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# Effects of boat noise on the singing behavior of humpback whales (Megaptera novaeangliae)

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EFFECTS OF BOAT NOISE ON THE SINGING BEHAVIOR OF

HUMPBACK WHALES (Megaptera novaeangliae)

A Thesis Presented to the Faculty of

Moss Landing Marine Laboratories

San Jose State University

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by

Thomas F. Norris

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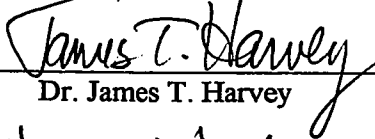
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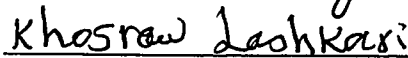
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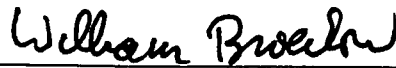
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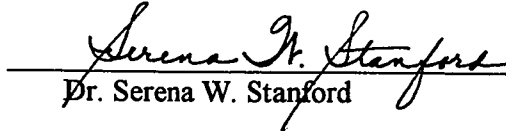
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# ABSTRACT

## EFFECTS OF BOAT NOISE ON THE SINGING BEHAVIOR OF HUMPBACK WHALES (Megaptera novaeangliae)

### by Thomas F. Norris

Songs from humpback whales (Megaptera novaeangliae) were recorded when noise from a small (5.5 m) boat was experimentally introduced, and when large (10-35 m) vessels passed nearby. Twelve variables characterizing the structure and patterns of humpback whale song were compared for periods before and during exposure to boat noise. Generally, singing humpback whales decreased the duration of song units (notes) resulting in an increase in the "tempo" of songs. The frequency structures of some song units were affected by noise from large boats. Statistical power analyses indicated that phrase and theme patterns probably were not affected. Spectral analysis of humpback whale song and noise produced by large and small boats indicated that masking of songs is more severe from noise by large boats than noise by small boats. Changes in song tempo may indicate disturbance in singing whales. The significance of these effects on the behavioral biology of humpback whales remains uncertain.

# ACKNOWLEDGMENTS

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# INTRODUCTION

Communication involves transmission of a signal through some medium to a receiver. In water, the acoustic channel is the most efficient pathway for sending and receiving signals. Consequently, many marine organisms have evolved the ability to communicate and sense their environment acoustically. Cetaceans are particularly well adapted for acoustic communication (Herman and Tavolga, 1980). In fact, some cetaceans (e.g. delphinids) have sound production, reception, and processing capabilities that are among the most sophisticated in the animal kingdom (Au, 1993). Although the acoustic capabilities of mysticetes are not as well understood, vocal behavior has been documented in ten of eleven species of baleen whales and complex acoustic signals have been documented in at least three species, bowhead whales (Balaena mysticetus), humpback whales (Megaptera novaeangliae), and right whales (Eubalaena glacialis; Clark, 1990). Generally, mysticetes vocalizations are lower in frequency and greater in duration than odontocete signals (Norris, 1969; Thompson et al. 1979; Clark, 1990). The largest mysticetes, blue whales (Balaenoptera musculus), fin whales (Balaenoptera physalus), bowhead whales, right whales, and humpback whales, produce extremely loud, low frequency signals that propagate great distances. Some researchers have proposed that such signals could function in long-range communication or echo-ranging of large-scale bathygraphic features (Payne and Webb, 1971; Gagnon and Clark, 1993). It is apparent that marine mammals, and mysticetes in particular, rely on information from the acoustic environment to survive.

Human-made noise in the ocean has increased dramatically since the industrial revolution. In fact, it has become the most significant source of low-frequency noise in the ocean (Ross, 1976). Although the causes of anthropogenic noise are known, its effects on marine mammals are not well understood (National Research Council, 1994). Traffic noise (i.e. noise from distant vessels), the main source of man-made noise, is pervasive throughout most of the world's oceans. Traffic noise contributes substantially to

deep-water ambient noise in the 20 Hz to 500 Hz range (Wenz, 1962). Moderate to heavy shipping activity in an area can increase noise levels as much as 25 dB more than "natural" ambient noise levels in the 20 to 300 Hz band (Fig.1; Urick, 1983). In deep water (>200 m), noise from ships up to 1,600 km distant can contribute substantially to ambient noise levels. Ambient noise levels in the hundreds of hertz frequency range are directly related to wind speed. In fact, traffic noise energy in the 200 to 500 Hz band can be exceeded by wind dependent noise (Ross, 1976). Although noise from small boats contains peak energy at higher frequencies than traffic noise and wind dependent noise (Richardson et al., 1991; pers. obs.), it still contributes significantly to shallow water noise in coastal regions with extensive fishing, recreational, and other small boat activity (Zakarauskas, 1986; Richardson et al., 1991). Generally, there are more noise sources (biological and man-made) in shallow than in deep water environments, thus ambient noise levels in shallow water are usually greater. Furthermore, the spectra of ambient noise in shallow water environments is extremely variable as a function of location and time (Richardson et al., 1991).

Numerous government, scientific, and conservation organizations have expressed concern about the effects of boats and boat noise on marine mammals (Acoustical Society of America, 1981, 1994; Tinney, 1988; NMFS, 1991; Inter-noise '95, 1995). Richardson et al. (1991) reviewed the few attempts made to quantitatively examine the effects of noise on large whales. In most studies, researchers examined conspicuous surface activities of whales, such as movements, respiration rates, and aerial behaviors in response to noise. Few of these studies incorporated quantitative measurements of noise near the whales being observed. Even fewer researchers have examined the effects of noise on the vocal behavior of marine mammals; however, none of these measured noise levels.

Most studies in which the effects of boat noise on the vocal behavior of marine mammals were deficient because investigators were not able to identify the individuals producing vocalizations. Also, they were not able to measure noise levels near the animals

being recorded and, in some cases, they did not have control of the noise source. For example, Terhune et al. (1979) examined the effects of vessel noise on the underwater vocal behavior of harp seals (Pagophilus groenlandicus) in the Gulf of St. Lawrence, Canada. The vocal activity of harp seals before and during the presence of an operating 36.5-m stern trawler was compared using indices based on the relative loudness of seal calls. They determined "a marked decrease in seal vocalizations occurred following the arrival of a vessel." Terhune et al. (1979) estimated that noise from the vessel was loud enough to mask seal calls within at least a two kilometer radius. Unfortunately, they could not attribute whether the reduction in vocalizations was due to a change in the number of vocalizations per animal, or to a decrease in the number of seals inhabiting the area. They stated the latter possibility was supported by "indirect evidence" from seal hunters who believed that noise from outboard motors frightened seals (Kapel, 1975). Although the boat producing the noise appeared to be part of a seal hunting operation, the authors gave no indication if harp seals in their study had prior experience with seal hunting operations. It seems possible these harp seals might have perceived boat noise as a threat or dangerous signal by associating it with previous encounters with seal hunting activities.

Lesage (1993) studied the effects of boat noise on the vocal behavior of the beluga whale (Delphinapterus leucas) in the St. Lawrence Estuary, Canada. She opportunistically recorded beluga whales in the presence of large (80 m) ferry boats. She also experimentally introduced noise using a 7-m Boston Whaler® powered by twin 70 h.p. outboard engines. Lesage proposed that beluga whale changed several aspects of their vocal behavior when they were exposed to boat noise. Her results indicated beluga whales reduced the diversity of call types produced, increased the duration and intensity of some signals, had a tendency to increase signal repetition, produced certain stereotyped vocalizations more frequently during boat-passes, and produced signals with frequency characteristics that [theoretically] would reduce interference by boat noise (Lesage, 1993).

Dahlheim et al. (1984) and Dahlheim (1987) recorded vocalizations of gray whales (<u>Eschrichtius robustus</u>) in the presence of boat noise at San Ignacio Lagoon, Baja California Sur, Mexico. Analyses of recordings indicated that boat noise spectra overlapped the spectra of gray whale vocalizations. She determined vocalization rates of gray whales increased in the presence of boat noise. After comparing the frequency distribution of gray whale and bottlenose dolphin vocalizations to the spectra of natural ambient noise, Dahlheim et al. (1984) proposed that signaling gray whales, and possibly bottlenose dolphins, might be taking advantage of "acoustical niches" (i.e. frequency bands with low levels of ambient noise). She suggested boat noise might interfere with whale vocalizations by "jamming" naturally occurring channels of communication.

Unfortunately, neither Lesage (1993) nor Dahlheim et al. (1984) could identify which individuals were producing sounds. Because some vocalizations probably were produced repeatedly by the same animal, it is probable that some samples (vocalizations) were not independent, possibly resulting in artificially inflated sample sizes and violations of certain assumptions of the statistical tests used. In fact, Lesage (1993) noted her sampling methods most likely resulted in non-independent observations and advised caution in the interpretation of her statistical results.

In many respects, humpback whales are ideal subjects for studying the effects of boat noise on free-ranging marine mammals. For example, singing humpback whales vocalize continuously for long periods (minutes to hours; Winn and Winn, 1978), usually are solitary, and often remain stationary. These behaviors allow individuals to be identified easily (Glockner, 1983) and make it possible to obtain long, but good quality recordings of their songs. The predictable structure of humpback song also allows the same variables to be examined for many different animals. Furthermore, the spectra of humpback whale song has a wide frequency range (50 Hz to 8 kHz) suggesting humpback whales have good hearing sensitivity over a similar range (Popper, 1980; Popov and Supin, 1990; Ketten, 1992). These spectra are similar to the spectra of noise produced by

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medium to large vessels (those smaller than tankers, freighters, and large cruise ships) that commonly occur in the same areas inhabited by humpback whales. Finally, humpback whales are protected by numerous laws (e.g. Endangered Species Act, Marine Mammal Protection Act), regulations (e.g. National Marine Fisheries Service whale-watching restrictions), and governing bodies (e.g. International Whaling Commission, U. S. Marine Mammal Commission). In Hawaii, much of their habitat is part of the recently designated Hawaiian Island Humpback Whale National Marine Sanctuary. It is apparent that there is great concern regarding any human impacts on humpback whales and their habitat.

Humpback whales migrate between temperate, cold water regions where they feed in summer and fall, to tropical and sub-tropical, warm water areas where they breed in winter and spring. In the North Pacific Ocean, humpback whales feed in biologically productive coastal waters off the northwest continental U.S.A., the Gulf of Alaska, the Bering Sea, and the Sea of Okhotsk (Johnson and Wolman, 1984). In late fall, humpback whales migrate south along undetermined migration routes to the Hawaiian Islands, the Bonin and Ryukyan Islands (Japan), the Revillagigedos Islands (Mexico), southern Baja California, and mainland Mexico (Baker et al., 1986; Urban, 1987; Perry et al., 1990; Darling, 1991). The Hawaiian Islands, however, are considered the main wintering area for the North Pacific population of humpback whales (Baker et al., 1986).

The population of humpback whales in the North Pacific Ocean was estimated at 15,000 individuals before whaling activities reduced it to as few as 1,000 animals (Rice, 1978). Because of this dramatic decline in the population, humpback whales were protected internationally in 1965 (Rice, 1978). Estimates of the humpback whale population in Hawaiian waters are very imprecise. Over the last twenty years, estimates have generally increased from a few hundred whales, based on results from vessel surveys in the mid 1970's (Rice and Wolman, 1978; Johnson and Wolman, 1984) to approximately 2,000 animals using mark-recapture techniques in the late 1970's (Baker et al., 1986; Darling and Morowitz, 1986). Recently, Cerchio (1994) used several mark-recapture

methods of analyses on photographic data collected from 1990 to 1993 to calculate population estimates of between 2,000 and 4,000 individuals. Although, part of the increase in these population estimates may be attributed to different methods, variable sample sizes, violations of model assumptions, and unequal levels of effort for each study, the general consensus among most humpback whale biologists is that the population of humpback whales in the North Pacific is increasing.

Surface behaviors of humpback whales in breeding areas are very conspicuous and, as a result, have been studied quite extensively (Baker and Herman, 1981; Bauer, 1986). Because underwater behaviors of whales are more difficult to observe, they are just beginning to be documented systematically (Anonymous, 1995; Clark, 1993). Probably the most frequently studied and most fascinating underwater behaviors of humpback whales is singing.

Humpback whale song is one of the most complex acoustic displays in the animal kingdom (Wilson, 1975; Payne et al., 1983). Although recordings and accounts of sounds attributed to humpback whales have been documented earlier (Schreiber, 1952; Schevill and Watkins, 1962; Levenson, 1972), Payne and McVay (1971) were the first to categorize as songs the long, repetitive, and structurally complex sounds produced by humpback whales in tropical and sub-tropical waters. Payne and McVay (1971) described humpback whale songs as being organized hierarchically in units, phrases, and themes (Fig. 2). Units (analogous to notes in human music and elements or figures in bird song) are the most basic component of humpback whale song. Groups of units, arranged in a similar pattern, compose a phrase. Phrases are repeated consecutively, a variable number of times, to produce a theme. Themes occur in a non-reversible order to complete a song. Songs are repeated continuously, without pause, during a song session. Singers usually breathe during the same theme, sometimes called the "surface ratchet" (Winn and Winn, 1978), because it resembles the noise produced by a ratchet mechanism. Song sessions can range from few minutes to more than 24 hours in duration (Winn and Winn, 1978).

Generally, humpback songs are very repetitive and have rhythmical characteristics that are not obvious to the human ear unless recorded songs are played back at fast speed (pers. obs).

Several functions for singing behavior in humpback whale have been proposed. Payne and McVay (1971) first suggested that songs may be used by males to attract mates. Since then, there has been much evidence to indicate singing whales are sexually mature males (Winn et al.,1973; Glockner, 1983; Lambertson et al., 1988; Medrano et al., in press). Some researchers have suggested singing is a form of sexual advertisement (Winn and Winn, 1978; Tyack, 1981). Darling (1983) proposed that singing is used to establish and maintain a dominance hierarchy among males, whereas Baker and Herman (1984) suggested singing synchronizes ovulation in females. Winn and Winn (1978) hypothesized that the combined effect of many singing animals could function as an acoustic beacon for whales migrating to winter areas. Makris and Cato (1994) even suggested songs can be used as an acoustic source to detect non-singers from reflected sounds. Of course, these functions are not all mutually exclusive. As with most complex behaviors, singing by humpback whales probably has several functions; however, most humpback whale researchers agree that the primary function of singing is related to reproductive behavior (Tyack, 1983; Baker, 1985; Frankel, 1994).

Acoustic experiments using sound playbacks and hydrophone arrays have clarified the function of singing in humpback whales. Tyack (1983) first performed playbacks of songs and "social sounds" (produced in tropical breeding areas when a group of males are actively pursuing a female) to humpback whales in Hawaii. He determined that song playbacks resulted in "avoidance" of the sound source, whereas social sounds elicited a "charge" response. Mobley et al. (1988) performed similar playback experiments using a more rigorous experimental design that included controls. They determined humpback whales were least attracted to the most recent song version, and were greatly attracted to other sounds, including social sounds and particularly "feeding calls" (i.e. calls associated

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with feeding behavior in high latitudes), lending further support to Tyack's (1983) conclusions. Mobley et al. (1988) suggested whales were attracted to feeding calls and social sounds because of the possibility that food or females were present. They reasoned that the least attractive sounds were songs, because these are usually produced by solitary males.

Using a fixed hydrophone array, Frankel (1994) determined singers were uniformly distributed in areas where several animals were singing. He proposed, as others before him have (Tyack 1981), that one function of humpback whale song is to space apart males. Frankel (1994) also discovered that singing whales sometimes affiliated with other (non-singing) whales. It has been suggested these affiliations might function in courtship, possibly by "serving as a basis for female choice" (Helweg et al. 1992). Regardless of the actual function of singing behavior, the complexity of humpback whale song structure most probably is the result of strong sexual selection (Tyack 1981).

Using models and theories of communication from statistics, electrical engineering, and psycho-physics, predictions can be made about how a signaler (singing whale) can maximize the probability that a receiver (listening whale) will detect and correctly discriminate a signal in noise. Noise interferes with communication by reducing the probability of signal detection and discrimination by a receiver. Information theory (Shannon and Weaver, 1949; Raisebeck, 1949), statistical communication theory (Harman, 1963; Blachman, 1982) and signal detection theory (Green and Swets, 1966; Swets and Birdsall, 1978) all predict that increasing redundancy (e.g. signal repetition) should increase the probability of signal detection in noise. Auditory masking theory, predicts that noise present in a band corresponding closely to the frequency band of the signal will have the greatest effect on signal detection and discrimination (Greenwood, 1961; Moore, 1975). Based on these models, it can be predicted that the effects of noise could be reduced if a signaler altered the frequency structure of signals so they do not overlap with frequencies containing the greatest noise energy. Also, increasing

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redundancy using signal repetition would effectively increase the signal-to-noise ratio (S/N) at the receiver, further increasing the probability of signal detection and discrimination by a receiver.

