. Codas that were the first recorded in any session were eliminated from this analysis as were those coda types with a total sample size of less than 80. Compared with other coda types, a greater proportion of type 5 codas (relative to the total number of type 5 codas) were preceded by over 30 s of coda-free time (Table 2). While the difference between coda type 5 and other coda types was not significant ($p > 0.05$; χ^2 test), this result does support those from the overlap analysis, which showed that type 5 was second in an overlap less often than expected.

Co-occurrence of coda types within recording sessions

To describe the correlations of occurrence rates within sessions among the 23 coda types, a principal components analysis was performed on counts of each coda type per session (51 sessions). Counts of each coda type were standardized by dividing by the total number of codas of the 23 types for each session to give relative proportions of each coda type. The first two principal components accounted for about 30% of the total variance (21.6% for the first; 10.1% for the second), after which the percentage of total variance explained dropped off to 8% for the third and 7% for the fourth principal components. The vector plot of component 1 versus component 2 (Fig. 5) 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 comprised regular codas and the other major grouping contained irregular codas. The third grouping was made up of types 3, 3var, 4, and 2+1+1, which were not significantly correlated with most of the other coda types. The second principal component, although the separation was less perfect, seemed to distribute codas roughly by the number of clicks they contained, codas with fewer clicks being lower on the plot. Therefore, it seems that codas which were similar in length and pattern (i.e., evenly spaced or not) tended to occur within the same 5-min session.

Discussion

The type of sperm whale vocalization known as a coda occurs in a highly clustered fashion over time, large numbers of codas being heard only occasionally. They appear to be reserved principally for specific contexts. Watkins and Schevill (1977) proposed that the temporal patterning within codas is

