Analysis of calls of killer whales, *Orcinus orca,* from Iceland and Norway

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ABSTRACT

Underwater recordings of killer whale calls were made off Norway and Iceland from 1983 through 1986 in association with efforts to photograph dorsal fins and saddles for identification of individual whales. Researchers collected eight hours of recordings near at least two pods off Norway and eight hours of recordings near at least five pods off Iceland. A preliminary description of discrete call types for whales from each area was completed using methods developed on well known pods of killer whales off British Columbia and Washington. Twenty-four discrete calls were described for whales off Iceland; 23 discrete call types were identified for whales off Norway. There was little evidence of calls shared between Icelandic and Norwegian pods.

INTRODUCTION

Effective management of cetaceans requires specific information about abundance, movements and reproductive isolation of subpopulations ("stocks") of the species. Some relatively new techniques applied to the management of killer whales *(Orcinus orca)* involve analysis of geographic variation in colouration and vocalizations, identifying stereotypic, pod-specific calls and photoidentifying individuals. Killer whales of the world have been provisionally divided into five distinct stocks based on geographic variation in colour patterns (Evans *et al.* 1982). Two distinct races of killer whales in the Antarctic have been recognized, based on differences in osteology and size (Berzin and Vladimirov 1983). Variations in colour patterns have been related directly to genetic differences in some other cetaceans, such as *Stenella* spp. (Perrin *et al.* 1987). In addition, differences in the calls recorded from killer whales in the Northern and Southern Hemispheres have been recognized (Jehl *et al.* 1980; Awbrey *et al.* 1982), although this topic has been little explored. The pulsed calls recorded from Antarctic killer whales were similar in gross structure to those recorded from killer whales in the Northern Hemisphere, but were of a higher frequency (Awbrey *et al.* 1982). Also, subunits of some Antarctic calls ("components") were produced in a fixed order that differed from that of calls in the Pacific Northwest (Awbrey, pers. comm.).

Comprehensive photoidentification studies of wild populations of killer whales have been conducted off British Columbia and Washington since 1973 and 1976, respectively (Bigg 1982; Balcomb *et al.* 1982). These studies have relied on high-resolution photographs of dorsal fins and post-dorsal-fin "saddles" to identify individual whales. Nearly all killer whales in the British Columbia study area are thought to have been identified in this manner, so the social structure and natural history of this population is relatively well known. A five-year bioacoustic study carried out in association with the photoidentification efforts culminated in the description of pod-specific dialects for these British Columbia whales (Ford 1984; Ford and Fisher 1982, 1983). Although each pod produced a repertoire of 7 to 17 readily identifiable calls, some pods shared some call types. Call sub-categories (hereafter called subtypes) were produced by particular pods, and were identified as such because they were themselves relatively invariant and were similar in the organization of components and tonal quality to calls given by other pods. Pods that shared some calls composed a "clan" (Ford 1984). Sixteen resident pods off the coast of British Columbia were separated into four such clans, each with a unique set of discrete calls. It is not yet clear whether there is genetic flow among these clans (Ford 1984). Local variants of call traditions (hereafter called "dialects") may be a genetic isolating mechanism in other species, notably birds (Baker 1982).

Similar photoidentification studies were begun off Argentina in 1975 (Lopez and Lopez 1985) and off south Alaska in 1976 (Leatherwood *et al.* 1984, 1986; Ellis *et al.* in press). These studies are not yet as comprehensive as those conducted in the Pacific Northwest, however, so that social structure and call repertoires for the population are poorly known.

In 1981 the Scientific Committee of the International Whaling Commission (IWC) convened a workshop on the identity and natural history of killer whale populations worldwide. The workshop recommended that the studies conducted in the Pacific Northwest be replicated in other areas, specifically off Iceland and Norway (Perrin 1982). Killer whales are common off eastern Iceland and western Norway, particularly during periods in late summer and fall when herring *(Clupea harengus)* spawn (Christensen 1982, 1988 – this volume; Sigurjónsson 1984; Sigurjónsson *et al.* 1988 – this volume). Photographs and acoustic recordings were taken in coastal waters of Norway during the fall of 1983 and 1984 (Lyrholm 1985, 1988 – this volume; Lien *et al.* 1988 – this volume) and off the east coast of Iceland in the fall of 1985 and 1986 (Lyrholm *et al.* 1986; Sigurjónsson *et al.* 1988 – this volume). The acoustic recordings were made available to us for analysis. Calls were differentiated into categories, called discrete calls, by examining sonograms and listening. The method is described in detail by Ford (1984, 1987) and is frequently used in studies of bird vocalizations (Becker 1982). The process is similar in practice to that used in photoidentification, and has similar benefits and pitfalls, i.e. the scoring is somewhat subjective, so there is a small percentage of inter-observer variability in the identifications. In fact, however, the human eye and ear are better able to perform this complex pattern-matching task than are other standard means of acoustic analysis.

The analysis of North Atlantic killer whale calls began in early 1987. The classification presented herein is preliminary. Nevertheless, it includes a catalogue that can be expanded and modified as additional recorings from these areas are analyzed.

MATERIALS AND METHODS

Study area and recording procedures

Underwater recordings were made near killer whales off eastern Iceland and northwestern Norway by field observers engaged in photoidentification studies (Lyrholm *et al.* 1987; Sigurjónsson *et al.* 1988 – this volume; Lyrholm 1985, 1988 – this volume; Lien *et al.* 1988 – this volume). All recordings from Norway were made near Lofoten; those from eastern Iceland were made at eight locations (Fig. 1; Table 1). Recordings were made from small inflatable skiffs launched from a herring seiner or research vessels, or, less frequently from small motorized boats launched from shore. Field workers conducting the photoidentification studies obtained the recordings. Wherever possible, tape recordings were labelled to indicate the pod(s) present, with

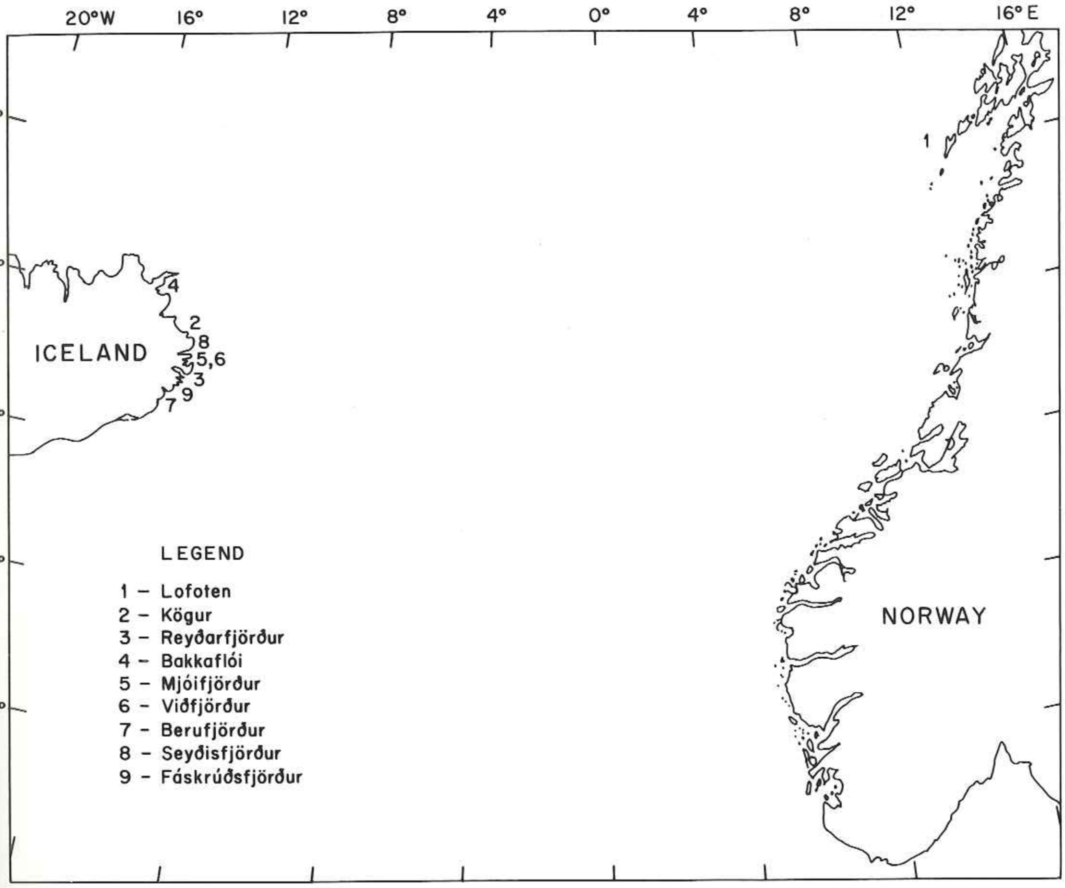


Fig. 1. Locations off Iceland and Norway where recordings of killer whale calls were made.

"I" indicating an Icelandic group and "N" a Norwegian group. Recording systems differed slightly among years, but always consisted of a good-quality cassette recorder and hydrophone. The frequency responses ranged from 50Hz to 15kHz ± 3dB at 4.75 cm/s (Tables 1 and 2).

Call classification and analysis

Calls were classified following the methods of Ford (1984, 1987). Discrete calls were composed of trains of pulses and contained one distinct component or more. A call component was defined by an abrupt shift in the interval between frequency bands in the sonograms, called a side-band interval or SBI (Ford 1984). The shifts in SBI were usually accompanied by a distinct change in tonal quality. According to Watkins (1967), the interval between the sidebands is equal to the pulse repetition frequency. We attribute differences in tonal quality of the call components to differences in pulse waveform and to changes in the pulse repetition frequency.

