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Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia

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Underwater vocalizations were recorded during repeated encounters with 16 pods, or stable kin groups, of resident killer whales (*Orcinus orca*) off the coast of British Columbia. Pods were identified from unique natural markings on individuals. Vocal exchanges within pods were dominated by repetitious, discrete calls. Pods each produced 7–17 (mean 10.7) types of discrete calls. Individuals appear to acquire their pod's call repertoire by learning, and repertoires can persist with little change for over 25 years. Call repertoires differed significantly among pods in the resident population. The 16 pods formed four distinct acoustic associations, or clans, each having a unique repertoire of discrete calls, or vocal tradition. Pods within a clan shared several call types, but no sharing took place among clans. Shared calls often contained structural variations specific to each pod or group of pods in the clan. These variants and other differences in acoustic behaviour formed a system of related pod-specific dialects within the vocal tradition of each clan. Pods from different clans often travelled together, but observed patterns of social associations were often independent of acoustic relationships. It is proposed that each clan comprises related pods that have descended from a common ancestral group. New pods formed from this ancestral group through growth and matrilineal division of the lineage. The formation of new pods was accompanied by divergence of the call repertoire of the founding group. Such divergence resulted from the accumulation of errors in call learning across generations, call innovation, and call extinction. Pod-specific repertoires probably serve to enhance the efficiency of vocal communication within the group and act as behavioural indicators of pod affiliation. The striking differences among the vocal traditions of different clans suggest that each is an independent matriline.

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Les cris sous l'eau ont été enregistrés au cours d'épisodes répétés, chez 16 bandes, ou groupes stables d'individus apparentés, d'Épaulards (*Orcinus orca*) de la côte de Colombie-Britannique. Les bandes pouvaient être reconnues grâce aux colorations propres à certains individus. Les échanges vocaux au sein des bandes étaient dominés par des cris répétés et distincts. Les bandes produisaient chacune 7–17 (moyenne 10,7) types de cris distincts. Les individus semblent faire l'acquisition du répertoire de cris de leur bande par apprentissage, et les répertoires peuvent persister plus de 25 ans sans modifications majeures. Les répertoires de cris différaient significativement d'une bande à l'autre chez la population résidente. Les 16 bandes formaient quatre associations acoustiques distinctes, ou « clans », chacune caractérisée par une tradition vocale exclusive c'est-à-dire un répertoire exclusif de cris distincts. Les bandes d'un clan particulier utilisaient plusieurs types de cris en commun, mais il n'y avait pas de cris communs entre les différents clans. Les cris communs comportaient souvent des variations structurales spécifiques à chaque bande ou groupe de bandes dans un clan. Ces variations et d'autres particularités du comportement acoustique constituaient un système de dialectes spécifiques aux bandes au sein de la tradition vocale de chaque clan. Les bandes de différents clans se déplaçaient souvent ensemble, mais les associations sociales observées étaient souvent indépendantes des relations acoustiques. Il est possible que chaque clan se compose de bandes apparentées issues d'un groupe ancestral commun. De nouvelles bandes sont apparues par croissance et division maternelle linéaire de la lignée. La formation de nouvelles bandes s'est accompagnée de la formation de nouveaux répertoires de cris issus de celui du groupe fondateur. Cette divergence a occasionné l'accumulation d'erreurs dans l'apprentissage des cris d'une génération à l'autre, la création de cris et l'extinction de cris. Les répertoires spécifiques aux bandes servent probablement à favoriser la communication vocale au sein d'un groupe et servent d'indicateurs comportementaux des affiliations. Les différences marquées entre les traditions vocales ou entre les clans semblent indiquer que chaque clan est une lignée maternelle indépendante.

[Traduit par la rédaction]

Introduction

Killer whales (*Orcinus orca*) are seen throughout all the world's oceans, but in only a few locations can they be found reliably in protected waters. One such area is off the coast of British Columbia and in adjacent waters of Washington State, where the species has been studied intensively since the early 1970s. These studies have relied on field identification of individual whales by means of natural markings on the dorsal fin or back (Balcomb et al. 1982; Bigg 1982; Bain 1989; Bigg et al. 1990). The killer whales of British Columbia are now among the best-known cetacean populations.

Approximately 325 killer whales have been identified from

the inshore waters of British Columbia (Bigg et al. 1987). These whales are of two different forms, referred to as *residents* and *transients*, which are sympatric but socially isolated from each other. The two forms differ in morphology, social behaviour, feeding habits, and movements. Residents, composing about 75% of the population, are found throughout the year but are most common during June–October. Transients are also present throughout the year, but are less common and less predictable in occurrence. Residents live in stable social groups containing 5–50 individuals and feed primarily on fish. Transients, in contrast, travel in smaller groups of 1–7 and appear to specialize on marine mammal prey. Resident groups associate only with other residents, and transients only with other transients.

Resident killer whales in British Columbia are better studied

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and understood than transients (Kirkevoold and Lockard 1986; Heimlich-Boran 1988; Bain 1989; Bigg et al. 1990; Olesiuk et al. 1990). Resident societies are organized largely on the basis of maternal genealogy (Bigg et al. 1990). The smallest social unit is the *matrilineal group*, which comprises individuals related by unilineal descent from a single living female. Matrilineal groups may contain up to four generations of animals, although two or three generations are typical. The next larger unit is the *subpod*, which contains one or more matrilineal groups that always travel together and are very likely closely related. Maximum longevity is estimated to be about 80 years for females and 50–60 years for males. Dispersal of individuals from their natal subpod appears to be extremely rare or absent: no whale has been seen to leave one subpod and join another permanently in over 15 years of study.

The usual social group of resident killer whales is the *pod*, which comprises one or more subpods. Although they remain together most of the time, subpods occasionally separate for periods of a few days or months. Subpods that gradually spend longer periods apart may eventually form new pods, although this process is likely to take many years.

The long-term stability of killer whale social structure in British Columbia has provided the opportunity to examine in detail the vocal behaviour of pods over extended periods. Ford and Fisher (1982, 1983) provided evidence that resident pods have repertoires of discrete calls that are consistent over several years and that these repertoires differ among pods. Similar findings were reported by Hoelzel and Osborne (1986) for part of this population. Dahlheim and Awbrey (1982) also noted variations in vocalizations of captive killer whales taken from different locations along the coasts of British Columbia and Washington State. Such dialectal differences are extremely rare among mammals (Connor 1980; Ford and Fisher 1983; Maeda and Masataka 1987). Ford and Fisher (1982) also suggested that similarities and differences in repertoires may reflect the ancestral relationships of pods.

Recently, I described the behavioural circumstances associated with the occurrence of discrete calls in resident pods (Ford 1989). During periods of activity, discrete calls dominate vocal exchanges among pod members. Most of the call types in the pod's repertoire are heard, regardless of the type of activity in which the group is engaged, which suggests that calls are largely context-independent. Each pod member is capable of producing most or all calls made by the group as a whole. I proposed that discrete calls generally serve as signals for maintaining contact within the pod, and that the use of repertoires of pod-specific calls enhances this function by conveying group identity and affiliation.

In this paper I describe the discrete call repertoires of all known resident pods in coastal British Columbia. I examine the similarities and differences in the structure of the calls that are shared by pods, and the typical patterns of call occurrence for each pod. Evidence is presented that pod-specific call repertoires can be retained for periods in excess of 25 years. I also develop a model to account for the observed call patterns in the population, and a genealogy based on acoustic relationships for resident pods. The acoustic behaviour and group-specific vocal variations of transient pods will be the subject of a future report.

Methods

The study animals

A total of 16 resident pods with 232 whales (1983 census) are known to occur in British Columbia waters. These pods are divided into

'northern' and 'southern' communities, with different distributions, as shown in Fig. 1. Pods from one community are rarely sighted within the range of the other. No pod appears to have an exclusive home range, and pods frequently associate with others within their community. No mixing takes place between the two communities.

Table 1 shows the size and composition of resident pods. The alphanumeric designations of Bigg (1982; Bigg et al. 1987) are used to name pods. Most pod names were assigned arbitrarily and do not imply degree of association or relatedness. During the present study, the northern resident community contained 13 pods with 154 whales, and the southern resident community contained 3 pods with 78 whales (1983 census). Recent analyses of social associations have led to a reevaluation of pod designations (Bigg et al. 1987, 1990). Several subpods of these original groups have been designated as separate pods, with the result that the northern resident community currently comprises 16 pods. In the analyses presented in this paper, I use pod designations as they existed in 1983.

Field observations and recordings

Between July 1978 and October 1983, I studied resident killer whales at a variety of locations in the waters to the east and south of Vancouver Island, British Columbia. Whales were encountered on 154 days during this period, mostly during June–September. All 16 resident pods known to occur in the area were encountered and recorded acoustically. A total of 426 'pod encounters' was made with residents (1 pod encounter is the interception and identification of one pod on 1 day), an average of 2.76 pods per observation day (range 1–10 pods/day). In addition, I examined 43 recordings of captive and wild killer whales made by other individuals, mostly prior to the onset of this study. Dates and pod identifications for both recent encounters and historical field recordings (and the sources for the latter) are tabulated in Ford (1984).

Whales were located either by patrolling waters known to be frequented by pods or with the help of volunteer observers who telephoned when they saw whales. All fieldwork was conducted from a 5-m boat powered with an outboard motor. Pods present were identified from photographs or visually. About 7500 photographs were taken using a motor-driven 35-mm single-lens-reflex camera with a 300-mm lens mounted on a shoulder brace, and black and white film exposed at ISO 1600 (see Bigg et al. 1986 for details of the procedure). Individual whales in the photographs were identified by M. A. Bigg and G. Ellis (Pacific Biological Station, Nanaimo, B.C.).

Acoustic recordings were made with a variety of equipment, mainly a Nagra IV-SJ recorder fitted with a custom preamplifier-filter unit and a Celesco BC-10 or BC-50 hydrophone. Frequency response of this system varied with tape speed. Tapes made at the maximum speed of 38 cm/s (15 ips) were flat (± 3 dB) from 100 Hz to 35 kHz. Cassette recorders (Sony TC-D5M and Superscope C-205) were used during 1982–1983. The responses of these systems were relatively flat from 100 Hz to 14 kHz.

Recording and identification of call repertoires

Recordings used to describe the call repertoire of each pod were made under the following circumstances. First, the pod, or a subgroup of the pod, was recorded while alone or at such a distance from other groups that the calls could be attributed unequivocally to that pod. Second, the recordings chosen were made in social and activity contexts that were as similar as possible. This helped to avoid the potentially complicating effects of situation-related variation in call usage or structure (Ford 1989). Foraging, the most common activity of resident killer whales, was selected as the standard context from which samples were drawn.

All recordings meeting the above criteria were used to describe the typical pattern of call usage for the pod. Also, representative samples of each call type were drawn from these tapes for quantitative structural analysis. Although most pods were encountered and recorded alone on several occasions, some common groups were seldom found apart from other whales, and other pods were simply rare in the study area. Pod A4, for example, was encountered on 62 days, but was alone on only three of those occasions. In contrast, pod R was encountered on only 3 days, each time in the presence of seven or more additional pods.

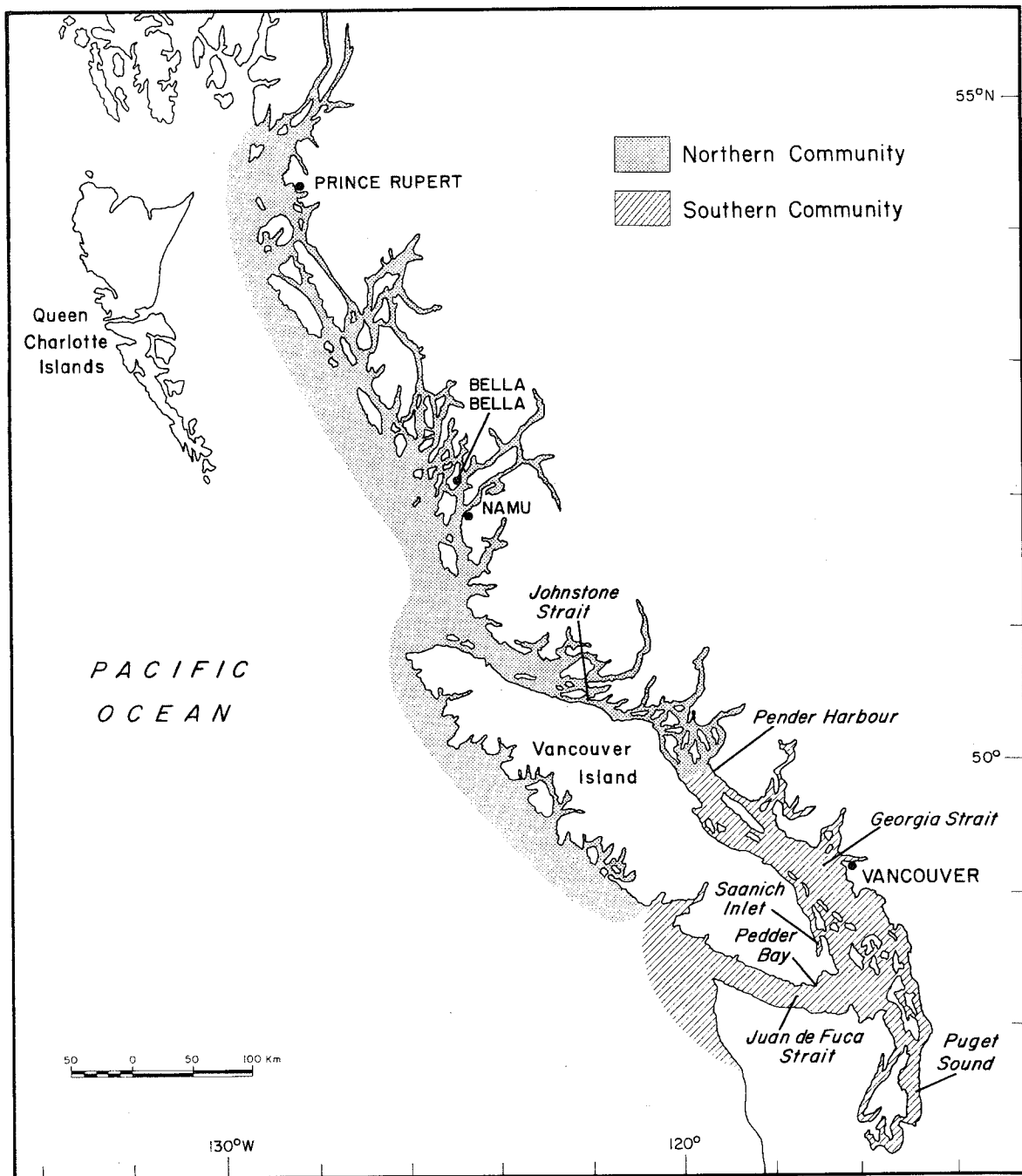


FIG. 1. Map of the known distributions of the northern and southern communities of resident killer whale pods, showing locations mentioned in the text. Data are from Bigg et al. (1987, 1990).

Despite the limited samples available for some groups, I am confident that most or all call types in each pod's repertoire have been identified and their relative frequencies of use correctly determined. Repeated encounters with common pods indicated that most calls in a pod's repertoire could be heard in only one or two 10-min samples from periods of vocal activity (Ford 1989).

Unless otherwise mentioned, tapes made prior to 1978 were attributed to certain pods on the basis of call type because no photographic identifications were available. These early recordings were made in the same locations as those in this study. All pods assumed to have been present when the older tapes were made were also observed during this study. All call repertoires present in pre-1978 tapes were also recorded during 1978–1983.

Acoustic analyses

Most social signals, or calls, of killer whales could be classified by

ear into discrete categories based on distinctive structural characteristics. For initial classification, sounds were transcribed using symbolic notations that reflected the pitch and temporal patterning of the calls. Later, clear examples from each category were selected and analyzed on a Kay Elemetrics 7029A spectrum analyzer. Most spectrograms, including all those illustrated in this report, were made using an 80- to 8000-Hz frequency range with a 45-Hz filter bandwidth. These analyses served to clarify call classification and permitted quantitative definition and comparisons of call types to be made.

Discrete call classification

Discrete calls of killer whales were typically made up of rapidly emitted pulses which, to the ear, had a tonal quality. The repetition rate of these pulses, reflected in the harmonic or sideband interval (SBI) seen in spectral analysis, was usually modulated over the call's duration. Many calls contained several abrupt shifts in pulse repetition

TABLE 1. Size and composition of resident pods in 1983, and the number of encounters made with each pod during this study (1978–1983)

Original pod	Current pod	Size of pod	No. of bulls	No. of cows	No. of juveniles	No. of calves	No. of encounters*
Northern resident community							
A1	A01	15	5	4	6	0	86
A4	A04	9	1	4	3	2	62
A5	A05	12	1	4	7	0	86
B	B01	7	4	1	2	0	20
C	C01	9	3	2	4	0	17
D	D01	9	2	3	4	0	13
G	G01	20	4	5	11	0	3
	G12	7	0	2	5	0	4
H	H01	5	1	2	2	0	18
I1	I01	6	1	2	2	1	5
	I02	7	3	2	2	0	9
	I18	11	0	4	5	2	9
I11	I1	11	0	3	6	2	18
I31	I31	5	1	1	3	0	11
R	R01	17	6	6	5	0	3
W	W01	4	2	1	1	0	9
Southern resident community							
J	J01	19	3	8	8	0	18
K	K01	15	4	7	4	0	10
L	L01	44	6	18	20	0	12
Total		232	47	78	100	7	441

NOTE: Original pod identities are used in the text. Current pod designations result from recent analyses of social associations by Bigg et al. (1990).

