

Ontogeny of stereotyped calling of a killer whale calf, *Orcinus orca*, during her first year

Ann E. Bowles¹, W. Glenn Young² and Edward D. Asper³

¹ Sea World Research Institute, San Diego, CA 92109 USA

² Sea World of Texas, San Antonio, TX 72868 USA

³ Sea World of Florida, Orlando, FL 32821 USA

ABSTRACT

The ontogeny of stereotyped calls by a female killer whale calf (*Orcinus orca*), born at Sea World of Florida, Orlando, on 26 September 1985, is documented. The calf, her mother, a female companion and a subadult male were recorded during three three-day observation sessions, beginning when the calf was aged 12, 255 and 396 days, respectively. The adult whales were of Icelandic origin and used two or three different stereotyped call repertoires. None of these repertoires resembled those of wild pods recorded off Iceland in 1985 and 1986, even though all three whales were captured in the late 1970's in the same area. The calf never interacted with her father, captured in Puget Sound, State of Washington, in 1976. The calls of the calf at 14 days and 8 months did not resemble the stereotyped calls of either the Orlando whales or the father, although some elements of the mother's most common call could be detected occasionally. By eight months of age, the calf also produced clicks (peak frequencies 11–17 kHz) similar to clicks used by adults for echolocation.

At about one year of age, the calf was producing at most four of the 13 stereotyped calls she heard, but used only one commonly (90% of her calls). The mother's repertoire was distinguishable from that of her adult female companion by the frequent use of this same call type. As the mother's companion produced most of the calls heard in the pool, the calf must have learned the mother's distinguishing call selectively.

INTRODUCTION

Despite a substantial literature on calls of killer whales, almost nothing is known about the ontogeny of calling behaviour in this species. This information is of particular interest because at least some killer whales have stereotyped, pod-specific dialects that apparently are passed unchanged from generation to generation (Ford and Fisher 1982a, 1982b).

The present paper gives a preliminary analysis of a series of recordings made of a female killer whale calf born at Sea World of Florida on 26 September 1985 (Fig. 1; see Cornell and Leatherwood 1986). We also studied her vocal relationship with the mother, a female companion and a subadult

male, all sharing the same pool, and her father, kept in a separate pool.

Killer whales produce a wide variety of clicks, pops, whistles and pulsed calls (Schevill and Watkins 1966; Steiner *et al.* 1979; Dahlheim and Awbrey 1982; Ford and Fisher 1982a). However, 92% of the sounds recorded from wild killer whales were stereotypical pulsed calls, or "screams" (Ford 1984). For this paper, we have focused on chronicling the ontogeny of these stereotypical calls (hereafter "calls") and on cataloguing the repertoires of Icelandic whales at Sea World of Florida to determine what call-types the calf most likely heard in her environment.

The ontogeny of wild killer whale be-

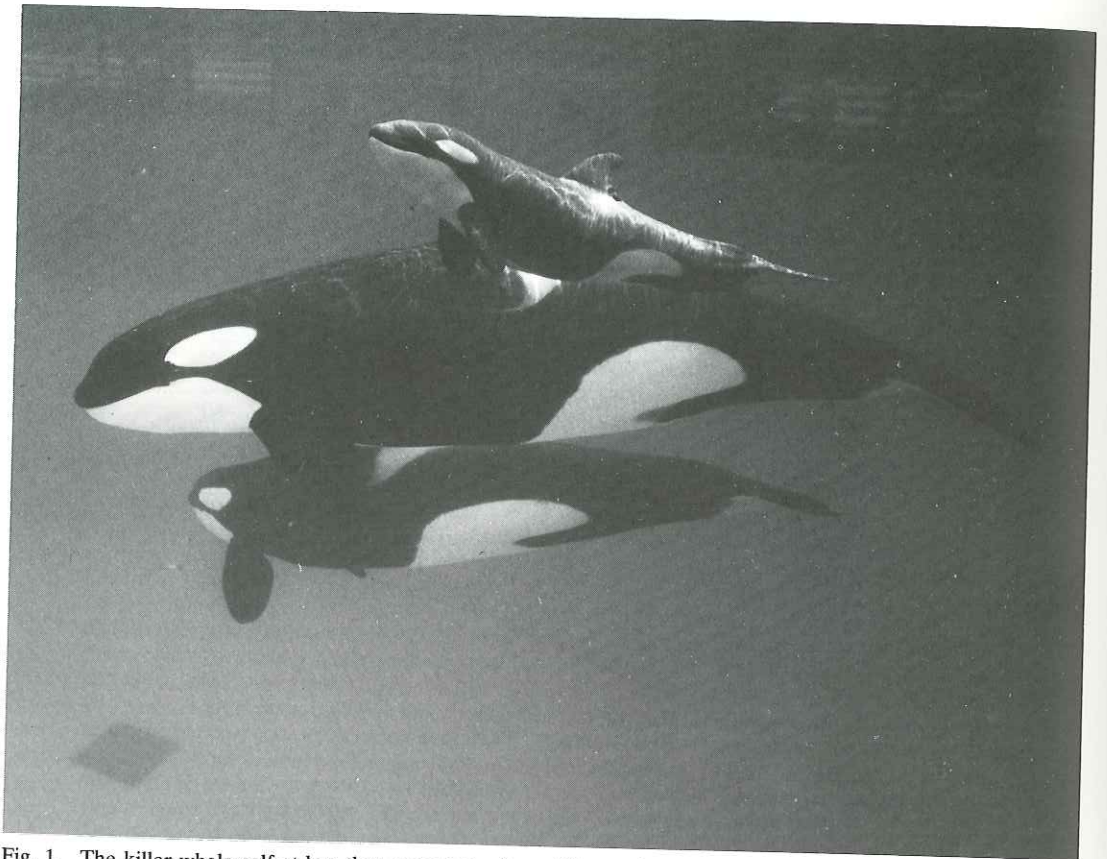


Fig. 1. The killer whale calf at less than one week of age. The mother is in the foreground, with the calf, and her companion is swimming below (Jerry Roberts, Sea World, Inc.).

haviour has been described in general terms by Haenel (1986) based on surface-based observations. Adult females were seen occasionally accompanying and apparently herding one or several calves which were not their own (see also Heimlich-Boran 1986), but no estimate could be made of the percentage of time calves spent in the presence of such "al-mothers". These observations suggest that calves may interact with several adults in their natal pod from an early age; therefore, these companions might influence call acquisition. For calves in these two studies, investigators knew the identity and pod-repertoire of the mothers but not of the fathers. Therefore, we can say nothing about the possible effect of the father on call development.

Mammalian calls can be genetically pre-de-

termined and acquired without exposure to conspecifics, as has been shown in squirrel monkeys (Winter *et al.* 1973) and some equids (Klingel 1977). However, call learning has been little studied in any mammals except humans. In birds, in which call learning has been studied extensively, most species possessing local "dialects" of the type described for killer whales have some learned component in their local repertoire (Marler and Mundinger 1971; Mundinger 1982). This is also the case with humans (Lieberman 1984). Thus, we hypothesize that the calls of killer whales are learned, at least in part.

Killer whale "dialects" have been described by Ford and co-workers for well-known pods in Puget Sound and British Columbia (Ford and Fisher 1982a, 1982b; Ford 1987). Such

dialects consist of calls constructed from trains or bursts of pulses (pulsed calls: Watkins 1967; Schevill and Watkins 1966), and are composed of one or several components, distinguished by rapid changes (of less than 20 milliseconds [ms]) in the characteristic pulse repetition rate and pulse waveform (Ford and Fisher 1982a). The pulse repetition rate is usually estimated by measuring the interval between bands on a sonagram. Hereafter we will call this interval the band interval.¹

The time-varying pulse repetition rate, time-varying pulse tone-frequency and characteristic aural quality (timbre) of the components, and the ordering of components in the call all are important features for categorizing calls. A few calls described to date have had an unusual overlapping component that was modulated independently of the other component(s), with a high tone-frequency. Ford described such independent components but did not measure their acoustic characteristics (Ford 1984, 1987). Hereafter we will refer to this component as an independently-modulated upper component (IMUC).

Ford (1984, 1987) categorized the calls largely by ear, although he then quantified them to look for interpod differences. He found that pods shared some calls, most of which could be broken into sub-categories unique to each pod. He measured the band intervals at selected points (e.g. beginning, middle, peak, end) in each component, the tone-frequency and the duration of each component (Moore *et al.* [1988 - this volume] provide a similar analysis). However, he did not quantify time-varying parameters or timbre.

The calls were often rather variable, with

¹ The terms "sideband interval" and "harmonic interval" were used by Ford and Fisher (1982a, 1982b) and Watkins (1967), respectively. We prefer the term "band interval" because it does not imply anything about the structure of the source waveform, whether pulsed or periodic. As we shall describe later, some components of killer whale calls apparently are periodic while others obviously are pulsed. The distinction cannot be made by looking at the sonagrams alone (Watkins 1967).

coefficients of variation ranging up to 50%. Therefore, a large number of parameters would have been needed to categorize them reliably by statistical means. The aural method of categorizing stereotyped calls is somewhat subjective; even so, we have adopted it, as subjective methods are usually used to categorize bird songs (Becker 1982) and other complex animal behaviours (Altmann 1974).

Nothing is known about how each individual whale uses its pod's repertoire of 8-15 different stereotyped calls. The repertoires of each individual within a given pod appear to be the same (Ford and Fisher 1982a; Ford 1984), although wild killer whales have only rarely been recorded in isolation. There is no obvious correlation between call types recorded during an encounter and the particular subset of a pod involved in that encounter (Ford 1984). Ford dismissed previous accounts of age- and sex-related differences in calls (Singleton and Poulter 1967; Dahlheim and Awbrey 1982) as dialect differences among whales from different pods.

For the present study, we hypothesized that the calf would acquire call types that she heard commonly, but we did not know whether she would select only her mother's calls or some more representative sample of the "pool" repertoire (the ensemble of all calls heard in the pool). Our *a priori* hypotheses were that: 1) the calf would learn at least some of the stereotyped calls commonly given by the other whales; 2) she would not learn any of her father's repertoire; and 3) her repertoire would resemble that of her mother more than those of the other whales in her environment.

METHODS

Acoustic recordings and behavioural observations of the calf were made during three short sessions in Orlando, Florida, in 1985 and 1986. The calf was housed in a 150 m × 50 m × 12 m pool with a plexiglass wall extending 2 m below the water line. Underwater visibility was in excess of 50 m during daylight. For the

first year, the calf was housed solely with three Icelandic killer whales, her mother, another adult female who often accompanied the mother and a subadult male who, for husbandry reasons, was frequently separated from the females by a visually and acoustically transparent gate. Two subadult females, added to the collection in September 1986, were usually kept separate from the calf. We made recordings on three successive days beginning when the calf was 12, 255 and 396 days of age, respectively. She spent most of her time with her mother and her mother's companion but occasionally interacted with the other whales.