Discrete calls identified twice or more were assigned a catalog number and described by measuring the duration and the sideband interval for each of it components. When the SBI of a call was relatively constant, only the center SBI was measured. Categories of subtypes were created when a call contained variant components but retained the identifiable aural qualities and basic component structure of that call type. As we usually could not as-

TABLE 1

Summary of recordings off Iceland (See also Fig. 1, Lyrholm et al. 1987 and Sigurjónsson et al. *1988 – this volume).*

	Date	*Tape no.*	*No. whales*	*Pods present*	*Location*	*Equipment*
1985	13 October	1505	12–30	IA, IB, Misc.	1. Kögur	Marantz PMD 360 recorder
	23 October	1504	20–25	IB, Misc.	2. Reyðarfjörður	custom preamp/hydrophone
						50 Hz to 15 kHz at 4.75 cm/s
1986	20 October	1514	60–80	IA, IB, IE	3. Bakkaflói	Sony WM-D6C recorder
	29 October	1515	15–18	IB	4. Mjóifjörður	InterOcean T-902 hydrophone
	30 October	1516	15–20	IB	5. Mjóifjörður	50 Hz to 15 kHz at 4.75 cm/s
	31 October	1517	16–20	IA, IB	6. Viðfjörður	
	7 November	1518	6	IF	7. Berufjörður	
	13 November	1519	9	IB	8. Seyðisfjörður	
	16 November	1520	15–19	IE	9. Fáskrúðsfjörður	

TABLE 2

Summary of recordings off Lofoten Norway (See location 1 in Fig. 1 and Lyrholm 1985, 1988 – this volume).

	Date	*Tape no.*	*No. whales*	*Pods present*	*Equipment*
1983	18 September	1521	?	NB, NC pods	Marantz PMD 360 recorder
	18 September	1523	20+	NB, NC pods	custom preamp/hydrophone
					50 Hz to 15 kHz at 4.75 cm/s
1984	30 November	1525	?	?	Uher 4400 IC Report Stereo
	1 December	1525	?	?	Gould CK-17U hydrophone
	2 December	1525	?	?	25 Hz to 20 kHz at 19 cm/s
	2 December	1526	?		
	3 December	1526	?		
1986	18 September	1522	?	NB pod	Same as 1983 system
	24 September	1524	?	?	Unknown; Tape from M. Schultz
	2 October	1524	?		
	23 October	1524		NC pod, NB pod	

sociate these subtypes with particular pods, the categories must be considered tentative.

All calls were analyzed in real time on a UNISCAN II digital sonograph (Multigon Industries) set at 10 kHz. The frequency resolution at this setting was ± 80 Hz, the time resolution ± 6 milliseconds (ms). The beginning and ending of components were identified by eye. Therefore, the time resolution probably varied by a few milliseconds, depending on the quality of the recording. The sideband interval was measured relative to the peak frequency. Some discrete calls contained overlapping, high-frequency components that had either no sidebands or, more likely, sidebands

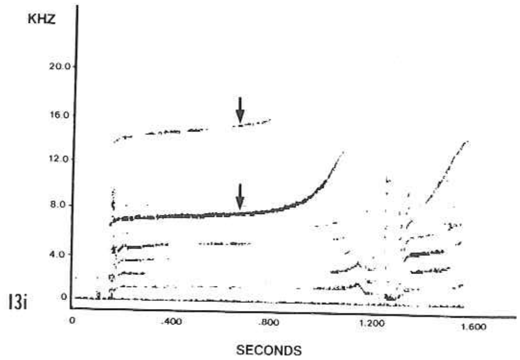


Fig. 2. An example of a discrete call containing a high-frequency, harmonically-unrelated component. Two side-band components are marked with arrows.

which were outside the flat range of the recording system (Fig. 2). The peak frequency for the beginning, ending or mid-point of these components was measured. Three or more calls of each type (or subtype) were measured for descriptive purposes.

Ford (1984) used single-link cluster analysis applied to measurements of call duration and SBI to estimate relatedness between calls. As yet this analysis on the Norwegian or Icelandic samples has not been completed. Here we present a general description of the relatedness of calls from the two areas based on our preliminary classifications.

RESULTS

Recordings from Iceland

Recordings were obtained during nine encounters with killer whales off eastern Iceland (Table 1). Of these samples, seven contained calls that could be analyzed, although boat noise occasionally obscured the data. Twenty-four discrete calls and nine call subtypes were

TABLE 3

Icelandic call types recorded in the presence of photoidentified pods.

Pods:	*IB, Misc*	*IA, IB Misc*	*IA, IB IE*	*IB*	*IB*	*IA, IB*	*IF*	*IB*	*IE*
Tape no.	*1504*	*1505*	*1514*	*1515*	*1516*	*1517*	*1518*	*1519*	*1520*
Call type									
I1			X						
I2i			X						
I2ii			X						
I2iii			X						
I2iv			X						
I3			X						
I4			X						
I5i			X						
I5ii			X						
I5iii			X						
I5iv			X						
I6			X						
I7			X			X(?)			
I8			X						
I9			X						
I10		X	X						
I11i			X					X	
I11ii			X						
I12	X		X			X			
I13i			X		X				
I13ii			X						
I14i		X	X						
I14ii	X		X						
I16						X			
I17			X	X					
I19						X			
I20					X				
I21						X		X	
I31		X	X			X			
I32			X						
I33			X						
I34					X				
I35		X							

identified (Table 3). Recordings made near Bakkaflói (see Fig. 1) on 20 October 1986 in the presence of over 60 feeding killer whales contained the greatest number of analysable calls, including representatives of eighteen discrete calls and nine subtypes. Because of the large number of whales in the area, it was impossible to assign the call types to any specific pod. Several of the discrete calls identified were subsequently found in recordings from other encounters, but no other recording contained calls of the same number and clarity. A total of six additional discrete calls were identified in three other encounters, including some recorded in the presence of a single pod (Table 3).

The components of Icelandic calls were most often swept or warbled pulsed sounds, buzzes, clicks and constant-frequency pulsed sounds. The reader is directed to Figure 3 and Appendix 1a for sonograms and measurements of acoustic parameters. Where possible the table also gives qualitative descriptions of the tone of the call components. In 24% of discrete calls, there was a harmonically-unrelated, high-frequency component which overlapped sections of the call. This component unquestionably was produced by the same animal, and was therefore considered another component of the call.

Five discrete call types from Icelandic whales were classified into subtypes. We do not have enough data to show whether these subtypes were associated with particular pods, except in one case. Recordings were made near the IB pod (see Sigurjónsson *et al.* 1988 – this volume) on three occasions when there were no other killer whales present. Therefore, a preliminary pod-specific repertoire of six discrete calls can be assigned to this group:

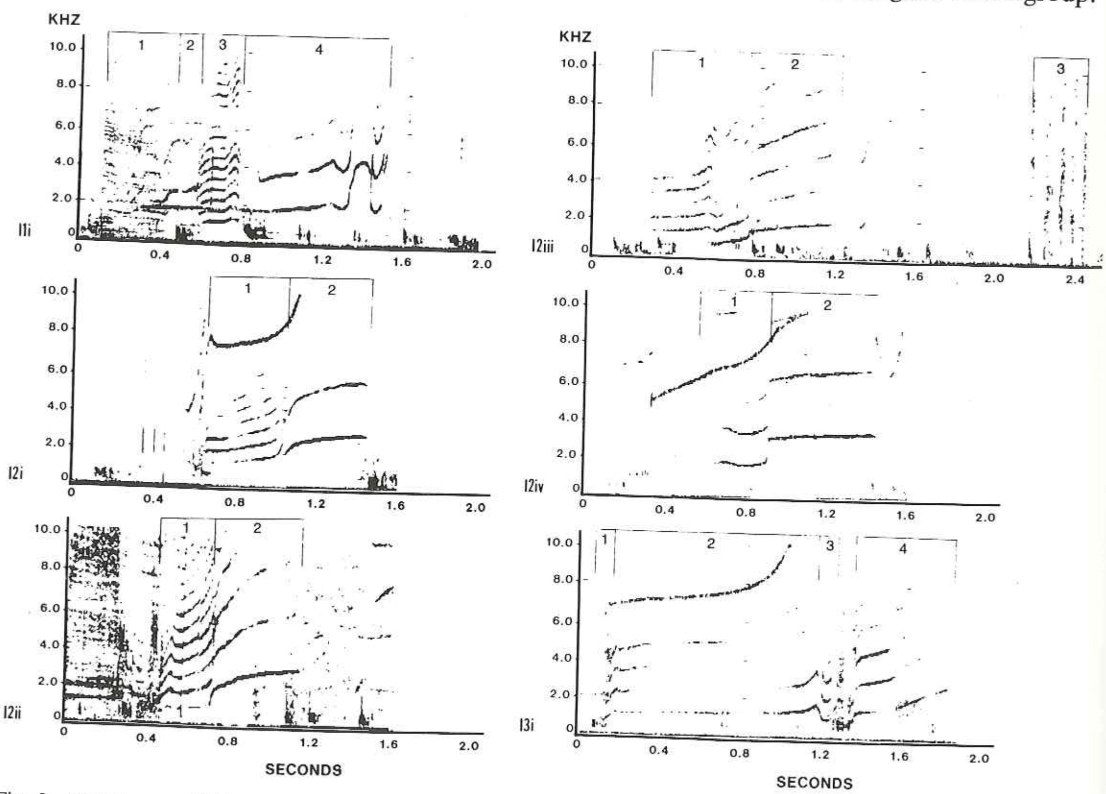
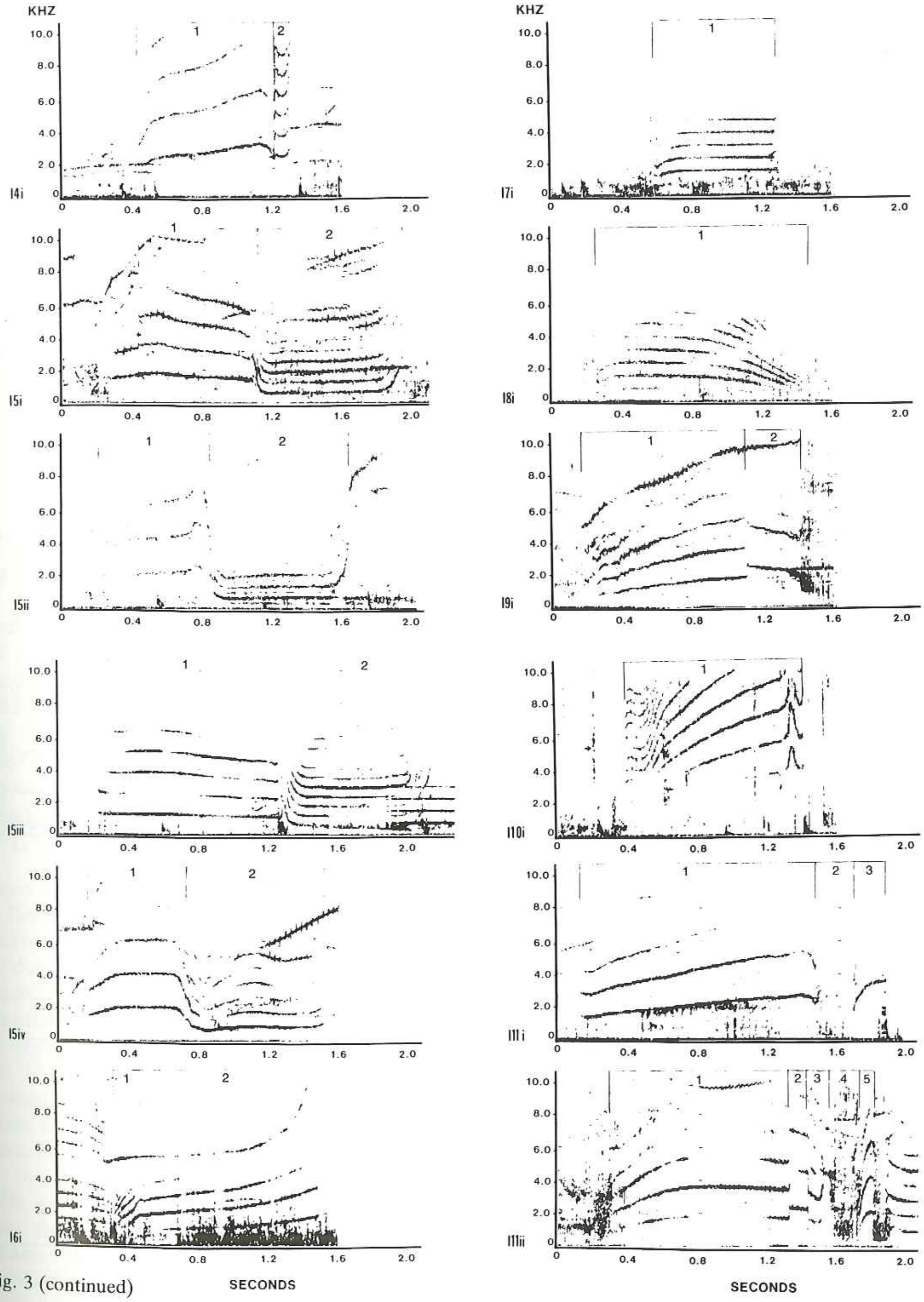