*Using current pod designations (total is 426 when original identities are used).

rate, which allowed the call to be divided into different segments, or 'parts.' Sound patterns on spectrograms were measured using frequency and duration variables appropriate to the structure of each call type. For simple, one-part calls, the overall duration and minimum and maximum sideband intervals were measured. In more complex calls, duration and SBI measurements were made for each distinct part, and other components, such as simultaneous narrow-band tones, were also measured.

An average of 8.4 (range 2–17) frequency and duration variables per call were measured from spectrograms of about 3600 calls. These measurements were made digitally using an Apple Computer Graphics Tablet. Means, ranges, and coefficients of variation (standard deviation \times 100/mean) were calculated for each variable. Measurements were compared using analysis of variance (ANOVA) with Bartlett's test for homogeneity of variances and Scheffé's pairwise comparison of means (Sokal and Rohlf 1981).

Discrete calls were classified alphanumerically. Numbers were assigned arbitrarily in the order in which calls were identified, regardless of which pod was responsible for their production. Call numbers are preceded by a letter indicating whether they were recorded from northern (N) or southern (S) community residents.

Most discrete call types were shared by several pods. However, shared calls were often rendered in consistently different forms specific to each pod or groups of pods. Some of these call-type variants were so modified that they were initially given separate call numbers. Later, however, they were judged to be homologous, from structural clues or from patterns of call association. Structurally unique variants of a discrete call are distinguished by different lower-case Roman numeral suffixes. An example of a typical call type is N9, shared by three pods, A1, A4, and A5, of the northern resident community, but given in a slightly different manner by each pod. These subtypes are identified as N9i, N9ii, and N9iii, respectively. A complete classification of call types identified in this study is given in Ford (1987), along with descriptive statistics and ANOVA comparisons of call variables.

A quantitative measure of similarity of call repertoires for each pair of pods was obtained by calculating an index from the degree of call

sharing. This index is based on Dice's coefficient of association (Morgan et al. 1976; McGregor and Krebs 1982), which normalizes the data to account for differences in repertoire size:

$$\text{index of similarity} = \frac{2(N_c + N_s)}{R_1 + R_2}$$

where N_c is the total number of call types shared, N_s is the total number of subtypes shared, and R_1 and R_2 are the repertoire sizes (call types plus subtypes) of the two pods. The index values were then used to calculate a hierarchical structure of acoustic similarity, displayed in the form of a dendrogram by means of single-link cluster analysis (Morgan et al. 1976).

Patterns of call occurrence

To examine the frequency distribution of call types and their patterns of occurrence, continuous sections of tapes were divided into 10-min periods. Proportions for each call type in each time period were calculated. An arcsine square-root transformation was applied to these data, which were then used as replicates in analyses of variance with Scheffé's test for determining the significance of differences among means. Associations of different call types were examined by calculating the frequencies with which calls preceded and followed each other within each minute of the 10-min periods. These transition frequencies for each call combination were summed and used to calculate an index of association, described in Ford (1989).

Results

Patterns of vocal variation in the resident population

Vocal variations were evident at two major levels among the 16 resident pods. First, certain pods shared a number of discrete call types and others had entirely different call repertoires. The population was thus divided into several distinct acoustic associations, each containing pods that shared a portion of their call repertoires. I refer to each set of acoustically related pods as a *clan*, since, as discussed later, it is probable that such pods

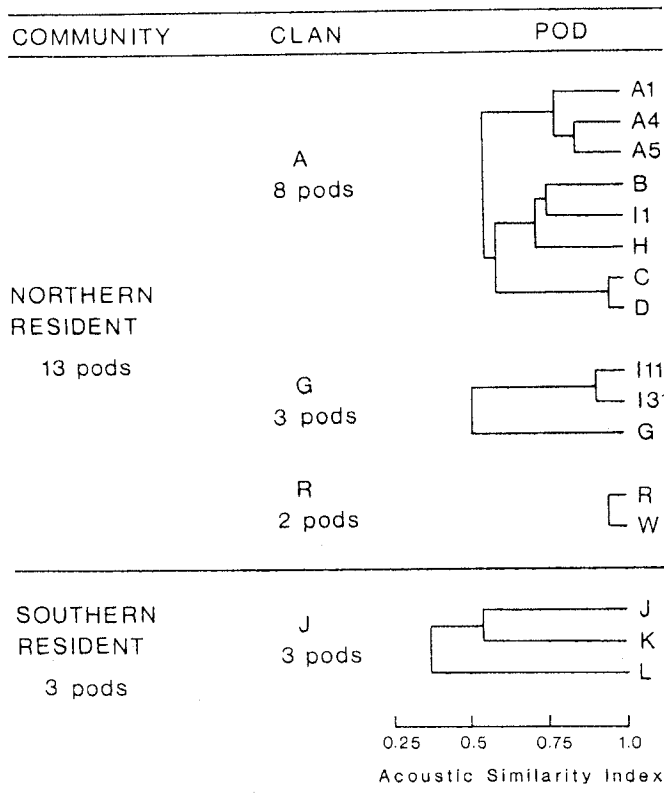


FIG. 2. Summary of acoustic relationships of resident pods in British Columbia. The two resident communities had exclusive ranges, while clans had exclusive vocal traditions. Pods in the three northern-community clans often associated with each other. All pods within a clan shared calls, yet many also had unique calls. The degree of acoustic similarity among pods in each clan is expressed as an index value, described in the text, and displayed as a dendrogram.

have descended from a common ancestral group. Each clan had a unique *vocal tradition*, comprising calls used by members of that clan and by no other pod. The resident population was found to contain four clans. The northern community comprised clans A, G, and R, each named after one of its member pods. The southern community consisted of a single clan, J.

The second level of vocal variation existed among pods within clans. All pods belonging to a clan shared a number of calls, but these shared calls were often rendered in consistently different forms by different pods. In addition, certain pods produced calls that were not used by the remainder of the clan. Such variations produced a set of related group-specific *dialects* within the vocal tradition of each clan. Pods that shared the majority of calls in their repertoire and formed distinct acoustic subgroups are referred to as a *subclan*.

The acoustic relationships of the 16 resident pods are illustrated in Fig. 2. Pods within clans are arranged in a dendrogram according to an index of acoustic similarity based on the proportion of calls shared, as described in the Methods. In the following sections, the call repertoire of each resident pod is described, using sample spectrograms to illustrate the variety of calls used by different clans and the structural variations of selected calls shared within clans. In addition, the typical frequency distribution of call types for each pod is examined. Each call type and subtype identified in this study is illustrated and defined quantitatively in Ford (1987).

TABLE 2. Call types and subtypes produced by pods belonging to clan A in the northern resident community

Call	Pod							
	A1	A4	A5	B	C	D	H	I1
N1								
i	x							
ii				x				x
iii					x	x		
iv							x	x
v		x						
N2	x	x	x					
N3	x	x	x	x	x	x	x	x
N4	x	x	x					
N5								
i	x	x	x	x			x	x
ii				x			x	x
N7								
i	x	x	x					
ii	x	x	x				x	x
iii								x
iv				x		x		
N8								
i	x	x	x				x	
ii					x	x		
iii				x				x
iv				x				x
N9								
i	x							
ii		x						
iii			x					
N10	x	x	x					
N11								
i	x	x	x	x				
ii				x	x	x	x	
N12	x	x	x	x	x	x	x	x
N13		x	x					
N16								
i				x				
ii					x	x		
iii							x	x
iv								x
N17			x					
N18				x	x			
N19		x						
N20				x	x	x		x
N21				x				
N27	x							
N47	x							
Total	14	14	13	14	9	8	9	13

NOTE: The clan designation includes pods that share call types.

Calls of northern-community resident pods

Clan A

Clan A consisted of 90 whales divided into eight pods, A1, A4, A5, B, C, D, H, and I1, all of which shared a portion of their call repertoires. The 19 clan A call types and the pods observed to produce them are summarized in Table 2. All eight pods shared a minimum of four call types, N3, N7, N8, and N12. A further three calls, N1, N5, and N11, were produced by all but one or two of the pods. The clan was divided clearly into two major acoustic subgroupings on the basis of the remaining call types. The first, subclan A, consisted of pods A1, A4, and A5.

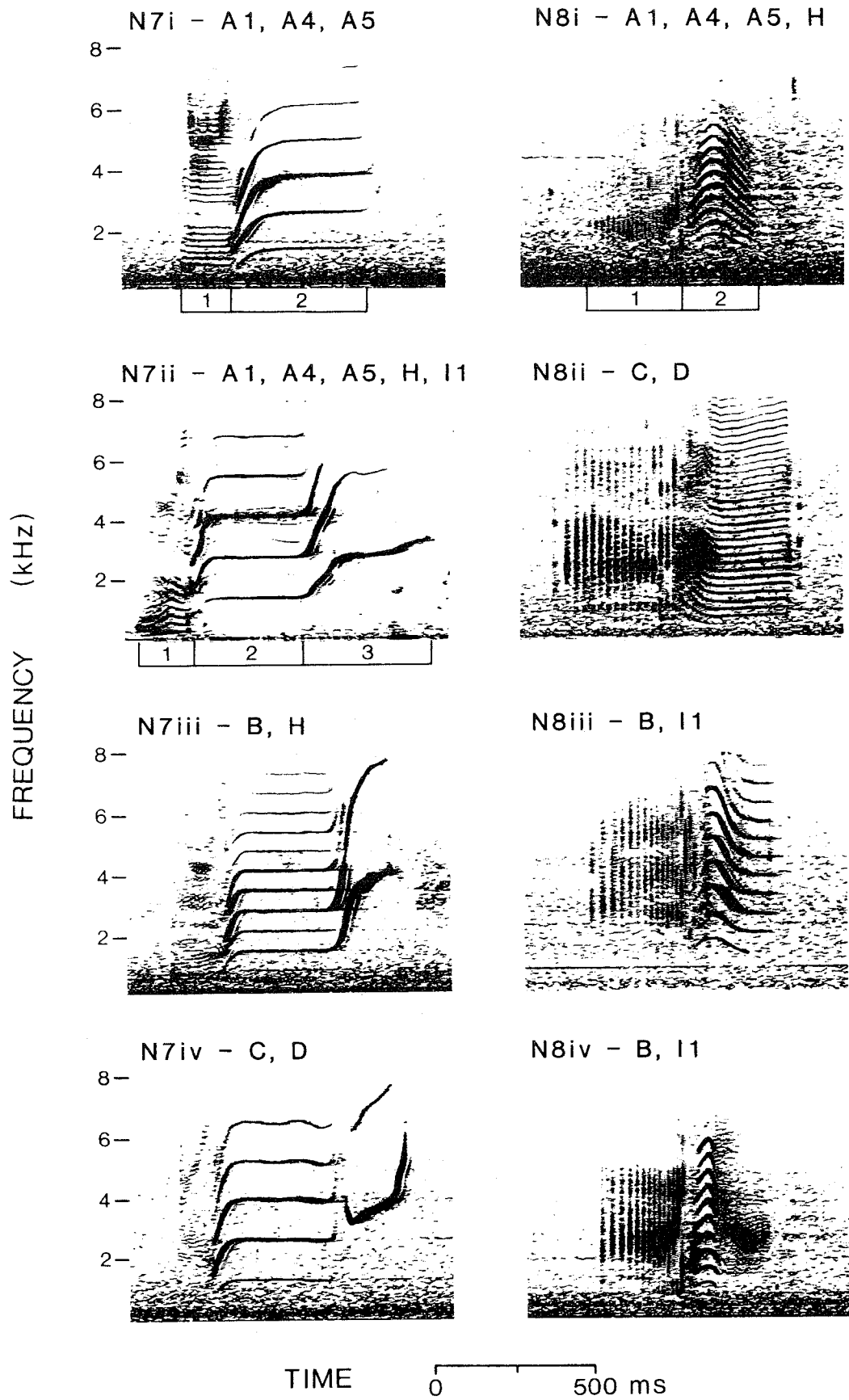
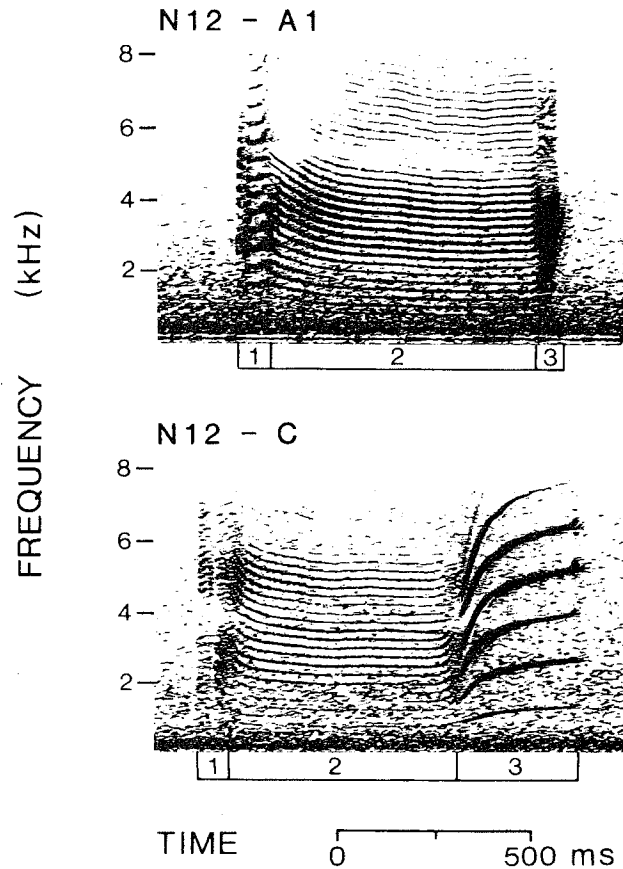


FIG. 3. Sample spectrograms of clan A call types N7 and N8. Above each spectrogram in this figure and Figs. 5, 6, 12, 13, 15, 17, 21, and 22 is the subtype identification and the pods that produce that variant, and below certain spectrograms are division marks separating calls into their component parts.

A.



B.

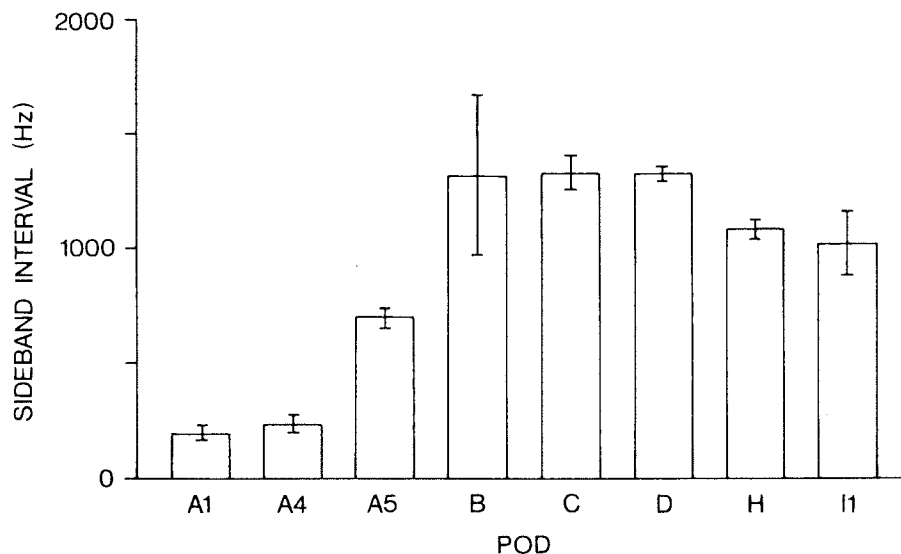


FIG. 4. Spectrograms and structural measurements of clan A call type N12. (A) Examples of typical renditions of call N12 by pods A1 and C. (B) Distribution of mean sideband intervals (with 95% confidence intervals) at the termination of part 3 in N12 calls sampled from clan A pods.

These pods shared four additional call types. The second acoustic group, subclan B, contained pods B, C, D, H, and I1, all of which produced call N16. These two subclans could be further subdivided according to the call types shared or absent in the repertoires of certain pods, and in the different variants of shared call types.

Call characteristics—Common clan A calls: Calls given by

representatives of both subclans A and B included N1, N3, N5, N7, N8, N11, and N12. Consistent pod-specific variations were evident in all but call N3, which was a simple sound heard most often when pods were resting (Ford 1989). Call N5 was not produced by pods C and D, call N1 was not given by pod A5, and N11 was absent in the relatively short samples available for pod I1. Calls N3, N7, N8, and N12 were used by all eight pods.

Representative examples of group-specific call variations within clan A are N7 and N8, which were common in each pod's repertoire. There were four distinct subtypes of each call, illustrated in Fig. 3. Some pods produced more than one subtype of each call. Call N7 was typically a three-part signal, beginning with a low pulse rate component (part 1), followed by a high-pitched middle component (part 2), and ending with an upsweep (part 3). Part 3 was absent in subtype N7i. Subtype N7ii differed from N7iii in the sideband interval (SBI) of part 2, which was consistently >1100 Hz in N7ii and <800 Hz in N7iii. In subtype N7iv, part 1 was very much reduced in intensity compared with other variants, and part 3 started at an SBI generally >1000 Hz higher in frequency than in N7ii and N7iii. Within each N7 subtype there were several significant pod-specific differences in structure, listed in Ford (1987).