According to the aforementioned theories, songs of humpback whales exhibit several design features that should reduce the effects of noise on a receiver. For example, humpback whale songs incorporate great redundancy in the form of phrase repetition which, interestingly, is also one of the most variable components of their songs (Payne et al., 1983). Although specific song units have stereotyped morphology (i.e. similar time-frequency structure), there is a wide range of frequencies used for different units. By examining the frequency structure and repetition of signals in humpback whale songs, it should be possible to determine if singing humpback whales are changing some aspect of their songs in an attempt to reduce the effects of noise on receivers Alternatively, it is possible noise is affecting the singing behavior of humpback whales, but changes in behavior are not related to maximizing S/N. By examining durations of signals and patterns of signals (e.g. tempo and rhythm of songs), other effects, such as disturbance responses to noise, can be investigated.

Objectives

The objectives of this study were to determine the effects of boat noise on the singing behavior of humpback whales, to measure absolute received noise levels near singing humpback whales before and during boat-passes, and to compare the power spectra of humpback whale songs to the power spectra of noise from different types and sizes of boats.

## METHODS

### Study Site

Humpback whales were studied in coastal waters off Kauai (22° 10″ N; 159° W), the most northwestern island of the main Hawaiian Islands (Fig. 3). The study area encompassed near-shore (< 4 km) waters off the leeward (southwest) corner of the island. Effort was concentrated off the southwest side of the island in within the 180 m contour line (Fig. 3). This region has the greatest density of humpback whales around Kauai (Mobley and Bauer, 1991) and, generally, has the most favorable sea conditions.

Natural and man-made ambient noise was pervasive in the study area. Major ambient noise sources of biological origin were snapping shrimp, fish, and other cetaceans. Snapping shrimp (probably Family Alpheidae) are the main source of noise in shallow (< 50 m) coastal waters (Norris et al. 1994) around the Hawaiian islands. Snapping shrimp produce intense broad-band clicks that collectively sound like water crackling in a frying pan. Songs from distant humpback whales were the predominant source of background noise in deep water (> 200 m). Occasionally, whistles and echolocation signals from dolphins (usually Stenella sp. or Tursiops truncatus) were audible.

Non-biological ambient noise in the 100 to 10, 000 Hz range typically is related to meteorological conditions. For instance, ambient noise levels in shallow water is related directly to wind speed and indirectly to sea state (Wenz, 1962; Willie and Geyer, 1984). Rain also affects ambient noise in the ocean (Wenz, 1962). Due to practical considerations of working from small boats, sea states during acoustic recordings usually were less than Beaufort four. Although heavy rain occasionally occurred in the study area, recordings usually were terminated if it was raining in the immediate vicinity. In winter, intense storms originating off the Aleutian Islands can produce large ground swells that can be up to 10 m in height when they arrive at the north and west coasts of the Hawaiian Islands. When recordings were made close to shore (< 1 km) during such periods of large swell activity, periodic pulses of low frequency noise often were detected.

These pulses of noise presumably were produced from sets of large waves breaking along shore (Wilson et al., 1985) or across offshore reefs.

Major sources of anthropogenic noise in, or near, the study area included boats, low-flying aircraft, and possibly submarines, many of which were associated with military operations. Boat traffic along the southwest coast of Kauai primarily consisted of small (5 to 10 m) commercial and sport-fishing vessels with engines ranging from small (50 h.p.) outboards to large (300 h.p.) inboard/outboards. Occasionally (once or twice per week), large (> 100 m) cruise-ships traveled at low speeds (< 15 km/hr) four to six kilometers offshore. Noise from slow-moving cruise ships was not audible (to the human ear) until they were nearby (< 0.5 km). Infrequently, low frequency (10 - 50 Hz) noise was audible, but no source was visible. Such noise possibly was related to submarine activity nearby or large vessels far offshore. Most large, non-military ship traffic occurred within shipping lanes approximately 7 km offshore of the north side of the island (pers. obs.). Therefore, most recordings were made in the acoustic shadow of noise from these vessels.

The U.S. Navy (USN) maintains a base, the Pacific Missile Range Facility, on the southwest corner of Kauai and operated frequently in waters near the study area (Fig. 3 ). The three types of naval vessels most commonly operated by the USN in the region were large (30 m) torpedo retrieving vessels (TRVs), medium (25 m) TRVs, and small (10 m) target vessels. Noise produced by TRVs was extremely loud (relative to noise from most other vessels) probably due to their large engines and metal hull construction. Although target vessels are smaller, and are constructed of wood and fiberglass, they also were very noisy relative to other boats of similar size.

There were numerous other sources of human-made sound in the study area that potentially could have affected humpback whale singing behavior. Most of these sounds were related to military exercises. For example, because a runway is located on the military base, airplane and helicopters frequently flew over the study area. Also, there were various types of unidentified man-made underwater sounds that presumably were

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associated with USN activities. These sounds included loud pings (pure tones > 2 kHz and < 5 sec. duration), engine sounds (probably torpedoes) and occasionally, underwater explosions. It is llikely such sounds were related to submarine and anti-submarine warfare exercises.

Equipment

All field work was conducted from small inflatable boats. A 4-m inflatable boat powered by a 25 h.p., two-stroke, outboard engine was used for approaching singing whales and to deploy recording equipment (recording vessel). A 5-m rigid-keel inflatable boat, powered by a 40 h.p, two-stroke, outboard engine was used to experimentally introduce noise to singing whales (passby vessel), and occasionally, to opportunistically record singers during passes by other vessels. Both vessels were equipped with portable VHF and CB radios for communication. Hand held compasses were used for triangulating positions.

In 1991, the acoustic recording system consisted of a 2 channel Marantz PMD-40 or Sony TCD-5M portable cassette-recorder (both professional models), a reference-tone-generator (RTG), and a modified sonobuoy hydrophone with external power supply (Fig.4). In 1992, the RTG was replaced by a step-attenuator. The step-attenuator (or RTG) was used to adjust (or determine) gain levels for the cassette recorder so that absolute received sound-pressure-levels (SPL) could be calculated during analysis.

Hydrophones were calibrated at the Naval Post Graduate School, Monterey, CA, using a comparison calibration technique (Bobber, 1988). All other components of the recording system were calibrated using a HP 35660A Dynamic Signal Analyzer. The effective frequency response of the recording system was flat from approximately 50 Hz to 15 kHz. System fidelity was verified in the field by recording calibration tones at the beginning of a cassette tape for each day. Calibration tones were measured before each analysis session to ensure the tape playback system was operating at the correct speed.

Locating and Recording Singing Whales

Singing whales were located acoustically using a technique termed "leap-frogging" that involved monitoring whale signals from two boats simultaneously. First, both research boats would separate by at least 100 m and deploy hydrophones. Underwater sounds from singing whales were transmitted from one boat to the other using a VHF radio. By aurally comparing the time delay of signal arrival, the boat which was closest to a singing whale could be determined (i.e. the boat which received the signal first was closer to the singer). Essentially, the two hydrophone-equipped boats functioned as a 2-element array. Next, both boats would move in the direction of the boat which was closer to the singing whale, while maintaining the same relative inter-boat position. After moving a few hundred meters, both boats would stop, deploy hydrophones, and repeat the procedure. When the location of a singing whale was subjectively determined to be within approximately one kilometer (by listening to the intensity of the signals relative to ambient noise), only one boat would move, while the second boat monitored the song. This "leapfrog" technique was used until a singing whale was sighted visually at the surface. Once a singing whale was sighted, the small 25-h.p. boat moved slowly to within 25 to 100 m of the whale and was positioned to begin recording. The positioning of the boat relative to the singing whale was based on prevailing wind and current conditions. The ideal location usually was a few hundred meters up-wind (or up-current) of the singing whale. Using this technique, a singing whale usually could be located within 30 minutes.

Singing whales were located visually during the recording by correlating their appearance at the surface with the "surface ratchet" theme of the song (Winn and Winn, 1978). Additionally, because the song signals attenuate as a singer approaches the surface to breathe, it usually was possible to correlate attenuation of signals with the singer's appearance at the surface. Furthermore, when respirations occurred, there were distinct pauses in the surface ratchet signals at the precise moment of the blow. By correlating these pauses with blows seen or heard from the animal at the surface, it usually was

possible to confirm that the animal sighted was singing. Finally, commentary of whale behaviors were recorded concurrently on the second channel of the audio tape. When the audio tape was reviewed later, it was possible to verify that an animal sighted at the surface was singing, by correlating singing behavior with notes from visual observations of the whale's blows and appearance at the surface.

Acoustic recordings of singing whales were made by lowering a hydrophone to a depth of 15 to 25 m. The exact hydrophone depth was dependent on the rate of drift. To reduce strumming (noise from hydrophone cable vibration) and variability of hydrophone depth, a sea anchor was deployed when the drift rate was greater than approximately 5 km/hr. Signal levels on the tape recorder were monitored continuously so that step attenuator settings could be adjusted appropriately. To investigate the possibility that factors other than boat noise might have been affecting humpback whale singing behavior, relevant data (e.g. surfacing and respiration events of other whales, other whale activities nearby, boat activities nearby, other potential sources of disturbance, sea conditions, and weather conditions) were recorded verbally on a second channel, and on data sheets.

Experimental Boat-Passes

Boat noise was introduced experimentally to individual singing whales using the passby vessel (40 h.p. outboard engine). At least one, but preferably two complete songs were recorded before boat-passes began. Boat-passes were initiated just after a singer surfaced, usually during theme 1A or 1B. The boat traveled in a straight line, passing between the whale and recording vessel, so that both were equidistant at the point of closest approach (PCA; Fig. 5). The boat was driven at the greatest speed possible (near maximum throttle) for approximately two to five minutes. When the boat-pass ended, the engine throttle was reduced to idle (or turned off) as the boat continued on a heading away from the singing whale and the recording vessel. Recordings continued for at least

20 minutes after the boat-pass, until the recording quality was considered unsuitable for analysis (e.g. low S/N), or until some outside event interrupted the singer or recording.

Opportunistic Boat-Passes

Several recordings of singers included uncontrolled passes by other vessels, hereafter referred to as "opportunistic boat-passes." If these boat-passes were near the singing whale and occurred during, or just before, theme 1B of the song, they were considered for inclusion as a sample. Because it was not possible to control the timing and direction of these boat-passes, distances and orientations of the boat relative to the singer and recording boat varied. The locations and movements of the boat and the singing whale were recorded verbally on a second channel during the recording. Vessels were photographed at the PCA so they could be identified later using registration numbers and vessel names on the hull.

Photographic Identification of Singing Whales

Singing whales were identified individually by photographing the ventral side of their fluke as it was raised vertically before diving (Katona et al., 1979). Flukes were photographed opportunistically during acoustic recordings if the whale dove nearby, or by approaching the whale after recordings were finished. Using the developed photographic images, patterns and markings on the flukes were compared to determine if repeat recordings of the same singer were made.

Signal Analysis of Recordings

Recordings were played back using a Marantz PMD-430 cassette recorder. Before each play-back session, the tape speed was adjusted based on the calibration tones recorded at the beginning of each recording session. Signals were high-pass filtered at 55 Hz to remove low frequency noise that could have resulted in inaccurate measurements of

sound levels (due to the non-linear low frequency response of the recording system), and also because 55Hz is approximately the lower frequency limit of humpback whale song units (pers. obs.). Signals were low-pass filtered at 40% of the sample rate (see below) to prevent aliasing during analog-to-digital conversion (Fig. 6).

Humpback songs and noise were analyzed using SIGNAL©, a DOS-based system for analyses of bio-acoustic signals. Song variables were measured using the SIGNAL program RTS (Real-Time Spectrographic display). This program acquires and displays a waveform and spectrograph of signals in real-time on a computer monitor so that time and frequency measurements can be made using a mouse driven cursor. Measured values were downloaded to a computer file and saved to the hard disk. Recordings used for analysis of song variables were sampled at 2.5 kHz (bandwidth = 1 kHz ), because this band contained the greatest energy for the specific signals analyzed. Ambient noise and boat noise signals were sampled at 12.5 kHz (bandwidth = 5 kHz) because of the greater frequency range of boat noise energy.

All acoustic recordings of boat-passes were reviewed before analysis. Potential sources of acoustic disturbance, both man-made and natural, were noted on a data sheet. Recordings were eliminated from analysis if they included other whales or boats nearby, loud acoustic disturbances (e.g. pinging), or other potential sources of disturbance. To reduce the possibility of confounding effects due to interactions with other singers, only recordings with faint (distant) or no background singers were analyzed. Furthermore, recording sessions were used as samples for experimental boat-passes analyses only if at least two complete "undisturbed" control songs (approximately 20 minutes) were recorded before the boat-pass. Recordings selected for opportunistic boat-passes analyses had at least one control song (approximately ten minutes) before the boat-pass. Some recordings of opportunistic boat-passes had PCAs that did not always occur during theme 1B, however, if boat noise during theme 1B was loud, the recording was still considered for analysis.

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Twelve song variables in each period (control and boat-pass) were measured (Table 1). Song variables were chosen that characterized signal structure and patterns of humpback whale songs and also were simple to measure. Time and frequency measurements of song units and phrases included unit duration, inter-unit duration, phrase duration, unit average frequency, unit minimum frequency, and unit maximum frequency (Fig 7). Song structure and patterns were quantified by counting units, phrases, and themes, and measuring durations of themes and songs.

Song variables were compared statistically using paired sample t-tests (Zar, 1984). Songs from experimental and opportunistic boat-passes were categorized into two periods for each individual: 1) before boat-passes (control), and 2) during boat-passes (BP). Phrase measurements and unit measurements (Table 1) were averaged from a group of phrases that corresponded with the PCA (Fig. 9). Phrase groups consisted of three consecutive phrases in experimental boat-pass recordings, and five consecutive phrases for opportunistic boat-pass recordings. When possible, the middle phrase of the grouping was chosen to correspond with the PCA. This procedure was used to control for any effects related to phrase repetition, because some variables appeared to be correlated with absolute position (repetition number) of the phrase in the theme.

Theme measurements (theme duration, and number of phrases per theme) for control and BP periods were compared for theme 1B only, because this theme occurred directly after the surface ratchet (i.e. when a singer surfaced), usually during the boat pass PCA. Song durations were compared between songs for control and BP periods.

Received Noise Level Measurements

Received sound pressure levels (SPLr) of ambient and boat noise were determined from recordings using SIGNAL-RTS and a computer routine created within SIGNAL. Ambient and boat noise signals from control and BP periods were extracted from brief

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( < 5 second) pauses between song units (inter-unit spaces; Fig. 7) and saved to disk using a mouse-driven cursor in RTS. The computer routine in SIGNAL was used to read digitized signals from the disk into a buffer, append noise signals (for each control or boat-pass period), and measure root mean square (Vrms) band level (5 kHz band) of the appended signals (Fig.8). Durations of appended noise signals were between five and twelve seconds. Recorded (uncorrected) Vrms values were converted to sound pressure density spectrum levels and corrected for system gain, step attenuation, and hydrophone sensitivity using the formula:

$$SPLr = 20\log [Vrms / (BW)^{1/2}] + HS + SA - RS$$

where:

| | | |
|---|---|---|
| SPLr | = | received sound pressure density spectrum levels (dB re: $1\mu Pa^2/Hz$) |
| Vrms | = | root mean square recorded levels (V) |
| HS | = | hydrophone sensitivity (dBV re: $1\mu Pa$) |
| SA | = | attenuation from step attenuator (dB) |
| RS | = | recording system gain (dB) |

Power Spectral Analysis

To describe the frequency characteristics of boat noise produced by vessels occurring in the study area, power spectral analysis was performed on recordings of boat noise from several vessels, including the 40 h.p. boat used to experimentally introduce noise. Recordings were made of the 40 h.p. boat from a distance of 100 m at the PCA. The distance of the PCA was determined precisely by tying a buoy to the end of a 100 m line that was attached to the recording vessel. Boat-passes were conducted at two shallow water sites (approximately 400 m offshore and 2 km offshore; both sites < 100 m water depth). Ambient noise was recorded before boat-passes were conducted. Ambient noise also was recorded at a deep-water site ( > 5km offshore; > 500 m depth) in the

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Kaulakahi Channel between Kauai and Niihau. Additionally, a large navy vessel and a whale watching vessel were recorded opportunistically when they passed near the recording vessel. The power spectra of ambient noise, boat noise, and humpback whale songs were measured using a HP 35660A Dynamic Signal Analyzer. Power spectra of boat noise was determined from multiple (80 - 120) averages of noise samples from the PCA. Absolute received levels were determined by correcting for system gain, attenuation, and hydrophone sensitivity.

Power spectra of humpback songs were analyzed from recordings of song units for three phrase types (1B, 2A, 3B). Recordings were made of units without inter-unit pauses by dubbing from recordings of complete songs (i.e. the recorder was paused during each inter-unit space). Average power spectra were calculated from multiple (>100) samples using a HP 35660A Dynamic Signal Analyzer.