ABSOLUTE LENGTHS

1/4-S INTERVALS

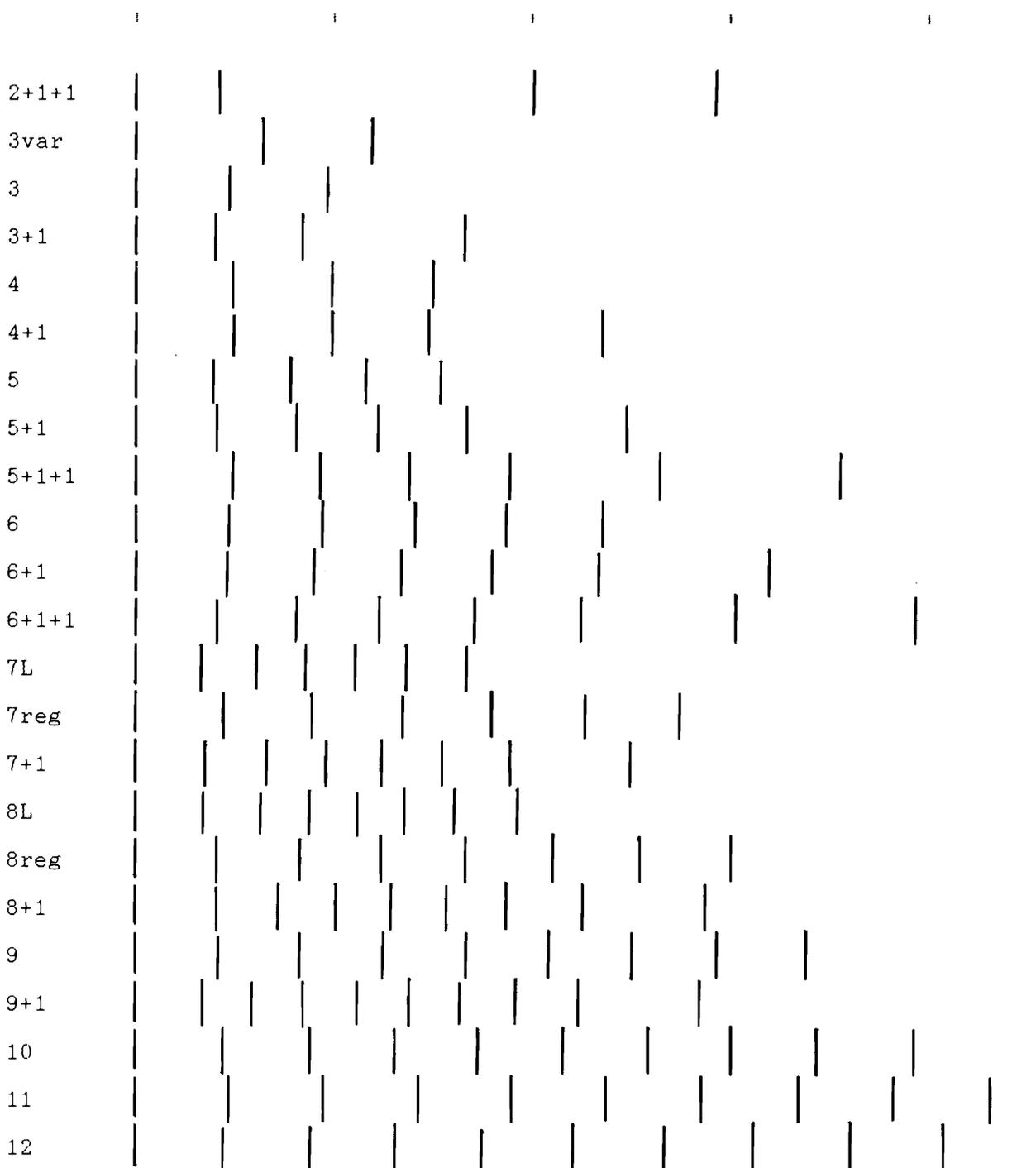


FIG. 3. Mean interclick intervals for each coda type.

primarily used as a means of individual identification. We find this unlikely for the Galápagos sperm whales, since only 23 principal coda types were discovered in a population of about 400 whales in the study area at any one time, in which there was considerable intermingling of stable units (Whitehead et al. 1991). Different coda types clearly appeared to be emitted by the same individual (as determined by tonal quality and intensity cues), whereas many different individuals could be heard

using the same coda type (cf. Watkins et al. 1985). Information on individual identity may be contained in some other characteristics of the codas that we did not examine in depth, such as spectral structure (cf. Backus and Schevill 1966; Adler-Fenchel 1980).

Group identification also does not clearly appear to be a principal function of codas. There was some indication of differences between stable groups of identified individuals (as deter-