As described in Ford (1989), the occurrence of call N8 was closely tied to that of N7. Call N8 was never heard without being preceded by N7, 1–4 s earlier, with both calls in each pair apparently given by the same individual. All variants of call N8 began with a low pulse rate (<50 Hz) component, followed by a rapid increase to a higher pulse rate in part 2. Subtypes of call N8 differed in the SBI and pitch contour characteristics of part 2. As with call N7, there were further pod-specific variations within each subtype. Note that the pods sharing a subtype of call N7 did not necessarily do so with call N8.

Call N12, which was also used by all clan A pods, did not fall into discrete subtypes, but group-specific variations were nonetheless apparent. These variations were primarily in the terminal component (part 3) of the call, which consisted of an upsweep in pitch (Fig. 4). Pods of subclan A tended to have a brief part 3 with a lower upsweep than the longer, high-pitched upsweep typical of subclan B.

Calls produced by subclan A only: Pods A1, A4, and A5 shared four call types, N2, N4, N9, and N10, which were heard from no other pods. In addition, N13 was shared by pods A4 and A5, N27 and N47 were given by A1 alone, and N17 and N19 were used solely by A5 and A4, respectively. Spectrograms of these call types can be seen in Ford (1989). Each of the four shared calls differed significantly in structure among the three pods (Ford 1987), but only N9 formed discrete subtypes. Examples of these are illustrated in Fig. 5.

Calls produced by subclan B only: The five subclan B pods produced four calls, N16, N18, N20, and N21, that did not occur in the repertoire of any other pod. Of these, N16 was the only call shared by all five pods, and it tended to be an important component in their repertoires. This distinctive signal occurred in four variant forms, shown in Fig. 6. Part 1 of the call tended to be similar in each subtype, but clear differences can be seen in parts 2, 3, and 4 (Ford 1987). Pods C, D, and I1 often produced abbreviated versions of call N16 that lacked the descending component of parts 3 and 4. Call N20 was recorded from all subclan B pods except H. Pods C and D produced similar renditions of the call, which were significantly different from those of pods B and I1. Call N18 was heard only from pods B and C, and N21 only from pod B.

Call usage—Subclan A: The frequency of use of discrete call types in the repertoires of pods A1, A4, and A5 during various activity contexts, and their pattern of occurrence from transition analyses, are described in Ford (1989). Several early (pre-1978) recordings made apparently in the presence of the three A pods were obtained and analyzed. The frequency distributions of call types recorded in these encounters and those identified from recordings of A1, A4, and A5 pods made while they were

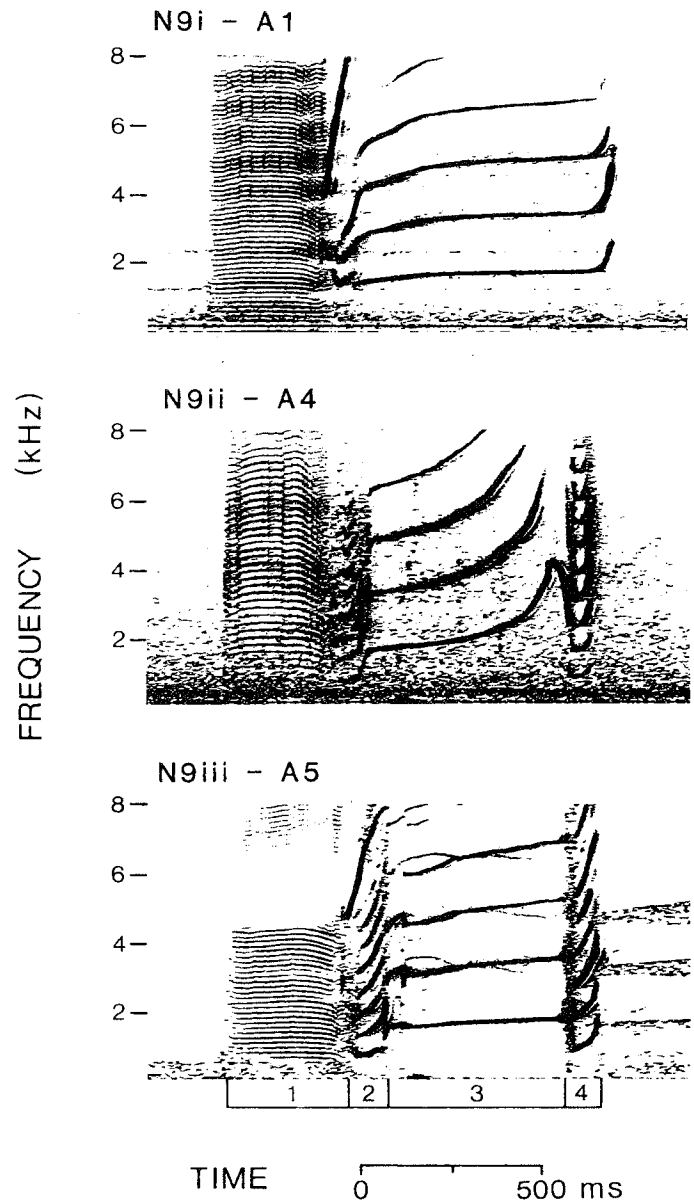


FIG. 5. Spectrograms of variants of call N9, recorded from clan A pods A1, A4, and A5. Note the variations in the structure of parts 3 and 4.

foraging together during 1978–1981 are shown in Fig. 7. There was considerable consistency in call usage from year to year. Analyses of variance with pairwise comparisons for calls N1–N12 among the samples for 1964, 1973, 1978, 1979, 1980, and 1981 revealed few significant differences. These consisted of a reduced occurrence of call N9 in 1964 compared with 1978 and 1979 (both $p < 0.01$), and also in 1981 compared with 1978 and 1979 (both $p < 0.05$). Calls N13, N17, N19, N27, and N47 were recorded too infrequently to warrant statistical comparison; however, all are represented in recordings made as early as 1973. Their absence in earlier samples may well be due to the short recordings available for those years.

There was significant variation in the frequency of use of shared calls by the three A pods. Pod A4 tended to produce N4 and N12 calls proportionately more often than did A1 ($p < 0.001$) and A5 ($p < 0.05$), and calls N5 and N9 less often (all $p < 0.001$). Call N10 occurred more frequently in the repertoire of pod A5 than in that of A1 or A4 ($p < 0.05$), and A1 used call

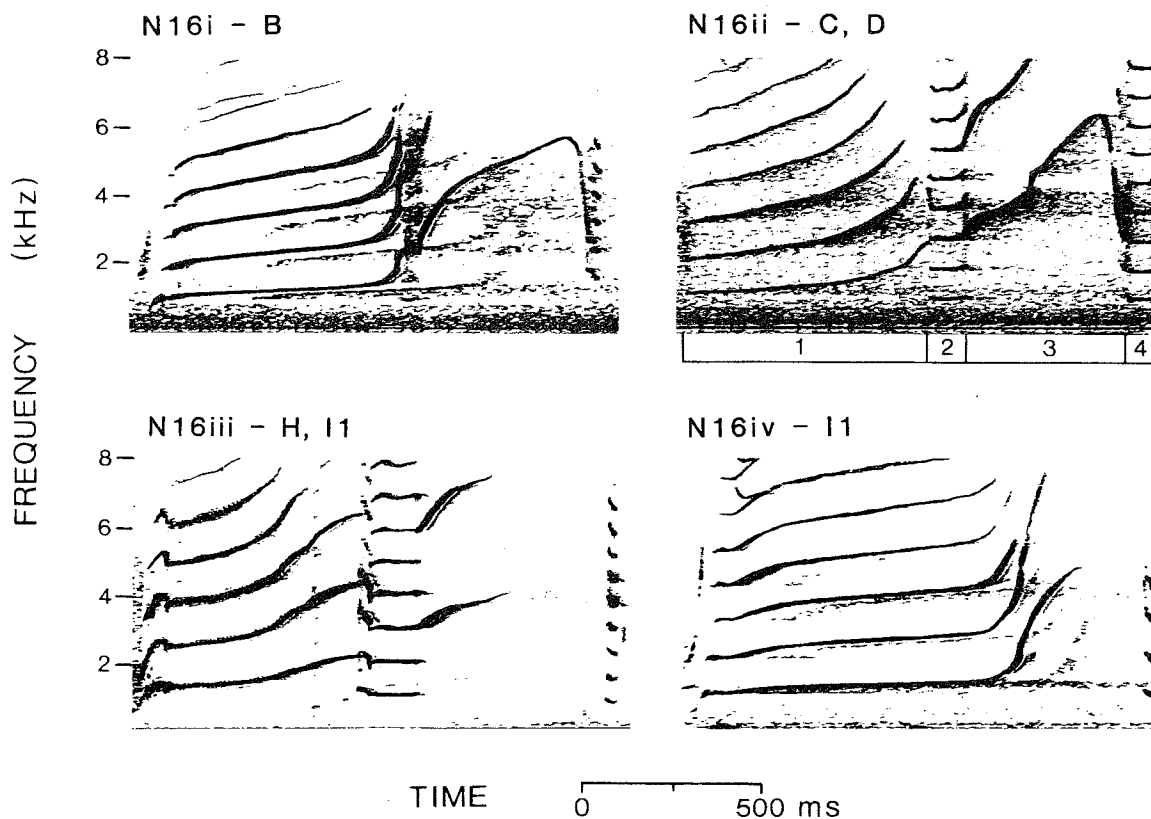


FIG. 6. Spectrograms of variants of call N16, produced by clan A pods B, C, D, H, and I1.

N1 more often than did A4 ($p < 0.001$). No differences were evident in the occurrence of calls N2, N7, N8, and N11.

The frequency distributions of call types recorded during encounters with pod A1 alone are shown in Fig. 8. The pre-1978 distribution was based on two short encounters combined. The first, made by P. Spong in the Johnstone Strait area on August 19, 1971, was recorded in the presence of a group containing a well-marked animal later determined to belong to pod A1. The second was recorded by E. Hoyt in Johnstone Strait on August 26, 1973. Photographs taken by M. Bigg and co-workers at this location on the same day contain A1 whales exclusively (M. Bigg, personal communication). Call types and variants recorded on both occasions were typical of pod A1. Comparing the frequency of use of calls N1–N12 and N47 in these early encounters and in pod A1 recordings made during 1978, 1979, 1981, and 1983 revealed no significant differences. The uncommon call N27 was recorded in the recent samples but not during 1971–1973.

Subclan B: The five subclan B pods could be further divided into two groups based on call use. The first contained B, H, and I1, which shared call N5 and some subtypes of other calls, and the second contained pods C and D, which did not produce N5 and shared subtypes of other calls. The frequency distributions of pod B calls during 1971 and 1973 combined, 1980, and 1981 are shown in Fig. 9. The 1973 recording, made by E. Hoyt in Johnstone Strait on August 24, 1973, contained calls characteristic of both the A pods and pod B. Identification photographs taken independently at the same time and location by M. Bigg (personal communication) confirmed that pods A1, A4, A5, and B were present in the area. All but the uncommon call N11 were present in the 1971–1973 samples, and comparisons of call

occurrence among these early samples and those from 1980 and 1981 revealed no significant differences. Contingency table analyses of a preceding–following transition matrix for all calls in pod B's repertoire except N3 and N21, which were used infrequently, indicate that call occurrence was nonrandom ($G = 850.5$, $df = 49$, $p < 0.001$). Calls N7 and N8 were very closely associated, as described for the A pods (Ford 1989). Other than this pair, no calls showed a strong tendency to occur together.

The occurrence of calls produced by pods H and I1 is illustrated in Fig. 10. Calls characteristic of pod H were present in two short recordings from 1970 and 1974. Although too few samples were available for statistical comparisons, the patterns of call use are similar between these early tapes and those made during 1978–1982. Calls N3 and N11, however, were absent in the older recordings. Pod I1's repertoire was not evident in any pre-1978 tape. Comparisons of the occurrence of call N5 revealed no significant variation among pods B, H, and I1, but all three groups produced the call more often than the A pods did ($p < 0.001$). Pod B produced call N1 less often than pod H did ($p < 0.05$); neither pod differed from I1 pod in the use of N1, but all produced the call more frequently than A1 and A4 did ($p < 0.001$). Occurrence of N7 was similar in B, H, I1, and the A pods, but N8 was used less often by the A pods ($p < 0.001$).

The considerable similarity in the structure of calls produced by pods C and D was paralleled, in most cases, in the frequency of their use of those calls (Fig. 11). The principal difference lay in the production of abbreviated and regular versions of N16. In pod D, the short form represented 39.5% of total call use, significantly greater ($p < 0.001$) than the 12.9% in pod C. Pod C's use of the long form of N16 amounted to 28.2% of all calls, in contrast to 3.9% in pod D ($p < 0.001$). The only other signif-

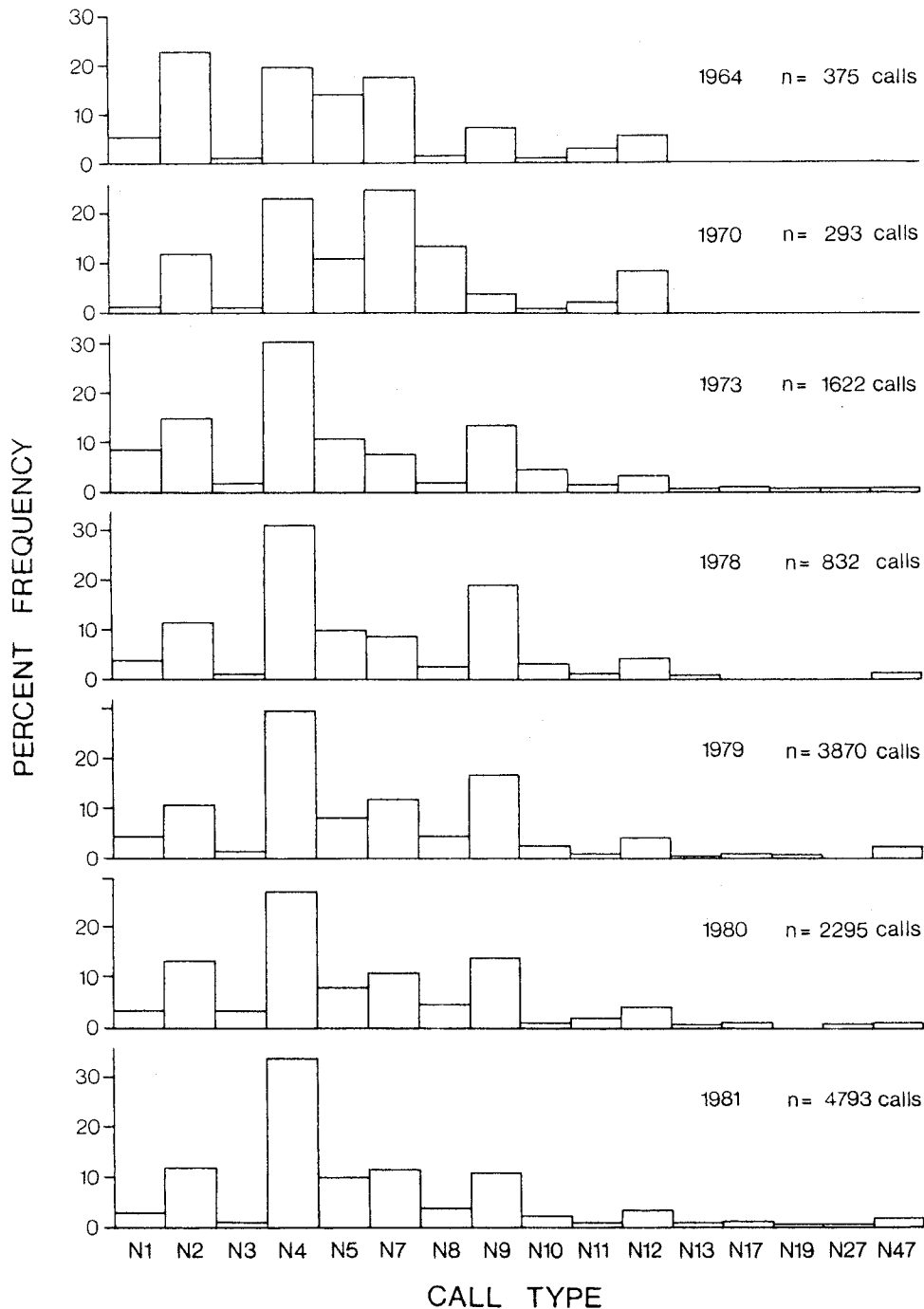


FIG. 7. Frequency distributions of call types of clan A pods A1, A4, and A5 while foraging together in 1978–1983, and from recordings made in 1964–1973, which are assumed, on the basis of call types recorded, to have involved the A pods.

icant variation between samples of the two repertoires was in N20, which occurred more often in pod D recordings ($p < 0.01$).

