

Development of behavior and sound repertoire of a rehabilitating gray whale calf

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Abstract

The rehabilitation of a gray whale calf, JJ, at SeaWorld of California in San Diego from 11 February 1997 to 31 March 1998 provided an opportunity to study the development of the sound repertoire in gray whales. Acoustic recordings were collected with an array of ITC hydrophones (one 6050H, eight 8212) from 1.5 mo after arrival until release. A total of 248 hr of simultaneous behavioral observations and sound recordings were collected. One previously-identified gray whale call type (type 1) proved to be divisible into two distinct types, termed 1a and 1b. JJ produced 3 of the 4 common wild gray whale call types (1a, 3, 4) by 1.5 mo of age and all four (1a, 1b, 3, 4) by 7 mo. Playback trials using calls of free-ranging gray whales (data from M. Dahlheim and N. Crane) were conducted from July through October 1997. JJ was exposed immediately prior to feeding during seven of 45 feedings per week. Initially, the playback stimulus presented type 1 calls at roughly the natural duty cycle (10/min). JJ did not respond for the first 13 trials. The rate and level of type 1 calls and level was then increased. She began to respond within the next five trials and responded to 10 of the following 11 trials (91%). During the sequence of playbacks that elicited responses, peak levels between 400 and 800 Hz, the frequencies with the best signal-to-noise ratio (SNR), were at or in excess of 79 dB re 1 $\mu\text{Pa}^2/\text{Hz}$ (95 dB re 1 μPa), just above the ambient noise in the pool. However, when animal care staff began to wean JJ to solid food thereafter, the reliability of the playback as a cue for feeding was reduced, and she ceased to respond to playback. Spontaneous development of all 4 elements of the gray whale call repertoire before the start of playback trials suggested that gray whales develop most of their repertoire with little need for exposure to calling adults. However, the delayed emergence of call type 1b as a common call and the disappearance of call type 3 after weaning suggested that

social context and/or reinforcement might play a role.

Key words: sound repertoire, gray whale, calf, rehabilitation, vocal development.

Introduction

Although research in captive settings can contribute much to understanding the behavior of cetaceans (e.g., Samuels & Gifford, 1997; Gubbins *et al.*, 1999), baleen whales rarely have been studied in captivity due to their substantial requirements for space and food. The rehabilitation of a gray whale calf, JJ, at SeaWorld of California provided a unique opportunity to study the development of gray whale behavior and call repertoire, to explore the behavioral context of various calls, and to use playback experiments to examine the extent to which an innate call repertoire might be modified or enhanced by exposure to conspecific sounds.

Playback of species-specific calls has been conducted on several species of baleen whales in the wild, including southern right whales, *Eubalaena australis*, (Clark & Clark, 1980), gray whales, *Eschrichtius robustus*, (Dahlheim, 1987), and humpback whales, *Megaptera novaeangliae*, (Tyack, 1983; Frankel *et al.*, 1995). Whales responded positively (with approach or calls in return) or neutrally (no obvious response). Consequently, we hypothesized that exposure of JJ to gray whale sounds would cause no harm and might serve as enrichment.

Three general mechanisms have been described for acquisition of a complete adult sound repertoire: (1) fully-formed at birth; (2) functional maturation; and (3) call learning. In general, the call repertoire of terrestrial mammals is fully-formed at birth (reviewed by Ehret, 1980). Features of particular calls in some birds (Podos *et al.*, 1995) and bats (Matsumara, 1979) appear in the call repertoire owing to developmental changes in the anatomy of

the vocal tract. In some oscine birds (Petrinovich & Baptista, 1987) and bats (Esser & Schmidt, 1989), the development of an adult repertoire requires exposure to calls of conspecifics when young. However, little is known about the development of sound production in marine mammals.

Among toothed whales (odontocetes), bottlenose dolphins, *Tursiops truncatus*, (Caldwell & Caldwell, 1979; Sayigh *et al.*, 1990; McCowan & Reiss, 1997), killer whales, *Orcinus orca*, (Bowles *et al.*, 1988), and sperm whales, *Physeter catodon*, (Watkins *et al.*, 1988) make non-stereotypical calls soon after birth. Complexity and stereotypy increase with age. Bottlenose dolphins can mimic computer-generated sounds (Richards *et al.*, 1984) and whistles of conspecifics (Tyack, 1986; Reiss & McCowan, 1993), suggesting that learning is one mechanism involved in the development of call behaviour in odontocetes. Killer whales may also be able to learn certain calls as repertoires appear to be stable within pods for several generations (Ford, 1991) and appear to be acquired from the mother regardless of the father's repertoire (Bowles *et al.*, 1988; Noonan, 1999).

Less is known about development in mysticetes. The call repertoires of humpback (Payne & Payne, 1985) and bowhead whales (Ljungblad *et al.*, 1982) evidently can change during a breeding season. In the case of the humpback whale, this change is most likely the result of learning, as all individuals in the population eventually converge on a common song. The few opportunistic data on sounds produced by baleen whale calves do not provide evidence for any developmental mechanism (Fish *et al.*, 1974; Ljungblad *et al.*, 1980; Würsig *et al.*, 1985).

The adult call repertoire of gray whales consists of 'cries', 'moans', and 'belches' (Asa-Dorian & Perkins, 1968; Cummings *et al.*, 1968). Dahlheim *et al.* (1984) described six call types designated by a number (1 to 6). The call types were: 1=a series or burst of pulses (sounding like knocks or clangs); 2=a single clang recorded only in the southern range and detected rarely; 3=low frequency moans (sounding like a cow's moo); and 4=grunts and groans (sounding like zippers or short grunts). Other types of sounds were bubble blasts (type 5) and bubble trails (type 6). Types 1, 3, and 4 are the most common calls and have been detected throughout the gray whale's range (Crane & Lashkari, 1996; Moore & Ljungblad, 1984).

Here, we describe the development of call repertoire and the behavioral context of calls in a stranded, rehabilitated gray whale calf (JJ) during her 14-mo stay at SeaWorld in San Diego from January 1997 through March 1998. We also describe a series of playback experiments used to explore the role of learning and context in the development of her repertoire.

Materials and Methods

We grouped all behavioral and acoustic data into four behaviorally significant time periods. Period A lasted from February through June, while JJ was still being fed formula and before the beginning of playback experiments. Period B lasted from July through October, during playback experiments and while JJ was slowly weaned from formula to solid food. Period C lasted from November, after playback experiments had ended, through December, the period when JJ was least active. Period D lasted from January 1998 through her release in late March 1998.

Development of behaviour

We observed JJ's behavior using *ad libitum* sampling (Altmann, 1974) from March 1997 through February 1998. We recorded, directly or on videotape, all behavioral events that occurred during four sampling periods per week, each lasting at least 90 min. After two, 24-h observations indicated that JJ's behavior was similar at night vs. during the day, we collected data primarily during the day. Observations were classed as either baseline (no playback of experimental stimuli) or experimental (a playback experiment was conducted). One observer was present during baseline observations and 4 observers were present during playback experiments. Simultaneous underwater recordings of sounds produced by JJ were collected during all observations. We also made recordings of noise sources in the pool, including normal husbandry activities (e.g., pool cleaning), killer whale calls originating from nearby pools, and noise made by SeaWorld guests to correlate with changes in JJ's behavior.

We categorized JJ's behaviors into seven states (Table 1) in addition to scoring individual events (e.g., breaching). Behaviors were assigned one of five locations within the pool (Fig. 1, inset).