The calf's parents undoubtedly had different call repertoires, as the father was captured in Puget Sound and the mother off southeastern Iceland. The calf was never exposed to her father's repertoire.

The stadium was monitored 16 hrs per day during each of the three sampling periods. Forty-five minute behavioural samples and simultaneous hydrophone recordings were collected at randomly selected times. (Results of behavioural observations are used herein only to interpret acoustic behaviour; they will be reported in detail elsewhere.) Whenever the whales began calling frequently, we made opportunistic high-quality recordings for 30 minutes with either an ITC 6050C hydrophone and a Nagra IV-SJ recorder (at 15 inches per second [IPS] = 38 cm/s) or a B&K 8103 hydrophone and a Racal Store 4D instrumentation recorder (at 15 or 30 IPS). The Racal recordings were used to document high-frequency clicks and check for the presence of very high frequency whistles. The recording hydrophone was immersed to 15 feet, 1.5 m from the plexiglass wall at one end of the pool.

During training sessions and at night, the young male occasionally was isolated in a back pool 50 m from the main stadium. At four such times we made 90 minute recordings using a Sony TCD5M cassette recorder; this provided a clean sample of attributable calls (calls that could be attributed to him alone). These samples were necessarily opportunistic,

as the male was not often thus confined. Usually, the whales were separated from one another by only a wide-meshed metal gate.

Recording sessions

Between 8 and 11 October 1985, sixteen 30-minute high-quality opportunistic recordings and 24 focal animal samples were taken. We also listened to the whales for additional 6-8 hours daily to establish the rates of nursing and the frequency of calling bouts during training sessions, performances, feeding and changes of nighttime staff.

Between 8 and 9 June 1986, strictly opportunistic recordings were taken, consisting of three 30-minute high-quality recordings of the calf when she was playing with the hydrophone and 240 minutes of cassette recordings of the adults at other times.

Between 27 and 28 October 1986, six opportunistic 30-minute recordings and ten focal animal samples were taken.

For preliminary analysis, the opportunistic recordings with attributable calls were singled out (Table 1). Once the random focal animal samples are analyzed, we may well find differences in the use of calls at other times. However, for this treatment we were mainly concerned with individual repertoires and did not find enough attributable calls to support any sort of statistical breakdown by context (time of day, weather, human activity, etc.). Screams or whistles that could not be categorized in any detail were not analyzed exhaustively, but we did examine a few screams that might have been confused with the calf's earliest calls. Clicks attributable to the calf when she was orienting towards the hydrophone were also examined, to determine when she might have started echolocating.

The calls of individuals were attributed in several ways. The best method was to detect the sound simultaneously in air and in water when a whale was at the surface near the hydrophone. At such times we could localize the caller reliably. When the callers were submerged, they had to be identified more cautiously. The whales often produced bubbles when calling, especially when they were very

TABLE 1

Details of the 19 opportunistic recordings with attributed calls, 8 October 1985–29 October 1986. The identities of the whales present during each recording are given in the last column (MO = mother, CA = calf, COM = female companion, MA = subadult male).

Date	Start Time	Duration (min)	Whale activity	Calls per minute of tape	Number of call types per tape	Whales in the stadium at the time of recording
10-7-85	1930	30	quiet swim	4.83	7	MO,CA,COM
10-8-85	0615	30	quiet swim	4.53	6	MO,CA,COM
10-8-85	0645	30	quiet swim	6.50	10	MO,CA,COM
10-8-85	0715	45	quiet swim	4.03	14	MA (isolated)
10-8-85	1000	45	training	4.36	10	MA (isolated)
10-8-85	1100	45	socializing	4.46	12	MA (isolated)
10-8-85	1800	45	training	10.63	15	MA (isolated)
10-8-85	1845	30	training	3.33	15	MO,CA,COM
10-8-85	1915	45	training	3.83	15	MA (isolated)
10-9-85	1700	30	quiet swim	2.26	7	MO,CA,COM
10-9-85	1730	30	quiet swim	6.36	7	MO,CA,COM,MA
10-10-85	1030	30	training	4.93	9	MO,CA,COM
10-10-85	1730	30	training, feeding	4.40	8	MO,CA,COM
10-11-85	1000	30	training	1.07	8	MO,CA,COM
6-8-86	1045	30	training, playing	9.86	15	MO,CA,COM,MA
6-8-86	1745	30	playing, resting	1.43	6	MO,CA,COM,MA
10-27-86	1100	30	socializing	3.93	11	MO,CA,COM
10-27-86	1226	30	socializing	1.73	8	MO,CA,COM
10-28-86	1730	30	socializing	1.13	11	MO,CA,COM,MA

active, as has been reported previously for bottlenose dolphins, *Tursiops truncatus*, (Caldwell and Caldwell 1979) and killer whales (Morton *et al.* 1986). In addition, we were able to guess the identity of a caller by using proximity cues. For example, when an isolated whale circled near the hydrophone, its calls were louder and less distorted than those of more distant whales. Neither method was completely reliable, of course; therefore, calls were attributed to a particular submerged individual only when it was well isolated from the others and very close (1–5 m) to the hydrophone or when it was relatively isolated and produced a string of calls and bubbles simultaneously.

It was easy to attribute calls to the young male when he was isolated in the back pool. Although he could hear and be heard by the other whales, he was at least 50 m from them, separated by several gates and the concrete mass of the main show stage. At such times, his calls a) were much louder than those from

the main stadium, b) did not, on a spectral display, show any evidence of distortion due to distance and/or c) did not sound distorted. We are confident that all the common calls in this whale's repertoire were identified, although his frequency of use of calls may have differed when he was with other whales from his frequency of calls during isolation. We did not record him immediately after he was placed in isolation. Instead, we made all the tapes at times when the whales call normally, such as after trainings and performances.

The sample of attributable calls is small. Only 116 were identified from the 19 opportunistic recordings that were analyzed. Thus, some rare calls in the repertoire of any individual may have been missed.

In 1984 the Nagra IV-SJ recorder and ITC hydrophone were used to make 30-minute recordings at Sea World of California of the calf's father, while he was completely isolated in a holding pool. Three hundred and five calls were identified. However, as the father's

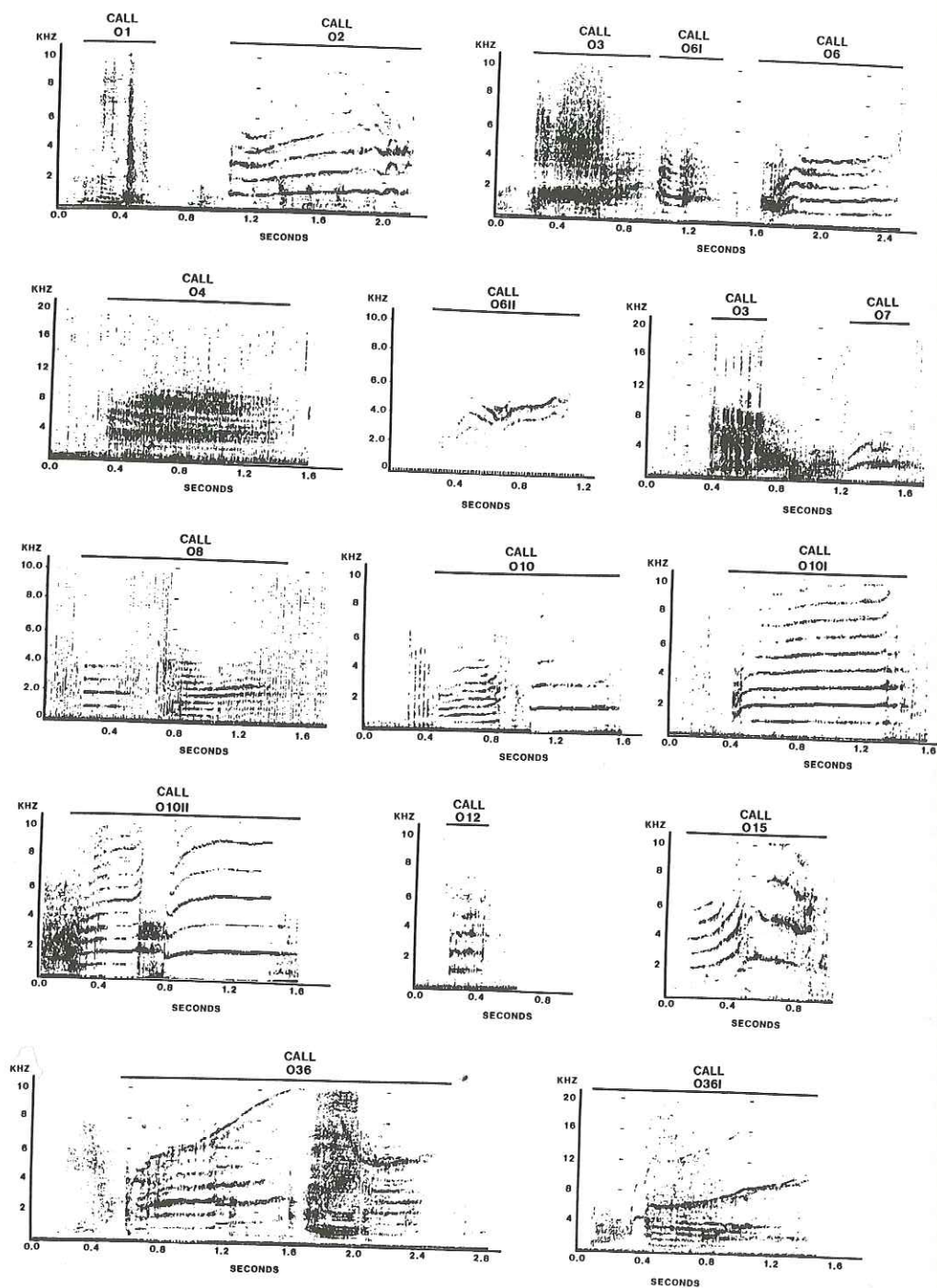


Fig. 2. Sonograms of the 16 calls produced by the adult whales in Orlando (see Table 2 for descriptions). Calls O1, O2, O3 and O6 are shown first in a typical sequence; the rest are shown in order by number.

behaviour was not quantified at other times, we cannot be sure we identified rare calls in his repertoire.

Calls of adults (and the young male, treated in this analysis with adults) and calf were identified and categorized by ear using the methods of Ford (1984). Sonograms were analyzed and plotted on a Multigon Industries UNISCAN II digital sonograph, and waveforms and spectra were analyzed on a Spectral Dynamics SD345 spectrum analyzer. The sampling rate was always twice the maximum frequency shown in each figure given below; the corresponding bandwidths are given with the figures.