There is substantial evidence that the repertoire of pod C had changed little since 1964. Recordings made apparently in the presence of the group in that year contained all but one (N3) of the calls used in recent years. Also, their frequencies of occurrence differ only in the short form of call N16, which was significantly ($p < 0.05$) less common in 1964 than in 1978–1980. Another indication of repertoire stability in the pod resulted from recordings of the whale *Namu*, which was captured

in 1965 from a group determined later from photos to be pod C (Bigg et al. 1991). This animal produced all calls typical of the pod except the uncommon N18 and N20, and the frequency distribution of these calls differed only in the short form of N16, which again was used less often ($p < 0.001$) than in 1978–1980. Transition analyses of common calls of pod C and *Namu* showed a similar pattern of call usage (Ford 1984). There were significant differences in some structural parameters of *Namu*'s calls compared with pod C's calls recorded during 1978–1980 (Ford 1987), but the overall forms of the signals were fundamentally

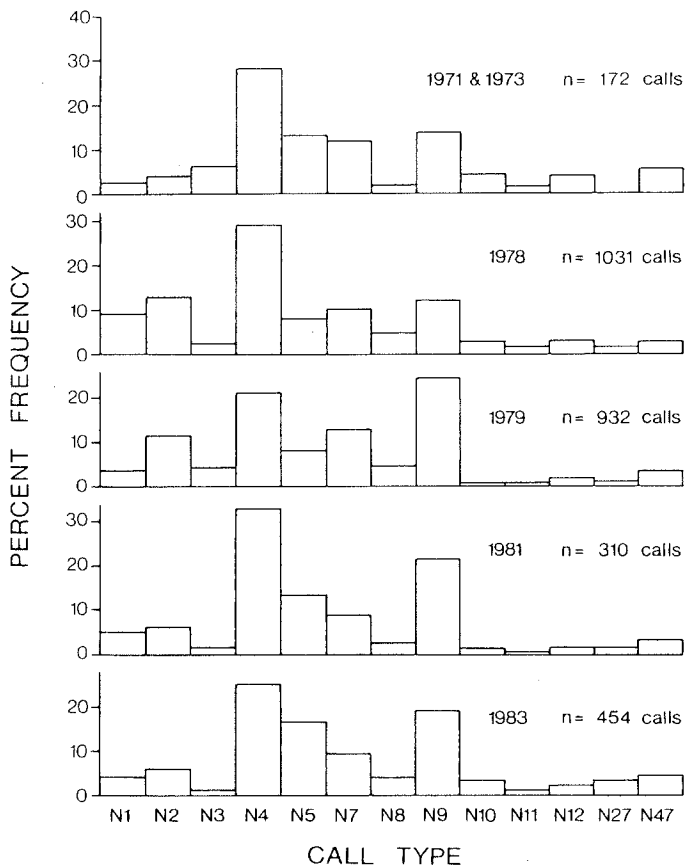


FIG. 8. Frequency distributions of call types produced by clan A pod A1 in 1971–1983. Recordings from 1971 and 1973 are known, from visual or photographic evidence, to have involved pod A1.

the same. Sample spectrograms of four pod C calls as they were produced by *Namu* and by pod C during 1978–1980 are shown in Fig. 12.

Summary of acoustic associations: clan A—A measure of acoustic associations within clan A was obtained by using an index of repertoire similarity for each pair of pods (Table 3), and arranging these values into a cluster diagram (Fig. 2). These show that within subclan A, pods A4 and A5 tended to be more closely related acoustically to each other than either was to pod A1. Similarly, within subclan B, pods C and D formed a distinct subgroup with a high level of similarity (0.963), and pods B, H, and I1 formed another subgroup with somewhat lower degrees of similarity. The pods of subclans A and B were related at the 0.571 level of similarity. It is noteworthy that pod I1 produced two versions of several call types. Some were unique to the pod, whereas others were shared with pod B or, more often, with pod H. Pod I1 has recently been subdivided into three pods, I1, I2, and I18 (Bigg et al. 1987), and these different versions of certain calls may have represented group-specific variations. For example, recordings of pod I2 made in 1986 contained only one version of call N16, subtype N16iv. Subtype N16iii may have been used by either pod I1 or I18, or both.

Clan G

Clan G comprised three pods, G, I11 and I31, containing 43 whales in 1983 (Table 1). The clan had a repertoire of 15 call types, one of which had two forms (subtypes). These calls and the pods observed to produce them are listed in Table 4. Four of the clan G call types were used by all three pods, and the rest

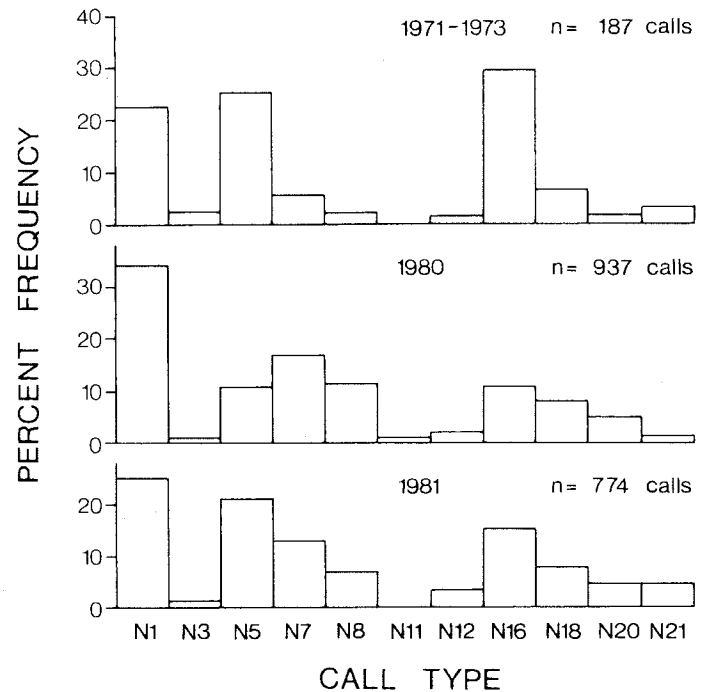


FIG. 9. Frequency distributions of call types produced by clan A pod B in 1971–1981. The sample from 1971 is assumed to have involved pod B, on the basis of call types recorded. There is photographic evidence of the presence of pod B in the 1973 sample (see text for details).

were produced only by one or two of the pods. The three pods formed two acoustically distinct subclans: G, which comprised pod G, and I, formed by pods I11 and I31. No clan G calls were shared with any other pod.

Call characteristics—The most common call of the clan G pods was N23, which occurred in two variant forms, N23i and N23ii. Subtype N23i was shared by pods I11 and I31, and N23ii was given exclusively by pod G. Subtypes of N23 and several other common clan G calls are illustrated in Fig. 13. Significant pod-specific variations were noted in the renditions of calls N23i, N24, and N30 by pods I11 and I31 (Ford 1987). Call N25 was important in the repertoires of pods I11 and G, but was not heard from I31. The terminal component, part 4, of the call was longer in the versions produced by pod I11 (mean 637 ms, range 384–1295 ms, $n = 32$) than in those produced by pod G (mean 185 ms, range 115–335 ms, $n = 26$) ($p < 0.001$). Calls N28 and N29, used exclusively by pod G, were related to N23 in the structure of part 1 (Fig. 13). All three call types were often preceded within 1 s by an ‘introductory note’ consisting of a short (<150 ms) pulse burst with repetition rates of 100–150 Hz. Clan G had a relatively large repertoire of six calls which were heard mainly when the pods were resting.

Call usage—The frequency distributions of calls produced recently by clan G pods are illustrated in Fig. 14, with the occurrence of calls in a tape recorded during 1973, apparently in the presence of pod I11 and, possibly, pod I31. These show that there was a strong tendency to use call N23 throughout the clan. For example, 61.8% of all calls recorded from pod I31 during 1981–1983 were of this type. The frequencies of occurrence of most of the remaining clan G call types differed markedly among the three pods. Although the sample for 1973 was small, the frequency distribution and structure of calls were similar to those recorded recently from encounters with pods I11 and I31 foraging together. Calls N38, N39, N40, N41, N45, and N46 were all

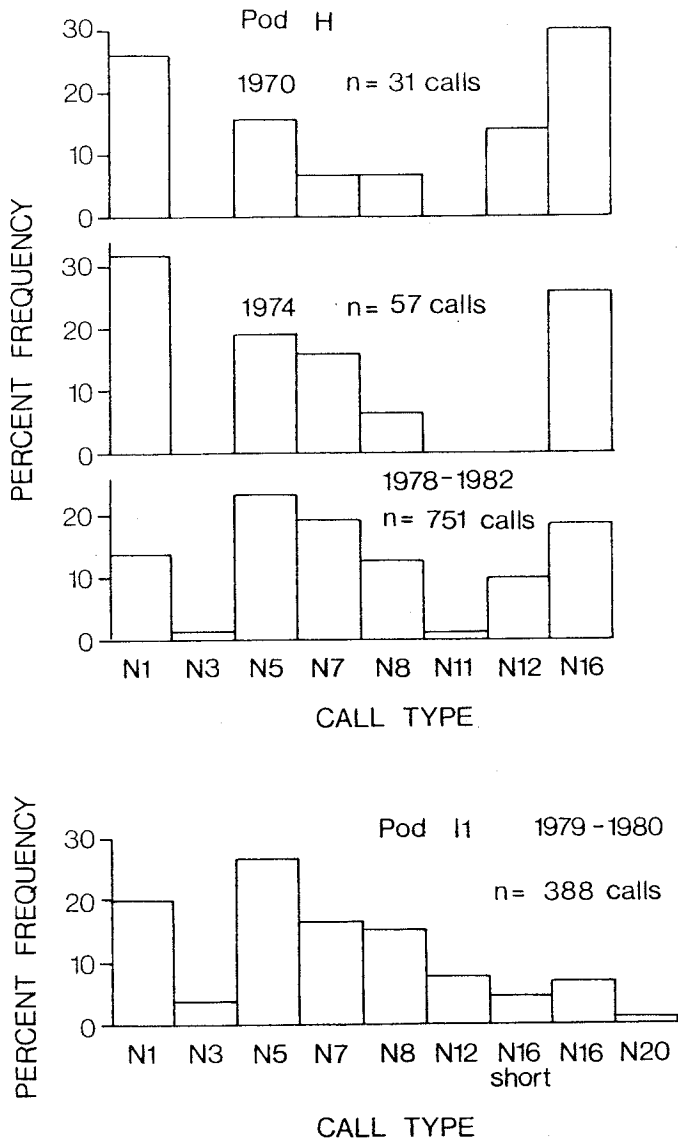


FIG. 10. Frequency distributions of call types produced by clan A pods H and I1. Tapes from 1970 and 1974 are assumed to have involved pod H, on the basis of the call types recorded.

strongly associated with low-arousal circumstances, as was call N3 in the clan A repertoires. Pod G produced N41 most frequently in these contexts, whereas I11 and I31 used N46 most often.

Transition analyses of clan G calls showed that, as with other clans, calls were typically emitted in repetitive series and certain calls in the repertoires tended to occur together. Individuals often emitted N45 less than 1 s prior to N25.

Summary of acoustic associations: clan G—The call repertoires of pods I11 and I31 were more similar to each other than either was to that of pod G. For this reason the two have been placed in the same subclan. Index of similarity values indicate that I11 and I31 were highly related acoustically, having a value of 0.909. Pods G and I11 had a lower similarity level, 0.522, and G and I31 had a similarity value of only 0.381.

Clan R

Clan R was a small acoustic association of two pods, R and W, which had 17 and 4 members, respectively, in 1983. The clan had a total repertoire of eight call types, N32, N33, N34, N35,

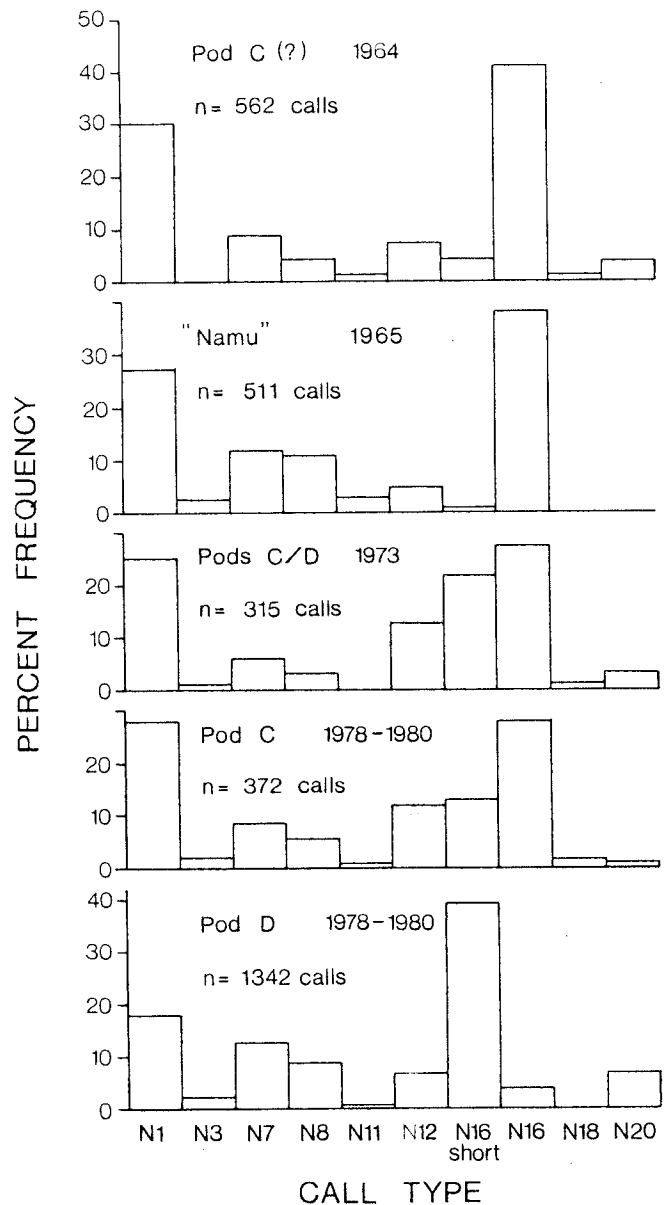


FIG. 11. Frequency distributions of calls produced by clan A pods C and D, and by the captive whale *Namu*, which was identified by Bigg et al. (1990) as having been taken from pod C in June 1965. Tapes from 1964 and 1973 are assumed to have involved pods C and (or) D, on the basis of the call types recorded.

N42, N43, N50, and N51, which was used by both groups. None of these call types was recorded from any other clan.

Call characteristics—The call repertoire of clan R is illustrated in Fig. 15. Call N32 occurred in two subtype forms: N32i was produced by both pods, but N32ii appeared to be made by pod R only. Calls N32i, N33, and N35 showed consistent pod-specific variations in structure. Clan R calls recorded in Johnstone Strait on August 29 and 31, 1964, were examined quantitatively and found to be similar in structure to those obtained recently from pods R and W (Ford 1987). Call N49 was present only in the 1964 recordings.

Call usage—The frequency distributions of clan R calls recorded in 1964 and 1973, and those recorded recently from pods R and W are shown in Fig. 16. All calls recorded from these pods during 1981–1983 were present in 1964, except the

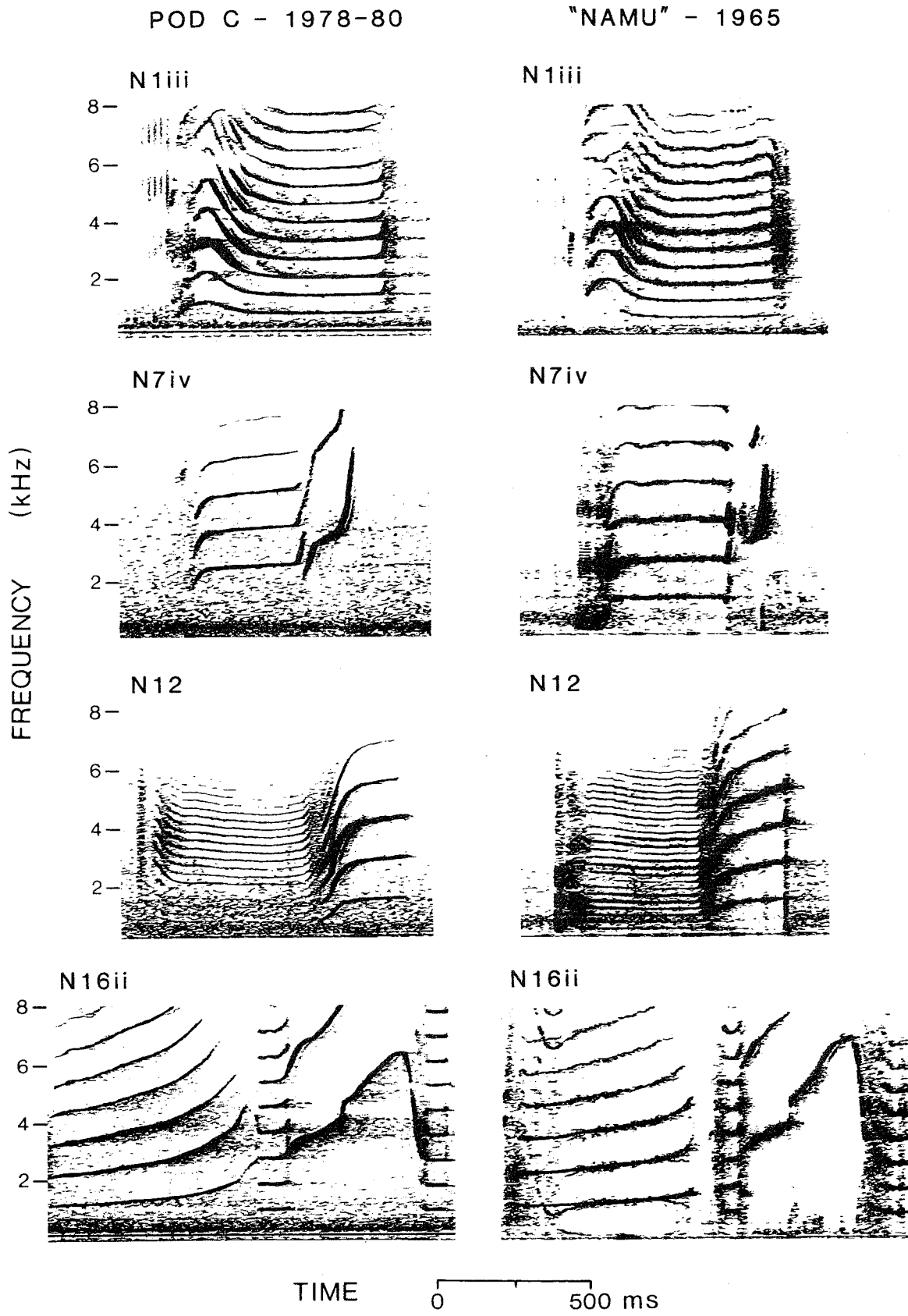


FIG. 12. Spectrograms of selected call types produced by clan A pod C in 1978-1980, and by the captive whale *Namu* in 1965.