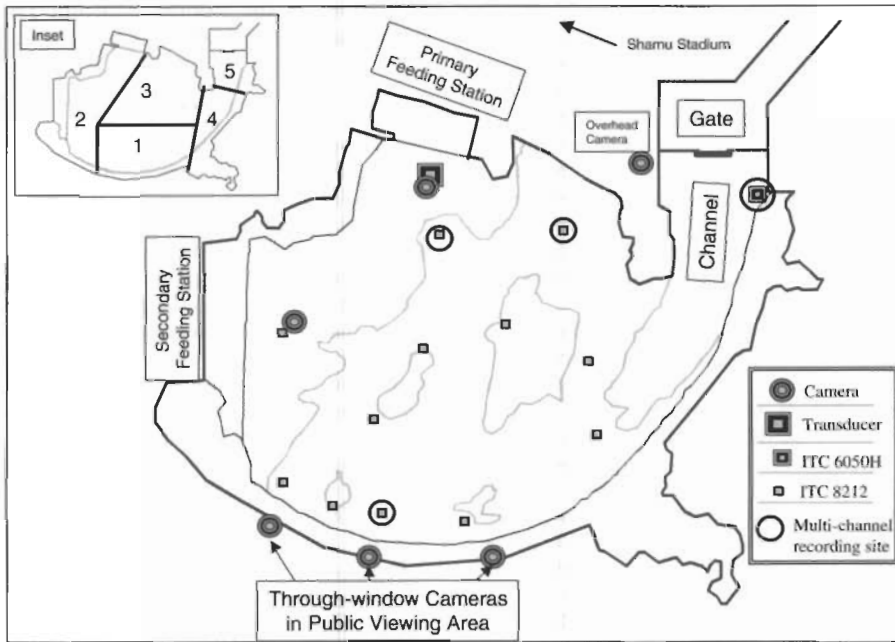
Development of call repertoire

We made recordings for at least 90 min at least 4 days each week. Recordings were collected from an array of nine hydrophones (one ITC 6050H, eight ITC 8212; frequency response 1 Hz–30 kHz) mounted in the concrete walls and rockwork of the pool (Fig. 1). Playback stimuli were delivered with an underwater loudspeaker (Lubell 964). The volume of the pool was 6343 m³, measured 9.1 m deep, 27 m wide, and 48.8 m long, and had a 21.3 m long acrylic underwater viewing panel.

We made video recordings with a JVC S-VHS video recorder connected to a four-channel multiplexer with input from 4 of 6 cameras distributed around the pool (underwater: two CoStar CV 730, three Sony SSC DC34; overhead: Sony SSC DC34).

Table 1. The seven behavioural states used to characterize activity of a rehabilitating gray whale calf (JJ).

State	Description
Stationary-Inactive	Remaining in one place, either completely motionless or very little movement. Includes behaviors such as resting and sleeping.
Stationary-Active	Remaining in one place, but active. Includes behaviors such as rolling, arching, and occasional spyhopping.
Unpatterned Swim	Unpatterned movements in the pool or channel.
Patterned Swim	Swimming in a repeated pattern near the viewing window or around the perimeter of the pool.
Highly Active	Energetic activities, such as swimming rapidly around the pool, porpoising, or surface-active behaviors (slapping head, breaching).
Feeding	Fed at surface by animal care staff or bottom feeding.
Play	Object manipulation, such as mouthing kelp, rolling in divers' bubbles, pushing an inflated bag (enrichment device).

**Figure 1.** Pool at SeaWorld in San Diego where JJ was housed, showing locations of hydrophones and cameras.

This configuration allowed us to monitor all areas of the pool simultaneously. We made sound recordings with a Sony TCD-D7 DATman (frequency response = 20 Hz to 22 kHz \pm 1 dB) and a four-channel TEAC RD101T DAT (frequency response 20 Hz to 20 kHz \pm 1 dB). The sampling rate of both recorders was 48 kHz. The frequency response of the entire system (20 Hz to 20 kHz \pm 1 dB) was adequate to detect all gray whale calls.

We digitized calls that had suitable signal-to-noise ratios (SNR) and then analyzed them using

Spectra Plus, Cool Edit, and Gram software programs. We calculated spectral levels using a SD380 real-time spectrum analyzer (25-Hz bandwidth). We characterized ambient sound levels by averaging spectra over 10 s intervals. We classified calls according to Dahlheim *et al.* (1984) based on frequency range, energy density across the spectrum, number of pulses, and duration. We then compared the spectral characteristics, rate of production, and relative use of calls made by JJ with those reported from the breeding/calving lagoons of Baja

California. We calculated rate of sound production as the number of sounds recorded per hour of observation.

Playback experiments

We obtained recordings of free-ranging gray whales in the breeding/calving lagoons (Dahlheim *et al.*, 1984), during migration near Monterey Bay, California (Crane & Lashkari, 1996), and on northern feeding grounds in the Bering Sea (Moore & Ljungblad, 1984). Call types 1 ('pops') and 3 ('moans') were chosen as sound stimuli for the playback experiments because they had good SNR in the available recordings and were the most common calls throughout the gray whale range.

We created playback stimuli using SpectraPlus[™] after first digitizing, low-pass filtering at 8 kHz, and reducing background noise (e.g., snapping shrimp) using Cool Edit[™]. Initially, we created a 30-min playback loop with stimuli presented at a rate of 10/min, roughly the natural rate on the source tapes. After the first 13 playback trials, pop rate was increased by selecting segments from the source tapes with high call rates and by removing intervals between bouts of calls. Average level was increased by 5 dB. The pops ranged in frequency from 50 to 2000 Hz (Fig. 2A). Durations ranged from 50 to 250 ms. Moans were later added to the last 25 min of the stimulus tape, ranging in frequency from 500 to 2500 Hz (Fig. 2B).

Playback stimuli were projected from the Lubell loudspeaker, which was located directly under JJ's feeding station. These sounds attenuated little within the reverberant main bowl of the pool (Fig. 3A), but were ~10–20 dB lower in the channel area (shadowed by rockwork from the main bowl) (Fig. 3B). Background noise in the pool was highest below 100 Hz due to pump and water noise; levels in this band were almost always above 100 dB re $1 \mu\text{Pa}^2/\text{Hz}$. Playback sounds were normally projected at lower levels, and would therefore have been inaudible or only intermittently audible in this range. From 100 Hz to 2500 Hz, background noise dropped from an average of 80 dB to around 45 dB re $1 \mu\text{Pa}^2/\text{Hz}$. In this range, pops in the pool exceeded the background noise under all conditions. In the channel, pops had levels within ± 5 dB of average background levels and below the highest levels (Fig. 3). Therefore, pops were just detectable in the channel. Moans had better SNR due to energy in the range from 1000 to 2500 Hz, from 20 to 30 dB in the main pool and 10 to 15 dB in the channel.

We conducted playback trials from July through October 1997 during seven of 45 scheduled feeding sessions per week, usually at the primary feeding station at the west end of the pool (Fig. 1). We presented stimuli during normal feedings because

we wanted JJ to associate natural gray whale sounds with food. At first, the stimulus tape consisted of pops only. Later, moans were added to the last 25 min segment of the tape.

We collected baseline observations of behavior for 30 min before each feeding session. Poolside observers were intentionally kept unaware of the start time of playbacks to prevent them from accidentally signaling the start of the experiment. We started playback trials approximately 1 min before feeding and continued through the feeding period (5 to 15 min/day) and for another 10 to 20 min, for a total of 30 min of playback time. We continued to observe JJ's behavior for 30 min after playbacks were terminated. We considered a positive response to the playback as: (1) an abrupt change in swimming direction; (2) direct movement towards the feeding platform within 45 s of playback onset; and (3) arrival at the feeding platform prior to the splash cue that normally signaled feeding.

Results

Development of behavior

JJ's behavior ranged from inactive to highly active states, like breaching, rapid swimming at the surface, and porpoising (Fig. 4). During periods A and B, while she was still being fed by hand, JJ spent time in both the main pool (61%) and the channel (39%) in active states, such as stationary-active (33%) and patterned swimming (21%; Fig. 4A). We observed 11 bouts of object manipulation during periods A and B, lasting a total of 43 min, which we classed as play, a rare occurrence (0.5 to 1.0% of activity). Play included mouthing kelp, rolling in and mouthing diver's bubbles, nosing a net placed in the pool during sea lion experiments (*cf.* Hurley *et al.*, 2000), and bumping or pushing an inflated bag that was introduced as an enrichment object.

