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Acoustic and visual tracking reveals distribution, song variability and social roles of humpback whales in Hawaiian waters

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ACOUSTIC AND VISUAL TRACKING REVEALS DISTRIBUTION, SONG VARIABILITY AND SOCIAL ROLES OF HUMPBACK WHALES IN HAWAIIAN WATERS

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This dissertation is dedicated to my parents, Patricia M. Frankel and Alan Arby Frankel, Ph.D.. I wish that he were here to see the next Dr. Frankel.

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Abstract

Acoustic and visual methods were used to track and observe humpback whales off Hawai'i. Chapter 3 found 62 singing whales were located acoustically in water depths from 10 to 305 fathoms. This indicates that singers are not confined within the 100 fathom contour, although near shore waters had a higher density of singers. The relative bearings from one singer to another indicated that singers predominantly oriented and moved away from other singers. A negative relationship was found between change-in-separation and the initial distance between singers, thus singers close to another were more likely to increase their separation. These observations suggest that 4 km is the preferred minimum spacing between singers off Northwestern Hawai'i. Some singers actively swam while singing and others continued singing while affiliating with or being joined by other whales. The correlation between breaching and the cessation of singing suggests that the sounds of aerial behavior can convey information to other whales.

Humpback whales song has been characterized as having the same structure shared by all individuals simultaneously. Chapter 4 found that the songs of individual whales were significantly different from one another at the level of the song unit. Significant differences were found in the duration, bandwidth, lowest frequency, frequency of peak amplitude and the source level of different singers. The implication of these findings is that these small scale differences allow for the possibility of assessment of the song and the singer by other animals.

The opposite end of the acoustic sensory modality was examined in Chapter 5. Whales responded to playbacks of biological and synthetic sounds. An empirically determined measurement of sound transmission loss allowed the received sound levels to be estimated when the stimulus was presented. The lowest sound level that produced a response was 102 dB re 1 μPa. This corresponds to a 16 dB signal-to-noise ratio. This

value is probably an underestimate of the response threshold and certainly an underestimate of their hearing threshold.

Taken together, these findings reported here suggest the need to expand the traditional interpretations of singing humpback whales as obtained from visual observations alone.

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List of Abbreviations

Abbreviation	Full Spelling	Description
dB	Decibel	A measure of sound pressure
μPa	microPascal	A reference sound pressure level
Hz	Hertz	A measure of sound frequency
dB re 1μPa^2/Hz	Decibel referenced to 1 micropascal squared per hertz	A measure of sound pressure in a 1 Hertz wide frequency band

Chapter 1
Introduction
OVERVIEW

Life is divided into two components: Survival and reproduction. It can be argued that every purposeful act of an animal directly or indirectly serves these goals. The migratory nature of humpback whales provides a unique opportunity to study these components, since mating and feeding appear to be both spatially and temporally separated by migration (Baker and Herman, 1984b).

Humpback whales (*Megaptera novaeangliae*) feed primarily during the summer, in the highly productive northern end of their range (Jurasz and Jurasz, 1979). Humpbacks subsist upon their energy reserves stored in the blubber while migrating and on the wintering grounds (Slijper, 1962; Brodie, 1975; Lockyer, 1981). The biology and behavior of humpback whales during the winter in the low latitudes is dominated by reproduction (Chittleborough, 1965; Dawbin, 1966).

Females return to the wintering ground either with or without a calf, and both of these classes may or may not mate that year. The average interval between calving years is between 2.4 and 2.8 years (Baker et al., 1987; Clapham and Mayo, 1987). There is considerable variation in this interval; the inter-calf interval can range from 0 to 9 years (Baker et al., 1987; Glockner-Ferrari and Ferrari, 1990).

During the winter, male humpbacks exhibit two modes of social behavior. The first is active physical competition between males for reproductive access to females (Tyack and Whitehead, 1983; Baker and Herman, 1984a; Clapham et al., 1992; Medrano et al., in press). The second is the singing behavior of males (Payne and McVay, 1971; Winn and Winn, 1978). Song appears to be a reproductive display, although its exact function remains unknown. Another unknown is how mate choice occurs, what role song plays in the mating system, and to what extent females exert mate choice.