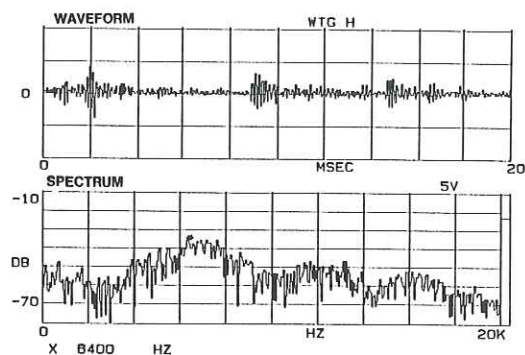
RESULTS

Adult call repertoires

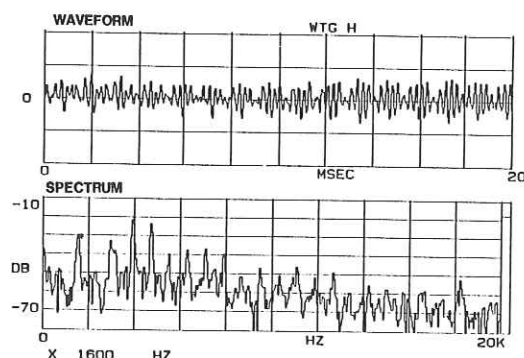
The "pool" repertoire of the three "adults" in Orlando consisted of sixteen stereotyped calls, each heard a total of four or more times on the nineteen selected tapes (Fig. 2). Call timbre varied greatly (including buzzy sounds, flute-like tones, screams, and hollow sibilants), but most calls could be classed as pulsed, in agreement with descriptions by previous authors (e.g. Schevill and Watkins 1966; Steiner *et al.* 1979; Ford and Fisher 1982a).

The distinguishing characteristics of the calls are summarized in Table 2. For this treatment, pulse repetition rates were estimated by measuring the band interval of each component. We defined a few subjective terms: a "burst" is a short, loud, broad-band noise; "sibilants", "raspberries", "squeals" and "screams" sound like human sounds of the same name; "hollow" sounds have a resonant timbre, as though they were made in an enclosed space; "flat" sounds have constant tone-frequencies. The waveforms of call components varied considerably, from obviously-pulsed (periodic waveforms composed of bursts of one or a few cycles with large duty cycles) to nearly-periodic (Fig. 3).

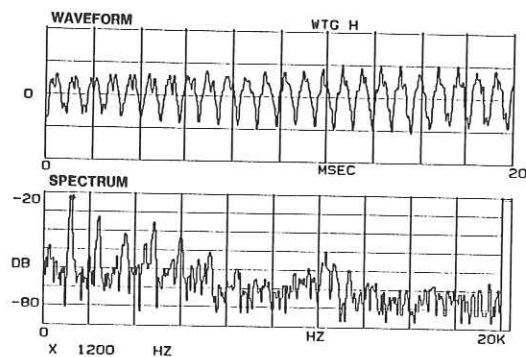
The statistical treatment of acoustic characteristics necessary to separate calls and components into categories quantitatively is beyond the scope of this paper. However, we



(A)



(B)



(C)

Fig. 3A-C. Waveforms and spectra of three selected segments of adult calls, showing the range from obviously pulsed-type calls to nearly-periodic ones. A) is a segment from call O1, B) from component 1 of call O36 and C) from component 3 of call O36. See Table 3 for ranges of pulse repetition rates and pulse tone-frequencies of these segments.

checked the most common call categories by selecting 20 ms segments from relatively constant portions of the most common calls and measuring the following: tone-frequency, calculated by measuring the period between successive peaks of the pulse waveform; pulse repetition rate, i.e. the period between successive pulses (in several cases the pulse wave-

form was absent, obscured or too long to detect in a 20 ms window); and the spectral peak, i.e. the spectral component with the highest amplitude (Table 3).

We have assumed that the call components were all pulsed and that any apparently periodic forms resulted from interactions among overlapping, independent upper com-

TABLE 2
*The distinguishing characteristics of the 16 call types used by the Orlando whales. Pulse repetition rates were estimated by measuring band intervals on the sonograms. Notations marked * refer to components of the call, including the IMUC.*

Call type	Duration (seconds)	Pulse repetition rate (kHz)	Subjective description
O1	0.2-0.4	0.2-0.4	short, harsh-sounding, upswept
O2	0.8-1.5	1.0-2.0	rising scream, often with a short onset burst
O3	0.3-0.5	0.1-0.2	low, harsh "raspberry" sound
O4	0.5-1.5	0.4-0.8	"hollow" sounding sibilant, composed of two overlapping pulsed components
O6	0.8-1.2	0.6-1.0	flat-sounding scream, similar to O2 but lacking distinctive upsweep
O6i	0.4-0.5	0.5-0.7	shortened version of O6, only occurred after O3 and before another O6
O6ii	0.8-1.2	0.6-1.2	warbled version of O6, similar in timbre; rare
O7	0.4-0.6	1.0-2.0	short upsweep; rare
O8	*C1:0.2-0.4	0.8-1.0	flat, high, pure tone
	*C2:0.8-1.0	0.4-0.6	flat, low, pure tone; interval between was about 0.2 sec; two distinct notes with no sharp transition bursts on leading or trailing end; rare
O10	*C1:0.4-0.6	0.4-0.8	flat, low, pure tone, sometimes with short upsweep at end; similar in timbre to C2 of O8
	*C2:0.4-1.0	1.5-2.5	flat, high, pure tone, trailing off at end; common; O8 may be a variant
O10i	1.0-1.5	1.0-2.0	flat sounding, high, pure tone; may be categorized as a separate call after sample sizes are increased because the harmonic intervals of the two calls differ slightly; difficult to distinguish from a call given by calf's father
O10ii	*C1:0.4-0.6	0.6-1.0	flat, low, pure tone, upsweeps sometimes present at end of C1, but not obvious to the ear
	*C2:0.1-0.2	—	burst; no obvious repetition rate, not buzzy like O3
	*C3:0.6-1.0	1.8-2.5	flat, high, pure note, trailing off at end; rare
O12	0.2-0.3	1.0-1.2	short, harsh, flat, high note; rare
O15	*C1:0.2-0.3	0.8-1.2	upswept rapidly over a range of 2-3 kHz, timbre of scream O2
	*C2:0.3-0.5	2.0-3.0	flat, high scream; abrupt downsweep at end making it sound "swallowed"; rare
O36	*C1:0.8-1.5	0.8-1.2	flat, shrill scream, slowly rising, occasionally with a short burst at beginning
	*IMUC:0.8-2.0	6.0-8.0	IMUC, contributing to the shrill timbre, loud, upswept from 6-12 kHz overlapping first component, end variable, but usually present overlapping C1, C2, C3
	*C2:0.3-0.4	0.2-0.4	burst, similar in quality to O3
	*C3:0.5-1.5	0.4-0.8	flat, shrill scream, similar to C1, but often shortened
O36i	*C1:0.1-0.3	0.8-1.2	short burst, buzzy, similar quality to O3, frequently absent
	*IMUC:1.0-1.2	4.0-6.0	IMUC, may begin before C2, trails off, high relative amplitude
	*C2:0.8-1.2	0.9-1.2	flat, shrill scream, slowly rising, trails off at end, same as C1 of O36

ponent (see further discussion below), pulse duty cycle, pulse repetition rate and pulse structure.

Eighty-two percent of the 1427 calls examined (116 attributable, 1311 unattributable) were in one of four categories (Fig. 4). Figure 5 shows the 116 attributable calls by call-

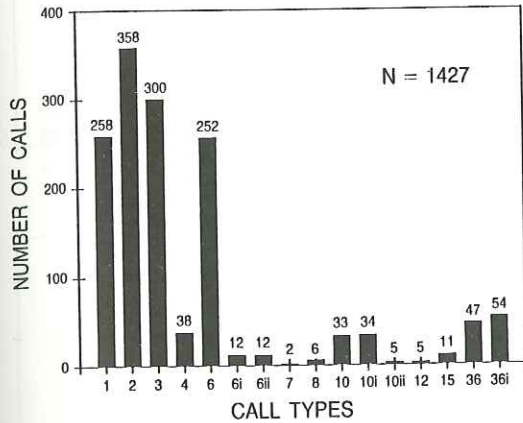


Fig. 4. Frequency of call use of the sixteen calls identified from the tapes collected in Orlando.

type and whale. The mother and her companion shared 6 of 7 call types but used different calls predominantly (Fig. 5; see Analysis below). The young male produced all six call types, characteristic of the adult females, but most commonly used four calls never attributable to the females (Fig. 5D). One of these was aurally similar to a call produced by the calf's father (call type O10i).

We did not attribute any calls to the two females introduced in September 1986. For the analysis discussed in this paper, we chose recordings of mother, companion and calf made when the newcomers were isolated and apparently quiet. As we identified no new call types in the sample selected, it seems unlikely the residents had acquired calls from the newcomers by that time.

Call Use

The whales tended to call frequently just after sunrise and at sunset, during or after interactions with humans or when anything unusual happened (e.g. a violent rainstorm, un-

TABLE 3
Acoustic characteristics of the six calls shared by the adult Orlando whales.

Call (see also Figure 3)	Tone frequency (range, in Hz)	Pulse repetition rate (range, in Hz)	Spectral peak (range, in Hz)	Comments
O3 (unattrib.)	6250-9090	141-174	6400	Pulses were bursts of 5-10 cycles with a pause 4-5 times the burst duration.
O1 (unattrib.)	3800-6250	400-512	3800	Pulses were bursts of 5-7 cycles with a pause 1-2 times the burst duration. A sonogram is given in Fig. 2, waveform in Fig. 3A.
O36 (Mother)	1900-2750	588-769	2900	Pulses were bursts of 1-3 cycles with a pause of around 1 cycle. The band interval is 950 Hz. A sonogram is given in Fig. 14A and a spectrum in Fig. 3B.
O2 (unattrib.)	3700-4400	775-950	3950	Pulses were bursts of 4-5 cycles with a pause of 1-2 cycles. Band intervals on the spectrum were 800-1400 Hz.
O6 (unattrib.)	1020-1220	—	1150	Calls contained pulses or modulations of long duration; the waveform is triangular with a slow modulation at 10 Hz. Waveform was variable.
O36 (Mother)	1225-1275	—	1200	This segment not obviously pulsed; had an apparently triangular waveform mixed with independent upper component at 6 kHz. Sonogram is given in Fig. 14A, waveform and spectrum in Fig. 3C.