High activity states, such as breaching and porpoise swimming, occurred only occasionally. Nearly all of these occurred in periods A and B and in the main bowl of the pool (Fig. 4B). We observed 12 bouts of breaching (5 min) during periods A and B, and 7 bouts porpoise swimming (6 min), five of them in periods A and B and two in period D.

Feeding was a small but constant proportion of her activity (<5%) in all periods. Formula feedings during periods A and B were signaled by slapping the water or wall at the feeding station. JJ turned within 15 s to 3 min of the start of this signal and swam directly to the feeding station. Once the formula was supplemented with solid food in mid-July, she responded more slowly to the signal, allowing large portions of the solid food to drop to the bottom of the pool, and often voluntarily ending the feeding sessions by moving away. However, she soon began to swim to the fallen food.

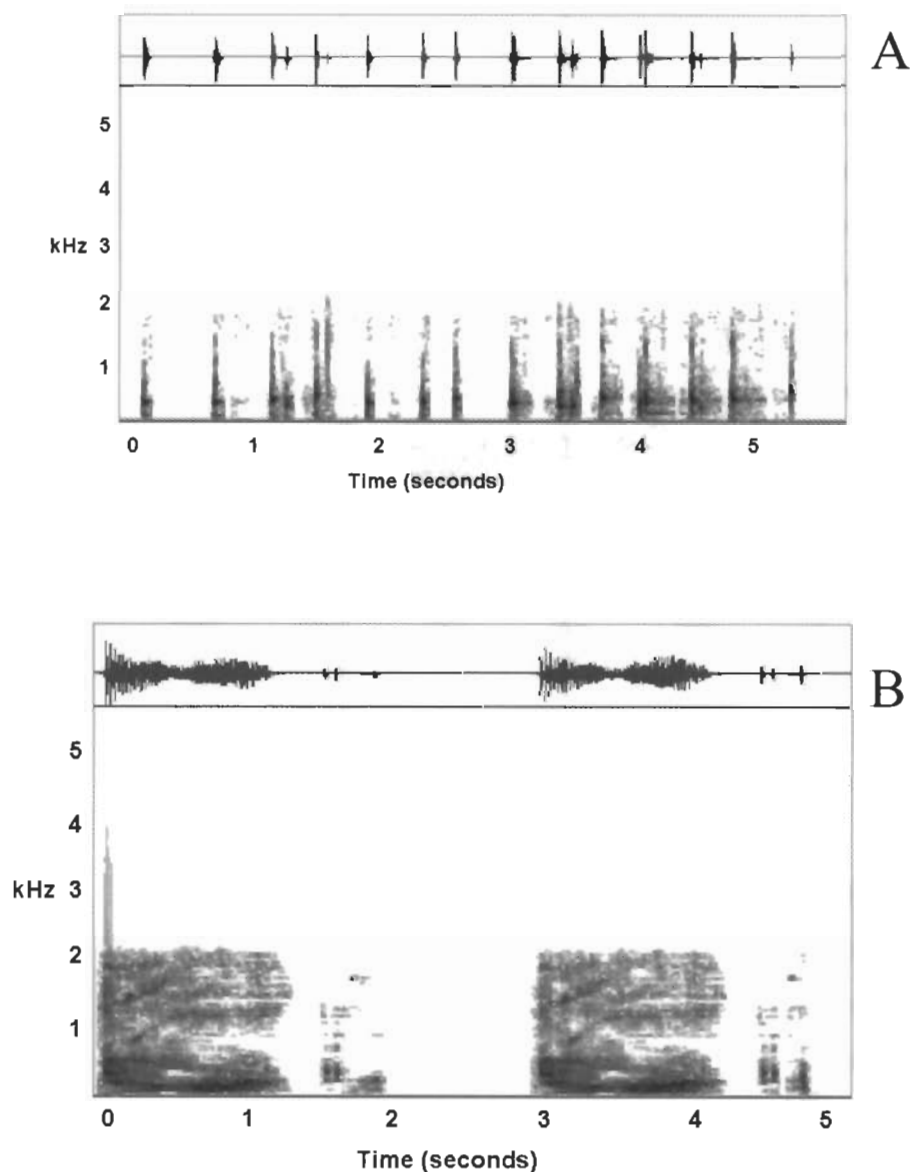
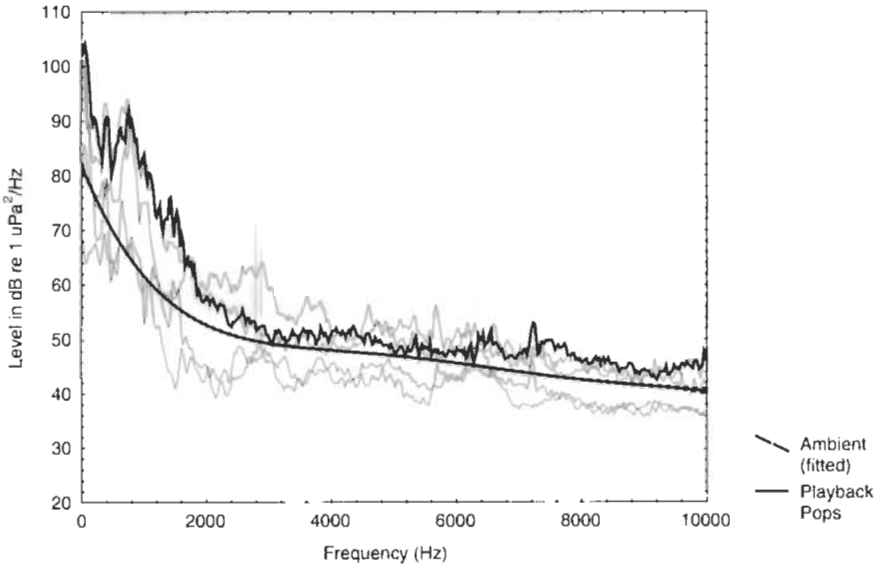


Figure 2. Spectrograms and waveforms of playback stimuli. A. Call type 1 ('pops'); B. Call type 3 ('moans').

turning on her right side sucking the food into her mouth and emitting a plume of debris from the left side of her mouth. This behavior was indistinguishable from feeding behavior of free-ranging gray whales (Nerini, 1984). She steadily increased bottom feeding time late in period C and in period D (Figs. 4A, 4B), losing interest in approaching and being hand led at the poolside feeding station.

JJ became less active after weaning. She spent only 1% of her time in patterned swimming in period C compared to 46% before then, while time spent in the channel area increased from 39 to 85%. The time she spent in the stationary-inactive state doubled from 12 to 24% and in the stationary-active state from 31 to 68%. After changes were made in feeding and care regimes during period D to encourage more activity, JJ spent

A



B

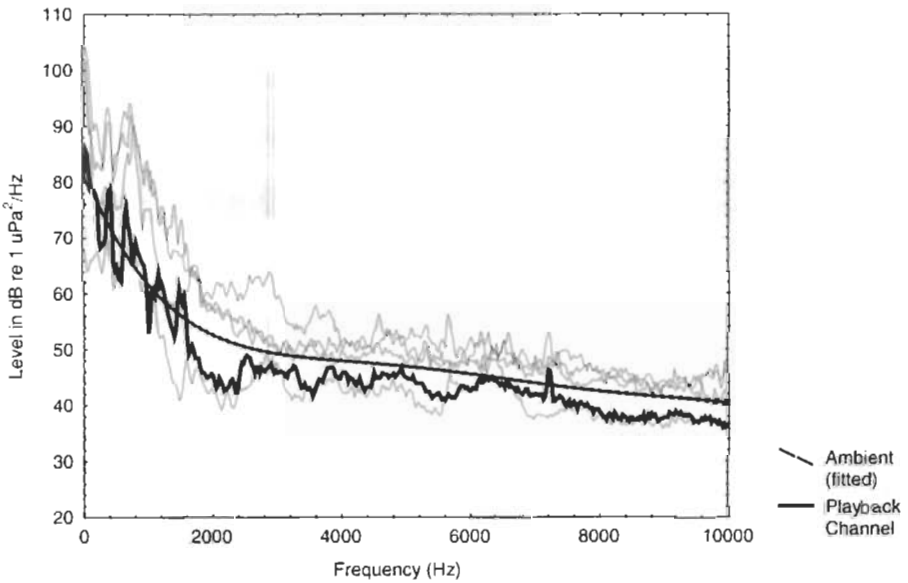


Figure 3. Power spectra of playback stimuli. A. playbacks in main bowl of pool; B. playbacks in channel. Spectra of stimuli shown in black; forty averaged ambient noise spectra shown in gray.