# RESULTS

## Experimental Boat-Passes

Songs of nine animals were analyzed from recordings of experimental boat-passes. Three of twelve variable means (unit 2 duration, inter-unit 1-2 duration, and phrase duration) were significantly less for boat-pass periods compared with control periods (Table 2, Appendix I ). Means of three variables characterizing durations (unit 1 duration, theme duration, and song duration), all four variables characterizing frequency structure (unit 1 minimum and maximum frequency, unit 2 minimum and maximum frequency), and both variables describing phrase and theme structure (unit and phrase counts), were not significantly different for boat-pass periods when compared with control periods (Table 2).

## Opportunistic Boat-Passes

Songs of seven animals were analyzed from recordings of opportunistic boat-passes. Means of all three variables describing unit and inter-unit durations (unit 1

duration, unit 1 duration, and inter-unit 1-2 duration) were significantly different in boat-pass periods compared with control periods (Table 3). All of these variables except inter-unit 1-2 duration were less during boat pass periods (Table 3; appendix IV). Additionally, means of two variables describing unit frequency structure (unit 1 and unit 2 maximum frequency) were significantly less in boat-pass periods compared with control periods (Table 3, Appendix VI).

Power Analyses

Statistical power (1-ß) was calculated for all t-tests with non-significant results. Statistical power was > 90% for seven of nine t-tests with non-significant results for song variables analyzed from experimental boat-pass recordings (Table 2). Only two of seven non-significant t-test results had power > 90% for song variables analyzed from opportunistic recordings of boat-passes (Table 3).

Photographic Identification

Seven of nine (78%) singers recorded during experimental boat-passes were photographically identified and determined to be different individuals. Only three out of seven (43%) singers recorded during opportunistic boat-passes were photographically identified, however, all three of these were different animals. It is not known if unidentified singers (i.e. those not photographed) were different animals. Cerchio (1993), however, used photographic data collected from the same study area in 1991 and determined the probability of recording the same singer more than once was low (10%).

Noise Levels

Mean received noise levels (dB re: $1\mu Pa^2/Hz$; 5kHz band) determined from control periods of experimental boat-pass recordings ranged from 58 to 76 dB with a mean of 69 dB for all control periods (Fig. 10A). Noise levels during the boat pass

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periods ranged from 77 dB to 87 dB with a mean of 82 dB. Noise levels were from 7 to 23 dB ( mean = 13 dB) greater in boat-pass periods than control periods.

Mean received noise levels for control periods calculated from recordings of opportunistic boat-passes ranged from 57 dB to 72 dB with a mean of 62 dB (Fig. 10B). Noise levels during the BP periods were 68 dB to 95 dB with a mean of 81 dB. Noise levels ranged from 6 to 35 (mean = 15 dB) greater in boat-pass periods than control periods.

Power Spectra

Most of the noise energy for the 40 h.p. inflatable research vessel was distributed between three and six kilohertz with a peak at 3.6 kHz and lower peaks at 4.6 kHz and 5.8 kHz (Fig. 11). Dominant noise energy produced by the Na Pali Queen, (a 28 m whale watching vessel) was concentrated below two kilohertz with a peak at 100 Hz (Fig. 12). Ambient noise levels for shallow water were between 67 and 80 dB (re: 1 $\mu Pa^2/Hz$; 12 kHz analysis window; Fig. 12). A ten decibel per octave increase in noise energy from 4 kHz down to 100 Hz for shallow water noise was due to "background" songs from humpback whales. A four decibel per octave increase from four to twelve kilohertz was attributed to snapping shrimp (Figs. 11 and 13). An eight to ten decibel decrease in noise levels was apparent in the 100 Hz to 3 kHz band for a recording made in extremely shallow (< 30 m) water (Fig. 13). Ambient noise measured at the deep water site (5 km offshore) had a six decibel per octave decrease from 100 Hz to 10 kHz. Most of this noise energy was attributed to distant, vocalizing humpback whales and possible other unidentified cetaceans.

Average power spectra for humpback song phrases 1B, 2A, and 3A indicated several distinct peaks (Fig. 14). As expected, these peaks were correlated with the fundamental frequencies of each particular phrase. Generally, the main energy in humpback whale song (all themes) was distributed between 60 Hz and 2 kHz.

# DISCUSSION

Results of song variable comparisons between control and boat-pass periods indicated boat noise affected unit and phrase structure of humpback whale songs (Tables 4 and 5). For example, durations of units and phrases generally were less when boat noise was present (however, one variable, inter-unit duration from opportunistic boat-pass recordings, increased slightly when boat noise occurred). Decreases in unit and phrase duration effectively resulted in an increase in the "tempo" of songs. Additionally, the frequency structure of some units were altered slightly when noise from large vessels occurred. The changes in duration and frequency structure detected indicated that the behavior of singing humpback whales was affected by boat noise. Interestingly, results of statistical power analyses indicated that other song variables, particularly those at the highest level of song structure (i.e. most complex patterns), were not affected by boat noise (Tables 4 and 5). It is possible, however, that the effect size was smaller than could be detected with the small sample size used in this study, or that the stimulus (boat noise) did not have the appropriate characteristics (e.g. loudness or frequency distribution) needed to elicit a response.

Information theory predicts that increasing S/N will increase the probability of a receiver detecting a signal in noise (Raisebeck, 1949). There are several strategies a signaling animal can use to maximize S/N. For example, increasing signal intensity, increasing repetition, and changing the frequency structure of the signal so it does not correspond with peaks in the noise spectra, all make signals easier to detect by effectively increasing the S/N at the receiver.

Due to limitations of the study design, the first possibility, increasing signal intensity, could not be examined. Although there is no direct evidence, it is possible that humpback whales are singing at, or near, the maximum intensity possible for extended periods (minutes to hours). Qualitative comparisons of received levels of songs with other humpback whale vocalizations (e.g. social sounds) indicated songs are much louder (pers.

obs.). Although estimates of peak source levels for humpback songs are inexact (170 and 174 dB re: 1µPa @ 1m ; Thompson et al.; 1986; Frankel, 1994, respectively), values are comparable to other species of mysticetes that produce loud signals designed to transmit over great distances (blue whales 188 dB re: 1µPa @ 1m; fin whales,155-186 dB re:1µPa @ 1m; Cummings and Thompson, 1971; Watkins, 1981; Watkins et al., 1987). Because songs probably are used for medium to long distance transmission (Winn and Winn, 1978; Tyack, 1981; Frankel, 1994) it would be advantageous for humpbacks to sing as loudly as possible, thus maximizing the range of signal propagation.

The second possibility, repetition, is a form of redundancy that can increase the probability of signal detection and discrimination in biological and man-made communication systems (Raisebeck, 1949; Pollack, 1959; Wiley and Richards, 1978, 1982). Repeating a signal allows a receiver to predict the entire signal from a part of it, or average parts of signals to determine the whole (Wiley and Richards, 1982). Humpback whale songs incorporate extreme redundancy in the form of phrase repetition. Although phrase repetition is one of the most variable components of humpback whale songs (Payne et al. 1983; Cerchio, 1993), it has not yet been correlated with any environmental variables or biological cycles (Payne et al., 1983). Increasing phrase repetition when ambient noise increases should be a simple, yet effective, strategy for singing humpback whales to overcome interference by noise; however, statistical power analyses results for t-tests of unit counts (i.e. unit repetitions) from opportunistic boat pass recordings, and unit and phrase counts from experimental boat-pass recordings indicated repetition did not change when boat noise occurred (Table 2).

Masking, the interference of signal reception by noise, is most severe in the frequency range in which the greatest noise energy occurs (Kryter, 1985; Richardson et al., 1991). Results of power spectral analyses indicated noise energy produced by large boats had a frequency distribution more similar to humpback whale songs than noise from

small boats was when compared with whale songs (Figs. 11 and 12). Therefore, large boats are more likely than small boats to mask humpback whale songs.

An alternative strategy for a signaler to effectively increase the S/N, is to alter the frequency structure of its signals so they do not correspond with frequencies containing the greatest noise energy. Several researchers have suggested cetaceans can change the frequency structure of their signals to reduce the effects of noise. Au et al. (1974) proposed bottlenose dolphins (Tursiops truncatus) were capable of shifting peak frequencies of echolocation clicks away from peak frequencies of ambient noise. However, results of a study examining the vocal behavior of two captive Atlantic bottlenose dolphins in a controlled, artificially noisy environment did not support their hypothesis (Au and Penner, 1981). The authors suggested that a "peak frequency shift was not detected because the animals probably project maximum energy at [another frequency range]." Later, Au et al. (1985) used a similar approach with a captive beluga whale (Delphinapterus leucas) and demonstrated evidence of frequency shifts away from noise in the beluga whale's vocalizations. Au et al. (1985) presented these latter results as demonstration of "adaptation" in the bio-sonar of beluga whales.

Lesage (1993) examined the effects of boat noise on free-ranging beluga whales, and suggested that beluga whales produced vocalizations with frequency characteristics that reduced the effects of noise. Dahlheim (1984) proposed vocalizing gray whales and probably bottlenose dolphins were taking advantage of an "acoustical niche" by signaling in a frequency band above the band containing noise; however, she did not present evidence that gray whales were able to shift the frequency structure of their calls to circumvent boat noise. Results of these studies indicate some cetaceans can adapt to noisy environments by altering the frequency structure of their vocalizations.

Humpback whales in this study did not appear to be behaving similarly. Although the frequency structure of some song units were affected by noise from large boats, it was not affected by noise from the small (40 h.p.) research vessel. Noise from small boats may

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not have been loud enough, or might not have had frequency characteristics that affected

singing behavior in humpback whales (Fig. 11). The changes detected in the frequency

structure of song units were not what would be expected if singing whales were trying to

reduce the effects of noise. For example, if behavioral responses similar to those

described in other cetaceans were occurring in singing humpback whales, low frequency

components of units (e.g. unit 1 and 2 minimum frequency) should have been shifted

upward in the presence of low frequency noise from boats. Instead, singing whales in this

study shifted high frequency components of units downward. According to signal

detection theory (i.e. maximizing the probability of signal detection by increasing S/N),

there should be no advantage in shifting the frequencies of signals to coincide with

frequencies containing most of the noise energy.

An alternative possibility is that changes in frequency were indicative of new or

different information being conveyed by singing whales. Morten (1977) presented a

model for communication in vertebrates in which he proposed that low frequency "growls"

and other structurally similar calls function as threats by communicating aggressive intent.

It is unlikely, however, that humpback whales exposed to boat noise are behaving

according to Morton's model because the frequency changes detected were so minor that

"boat-pass songs" were not substantially different from "control songs."

Decreased durations of units and inter-unit pauses indicated song tempo (singing

rate) increased, or was disrupted, in the presence of boat noise. The functional

significance of changes in song tempo is not clear. It is possible additional information is

conveyed with changes in song tempo. Bain (1992) presented a theoretical model for

examining the evolution of signal structure in vertebrate communication systems. Using

this model, a finite yet instantaneous representation of any signal is possible using a limited

number of functions (Gabor transforms). Bain's (1992) "multi-dimensional" model is

based on the concept that all vertebrate signals are structured hierarchically in levels.

Each level consists of modulation of a signal at another level with each additional level of

modulation adding a new "dimension" to the signal. Thus, any complex signal can be represented as multi-dimensional spectra. For example, using Bain's model, humpback whale songs would be categorized as amplitude modulated signals or units (1st dimension), that are frequency modulated (2nd dimension), arranged in patterns or phrases (3rd dimension), and repeated through time at some rate (4th dimension). According to this model, song tempo would be the fourth level in which information can be encoded. Therefore, changes in song tempo would correspond to a changes in information encoded in the 4th dimension. It is uncertain, however, whether or not this change would be detected by a receiver (listening whale), and more importantly, if this new information would affect a receiver's behavior. More information about the purpose of singing in humpback whales, particularly the function of tempo and rhythm in bio-acoustic signals, is necessary before further conclusions can be made.

To better understand the function of tempo and rhythm in humpback whale songs, it might be useful to examine singing behavior in terrestrial vertebrates. Like humpback whales, anurans produce simple calls that often are repeated in rhythmical patterns. Also, vocalizing male frogs frequently aggregate in a common area forming a "chorus." The function of calls and specific call parameters has been examined in several species of frogs using playback experiments. The function of calls is species-specific but generally serves some common functions: 1) to distinguish conspecifics from non-specific, 2) to attract females, and 3) to repel or threaten other males. Calling rates or rhythm have been examined in only a few species. Platz (1989) determined pulse (call) rates were used by female chorus frogs (Pseudacris triseriata) to distinguish conspecifics from non-specifics. In male cricket frogs (Acris crepitans blanchardi), the functions of pulse rate is both to attract females (high pulse rate) and threaten males (low pulse rate; Wagner, 1989a). Cricket frogs balance these competing demands by producing calls with low pulse rates at the beginning of a call group and calls with high pulse rates at the middle or end of a call group (Wagner, 1989b). Most frog calls are graded signals, that is, information is

encoded in some parameter (e.g. pulse rate) that can be varied along a continuum. Certain components of humpback song such as song tempo could be considered graded, however, until the functions of these components is determined, this will remain unknown.

Song is a specialized case of acoustic communication based on rule-governed rhythmical patterning of signals and combinations of signals, or (as in Bain's model), hierarchical levels of modulations. There are more species in the Order Aves (birds) that sing than any other taxonomic group. Not surprisingly, bird songs are the most studied and completely understood songs of any vertebrate. Like frog calls, bird songs vary greatly in form and function; however, most bird songs convey information such as individual identity, sex, location, readiness to mate, and readiness to defend a territory or engage in combative behavior. Marler (1977) stated that elaborate sequences of sounds such as bird songs are "especially associated with inter-male territorial spacing." Catchpole (1982), however, proposed that long, complex songs were the result of inter-sexual selection, and functions to attract mates, whereas short, stereotyped songs were considered the result of intra-sexual selection and functions to repel or exclude other males from their territory.

Tyack (1981) suggested humpback whale song has a reproductive function similar to that of bird song. It might be useful, therefore, to examine the function of bird songs that are similar in structure to humpback whale songs. Slater (1986) commented on the similarity between songs of humpback whales and songs of village indigo birds (Vidua chalybeata). Cerchio (1993) compared similarities and differences in cultural evolution of song and reproductive biology of humpback whales to caciques (Cacicus sp.) and village indigo birds. Caciques and village indigo birds have a polygynous mating system in which non-territorial males often engage in competitive behavior (Trainer, 1989). Songs of village indigo birds are similar to songs of humpback whales, in that individuals occupying a common area change their songs concurrently over time. Songs of adult male indigo birds with good breeding success seemed to be copied more often than songs of less

successful individuals (Payne, 1985). None of these researchers, however, examined the structure and function of specific components of bird songs or compared them to humpback whale songs.

A few researchers have studied the function of rhythm and tempo in bird songs, unfortunately, none have examined species with ecological constraints, mating systems, or songs that are similar to those of humpback whales. Emlen (1972) assessed which parameters of bird song function in species recognition by artificially altering specific components of songs from indigo buntings (Passerina cyanea), and measuring the level of agonistic response by males subjected to song playbacks. He determined that rhythm, tempo, and morphology of song figures (homologous to humpback song units) were important for species recognition. After reviewing studies of the structure and function of song components in ovenbirds, Serius aurocapillus, white-throated sparrows, Zonotrichia albicillis, wood larks (lullala arborea), and the European robins (Erithacus rubecula), Emlen (1972) proposed that song components with low variability within individuals and populations probably convey information about species recognition. He also suggested that parameters of bird song which are constant within an individual, but variable within a population, probably function in individual recognition. Finally, he proposed components of song which are variable within individuals might convey information about the motivational state of the individual. Green and Marler (1979), however, cautioned this was not the case for all bird songs.

As Emlen (1972) mentioned, the structure of song is the result of a compromise between numerous selective forces. The complexity of song in many species of birds, and humpback whales, suggests that many types of information (e.g. species identity, gender identity, individual identity) are conveyed. It follows that numerous selective forces were, or still are, acting upon the structure of humpback song. Such constraints must be considered when attempting to interpret results of this study.

Singing humpback whales in this study did not appear to respond to noise as might be predicted by various theories of communication. It is possible that the ability of humpback whales to respond to boat noise was limited because some other over-riding factor was regulating singing. Alternatively, singing humpback whales might have been incapable of reducing the effects of boat noise.

Most likely, humpback whales always have inhabited coastal regions. Because these regions are inherently noisy, ambient noise probably had a strong influence on the evolution of their singing behavior. Ryan and Brenowitz (1985) examined the song structure of several species of birds, and determined ambient noise played a significant role as an evolutionary force in determining frequency characteristics of their songs. He determined that songs were adapted to the characteristics of the acoustic environment inhabited by each species. Likewise, it would seem that humpback whales also have evolved adaptations to cope with noise. It must be emphasized, however, that sources of noise with characteristics similar to boat noise (i.e. dynamic, broad-band frequencies produced by a moving source) were non-existent when the acoustic abilities of humpback whales evolved. Because there were no selective pressures to reduce the effects of noise from boats or similar sources of noise , it is possible humpback whales never evolved mechanisms to cope with such interference (National Research Council, 1994). This might explain why humpback whales are not behaving optimally in the context of communication theory. Alternatively, it is possible that receivers, not signalers, somehow are reducing the effects of noise. Because no attempt was made to examine responses of receivers in this study, this possibility must await further investigation.