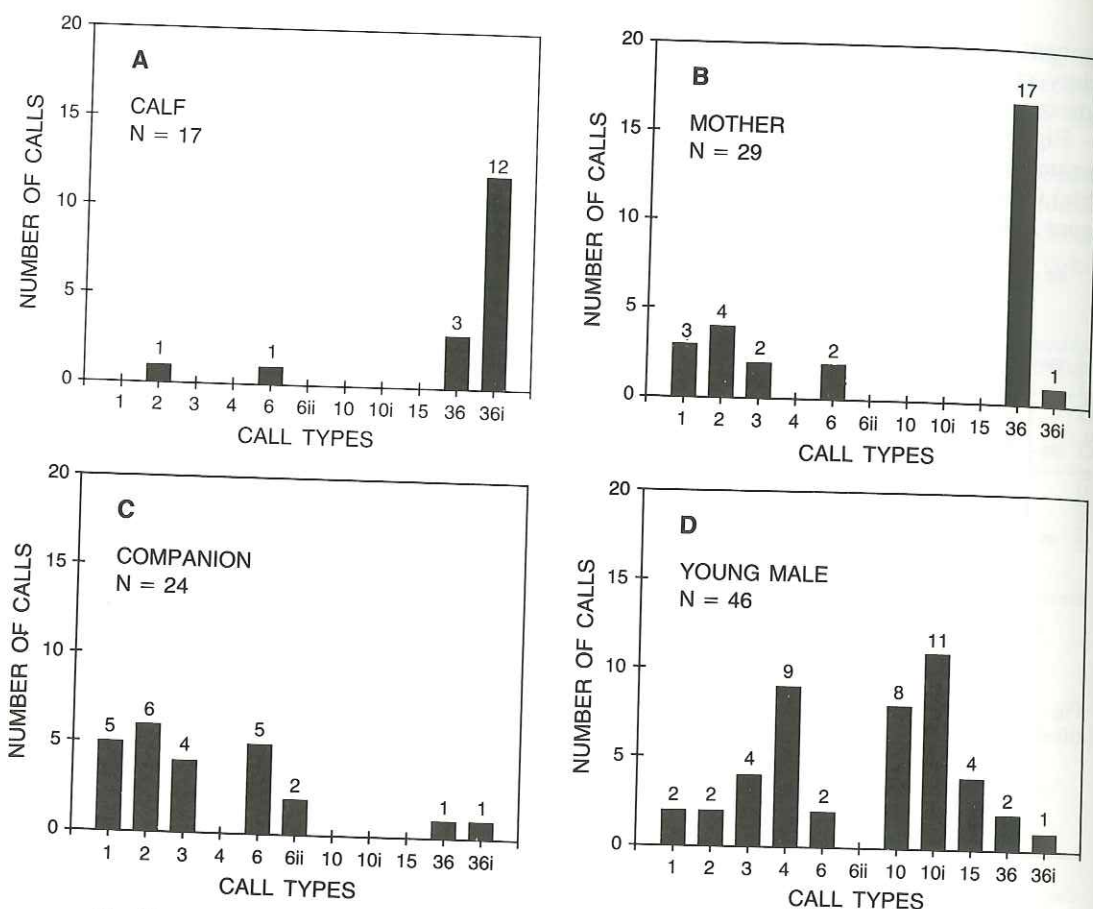


Fig. 5A-D. Frequencies of calls used by each whale, from the sample of 116 attributable calls.

expected visitors at night and divers working in the pool). The mean numbers of call types heard per 30 minute sample were 7.5 during quiet swimming and 11.0 during bouts of socializing or training. This difference was not significant ($N = 19$; $d.f. = 2, 12$; $F = 1.361$; $P > 0.05$) after we accounted for the tapes of the young male in isolation, whose call rate was significantly higher than that of other animals ($F = 7.78$; $d.f. = 1, 17$; $P < 0.05$).

We did not calculate rates for individuals because there were too few data. Calls were easier to attribute when the whales were in training or socializing; at such times "bubbling" was much more common and the whales did not spend as much time swimming in unison.

Using various means, we attributed 116 calls to individuals (Table 4). As only six of the young male's calls were attributable by methods other than isolation, we could not determine whether the frequency distribution of his calls differed by method of attribution. Calls from the mother were attributed mostly from bubbling; those of her companion mostly from calls at the surface. For example, call type O36 dominated the bubbling sample; all but two of them were attributable to the mother. Most of the calf's squeals were attributable by bubbling, as well.

When the whales were very active, calls were given in rather variable form, as described by Ford and Fisher (1982a) for socializing wild killer whales. These variations

TABLE 4

Summary of call types by whale and method of attribution (see text for definitions of methods).

Method of attribution	Call type	N All whales	N Mother	N Companion	N Young male	N Calf
Bubbling	1	4	2	2	0	0
	2	5	2	3	0	0
	3	5	2	3	0	0
	6	3	2	1	0	0
	6ii	1	0	1	0	0
	10	1	0	0	1	0
	36	13	13	0	0	0
36i	5	1	0	0	4	
Totals	8	37	22	10	1	4
Isolation (young male)	1	2	0	0	2	0
	2	2	0	0	2	0
	3	4	0	0	4	0
	4	8	0	0	8	0
	6	1	0	0	1	0
	7	1	0	0	1	0
	10	7	0	0	7	0
	10ii	10	0	0	10	0
	15	4	0	0	4	0
	36	1	0	0	1	0
	36i	1	0	0	1	0
	Totals	10	41	0	0	41
At surface	1	4	1	3	0	0
	2	5	1	3	0	1
	3	1	0	1	0	0
	6	5	0	3	1	1
	6ii	1	0	1	1	1
	10ii	1	0	1	0	0
	36	3	2	0	0	1
	36i	7	1	0	0	6
	Totals	8	27	5	12	2
Proximity	4	1	0	0	1	0
	6	1	0	1	0	0
	36	6	2	1	1	2
	36i	3	0	1	0	2
Totals	4	11	2	3	2	4
Table totals	—	116	29	24	46	17

took the form of warbling, especially at the end of the call, rapid changes in the band interval of components of the call, changes in call duration and "squealing" a harsh-sounding change in the timbre of the call. Despite these variations, we were often able to identify call types by the types and ordering of components and harmonic intervals. We discarded any that were difficult to categorize.

Calls O1, O2, O3 and O6 were usually given in sequence. Even so, for this analysis we classed them as separate call types. They were separated by a relatively long interval (100 ms), any one might be missing from the sequence and all of them occurred in isolation from time to time. The O1-O6 sequence was so common that we might as easily have scored it as a single call with variants. In the

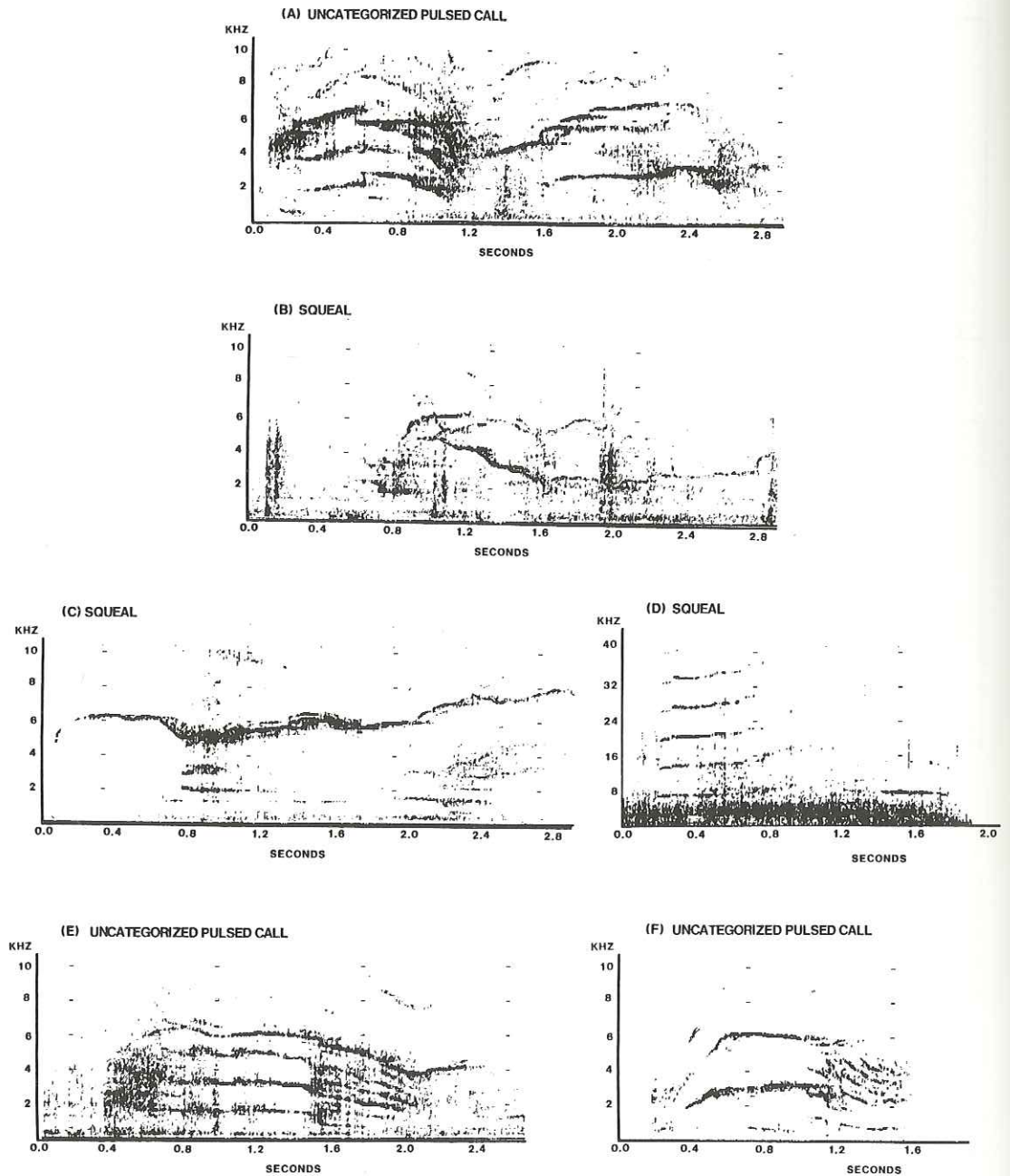


Fig. 6. Sonograms of the types of calls attributable to the killer whale calf at 12–15 days. A) a rough squeal following an O36 call from the mother. B) an irregular squeal with 2–3 independent components, the calf's most common call. C) a squeal, showing the occasional lapses into pulsed-type, lower-frequency components. D) a squeal showing the broad bandwidth of the calf's productions. E) and F) screams more closely resembling the adult calls but not of any categorizable type. The filter bandwidth was 80 Hz for sonograms A–C, E, F, 320 Hz for sonogram D.