I will primarily address the role of song and singers: however, the role of females is critical to the social system. In order to better develop hypotheses about these questions, the basic biology of humpback whales will first be reviewed.

BACKGROUND BIOLOGY

Alaskan Feeding Behavior

Jurasz and Jurasz (1979) described in detail the humpback feeding behaviors: lunge feeding and bubblenetting. Lunge feeding is used to take euphausids and small fish. Lunge feeding refers to a whale rushing through a shoal of prey with its mouth open, collecting prey items. Such lunge feeding occurs vertically, when the whale rises straight out of the water with its mouth open, or laterally, where the whale rushes along the surface with its body parallel to the surface and mouth open. The whale then snaps its mouth shut and strains the prey with its baleen.

Echelon feeding is a cooperative version of lateral lunge feeding (Jurasz and Jurasz, 1979; Baker and Herman, 1984b). In echelon, feeding two whales laterally lunge feed in unison with the lower jaw of the leading whale almost touching the rostrum of the trailing animal. Presumably this confers some foraging advantage to one or both of the animals, because it requires the cooperation of both (Baker and Herman, 1984b).

Bubblenetting is a specialized form of vertical lunge feeding. Bubblenetting begins with the whale circling below a school of fish, releasing bubbles of air from its blowholes. As the bubbles rise they burst into smaller bubbles that forms the bubblenet around the fish, possibly corralling and concentrating the fish. The whale then lunges vertically through the bubblenet, ingesting large numbers of the fish. Bubblenetting can occur singly, or more dramatically in large groups.

Baker (1985) presents evidence that structurally stable groups of individuals, possibly related, engage in this group foraging strategy. This coordinated feeding may be acoustically mediated as suggested by several observations of a humpback pod engaged in

group feeding. One of the whales was consistently the first whale to lunge through the surface. This whale, believed to be female, was the group leader and emitting a stereotyped "feeding call" consisting of a series of short 440-550 Hz tones produced while the whales are underwater, and culminated in a longer call that slowly increased in frequency and ended as the whales emerged from the water. The feeding call was recorded in Southeast Alaska in 1981 and 1984 and showed little difference between years (Baker, 1985).

Pod Structure

Humpback whales form social groups of varying size called pods. Pods range in size from one to twelve or more animals. In Hawai'i, the mean size for pods with a calf is three animals, while pods without a calf have a mean size of two (Herman and Antinoja, 1977; Herman et al., 1980; Mobley and Herman, 1985). The whale accompanying a cow-calf pair was first described by Herman and Antinoja (1977) and termed an "escort." Escorts have been sexed by both photographic and genetic methods; all have been found to be males (Whitehead, 1981; Glockner, 1983; Baker and Herman, 1984a; Glockner-Ferrari and Ferrari, 1990; Clapham et al., 1992; Medrano et al., in press).

Migration and the Seasonality of Behavior

Humpback whales (*Megaptera novaeangliae*) are migratory baleen whales found in all oceans of the world. The classic view of their migratory pattern describes feeding during summer in high-latitude waters (Jurasz and Jurasz, 1979). In winter, they migrate to tropical waters where they feed little if at all and where breeding and calving is thought to occur (Chittleborough, 1965; Baker et al., 1986; Daring and Jurasz, 1983; Mattila et al., 1988; Winn and Winn, 1985). A comparison of the blubber thickness of migrating whales found that whales caught leaving high latitudes for low latitudes had much higher fat content than those on the return migration, as shown by the amount of oil rendered (Lockyer, 1981). Furthermore, whales caught while heading toward low-latitude waters

had stomachs filled with prey, while those caught while migrating toward higher latitude waters had empty stomachs (Chittleborough, 1965; Dawbin, 1966) The implication is that the majority of feeding occurs while in productive low-temperature water and that whales use stored energy reserves while in the low productivity semi-tropical and tropical waters (Slijper, 1962; Brodie, 1975; Lockyer, 1981). This is supported by the frequent descriptions of feeding behavior in high-latitude waters (Jurasz and Jurasz, 1979; Hain et al., 1982) and the rarity of observations of feeding in low latitudes (Salden, 1989; Baraff et al., 1991).