Why, then, did changes in singing behavior occur, and what do these changes mean? It is possible that singing humpback whales were perceiving boat noise merely as a "disturbance," and consequently, they responded as they would to any disturbance. Behavioral responses to noise have been documented in most terrestrial mammals in which effects of disturbance from noise have been studied. Disturbance from noise generally

results in a reduction or cessation of behaviors, sometimes followed by a flight response if the disturbance is severe, or if it potentially signifies immediate danger (Richardson et al., 1991). The biological significance of such acute responses to noise are probably negligible if the disturbance does not occur often, however, chronic or repeated disturbances can result in increased stress. Stress can be defined as any physiological response of an animal to some external stimuli that allows that animal to cope with dangerous or life-threatening situations (Seyle, 1973). Chronic activation of stress-related mechanisms can lead to harmful physiological effects (Seyle, 1973).

Stress in aquatic mammals is difficult to monitor. Thomson and Geraci (1986), however, determined marine mammals exhibit symptoms of stress similar to those found in terrestrial mammals. The only study in which stress induced by noise has been examined in marine mammals was by Thomas et al. (1990) who measured levels of catecholamines (a stress related hormone) in captive beluga whales. They exposed beluga whales to playbacks of noise recorded from semi-submersible drill rigs, but did not find elevated levels of catecholamines. Because beluga whales were exposed to very short durations of noise, Richardson et al. (1991) cautioned that the significance of this study is uncertain.

Physiological responses to disturbance from noise can occur in mammals even when overt behavioral responses are not observed. Studies of terrestrial mammals have determined various physiological responses to noise, including elevated heart rates. For example, heart rates of bighorn sheep, Ovis canadensis, and white-tailed deer ,Odocoilus virginianus (ungulates are closely related to mysticetes), increased when disturbed by humans and mechanical sounds (MacAurthur et al., 1982; Moen, 1982). Because many researchers did not detect obvious changes in some animals that exhibited physiological responses, Richardson et al. (1991) suggested heart rates might be a more sensitive indicator of disturbance, and therefore stress, in marine mammals. Due to the difficulties associated in monitoring physiological variables in marine mammals, the effects of noise or other acoustic disturbances on heart rates have not yet been determined in cetaceans.

Heart rates in marine mammals are highly variable (compared with terrestrial mammals), therefore, the utility of monitoring heart rates for detecting disturbance by noise in marine mammals is probably low (T. Williams, pers. comm.).

Interestingly, some components of humpback whale song such as unit and phrase durations (i.e. song tempo) have very low variability and potentially could be sensitive indicators of disturbance. There would be many advantages to using songs of humpback as an indication of disturbance. For example, songs can be monitored and recorded remotely. This simple procedure allows data to be collected passively without capturing, tagging or using other invasive and stressful techniques often required to collect physiological data from wild animals. Obviously, further study is necessary to verify the relationship between song tempo and disturbance before the feasibility of using songs to monitor disturbance in humpback whales is proven.

Behavioral responses of humpback whales to industrial and boat noise have been examined by several researchers. Baker et al. (1983) and Bauer (1986) conducted comprehensive investigations of the effects of boat noise on respiration rates, diving behaviors, aerial behaviors, and movement patterns of humpback whales. Bauer (1986) examined short-term reactions of humpback whales to small and medium size vessels in Hawaiian waters. He determined humpback whale behaviors were correlated with vessel abundance, proximity, speed, and direction changes. Generally, his results indicated humpback whales were avoiding and possibly even directing threat displays towards vessels. "Avoidance behaviors" observed included increased frequency of emergence at the surface without breathing, and diving without flukes being raised. Most detectable effects occurred when vessels were within one-half to one kilometer of the whales.

In a more detailed study, Baker et al. (1983) examined the effects of large cruise ships on the behavior of humpback whales in feeding areas off southeast Alaska. Their study is one of the few which included acoustic monitoring of noise and modeling of ship noise levels in locations where whales were being observed (Miles and Malme, 1983).

Based on their results, Baker et al. (1983) proposed humpback whales were using two different strategies of boat avoidance: 1) vertical avoidance, and 2) horizontal avoidance. Vertical avoidance behaviors were detected in whales when boats were within two kilometers. Whales increased duration of dives, decreased blow intervals, and decreased swimming speeds (i.e. they remained submerged more). Horizontal avoidance occurred when boats were within two to four kilometers of the whale. Whales decreased durations of dives, and increased swimming speeds (i.e. they swam away quickly).

If singing humpback whales in this study were responding to noise in a similar manner, song durations (a direct indication of dive duration) should have been greater when boat noise was present. However, the opposite trend was observed. It might also be expected that some singing whales would have moved away when boats approached. Although whale movements were not systematically documented for this study, notes from visual observations made during recordings indicated this probably did not occur.

Because of the inherent constraints of studying free ranging cetaceans, there were several limitations on the experimental design, samples, and statistical analyses that could be used in this study. For example, results of song variable comparisons indicated most changes in singing behavior that occurred when boat noise was present were minor when compared with normal variability of humpback whale song (Tables 2 and 3; Appendices I, IV, and VI). Also, the paired sample t-test that was used to analyze song variables is relatively simple test because it does not incorporate within-subject variability. Furthermore, post boat-pass control periods were not used to determine if singing behavior returned to "pre-disturbed" conditions. A more rigorous statistical test (e.g. repeated measures ANOVA) incorporating these experimental design considerations would have yielded greater internal validity (Altmann, 1974). Unfortunately, the stringent guidelines used to ensure adequate controls limited the number of samples available and, consequently, the types statistical test that could be used. These constraints made

interpretation of statistical test results problematic. Therefore, any conclusions should be considered with the limitations of the study design in mind.

Although responses to noise by singing whales appear to be relatively minor, it is still possible that significant biological impacts occurred, but could not be detected. For example, masking is difficult, if not impossible, to examine in free ranging marine mammals; however, this psycho-physical phenomena has been demonstrated in many species of captive marine mammals examined under controlled conditions (Johnson, 1968; Terhune, 1981; Au and Moore, 1990; Turnbull and Terhune, 1990). Because masking interferes with signal reception, it is a problem experienced by receivers, not senders. Data was not collected on receivers; therefore, only indirect evidence that masking occurred could be examined.

Masking is most severe in the frequency band where the noise energy is greatest (Kryter, 1985); thus, it is important to examine the frequency characteristics of the masking noise. The energy in noise emitted from large (30 - 50 m) boats is concentrated between 50 and 1000 Hz (Fig. 12). This range is similar to the frequency range of peak energy in humpback song units (the low hundreds of hertz ; Fig. 11). Because the power spectra of humpback whale songs and noise from large boats overlap, masking of humpback whale songs probably occurred (Fig. 11). Noise from small boats (e.g. outboards) probably does not result in severe masking because the noise energy is concentrated at much higher frequencies (Fig.10; Young and Miller, 1960). Until the function of high frequency components of humpback whale songs is determined, any biological significance regarding the results of this study must be considered with caution.

# CONCLUSIONS

The biological significance of changes in the singing behavior for humpback whales exposed to boat noise remains uncertain. Although sample sizes and statistical tests used in this study were limited, results indicated that singing humpback whales were not responding in a way that would reduce the effects of noise on receivers. Boat noise in the ocean is a recent phenomena with no natural analogue. When singing behavior and acoustic capabilities evolved in humpback whales, it is likely there were no selective pressures to reduce the effects of boat noise. The changes in songs that were observed when boat noise occurred, such as changes song tempo and a shift downward in frequencies of some units, could be an indication of disturbance; however, further study is necessary to verify this hypothesis. Finally, the lack of predictable responses to noise does not exclude the possibility that receiver problems, such as masking, were occurring. Large boats produce intense noise energy with a frequency distribution of that overlaps the frequencies in humpback whale songs more closely than noise produced by small boats overlaps whale songs. Therefore, large vessels have greater potential to mask songs of humpback whales. Additional studies are necessary to examine the responses of singing whales to boat noise in greater detail, and more importantly, to investigate responses of receivers to boat noise.

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TABLE 1. Variables analyzed from hunpback whale songs recorded during experimental and opportunistic boat-pass recordings (X). Small "x" indicates variable measured only for experimental boat-pass recordings. Dashes ( -- ) indicate no measurements made. Complexity of song structure increases from top to bottom of table.

| TIME and FREQUENCY MEASUREMENTS | | | | |
| --- | --- | --- | --- | --- |
| Variable | Duration | Frequency (Hz) | | |
| | | Min. | Avg. | Max. |
| Unit 1 | X | X | x | X |
| Unit 2 | X | X | -- | X |
| Inter-unit 1-2 | X | -- | -- | -- |
| Phrase 1B | X | -- | -- | -- |
| Theme 1B | X | -- | -- | -- |
| Songs | X | -- | -- | -- |

| SONG PATTERNS and STRUCTURE | | |
| --- | --- | --- |
| Variable | Unit counts | Phrases counts |
| Phrase 1B | X | -- |
| Theme 1B | -- | X |

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Table 2. Results of paired t-tests for song variables analyzed from recordings of experimental boat-passes (n = 9). Means ($\bar{X}$) and standard errors (SE) are presented for descriptive purposes only (see appendices for data used in paired t-test analyses). Dashes (--) indicate no measurements. Non-significant results are indicated by "ns".

| VARIABLE | Control | | Boat-noise | | t value | P value | Power |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | $\bar{X}$ | SE | | | $(1 - \beta)$ |
| **DURATION (sec.)** | | | | | | | |
| Unit 1 | 2.14 | 0.20 | 2.06 | 0.17 | 1.08 | ns | .89 |
| Unit 2 | 1.86 | 0.15 | 1.57 | 0.18 | 4.23 | < .01 | -- |
| Inter-unit 1-2 | 1.98 | 0.09 | 1.88 | 0.12 | 2.80 | < .05 | -- |
| Phrase 1B | 11.06 | 0.47 | 10.61 | 0.37 | 2.33 | < .05 | -- |
| Theme 1B | 159.9 | 19.9 | 159.8 | 32.2 | 0.003 | ns | .99 |
| Song | 774 | 72.34 | 727 | 61.13 | 1.05 | ns | .89 |
| **FREQUENCY (Hz)** | | | | | | | |
| Unit 1 Minimum | 121 | 4.8 | 124 | 8.4 | -0.52 | ns | .98 |
| Unit 2 Minimum | 223 | 12 | 214 | 8.4 | 0.99 | ns | .96 |
| Unit 1 Average | 145 | 4.0 | 144 | 8.5 | 0.17 | ns | .90 |
| Unit 2 Maximum | 498 | 113 | 607 | 233 | -0.90 | ns | .92 |
| **COUNTS (no.)** | | | | | | | |
| Units / Phrase 1B | 3.04 | 0.12 | 3.04 | 0.04 | $-3 \times 10^{-15}$ | ns | .99 |
| Phrases / Theme | 14.8 | 2.2 | 15.7 | 3.3 | -0.47 | ns | .97 |

Table 3. Results of paired t-tests for variables analyzed from recordings of opportunistic boat-passes (n = 7). Means ($\bar{X}$) and standard errors (SE) are presented for descriptive purposes only (not used in paired t-test analyses). Dashes (--) indicate no measurements. Non-significant test results indicated by "ns".

| VARIABLE | Control | | Boat-noise | | t value | P value | Power |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | $\bar{X}$ | SE | | | $(1 - \beta)$ |
| **DURATION (sec.)** | | | | | | | |
| Unit 1 | 2.22 | 0.26 | 2.00 | 0.28 | 3.13 | < .05 | -- |
| Unit 2 | 1.91 | 0.14 | 1.69 | 0.19 | 2.67 | < .05 | -- |
| Inter-unit 1-2 | 1.94 | 0.10 | 2.07 | 0.12 | -2.46 | < .05 | -- |
| Phrase 1B | 10.97 | 0.65 | 10.74 | 0.58 | 0.97 | ns | .93 |
| Theme 1B | 148 | 21 | 302 | 94 | -1.54 | ns | .82 |
| Song | 738 | 32 | 646 | 63 | 1.78 | ns | .75 |
| **FREQUENCY (Hz)** | | | | | | | |
| Unit 1 Minimum | 108 | 9.8 | 98 | 8.7 | 2.44 | = 0.05 | .50 |
| Unit 2 Minimum | 221 | 18 | 202 | 9.5 | 1.24 | ns | .89 |
| Unit 1 Maximum | 156 | 10 | 139 | 13 | 4.62 | < .01 | -- |
| Unit 2 Maximum | 437 | 22 | 381 | 8.9 | 3.12 | < .05 | -- |
| **COUNTS (no.)** | | | | | | | |
| Units / Phrase | 2.9 | 0.24 | 2.9 | 0.31 | 0.06 | ns | .99 |
| Phrases / Theme | 14 | 2.5 | 20 | 3.6 | -1.94 | ns | .68 |

Table 4.  Significant results and statistical power for paired t-tests analyses of experimental boat-pass recordings.  Variables significant at P < 0.05 are indicated by "S." Non-significant test results with power (1-β) > 95% are indicated with "X."  Small "x" indicates power between 90% and 95%.  Non-significant test results with power < 90% are indicated by "ns."  Double dashes (--) indicate no measurements.  Complexity of song structure increases from top to bottom of table.

| TIME and FREQUENCY MEASUREMENTS | | | | |
|---|---|---|---|---|
| Variable | Duration | Frequency (Hz) | | |
| | | Min. | Avg. | Max. |
| Unit 1 | ns | X | x | -- |
| Unit 2 | S | X | -- | x |
| Inter-unit 1-2 | S | -- | -- | -- |
| Phrase 1B | S | -- | -- | -- |
| Theme 1B | X | -- | -- | -- |
| Songs | ns | -- | -- | -- |
| SONG PATTERNS and STRUCTURE | | | | |
| Variable | Unit counts | Phrases counts | | |
| Phrase 1B | X | -- | | |
| Theme 1B | -- | X | | |

Table 5. Significant results and statistical power for paired t-tests analyses of opportunistic boat-pass recordings. Variables significant at P < 0.05 are indicated by "S." Non-significant test results with statistical power $(1-\beta) > 95\%$ are indicated with "X." Small "x" indicates power between 90% and 95%. Non -significant test results with power < 90% are indicated by "ns." Marginally insignificant results (P = 0.05) are indicated with an asterisk (*). Double dashes (--) indicate no measurement. Complexity of song structure increases from top to bottom of table.

| TIME and FREQUENCY MEASUREMENTS | | | | |
|---|---|---|---|---|
| Variable | Duration | Frequency (Hz) | | |
| | | Min. | Avg. | Max. |
| Unit 1 | S | ns* | -- | S |
| Unit 2 | S | ns | -- | S |
| Inter-unit 1-2 | S | -- | -- | -- |
| Phrase 1B | x | -- | -- | -- |
| Theme 1B | x | -- | -- | -- |
| Songs | ns | -- | -- | -- |

| SONG PATTERNS and STRUCTURE | | |
|---|---|---|
| Variable | Unit counts | Phrases counts |
| Phrase 1B | X | -- |
| Theme 1B | -- | ns |

Figure 1. Model of deep water ambient noise spectra for different levels of shipping traffic and sea states with the low frequency boundary (seismic and pressure fluctuations) and high frequency boundary (molecular agitation) (from Urick, 1983).