TABLE 3. Degree of similarity of discrete call repertoires of the eight clan A pods

Pod	Pod						
	A1	A4	A5	B	C	D	H
A4	15 (0.750)						
A5	15 (0.789)	16 (0.842)					
B	9 (0.450)	9 (0.450)	8 (0.421)				
C	6 (0.353)	6 (0.353)	5 (0.312)	10 (0.589)			
D	6 (0.364)	6 (0.364)	5 (0.323)	9 (0.545)	13 (0.963)		
H	10 (0.571)	10 (0.571)	9 (0.545)	11 (0.629)	8 (0.522)	8 (0.571)	
I1	8 (0.421)	9 (0.514)	7 (0.389)	14 (0.737)	7 (0.438)	7 (0.452)	12 (0.727)

NOTE: Values are given as the total number of call types and subtypes shared by each pair of pods, and the number in parentheses show the index of similarity based on this number. See text for an explanation of derivation of this index.

TABLE 4. Call types and subtypes produced by pods of clan G in the northern resident community

Call	Pod		
	G	I11	I31
N23			
i		x	x
ii	x		
N24		x	x
N25	x	x	
N26		x	x
N28	x		
N29	x		
N30		x	x
N38	x		
N39		x	x
N40	x	x	x
N41	x	x	x
N44	x		
N45	x	x	
N46		x	x
N48	x	x	x
Total	10	11	9

uncommon call N51. However, call N49, which comprised 8.1% of the 422 clan R calls identified from the 1964 tapes, was not represented in either the 1973 or the 1981–1983 samples. It is possible that the call had been lost from the repertoires of pods R and W, or that the call was specific to some clan R pod not present in the area during the study, though this is less likely.

When the frequencies of occurrence of the remaining calls were compared, no significant differences were apparent in the use of calls N32, N33, N34, N35, or N43 between the recordings made in 1964 and recent recordings of pods R and W. Call N42, however, was significantly less frequent in pod W's calling than in pod R's (0.7 vs. 13.5% of total calls, respectively; $p < 0.001$). The uncommon calls N50 and N51 were not tested,

but the proportions of both were small in both early and recent samples. These signals appeared to be associated with resting, as were certain calls in the repertoires of clans A and G. Transition analyses of clan R call sequences revealed a strong association between calls N34 and N43.

Summary of acoustic associations: clan R—The two pods making up clan R were very closely related acoustically. The only major difference appeared to be in subtype N32ii, which was recorded from pod R but not from pod W. The index of similarity between the two groups was 0.947, which is one of the highest observed in resident pods (Fig. 2).

Calls of southern-community resident pods

Clan J

The southern community comprised three pods, J, K, and L, which belonged to a single acoustic association referred to as clan J. Pods J, K, and L contained 19, 15, and 44 individuals, respectively, in 1983 (Table 1). Twenty-six call types, listed in Table 5, were described from recordings of clan J pods. None of these calls was heard from any northern-community pod.

Call characteristics—Pod J produced 17 call types, pod K had 10, and pod L had 15. Spectrograms of the most common of these signals are shown in Fig. 17. Four calls, S6, S8, S10, and S42, were shared by all three pods, 9 were given by two pods, and 13 were exclusive to single pods. Four of the 26 clan J calls had two or three discrete subtypes. Pod J produced two subtypes of call S2, while L pod produced a third. Pods J and L similarly shared subtypes of calls S13 and S37. Subtype S8i was produced by pods J and K, and S8ii by pod L only. Six calls were recorded from pod J only and seven appeared to be used by pod L only. No calls were unique to pod K.

Although unrelated to the call types discussed here, another noteworthy feature of clan J sound production was the tendency for whistles to be emitted in long, repetitive series of pulses, especially during socializing activities. Each whistle pulse was 100–400 ms in duration, and had a constant pitch within a bandwidth of about 4000–8000 Hz. These pulses were repeated at rates of 1–8/s for periods of 3 to >30 s. Whistle pulses within a series were often given at alternating frequencies up to

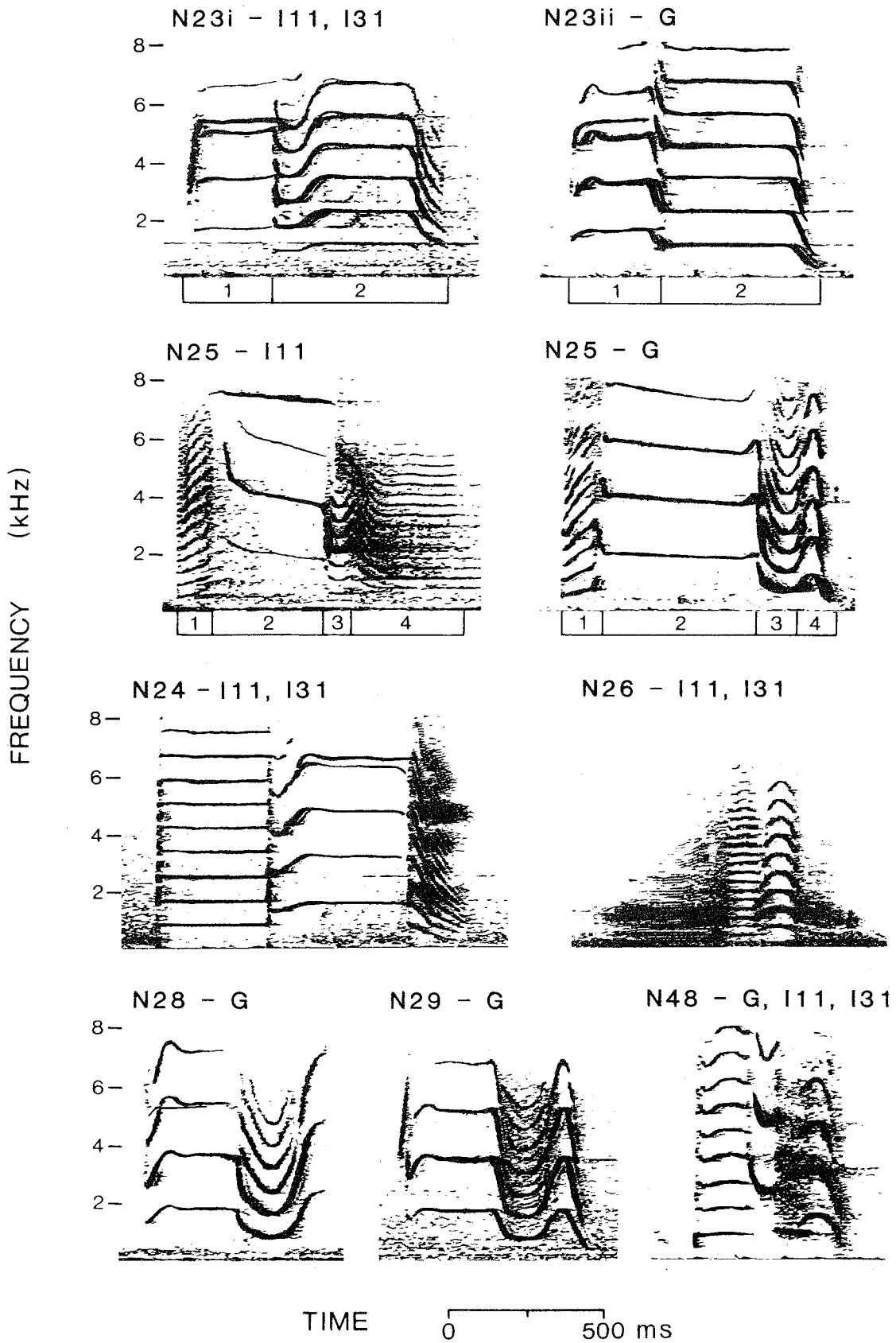


FIG. 13. Spectrograms of common call types produced by clan G pods G, I11, and I31. Renditions of call N25 by pods G and I11 differ in the duration of part 4.

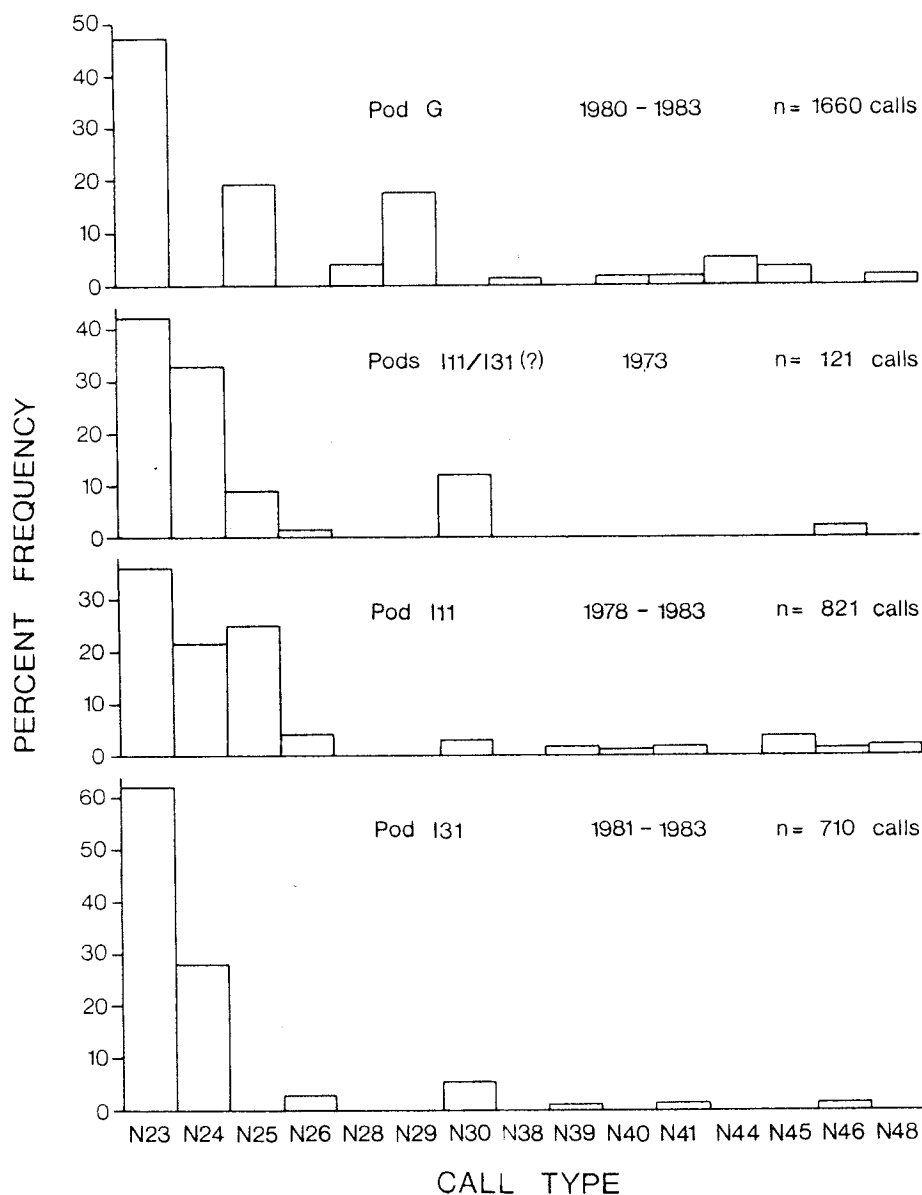


FIG. 14. Frequency distributions of call types produced by clan G pods G, I11, and I31. The sample from 1973 is assumed to have involved pods I11 and possibly I31, on the basis of the call types recorded.

3000 Hz apart. Series of pulsed whistles were not recorded from any other clan.

Call usage—The frequencies of occurrence of call types produced by pod J during foraging and travelling in 1979–1983 are illustrated in Fig. 18. There were many significant differences in call usage between these activities in this pod. Calls S1, S4, and S7 tended to predominate in foraging contexts, whereas S2, S44, S42, and S1, in that order, were the most common calls during travelling. Call production by pod L also differed significantly in these two contexts (Fig. 19). Calls S18, S19, and S22 were heard most often while the group was foraging, but S2, S8, and S40 were dominant during travelling. Such a degree of variation in vocal behaviour during foraging and travelling was not observed in northern-community pods (Ford 1989). Pod K was recorded only while foraging. Calls S16, S17, S1, and S4 were the most common signals of this group. No calls were associated with group resting activity in clan J; unlike northern-community whales, pods J, K, and L rested in silence.

Three historical field recordings made apparently in the presence of pod J in 1958–1961 contained 14 of the 17 calls used by the group in 1979–1983 (Fig. 18). Two of these recordings were made in Saanich Inlet, Vancouver Island, and the third in Puget Sound. Pod J has been the most common resident group observed in these locations since monitoring of the population began in 1973 (M. A. Bigg, personal communication). A brief recording of pod J made in March 1986 contained 10 of the 17 calls described for the group. Thus, most calls in the repertoire have persisted over a period of 28 years.

No calls appeared to be strongly associated in transition analyses of pod J sound production. However, the calls of pod L exhibited several clear associations, especially in the tendency for S22 to follow S18 and for S17 to follow S16 (the latter also occurred in the call patterns of pod K).

Summary of acoustic associations: clan J—Indices of similarity of clan J call repertoires were low compared with those of northern-community clans (Fig. 2). This was largely a

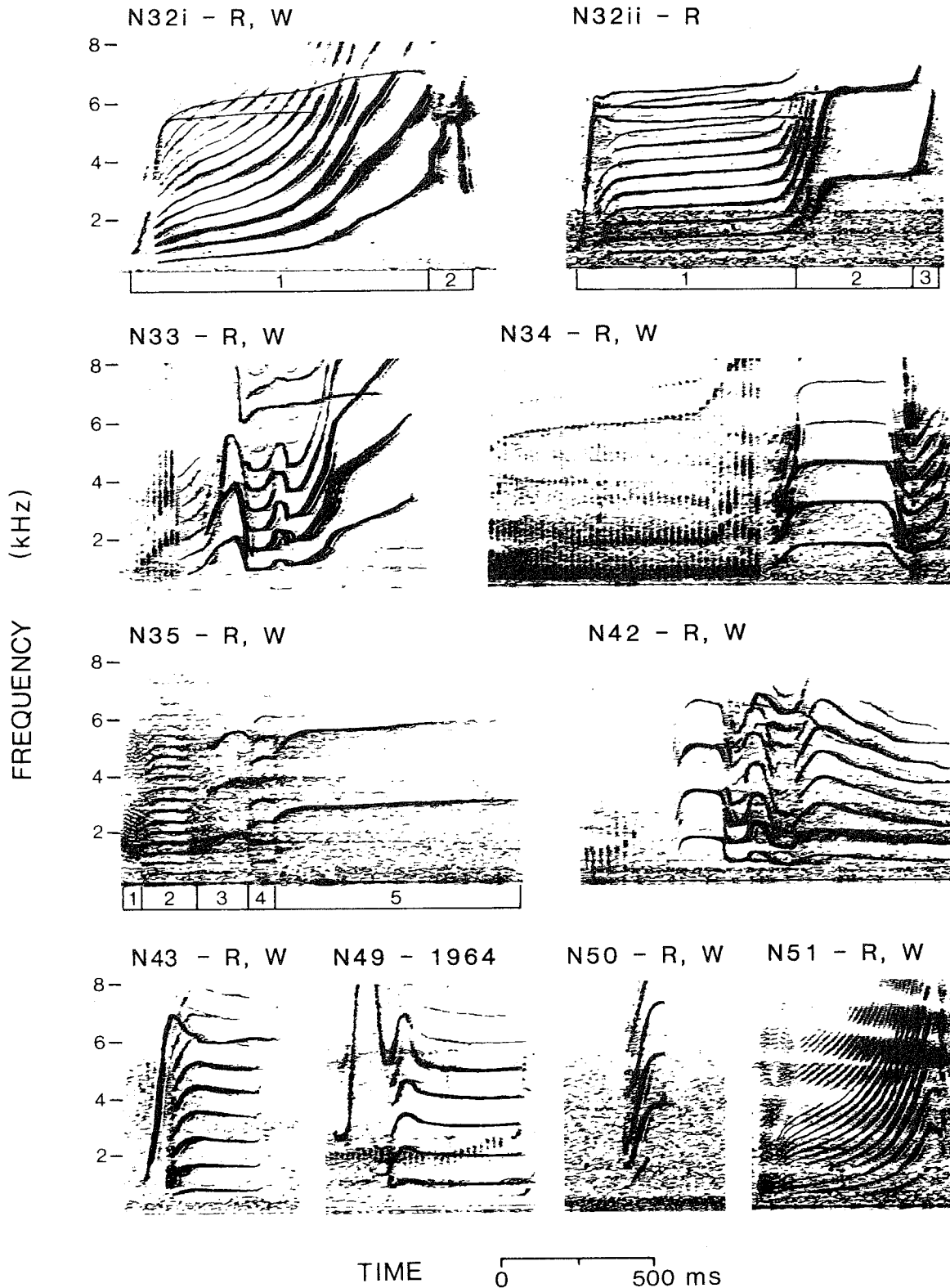


FIG. 15. Spectrograms of call types produced by clan R pods R and W.

result of the numerous calls exclusive to either pod J or pod L. Pods J and K were most similar acoustically, with an index of 0.545; pods K and L were next, with an index of 0.387, and finally J and L at 0.333.