Fig. 3. Sonograms of discrete call types recorded off Iceland. Components are bracketed and numbered at the top of each figure. The catalogue number of each call type is given at the lower left of each sonogram. Cont'd pp. 231–233.



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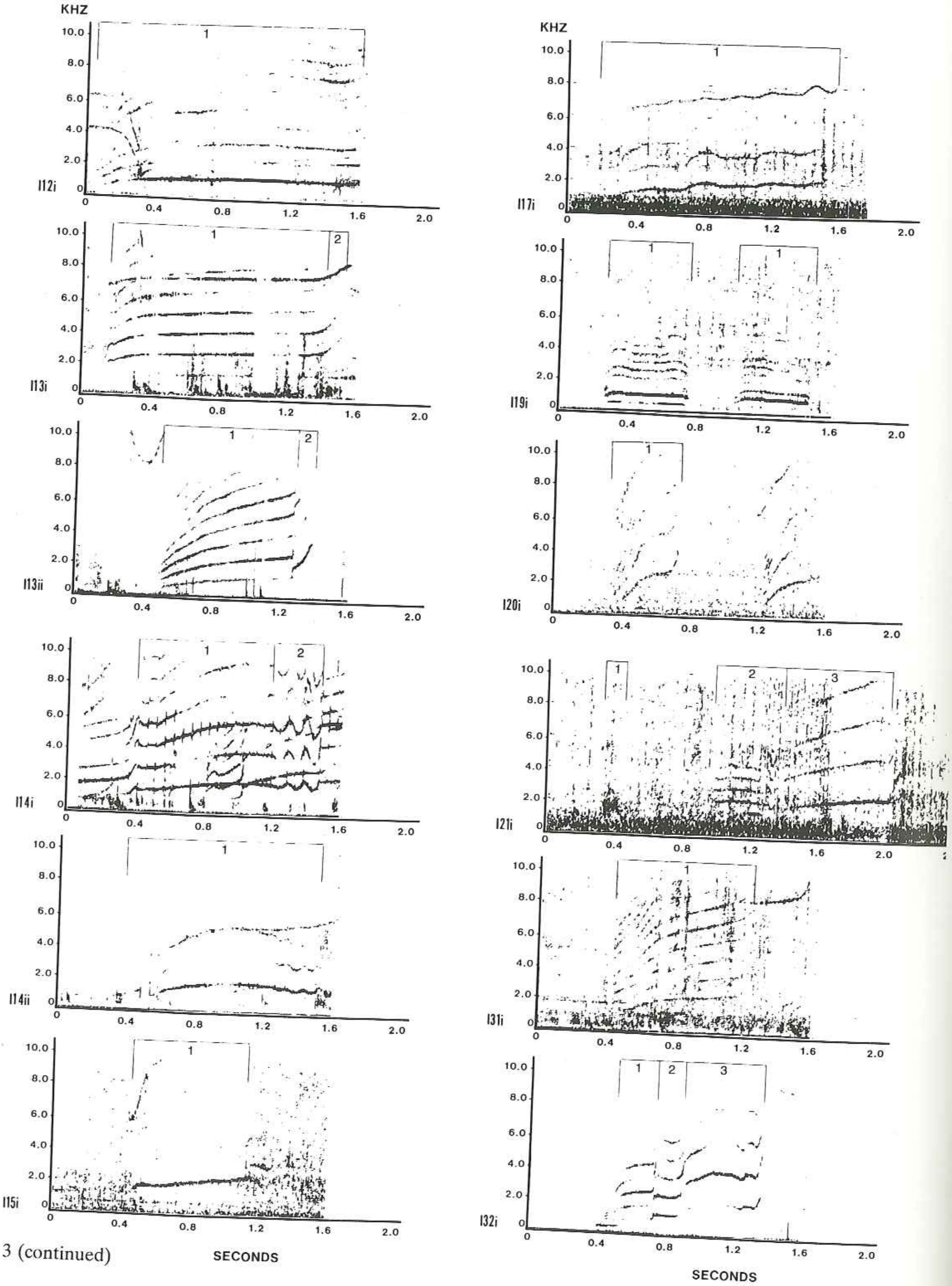

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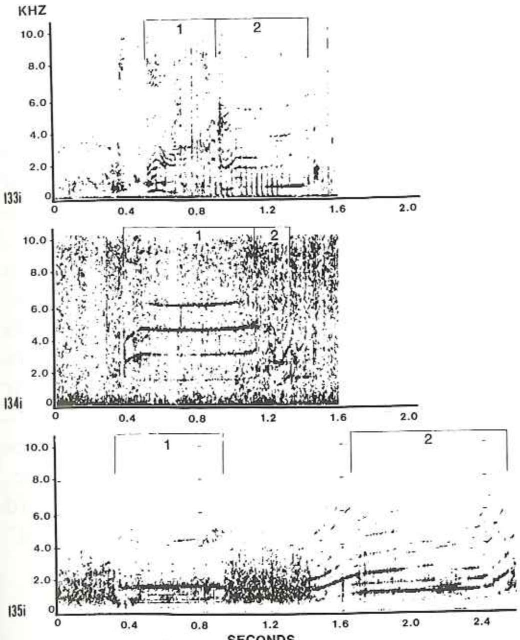


Fig. 3 (continued)

four calls (I13i, I17, I120 and I34) recorded on 29 and 30 October 1986 while the pod was feeding off Mjóifjörður and two call types (I11i and I21) were recorded on 13 November off Seyðisfjörður. Notably, three of these six discrete call types were not identified from the recordings of the encounter with the large group recorded off Bakkaflói, although the IB pod was present.

Recordings from Norway

Recordings were made on nine days in Norwegian waters near killer whales that were feeding or travelling (Table 2). Twenty-three discrete call types and 15 call subtypes were identified from these recordings (Table 4). The reader is directed to Figure 4 and Appendix 1b for sonograms and measurements of acoustic parameters. Like the discrete calls from killer whales in Icelandic waters, calls from Norwegian killer whales contained one to four components. However, Norwegian calls were different in their detailed component structure from calls described for killer whales from Iceland (see above) and the Pacific Northwest (Ford 1984).

Seven call subtypes were identified in the presence of the NB pod (see Lyrholm 1988 – this volume), when it was alone. Two contained high-frequency, harmonically unrelated components. We found no evidence of pod-specific subtypes.

Some call types occurred together consistently. For example, N18 frequently followed

TABLE 4

Norwegian killer whale call types recorded in the presence of photoidentified pods.