Activity on the low latitude areas appears to be dominated by reproduction. Many apparently newborn calves are seen in Hawai'i and other low-latitude waters (personal observation; Glockner-Ferrari and Ferrari, 1990). The gestation period of humpbacks has been established by whaling studies. Chittleborough (1954) measured the reproductive condition of females over the course of a winter season by examining the mammary gland and ovaries of whales taken off western Australia. The highest occurrences of both ovulations and births occurred in late July and early August (equivalent of January and February in the northern hemisphere). He concluded that the gestation period lasts approximately 12 months and that lactation lasts approximately 10.5 months. The cow nurses the calf for the year during one migratory cycle, returning to the wintering grounds with her yearling (Glockner and Venus, 1983; Baker, 1985; Baker et al., 1987). Some calves may be weaned earlier, while on the feeding grounds (Baraff et al., 1991)

The timing of female reproductive activity is matched by the males, as shown by the seasonal variation in testis weight and sperm presence in the seminiferous tubules (Matthews, 1937; Omura, 1953; Chittleborough, 1955; Nishiwaki, 1959). Spermatogenesis is found from June to October in the southern hemisphere, corresponding to December through April in the northern hemisphere.

While the overall pattern of the spatial and temporal separation of feeding and reproduction holds true, it is probably not a simple matter of poleward in the summer and toward the equator in the fall. This traditional migration pattern has been called into question by recent results from the tracking of mysticetes (Gagnon and Clark, 1993). A single blue whale (*Balaenoptera musculus*) was tracked in February, 1993 using U.S. Navy SOSUS arrays, a system of fixed hydrophone arrays. The whale vocalized nearly constantly for 43 days, permitting it to be tracked for that time. The whale swam 1450 nautical miles from a position east of new England to a position 200 nautical miles northeast of the Bahamas Islands and then reversed course and returned to Bermuda. This basin-scale wandering calls into question the commonly held idea that migration is just a rectilinear movement between mating and feeding grounds for blue whales and perhaps other mysticetes as well.

Mating: Operational Sex Ratio and the Availability of Females

Having established the seasonal nature of reproduction, it is important to examine the sex ratio. The sex ratio of the population is a typically mammalian 1:1 (Chittleborough, 1958; Glockner-Ferrari and Ferrari, 1990). (Emlen and Oring, 1977) defined the operational sex ratio (OSR) as the ratio of reproductively active males to females. The OSR in humpback appears to be biased towards males for a number of reasons. The general reproductive cycle of females has been described as alternating years between gestation and lactation (Dawbin, 1966). Examination of the sighting records of individual females has shown an average inter-calf interval from 2.4 years (Clapham and Mayo, 1987) to 2.8 years (Baker et al., 1987). Assuming that the number of failed pregnancies is small, this would indicate an operational sex ratio of approximately 2.5 males to 1 female. Classical ecological theory predicts that any system with an imbalance between need and availability will lead to competition for the limiting resource (Wilson, 1975).

Males appear to compete for reproductive access to females in large groups known as surface active pods. Studies conducted in Hawai'i and the Caribbean have investigated these pods. Tyack and Whitehead (1983) demonstrated that the structure of these pods consist of a nuclear animal (NA), a primary escort (PE) and a secondary escort (SE). The nuclear animal was often the mother of a mother and calf pair, thus inferred to be female. Recent genetic work has confirmed that the nuclear animal is often, but not always, female (Clapham et al., 1992). The animal that maintains closest proximity to the nuclear animal was referred to as the primary escort. Any additional escorts in the pod were referred to as the secondary escorts. Observations of these pods showed that secondary escorts attempt to replace the primary escort, which in turn attempts to maintain its position and displace (force) the secondary escorts out of the pod. Tyack and Whitehead (1983) concluded that the escorts were reproductively active males, competing for reproductive access to the female nuclear animal.