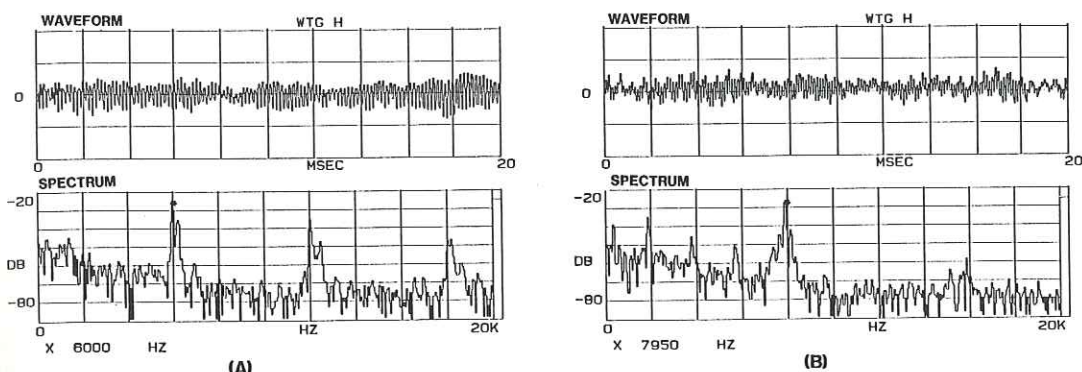


Fig. 7A-B. Waveforms of a representative calf squeal. A) a segment taken from the beginning of the squeal in Figure 6C. Note the distinct spectral peak (*) at the tone frequency and its harmonics, and the evidence of some slow modulation in both the waveform and the spectrum (secondary peaks at 6.1, 12.5, and 18.5 kHz). B) a segment taken from the center of the squeal in Figure 6C. The waveform is more distinctly pulsed, and spectral peaks are evident at roughly the pulse repetition rate (around 1900 Hz). The filter bandwidth was 50 Hz.

father's repertoire, three calls were similarly associated. Calls in sequences accounted for 82% of the sample in Orlando and 76% of the sample from the father (such sequences are reported by Ford [1984], Bain [1986] and Ford and Fisher [1982a]).

Acoustic characterization of the calls

The most important acoustic parameters of the calls are summarized in Table 2. Although we could not assign call types to pod-specific variants, we did notice that a few calls were very similar in timbre and component structure. These were classed as variants of one another, denoted by a subscript "i" for the first variant, "ii" for the second, and so on. For example, call O36 was composed of three components, a scream, a buzzy burst and a second scream like the first but with a somewhat lower pulse repetition rate (Table 2). These components were produced without pausing and the call always had an independently-modulated upper component (IMUC). Variant O36i contained the initial scream, including the IMUC. Call O36 often had only a rudimentary third component, suggesting that it was often truncated; thus, it is reasonable to expect that a version of the call might arise with the last components habitually truncated. Both versions were sometimes preceded by a variable burst.

IMUCs were found only in calls O36 and O36i. The IMUC gave the call a shrill timbre and possibly contributed to the rather periodic appearance of the waveform (Fig. 3C). Its band interval always increased with increasing frequency, suggestive of a harmonic function. The first component of the IMUC was always of higher amplitude than the others, also suggestive of a harmonic function.

The band interval of the adult calls ranged from 0.1–12 kHz. The band with the greatest amplitude was usually the first, second or third. The independent upper component of some calls had a wide harmonic interval (7–8 kHz with bands detectable to 25 kHz). Some of the buzzes reached also up to about 20 kHz (see Fig. 2, Call O36). Call components ranged in duration from 0.2–1 second (s). As might be expected, calls composed of several components were of longer duration (1–2 s) and the sequence O1-O2-O3-O6 lasted over 4 s. The harmonic intervals of the calls varied from 0.1 kHz to 2 kHz.

Repertoire of the calf at 12–15 days. The twenty-six calls attributable to the calf during the first study session were variable but shared a harsh, shrill timbre (Fig. 6). Eighteen were attributable by bubbling. We called these calls squeals (80% of the calf's calls, Fig. 6A–D) or in the case of her few more adult-like produc-

TABLE 5
Acoustic characteristics of the calf's most common calls.

Call	Tone frequency (Hz)	Pulse repetition rate (Hz)	Spectrum peak (Hz)	Comments
Squeal (Calf) Fig. 7A	4166-5263	1428-1960	5800	Call irregularly pulsed; independent upper component has peaks at 5.8, 11.55 and 17.3 kHz; the pulse repetition rate was difficult to measure. A sonogram is given in Fig. 6A.
Squeal (Calf) Fig. 7B	5550-6666	—	6000	Call was not obviously pulsed; this segment was taken from the beginning of the squeal in Fig. 6C.
Squeal (Calf) Fig. 7C	7500-9500	—	7950	Pulses are not obvious in the waveform, the bands appear in spectrum at interval 1800-2100 Hz; segment has two independently modulated components. This segment was taken from the call in Fig. 6C, at 0.85 sec.
O36 (Calf) Fig. 14A	1800-2500	750-1050	1950	The call is pulsed, but pulse duration and interval are difficult to measure; the upper component has bands at 6.1, 12.2 and 18.3 kHz. The sonogram is given in Fig. 12B.
Independently modulated upper component O36i (Calf; see Fig. 14B)	10869-11250	1329-1524	10875	Pulses are not obvious in this call; it is roughly a triangular wave, amplitude modulated with a period of 10 Hz. A sonogram is given in Fig. 12C

tions, uncategorized pulsed calls (Fig. 6E-F). The adults occasionally squealed when highly aroused, but we have no good recordings of these sounds. The band intervals of the calf's squeals ranged from 2-8 kHz, with detectable bands up to 40 kHz (Fig. 6D), well above the adult range. Squeals sometimes had 2-3 independently-modulated components (Fig. 6B). The waveforms of squeals were not clearly pulsed (Fig. 7, Table 5). They lasted 2-4 seconds, approximately the length of the longer calls and call sequences of the adults. Squeals often lapsed into noisy, sibilant sounds (Fig. 6B).

In three cases, the calf's uncategorized pulsed calls had an IMUC like those in O36 and O36i (Fig. 6A and 8B). The presence of such an IMUC is very characteristic of the mother's preferred calls, but not of the calls of any of the other whales.

Two sequences of calls involving mother and calf were documented. In the first, the mother produced an O36 (Fig. 8A), followed by a call from the calf (Fig. 8B) that contained

two similar components overlapped by an independent component. In the second (Fig. 8C), the calf's squeal bore no obvious resemblance to the mother's O36i call. It overlapped the end of the O36 call and rose slowly in frequency like the mother's IMUC, such that it could have been an imitation of that component only.

Repertoire of the calf at 8 months. The calf produced a wider variety of sounds during the second recording session than during the first (Fig. 9). This variability may have been unusual: she was much more interested in the hydrophone at this stage and spent the better part of an hour making sounds at it after it was introduced into the stadium. (All calls from this session attributable to the calf were, in fact, produced during this hour.) However, the variety of sounds is at least indicative of her abilities at this stage.

The 20 attributable calls included squeals, low groans with pulse repetition rates of around 75 Hz (Fig. 9A), bursts of clicks (Fig.

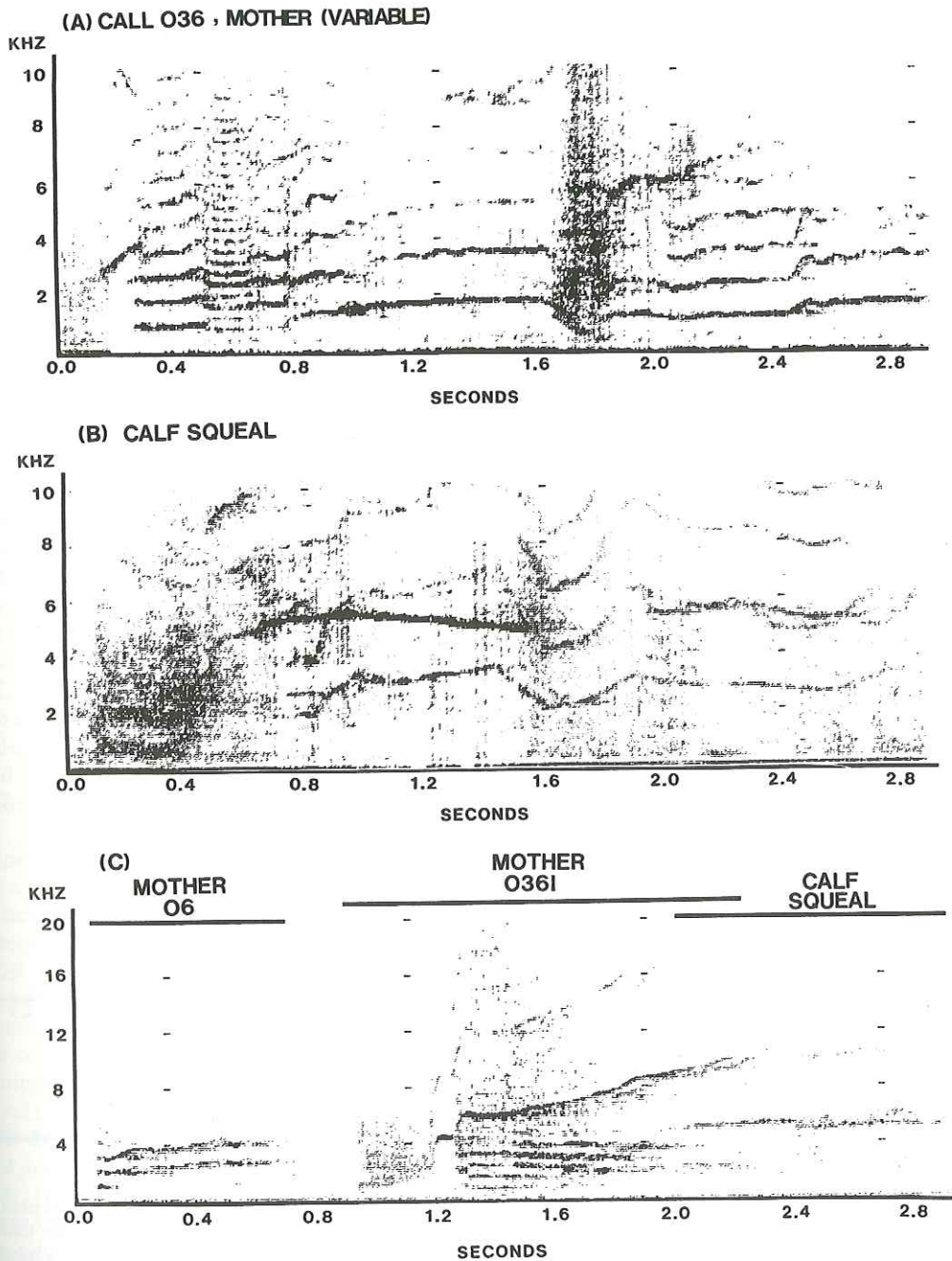


Fig. 8A-C. Sonograms of two sequences of calls attributable to the mother and calf. An O36 call from the mother (A) is followed by a squeal from the calf (B). The calf's response is broken into segments with timing similar to the mother's call and has an IMUC. The next example (C) shows an O36i from the mother overlapping a squeal from the calf, showing the similarity between her IMUC and the calf's squeal.