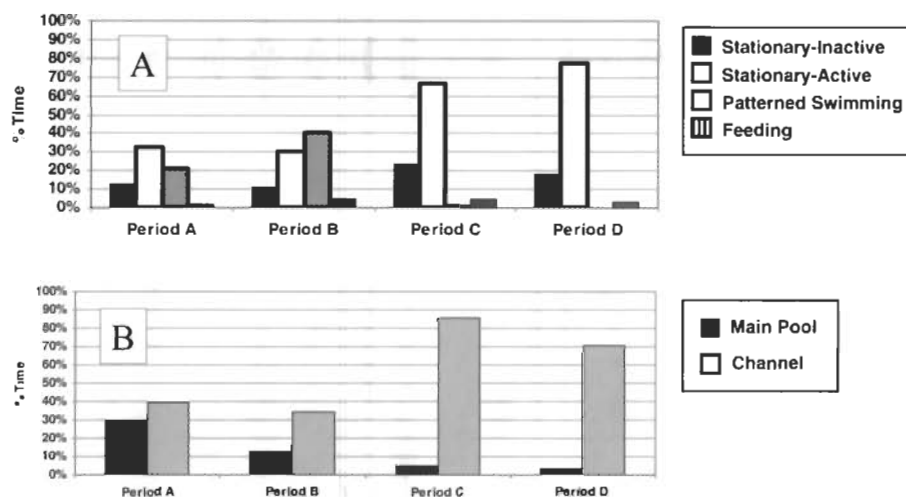


Figure 4. A. Changes in percentage time spent in behavioral states over four periods: February through June 1997 (Period A), July through October 1997 (Period B), November through December 1997 (Period C), January through March 1998 (Period D). B. Changes in percentage time spent in the main pool vs. channel over the four periods.

marginally less time in the channel (70% vs. 85%), more time in the stationary-active states (77% vs. 68%), and less time in the stationary-inactive state.

Development of call repertoire

We made the first recordings when JJ was 1.5 mo old. By then, she produced the three most common call types that have been reported for free-ranging gray whales (Dahlheim *et al.*, 1984). Type 1 was the most common (80%), type 3 was least common (2%), and type 4 occurred 18% of the time. We never recorded call type 2 reported by Dahlheim *et al.*

We found that call type 1 could be divided into two distinct types, type 1a ('croak') and type 1b ('pop'; Fig. 5). Both were similar in frequency range (70 Hz to 4 kHz) and were composed of pulses. However, type 1a had shorter pulses (*t*-test for unequal variances, $t = -7.07$, $df = 12$, $P < 0.001$) (Table 2), shorter inter-pulse intervals ($t = -4.98$, $df = 12$, $P < 0.001$), and more pulses ($t = 2.40$, $df = 12$, $P = 0.03$). JJ produced type 1a at 1.5 mo of age, but call type 1b did not appear until July 1997, at 7 mo of age.

Call type 3 (Fig. 6A) was a moan lasting 440 ± 200 ms and ranging in frequency from 80 to 2120 Hz (± 75 Hz; peak frequency = 270 ± 70 Hz). Call type 4 (Fig. 6B) was a grunt lasting 340 ms (± 90 ms), on average, and ranging in frequency from 70 to 5000 Hz (± 100 Hz; peak frequency = 890 ± 100 Hz). We also recorded several other types of sounds, including 'bubble-blasts' (type 5), flatulence, and miscellaneous intestinal rumblings (Fig.

7). We did not observe bubble trails (type 6). No particular behavior appeared to be associated with these sounds.

We observed a shift in JJ's call use over time (Fig. 8). JJ produced call type 1a most commonly in periods A and B (59% and 42%, respectively). In periods C and D, she produced call type 1b most commonly (50% and 68%, respectively), while call type 1a was produced second most commonly (33% and 24%, respectively). Call type 3 was produced infrequently, occurring only 26% of the time during period A, decreasing to 3% in period B, and completely disappearing in periods C and D. Most of the type 3 calls in period A (54 of 63, 86%) were recorded over a two-day interval. Call type 4 was produced in all four time periods, but was not common (8–28% of calls). Call types were not associated with any particular behavior, except perhaps for type 1a, which seemed to be produced most often (4.5 calls/min) when JJ was highly active. At other times, call type 1a was produced infrequently 0.001/min.

Playback experiments

Acoustic environment in the pool—Noise levels in JJ's pool were greatest below 1500 Hz, dropping to ~ 40 dB re $1 \mu\text{Pa}^2/\text{Hz}$ above ~ 3000 Hz. During the evening, night, and early morning, background noise was produced mainly by water motion, pumps, skimmers, and sumps. During the day, human activities produced noise. Of these, scrapers used to clean the surfaces of the pool several times a month produced the highest levels (Fig. 9A). Scraping produced levels above 64 dB re $1 \mu\text{Pa}^2/\text{Hz}$

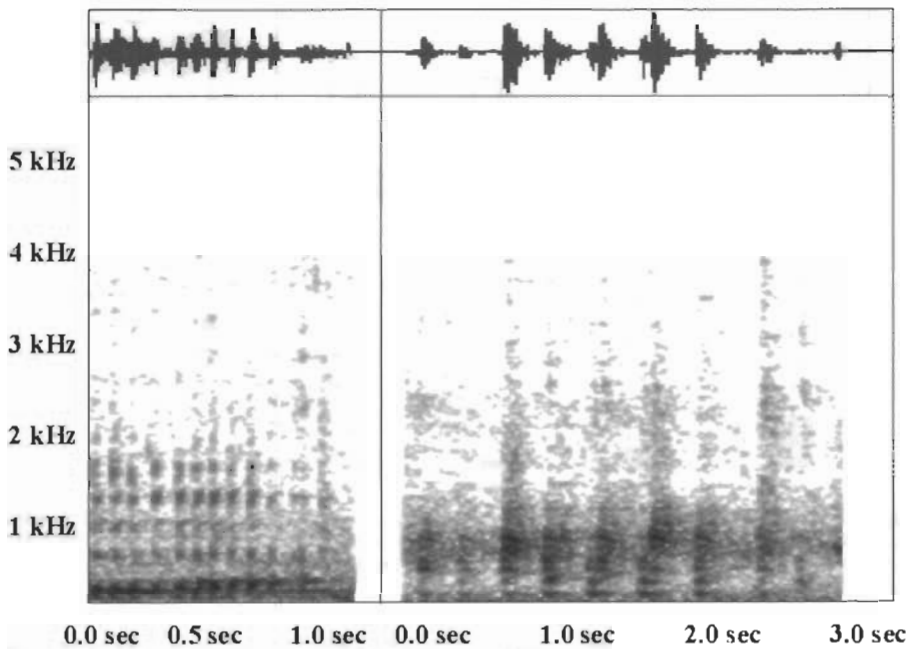


Figure 5. Spectrogram and waveform of call types 1a and 1b produced by a rehabilitating gray whale calf (JJ). Notice difference in pulse duration and inter-pulse interval.