RELATIVE

0.2X TOTAL LENGTH

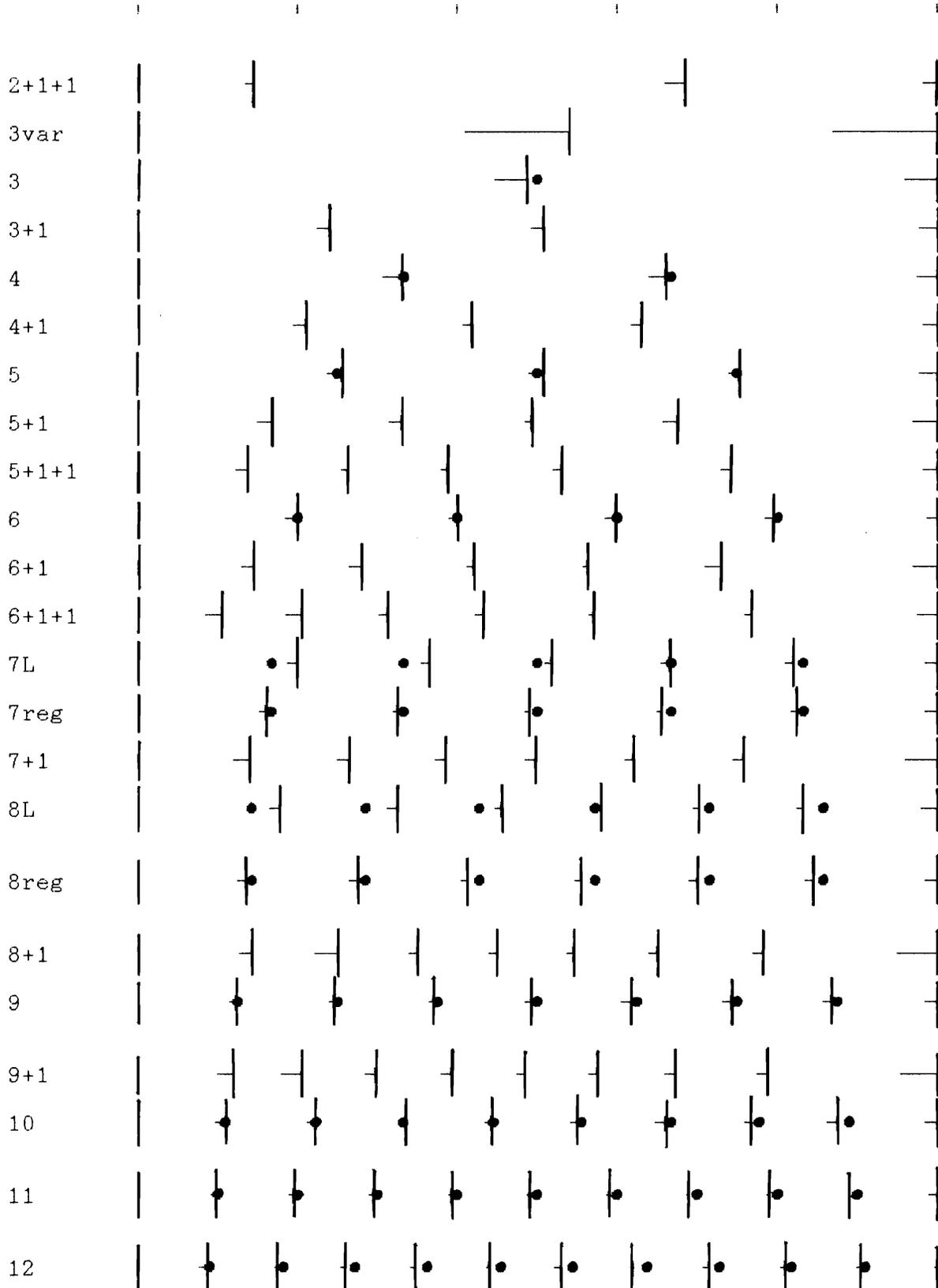


FIG. 4. Mean relative intervals (proportions of the total coda length) for each coda type. Black dots denote expected positions of clicks for perfectly regularly spaced codas, and horizontal bars indicate standard deviations of the previous interval.

TABLE 2. Comparisons between coda types of the number of times that a previous coda was not heard for the preceding 30 s or more

Coda type	Total	Without coda in previous 30 s	
		No.	Proportion
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
Total of all 23 coda types	1288	46	0.036

NOTE: Only coda types with sample sizes of >80 are given.

mined by the methods of Whitehead and Waters 1990) in the numbers and proportions of certain coda types they used, but we did not have sufficient data nor were they complete enough to fully determine whether group-specific codas existed (Weilgart 1990). In killer whales (*Orcinus orca*) off British Columbia, where group dialects have been found, each of 16 pods has a group-specific repertoire of 7–17 call types (Ford 1989), but we could identify only 23 coda types from a total of 20 different groups of sperm whales (Whitehead and Waters 1990).

Codas are heard away from, as well as on, the breeding grounds (Mullins et al. 1988), and calves as well as adults emit codas (Watkins et al. 1988), so mating must be excluded as the sole purpose of coda vocalizations. Since whales tend to aggregate at the surface and generally appear to be resting while codas are emitted (Whitehead and Weilgart 1991), it seems improbable that codas are mainly used to coordinate immediate group movement, especially over long distances. Intentions of moving may be communicated, however.