Pod(s)	*NB, NC*	*NB, NC*	*NA*	*NA*	*NB*	*NB, NC*
Tape no.	*1521*	*1523*	*1525*	*1526*	*1522*	*1524*
Call type						
N1i		X				X
N1ii		X				X
N1iii		X	X			
N1iv		X				
N2i	X	X				
N2ii	X	X				
N2iii	X					
N2iv	X					
N3i	X	X	X	X	X	
N3ii				X	X	
N4	X					X?
N5	X	X	X?	X?		
N6i	X	X				
N6ii	X	X				
N7	X	X	X	X?	X	X
N8ii		X	X	X		
N8ii		X				X?
N9	X	X	X	X		
N10i		X	X	X		
N10ii		X	X			
N11i		X	X?			
N11ii			X			
N12	X		X?		X	
N14i	X	X			X	
N14ii	X					
N15			X	X		
N16			X	X		
N17i	X	X	X		X	X
N17ii	X	X	X	X?		
N18		X	X?		X?	
N19	X	X	X	X		
N20			X	X		
N21			X			
N22			X			
N23			X			
N24i				X		
N24ii				X		

N17i. Such association are suggestive of higher-order structure in the call types as has been described by Ford (1984). We also found an instance in which two call types (N1ii and N11) were emitted between components one and two of an N6 call. The timing and amplitude of the composite call indicated it was produced by one individual. This observation suggests that components can be somewhat independent of one another.

Degree of overlap of call repertoires from Iceland and Norway

Most calls identified to date are area-specific to Iceland or Norway, although a few discrete calls may represent variants of the same call type; these are discussed in detail below. Our conclusion must be considered tentative until we have analyzed a more extensive sample. Even so, qualitative clues lead us to conclude that the repertoires are distinct.

The few similarities in the call types from Iceland and Norway are instructive. Most were single component calls that are particularly difficult to categorize. For example, types N5 and I8 sound different, even to an inexperienced listener, but have similar component structure. The small sample of N5 calls was of poor quality, so we could not measure the differences more rigorously. Other similar calls included the single-component pairs I7–N7, I17–N17 and I19–N19, and two-component pairs I21–N15 and I31–N18. Of these, some (e.g. I17 and N17, N18) were what Ford (1984) describes as "variable" and "aberrant"

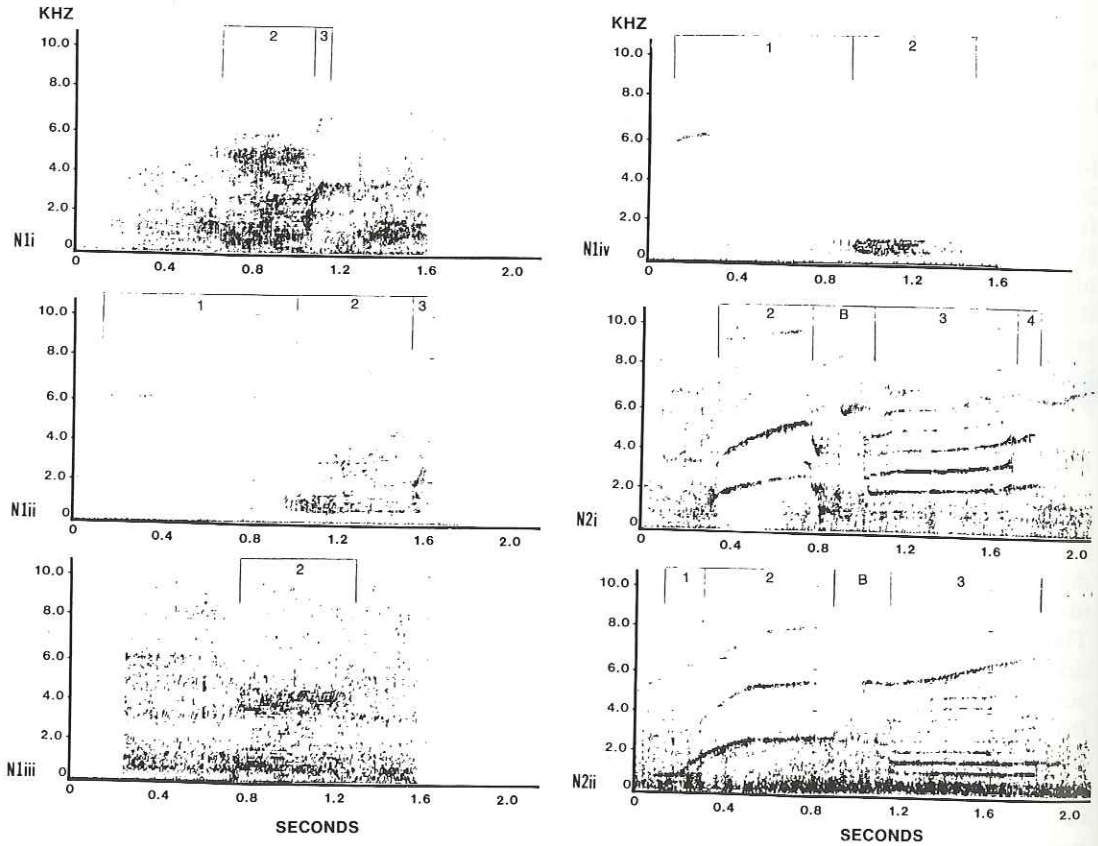
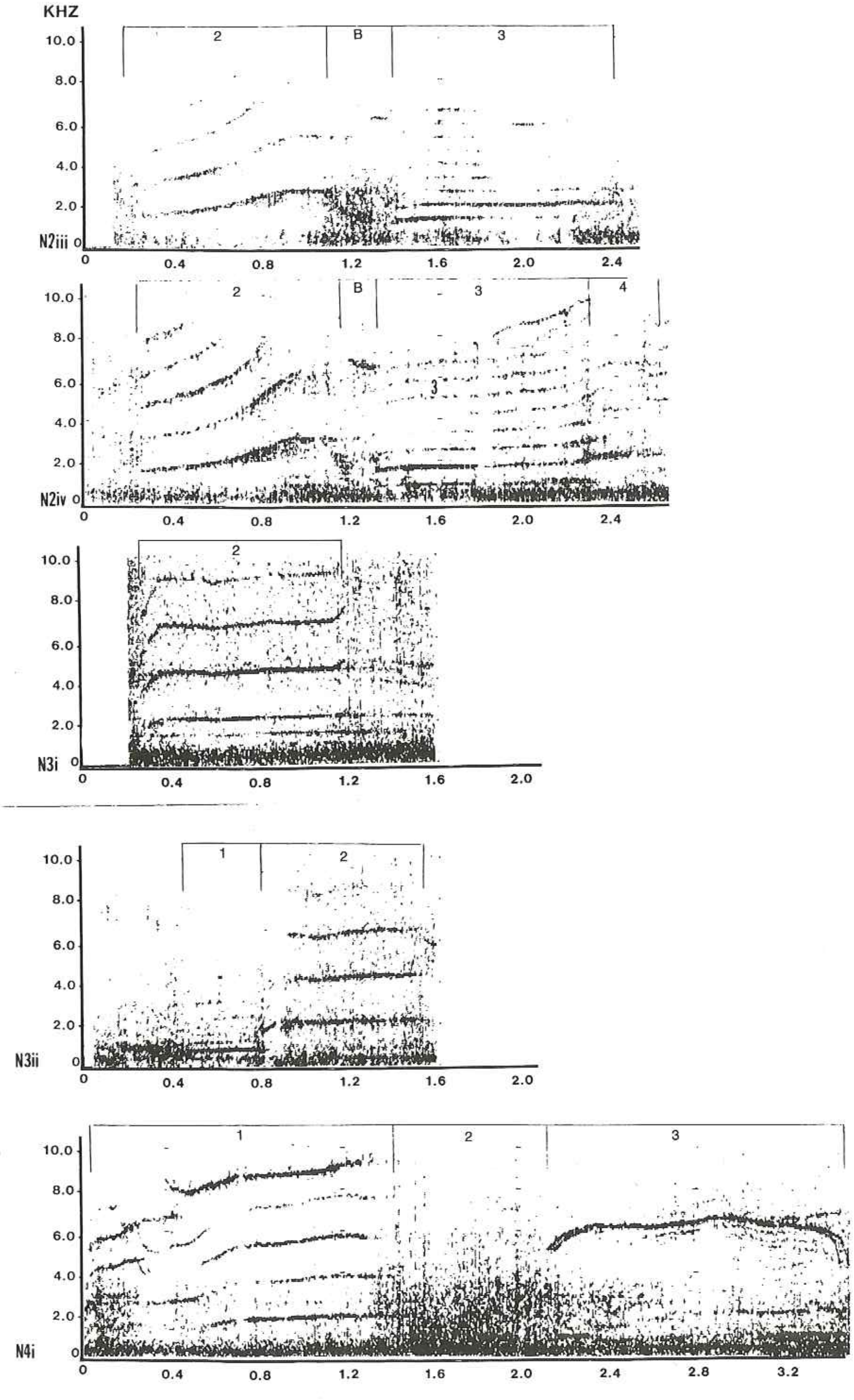


Fig. 4. Sonograms of discrete call types recorded off Norway. Components are bracketed and numbered at the top of each figure. The catalogue number of each call type is given at the lower left of each sonogram. Cont'd pp. 235–238.