Call repertoire similarities and comparison of pod ranges

Of the four resident clans, only clan J, which comprised the

entire southern resident community, appeared to have an exclusive range. The ranges of the three northern resident clans overlapped considerably. The frequencies of occurrence of northern resident pods off northeastern Vancouver Island during 128 days in 1978–1983 are shown in Fig. 20. Although all pods in the community occurred in the area, their distribution was clearly nonrandom. Pods A1, A4, and A5 were by far the most

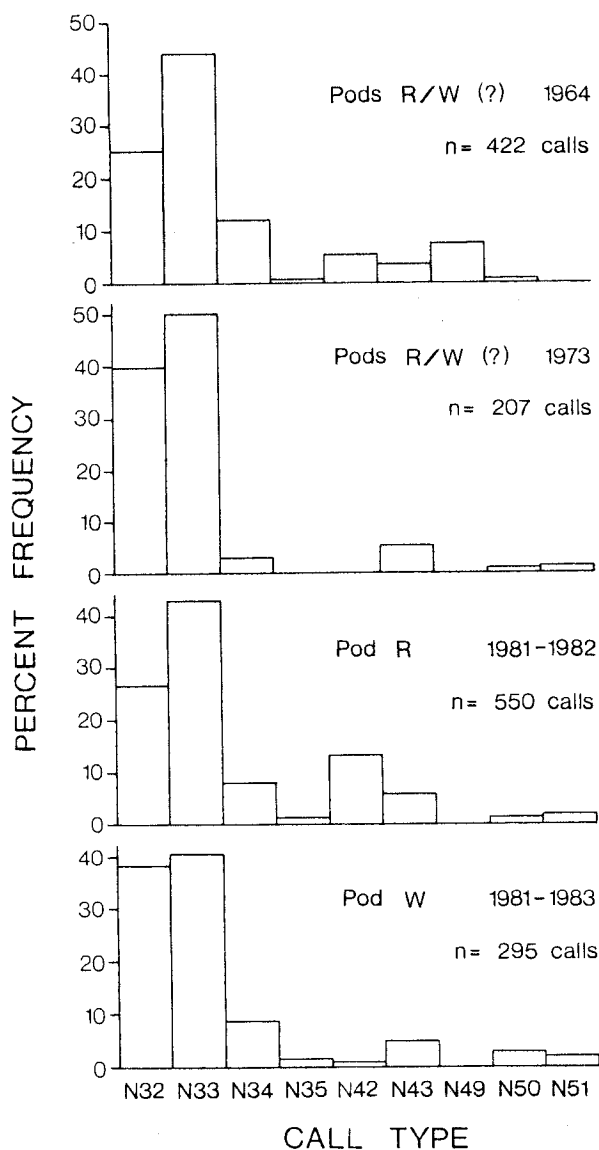


TABLE 5. Call types and subtypes produced by pods of clan J in the southern resident community

Call	Pod		
	J	K	L
S1	x	x	
S2			
i	x		
ii	x		
iii			x
S3	x		
S4	x	x	
S5	x	x	
S6	x	x	x
S7	x	x	
S8			
i	x	x	
ii			x
S9	x		
S10	x	x	x
S12	x		
S13			
i	x		
ii			x
S14	x		
S16		x	x
S17		x	x
S18			x
S19			x
S22			x
S31			x
S33			x
S36			x
S37			
i	x		
ii			x
S40			x
S41	x		
S42	x	x	x
S44	x		
Total	18	10	15

FIG. 16. Frequency distributions of call types produced by clan R pods R and W. The 1964 and 1973 samples are assumed, from the call types recorded, to have involved pods R and (or) W.

commonly encountered, each being present on >48% of encounter days. Next was pod B, which was seen on 25.8% of the total number of days on which whales were encountered. The remaining clan A pods were each seen on <16% of the days. All three clan G pods were relatively uncommon in the area. Of the three, I11 was the most often observed, being present on 13.3% of encounter days. The two clan R pods, R and W, were the rarest in the area: R was seen on only 3 days (2.3%) and W on only 9 days (7.0%).

Pod occurrence also varied from year to year. The three A pods were the most consistently seen, although A1 apparently left the study area for most of the 1980 field season (July–October). Many of the less common pods appeared sporadically. Some were observed several times in certain years, but not at all in others (Ford 1984).

These patterns of occurrence suggest that pods had preferred areas within the overall range of the northern community. The waters off northeastern Vancouver Island, especially Johnstone Strait, appeared to be the centre of distribution, or core area, of pods A1, A4, and A5 during the summer. All three pods were

absent on only 18 of the 128 days (14.1%) that whales were observed at this location during 1978–1983. The remaining clan A pods, as well as clans G and R, spent most of their time outside the study area, probably to the north and west. Unfortunately, too few encounters have been made in these regions to permit possible core areas for these pods to be identified. There is some indication that clan R may reside predominantly in the northern portions of the community range. On four of the eight occasions on which pod R was encountered between 1973 and 1983, it was north of Bella Bella, some 200 km north of the Johnstone Strait area (Fig. 1). Pods from the other northern-community clans have also been sighted in these northern areas, but rarely, compared with their occurrence in the southern portions of the community range.

In summary, the southern resident community comprised a unique acoustic group, clan J, with an exclusive range. In the northern community, clans A, G, and R overlapped geographically, although each may have had separate core areas within the community range. In the case of clan A, pods A1, A4, and A5, which formed an acoustic subclan (Fig. 2), appeared to have a

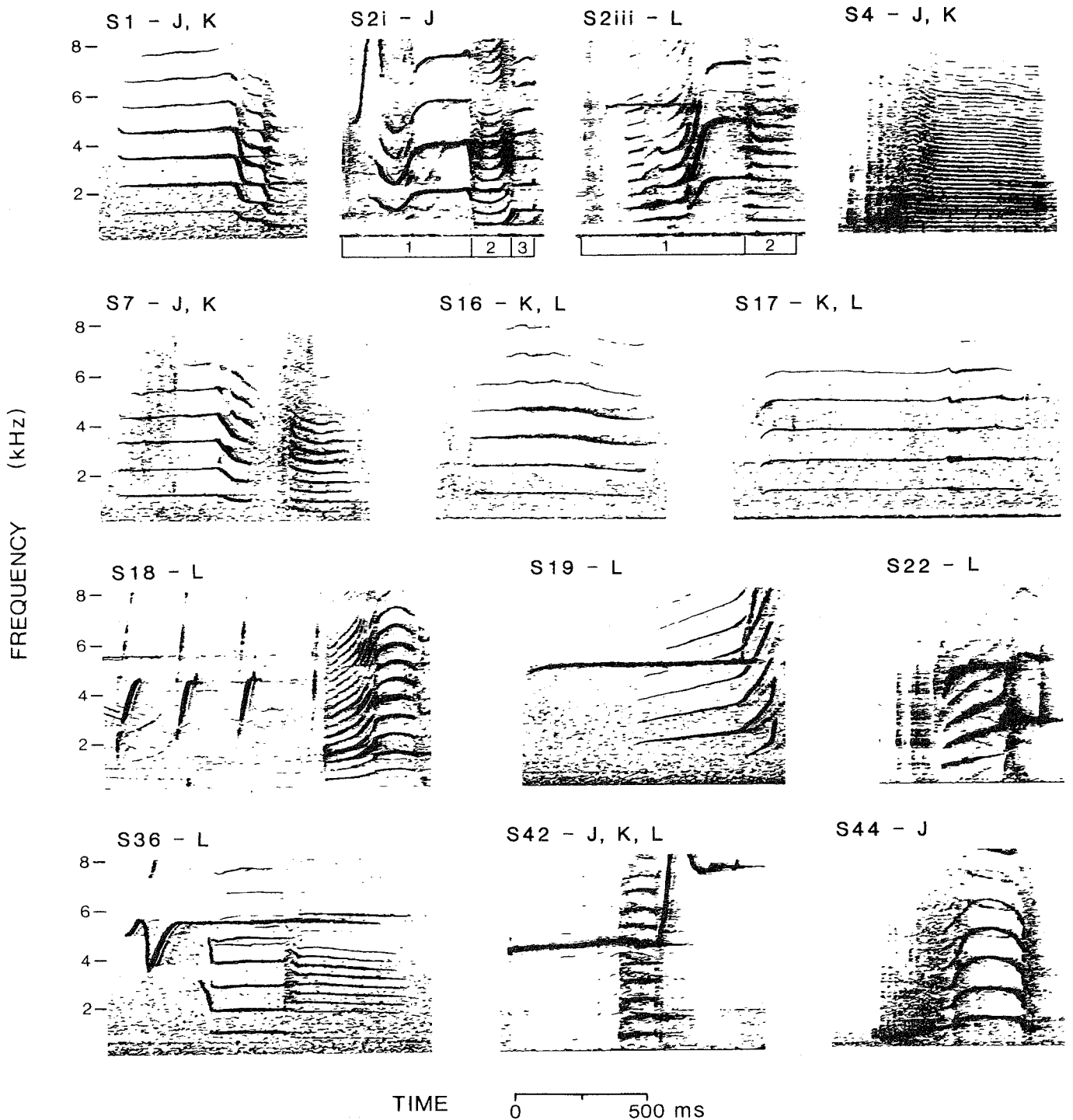


FIG. 17. Spectrograms of common call types produced by clan J pods J, K, and L.

different core area from the remainder of the clan. It should be noted that most northern resident encounters were made in June–October. Pod distributions at other times of the year are mostly unknown.

Call repertoire similarities and comparisons of pod associations

To examine the relationship between repertoire similarity and the degree of social association of pods, an index of association (Dice's index, described in Morgan et al. 1976) was calculated from the total number of days on which each pair of pods was sighted together. To provide as large a sample as possible, all

pod encounters observed or documented by M. A. Bigg prior to and during this study were included in this analysis. The association matrix for the northern resident community (Table 6) was based on 773 pod encounters made on 353 days during 1973–1983, an average of 2.19 pods/day. There was considerable variation in the number of occasions on which each pod was encountered while travelling alone. Thus, to arrive at an accurate measure of interpod association unaffected by each pod's degree of sociability (i.e., tendency to mix with other groups), these 'lone' encounters were removed from the total for each pod before the association index was calculated.

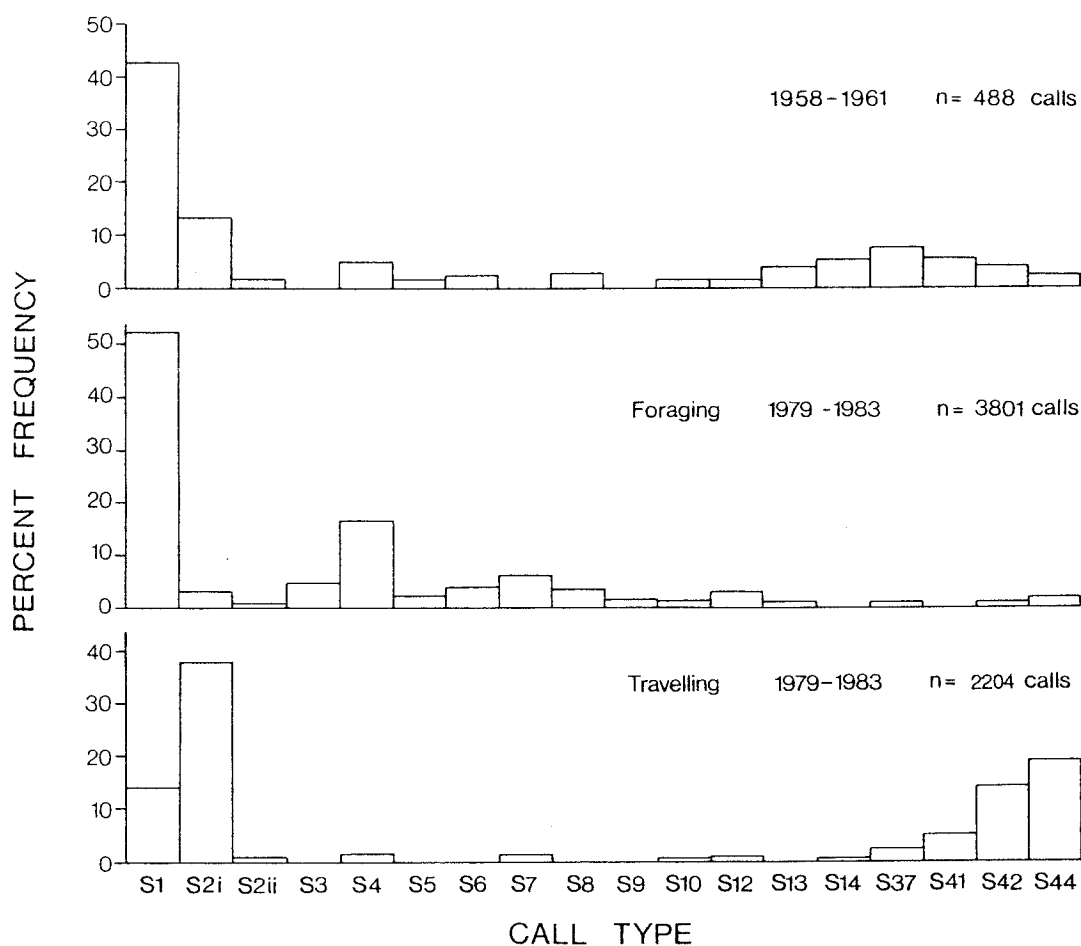


FIG. 18. Frequency distributions of call types produced by clan J pod J while foraging and travelling in 1979-1983, and from recordings of unidentified killer whales in the southern community area during 1958-1961. See text for further details.

Since the distribution of northern resident pods was non-random, and most sampling was conducted in a small portion of the community range, the association indices must be interpreted with care. As mentioned previously, the main study area of western Johnstone Strait appeared to be the core area for pods A1, A4, and A5. Other pods entered this area irregularly and usually joined with the A pods for the duration of their visit. For this reason, the high index values between the three A pods and many other northern-community pods are very likely over-representations of the actual year-round relationships of these pods outside Johnstone Strait.

Almost all northern resident pods were observed to associate with each other, but there was no consistent relationship between the acoustic similarities of pods and their association patterns. Within clan A there was a strong correlation between the close travelling associations of the subclan A pods A1, A4, and A5 and the similarity of their call repertoires. Among the subclan B pods, C and D had the most similar repertoires in the northern community, with an index of similarity of 0.963. These two pods travelled more with each other than with any other northern-community pod, although their association index of 0.343 was not particularly high. The second-highest association for pod C was with pod W of clan R (0.245). Pods B, H, and I1 formed a distinct acoustic subgroup within clan A, and in some cases this was reflected in their social relationships. Pods H and I1 had an association index of 0.333, the highest value for both pods. Pod B, however, had a stronger association with pod G (0.270) than with any other northern resident pod except the A pods. Pod B's

association with H was higher than with any other clan A pods, again excluding the A pods, but it had a weak association with I1 (0.102).

Of the three clan G pods, I11 and I31 were closely related, in both call repertoire (similarity index 0.909) and occurrence (association index 0.627). Pod G's highest association was with I11 (0.475), but its association with I31 was lower (0.261) than with W (0.333). Within clan R there was little indication from occurrence patterns of the close acoustic relationship between pods R and W. Although the highest association for R was with W, the latter associated more with C, G, I11, and I31 than with R.

Interpod associations in the southern resident community were confined to the three clan J pods (Table 7). The strongest association was between K and L (0.461). Pod J associated to a similar degree with both K (0.353) and L (0.337). Pod J appeared to spend most of its time within Georgia Strait and Puget Sound, whereas pods K and L travelled regularly through Juan de Fuca Strait to areas off the west coast of Vancouver Island (Fig. 1). Acoustic relationships within clan J did not coincide closely with these association patterns. Pods J and K had the highest repertoire similarity index, 0.545, followed by K and L (0.387) and J and L (0.333).

Discussion

Regional variation of vocalization is far less common in mammals than in birds, where it is a well-known and widespread phenomenon. Regional differences in bird song exist at two

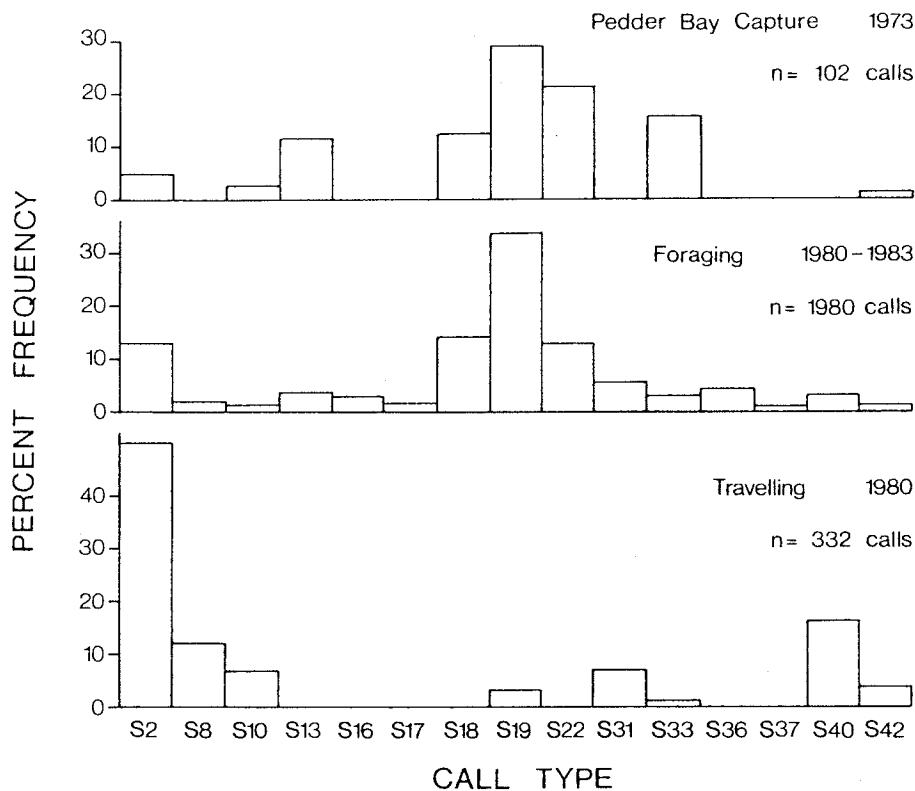


FIG. 19. Frequency distributions of call types produced by clan J pod L while foraging and travelling in 1980-1983, and from captive whales held at Pedder Bay, Vancouver Island, in August 1973.