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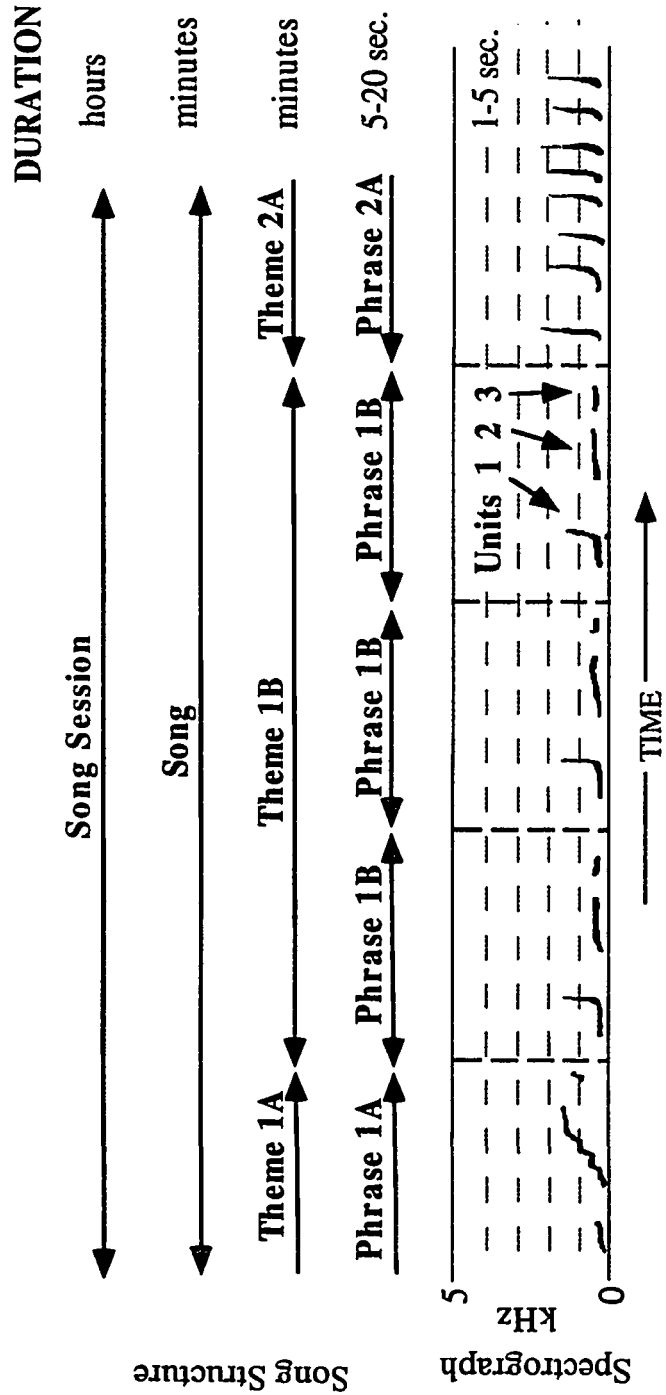
Figure 2. Structure and organization of humpback whale song. Song components are organized hierarchically from the most basic (bottom) to the most complex (top). Three phrase types are represented in the tracing of a spectrograph of the song at very bottom. Phrases are categorized subjectively based on similarities in patterns of units. Representative durations of each song component are presented at far right (layout from Payne et al. 1983).
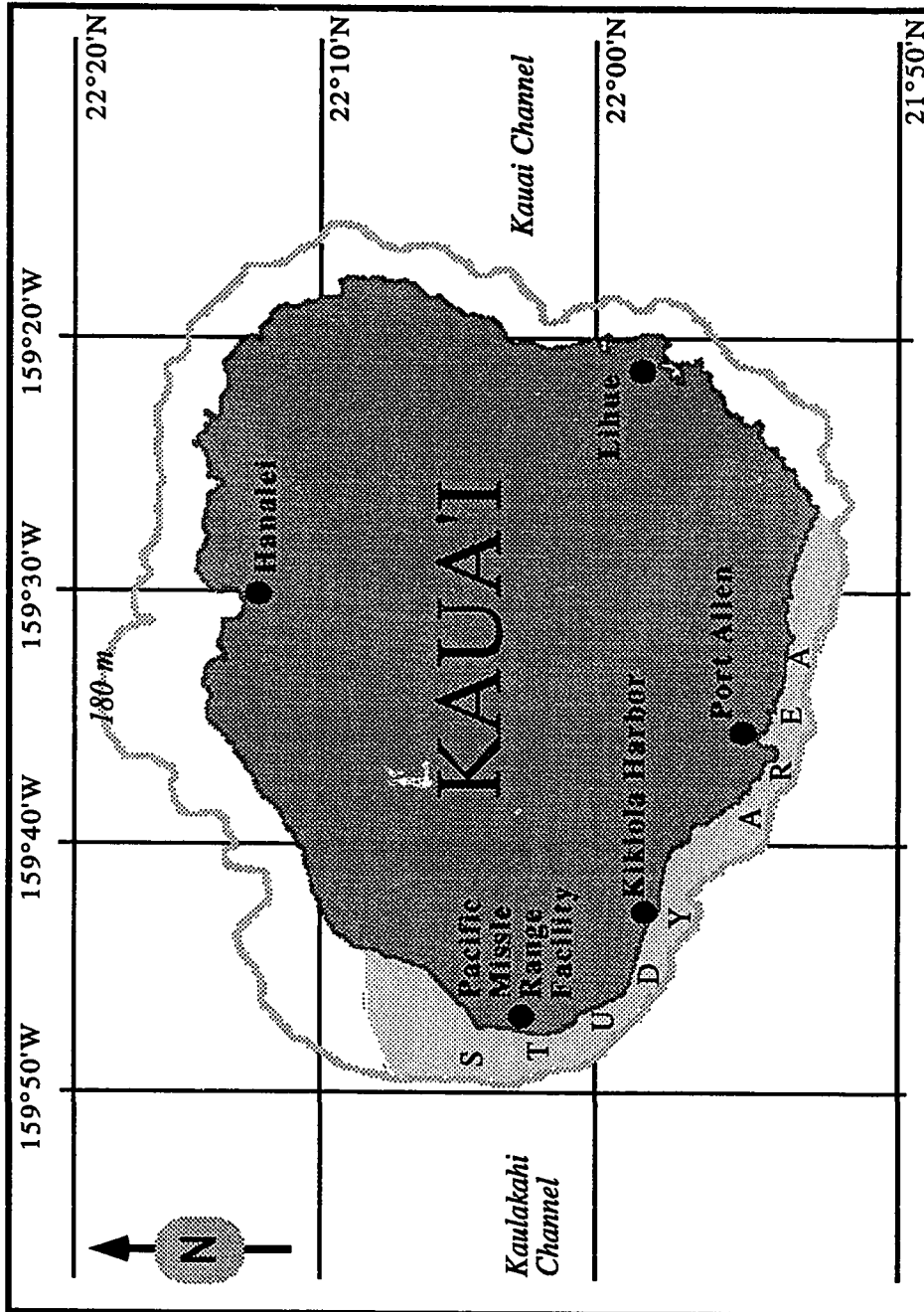
Figure 3. The study area (light shaded region) encompassed nearshore waters (within 180 m isobath) off south-west Kauai that included the region with the greatest concentrations of humpback whales around Kauai (Mobley and Bauer, 1991).
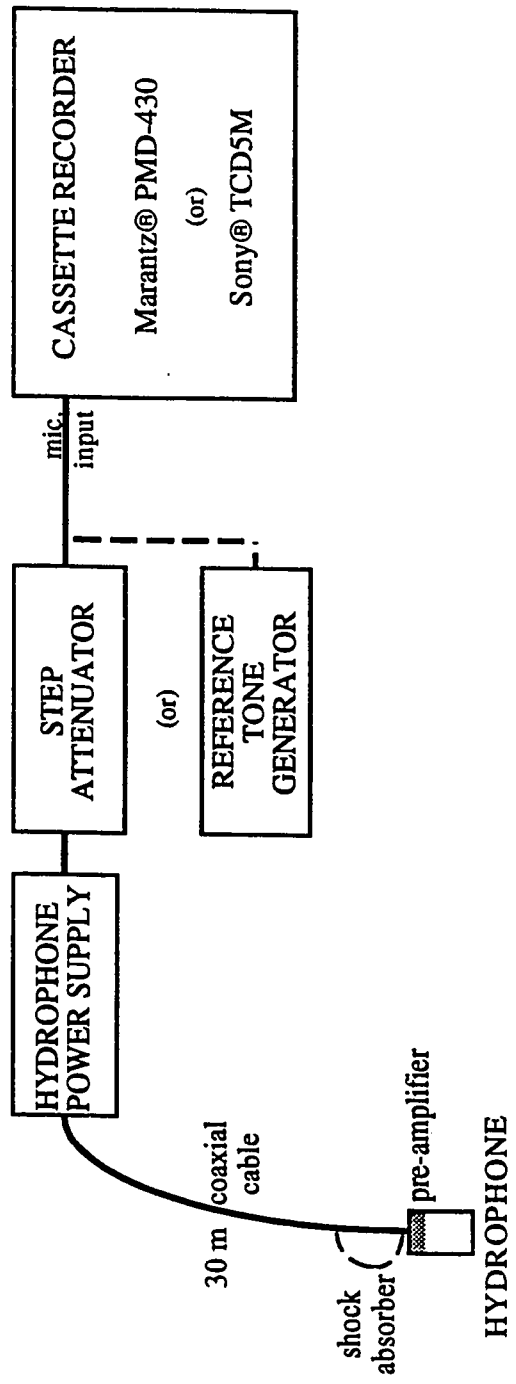
Figure 4. Block diagram of audio recording system. System frequency response was flat from 50 Hz to 15 kHz.
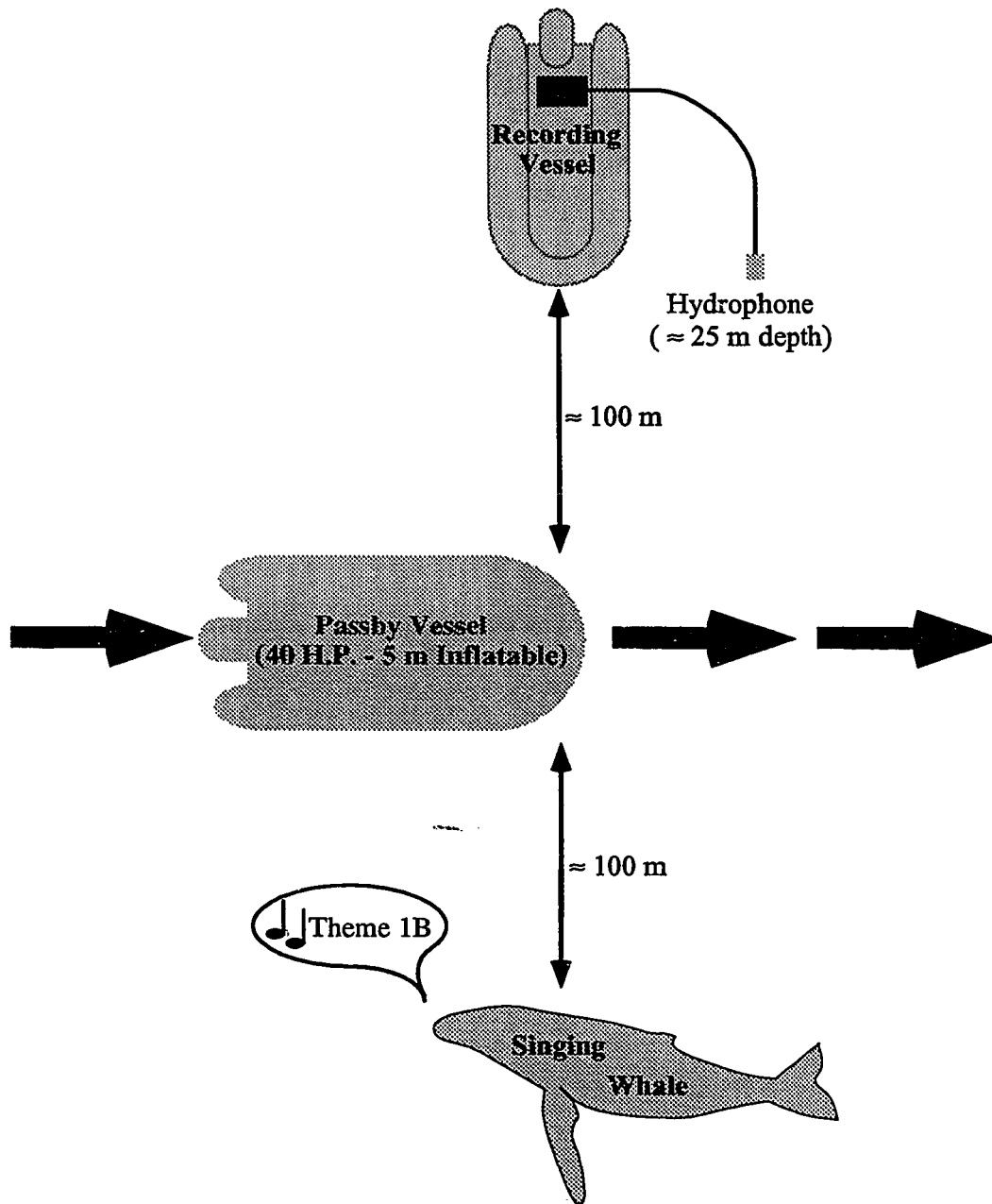
Figure 5. Procedure for experimental boat-passes. Recording vessel was positioned near singing whale and recorded for at least 20 minutes before the boat-pass was initiated. The passby vessel travelled at approximately full throttle as it passed between the singing whale and recording vessel. It was assumed that the whale heard boat noise that was similar in intensity to the recorded signals.

CASSETTE
RECORDER
Marantz®
PMD 430

HIGH PASS FILTER
Circuit Corp.

LOW PASS FILTER
Frequency Devices® 901

486 Personal Computer

A/D
BOARD

SIGNAL-RTS
SOFTWARE©

Signal Playback

Signal Conditioning
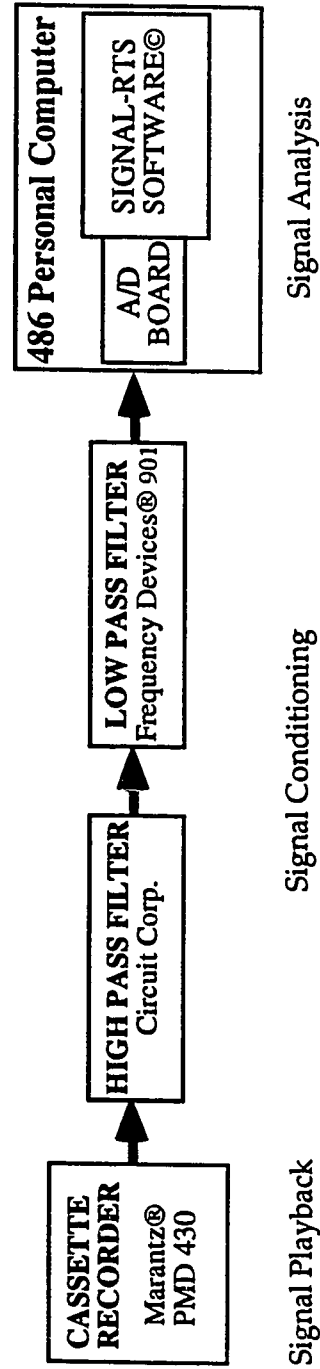
Signal Analysis

Figure 6. Block diagram of signal playback and analysis system. High-pass filter cutoff set at 55Hz. Low-pass filter cut-off set at 40% of the sample rate (for anti-aliasing during analog-to-digital conversion).

55
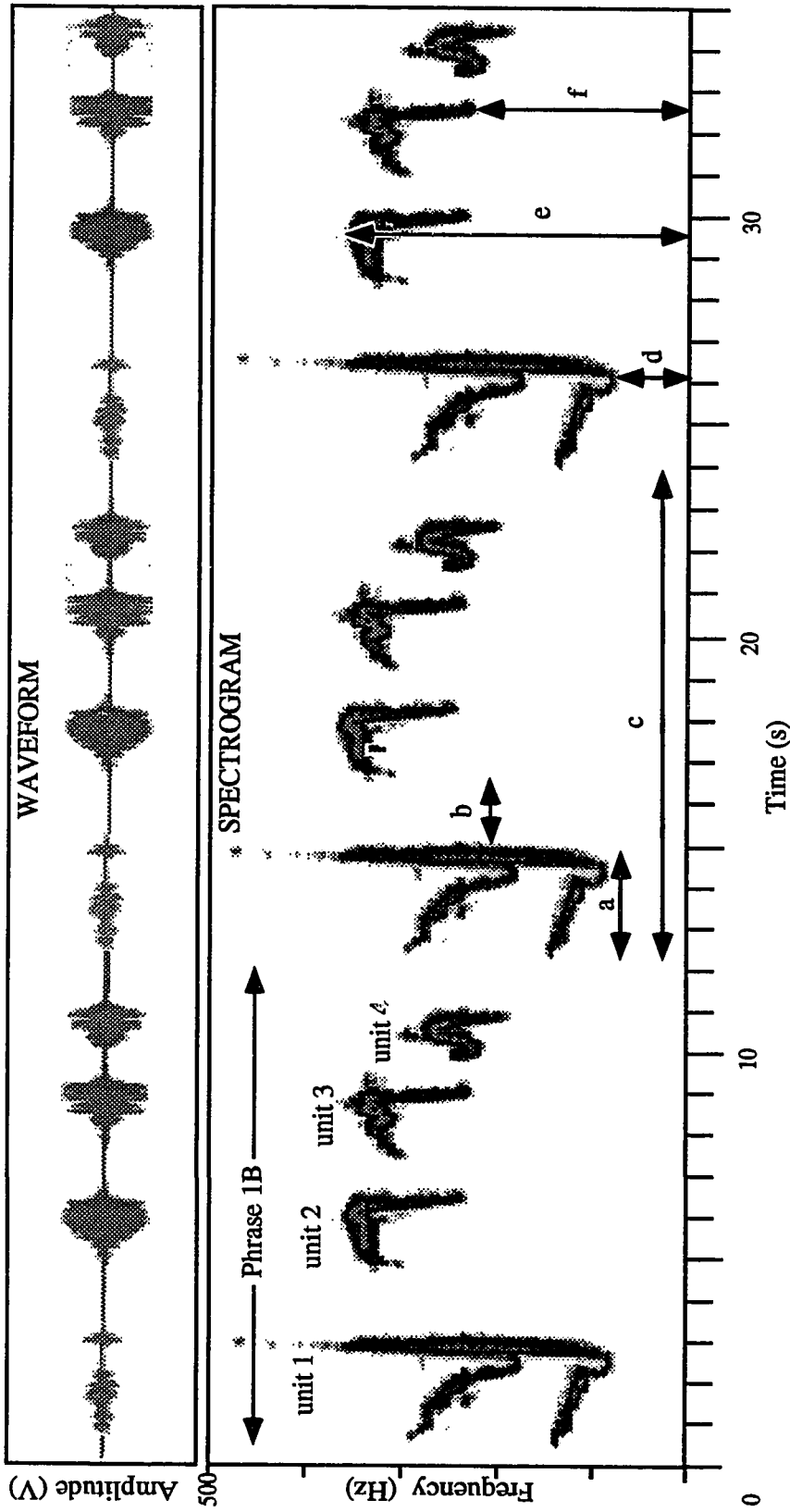
Figure 7. Example of song variable measurements for phrase 1B. Waveform is of same signals as spectrograph. Double ended arrows depict examples of variables measured: (a) unit duration, (b) inter-unit duration, (c) phrase duration, (d) unit 1 minimum frequency, (e) unit 2 maximum frequency, and (f) unit minimum frequency (terminal downsweep). A mouse driven cursor was used to make these measurements. Units (per phrase) and phrases (per theme) were counted visually. Theme and song duration were calculated by summing phrase durations (in a spreadsheet) for themes or songs.