Table 2. Acoustic characteristics of call types 1a and 1b. Mean, standard deviation, and *P*-value are shown; number of pulses, pulse duration, and inter-pulse interval differed significantly between the two call types (*t*-test for unequal variances, two-tailed).

	Minimum frequency (Hz)	Maximum frequency (Hz)	Total duration (ms)	Number of pulses	Pulse duration (ms)	Inter-pulse interval (ms)
Type 1a	70 ± 30	2810 ± 910	910 ± 130	12 ± 2	39 ± 12	37 ± 25
Type 1b	70 ± 40	3090 ± 650	1200 ± 580	8 ± 5	72 ± 27	78 ± 48
<i>P</i> -value	—	—	0.162	0.033	<0.001	<0.001

across the range from 50 Hz to 10 kHz, peaking at 1 to 200 Hz in excess of 84 dB re 1 $\mu\text{Pa}^2/\text{Hz}$ (105 dB re 1 μPa). Above 2 kHz, the SNR of this activity was high, over 40 dB. Early on, JJ appeared to react aggressively to the scrapers at least once. She approached the scraping crew, tipped her flukes toward them, emitted bubble clouds, and made several sharp head movements at them. Sharp jerks of the head were associated with negative reactions in other contexts, as when someone touched her unexpectedly. Two bouts of porpoising and two of breaching were stimulated by the scrapers as well. JJ evidently habituated behaviorally to the activity and thereafter reacted little when the cleaning crew entered the pool.

Divers' SCUBA-gear produced similarly high levels of noise during daily efforts to scoop uneaten

food from the pool bottom (Fig. 9A). At first, JJ occasionally approached the divers, but without obvious aggression despite peak sound levels below 2000 Hz similar to those made during scraping. On occasion, she approached the divers for play, mouthing or rolling in their bubbles.

Noise from SeaWorld guests, mostly knocking on the acrylic viewing panels, and killer whale calls had lower SNR, around 15 to 25 dB above background levels at most. Guest noise ranged from 200 to 1800 Hz, reaching 79 dB re 1 $\mu\text{Pa}^2/\text{Hz}$ (95 dB re 1 μPa) at around 800 Hz. Killer whale calls propagating from other areas of the pool complex occasionally reaching SNR of 15 dB in the range from 500 Hz to 10 kHz (Fig. 9B).

Detection of playback stimuli—JJ did not approach the feeding station spontaneously when

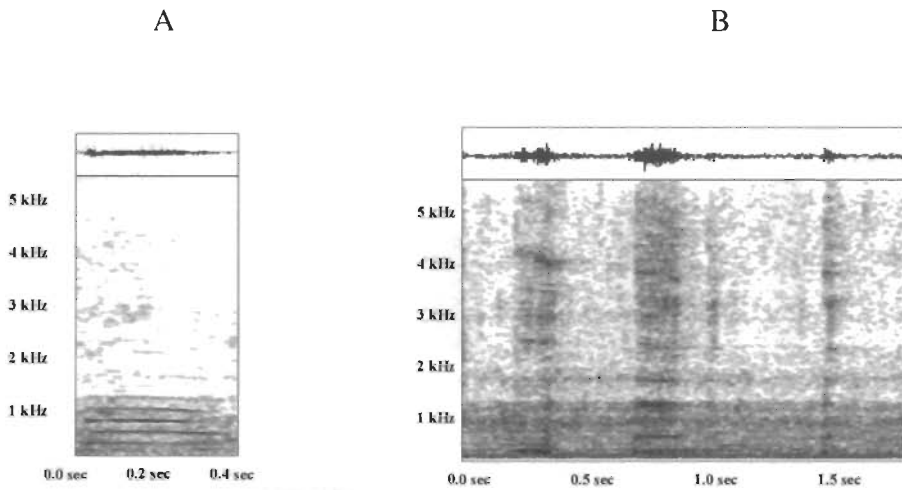


Figure 6. A. Spectrogram and waveform of call type 3 produced by a rehabilitating gray whale calf (JJ). This call is not pulsive and all energy is below 2 kHz. B. Spectrogram and waveform of three type 4 calls produced by a rehabilitating gray whale calf (JJ). This call is not pulsive, energy is present up to 5 kHz, and each call is very brief.

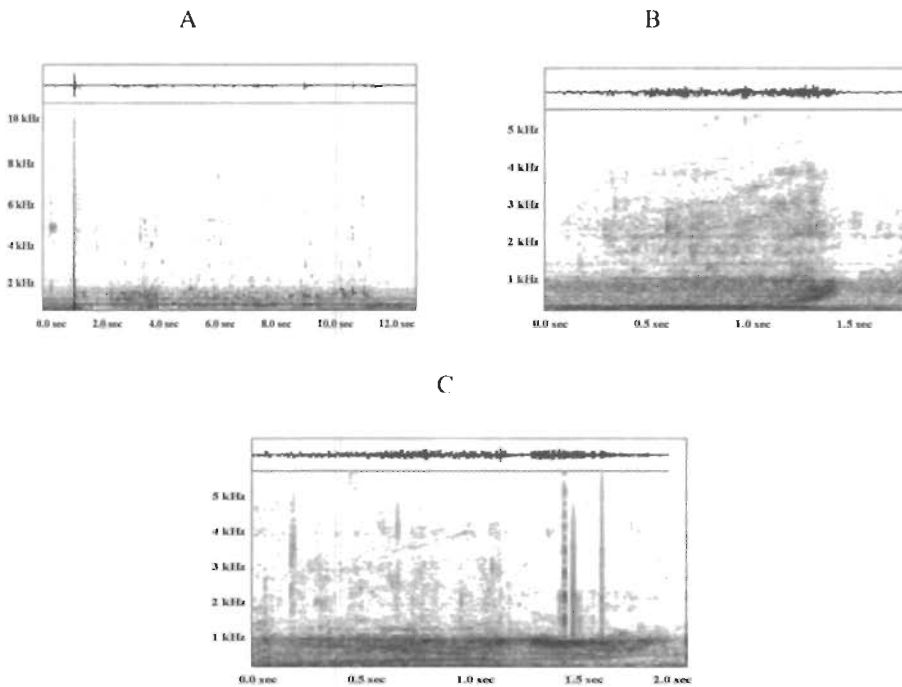


Figure 7. Spectrograms and waveforms of three miscellaneous sounds recorded in the presence of JJ.

exposed to anthropogenic sounds that did not signal a feeding or during control (blank) trials. During 280 hr of non-experimental behavioral observations, she never responded with an abrupt turn and approach of the feeding station unless she had

received a signal. Thus, her false response rate to playback trials was functionally 0.

During the first 13 trials, JJ did not respond to playback stimuli in any detectable way. In these trials, stimulus pops were produced at 10/min and a

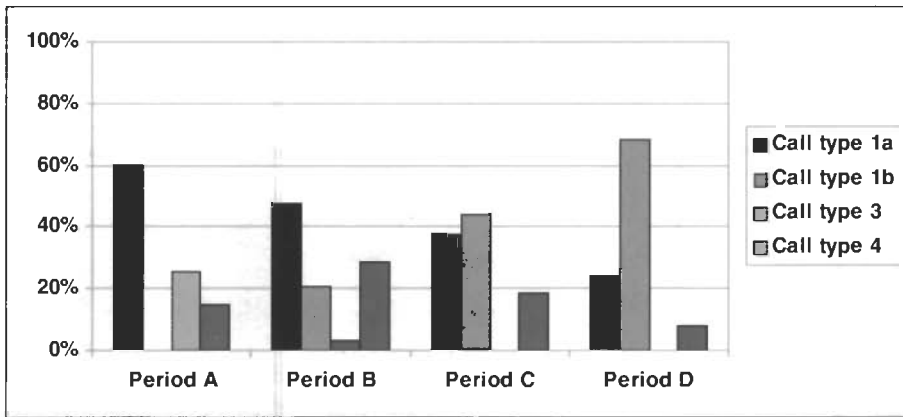


Figure 8. Recorded number of calls per hour produced by a rehabilitating gray whale calf (JJ) over four behavioral time periods. A. February through June 1997. B. July through October 1997. C. November through December 1997. D. January through March 1998. Total number of calls (n) and total number per hour recorded (parentheses) indicated at top.

level of 74 dB re $1 \mu\text{Pa}^2/\text{Hz}$ (maximum 92.5 dB re $1 \mu\text{Pa}$). Under the quietest conditions, the stimuli had an SNR of 34 dB, but during the day when guests were present the SNR was 0 dB. So, the stimuli may not have aroused her attention or they may have been difficult to detect against the background of other noises in the pool.