The most plausible primary function of sperm whale codas is the maintenance of social bonds. In primates, certain call types occur during times when individuals are resting close together, affiliating, or engaged in care-giving behaviour (e.g., Gautier and Gautier 1977; Smith et al. 1982). Vocal exchanges may be especially important in reaffirming the social cohesion within stable groups following periods of dispersion or separation (Gautier and Gautier 1977; Smith et al. 1982), as occurs when sperm whales are foraging (Whitehead 1989).

The distinctions sperm whales seem to make between different coda types (e.g., between type 5 and the rest of the coda types; cf. Weilgart 1990) and the nonrandom order in which coda types overlap one another suggest that codas could represent a somewhat sophisticated level of communication. The fact that certain coda types tend to be heard first or second in overlaps suggests that the pattern of coda exchanges has a sequential structure. Sperm whales also seem to distinguish between regular and irregular coda types. This shows that there may be information in the gap that represents the "skipped" click(s) of irregular codas.

Symmes and Biben (1988) offer three criteria that may indicate primitive forms of "conversation": (i) "turn taking," or ordered nonrandom vocalizing, which implies that interactants listen to each other and share rules about vocal behaviour; (ii) "directionality," i.e., conversations are not reversible: the order matters; and (iii) a change in the vocal pattern of the

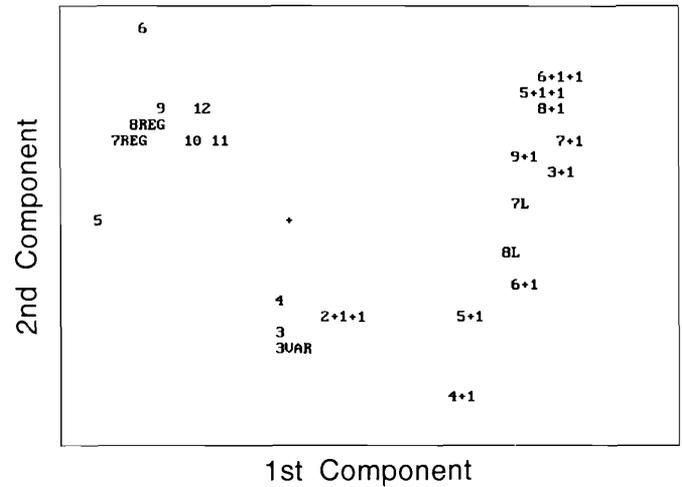


FIG. 5. Factor loading vector plot of the first two principal components using the standardized 23 coda types (51 sessions). Types plotted close together tended to occur in the same 5-min recording session; "+" denotes the origin.

first speaker as a reaction to the vocal response given by the listener. Squirrel monkeys (*Saimiri* spp.) showed evidence that the above three conditions were fulfilled (Symmes and Biben 1988). "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 (Watkins and Schevill 1977; L. Weilgart, personal observation). Their order of vocalizing is also nonrandom and tends to have directionality. Certain coda types tend to follow or overlap other coda types, and type 5 tends to initiate exchanges. The fact that regular coda types had longer than expected final interclick intervals relative to their total length may signify to conversational interactants that the coda will soon end. Longer sequences of codas need to be studied to determine if the first caller changes its vocal pattern as a result of the listener's response (i.e., criterion *iii* above for primitive conversations).

Species in which complex social interrelationships exist and communicants are familiar with one another are predicted to have a greater prevalence of graded signals, defined as signals that vary continuously along a given dimension (Green and Marler 1979). In addition, Green and Marler (1979) describe such socially complex species as tending to be long-lived and found in stable groups with overlapping generations. While the social system of female sperm whales and their young fits this description, coda types characterized by relative interclick intervals show little gradation from one type to another. Codas, then, genuinely seem to possess prominent characteristics that allow them to be classified into discrete units or types, as is the case with the sounds used in human language, another notable exception to Green and Marler's (1979) theory.

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