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recorded signals

**486 Personal Computer**

analog-to-digital board → SIGNAL-RTS software© → hard disk → SIGNAL© software → EXCEL© spreadsheet

1.) Real-time signal aquisition, digitization, and display. Mouse driven cursor used to "capture" noise signals.

2.) Captured noise signals saved to hard disk.

3.) noise signals appended and $V_{rms}$ measured.

4.) $V_{rms}$ values corrected for gain, attenuation, and hydrophone sensitivity.

Figure 8. Block diagram of equipment and procedure used to determinine noise levels.

Time →

| Phrase | 1A | 1B | 1B | 1B | 1B | 1B | 1B | 1B | 1B | 1B |
|---|---|---|---|---|---|---|---|---|---|---|
| Repetition # | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |

Song Spectrogram

start of boat-pass

PCA
← experimental →
← opportunistic →

PHRASES USED IN ANALYSIS

| Phrase | 1B | 1B | 1B | 1B | 1B | 1B | 1B | 2A | 2A |
|---|---|---|---|---|---|---|---|---|---|
| Repetition # | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 1 | 2 |

boat-pass continues

end of boat-pass
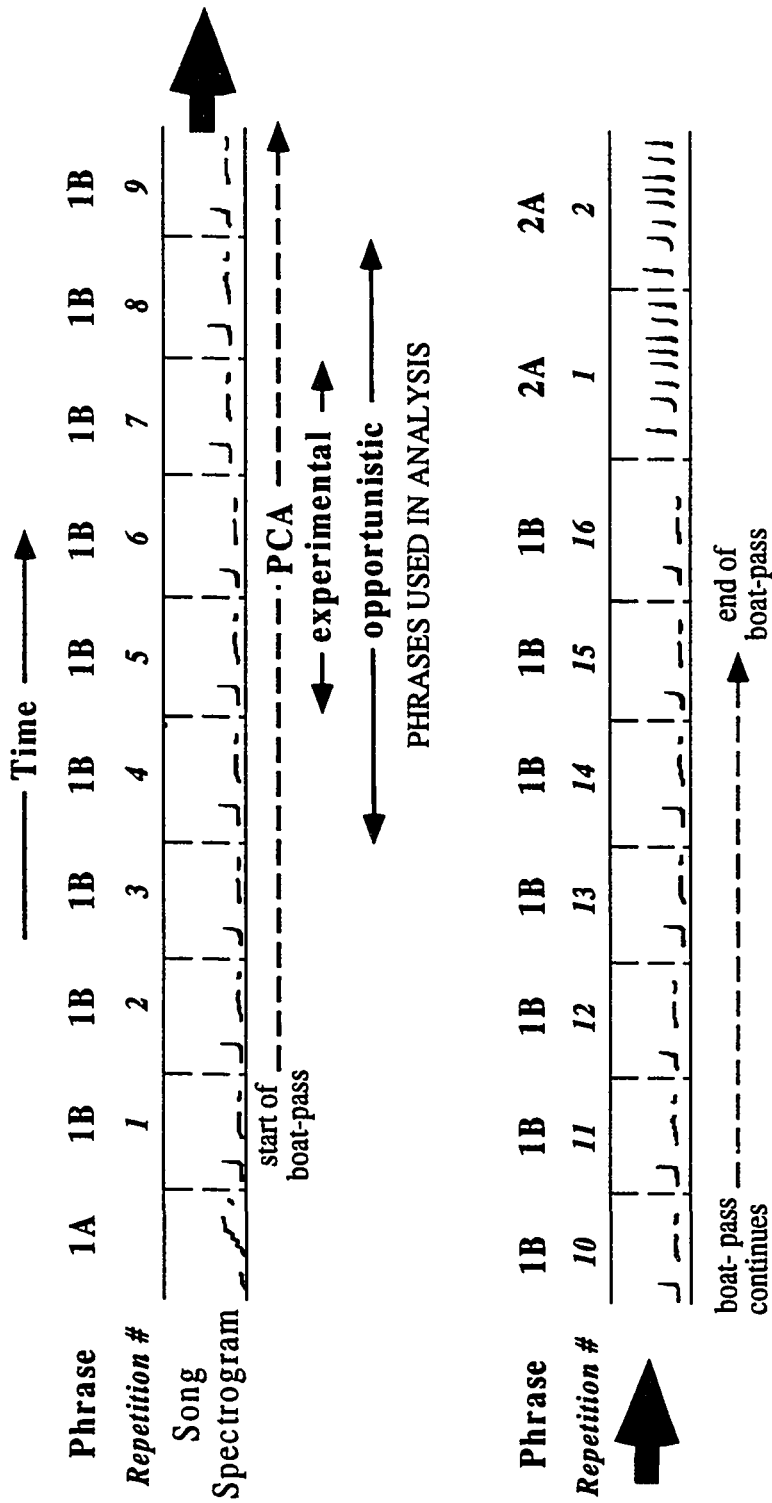
Figure 9. Example of protocol used to determine which phrases to use for song variable measurements. Phrases were grouped according to their position relative to the PCA (Point of Closest Approach) of the boat-pass. The middle phrase of the group (e.g. phrase repetition # 6) was always chosen to correspond to the PCA. Five phrases (e.g. repetitions # 4 - 8) were used for analyses of opportunistic boat-passes, and three phrases (e.g. repetition # 5, 6, & 7) were used for analyses experimental boat-passes. Fewer phrases were analyzed for experimental boat passes because of the short period in which boat noise was loud due to the small boat used. Phrase groupings for control songs (before boat-pass) consisted of the same phrase repetitions as boat-pass songs (e.g. phrase repetition # 5, 6, & 7 from boat-pass and control songs for experimental boat-passes). This protocol was used to control for phrase repetition effects, because some variables (e.g. unit minimum frequency) varied as function of phrase repetition.

58
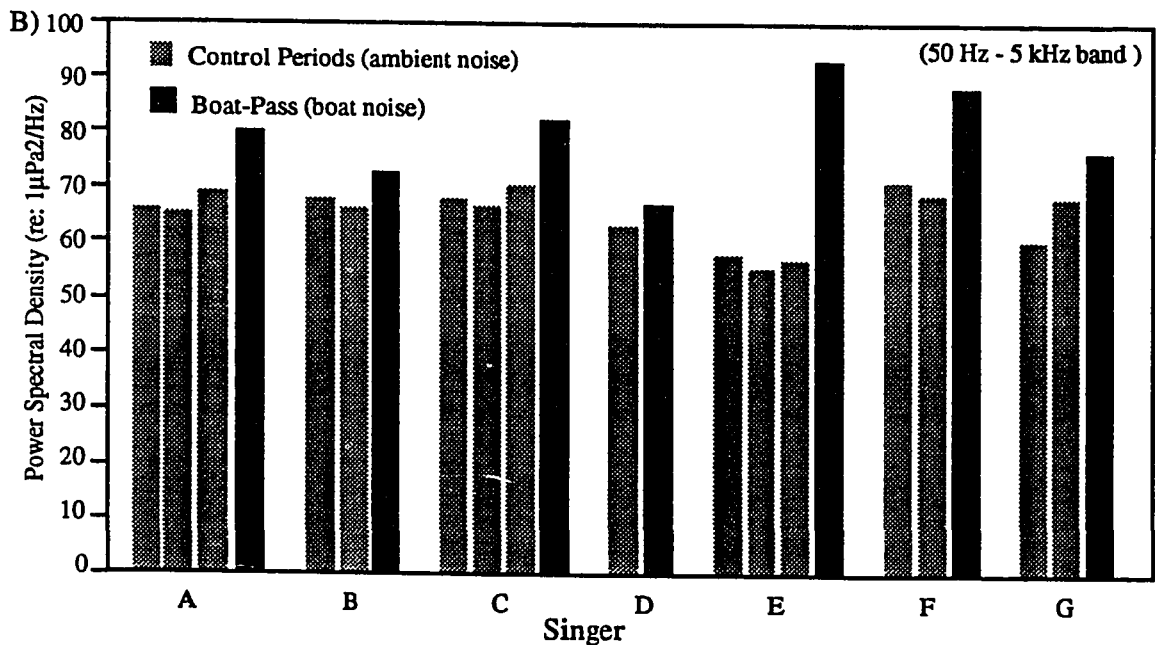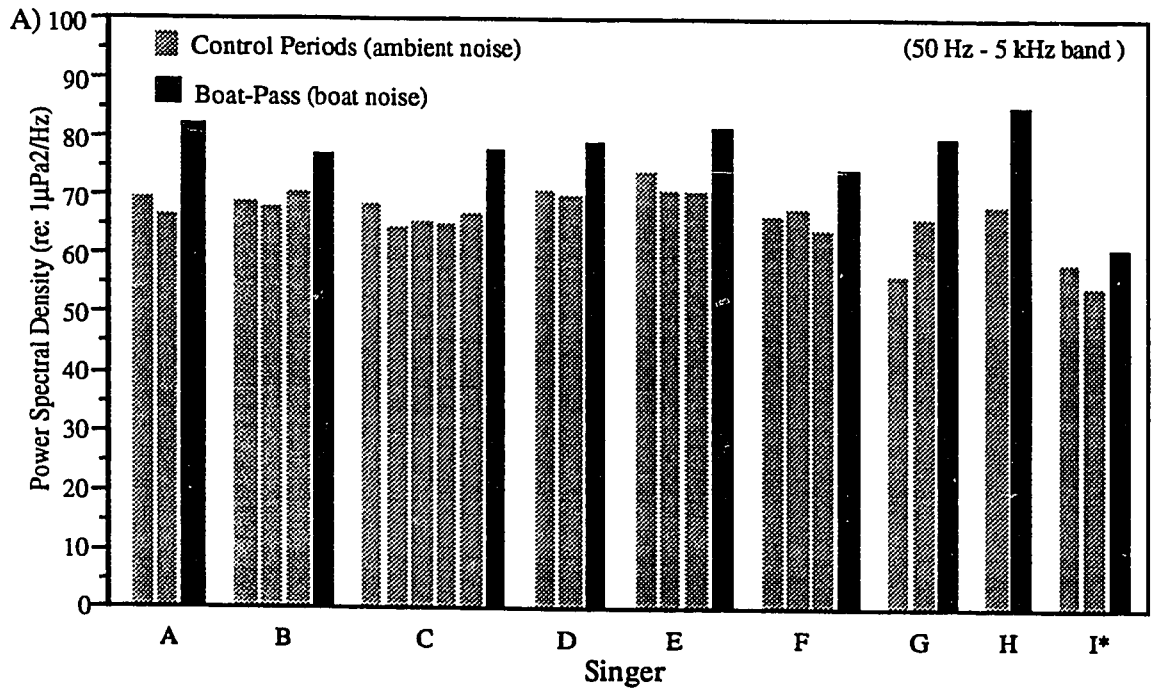
Figure 10 A & B. Noise levels (PSD re: $1\mu Pa^2/Hz$) for: A) experimental boat-passes, and B) opportunistic boat-passes. Noise was measured for the same groups of phrases (see Fig. 9) from control periods (shaded bars) and boat-pass periods (black bars). The number of control periods measured varied (between one and five) depending on the duration and quality of the recording before the boat-pass. (* noise levels for singer I were low because signals were high-pass filtered at 312 Hz to remove low-frequency noise from an unknown source that was prevalent throughout recording).