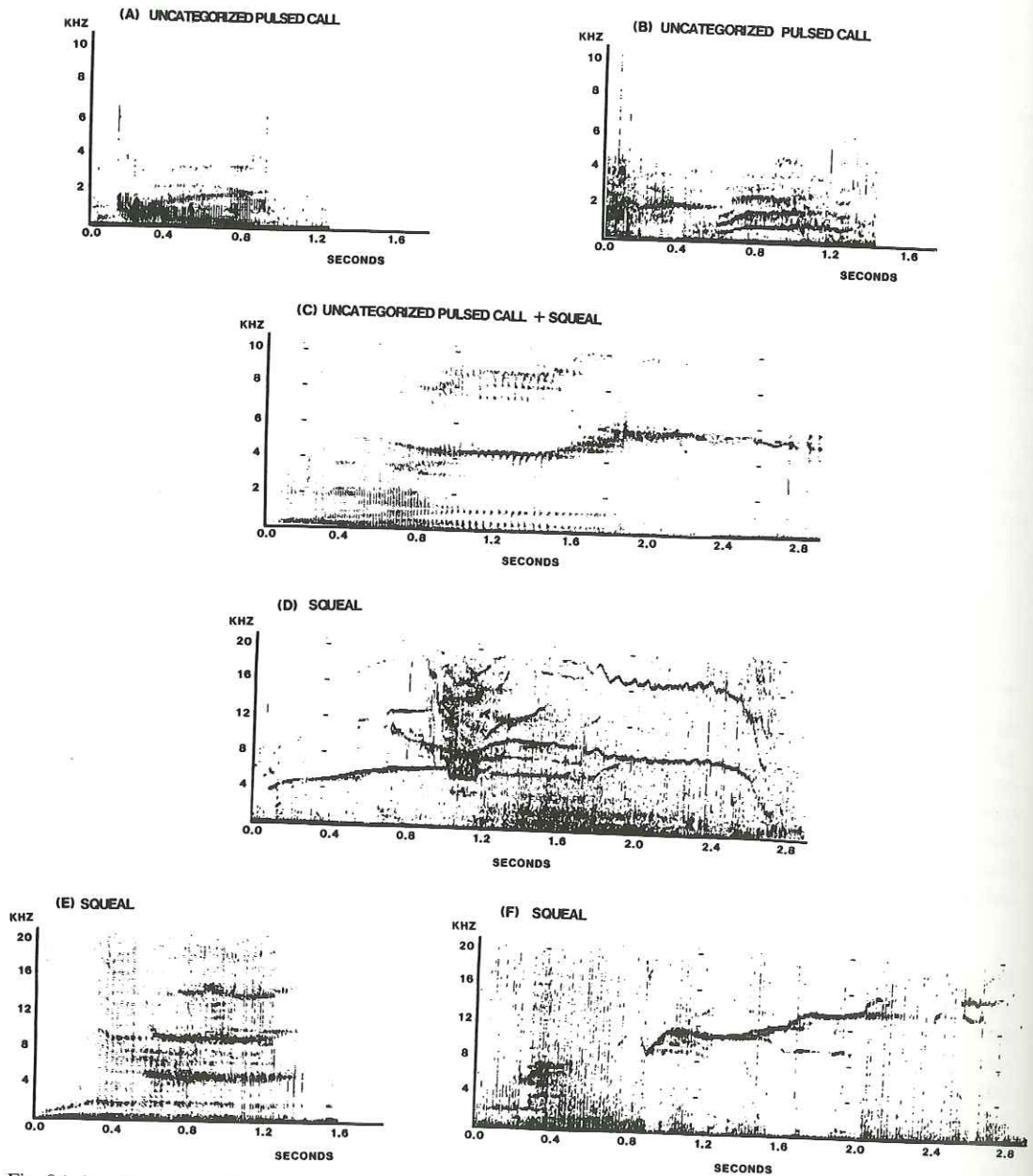


Fig. 9A-F. Sonograms of the call types attributable to the calf at 255-256 days. A) a low groan with pulse repetition rate of around 75 Hz, in the range of normal adult calls such as O3 and O4, but lacking their characteristic timbre. B) a pulsed-call of the adult type. It was never repeated and did not resemble any of the adult calls. C) a burst of pulses that graded into a squal, suggestive of two independent components, one pulsed and one periodic, as in the mother's O36i calls. D) a squal showing the presence of IMUCs; timing similar to the mother's O36 call. The low-frequency burst from 1.2-1.6 sec is in the background. E) a harsh screech the calf made several times while playing with another whale. F) a randomly-modulated high-pitched squal, like call 6C, showing that the calf still retained the most characteristic element of her early repertoire. The filter bandwidth was 80 Hz (A-C) and 160 Hz (D-F).

10 and 11) and a few adult-like screams (Fig. 9B) with harmonic intervals of 1–2 kHz and durations of 0.5–2 sec, none of which could be categorized. The squeals had IMUCs (Figs. 9D and F) and were highly variable. One (Fig. 9D) had roughly the correct component timing for the O36 call (two squeals separated by a harsh and undefinable burst) but was otherwise unlike it. Although admittedly sparse, these data show that, 1) the calf was producing sounds with roughly the correct timing and frequency range for most calls attributable to the adults, 2) none of her calls could be categorized at this stage and 3) many were distinctly pulsed, with pulse repetition rates and tone-frequencies in the range normal for the adults (e.g. Figs. 9A and C).

In the first session, the waveforms of the calf's squeals were not always distinctly pulsed and the sonagrams showed only subtle sidebands (Fig. 7). The waveforms were most similar to the IMUC of the mother's most common calls. In this second session we saw several instances, illustrated best by Figure 9C, when the calf's call ranged slowly from obviously pulsed to an ambiguous squeal. The pulsed part of the call and the squeal overlapped; so, they were apparently produced by different sources.

Repertoire of the calf at approximately 1 year. At age 396–398 days, the calf was, in addition to her squeals, producing calls which could be categorized and were similar to the mother's most common calls (Figs. 12A and 12E), although the calf's version was somewhat different from those of the adult. For example, the tone-frequency of the independent upper component often changed in sharp steps instead of rising evenly (Fig. 12A), and her O36 calls had greater ranges of duration (0.8–3 s) and harmonic interval (0.5–1.5 kHz). However, the number and order of components in these calls and the band intervals were within the adult range and the waveforms were distinctly pulsed (Fig. 13A).

Twelve of the calf's 17 calls were classified as O36i, three as O36. In the four instances when categorizable calls occurred in call se-

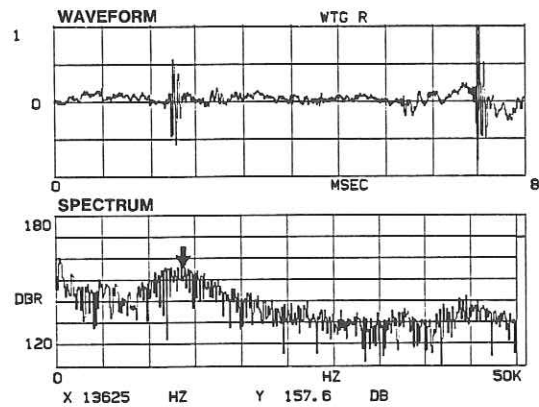


Fig. 10. An oscillogram and spectrum of two clicks from a train emitted by the calf as she approached the hydrophone and grabbed it. The peak frequency of clicks in this train ranged from 10 to 17 kHz. The clicks resembled echolocation pulses of adult killer whales. The filter bandwidth of the spectrum is 125 Hz.

quences with the mother (two are shown in Fig. 14) the calf used the O36i call.

Ninety percent of the calls attributable to the calf were of the same type as the two most characteristic calls of the mother, even though 38% of the mother's calls and 82% of the calls in the pool were of other types. A sequence of calls was rarely attributed to both mother and calf. Even so, whenever the calf was calling, sequences of the type shown in Figure 14 could be found. The calf favoured the shortened version of the mother's favoured call but was capable of producing the whole call (Fig. 12A and possibly 12F).

Although several of the calf's calls were assigned tentatively to other call categories (e.g. O6 in Fig. 12B), these could have been reduced or altered versions of the O36 call. No call types were detected from the calf that were recognizably unique to the young male or the father.

The calf tended to extend the IMUC beyond the normal end of the call. Thus, waveform and spectrum of this component could be studied undistorted by the other portions of the call (Fig. 13B). The waveform appears to be harmonic, like a triangular wave (see also Table 5). The tone-frequency is approximately 11 kHz, very weakly amplitude-

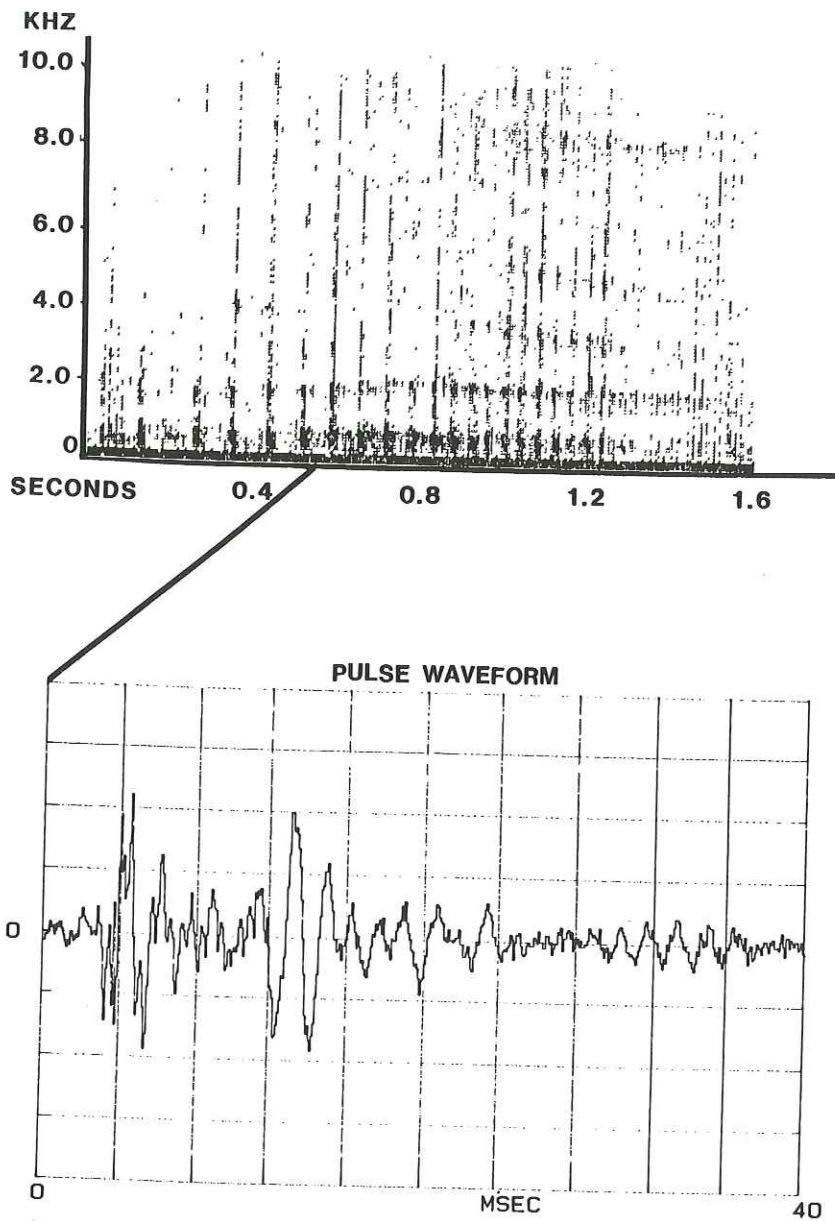


Fig. 11. A sonogram of a train of hollow-sounding, low-frequency clicks made while the calf oriented on the hydrophone. The waveform of one such click is shown in detail. The second mode in this click may be a reflection from the water's surface.

modulated at around 1500 Hz; at 12.5 kHz it appears as a single peak in the spectrum.