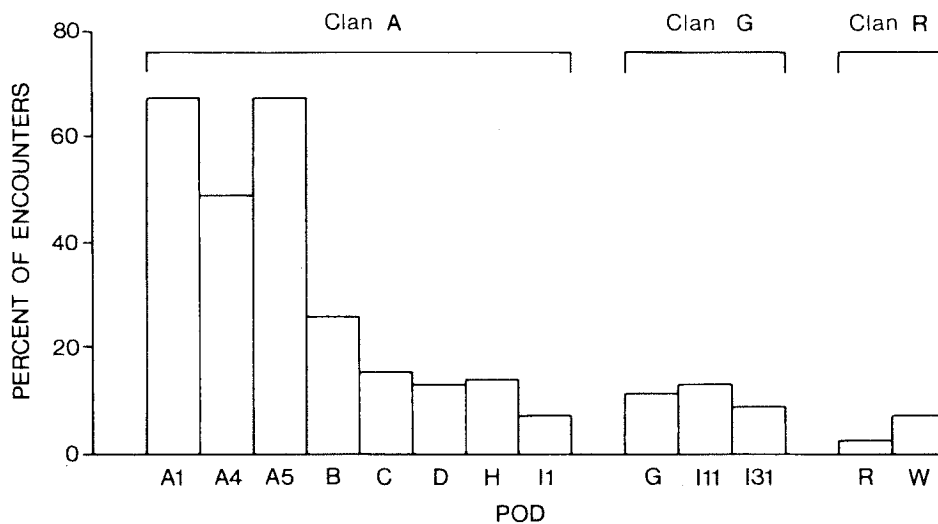


FIG. 20. Frequencies of occurrence of northern resident pods off northeastern Vancouver Island in 1978-1983. Percentages refer to the proportion of days on which each pod was present during the total 128 days that whales were observed in the area ($N = 386$ pod encounters).

major levels: (i) as 'geographic variation' between isolated populations, and (ii) as 'dialects' among neighbouring groups that can potentially mix and interbreed (Krebs and Kroodsma 1980; Conner 1980; Mundinger 1982). Geographic variation is generally considered to result from acoustic adaptations to differing environmental conditions at each site, or to reflect functionless cultural or genetic divergence caused by isolation. On the other hand, the functional significance of dialects that develop among local populations is the subject of controversy. Some maintain that dialects are epiphenomena of song learning and

social adaptation, whereas others believe that they play a role in assortative mating and are of evolutionary significance (see reviews by Krebs and Kroodsma 1980; Payne 1981; Baker 1982; Mundinger 1982; Slater et al. 1984; Baker and Cunningham 1985; Baptista 1985).

Virtually all previously reported cases of regional intraspecific variation in the acoustic signals of mammals involve isolated populations, i.e., populations separated by geographic barriers (Green 1975; Conner 1980; Ford and Fisher 1983; Thomas and Stirling 1983; Masataka 1988). These represent geographic

TABLE 6. Social associations of northern resident community pods, based on the number of occasions on which pods were observed together during 1973-1983

Pod	A1	A4	A5	B	C	D	G	H	II	III	I31	R	W
A1	28 (0.169)												
A4	79 (0.678)	6 (0.059)											
A5	102 (0.734)	76 (0.647)	39 (0.218)										
B	28 (0.303)	17 (0.239)	30 (0.321)	33 (0.413)									
C	23 (0.267)	17 (0.264)	20 (0.230)	6 (0.148)	3 (0.081)								
D	11 (0.131)	11 (0.176)	24 (0.283)	6 (0.156)	11 (0.343)	2 (0.063)							
G	15 (0.182)	10 (0.164)	14 (0.168)	10 (0.270)	4 (0.131)	3 (0.105)	19 (0.413)						
H	16 (0.190)	9 (0.144)	15 (0.176)	9 (0.234)	6 (0.188)	4 (0.133)	5 (0.175)	1 (0.032)					
II	5 (0.67)	4 (0.075)	4 (0.053)	3 (0.102)	1 (0.043)	2 (0.095)	1 (0.051)	7 (0.333)	10 (0.454)				
III	13 (0.153)	8 (0.126)	14 (0.163)	8 (0.203)	6 (0.182)	2 (0.065)	14 (0.475)	6 (0.194)	3 (0.136)	3 (0.086)			
I31	9 (0.115)	8 (0.140)	12 (0.151)	3 (0.091)	3 (0.113)	1 (0.041)	6 (0.261)	6 (0.245)	4 (0.258)	16 (0.627)	1 (0.050)		
R	3 (0.42)	3 (0.061)	3 (0.042)	1 (0.039)	2 (0.105)	0 (—)	3 (0.194)	3 (0.176)	1 (0.125)	2 (0.111)	2 (0.174)	4 (0.500)	
W	9 (0.118)	8 (0.145)	6 (0.077)	2 (0.065)	6 (0.245)	0 (—)	7 (0.333)	3 (0.133)	2 (0.148)	12 (0.511)	7 (0.412)	2 (0.210)	1 (0.063)
Total	166	101	179	80	37	32	46	31	22	35	20	8	16

NOTE: Values along descending diagonal (e.g., A1 with A1) are the number of occasions on which each pod was seen alone. Numbers in parentheses below these values show the proportion of total encounters in which the pod was alone. All other values are the number of encounters during which different pods were observed in association, and numbers in parentheses show the index of association (see text) ($N = 773$ pod encounters).

TABLE 7. Social associations of southern resident community pods

Pod	Pod		
	J	K	L
J	105 (0.761)		
K	30 (0.353)	8 (0.133)	
L	28 (0.337)	47 (0.461)	30 (0.375)
Total	138	60	80

NOTE: See Table 6 for explanation of the derivation of these values ($N = 278$ pod encounters).

variations, in accordance with the accepted definitions given above, but have occasionally been inappropriately referred to as 'dialects' (Conner 1980; Payne and Guinee 1983). Earlier reports of local dialects within a population of northern elephant seals (*Mirounga angustirostris*) (Le Boeuf and Peterson 1969) involved short-lived phenomena resulting from population expansion and colonization of new rookeries (Le Boeuf and Petrinovich 1974). These variants have since disappeared (Shiple et al. 1981). An unusual case of locale-specific variation has been reported in calls that developed and spread within three isolated troops of Japanese monkeys (*Macaca fuscata*) as a direct result of artificial feeding (Green 1975). Dialects apparently do not occur naturally in this species, nor have they been found in the vocalizations of most other nonhuman primates (Snowdon 1985). Indeed, the calls of primates are typically so consistent over wide geographic areas that they are often used as taxonomic markers (e.g., Newman and Symmes 1982; Oates and Trocco 1983).

Other than killer whales, the only nonhuman mammal which appears to have local dialects that seem not to involve genetic differences is the red-chested moustached tamarin (*Saguinus labiatus labiatus*). The long calls given by this species have been found to vary in acoustic structure between contiguous populations in Bolivia (Maeda and Masataka 1987). It is speculated that these variations may function in assortative mating, whereby females choose mates that have the same natal dialect (Masataka 1988).

Patterns of vocal variation described here for killer whales appear to be unique in that they are associated with social groups that are not tied to any particular locale. In birds, different dialect populations are nearly always restricted to specific geographic localities (Krebs and Kroodsma 1980; Mundinger 1982). Flock-specific vocal variation occurs in a few bird species (e.g., Feeke 1982; Nowicki 1983), but such groups are territorial. In red-chested moustached tamarins, different vocal populations may abut one another, but there is no evidence of interaction between them (Masataka 1988). Within resident communities of killer whales, pods having entirely independent repertoires of calls not only occupy the same range, but routinely intermix. The closest parallel to this situation can be seen in urban human communities that are stratified both socially and linguistically (Trudgill 1983).

Acquisition of call repertoires

Interpretation of the origin, maintenance, and possible

adaptive significance of dialects in killer whales requires consideration of the manner by which individuals acquire their calls. Vocal development in most mammals appears to be primarily under genetic control (Nottebohm 1972, 1975; Ehret 1980; Newman and Symmes 1982; Ralls et al. 1985; Snowdon 1985; Masataka and Fujita 1989). In cetaceans, however, the ability to mimic and learn new vocal patterns has been well documented. The complex, ever-changing songs of humpback whales (*Megaptera novaeangliae*) appear to be acquired by learning (Payne and Payne 1985), and captive delphinids are well-known vocal mimics (Caldwell and Caldwell 1972; Herman 1980; Richards et al. 1984; Tyack 1986). Whether learning plays an important role in the normal development of vocal behaviour in delphinids has yet to be determined, although this is generally assumed to be the case (e.g., Caldwell and Caldwell 1979).

There is good evidence that killer whales share the capacity for vocal learning with other delphinids. Van Heel et al. (1982) were able to train a captive killer whale to reproduce artificial tones. Individuals held in captivity with whales from different pods occasionally imitate the alien calls of their pool mates and incorporate them into their own repertoire (Bain 1989; J. K. B. Ford, unpublished data). Bowles et al. (1988) studied the vocal ontogeny of a captive-born killer whale calf and found that it learned and reproduced only the calls of its mother, and apparently ignored the different repertoires of calls used by other conspecific individuals held in the same pool. The calf was never exposed to the call repertoire of its father, which differed from that of its mother. In the present study, killer whales were on rare occasions observed to imitate call types belonging to different pods, even those from other clans. Examples of such mimicry are shown in Fig. 21.

It thus seems most reasonable to assume that a killer whale's repertoire of discrete calls is acquired through imitation and learning, and thus is passed from generation to generation by cultural, rather than genetic, transmission (see also Bain 1989). It is noteworthy that development of local dialects in birds is dependent on song imitation and learning (see reviews by Nottebohm 1972; Krebs and Kroodsma 1980; Mundinger 1982).

Origins of dialects within clans

It is unlikely that group-specific dialects would exist among resident pods were it not for the unusual social organization of the population. As mentioned previously, the social system of residents is based strongly upon maternal kinship. Resident pods comprise one or more matrilineal groups, each consisting of one to four generations of animals related by unilineal descent. No individual has been observed to disperse from its natal group since monitoring of the population began in 1973 (Bigg et al. 1990). Formation of new pods appears to result from the gradual splitting of older, larger pods. Over a period of several years, subpods of the original pod would spend increasing amounts of time separated, each group eventually travelling apart for most of the time. At this point, each subpod would be considered an independent pod. This process of group fission appears to be currently underway among certain northern-community pods (Bigg et al. 1990).

I propose that the process of group splitting leading to the formation of new pods is accompanied by divergence of the vocal repertoire of the original pod. Newly formed pods would have essentially the same repertoire of calls as their ancestral pod. With time, however, call structure and pattern of usage would evolve independently in each new pod, leading to pod-specific dialectal variations. As these pods grew and divided,

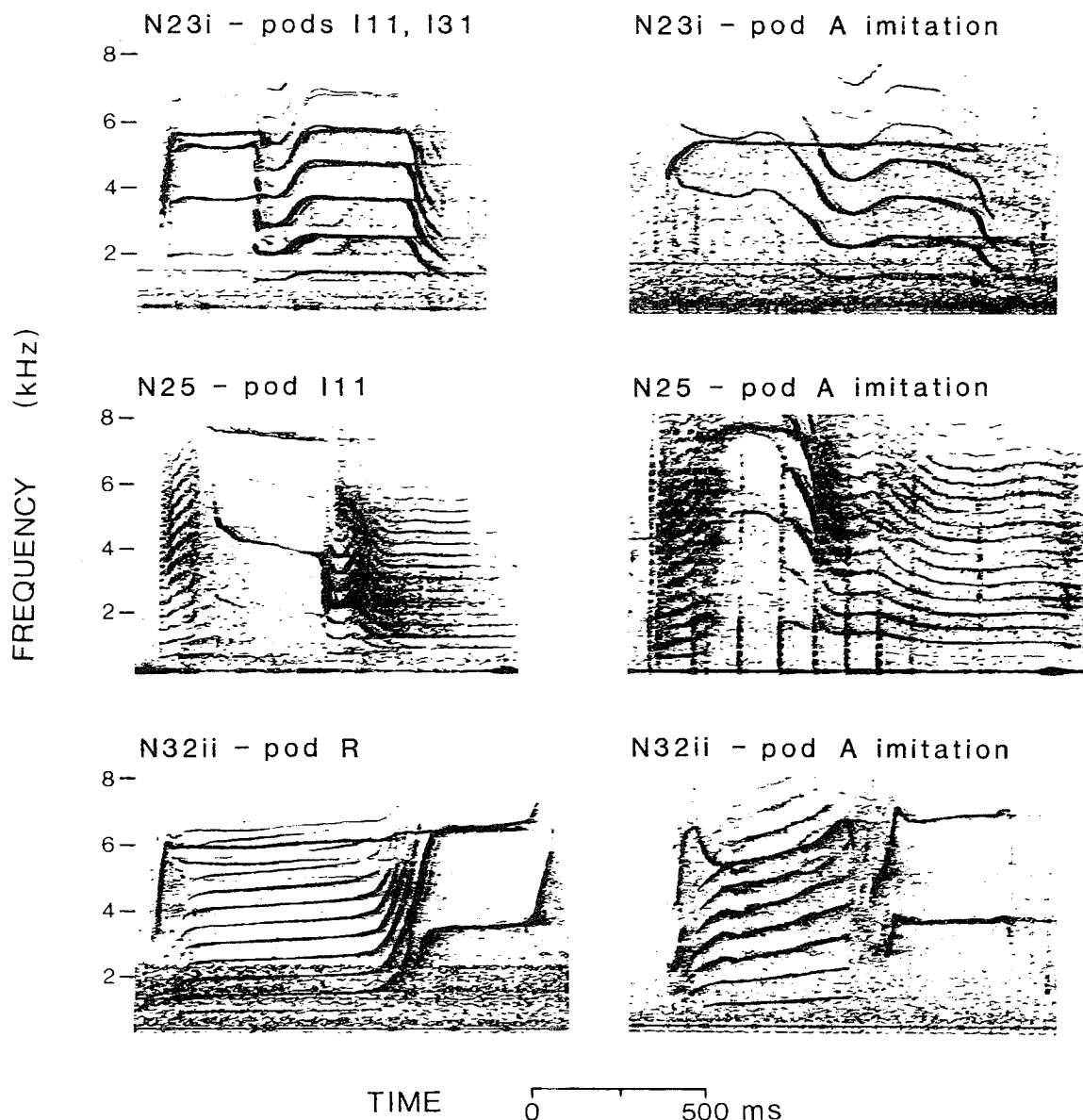


FIG. 21. Spectrograms of northern resident call types N32i, N25, and N23ii, and imitations of these calls by clan A pods A1, A4, and A5. Calls N23i and N25 were from the repertoires of clan G pods, and N32ii was from the clan R repertoire. None of these pods was in the area when the A pods emitted these imitations. Such mimicry was recorded only during socializing episodes (see Ford 1989).

further divergence of the original call tradition would occur. The lack of dispersal of individuals from the natal group would serve to confine the vocal tradition to descendant pods in the lineage.

This process would result in such situations as those seen within the four resident clans. All pods within a clan share calls, indicating that they have likely descended from a common ancestral group. Pods with very similar call repertoires can be assumed to have split more recently, and to be more closely related, than pods having fewer calls in common. Pod-specific dialects in the vocal tradition of the clan can thus be viewed as behavioural reflections of the common heritage of the clan's pods and the manner in which the lineage has diverged over time.

The vocal tradition of a killer whale clan appears to represent a 'cultural institution,' defined by Mundinger (1980) as a "single lineage of ancestral descendant populations of models (= acquired behavioural traits) that maintains its identity from other

such lineages and which has its own evolutionary tendencies and historical fate." Cultural institutions retain their distinctiveness despite significant periods of contact with other such institutions, and are generally maintained by geographic, psychological, or socially isolating mechanisms. As examples of cultural institutions, Mundinger (1980) cites specific human languages, each with sets of related speech dialects, and systems of related song dialects in the house finch (*Carpodacus mexicanus*).