Baker and Herman (1984a) reported similar findings and were able to describe the sequence of behaviors used in such contests. They reported a general pattern of increasing agonistic intensity as the encounters proceeded. A typical low-level agonistic display lowest in intensity is the broadside threat display, or bodily interposition of the primary escort between the female and the challenging male. The next level of aggression includes headlunging and bubbling. The underwater release of air or "bubbling" is often associated with headlunging, most commonly as underwater blows or bubble-trails, possibly to disorient the intruding whale (Baker and Herman, 1984a). Intermediate levels included headlunges. Headlunging refers to the whale lunging forward at the surface with its rostrum raised above the water's surface. The ventral pleats are often distended during headlunging, thereby increasing the animal's size. This display may be analogous to piloerection in the threat displays of other mammals (Baker and Herman, 1984a). Headlunges range from simple lunging at the surface, through lunging with the ventral

pleats partially expanded to lunging over the back of another animal. Animals lunging over the back of another appear to be attempting to hold it underwater, forcing the animal to move toward the back of the pod to escape and breathe. If the combination of headlunging and bubbling have not dissuaded an intruding animal, agonism may escalate to the highest level, the charge-strike. Three forms of the charge-strike have been observed: butting, lateral fluke strikes and peduncle strikes. Butting involves one whale, usually the primary escort, ramming another whale with its rostrum. Lateral fluke strikes occur between whales swimming side by side while lashing out at each other with their flukes. The most violent form is the peduncle strike. One escort may swim underneath another male and throw its peduncle upwards, often throwing the posterior portion of the whale on the receiving end of the strike clear of the water. These behaviors can either be used to displace challenging escorts from the pod, or can be used by challengers in an attempt to remove the primary escort.

Some of the nuclear animals were identified as females, either by the presence of a calf (Tyack and Whitehead, 1983), direct photographs of the genital area (Baker and Herman, 1984) or by fluke identification photographs compared to the catalog of known individuals (Tyack and Whitehead, 1983; Baker and Herman, 1984a). Escorts were also identified as males, presumably engaged in male-male competition for reproductive access to the females. This view of surface active groups has been largely confirmed through recent genetic work. Clapham et al. (1992) collected tissue samples from all of the individuals in 21 surface active groups. None contained more than one female, 17 of 22 nuclear animals were sexed as female, and 23 of 24 primary escorts were male, as were all 24 secondary escorts. Similarly, Medrano et al. (in press) found that 17 of 18 whales in surface active groups were male. Thus the overall hypothesis that surface active groups are mainly arenas for male-male physical competition for reproductive access to females appears to be confirmed.

Pod composition on the mating grounds is quite fluid. Mobley and Herman (1985) reported that a change in membership occurs in 14 percent of the whale pods within an hour. Agonistic behaviors contribute greatly to that fluidity. The primary escort usually displaces challenging males (secondary escorts) to the rear of the pod or from the pod entirely. However, secondary escorts periodically replace the primary escort. Tyack and Whitehead (1983) reported that the primary escort is replaced once every 7.5 hours on average. Baker and Herman (1984) additionally reported no affiliations between individuals longer than 24 hours. Moreover, whales are more likely to join a pod with a calf than one without a calf. This is probably due to the attractiveness of sexually mature cows to competing males (Mobley and Herman, 1985).

Vocalizations

Whales in these agonistic surface-active pods produce various grunts, whistles and the sounds of bodily contact. These are referred to as "social sounds" (Tyack, 1983; Silber, 1986). Silber (1986) demonstrated that the number of social sounds produced in a pod increased with increasing number of whales in a pod. Furthermore, the numbers of calls per whale did not differ with pod size. Finally, overlapping calls were heard. He therefore concluded that the male escorts in the pod were responsible for the production of the social sounds. He went on to suggest that such calls are produced as acoustic threats.