Ontogeny of echolocation clicks. Caldwell and Caldwell (1977) observed that bottlenosed dolphin calves click from birth. We cannot confirm that killer whales do so.

During the first session the calf passed by the hydrophone on several occasions in isolation from the mother but evidenced no interest in it, did not orient towards it or grab it and apparently produced no clicks.

During the brief second recording sessions, the calf spent an hour on two separate occa-

sions playing with the hydrophone, nudging it and producing a wide variety of sounds, including clicks. One click sounded like an adult echolocation train and was spectrally similar to killer whale echolocation clicks reported elsewhere (Schevill and Watkins 1966; Diercks *et al.* 1971). She emitted the click in Figure 10 when she was approaching the hydrophone, at a range of 1–2 m, oriented di-

rectly towards it and at right angles to the plexiglass wall. The peak frequency was 10–17 kHz. The levels were roughly 158 dB re 1 μ Pa.

The second type of click attributable to the calf was a version of a train of low-frequency clicks sometimes heard from the adults sounding like hollow pops or claps (Fig. 11). This click has been described for other captive

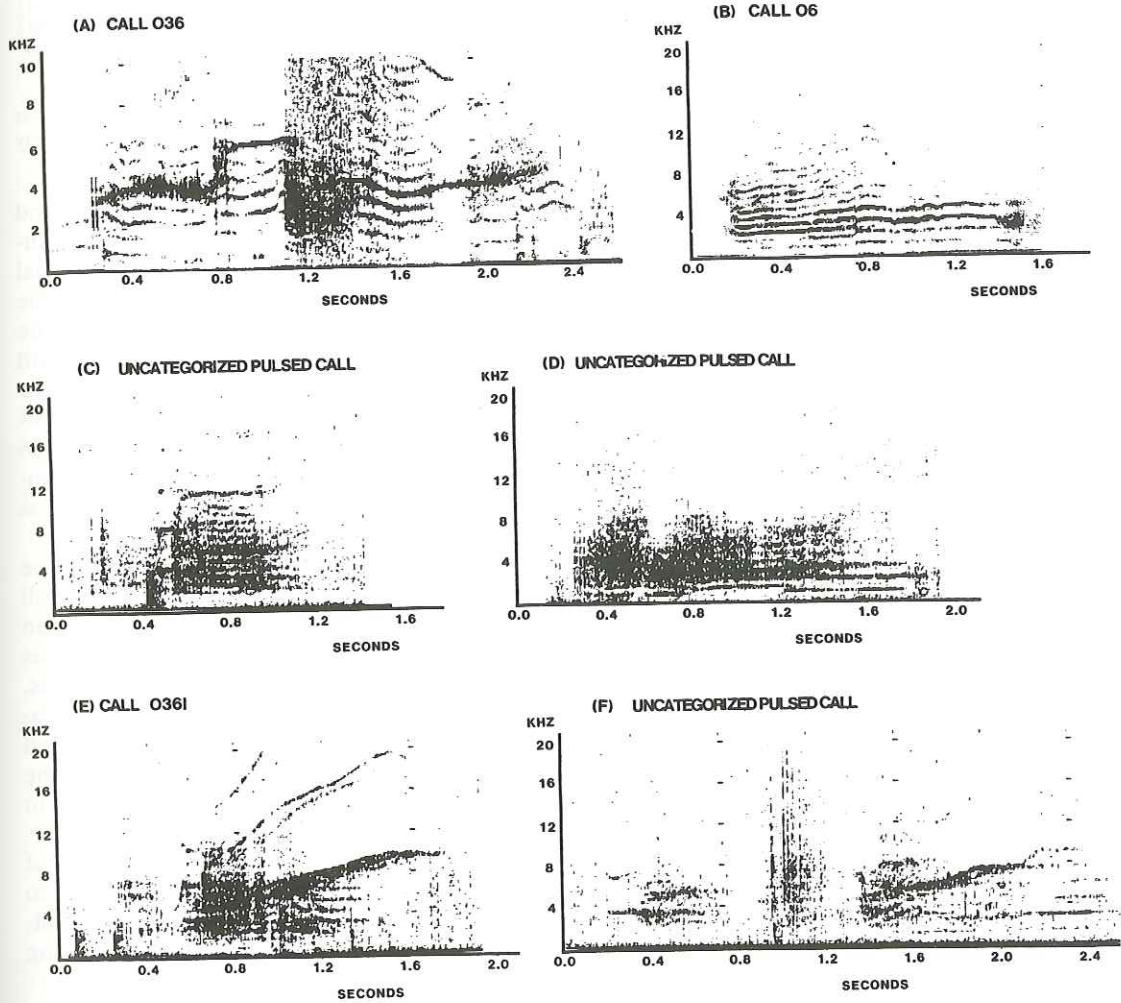


Fig. 12A–F. Sonograms of call types attributable to the calf at approximately one year. A) a version of the O36 call, with all the correct components. B) an O6 or an O36i without the inharmonic component. C) a short pulsed call with obvious similarities to O36i. D) a low honk that could not be categorized. E) a categorizable version of O36i. F) a probable O36, although it could also be categorized as a sequence O6-O3-O36i. As a result of this ambiguity it was not categorized. These sonograms show the variability of the calf's calls. The filter bandwidth was 80 Hz (A) and 160 Hz (B–F).

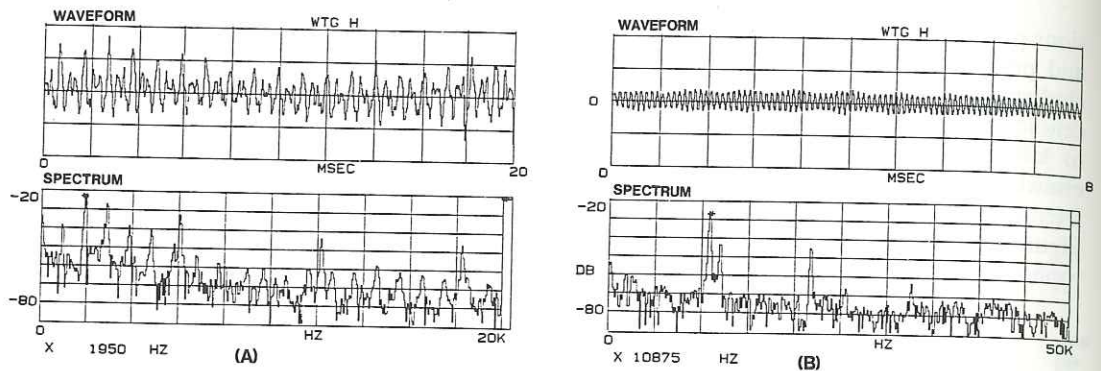


Fig. 13A-B. A sequence of calls, first from mother, then from calf, collected when it was approximately one year old. A) is an O36 call from the mother. B) and C) show a sequence of O36i calls given by the calf immediately following. The filter bandwidth of all three was 160 kHz.

killer whales (Dahlheim and Awbrey 1982) and wild killer whales (John Hall, pers. comm.). The calf swept her head broadly from side to side as she emitted these clicks, as though eyeing the hydrophone. The clicks were composed of single or possibly double bursts with peak frequencies at around 500–700 Hz and a secondary peak at around 2 kHz. The click repetition rate was around 20 Hz, and the interval between the first and second burst was 8 ms, a reasonable interval for a reflection from the surface.

ANALYSIS

As discussed by Ford (1984), calls that tend to occur in stereotypical sequences complicate any statistical treatment of call frequency, because they are not independent events. The calls in our sample, as in Ford's (1984) sample from wild killer whales, often occurred in sequences. To avoid bias, Ford measured the presence or absence of call types in the repertoires of different pods rather than relative call frequencies. He compared pod repertoires using single-link cluster analysis on an index of similarity that accounted for differences in repertoire size (Morgan *et al.* 1976).

Following these methods we calculated an index of similarity (IS) for all possible pairs of the four whales in our study according to the formula:

$$IS = 2 \times N_o / (R_1 + R_2)$$

where N_o is the total number of call types and subtypes shared, R_1 is repertoire size of individual 1 and R_2 is repertoire size of individual 2. The results are given in Table 6. The greatest similarities were found between the mother and her companion ($IS = 0.92$) and the mother and calf ($IS = 0.80$). The value for mother and calf would be much smaller ($IS = 0.44$) if the single instances of calls O2 and O6 were erroneously attributed. Thus, it was important to look at frequencies of call use as well as similarities between repertoires.

We were unable to distinguish reliably one of the father's calls from the young male's call O10i. This links them as expressed by an index of similarity of 0.11. The two whales cannot have come from the same wild pods. But, as they have been housed together occasionally, the young male may have imitated the father. The mother was housed with the father for over a year but was not heard to produce this call.

The young male commonly produced at least four calls that were never attributable to the females; hence his generally lower IS values. The calf was less similar to the young male than to the females.