During trials 14 to 18, the tape with higher pop rate and level was used. JJ began to respond to these stimuli by trial 18. She responded to 91% (10) of the next 11 trials (19 to 29), indicating that she detected the new stimulus. After trial 30, moans were added to the last 25 min of the stimulus in an effort to transfer the association between pops and feedings to moans. Unfortunately, it is difficult to know whether this change had any effect. During this period, JJ was weaned from hand-feeding of formula to solid food distributed on the bottom of the pool. Food given to her at the surface was substantially reduced and then terminated. From trials 30 to 45, her proportion of positive responses declined to 59% (still well above chance levels, estimated at $\ll 1\%$ in any 2-min period).

Solid food was distributed by two divers, who entered the water with a large bag of fish and krill and distributed it on the bottom. We began playback trials approximately 1 min before the divers entered the water. After they entered, it only took a few minutes to distribute the food. In principle, the playback should thus have continued to be an adequate signal for food. However, JJ quickly began to wait for the sound of the divers before approaching. The effort to measure responses to playback stimuli was discontinued after trial 54 as a result. Randomly interspersed pops and moans were presented as acoustic enrichment during

feedings until October. Response delay (latency)—From trials 18 to 29, when JJ routinely responded to the playback stimuli, response latency was similar to her responses to the splashing signal made by animal care staff, averaging ~ 39 s (range 15 to 114 s). Feedings began an average of 139 s after the start of playback (45 to 285 s), so the playback stimuli were a reliable cue for the onset of feeding. Even though JJ responded less often during trials 30 to 45, the latency of her responses changed little, averaging 40 s (range 23 to 96 s). From trials 46 to 54, JJ responded only three times, with latencies of 35, 92, and 30 s. After trial 54, when she ate entirely at the bottom of the pool, JJ no longer responded to playback sounds.

Minimum level at which JJ responded—During the first 13 trials, JJ did not respond to playback stimuli in any detectable way. In these trials, stimulus pops were produced at 10/min and a level of 74 dB re $1 \mu\text{Pa}^2/\text{Hz}$ (maximum 92.5 dB re $1 \mu\text{Pa}$). Under the quietest conditions, the stimuli had good SNR (34 dB), but during the day when guests were present the SNR was 0 dB. So, the stimuli may not have aroused her attention or they may have been difficult to detect against the background of other noises in the pool. Later, after she began to respond, she detected playback stimuli from anywhere in the pool, although most trials began when she was in the main pool (areas 1–3, Fig. 1). SNR was always at least 5 dB and reached 39 dB under quiet conditions. In the channel, where the lowest SNR was found, JJ was able to respond to 3 of 3 trials that began while she was resting there. For the lowest frequency band examined (12 to 38 Hz), channel playback levels reached 98 dB re $1 \mu\text{Pa}$ (82 dB re $1 \mu\text{Pa}^2/\text{Hz}$). However, there was always

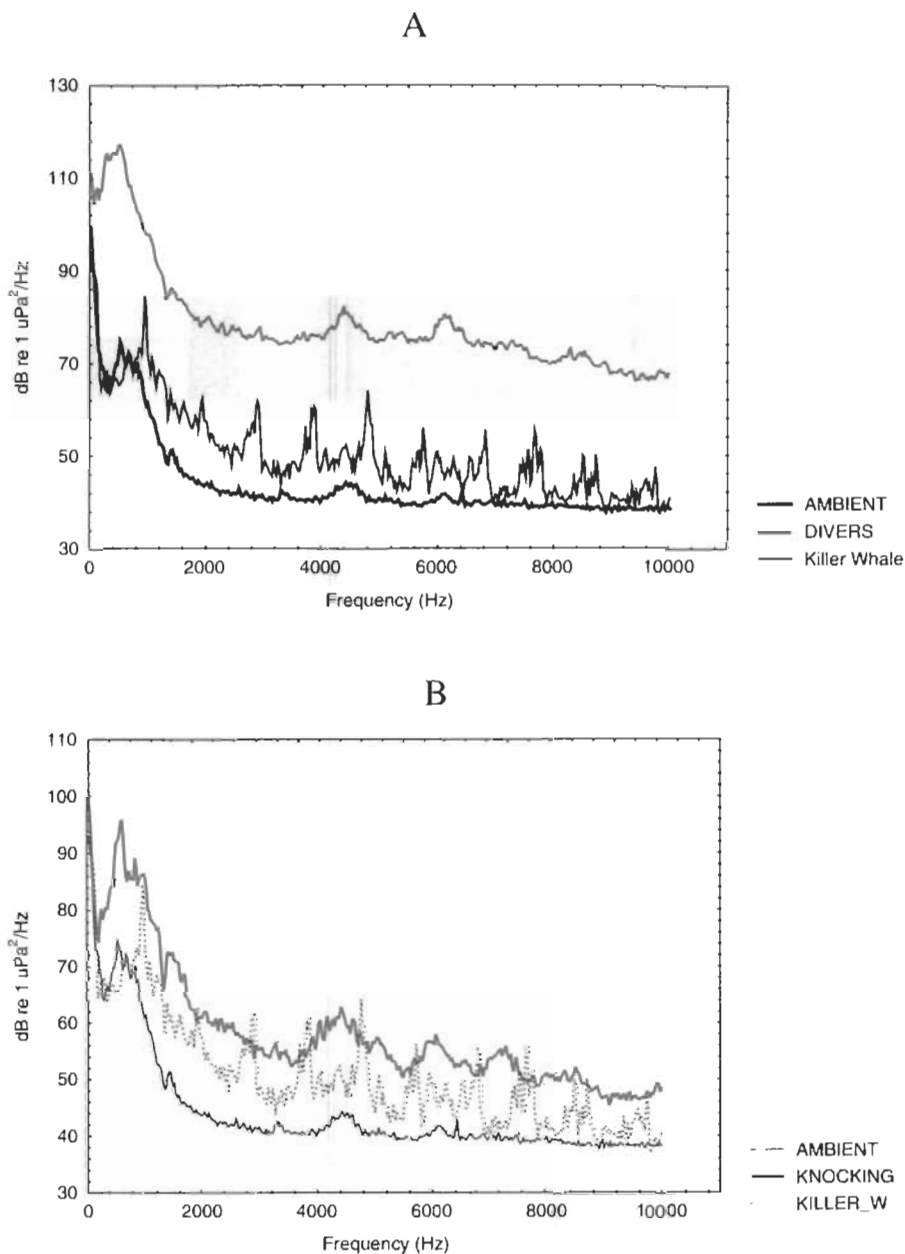


Figure 9. Power spectra of ambient sound levels. A. Ambient levels in main bowl of pool, B. Ambient levels in channel.

substantial noise in that range, often more than 10 dB above playback sound levels. Consequently, detection would have been difficult at those frequencies. Components between 400 and 800 Hz more reliably exceeded the background. In the channel, levels from 400 to 800 Hz peaked at 95 dB re $1 \mu\text{Pa}$ (79 dB re $1 \mu\text{Pa}^2/\text{Hz}$; Fig. 3B). This is the

best estimate of the minimum level at which JJ responded.