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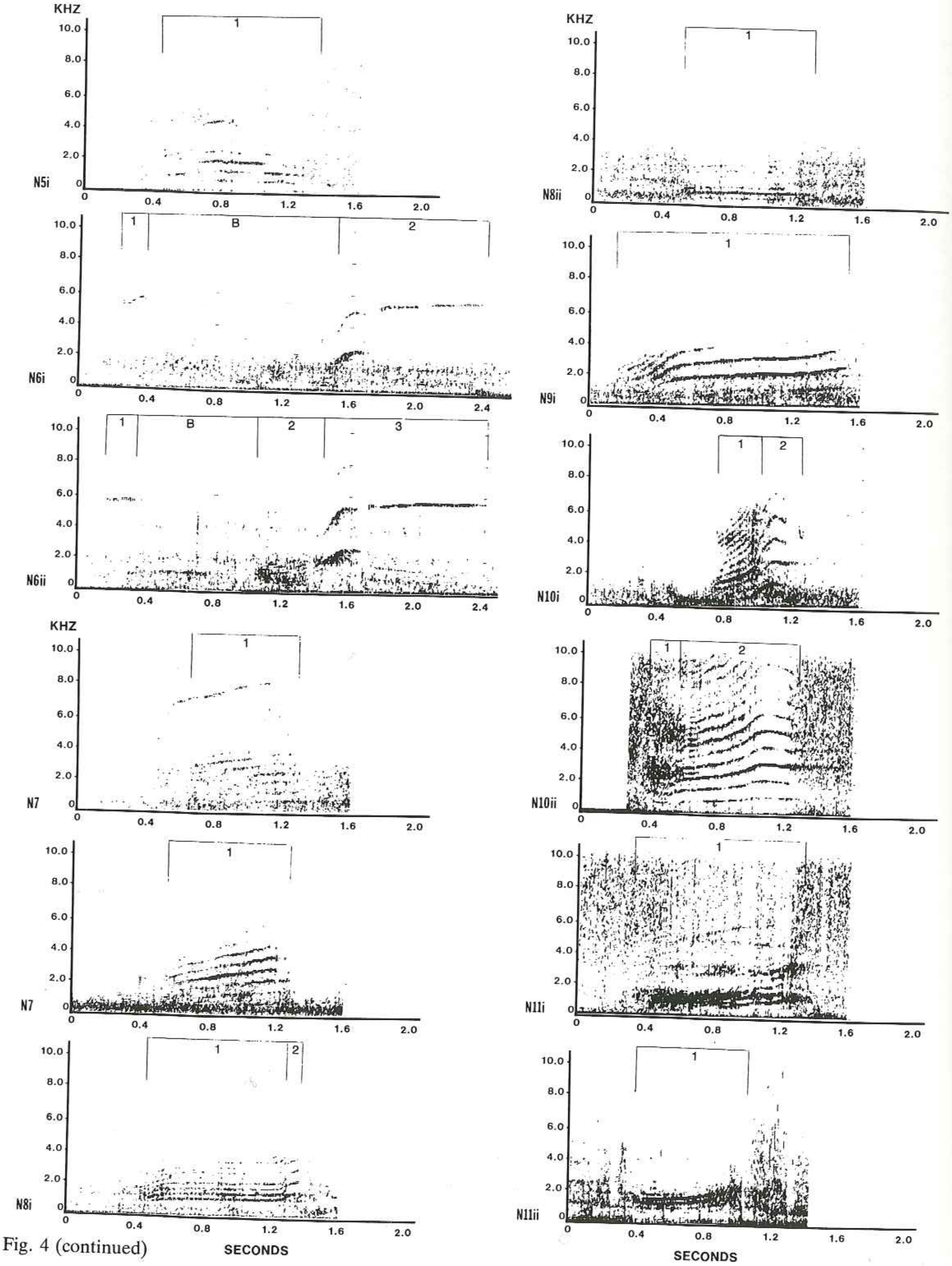

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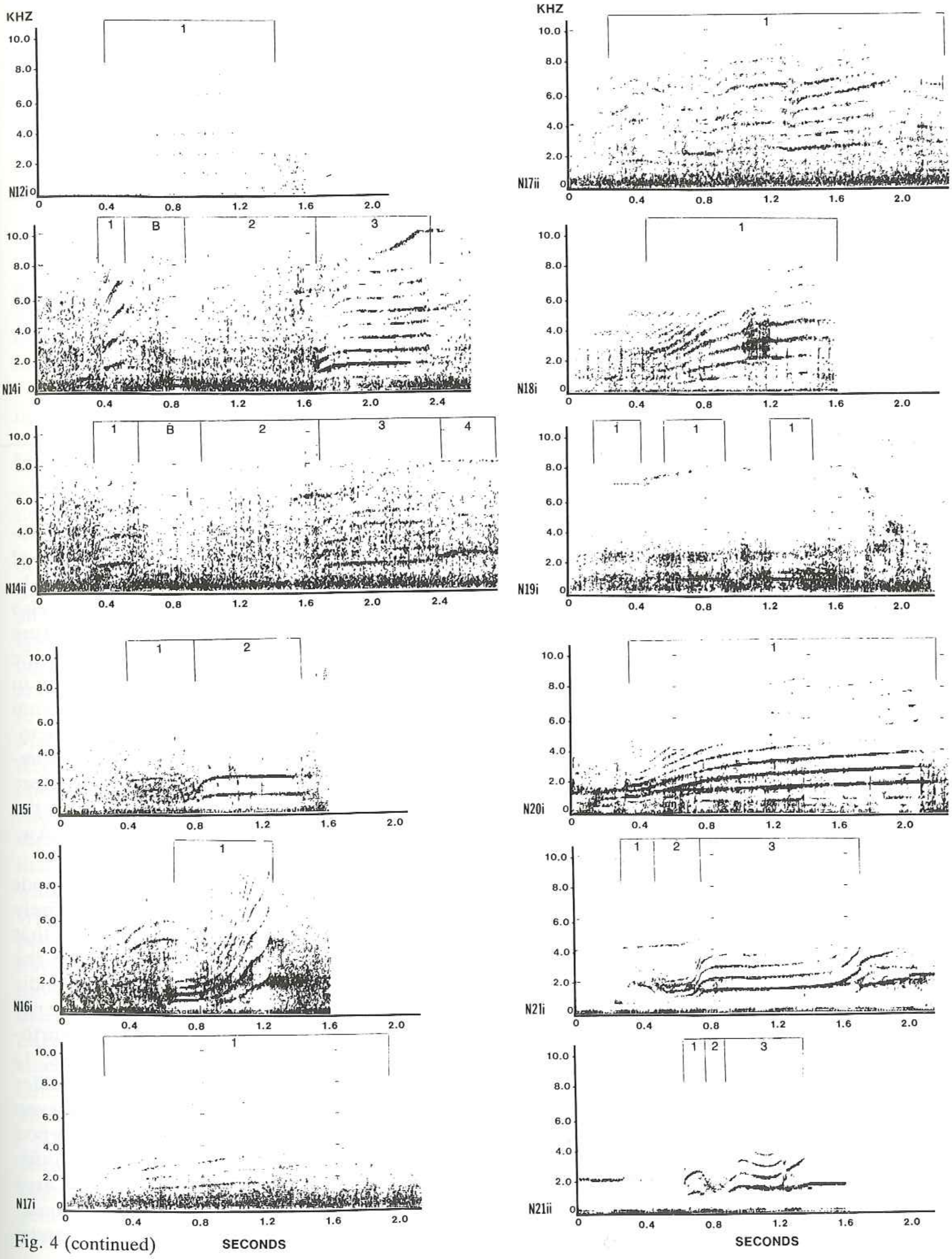

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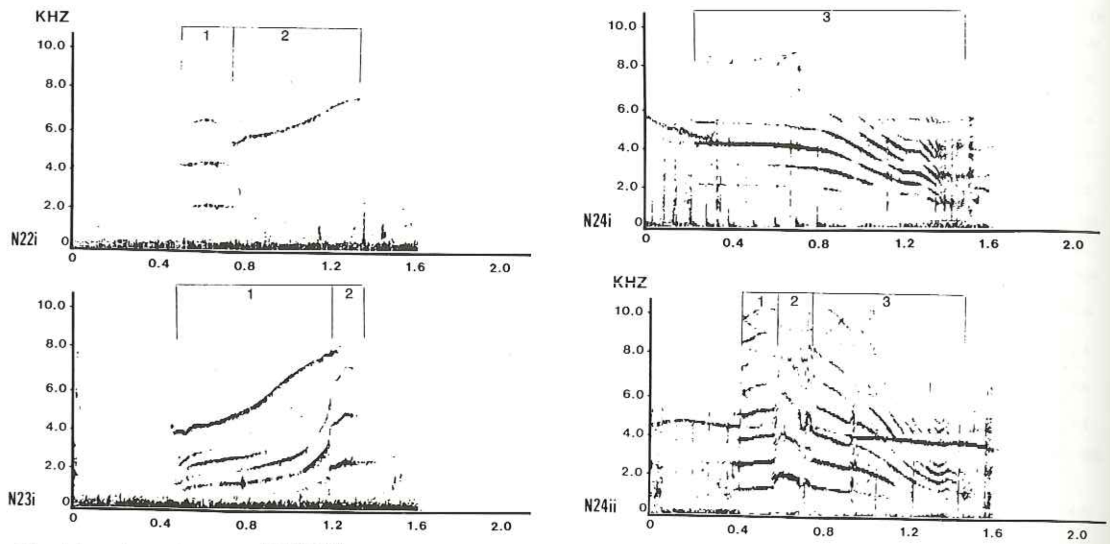

Fig. 4 (continued)

calls, which do not fall clearly into any category. Such calls may be readily identifiable when the call types are already well understood, but not when the call repertoires are relatively unknown.

We also found unique aural qualities common to many calls that may distinguish repertoires of the two areas. For example, calls from Norway that were particularly distinctive to the ear included types N1i, N4, N14 and N19, each of which had a "buzzy" or "raspy" quality not found in Icelandic calls. This difference is suggestive of a higher-order difference between repertoires of the two areas, as has been reported for North Pacific and Antarctic killer whales (Awbrey *et al.* 1982). However, we need more data to substantiate this observation, as we cannot exclude the possibility that all these sounds were made by members of only one pod.

DISCUSSION

Preliminary analysis of killer whale calls from Norwegian and Icelandic coastal waters indicates that the sampled population in each region has a distinct repertoire of discrete calls, with little evidence of call sharing between the regions. Discrete calls from both regions were similar in frequency and component structure, but unique in the patterning of the call components and readily distinguishable by ear. Calls from both areas were also similar in frequency and component structure to those of killer whales from the Pacific Northwest (Ford 1984, 1987), but different in frequency and component patterning from those recorded in the Southern Hemisphere. Norwegian and Icelandic killer whales commonly produced "click-burst" sounds before and between frequency sweeps, unlike the Antarctic whales (Awbrey *et al.* 1982; Awbrey, unpubl. data).