This view was supported by the results of playback experiments, in which social sounds were presented to humpback whales. (Tyack, 1983) demonstrated that social sounds were an attractive stimulus. Nine of 16 whales that he presented with the sound charged toward the boat in response. Mobley et al. (1988) played back these social sounds and the feeding call to whales. Playback of both of these sounds produced rapid approach responses. However the feeding call produced far more approaches (19 v. 3 out of a total of 143 trials). This difference in attractiveness was attributed to the presumed sexual information in the call. The feeding call was believed to have been produced by a lone

female, and social sounds are produced by males accompanying a female. The lowered attractiveness of social sounds was attributed to their indicating male presence.

Another vocalization produced on the wintering grounds is song. The song has a typical length of 8 to 16 minutes and fundamental frequency range of 30 to 4000 Hz (Payne and Payne, 1985). Payne and McVay (1971) described the hierarchical structure of the song, beginning with a series of units, which are defined as "the shortest sound that is continuous to our ears when heard in 'real time'." Units appearing in regular sequence constitute a phrase. Likewise, a regular combination of phrases forms a theme. The song itself is composed of several themes. A single animal sings the song repeatedly in a song session.

Payne and Payne (1985) examined songs over a 19-year period and found that songs typically had between five and nine themes in any year. They also separated themes into three categories: 1) Static, where the phrases are nearly identical for every production. 2) Shifting themes, where the successive phrases evolve in structure from one form to another. 3) "Unpatterned" themes, where there are a variable number of units and no clear organization. Such themes cannot be divided into phrases.

Unlike many other vocalizations, humpback whale song changes from year to year and within seasons (Payne and Payne, 1985; Payne, Tyack and Payne, 1983). This variation is expressed as a slow progressive change in the structure of the song. Themes are constantly being added and lost. Guinee et al. (1983) demonstrated that the progressive change of song results from the simultaneous modification of each individual's song, rather than a change in the singing population. While song changes continuously, most individuals at a given time sing the same basic version (Payne and Payne, 1985; Payne, Tyack, and Payne, 1983). Convergence on a single song type within a population is not, however, absolute. A few whales deviate from the pattern, and are referred to as aberrant singers (Frumhoff, 1983). Payne and Payne (1985) reported that inter- and intra-

individual variation was found in their large sample of 163 songs collected over 19 years. They stressed, however, that the degree of this variation was far less than the variation in song structure from year to year.

Winn and Winn (1978) argued that the homogeneity of the song within a population is the result of learning. Comparison of songs from different breeding areas of different oceans has shown that whales within an ocean basin sing very similar songs. The songs of whales from northern and southern hemispheres or between oceans show great differences. These similarities have been used to define populations (Winn et al., 1981; Payne and Guinee, 1983; Helweg et al., 1990; Helweg et al., 1992).

The exact function of song remains undetermined; however it is believed to play a role in the mating system (Tyack, 1982; Baker, 1985). Song is rarely heard while the whales are feeding in high latitude waters in the summer (Mattila et al., 1987; McSweeney et al., 1989). Song has been heard along the migration route (Clapham and Mattila, 1990). The vast majority of singing, however, occurs during winter, in low latitude waters. Humpback whales are believed to mate during this time. Winn and Winn (1978) first demonstrated that singers were typically alone. They also provided evidence to suggest that the singers were sexually mature males. Subsequent observations revealed that escorts occasionally sang as well (Herman and Tavolga, 1980; Tyack, 1981; Glockner and Venus, 1983; Baker and Herman, 1984a). A number of singers have been photographically or genetically sexed, and all have been male (Winn et al., 1973; Glockner, 1983; Lambertsen et al., 1988; Clapham et al., 1992; Medrano et al., in press).

The hypothesis that song is important in the mating system is supported by the considerable time investment made by singers. Winn and Winn (1978) reported that a single whale may sing continuously for as long as 22 hours. Levenson (1972) estimated a source level of 155.4 dB re 1 μPa at 1m (level in decibels referenced to one micro Pascal at a distance of one meter) for humpback whale song. Sound levels of this magnitude have

allowed detection of singing whales at ranges of 32 km (Winn and Winn, 1978). Estimates of its biologically effective range vary between 7.5 and 10 km (Tyack, 1981).