Behavior and calls during playback—JJ spent most of her time in the main pool before and during playback trials (71% and 72%, respectively; Fig. 10; Table 3). She spent most of the 30 min before playback trials in the stationary-active (36%) and

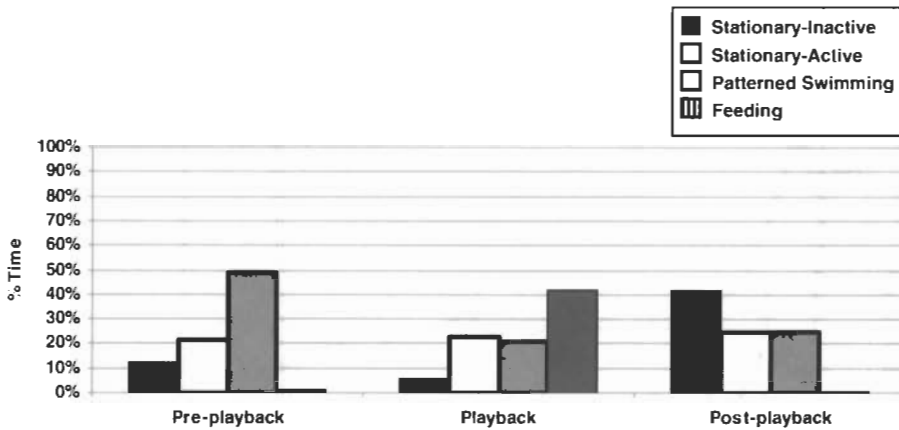


Figure 10. Behavior changes during playback period. The pre-playback period was 30 min prior to the start of the playbacks, the playback period was during exposure to the 30-min playback tape, and the post-playback period was 30 min after playbacks were terminated.

patterned swimming (32%) states. She was stationary-inactive only 16% of the time. During the first 5–10 min of playback, she was usually feeding. After feeding, she continued in the patterned swimming (49%) and stationary-active (24%) states. She was stationary-inactive only 11% of the time. After playback trials, patterned swimming decreased dramatically (1%) and she spent most of her time in stationary-active (67%) or stationary-inactive (27%) states, primarily in the channel (91%).

JJ did not produce many sounds at any time, but was most silent around feeding times and during the playback trials. Consequently, it is not possible to compare call rates before, during, and after playbacks. The playbacks certainly did not cause a noticeable increase in calling.

JJ began making pops (call type 1b) at higher rates during non-playback recording sessions in period B. Type 1b later emerged as her most common call (period D). Moans (call type 3) were made most often during period A, were rare in period B, and were never heard again after the end of period B, even though they were introduced into the playback stimuli.

Discussion

Development of behavior

Because of concerns about imprinting on humans, JJ was handled as little as possible during her rehabilitation. This may explain her low activity during periods C and D. Alternatively, the decrease in activity may have occurred naturally after JJ was weaned. Free-ranging southern right whale calves become more active during the first two months after birth (Taber & Thomas, 1982), as do gray

whales (Norris *et al.*, 1977; S. Wisdom, pers. obs.), but yearlings are substantially less active. JJ was most active during the period when she was being fed by hand, when she had most contact and social stimulation by humans. Activity levels declined substantially after JJ started taking solid food at the bottom of the pool and as interactions with human feeders declined. When JJ's inactivity aroused concern near the end of period C, SeaWorld animal care staff began altering the feeding schedule to stimulate more activity. This resulted in only a marginal increase in activity in period D.

If contact was a factor, it was the result of direct physical and social contact during surface feedings. After weaning, JJ was exposed to divers daily, a California sea lion, *Zalophus californianus*, for short periods (*cf.* Hurley *et al.*, 2000), and a common dolphin for brief periods. JJ reacted little to these potential social partners. They had no effect on her overall activity levels. JJ always reacted strongly and negatively to unexpected contact, as when a person reached into the pool near her in an area where she was not normally approached.

Development of call repertoire

Development of an adult call repertoire seems to be innate in most mammals (Ehret, 1980), though it may be affected by maturation of the vocal tract and motor and neuronal control. Nonetheless, young mammals may need experience to use calls in an appropriate context and give an appropriate response to calls of conspecifics.

JJ produced all the calls of free-ranging adult gray whales shortly after birth, despite very limited contact with her mother and other whales (at most a few days, during which her condition was poor). She had no further exposure to gray whale sounds

Table 3. Time spent by a rehabilitating gray whale calf (JJ) in each activity and area of the pool during the pre-playback (3a), playback (3b), and post-playback periods (3c).

	Main Pool		Channel		Totals	
	Hours	Percent	Hours	Percent	Hours	Percent
3a. Pre-playback						
Stationary-Inactive	5.04	14%	3.04	21%	8.08	16%
Stationary-Active	7.35	21%	10.48	74%	18.23	36%
Unpatterned Swim	5.41	15%	0.16	2%	5.57	12%
Patterned Swim	16.41	45%	0.00	0%	16.41	32%
Highly Active	0.03	0%	0.00	0%	0.03	0%
Feeding	1.23	4%	0.00	0%	1.23	3%
Play	0.25	1%	0.25	3%	0.50	2%
Grand total	36.52	72%	14.33	28%	50.85	100%
3b. During playback						
Stationary-Inactive	1.22	2%	7.42	32%	9.04	11%
Stationary-Active	4.36	8%	15.32	64%	20.08	24%
Unpatterned Swim	6.48	11%	0.29	2%	7.17	9%
Patterned Swim	41.09	69%	0.00	0%	41.09	49%
Highly Active	0.20	1%	0.01	0%	0.21	0%
Feeding	3.51	6%	0.00	0%	3.51	5%
Play	1.28	2%	0.21	1%	1.49	2%
Grand total	59.34	71%	24.05	29%	83.39	100%
3c. Post-playback						
Stationary-Inactive	0.00	0%	9.16	29%	9.16	27%
Stationary-Active	1.26	47%	21.47	69%	23.13	67%
Unpatterned Swim	0.30	16%	0.02	0%	0.32	2%
Patterned Swim	0.18	10%	0.00	0%	0.18	1%
Highly Active	0.00	0%	0.00	0%	0.00	0%
Feeding	0.50	27%	0.29	2%	1.19	4%
Play	0.00	0%	0.00	0%	0.00	0%
Grand total	3.04	9%	31.34	91%	34.38	100%

until playback experiments began when she was eight mo old. She was making 3 of 4 common gray whale calls by the time she was 1.5 mo old and the full repertoire by 7 mo of age. She produced these in proportions similar to those of free ranging whales (Fig. 11).

The division of call type 1 into two types is consistent with earlier reports. Dahlheim *et al.* (1984) described type 1 calls as either a 'burst' of pulses (our type 1a) or as a 'series' of pulses (our type 1b). We found that the pulse burst type 1a sounds were made when JJ was very young whereas type 1b sounds emerged when she was around 7 months old. Afterwards, type 1b was heard substantially more often. The use of the call increased gradually after playback experiments began. It seems likely that the sound was a part of her innate repertoire, but use of the call could have been reinforced by playback experiments. The other playback call (moan, type 3) decreased in usage

during the period of the playback experiments, but was never projected as the signal for feeding. Thus, if changes in usage of the type 1b call were stimulated by playback, it was the association with feeding that produced the change.

The early and complete emergence of the repertoire is only one line of evidence that call learning does not occur in gray whales. Generally, animals that must learn how to produce calls start with a 'babbling' or 'plastic' phase during development. For example, bottlenose dolphins (McCowan & Reiss, 1997), humans (Locke, 1990), and killer whales (Bowles *et al.*, 1988) go through a plastic phase before producing adult-like calls. We have no evidence for plasticity in JJ's repertoire; although relative usage of call types changed as JJ aged, the calls themselves did not.