Ford (1984) noted that killer whale pods sharing the same area sometimes had entirely different repertoires of calls, a finding that confounds any attempt to conclude that the differences we observed between Icelandic and Norwegian call repertoires are necessarily geographical differences. In the Pacific Northwest, call variation occurs at two levels: 1) within clans and 2) between clans. Killer whale pods within a clan share calls, but even shared calls often vary in structure from pod to pod. Pods of different clans share no discrete calls, but can share a geographic area and associate with one another, at least occasionally. The differences between Antarctic and British Columbia repertoires appear to be greater than the interpod differences in British Columbia (Awbrey *et al.* 1982; Awbrey, unpubl. data), suggesting that differences in call repertoires may increase with increasing geographic and temporal isolation. Our observations of unique tonal qualities common to many Norwegian calls but absent in all Icelandic calls, may suggest the same.

The adaptive significance of discrete call repertoires in killer whales is still a matter of speculation. Killer whales have developed true dialects as well as geographical variation in vocal behavior (Conner 1980; Ford and Fisher 1983). A true dialect is defined as a variant in signaling behaviour which is confined to a social group or sub-population that is sympatric with other groups or populations of conspecifies, as opposed to geographic variation which is the result of allopatric drift.

Ford (1984) hypothesized that call dialects of clans developed during long periods of geographic isolation, and could thus also be an indicator of genetic drift. He suggested that discrete calls function as "contact" or "spacing" calls and that "graded" or "variable" calls are used among socializing animals, as is true for the calls of some primates (Marler 1976; Marler and Tenaza 1977; Byrne 1982). If the discrete calls of killer whales are used in situations involving long-range communication, and variable or graded signals are common in social situations, it is particularly important that researchers note the activity of the whales while recording. Criteria for categorizing call types in the Pacific Northwest sometimes depended on detailed knowledge of social behaviour of the whales. Ordinarily, detailed behavioural information is not readily available in a study of broader geographic areas, such as ours. To use discrete calls of killer whales as a stock assessment tool, one must know the variance of not only the discrete calls but also of any calls that might be confused with them.

The discrete call repertoires of killer whale pods can be used to measure associations, migration and, potentially, the structure and genetic affinities of a population. In British Columbia new pods are postulated to form by the division of larger groups (Bigg 1982). In social primates, similar group fission has been documented (Nash 1976; Oliver *et al.* 1981), resulting in matrilines that are genetically distinct. Ford (1984) suggests that the dialects and "call traditions" of killer whales of the Pacific Northwest reflect the phylogenetic history of the population. As previously noted, however, patterns of acoustic divergence do not necessarily correspond with geographic separation in North Pacific killer whales, at least in the short-term. Therefore, the relationship between call divergence and genetic differentiation still must be clarified.

Bioacoustic studies deserve more emphasis than they have received in the past, despite the difficulties inherent in acoustic analysis. Because calls can be readily collected even under adverse conditions, such as darkness and fog, or when whales are underwater or at great distances, they are at the very least an important means of tracking movements of pods and clans. If they actually provide a reliable index of genetic variability, they can be useful management tool. It is important to clarify the relationship between genetic variability and similarities/differences in vocal dialects. Since various techniques are now available to describe the genetic relationships among groups and individuals (Hoelzel and Dover 1987), it is time to collect samples of calls and morphological or genetic material from the same areas. The combined use of photoidentification, genetic and bioacoustic techniques will help us to understand genetic affinities of killer whales worldwide.

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APPENDIX 1a

Descriptive statistics of call types collected off Iceland (x = mean, s = standard deviation, n = sample size, C.V. = coefficient of variation, (S) = start, (C) = center, (E) = end, SBI = sideband interval, C = component, UC = harmonically-unrelated, high-frequency component). Frequencies were generally measured in the steady-state portion of a component; where this was impossible, a starting and ending frequency were measured. A note under "description" is included where the qualitative features of the component can be described in common language (BZ = buzz, CF = constant-frequency, US = upsweep, DS = downsweep, CL = clicks, UCH = chirp (rising), DCH = chirp (falling), W = warble).

Call type	*Duration(s)*					*Side-band interval(Hz)*				
I1	Tot	C1	C2	C3	C4	SBI1	SBI2	SBI3	SBI4	
x = ...	1.454	0.314	0.192	0.217	0.729	200	2251	516	1844	
s = ...	0.015	0.075	0.054	0.028	0.099	12	228	42	120	
n = ...	11	11	11	11	11	11	11	11	11	
C.V. = . . .	10.1	23.1	28.3	13.1	13.6	5.9	10.1	8.1	6.5	
Description		BZ	US	US-UCH	US-W					
I2i	Tot	C1	C2	UC(Tot)		SBI1	SBI2	UC(C)		
x = ...	0.776	0.387	0.364	–		720	2500	7280		
s = ...	0.039	0.013	0.060	–		0	136.6	445		
n = ...	4	3	4	–		4	4	3		
C.V. = . . .	4.9	3.2	16.6	–		0	0.5	6.1		
Description		US	US							
I2ii		Tot	C1	C2		SBI1	SBI2			
x = ...	0.673	0.225	0.448			807	2593			
s = ...	0.032	0.018	0.031			53.2	119.7			
n = ...	6	6	6			6	6			
C.V. = . . .	4.7	8.2	6.9			6.6	4.6			
Description		US	US							
I2iii	Tot	C1	C2	Gap	C3	SBI1	SBI2			
x = ...	1.071	0.594	0.478	1.312	–	840	1440			
s = ...	0.225	0.124	0.101	0.477	–	56.5	0			
n = ...	2	2	2	2	–	2	2			
C.V. = . . .	21	20.1	21.3	36.3	–	6.7	0			
Description		US	US	–	CL					
I2iv	Tot	C1	C2			SBI1	SBI2			
x = ...	0.905	0.368	0.537			1800	3280			
n = ...	1	1	1			1	1			
Description		UCH	US							
I3	Tot	C1	C2	C3	C4	SBI1	SBI2	SBI3	SBI4	UC(S)
x = ...	2.142	0.072	1.365	0.097	0.394	400	1360	320	1600	6800
s = ...	0.193	0.013	0.385	0.005	0.151	–	113.1	–	–	113.1
n = ...	2	2	2	2	2	1	2	1	1	2
C.V. = . . .	9.1	18.8	28.2	5.1	38.3	–	8.3	–		1.6
Description		BZ	US-CF	W	US					

Appendix 1a (continued)

Call type	*Duration(s)*				*Side-band interval(Hz)*			
I4	Tot	C1	C2		SBI1	SBI2		
x = ...	0.966	0.864	0.102		2427	1147		
s = ...	0.105	0.118	0.013		46.2	46.2		
n = ...	3	3	3		3	3		
C.V. = . . .	10.9	13.7	12.9		1.9	4.1		
Description		US	W		C2 has metallic quality			
I5i	Tot	C1	C2		SBI1	SBI2		
x = ...	1.714	0.858	0.856		1870	691		
s = ...	0.150	0.109	0.095		119	73.9		
n = ...	12	12	12		12	11		
C.V. = . . .	8.8	12.7	11.1		6.4	10.7		
Description		US-DS	DS-CF-US					
I5ii	Tot	C1	C2		SBI1	SBI2		
x = ...	1.390	0.588	0.782		2220	656		
s = ...	0.109	0.025	0.089		410	67		
n = ...	5	5	5		5	5		
C.V. = . . .	7.8	4.3	11.4		18.6	10.2		
Description			DS-CF-US		5ii has stronger DS, US			
I5iii	Tot	C1	C2		SBI1	SBI2		
x = ...	1.937	1.062	0.875		1120	560		
n = ...	1	1	1		1	1		
Description		DS	DS-CF-US					
I5iv	Tot	C1	C2		SBI1	SBI2(S)	SBI3(C)	SBI2(E)
x = ...	1.370	0.537	0.883		1946	600	1067	747
s = ...	0.070	0.062	0.070		46.2	56.6	166.5	46.2
n = ...	3	3	3		3	3	3	3
C.V. = . . .	5.1	11.5	8.4		2.4	9.4	15.6	6.2
Description		US-DS	CF-W					
I6	Tot	C1	C2	UC(Tot)	SBI1	SBI2	UC(S)	UC(E)
x = ...	1.369	0.160	1.209	1.326	575	1221	5237	8762
s = ...	0.430	0.034	0.454	0.381	44.8	153	117	944.5
n = ...	13	8	7	17	11	15	17	17
C.V. = . . .	31.4	4.7	37.7	28.7	7.8	12.5	2.2	10.7
Description		US	US					
I7	Tot	C1			SBI(S)	SBI(E)		
x = ...	0.723	0.061			468	772		
s = ...	0.143	0.015			62.7	106.3		
n = ...	20	7			10	20		
C.V. = . . .	19.9	24.6			13.4	13.7		
Description	UC-CF	C1 is short chirp at start			mew-like quality			
I8	Tot	C1			SBI(S)	SBI(E)		
x = ...	1.163	0.058			542	832		
s = ...	0.248	0.010			82.7	125.1		
n = ...	13	7			9	22		
C.V. = . . .	21.3	17.5			15.3	15		
Description	US	C1 is short chirp at start						

Appendix 1a (continued)