Based on the frequency of call use, there seemed to be differences among all three adults, although the repertoires of the two females are very similar (Fig. 5). Our sample may be biased, of course, since the attributable calls were not drawn at random and sam-

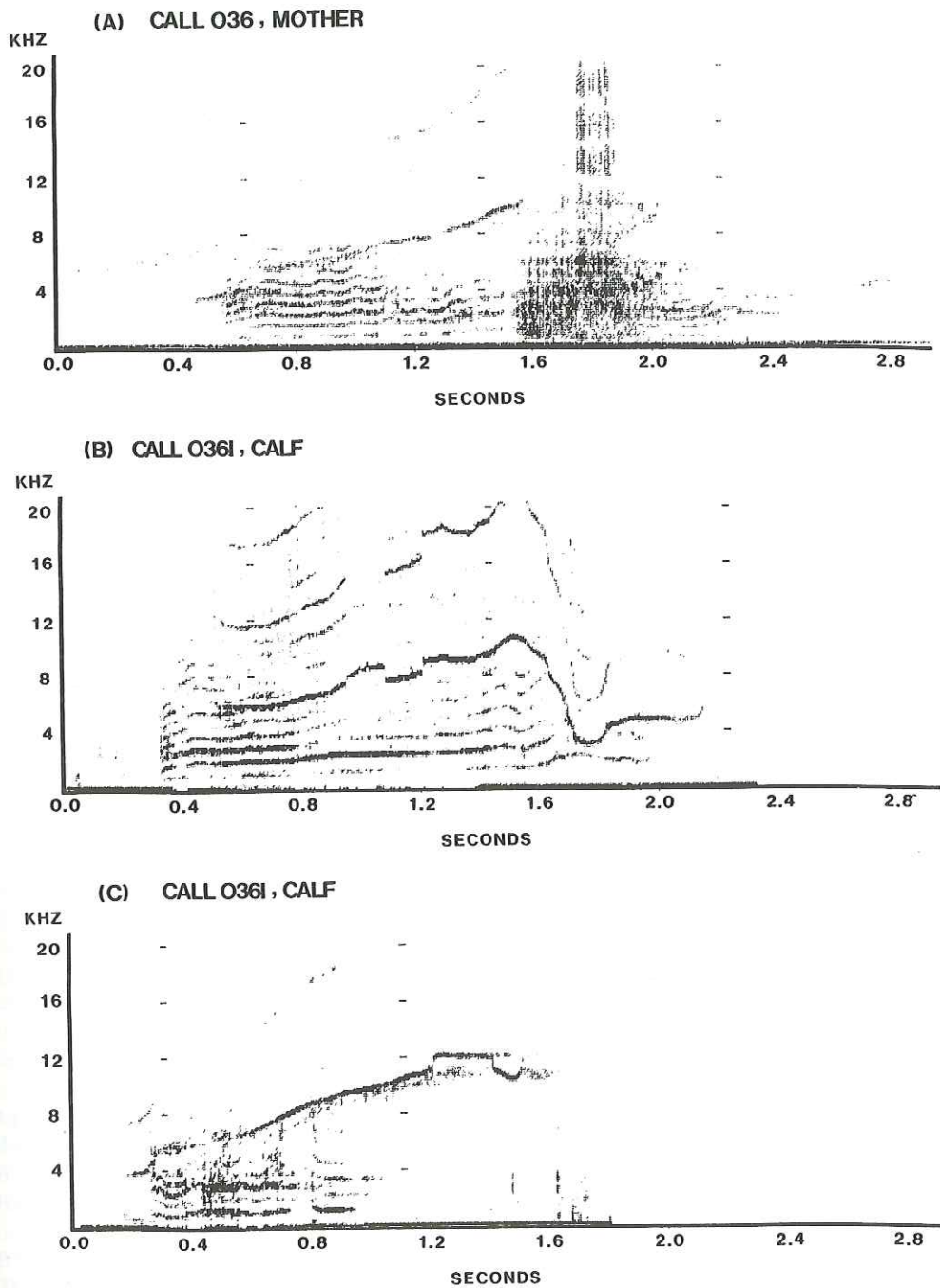


Fig. 14A-C. Waveforms taken from the calf's O36i call. A) a segment (obviously pulsed) taken from the beginning of the call in Figure 13B. B) a segment taken from the end of the same call, after the lower component ended, to show the waveform of the upper component. The filter bandwidth of A) is 50 Hz and of B) 125 Hz.

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TABLE 6

Similarities among repertoires of the five study subjects. The individual cells show the overlap in individual repertoires and the index of similarity (in parentheses) for each pair of whales. The marginal totals indicate repertoire size for each individual.

Individual	No. of overlapping calls (Index of similarity)				Individual repertoire (Number of calls)
	Calf	Mother	Female Companion	Sub adult male	
Calf					4
Mother	4 (0.80)	6			7
Female Companion	4 (0.73)	6 (0.92)			7
Subadult Male	4 (0.53)	6 (0.71)	6 (0.66)		11
Father	0 (0)	0 (0)	0 (0)	1 (0.11)	7

ple sizes were small. However, as the differences appeared to be quite marked, a further test for heterogeneity in the frequencies of the calls shared by all three adults (O1, O2, O3, O6 and the variants O36 and O36i) was performed. Sequences of calls were treated as single samples to ensure sample independence, and, since calls O36 and O36i were variants of one call-type, they were pooled. Such pooling obscures a difference in call use between mother and calf, the calf preferring the simpler variant O36i, but ensures an adequate sample size for comparisons.

There was heterogeneity among all individuals in their use of call types ($X^2 = 9.939$; $P < 0.05$; d.f. = 3, Table 7). Pairwise comparisons were made using Fisher's Exact Test. They failed to distinguish mother from calf but did show that the calf's repertoire differed significantly from those of the young male and companion female ($P < 0.05$; d.f. = 1). Although the young male's frequency distribution was not significantly different from that of the females, his repertoire was distinguished absolutely by four calls, as discussed earlier. The repertoires of the mother and her companion were significantly different ($P < 0.001$; d.f. = 1).

The frequency distribution of all the calls in the pool (Fig. 4) is remarkably similar to the

distribution of calls of the companion female (Fig. 5C). We tested the fits of the distribution of each individual's attributable calls against the distribution of unattributable calls ($N = 1311$, Table 7). In this case call variants were pooled first, then call types were pooled arbitrarily to ensure adequate cell sizes.

Again, there is some possibility that the samples of individual calls were biased by the circumstances of attribution. However, we do not believe such biases were large, based on Ford's (1984) report and on a comparison of the few calls attributable to the young male in the main pool. Of the 6 attributable calls heard when he was with the females in the main pool, one was an O15, one an O4, two O10's, and two O6's. This sample is too small for any statistical test, but it certainly does not suggest that the young male was using different calls when isolated.

The mother's companion may have produced the bulk of the unattributed calls, as the frequency distribution of her calls could not be distinguished from the distribution of unattributed calls (X^2 goodness-of-fit test; d.f. = 3; $P > 0.05$). If so, it is curious that we did not detect many more calls attributable to her. It can only be suggested that behaviours that make calls attributable are most common when all the whales are calling.

TABLE 7
 Statistical comparisons among the frequency distributions of call types for the whales at Sea World of Orlando (N/S = difference not significant).

Individual	Calf	Mother	Female	Comparison with distribution of all unattributed calls	Number of calls in category	
					O1-O6 Sequence	O36
Calf				P < 0.001	1	15
Mother	N/S			P < 0.05	4	18
Female Companion	P < 0.01	P <	0.01	N/S	4	2
Subadult Male	P < 0.05	N/S	N/S	P < 0.001	6	3
All counts				P < 0.001	15	38

DISCUSSION

By the age of 398 days the calf had not acquired any portion of her father's dialect nor the most common calls in the companion female's repertoire. Thus, our evidence to date suggests that killer whale calves selectively learn their repertoires from their mothers. We cannot rule out the possibility of genetic influences, of course, as studies on other species suggest that call-learning is influenced by genetically-determined factors (Marler and Mundinger 1971; Lieberman 1984).

Observations suggest that the calf learned selectively from her mother. Firstly, a few sequences of calls were heard, first mother then calf, that were attributable. In many instances the mother's calls overlapped with the calf's squeals. The calf was never heard calling in such sequences with any whale but her mother, nor did her calls appear in such sequences with calls characteristic of other whales. Secondly, the calf's earliest calls with component timing and structure similar to adult calls, most resembled her mother's favoured calls. These vaguely-recognizable calls appeared most often when the mother was also calling.

The IMUC in the mother's most characteristic calls served as a "marker" in our analysis of the calf's calls, showing that the calf's earliest sounds shared important fea-

tures with her mother's calls. This component is present in killer whale calls from the North Atlantic (Moore *et al.* 1988 - this volume), Puget Sound (Ford 1984) and the Antarctic (Awbrey, pers. comm.); thus, it is a common addition to the more typical pulsed-calls of killer whales. Interestingly, the calf's earliest sounds are most similar to this component. The IMUC may thus be a stereotyped imitation of calf sounds or the product of a sound-producing mechanism, well-developed at birth but only infrequently used in adult life.

We have only sketched the development of the calf's calls. The data collection sessions were short, considering the complexity of calling behaviour in this species. Moreover, the calls we could attribute obviously did not occur at random. Despite its limitations, the study leads us to some interesting speculations about call-learning in killer whales. For example, the data hint that the mother was actively encouraging or "training" her calf to call by calling frequently in sequence with her. If killer whales are like humans and birds in this regard, the calf needed such exposure and interaction with the mother to learn the repertoire (Marler and Peters 1977; Baptista and Petrinovich 1984; Lieberman 1984).

If killer whales learn selectively from certain individuals, we can also more easily explain some conflicting reports in the literature. Killer whales are known to imitate some

novel sounds (e.g. the young male in Orlando produces a convincing imitation of the bridging whistle used in training; see also Bain 1986). However, Ford's (1984) data suggest that their repertoires remain stable and conservative for generations. Work on other species suggests such selectivity might arise from some sort of a learning "window" early in life, when whales can acquire new calls, as documented in humans and some birds (Lieberman 1984; Marler and Mundinger 1971). For example, the repertoire of the young male in Orlando is larger than that of the females, apparently because he occasionally uses their more common calls while they do not produce any of his. Had the females and the young male shared elements of their repertoires because they came from closely-related pods, one would not have expected the overlap to be so one-sided. Also, a young Icelandic female held in captivity in British Columbia rapidly learned elements of the Puget Sound repertoire from her companions (Bain 1986).

Social factors may also play an important role in determining the selection of a call "role-model". Given the pattern of call-sharing among the Orlando whales, it is likely that killer whales only imitate close companions or dominant individuals, such as the mother, as has been shown in primates (Meador *et al.* 1987). The calf shared most calls with her mother, her mother shared most calls with her closest companion and the young male (who is subordinate to the females) shared calls with both females.

We cannot say whether individual whales use subsets or variants of their pod's repertoire, as we do not know the natal repertoires of any of the whales in the Orlando facility. Whales in wild pods all share the same repertoires (Ford 1984). Thus, the two females in Orlando could have come from separate pods and copied one another in the course of their close companionship, or they could have come from different but closely-associated pods (e.g. the A-clan in British Columbia; Ford and Fisher 1982a). The young male probably had a different repertoire at capture.

It is clear from comparison of available acoustic data that the natal pods of the Orlando whales are not among those four pods that have been identified acoustically in the wild (Moore *et al.* 1988 – this volume), as they produce none of the call types collected while censusing wild Icelandic killer whales in 1985 and 1986. The whales in Orlando were captured in the late 1970's, recently enough that the dialects of the Icelandic whales would not have drifted significantly (given the evidence from whales in British Columbia). Thus, there were at least two and probably three pods off Iceland at the time of capture in addition to the four that were identified recently (Lyrholm *et al.* 1987; Sigurjónsson *et al.* 1988 – this volume; Moore *et al.* 1988 – this volume).

ACKNOWLEDGEMENTS

We thank the staff of Sea World's Animal Behavior and Animal Care departments, particularly Mark McHugh, Stan Searles and Ted Turner, for their support and help during recording sessions. Stephen Leatherwood and John K. B. Ford provided initial inspiration and considerable encouragement along the way. Without their enthusiasm, the project would never have been done. We also thank Peter Tyack for a thoughtful review of this manuscript. Sheldon Fisher made the recordings of the calf's father.

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