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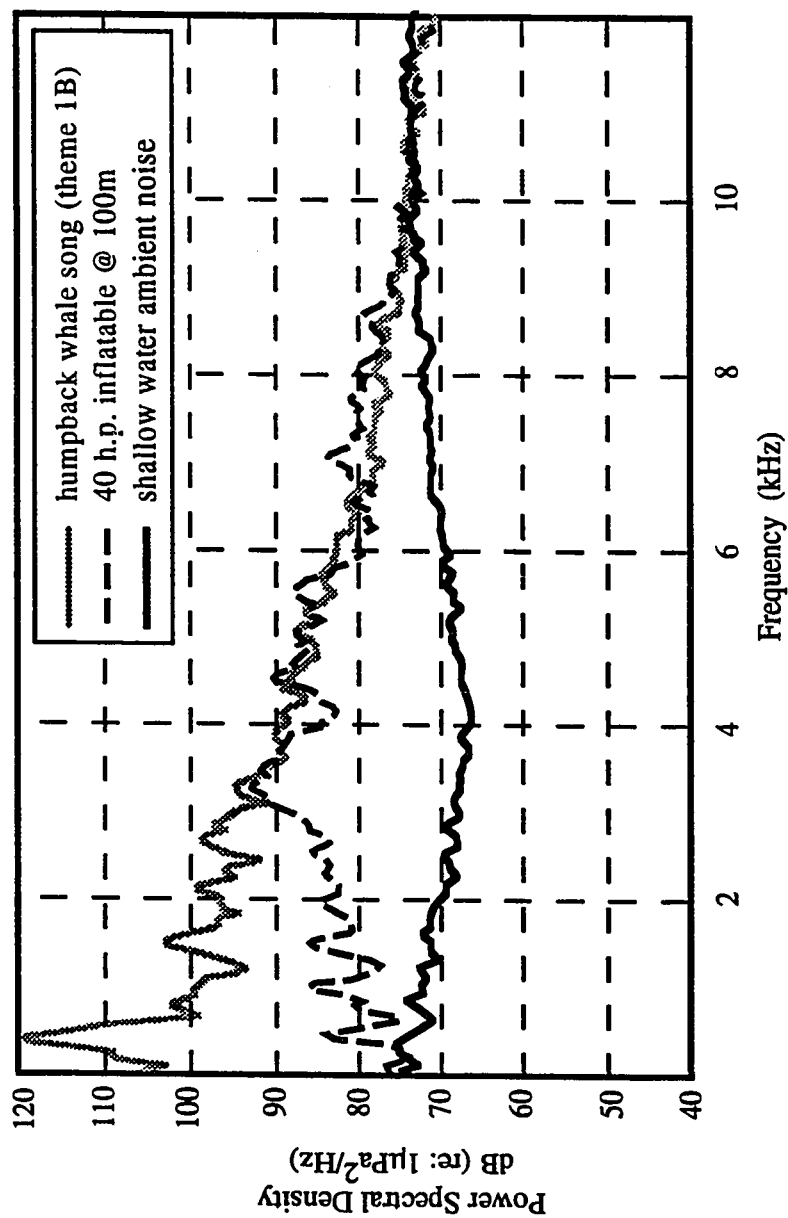
Figure 11. Average power spectra of ambient noise (solid line), the 40 h.p. inflatable boat used in experimental boat-passes (dashed line), and theme 1B of humpback whale song (shaded line). Intensity of humpback whale song is relative (i.e. distance dependent).
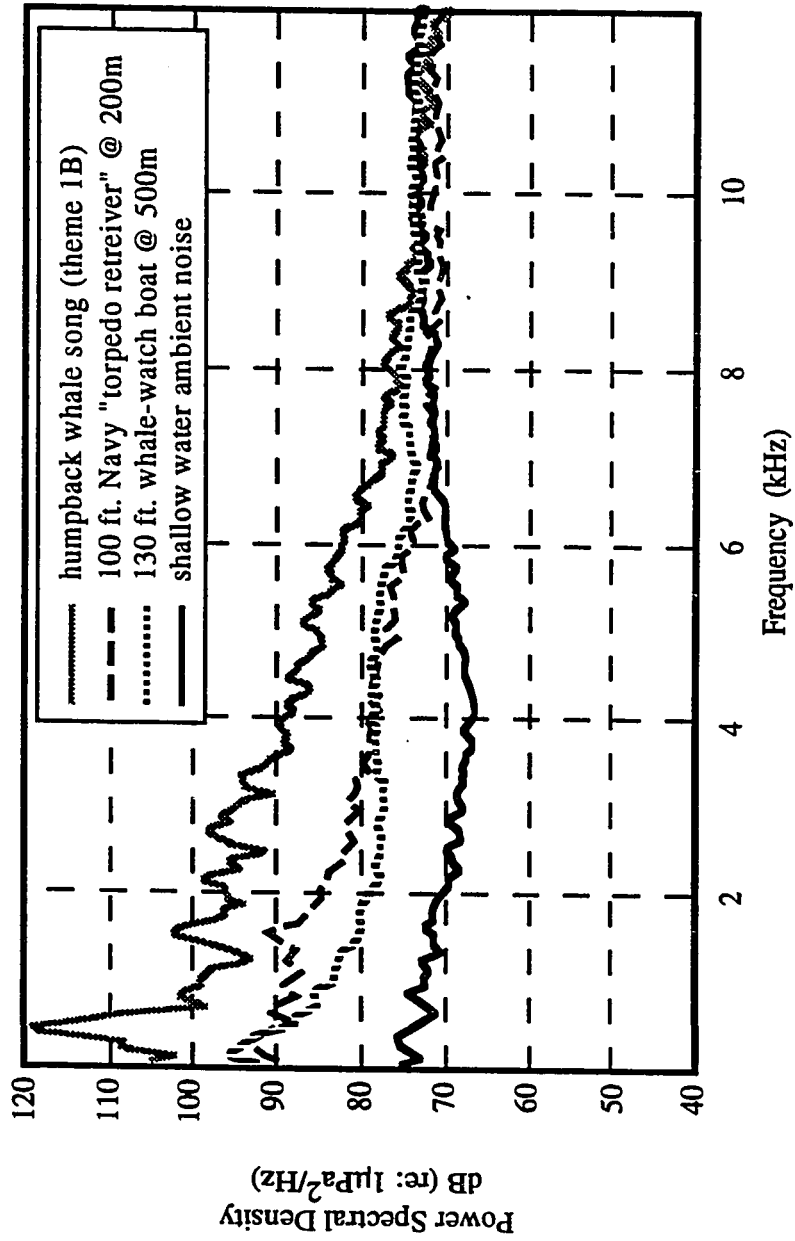
Figure 12. Average power spectra of ambient noise (bottom curve), two medium-size boats (two middle curves), and humpback whale song (top curve). Intensitiy of whale song is relative (distance dependant).
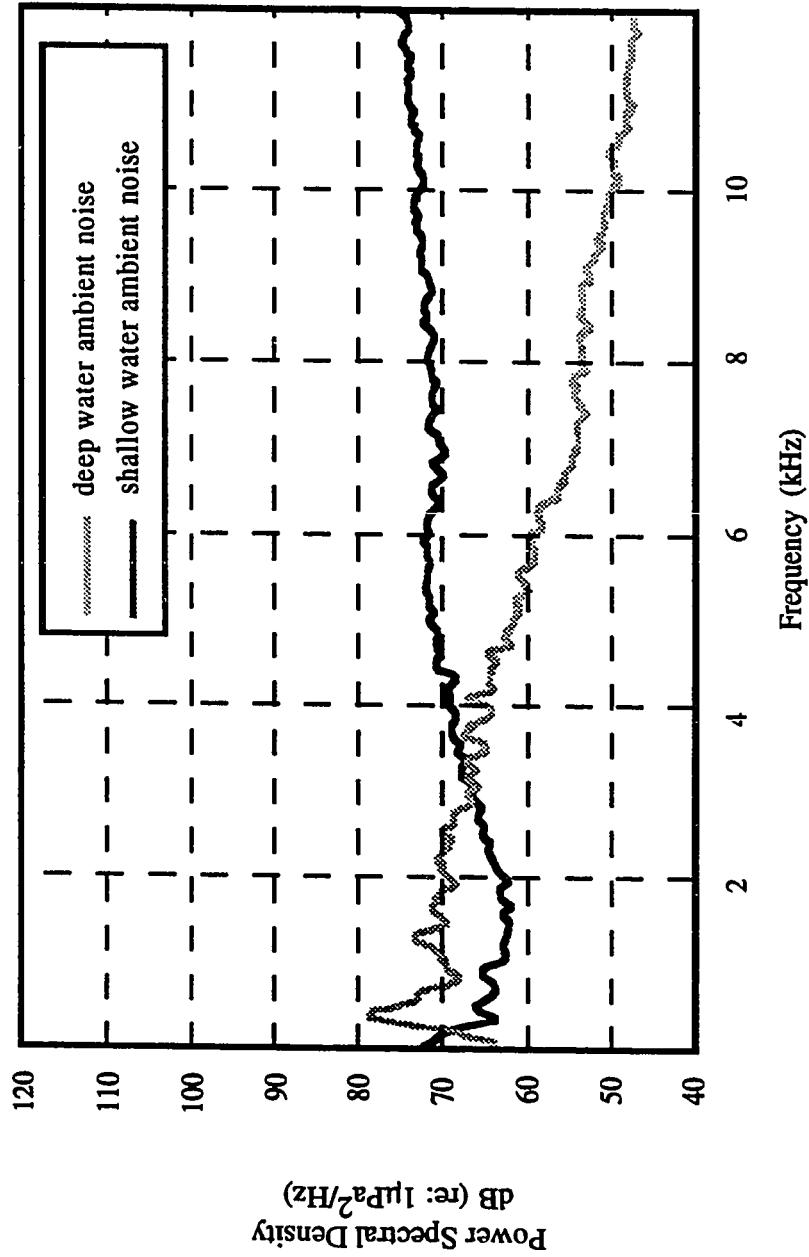
Figure 13. Average power spectra of ambient noise in shallow ( <30 m) and deeper water ( >100 m). The rise in noise levels from 2 to 12 kHz for the shallow water curve is probably due to snapping shrimp.
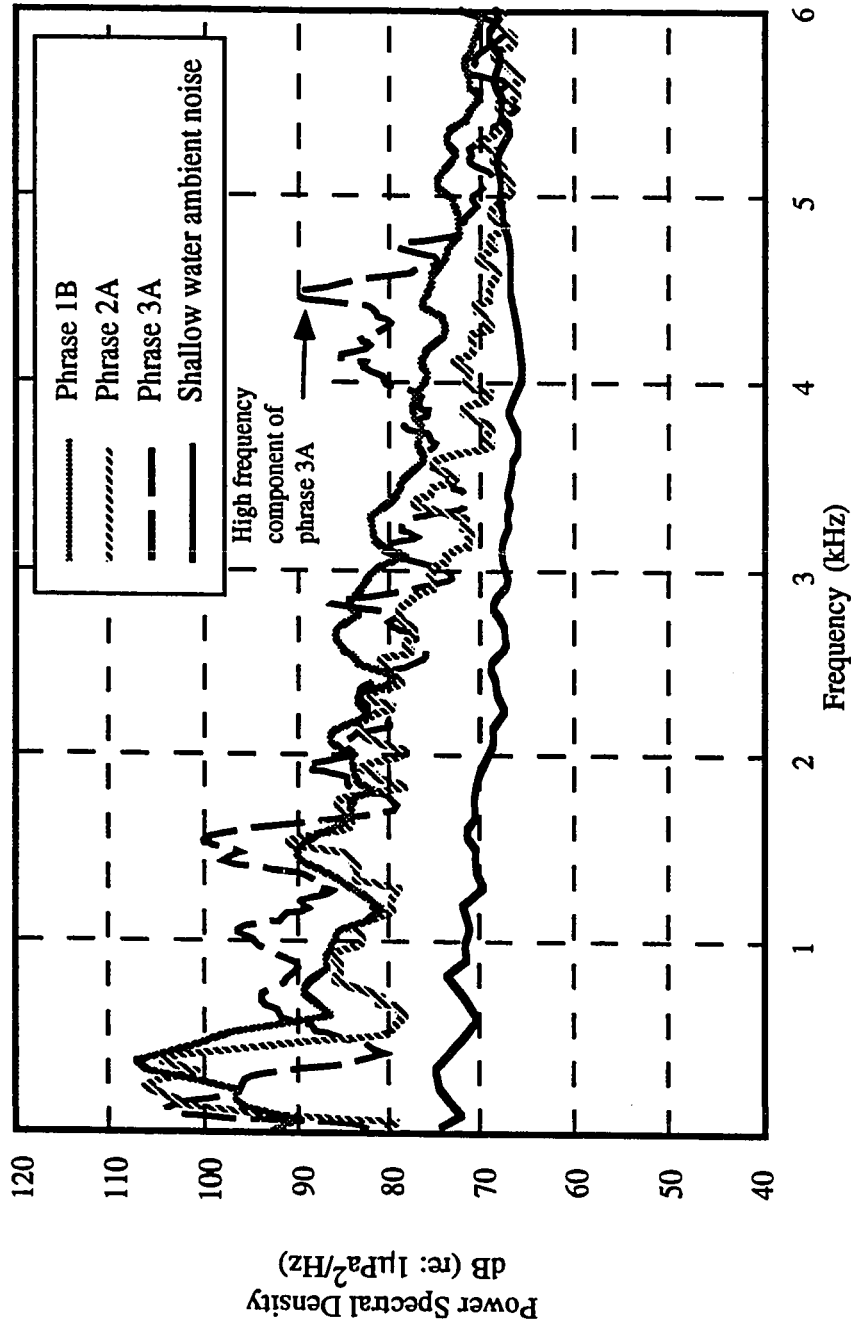
Figure 14. Power spectra of three types of humpback whale song phrases and shallow water ambient noise. All song phrases were anlyzed from recordings with high S/N. Songs were recorded from whales that were nearby (generally < 0.5 km); however, amplitudes are relative (distance dependant) because precise distances were not known. Peaks correspond to tonal (narrowband) components of song units. Most energy in song phrases is concentrated below 2 kHz, although a peak corresponding to a high frequency component is evident at approximately 4.5 kHz.

Appendix I. Mean, standard error, sample size, and the difference of means between control periods and boat-pass periods for: (A) unit 1 duration, (B) unit 2 duration, (C) inter-unit duration, and (D) phrase duration measured from experimental boat-pass recordings. Variable means for each singer and period were used to calculate differences ($\overline{X}c - \overline{X}bp$) used in paired t-tests.

(A)

**UNIT 1 DURATION**

| Singer | Control X | SE | n | Boat Pass X | SE | n | Difference $\overline{X}c - \overline{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 2.42 | 0.12 | 6 | 2.40 | 0.14 | 3 | 0.02 |
| B | 2.62 | 0.12 | 9 | 2.07 | 0.12 | 3 | 0.55 |
| C | 2.28 | 0.05 | 15 | 2.20 | 0.10 | 3 | 0.08 |
| D | 3.09 | 0.04 | 6 | 2.84 | 0.14 | 3 | 0.25 |
| E | 2.57 | 0.08 | 9 | 2.58 | 0.09 | 3 | -0.01 |
| F | 1.44 | 0.07 | 9 | 1.30 | 0.05 | 3 | 0.14 |
| G | 1.50 | 0.11 | 6 | 1.60 | 0.08 | 3 | -0.10 |
| H | 1.89 | 0.05 | 6 | 1.98 | 0.15 | 3 | -0.09 |
| I | 1.46 | 0.09 | 6 | 1.60 | 0.09 | 3 | -0.14 |

(B)

**UNIT 2 DURATION**

| Singer | Control X | SE | n | Boat Pass X | SE | n | Difference $\overline{X}c - \overline{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 1.77 | 0.10 | 6 | 1.47 | 0.11 | 3 | 0.30 |
| B | 1.69 | 0.11 | 9 | 1.36 | 0.04 | 3 | 0.33 |
| C | 2.29 | 0.22 | 6 | 2.19 | 0.23 | 3 | 0.10 |
| D | 2.01 | 0.08 | 6 | 1.54 | 0.07 | 3 | 0.47 |
| E | 1.33 | 0.08 | 9 | 1.20 | 0.05 | 3 | 0.13 |
| F | 1.10 | 0.10 | 9 | 0.83 | 0.03 | 3 | 0.27 |
| G | 1.76 | 0.30 | 5 | 1.04 | 0.10 | 3 | 0.72 |
| H | 2.31 | 0.23 | 6 | 2.22 | 0.09 | 3 | 0.09 |
| I | 2.44 | 0.23 | 6 | 2.26 | 0.07 | 3 | 0.18 |

(C)

**INTER-UNIT DURATION**

| Singer | Control X | SE | n | Boat Pass X | SE | n | Difference $\overline{X}c - \overline{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 2.09 | 0.14 | 6 | 2.04 | 0.12 | 3 | 0.05 |
| B | 2.14 | 0.12 | 6 | 2.03 | 0.06 | 3 | 0.11 |
| C | 2.25 | 0.07 | 15 | 2.26 | 0.08 | 3 | -0.01 |
| D | 1.89 | 0.05 | 6 | 1.87 | 0.09 | 3 | 0.02 |
| E | 2.20 | 0.06 | 9 | 2.20 | 0.12 | 3 | 0.00 |
| F | 2.30 | 0.03 | 9 | 2.16 | 0.08 | 3 | 0.14 |
| G | 1.81 | 0.06 | 5 | 1.75 | 0.03 | 3 | 0.06 |
| H | 1.59 | 0.18 | 6 | 1.25 | 0.12 | 3 | 0.34 |
| I | 1.51 | 0.05 | 6 | 1.36 | 0.09 | 3 | 0.15 |

(D)

**PHRASE DURATION**

| Singer | Control X | SE | n | Boat Pass X | SE | n | Difference $\overline{X}c - \overline{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 11.58 | 0.20 | 6 | 11.14 | 0.55 | 3 | 0.44 |
| B | 12.52 | 0.28 | 9 | 10.82 | 0.12 | 3 | 1.70 |
| C | 11.86 | 0.13 | 15 | 11.72 | 0.22 | 3 | 0.14 |
| D | 12.82 | 0.48 | 6 | 11.93 | 0.54 | 3 | 0.89 |
| E | 11.98 | 0.09 | 9 | 11.83 | 0.17 | 3 | 0.15 |
| F | 8.86 | 0.19 | 9 | 9.21 | 0.17 | 3 | -0.35 |
| G | 10.30 | 0.11 | 6 | 9.84 | 0.13 | 3 | 0.46 |
| H | 9.74 | 0.11 | 6 | 9.64 | 0.38 | 3 | 0.10 |
| I | 9.86 | 0.15 | 6 | 9.32 | 0.07 | 3 | 0.54 |

Appendix II. Mean, standard error, sample size, and difference of means between control periods and boat-pass periods for: (A) theme 1B duration, (B) song duration, (C) units per phrase 1B, and (D) phrases per theme 1B measured from experimental boat-pass recordings. Variable means for each singer and period were used to calculate differences ($\bar{X}c - \bar{X}bp$) used in paired t-tests.

(A)

**THEME 1B DURATION**

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c - \bar{X}bp$ |
| A | 127 | 1.3 | 2 | 182.53 | -- | 1 | -55.23 |
| B | 126 | 24 | 3 | 55.46 | -- | 1 | 70.64 |
| C | 207 | 33 | 5 | 212.13 | -- | 1 | -4.84 |
| D | 145 | 21 | 2 | 86.97 | -- | 1 | 57.91 |
| E | 112 | 4.1 | 4 | 59.96 | -- | 1 | 52.31 |
| F | 114 | 26 | 3 | 204.89 | -- | 1 | -91.27 |
| G | 280 | 12 | 2 | 353.44 | -- | 1 | -73.82 |
| H | 114 | 14 | 2 | 92.40 | -- | 1 | 21.55 |
| I | 214 | 6.9 | 2 | 190.57 | -- | 1 | 23.27 |

(B)

**SONG DURATION**

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c - \bar{X}bp$ |
| A | 722 | -- | 1 | 829.64 | -- | 1 | -107.23 |
| B | 504 | 23 | 3 | 524.61 | -- | 1 | -20.96 |
| C | 656 | 41 | 5 | 586.79 | -- | 1 | 69.52 |
| D | 1138 | 123 | 2 | 1060.65 | -- | 1 | 77.48 |
| E | 830 | 19 | 5 | 557.45 | -- | 1 | 272.64 |
| F | 658 | 32 | 3 | 665.41 | -- | 1 | -7.04 |
| G | 837 | 40 | 2 | 897.72 | -- | 1 | -60.45 |
| H | 552 | 41 | 2 | 599.61 | -- | 1 | -47.58 |
| I | 1065 | 32 | 2 | 819.89 | -- | 1 | 245.32 |

(C)

**UNITS per PHRASE**

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c - \bar{X}bp$ |
| A | 3.33 | 0.21 | 6 | 3.33 | 0.33 | 3 | 0.00 |
| B | 3.56 | 0.18 | 9 | 3.00 | 0 | 3 | 0.56 |
| C | 3.00 | 0 | 15 | 3.00 | 0 | 3 | 0.00 |
| D | 3.33 | 0.21 | 6 | 3.00 | 0.30 | 3 | 0.33 |
| E | 3.00 | 0 | 9 | 3.00 | 0 | 3 | 0.00 |
| F | 2.44 | 0.18 | 9 | 3.00 | 0 | 3 | -0.56 |
| G | 2.83 | 0.31 | 6 | 3.00 | 0 | 2 | -0.17 |
| H | 3.17 | 0.17 | 6 | 3.00 | 0 | 3 | 0.17 |
| I | 2.67 | 0.21 | 6 | 3.00 | 0 | 3 | -0.33 |

(D)

**PHRASES per THEME**

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c - \bar{X}bp$ |
| A | 11.0 | 7.6 | 2 | 16 | -- | 1 | -5.00 |
| B | 8.3 | 9.7 | 3 | 5 | -- | 1 | 3.33 |
| C | 16.0 | 5.9 | 5 | 18 | -- | 1 | -2.00 |
| D | 12.0 | 4.1 | 2 | 8 | -- | 1 | 4.00 |
| E | 9.3 | 6.3 | 3 | 5 | -- | 1 | 4.33 |
| F | 13.0 | 3.5 | 3 | 24 | -- | 1 | -11.00 |
| G | 29 | 13 | 2 | 35 | -- | 1 | -6.50 |
| H | 13 | 18 | 2 | 10 | -- | 1 | 2.50 |
| I | 23 | 29 | 2 | 20 | -- | 1 | 2.50 |

Appendix III. Mean, standard error, sample size, and difference of means between control and boat-pass periods for: (A) Unit 1 average frequency, (B) unit 1 minimum frequency, (C) unit 2 minimum frequency, and (D) unit 2 maximum frequency all measured from experimental boat-pass recordings. Variable means for each singer and period were used to calculate differences $(\bar{X}_c - \bar{X}_{bp})$ used in paired t-tests.