Singing may facilitate the affiliation of the singer with a pod. When singers do join a pod they typically stop singing and assume an escort role (Tyack, 1981), although some escorts continue to sing (personal observation). This supports the hypothesis that humpback whale song functions to facilitate association with females. However, playback experiments that presented recordings of song to whales failed to produce any significant approach response (Tyack, 1983; Mobley et al., 1988)

Tyack (1981) reported that singers are always 5-10 km distant from other singers and that they may avoid each other. If avoidance leads to regular spacing of individuals, it may represent a communal display, such as in a lek (Herman and Tavolga, 1980). (Leks are mating systems where males defend very small territories that serve only for mating. Females visit males on the lek and mate there.) However, Whitehead (1981) found singers within 100-500 meters of one another on Silver Bank in the Caribbean. Additionally, when the local population was high, singers in Hawai'i have been seen within 100s of meters of each other (Cerchio, personal communication). The western North Atlantic population is larger than the Pacific (Baker and Herman, 1987; Katona and Beard, 1990), and the density on the wintering grounds is greater in the Atlantic (Whitehead, 1981). Spacing between individual singers may be density-dependent, but this has not been addressed {move to discussion?}.

Mating System: Preliminary Description

The mating system of humpbacks is characterized by no long-term pair-bonds between adults (Baker and Herman, 1984a; Mobley and Herman, 1985). Without pair bonds, it is unlikely that the father can provide parental care. In any case, the feeding methods of humpbacks prohibit male provisioning. Female humpbacks are mobile and their range is not defensible as in seal harems (Le Boeuf, 1974). Females are rarely found

in the same pod on the wintering grounds (Clapham et al., 1992) and may avoid each other (Tyack, 1981). Mammalian mating systems with these characteristics are likely to be a form of polygyny or a lek (Clutton-Brock, 1989). The prevalent agonistic behavior between males supports this conclusion. The mating system appears to be female defense polygyny or possibly promiscuity (Herman and Tavolga, 1980; Darling et al., 1983; Baker and Herman, 1984; Mobley and Herman, 1985; Brownell and Ralls, 1986).

Sexual Selection and Reproductive Displays

Reproduction typically includes two types of interactions. Intrasexual, typically male-male interactions include establishment and defense of a territory or control of a mate. Intersexual interactions usually involve attracting a mate. The outcome of both types of interactions can affect the reproductive success of an individual (Harvey and Bradbury, 1991)

Of the two, intra-sexual selection has been more widely accepted. It is easy to realize that larger horns increase a male ungulate's fighting ability. Nevertheless, experimental manipulation of tail length in widow birds has shown a distinct female preference for longer tails (Andersson, 1982). Female preferences are assumed in many models of sexual selection that attempt to explain the evolution of extravagant male characters, such as in Fisher's (1958) original runaway sexual selection theory.

The effects of sexual selection on bird song have been extensively investigated. Catchpole (1982) compared the functions, selective pressures and structures of the songs of birds. Songs that functioned primarily for female attraction showed a trend toward longer and more complex structures and were the result of intersexual selection. Conversely songs for male repulsion were shorter, more stereotyped, and resulted from intrasexual selection.

For example: Sedge warblers, which have a complex song, are migratory, and have little time to establish relationships with neighboring males and must quickly attract

females. In this species, song stops after a mate is acquired, thus song in this species is functions to attract females (Catchpole, 1982). In contrast, great tits have a comparatively small repertoire and they continue to sing after pairing. Higher repertoire size in this species contributes to the acquisition of better territory (McGregor et al., 1981) Song in great tits has an intersexual function, the maintenance of territories.