Call type	*Duration(s)*						*Side-band interval(Hz)*			
I9	Tot	C1	C2				SBI1	SBI2		
x = ...	1.306	0.981	0.322				1680	2240		
s = ...	0.177	0.168	0.013				0	0		
n = ...	2	2	2				2	2		
C. V. = ...	13.5	17.2	4.2				0	0		
Description		US	DS							
I10	Tot						SBI1(S)	SBI1(E)		
x = ...	0.726						1712	2464		
s = ...	0.199						292	285		
n = ...	5						5	5		
C.V. = ...	27.4						17	11.6		
Description	US-W						peak frequency 5-8 KHz			
I11i	Tot	C1	Gap	C3			SBI1	SBI3(S)	SBI3(E)	
x = ...	1.840	1.367	0.255	0.194			1907	2053	2967	
s = ...	0.297	0.248	0.104	0.048			126	432	458	
n = ...	13	11	13	13			13	12	12	
C.V. = ...	16.1	18.1	40.7	24.5			6.6	21	15.4	
Description		US-DS								
I11ii	Tot	C1	C2	C3	Gap	C4	SBI1	SBI2	SBI3	SBI4
x = ...	1.495	1.073	0.108	0.083	0.195	0.089	1760	2280	1480	2160
s = ...	0.086	0.050	0.025	0.014	0.013	0.016	0	57	57	113
n = ...	3	3	3	3	3	3	3	3	3	2
C.V. = ...	5.7	4.7	23.4	17.3	6.7	17.6	0	2.4	3.8	5.2
Description		US-CH								
I12ii	Tot						SBI1			
x = ...	1.300						848			
s = ...	0.326						70			
n = ...	9						10			
C.V. = ...	25						8.3			
Description							hollow quality			
I13i	Tot	C1	C2				SBI1	SBI2(S)	SBI2(E)	
x = ...	1.391	1.138	0.216				1200	1371	2343	
s = ...	0.365	0.356	0.043				137	108	452	
n = ...	8	7	7				9	7	7	
C.V. = ...	26.2	31.3	19.7				11.4	7.8	19.3	
Description		US-CF	US							
I13ii	Tot	C1	C2				SBI1	SBI2(S)	SBI2(E)	
x = ...	0.955	0.832	0.145				989	1865	2717	
s = ...	0.130	0.129	0.062				88	405	495	
n = ...	10	10	10				11	11	12	
C.V. = ...	13.6	42.9	42.9				8.9	21.7	18	
Description		US	US							
I14i	Tot						SBI1	SBI2		
x = ...	1.353						1552	1440		
s = ...	0.244						269	203		
n = ...	5						5	5		
C.V. = ...	18						17.3	14.2		
Description	US-CF-W						Variable number of warbles			

Appendix 1a (continued)

Call type	*Duration(s)*					*Side-band interval(Hz)*		
I14ii	Tot					SB1(S)	SB1(E)	
x = ...	1.160					1787	1520	
s = ...	0.215					201	277	
n = ...	3					3	3	
C.V. = . . .	18.5					11.2	18.2	
Description	US-W							
I15	Tot	UC(Tot)				SBI1(S)	SBI1(E)	UC(S)
x = ...	0.671	–				1467	2160	6213
s = ...	0.056	–				122	80	532
n = ...	3	–				3	3	3
C.V. = . . .	8.4	–				8.3	3.7	8.5
Description	US							
I17	Tot					SBI1(S)	SBI1(E)	
x = ...	1.719					780	2000	
s = ...	0.622					101	173	
n = ...	4					4	4	
C.V. = . . .	36.2					12.9	8.6	
Description	US							
I19	Tot					SBI1(S)	SBI1(C)	SBI1(E)
x = ...	0.481					400	520	400
s = ...	0.035					0	56.6	0
n = ...	2					2	2	2
C.V. = . . .	7.3					0	10.8	0
Description	W-CF-W					often occurs in pairs		
I20	Tot					SBI1(S)	SBI1(E)	
x = ...	0.355					550	2240	
s = ...	0.085					202	429	
n = ...	5					4	5	
C.V. = . . .	23.8					36.8	19.1	
Description	US							
I21	Tot	C2	C3	Gap	Buzz (Tot)	SBI2	SBI3	
x=	0.977	0.299	0.827	0.521	0.145	640	2240	
s = ...	0.303	0.026	0.113	0.038	0.079	113	65.3	
n = ...	4	2	4	3	3	2	4	
C.V. = . . .	31	8.7	13.6	7.2	54.3	17.7	2.9	
Description		CF	US		US			
I31	Tot	C1	C2			SBI1	SBI2	
x = ...	0.856	0.240	0.660			896	1128	
s = ...	0.146	0.038	0.164			92.1	43.8	
n = ...	4	5	5			5	5	
C.V. = . . .	17.1	15.9	24.8			10.2	3.9	
Description		US	US					
I32	Tot	C1	C2	C3		SBI1	SBI2	SBI3
x = ...	0.963	0.340	0.162	0.460		800	1291	2000
s = ...	0.183	0.120	0.068	0.071		124	108	170
n = ...	7	7	7	7		6	7	5
C.V. = . . .	19	35.2	41.7	15.4		15.5	8.3	8.5
Description		US	CF	US-UCH				

Appendix 1a (continued)

Call type	Duration(s)				Side-band interval(Hz)		
I33	Tot	C1	C2		SBI1	SBI2	
x = ...	0.884	0.378	0.506		460	560	
s = ...	0.004	0.031	0.027		28.3	0	
n = ...	2	2	2		2	2	
C.V. = ...	0.5	8.2	5.3		6.1	0	
Description ..		UCH	DCH				
I34	Tot	C1	C2		SBI1	SBI2	
x = ...	0.962	0.762	0.200		1520	1840	
n = ...	1	1	1		1	1	
Description ..		US-CF	W				
I35	Tot	C1	Gap	C2	SBI1	SBI2	SBI3
x = ...	1.574	0.618	0.700	0.956	160	600	1040
n = ...	1	1	1	1	1	1	1
Description ..		US-CF		CF-US			

APPENDIX 1b

Descriptive statistics of call types collected off Norway (x = *mean*, s = *standard deviation*, n = *sample size*, C.V. = *coefficient of variation*, (S) = *start*, (C) = *center*, (E) = *end*, SBI = *sideband interval*, C = *component*, UC = *harmonically-unrelated, high-frequency component*). *Frequencies were generally measured in the steady-state portion of a component; where this was impossible, a starting and ending frequency were measured. A note under "description" is included where the qualitative features of the component can be described in common language* (BZ = *buzz*, CF = *constant-frequency*, US = *upsweep*, DS = *downsweep*, CL = *clicks*, UCH = *chirp (rising)*, DCH = *chirp (falling)*, W = *warble*).

Call type	Duration(s)					Side-band interval(Hz)			
N1i I	Tot	C1	C2	C3	C4	SBI2(S)	SBI2(E)	SBI3	
x = ...	0.558	–	0.473	0.085	–	187	187	560	
s = ...	0.066	–	0.046	0.025	–	23	23	560	
n = ...	3	–	3	3	–	3	3	2	
C.V. = ...	11.8	–	9.7	29.4	–	12.3	12.3	100	
Description			BZ-US			N1 often heard in sequences of 2–3			
N1ii	Tot	C1	C2	C3	C4	SBI2(S)	SBI2(E)	SBI3	UC
x = ...	1.427	0.860	0.502	0.066	–	240	293	580	6053
s = ...	0.050	0.014	0.040	0.003	–	69	162	141	167
n = ...	3	3	3	3	–	3	3	2	3
C.V. = ...	3.6	1.6	7.9	4.5	–	28.8	55.3	24.4	2.8
Description		CF	BZ-US						
N1iii	Tot	C1	C2	C3	C4	SBI2(S)	SBI2(E)		
x = ...	0.456	–	0.456	–	–	173	173		
s = ...	0.013	–	0.013	–	–	23	23		
n = ...	3	–	3	–	–	3	3		
C.V. = ...	2.9	–	2.9	–	–	13.3	13.3		
Description			BZ						

Appendix 1b (continued)

Call type	*Duration(s)*					*Side-band interval(Hz)*					
N1iv	Tot	C1	C2	C3	C4	SBI2(S)	SBI2(E)	UC			
x =	1.320	0.620	0.520	–	–	160	180	5880			
s =	0.120	0.110	0.040	–	–	0	23	139			
n =	4	4	4	–	–	4	4	4			
C.V. =	9.1	17.7	7.7	–	–	0	12.8	2.4			
Description		CF	BZ								
N2i	Tot	C1	C2	C3	C4	SBI2(S)	SBI2(E)	SBI3(S)	SBI3(E)	SBI4(S)	SBI4(E)
x =	1.727	–	0.725	0.737	0.098	1493	2613	560	560	2427	2640
s =	0.149	–	0.062	0.190	0.001	244	122	80	80	46	0
n =	3	–	3	3	3	3	3	3	3	3	3
C.V. =	8.6	–	25.8	21.0	16.3	4.7	14.3	14.3	1.9	0	0
Description			US	DCH-US	US						
N2ii	Tot	C1	C2	Gap	C3	SBI1	SBI2	SBI3(S)	SBI3(E)		
x=	1.910	0.15	0.791	0.23	0.856	1504	2544	544	600		
s=	0.120	0.038	0.080	0.109	0.083	307	131	88	89		
n=	5	5	5	5	5	5	5	5	5		
C.V.=	6.3	25.3	10.1	47.4	9.7	20.4	5.2	16.2	14.8		
Description		CF	US	DCH-US							
N2iii	Tot	C1	C2	Gap	C3	SBI2(S)	SBI2(E)	SBI3(S)	SBI3(E)		
x =	1.661	–	0.813	0.296	0.841	1474	2617	589	640		
s =	0.364	–	0.096	0.138	0.225	78	128	76	69		
n =	7	–	7	7	7	7	7	7	7		
C.V. =	21.9	–	11.8	46.6	26.8	5.3	4.9	12.9	10.8		
Description			US		DCH						
N2iv	Tot	C2	Gap	C3	C4	SBI2(S)	SBI2(E)	SBI3(S)	SBI3(E)	SBI4(S)	SBI4(E)
x =	1.743	0.897	0.289	1.075	0.229	1333	2667	640	827	2240	2293
s =	0.577	0.061	0.089	0.082	0.087	185	46	113	46	487	378
n =	3	3	3	3	3	3	3	3	3	3	3
C.V. =	33.1	6.8	30.8	7.6	38.0	13.9	1.7	17.7	5.6	21.7	16.5
Description		US		DCH-US							
N3i	Tot					SBI1(S)	SBI1(E)				
x =	0.778					1584	1840				
s =	0.223					381	515				
n =	5					5	5				
C.V.	28.7					24.1	28.0				
Description	US-CF										
N3ii	Tot	C1	C2			SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)		
x =	1.495	0.716	0.779			293	360	2080	2133		
s =	0.276	0.203	0.072			46	40	80	46		
n =	3	3	3			3	3	3	3		
C.V. =	18.5	28.4	9.2			15.7	11.1	3.9	2.2		
Description		BZ	US-CF			C2 equivalent to N3i above					
N4i	Tot	C1	C2	C3		SBI1(S)	SBI1(E)	SBI3(S)	SBI3(E)		
x =	3.080	1.119	0.931	0.950		853	1520	1280	1920		
s =	0.827	0.428	0.387	0.453		323	212	367	80		
n =	3	3	3	3		3	3	3	3		
C.V. =	26.9	35.7	41.6	47.7		37.9	13.9	28.7	0		
Description		W-US	BZ	US							