(A)

UNIT 1 AVERAGE FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}_{CP} - \bar{X}_{BP}$ |
| A | 135 | 13.8 | 6 | 98.96 | 3.4 | 3 | 35.8 |
| B | 143 | 5.9 | 9 | 125 | 7.8 | 3 | 17.8 |
| C | 140 | 5.1 | 15 | 148.4 | 0.0 | 3 | -8.9 |
| D | 140 | 4.2 | 6 | 130.2 | 7.9 | 3 | 9.8 |
| E | 164 | 6.4 | 9 | 181 | 10.6 | 3 | -17.0 |
| F | 161 | 2.2 | 9 | 174.5 | 4.7 | 3 | -13.5 |
| G | 154 | 2.4 | 6 | 157.6 | 1.3 | 3 | -3.3 |
| H | 131 | 5.6 | 5 | 141.9 | 3.4 | 3 | -10.7 |
| I | 134 | 3.1 | 6 | 135.4 | 3.4 | 3 | -1.3 |

(B)

UNIT 1 MINIMUM FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}_{CP} - \bar{X}_{BP}$ |
| A | 108 | 13.0 | 6 | 75.5 | 1.3 | 3 | 32.6 |
| B | 113 | 6.9 | 9 | 108.1 | 15.8 | 3 | 5.2 |
| C | 117 | 5.7 | 15 | 128.9 | 2.3 | 3 | -11.5 |
| D | 100 | 1.3 | 6 | 102.9 | 12.8 | 3 | -3.3 |
| E | 125 | 5.5 | 9 | 139.3 | 19.4 | 3 | -14.7 |
| F | 145 | 2.3 | 9 | 160.2 | 4.5 | 3 | -15.2 |
| G | 139 | 3.7 | 6 | 144.5 | 0.0 | 3 | -5.2 |
| H | 122 | 4.1 | 6 | 132.8 | 2.3 | 3 | -11.1 |
| I | 122 | 3.9 | 6 | 122.4 | 3.4 | 3 | 0.0 |

(C)

UNIT 2 MINIMUM FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}_{CP} - \bar{X}_{BP}$ |
| A | 194 | 7.6 | 6 | 198 | 8.5 | 3 | -3.3 |
| B | 221 | 9.7 | 9 | 186 | 5.2 | 3 | 35.6 |
| C | 210 | 5.9 | 15 | 229 | 13.8 | 3 | -18.7 |
| D | 225 | 4.1 | 6 | 221 | 14.7 | 3 | 4.6 |
| E | 185 | 6.3 | 9 | 179 | 3.4 | 3 | 6.9 |
| F | 219 | 3.5 | 9 | 237 | 15.8 | 3 | -17.8 |
| G | 189 | 13.5 | 5 | 203 | 17.9 | 3 | -13.7 |
| H | 280 | 17.7 | 6 | 257 | 4.7 | 3 | 23.6 |
| I | 281 | 29.2 | 6 | 215 | 2.3 | 3 | 66.4 |

(D)

UNIT 2 MAXIMUM FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}_{CP} - \bar{X}_{BP}$ |
| A | 432 | 15.9 | 6 | 359 | 6.1 | 3 | 73.1 |
| B | 347 | 17.4 | 9 | 356 | 31.8 | 3 | -8.7 |
| C | 383 | 8.8 | 15 | 409 | 2.6 | 3 | -25.8 |
| D | 377 | 3.9 | 6 | 385 | 1.3 | 3 | -8.5 |
| E | 334 | 7.6 | 9 | 346 | 12.4 | 3 | -12.1 |
| F | 394 | 6.2 | 8 | 400 | 8.5 | 3 | -5.7 |
| G | 1402 | 334 | 5 | 2474 | 26.3 | 3 | -1071.8 |
| H | 370 | 4.7 | 6 | 358 | 1.3 | 3 | 12.4 |
| I | 440 | 13.2 | 5 | 373 | 2.0 | 2 | 66.8 |

Appendix IV. Mean, standard error, sample size, and the difference of means between control periods and boat-pass periods for: (A) unit duration, (B) unit 2 duration, (C) inter-unit duration, and (D) phrase duration measured from opportunistic boat-pass recordings. Variable means for each singer and period were used to calculate differences ($\bar{X}c - \bar{X}bp$) used in paired t-tests.

(A)

UNIT 1 DURATION

| Singer | Control $\bar{X}$ | SE | n | Boat Pass $\bar{X}$ | SE | n | Difference $\bar{X}c - \bar{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 1.91 | 0.09 | 12 | 1.49 | 0.11 | 4 | 0.42 |
| B | 2.61 | 0.08 | 6 | 2.1 | 0.19 | 3 | 0.51 |
| C | 2.88 | 0.19 | 8 | 2.70 | 0.09 | 4 | 0.18 |
| D | 3.15 | 0.13 | 5 | 3.17 | 0.19 | 5 | -0.02 |
| E | 1.60 | 0.06 | 15 | 1.44 | 0.05 | 5 | 0.16 |
| F | 2.12 | 0.14 | 10 | 2.01 | 0.04 | 12 | 0.11 |
| G | 1.26 | 0.04 | 10 | 1.1 | 0.09 | 5 | 0.16 |

(B)

UNIT 2 DURATION

| Singer | Control $\bar{X}$ | SE | n | Boat Pass $\bar{X}$ | SE | n | Difference $\bar{X}c - \bar{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 1.66 | 0.13 | 12 | 1.08 | 0.08 | 4 | 0.58 |
| B | 1.74 | 0.10 | 6 | 1.34 | 0.11 | 3 | 0.40 |
| C | 2.11 | 0.17 | 8 | 2.01 | 0.13 | 4 | 0.10 |
| D | 1.46 | 0.11 | 5 | 1.42 | 0.11 | 5 | 0.04 |
| E | 2.58 | 0.08 | 15 | 2.6 | 0.14 | 5 | -0.02 |
| F | 2.08 | 0.08 | 10 | 1.78 | 0.05 | 12 | 0.30 |
| G | 1.73 | 0.21 | 10 | 1.6 | 0.33 | 5 | 0.13 |

(C)

INTER-UNIT DURATION

| Singer | Control $\bar{X}$ | SE | n | Boat Pass $\bar{X}$ | SE | n | Difference $\bar{X}c - \bar{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 2.31 | 0.09 | 11 | 2.52 | 0.13 | 4 | -0.21 |
| B | 2.21 | 0.14 | 6 | 2.42 | 0.08 | 3 | -0.21 |
| C | 1.99 | 0.10 | 7 | 1.9 | 0.03 | 4 | 0.09 |
| D | 1.95 | 0.08 | 5 | 2.08 | 0.09 | 5 | -0.13 |
| E | 1.54 | 0.04 | 15 | 1.62 | 0.06 | 4 | -0.08 |
| F | 1.64 | 0.10 | 10 | 2.01 | 0.01 | 12 | -0.37 |
| G | 1.95 | 0.05 | 10 | 1.94 | 0.11 | 5 | 0.00 |

(D)

PHRASE DURATION

| Singer | Control $\bar{X}$ | SE | n | Boat Pass $\bar{X}$ | SE | n | Difference $\bar{X}c - \bar{X}bp$ |
|---|---|---|---|---|---|---|---|
| A | 12.22 | 0.21 | 12 | 12.75 | 0.14 | 4 | -0.53 |
| B | 11.76 | 0.21 | 6 | 11.78 | 0.70 | 3 | -0.02 |
| C | 11.74 | 0.15 | 8 | 11.07 | 0.10 | 4 | 0.67 |
| D | 13.31 | 0.38 | 5 | 11.98 | 0.16 | 5 | 1.33 |
| E | 8.91 | 0.06 | 15 | 8.9 | 0.19 | 5 | 0.01 |
| F | 8.87 | 0.06 | 10 | 9.1 | 0.05 | 11 | -0.25 |
| G | 9.99 | 0.15 | 10 | 9.6 | 0.20 | 5 | 0.39 |

Appendix V. Mean, standard error, sample size, and difference of means between control periods and boat-pass periods for: (A) theme 1B duration, (B) song duration, (C) units per phrase 1B, and (D) phrases per theme 1B measured from opportunistic boat-pass recordin Variable means for each singer and period were used to calculate differences ($\bar{X}c$ - $\bar{X}bp$) used in paired t-tests.

(A)

THEME 1B DURATION

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c$ - $\bar{X}bp$ |
| A | 130 | 25 | 3 | 112 | -- | 1 | 18.74 |
| B | 154 | 28 | 2 | 104 | -- | 1 | 49.83 |
| C | 92 | 0 | 2 | 814 | -- | 1 | -721.44 |
| D | 90 | -- | 1 | 159 | -- | 1 | -68.72 |
| E | 192 | 22 | 3 | 397 | -- | 1 | -205.53 |
| F | 137 | 4 | 2 | 269 | -- | 1 | -132.85 |
| G | 243 | 41 | 2 | 260 | -- | 1 | -17.64 |

(B)

SONG DURATION

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c$ - $\bar{X}bp$ |
| A | 599 | 28 | 3 | 556 | -- | 1 | 42.57 |
| B | 776 | 54 | 2 | 585 | -- | 1 | 191.22 |
| C | 726 | 29 | 2 | 497 | -- | 1 | 228.85 |
| D | 759 | -- | 1 | 517 | -- | 1 | 241.73 |
| E | 672 | 149 | 3 | 604 | -- | 1 | 68.23 |
| F | 765 | 4 | 2 | 895 | -- | 1 | -130.39 |
| G | 871 | 34 | 2 | 869 | -- | 1 | 1.49 |

(C)

UNITS per PHRASE

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c$ - $\bar{X}bp$ |
| A | 3.6 | 0.15 | 12 | 4.0 | 2.0 | 4 | -0.42 |
| B | 3.2 | 0.17 | 6 | 3.8 | 2.5 | 5 | -0.63 |
| C | 3.3 | 0.16 | 8 | 3.0 | 1.9 | 4 | 0.25 |
| D | 3.4 | 0.24 | 5 | 3.0 | -- | 5 | 0.40 |
| E | 2.1 | 0.07 | 15 | 2.2 | 2.2 | 5 | -0.13 |
| F | 2.0 | 0.00 | 10 | 2.0 | 0.5 | 5 | 0.00 |
| G | 2.6 | 0.16 | 10 | 2.0 | 5.0 | 5 | 0.60 |

(D)

PHRASES per THEME

| Singer | Control | | | Boat Pass | | | Difference |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | SE | n | $\bar{X}$ | SE | n | $\bar{X}c$ - $\bar{X}bp$ |
| A | 11.0 | 2.04 | 3 | 9 | -- | 1 | 2.00 |
| B | 13.5 | 2.50 | 2 | 9 | -- | 1 | 4.50 |
| C | 8.0 | 1.90 | 2 | 25 | -- | 1 | -17.00 |
| D | 7.0 | -- | 1 | 13 | -- | 1 | -6.00 |
| E | 21.3 | 2.19 | 3 | 28 | -- | 1 | -6.67 |
| F | 15.5 | 0.50 | 2 | 31 | -- | 1 | -15.50 |
| G | 25.0 | 5.00 | 2 | 28 | -- | 1 | -3.00 |

Appendix VI. Mean, standard error, sample size, and difference of means between control and boat-pass periods for: (A) Unit 1 minimum frequency, (B) unit 1 maximum frequency, (C) unit 2 minimum frequency, and (D) unit 2 maximum frequency all measured from opportunistic boat-pass recordings. Variable means for each singer and period were used to calculate differences ($\overline{X}_{CP} - \overline{X}_{BP}$) used in paired t-tests.

(A)

UNIT 1 MINIMUM FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
| | $\overline{X}$ | SE | n | $\overline{X}$ | SE | n | $\overline{X}_{CP} - \overline{X}_{BP}$ |
| --- | --- | --- | --- | --- | --- | --- | --- |
| A | 134 | 6.1 | 8 | 131 | 7.6 | 4 | 3 |
| B | 122 | 6.4 | 6 | 117 | 6.5 | 3 | 5 |
| C | 89 | 2.6 | 8 | 75 | 1.9 | 3 | 14 |
| D | 88 | 7.7 | 5 | 86 | 12.5 | 5 | 2 |
| E | 149 | 3.6 | 15 | 117 | 4.6 | 5 | 32 |
| F | 89 | 2.2 | 10 | 75 | 2.6 | 5 | 14 |
| G | 88 | 1.6 | 10 | 86 | 5.3 | 5 | 2 |

(B)

UNIT 1 MAXIMUM FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
| | $\overline{X}$ | SE | n | $\overline{X}$ | SE | n | $\overline{X}_{CP} - \overline{X}_{BP}$ |
| --- | --- | --- | --- | --- | --- | --- | --- |
| A | 170 | 6.2 | 8 | 165 | 8.0 | 4 | 5 |
| B | 158 | 8.2 | 6 | 155 | 9.1 | 3 | 3 |
| C | 118 | 3.6 | 8 | 90 | 3.9 | 4 | 28 |
| D | 179 | 4.0 | 5 | 158 | 10.9 | 5 | 21 |
| E | 173 | 3.1 | 15 | 155 | 69.5 | 5 | 18 |
| F | 118 | 3.3 | 10 | 90 | 6.7 | 5 | 28 |
| G | 179 | 1.5 | 10 | 158 | 2.3 | 5 | 21 |

(C)

UNIT 2 MINIMUM FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
| | $\overline{X}$ | SE | n | $\overline{X}$ | SE | n | $\overline{X}_{CP} - \overline{X}_{BP}$ |
| --- | --- | --- | --- | --- | --- | --- | --- |
| A | 224 | 6.7 | 8 | 217 | 7.2 | 4 | 7.2 |
| B | 220 | 9.5 | 6 | 198 | 2.0 | 2 | 22.1 |
| C | 232 | 13.1 | 8 | 230 | 2.5 | 4 | 2.4 |
| D | 170 | 9.0 | 5 | 170 | 5.9 | 5 | -0.8 |
| E | 308 | 15.5 | 15 | 198 | 14.4 | 5 | 109 |
| F | 224 | 5.5 | 10 | 230 | 10.6 | 5 | -5.3 |
| G | 170 | 12.4 | 10 | 170 | 30.4 | 4 | -0.8 |

(D)

UNIT 2 MAXIMUM FREQUENCY

| Singer | Control Period | | | Boat - Pass | | | Difference |
| | $\overline{X}$ | SE | n | $\overline{X}$ | SE | n | $\overline{X}_{CP} - \overline{X}_{BP}$ |
| --- | --- | --- | --- | --- | --- | --- | --- |
| A | 368 | 16.6 | 8 | 374 | 4.9 | 4 | -6.5 |
| B | 450 | 15.2 | 6 | 416 | 21.9 | 3 | 35 |
| C | 415 | 17.3 | 8 | 365 | 9.4 | 3 | 50 |
| D | 404 | 15.7 | 5 | 368 | 14.2 | 5 | 36 |
| E | 542 | 27.2 | 15 | 416 | 51.7 | 5 | 126 |
| F | 477 | 8.5 | 10 | 365 | 3.4 | 5 | 112 |
| G | 404 | 22.0 | 10 | 368 | 26.4 | 4 | 36 |