Songs can be used by females for mate selection based upon phenotypic or genotypic characters rather than territory quality. Female leptodactylid frogs select larger males by using the dominant frequency of the male's advertisement call as an indicator of size (Ryan, 1980). Selecting larger males increases the female's reproductive success (Ryan, 1983). Female mate choice based upon the proximate characteristic of body size has been shown to affect the frequency of alleles that influence body size (Ryan et al., 1990)

The sender's body size determines the dominant frequency of these calls. Larger bodies produce lower frequency sounds (Ryan, 1980). This is an example of an "unbluffable" or honest signal. It has been suggested that sexual selection should favor signals that positively correlate with the genetic quality of the male. Intersexual selection may have shaped the use of this signal for male advertisement by females choosing males that used this low frequency call. Females should select mates based on these traits because they do reflect the male's fitness (Kodric-Brown and Brown, 1984).

Not all communication associated with reproduction is "honest." The song of the Great Tit appears to function primarily in male aversion. Studies of great tits have revealed that some males have larger song repertoires than others. It has been suggested that this serves to deceive competing males that the area from which the signal is emitted is already crowded (Krebs, 1977) This hypothesis is also supported by similar work done on red-winged blackbirds (Yasukawa, 1981). Such a mechanism could have been brought about through intrasexual selection.

Studies of indigo buntings reveal that a great deal of mimicry or song-matching occurs. Observation has revealed that birds are mimicking older birds with higher reproductive success. These song-matchers in turn realize an increase in their reproductive success through an enhanced intra-sexual competitive ability (Payne, 1982).

Village indigobirds also perform song-matching. However, unlike indigo buntings, indigobird song appears to function in both intra- and inter-sexual encounters. Indigobird song does not have a constant structure, rather it is continuously modified with all males making the same changes. After a period of five years, the song is no longer recognizable. This process of song-matching creates separate song populations that all share the same song, and the song is continually being modified (Payne, 1985).

Furthermore, the rate of change in structure does not differ between intrasexual and intersexual song types. Some of the changes in song structure were associated with an increase in reproductive success, suggesting that the members of a song population were matching the song of the most successful individual (Payne, 1985). If so, it suggests that the changes in both types of song improve success in both intra-sexual and inter-sexual encounters.

A similar situation occurs in humpback whales. Males sing during the breeding season (Payne and McVay, 1971; Winn, et al, 1971). At any given point in time, the songs of individual whales are very similar (Payne, Tyack, and Payne, 1983). However, the song slowly undergoes changes in its structure both within and between breeding seasons (Payne and Payne, 1985; Payne, Tyack, and Payne, 1983). These changes appear to be made by all members of a population (Payne and Guinee, 1983).

Hypotheses of Humpback Song Function

Migration Beacon

One of the puzzles of migration is how animals orient during migration. Payne and McVay (1971) suggested that large numbers of humpback singers could produce an

acoustic beacon. Whales migrating toward the wintering area could orient toward the acoustic display. This suggestion does not explain how the initial singers would locate the wintering grounds. Whales may use other methods to orient to their migratory termini. Suggestions include following currents (Baker and Herman, 1981) and most recently, magnetic orientation (Bauer et al., 1985)

Mating and Courtship

The temporal association of song production and reproduction makes the functions of mating and courtship an obvious suggestion. Payne and McVay (1971) made the original suggestion of a mating function for song. This early paper went on to suggest that it may function in pair bonding as well. Later work demonstrated no evidence for stable associations between adults on the wintering grounds (Tyack and Whitehead, 1983; Mobley and Herman, 1985). The question that remains is more specific: what role does song play in the mating system?

Payne & McVay (1971) also suggested that song might function in courtship. Because courtship is poorly understood in humpbacks, this remains a viable hypothesis. While the majority of singers are alone while singing (Winn and Winn, 1978; Tyack, 1981; Chu, 1988),, escorts in mother, calf and escort pods are sometimes reported to be singing as well (Baker & Herman, 1984a; personal observation). Singing in this context would seem to have multiple possible functions: courtship as already suggested, or a signal to other males to stay away. However, if song reliably kept other males at a distance, it should be produced by all escorts in mother, calf and escort pods. The occurrence of singing escorts is relatively rare.