Appendix 1b (continued)

Call type	*Duration(s)*					*Side-band interval(Hz)*					
N5i	Tot					SBI1(S)	SBI1(C)				
x = ...	0.875					427	613				
s = ...	0.200					61	180				
n = ...	3					3	3				
C.V. = ...	22.9					14.3	29.4				
Description	UCH										
N6i	Tot	C1	Gap	C2		UC1(S)	UC1(E)	SBI2(S)	UC2		
x = ...	1.560	0.172	1.080	0.901		5660	5920	2040	5640		
s = ...	0.760	0.024	0.551	0.06		264	643	201	167		
n = ...	4	4	4	4		4	4	4	4		
C.V. = ...	48.7	13.9	51	5.1		4.6	10.9	10	2.9		
Description		US									
N6ii	Tot	C1	Gap	C2	C3	SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)	SBI3	UC1
x = ...	1.924	0.185	0.766	0.935	0.375	5733	5813	200	253	2027	5707
s = ...	0.368	0.003	0.213	0.035	0.044	244	201	0	23	201	185
n = ...	3	3	3	3	3	3	3	3	3	3	3
C.V. = ...	19.1	1.6	27.8	3.7	11.7	4.3	3.5	0	9.1	9.9	3.2
Description		US		CF	BZ	C2 sometimes preceded by a buzz					
N7	Tot	UC(Tot)				SBI1(S)	SBI1(E)				
x = ...	0.715	–				431	531				
s = ...	0.121	–				100	129				
n = ...	18	–				18	18				
C.V. = ...	16.9	–				23.2	24.3				
Description	US					N7 often occurs with N12 in sequence					
N8i	Tot	C1	C2			SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)		
x = ...	0.976	0.838	0.139			270	380	740	770		
s = ...	0.100	0.092	0.035			20	23	95	50		
n = ...	4	4	4			4	4	4	4		
C.V. = ...	10.3	11	25.2			7.4	6.1	12.8	6.5		
Description		US	US			Buzzy quality					
N8ii	Tot	C1	C2			SBI1(S)	SBI(E)				
x = ...	0.679	0.679	–			320	360				
s = ...	0.050	0.050	–			0	57				
n = ...	4	4	–			4	4				
C.V. = ...	7.4	7.4	–			0	15.8				
Description		US									
N9i	Tot					SBI1(S)	SBI1(E)				
x = ...	1.027					360	1160				
s = ...	0.172					40	106				
n = ...	3					3	3				
C.V. = ...	16.7					11.1	9.1				
Description	US										
N10i	Tot	C1	C2			SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)		
x = ...	0.470	0.273	0.197			387	547	1347	1587		
s = ...	0.074	0.040	0.050			83	83	295	234		
n = ...	3	3	3			3	3	3	3		
C.V. = ...	15.7	14.7	25.4			21.5	15.2	21.9	14.7		
Description		US	UCH			N10 calls occur in pairs or series					

Appendix 1b (continued)

Call type	*Duration(s)*					*Side-band interval(Hz)*					
N10ii	Tot	C1	C2			SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)		
x = ...	0.808	0.154	0.654			387	453	693	960		
s = ...	0.013	0.014	0.004			83	46	46	80		
n = ...	3	3	3			3	3	3	3		
C.V. = ...	1.6	9.3	0.5			21.5	10.2	6.7	8.3		
Description		US	UCH								
N11i	Tot					SBI1(S)	SBI1(E)				
x = ...	0.930					150	410				
s = ...	0.045					20	119				
n = ...	4					4	4				
C.V. = ...	4.8					13.3	29				
Description	BZ					These calls occur in pairs					
N11ii	C1(1st)	C1(2nd)				SBI(S)1st	SBI(E)1st	SBI(S)2nd	SBI(E)2nd		
x = ...	0.331	0.604				347	453	320	613		
s = ...	0.048	0.025				46.2	46.2	0	166.5		
n = ...	3	3				3	3	3	3		
C.V. = ...	14.7	4.3				13.3	10.2	0	27.2		
Description	CF-US	CF-US				These calls occur in pairs. (1st and 2nd)					
N12i	Tot					SBI(S)	SBI(E)				
x = ...	0.960					1336	1480				
s = ...	0.076					102	142				
n = ...	10					10	10				
C.V. = ...	7.9					7.6	9.6				
Description	US										
N14i	Tot	C1	Gap	C2	C3	SBI1(S)	SBI1(E)	SBI2	SBI3(S)	SBI3(E)	
x = ...	1.951	0.202	0.197	0.776	0.825	1093	1593	509	600	794	
s = ...	0.323	0.078	0.053	0.065	0.122	0.452	0.137	0.149	95	43	
n = ...	7	7	7	7	7	7	7	7	7	7	
C.V. = ...	16.6	38.6	26.8	8.4	14.8	41.4	8.6	29.3	15.8	5.4	
Description		US		BZ	CF						
N14ii	Tot	C1	C2	C3	C4	SBI1	UC1	SBI3(S)	SBI3(E)	SBI4(S)	SBI4(E)
x = ...	1.994	0.212	0.897	0.845	0.316	1573	333	573	773	1827	2013
s = ...	0.566	0.028	0.224	0.046	0.010	46	23	61	46	61	101
n = ...	3	3	3	3	3	3	3	3	3	3	3
C.V. = ...	28.1	13.2	25	5.4	3.2	2.9	6.9	10.7	5.9	3.3	5
Description		US	BZ	CF	US						
N15i	Tot	C1	C2			SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)		
x = ...	0.958	0.379	0.579			293	347	1387	1653		
s = ...	0.031	0.003	0.029			46.2	46.2	743	789.3		
n = ...	3	3	3			3	3	3	3		
C.V. = ...	3.2	1.0	5.1			15.8	13.3	53.6	47.7		
Description		CF	US-CF								
N16i	Tot					SBI1(B)	SBI1(E)				
x = ...	0.733					400	2320				
s = ...	0.225					80	138.6				
n = ...	3					3	3				
C.V. = ...	30.8					20.0	5.9				
Description	US										

Appendix 1b (continued)

Call type	*Duration(s)*				*Side-band interval(Hz)*					
N17i	Tot				SBI1(S)	SBI1(E)				
x = ...	1.598				768	1136				
s = ...	0.460				156	301				
n = ...	5				5	5				
C.V. = ...	28.8				20.3	26.5				
Description	US									
N17ii	Tot				SBI1(S)	SBI1(E)				
x = ...	2.028				693	441				
s = ...	0.164				46	483				
n = ...	3				3	3				
C.V. = ...	8.1				6.6	9.1				
Description	US-DS				variable call					
N18i	Tot				SBI1(S)	SBI1(E)				
x = ...	1.199				400	1147				
s = ...	0.198				160	46				
n = ...	3				3	3				
C.V. = ...	16.5				40	4.0				
Description	US				Often preceded by N17i					
N19i	Tot				SBI1(S)	SBI1(E)				
x = ...	0.466				216	248				
s = ...	0.040				83	91				
n = ...	5				5	5				
C.V. = ...	8.6				38.4	36.7				
Description	US									
N20i	C1				SBI(S)	SBI(E)				
x = ...	1.701				340	900				
s = ...	0.334				76.6	40				
n = ...	3				3	3				
C.V. = ...	19.6				22.5	4.4				
Description	US									
N21i	Tot	C1	C2	C3	SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)	SBI3(S)	SBI3(E)
x = ...	1.292	0.159	0.246	0.887	920	880	280	400	680	1160
s = ...	0.142	0.042	0.048	0.098	56.6	113.1	56.6	0	56.6	56.6
n = ...	2	2	2	2	2	2	2	2	2	2
C.V. = ...	11.0	2.6	19.8	11.0	6.1	12.9	20.2	0	8.3	4.9
Description		DS	US	US						
N21ii	Tot	C1	C2	C3	SBI1(S)	SBI1(E)	SBI3(S)	SBI3(E)		
x = ...	0.596	0.105	0.137	0.353	960	1240	680	840		
s = ...	0.30	0.018	0.085	0.042	113.1	282.8	56.6	56.6		
n = ...	2	2	2	2	2	2	2	2		
C.V. = ...	0.1	16.7	6.2	1.2	11.8	22.8	8.3	6.7		
Description		US		US-DS						
N22i	Tot	C1	C2		SBI1(S)	SBI1(E)	UC(S)	UC(E)		
x = ...	0.753	0.206	0.548		1973	2000	5120	7707		
s = ...	0.033	0.010	0.135		122.2	80	138.6	468.8		
n = ...	3	3	3		3	3	3	3		
C.V. = ...	17.9	16.0	18.8		6.2	4.0	2.7	6.1		
Description		CF	US							

Appendix 1b (continued)

Call type	*Duration(s)*				*Side-band interval(Hz)*					
N23i	Tot	C1	C2		SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)		
x =	0.785	0.652	0.133		507	853	1467	2160		
s =	0.034	0.092	0.041		46.2	92.4	488.8	80		
n =	3	3	3		3	3	3	3		
C.V. =	4.4	6.4	6.9		9.1	10.8	33.3	3.7		
Description		US	UCH							
N24i	C3				SBI3(S)	SBI3(E)				
x =	1.039				1200	400				
s =	0.258				160	240				
n =	3				3	3				
C.V. =	24.8				13.3	60.0				
Description	DS									
N24ii	Tot	C1	C2	C3	SBI1(S)	SBI1(E)	SBI2(S)	SBI2(E)	SBI3(S)	SBI3(E)
n=1	1.073	0.168	0.187	0.718	1200	1280	1760	1600	1360	480