Origin of clans

Since different clans have no call types in common, it is probable that they have no recent common ancestry. If clans were descended from a single matrilineal group, one would expect that some pods would have intermediate dialects with features of more than one vocal tradition. It may be that the four resident clans split from a common matriline so long ago that shared calls have been lost or are no longer recognizable as

homologues. An alternative explanation is that the vocal traditions of each of the four resident clans developed independently in geographic isolation. Their occurrence on the coast of British Columbia might then be the result of a series of unrelated founding events. The founding pod of each local clan may have dispersed from a distant core area and become established on the British Columbia coast. It is also possible that founding pods may have shifted from a nomadic life-style, such as that seen in transient pods (Bigg 1982; Bigg et al. 1987), to one of seasonal philopatry. Historical founder effects are important in the origin and spread of human languages and dialects (Friedlaender et al. 1971; Spielman et al. 1974; Trudgill 1983) and in the song traditions of birds (Payne 1981; Mundinger 1982; Baker and Thompson 1985; Baker and Jenkins 1987). For example, Mundinger (1975, 1980) has proposed that many song institutions among house finches on the American east coast evolved in isolation as a form of 'allopatric cultural speciation,' and subsequently diverged into complex systems of related dialects.

Of the four resident clans of killer whales in British Columbia, only clan J appears to occupy an exclusive range. Its vocal tradition may thus be maintained through geographic isolation from other clans. On the other hand, clans A, G, and R of the northern resident community overlap in range and interact socially, yet each maintains a unique vocal tradition. Behavioural isolating mechanisms are probably important in preserving the integrity of these sympatric traditions. Assuming that pods in a clan are descended from a common founding group, dialects within the clan's vocal tradition most likely developed locally as the lineage evolved.

Mechanisms of dialect development

Several mechanisms of vocal change leading to dialect formation have been identified in birds and humans (Lemon 1975; Slater and Ince 1979; Slater et al. 1980; Krebs and Kroodsma 1980; Mundinger 1980, 1982; Payne 1981; Trudgill 1983). Those that may have had a role in the formation of killer whale dialects include cultural drift, innovation, and cultural diffusion.

Cultural drift results from the appearance of errors in vocal copying and the transmission of these changes across generations. These errors are typically neutral with respect to adaptation, and are simply incidental by-products of the process of vocal learning. As mentioned above, dialects in many bird species are considered to be epiphenomena of vocal learning and social insularity. In killer whales, errors in call transfer across generations might accumulate as pods grow and split, resulting in the complex group-specific modifications in the structure of calls shared within clans.

It is quite likely that young killer whales learn their repertoire of calls selectively from their mother, as is suggested from captive studies (Bowles et al. 1988), as well as from other members of their natal matrilineal group. For the first few years of life, offspring travel in close proximity to their mothers, grandmothers, and siblings, and associate less frequently with other members of the pod (Heimlich-Boran 1986; Bain 1989; Bigg et al. 1990). There is thus the potential for minor variations in a pod's dialect to become established among matrilineal groups and subpods early in the process of new pod formation.

Cultural drift resulting from errors in vocal copying would only involve established call types in a vocal tradition. The creation of new calls in a pod's repertoire seemingly requires innovation and subsequent imitation of novel sounds. It is likely that both drift and innovation have been involved in the develop-

ment of dialects in killer whales. Of the 69 call types identified in the resident population, 46 (66.6%) were shared by two or more pods. Of these, 13 (28.3%) were differentiated into discrete subtypes, and most of the remaining shared calls showed significant pod-specific variation in structure (Ford 1987). Many of these variants may well have arisen by some process of cultural drift. However, 23 of the call types identified (33.3%) were produced only by a single pod. Such calls probably represent vocal innovations by the pod using them, or the calls could have been lost from the repertoires of other pods in the clan.

If cultural drift has resulted in pod-specific variation in the structure of shared calls, it appears not to have acted randomly throughout vocal traditions. In each tradition, some calls show little variation, whereas others differ markedly from pod to pod. One might predict that more structurally complex calls would show greater variation because they would be more susceptible to copying errors during learning. This, however, does not seem to be the case. For example, call N3 was produced in basically the same manner by all eight pods of clan A, yet call N8, a sound with a comparably simple structure, showed considerable variation. It may be significant that N3 was a call given primarily in low-activity behavioural states by all pods in the clan. The resting calls of other clans also tended to show little variation compared with calls used primarily in active contexts.

There are other indications that some call variants are not a result of chance copying errors. As an example, pod A5's version of 5 of the 11 calls shared by the three A pods had strongly emphasized terminal components, in both duration and frequency shift. In pods A1 and A4, however, these calls all had weakly developed or nonexistent terminal parts. Another example can be seen in the convergence of structure in the versions of calls N1 and N8 emitted by pod H (Fig. 22). These two calls showed no structural similarity in other clan A repertoires, yet in pod H they appear to have acquired the same very distinctive sound quality. This evidence suggests that the development of dialects within vocal traditions may have been influenced by unique behavioural trends within each pod. Thus, a portion of the vocal divergence in the three closely related A pods, for example, may have been directed by a generalized predisposition towards strong call endings in pod A5 (or an ancestral group), or towards reduced call endings in pods A1 and A4.

Cultural diffusion can be an important source of vocal variation in birds and humans. New sounds are introduced into a vocal tradition by immigrants, and these sounds spread into the recipient population's repertoire (Mundinger 1980; Slater et al. 1980; Payne 1981). Diffusion may also result from temporary contact with different vocal traditions, especially in human populations (Spielman et al. 1974; Trudgill 1983). There is, however, no indication that diffusion is involved in the formation of call dialects in killer whales. As individuals do not disperse from their natal matrilineal group, this potential source of diffusion is eliminated. If transfer of whales between pods did occur, such individuals would presumably introduce their original pod's repertoire into the group they join, which would then have a blend of dialects. The outcome of this would be the loss of the acoustic integrity of the pod or clan. There is a possibility, however, that a transferring animal might switch its call repertoire to that of its new group.

Call innovation and the structural differentiation of shared calls seem to have taken place without the use of any vocal patterns from other traditions to which a pod is exposed. As

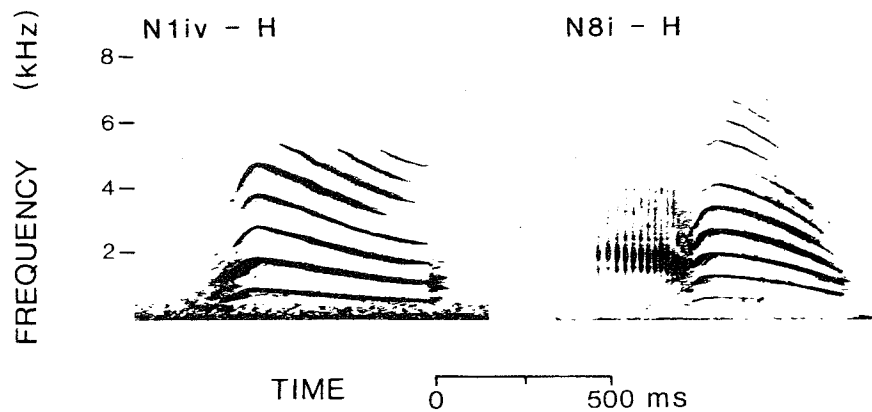


FIG. 22. Examples of call types N1 and N8 as produced by pod H of clan A. These two call types appear to have become structurally modified in a similar manner in this pod's repertoire.

mentioned above, rare cases of mimicry of calls from other clans indicate that the whales are aware of and can reproduce calls of neighbouring groups. However, no call transfer has taken place among the four vocal traditions in the resident population. Thus, it would seem that there is strong conservatism in the process of vocal divergence which prevents diffusion from unrelated dialects and serves to preserve the distinctiveness of each tradition.

Finally, vocal divergence within clans appears also to have involved changes in the frequency of use of call types. Each pod has a typical frequency distribution of calls which varies only slightly with most behavioural circumstances (Ford 1989). This distribution may change differentially among descendant pods, certain calls being favoured and others falling into disuse. This process may lead to the extinction of calls from pod-specific repertoires. A possible example is pod J's use of call S14. This signal seemed to be very common in the early 1960s, typically comprising almost 10% of call production (Ford 1984). During 1979–1983, however, the call was heard only twice in over 6000 calls recorded and identified from pod J. Similarly, call N49 comprised 8.1% of the signals recorded from a clan R pod in 1964, but did not occur in clan R samples from 1973 or 1981–1983. There are numerous cases of calls apparently being lost from the repertoires of certain pods in a clan but not from others. Pod A5, for example, is the only one of the eight clan A pods that does not have some version of call N1. Similarly, call N5 seems to have been dropped by pods C and D, whereas it remains a common component in the repertoires of the rest of the clan.

Rates of vocal differentiation

Assigning a time scale to the process of pod evolution and dialect development within clans is difficult. Examination of historical recordings revealed few differences in the repertoires of resident pods between as early as 1958 and 1986. Without an accurate measure of the rate of vocal change, it is not possible to apply quantitative techniques in estimating the time required for linguistic divergence (e.g., Spielman et al. 1974; Payne et al. 1981).

The rate of dialect formation in other species may provide some basis for estimating the timing of vocal divergence in killer whales. However, this information must be interpreted with caution because of the diversity of social structure, function of acoustic signals, and adaptive significance of the dialects. During long-term studies of song dialects in several bird species, the

persistence of local song types across many generations has been documented. Dialects of white-crowned sparrows (*Zonotrichia leucophrys*) at one location were found by Trainer (1983) to have retained the same basic structure over 18 years. Mundinger (1975, 1980) has been able to trace the development of song institutions and dialects in a population of house finches back from 1974–1975 to periods of population expansion and colonization in the early 1960s. This period represents about 10–15 generations. Basic features in the song traditions of chaffinches (*Fringilla coelebs*) in the Chatham Islands have been retained since colonization in about 1900, which represents some 35 generations (Baker and Jenkins 1987). Baker and Thompson (1985) postulate that dialect differences between adjacent populations of white-crowned sparrows in coastal California have persisted for as many as 80 generations, or about 100–200 years. Words in human languages tend to persist, the half-life averaging 30–40 generations (Payne et al. 1981).

The approximate rate of dialect differentiation in resident pods of killer whales can be estimated using data on reproductive dynamics and recent age and sex structure of selected groups. For example, pods A1, A4, and A5 are clearly related in both dialect and social association patterns. Assuming that these three pods have descended from a common matrilineal group, their founding matriarch was likely born no later than 1840 (M. A. Bigg, personal communication). This period represents about six generations at 24.8 years/generation (Olesiuk et al. 1990). During this time, the three descendant pods have retained 10 calls in common, 1 of which has diverged into pod-specific subtypes. Pod A5 appears to have lost one shared call (N1), whereas pod A1 has perhaps lost another (N13). In addition, pods A4 and A5 have each incorporated a single unique call into their repertoires, and pod A1 has developed two such calls.

It may be more appropriate to measure rates of dialect formation in terms of a *cultural generation*, which would be the period over which individuals may have an influence on the vocal development of others in the group. This period would be equivalent to the mean life expectancy of females, which is about 50 years (Olesiuk et al. 1990). If call structure and usage change only slightly between cultural generations, group-specific dialects may persist in similar form for several centuries.

The adaptive significance of dialects

Are vocal dialects simply functionless by-products of vocal learning and the closed social system of resident killer whales, or do they have some selective value? To address this question,

one must consider the role played by repertoires of discrete calls in the communication system of pods. This was examined by Ford (1989), and can be summarized as follows. Discrete calls appear to be used to maintain contact among pod members, especially when the pod is dispersed, such as during episodes of foraging. Most calls in the pod's repertoire are produced in every behavioural circumstance in which the pod is alert and active. Context-dependent and individualized variations on the standard format of each call likely convey information about the identity and behaviour state of the vocalizing animal, as do changes in the frequency of use of different calls.

It seems reasonable to assume that the efficiency of intrapod communication would be enhanced by the use of pod-specific signals. Individuals may be better able to recognize fellow pod members at a distance, which would be of value in coordinating group behaviours and maintaining pod cohesion and integrity. Repertoires of pod-specific calls may improve the reliability of intrapod signalling by providing greater contrast to external sounds than would be possible with a single call (Andrew 1962).

There is probably considerable selective pressure on an individual to copy the traditional call repertoire of its pod. Using the group's calls might provide the animal with an acoustic 'badge' of pod affiliation, which could be important for its acceptance by the group and continued access to the benefits of group living. Being long-term social units comprising several overlapping generations, killer whale pods are likely to have strong cultural traditions which have developed over many years. The overall range of the pod, the timing of its movements to coincide with the distribution of its migratory prey, cooperative foraging strategies, and social activities may all be dictated by tradition. Beach rubbing, for example, is an important traditional activity conducted regularly at a specific site on Vancouver Island by certain northern resident pods (Ford 1989). These pods have rubbed at this site almost daily during the summer months since at least 1973 (I. B. MacAskie, personal communication), yet southern resident pods have no such tradition.

Given the probable pressure for acoustic conformity among pod members and the lack of dispersal from the group, it is perhaps not surprising that pod repertoires have such long-term stability. It is these factors which suggest that natural selection has not actively promoted the development of dialects among related pods, but rather has favoured the homogeneity of signals used by pod members. If vocal divergence of pods was encouraged by selection, one would expect more rapid evolution of dialects, especially among pods that associate frequently. Dialects are more likely to have arisen as incidental by-products of the evolution of a reliable and efficient system of intrapod communication.

Although selection may not act directly to maximize vocal differentiation among pods, this does not preclude the possibility that dialects have some functional significance. Different pods frequently travel and forage in association, and calls often appear to be exchanged between groups at such times. It would seem most probable that individuals can recognize other pods from their vocalizations, and this may in turn affect social interactions within the clan or community. Dialects appear to encode information on pod genealogy, and whales may be able to use this to discriminate between relatives and nonrelatives. This ability may serve in determining patterns of association or perhaps in mate selection. It is highly probable that breeding occurs between pods, but whether it is endogamous within the clan or community is unknown. Song dialects in some species of birds have been proposed to function ultimately as a mechanism for avoiding inbreeding (Treisman 1978; Grant 1984).

Dialects, vocal traditions, and population structure

Vocal variation among resident killer whale pods provides a useful means of gaining insight into historical patterns of population growth and differentiation on the British Columbia coast. Similar applications are often made of bird song dialects, which have been used to reconstruct processes of colonization and expansion of populations in a variety of species (e.g., Baptista 1975; Mundinger 1975, 1980; Jenkins 1978; Payne et al. 1981; Baker and Thompson 1985). Linguists studying the origin and spread of human languages frequently use geographical distribution of word usage to infer historical migration routes and occupancy patterns (e.g., Spielman et al. 1974; Trudgill 1983).

It is assumed in this discussion that killer whale pods with similar dialects are more closely related than those with different dialects. The simplest explanation of dialects within vocal traditions, and the one that is most compatible with the social system of resident whales, is that pods belonging to the same clan are related by matrilineal descent from a single ancestral pod, and that cultural evolution of the original pod's call repertoire has taken place concurrently with growth of the lineage. Dendrograms showing the acoustic relationships of pods (Fig. 2) may therefore also indicate their genealogical relationships within the clan.

If the pod genealogies indicated in Fig. 2 are correct, the degree of relatedness of pods is not consistently reflected in their patterns of travel association. Comparisons of the data in Tables 6 and 7 with the genealogies of resident pods shown in Fig. 2 revealed that pods which showed strong associations were frequently not the most closely related acoustically. Several northern resident pods were more often observed travelling with members of a different clan than with pods of their own clan. A similar analysis by Bigg et al. (1990), using additional association data, yielded somewhat different patterns of pod travel preference but the same conclusion: variations in dialects and vocal traditions provide a very different picture of pod relationships than do observed associations.

It is probable that pod ancestry is more accurately represented by dialect similarities than by association patterns, as was also concluded by Bigg et al. (1990). Pod associations vary within and among years, and are likely to be influenced by a range of social and ecological factors. Dialects, which are stable over many years, seem to be the more conservative and reliable measure of pod genealogy within the clan. The relationships between clans are obscure, as each is acoustically independent.

Acoustic relationships among resident pods of killer whales may also provide an outline of the genetic structure of the population. If clans are independent lineages, it is probable that each is genetically distinct to some extent. This may also be true of pods within the clan. Social groups in some species of primates form by matrilineal division and, under certain demographic conditions, significant variations in gene frequencies may exist among descendant groups (Cheney and Seyfarth 1983; Melnick and Kidd 1983; Olivier et al. 1981). Similar genetic divergence, or 'lineal effects,' have been observed among villages of American Indian tribes that form by matrilineal division (Neel and Ward 1970), and in the case of the Yanomama Indians of South America, such genetic differentiation correlates with linguistic divergence among villages (Spielman et al. 1974). Genetic studies are needed to determine whether acoustic divergence is accompanied by genetic differentiation in killer whales.

Are group-specific dialects typical of the species?

Studies of the acoustic behaviour of other killer whale

populations indicate that group-specific dialects are not unique to the resident pods in British Columbia. Transient killer whales, which are sympatric with, but socially isolated from, resident killer whales in British Columbia (Bigg et al. 1990), produce discrete calls unlike those of resident pods. Call repertoires of transient pods, although reduced in size, also exhibit pod-specific dialectal variations (Ford 1984). Killer whales in Prince William Sound, Alaska, form long-term pods with matrilineal structure (Leatherwood et al. 1984; von Ziegler et al. 1986; G. Ellis, personal communication), and these also appear to have pod-specific repertoires (Englund 1985). Similarly, photo-identification studies in Norway and Iceland have documented pods with stable membership (Lien et al. 1988; Lyrholm 1988; Sigurjónsson et al. 1988). Preliminary acoustic studies of these populations also suggest the existence of pod-specific dialects (Moore et al. 1988). It seems probable that local acoustic traditions with pod-specific dialects are characteristic of killer whale populations throughout the world.

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