Call learning usually occurs in species that must be able to distinguish and recognize certain conspecifics (e.g., bottlenose dolphins, Caldwell

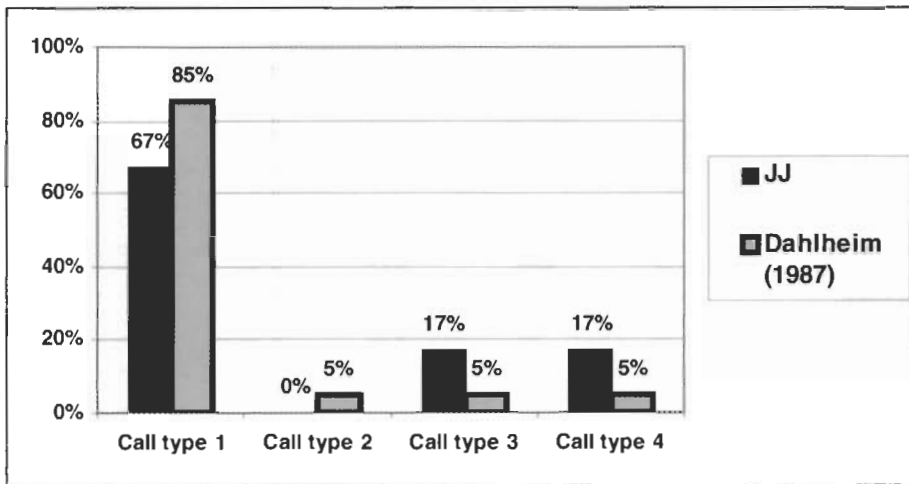


Figure 11. Percent call use by a rehabilitating gray whale calf (JJ) and free-ranging gray whales in breeding lagoons at Laguna San Ignacio, Baja California (from Dahlheim *et al.*, 1984).

et al., 1990; killer whales, Ford, 1991; big brown bats, Rasmuson & Barclay, 1992; bannertail kangaroo rats, Randall, 1995). As yet, there is no evidence that gray whales use calls to recognize each other or for other social purposes.

However, use of particular sounds often requires experience, even in animals with innately determined vocal repertoires. Responses of vervet monkey adults (Seyfarth & Cheney, 1997) facilitate the development of alarm call usage in infants by reinforcing situations in which an infant produces the correct alarm call for the appropriate predator. In other words, the infant knows how to make the calls without access to a model, but learns the appropriate context in which to use a particular call through reinforcement by adults. Thus, although JJ was able to make all the gray whale call types with little or no access to other gray whales, she may not have known the appropriate context in which to use the calls without being reinforced by conspecifics. Such contextual or social cues may explain the temporal shift in the proportionate usage of call types that we observed. For example, call type 3 was only observed during periods A and B and not in periods C or D. Clark (1982) suggested that tonal calls are primarily contact calls in southern right whales. Call type 3, a tonal call, was absent later in development, perhaps due to lack of contact with conspecifics.

Behavioral evidence from two studies suggested that gray whales may also use pulsed sounds to maintain contact with conspecifics. Fish *et al.* (1974) and Norris *et al.* (1977) reported the presence of pulses upon release of gray whale juveniles from short-term and long-term captivity. Pulses (type 1b) were not observed in JJ's call repertoire initially,

perhaps because the reinforcement of a response was needed. They did become more common after playback experiments began, which could have served as reinforcement.

Usage of call types 1a and 1b did not suggest any similarities in usage between the two calls. JJ made bursts of call type 1a more often when she was young, particularly when she was very active (e.g., breaching or porpoise swimming), though it did occasionally occur at other times. It was therefore the increased use of the call that was associated with periods of greater activity rather than the call itself. Call type 1a may then be used to indicate high states of arousal, whereas 1b could serve to maintain contact, as suggested by previous authors.

Playback experiments

Playback experiments on humpback whales, southern right whales and gray whales have all stimulated approaches (positive responses) to species-specific calls (Clark & Clark, 1980; Tyack, 1983; Dahlheim & Ljungblad, 1990; Frankel *et al.*, 1995). However, JJ did not approach gray whale sounds until she learned to associate them with food, suggesting that the tendency to approach conspecific sounds requires experiences that associate the sounds with reinforcing experiences.

JJ's lack of response was less surprising. Bowhead whales increased the rate of calls during approaches (Clark & Clark, 1980) to playback sources, but humpback and gray whales approached silently (Tyack, 1983; Dahlheim & Ljungblad, 1990; Frankel *et al.*, 1995), perhaps a defensive response in the presence of an unknown caller. However, the initial low SNR in playback

trials with JJ probably provides a more parsimonious explanation for her failure to respond. JJ was exposed to human-made sounds in the pool before the start of playback trials, many of which had as great or greater amplitude than the playbacks. There was nothing in the context of the initial playbacks to call playback sounds to her attention. Indeed, we found it necessary to make the sounds more obvious to her before she could establish an association between the sounds and food and/or social contact. When playback level and rate were increased after 13 trials, it took only five trials for JJ to learn to respond with approach. However, once she learned to associate playback sounds and feedings, she was able to detect the playback sounds within (5 dB of the background within 2 min of the start of exposure in the channel, even when there were sounds with greater amplitude present in the pool at the same time (fan noise, humans banging on glass). Thus, pairing the sounds with food and/or social interaction evidently motivated her to listen for playback sounds among the clutter of background noise. This suggests that a motivated whale might hear sounds at or just above background noise levels (Richardson *et al.*, 1995).

JJ learned to associate sounds with food readily. First, she learned that splashes and slaps at the feeding station were associated with food. Then, she associated playback of pops with food and responded by swimming to the feeding station in advance of the splashes. This association required only an adequate SNR. Finally, she learned to wait for the sounds of divers entering the water, extinguishing her previous responsiveness to playbacks. The rate at which she made associations was comparable to food-motivated learning rates in other marine mammals (pinnipeds, small odontocetes).

Our playback stimuli had energy in the range from 20 to 2500 Hz. That made it difficult to evaluate which frequencies were more important in evoking responses. However, our data are most consistent with the hypothesis that JJ could hear down to background noise levels down to at least 400 to 800 Hz. Frankel *et al.* (1995) reported similar findings for humpback whales, which were attracted to sounds of conspecifics at levels down to 102 dB re 1 μ Pa (broadband level, close to ambient level where their study was conducted). Dahlheim & Ljungblad (1990) conducted experiments using 500 Hz pure tone stimuli in the Baja California Lagoons and observed avoidance responses by gray whales at levels down to ambient (95 dB re 1 μ Pa).

Hearing thresholds of toothed whales and pinnipeds in the sensitive part of their range lie between 40 and 60 dB re 1 μ Pa (Richardson *et al.*, 1995). If baleen whales have best frequencies below 1 kHz, where their calls have the greatest energy (Ketten, 2000), oceanic ambient noise would limit detection

under most conditions (Wenz, 1962). In the absence of shipping noise, the highest ambient levels in the 20 to 800 Hz range drop from roughly 110 to 80 dB re 1 μ Pa²/Hz, determined in large part by wind-generated water noise and precipitation. Under very quiet conditions, levels drop from 60 to 30 dB re 1 μ Pa²/Hz in the same frequency range. Pinnipeds and small cetaceans have best sensitivities approaching quiet local ambient, as is also true of terrestrial carnivores (Fay, 1988; Richardson *et al.*, 1995). This suggests that baleen whale best sensitivities might be lower than our estimates based on JJ's performance and experiments on free-ranging whales suggest, perhaps as low as 70 dB re 1 μ Pa²/Hz at frequencies below 1 kHz (~85 dB re 1 μ Pa).

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