Synchronization of Ovulation

Seasonal peaks were found in both spermatogenesis and ovulation (Chittleborough, 1965). Both peaks were temporally correlated with respect to each other and to the migration. However, the timing of migration between years has varied by as much as three

weeks (Baker and Herman, 1981). It has been suggested that the communal singing display could function to synchronize ovulation and minimize time spent on the wintering grounds Baker & Herman (1984a) . This suggestion is supported by similar findings in canaries and parakeets (Hinde and Steele, 1978), mice (Whitten, 1956) and red deer (McComb, 1987).

Sexual Advertisement

Chu (1988) found differences in dive duration between different singers. The relationship between dive duration and the number of blows taken following a dive was shown to be different between individuals. Chu (1988) concluded individual whales were able to dive for different times, and that whales in better condition could dive longer. Dive duration would be communicated because song amplitude drops when the animal approaches the surface (Winn and Winn, 1978; Herman and Tavolga, 1980; Tyack, 1981), probably due to the Lloyd mirror effect (Urick, 1983). Chu (1988) concluded that diving ability, advertised via song, was an indication of higher phenotypic fitness in singers.

This conclusion is based upon the assumption that song is energetically costly to produce. Song production has been shown to be very costly in small terrestrial animals (Wells and Taigen, 1986; Wells and Taigen, 1989). However, there is less absolute pressure required to produce sound in water, due to the higher density of the transmission medium. A calculation based upon the source level of song, and assuming a 1% conversion efficiency from stored energy to acoustic energy, indicates that only 700 calories are required to sing for 24 hours, a vanishingly small portion of a whale's daily energy budget (Helweg et al., 1992). Chu's finding that recovery rates differ between singers may be correct, but the differences in energetic efficiency are probably due to basal metabolism rather than the activity of singing. A comparison between slow moving singers and non-singers might resolve the issue.

In any case, Chu (1988) concluded that song communicates the duration between surfacings, and therefore breath-holding ability. However, advertising breath-holding ability is not a complete explanation of song and song function.

Singers are mostly if not completely male (Winn et al., 1973; Glockner, 1983; Lambertsen et al., 1988; Clapham et al., 1992; Medrano et al., in press). Tyack (1981) found that singers were mostly alone (91 of 95 observed singers); three were in pairs and one in a trio. Tyack documented the affiliation of singers with other pod types. He reported that song always ceased when the singer joined a pod. While whales would approach and join with a singer, in most affiliations the singer would be the animal pursuing and joining with other whales. In these interactions, whales would tend to avoid the singer (Tyack, 1981). In one interaction, the whale that approached and joined with a singer later started singing itself, indicating that it was a male. Playback of songs produced very few approaches by whales and non rapid approach responses (Tyack, 1983; Mobley et al., 1988). The cessation of singing when joining another whale, and the scarcity of female approaches, suggested that singers are advertising, but not attracting, females.

Sexual Attraction

Singing males are almost certainly advertising their species and location, even if unintentionally. Song may also contain some indication of male quality. The critical factor in determining song's function is the reaction of the receivers (McGregor, 1991). Early reports offered little evidence of female approach to singers (Tyack, 1981). Controlled presentation of humpback sounds found strong approach reactions to social sounds and to feeding call, while song produced very few responses (Tyack, 1983; Mobley et al., 1988).

Animals have been observed to approach singers (Tyack, 1981; Frankel et al., 1989) but in most instance it was difficult to determine the sex of the animal approaching the singer. In some instances it was clearly male (Tyack, 1981; Darling, 1983). Singers have been seen to join with mothers and calves (Tyack, 1981) and recently females have

been observed to join singers (Medrano et al., in press). The incidence of females joining with singers is probably low, but its occurrence lends new support for the idea that songs can function to physically attract females.

Dominance Theory

The broadcast of song by males is certainly heard by many animals in the vicinity. Again, this proposed function is an interpretation of how that broadcast information is used. Darling (1983) proposed that males use song to establish dominance over one another, and that this dominance hierarchy would be used to determine reproductive access to females.

The existence of a dominance hierarchy is unlikely in humpback whales, given the unstable nature of humpback groups (Mobley and Herman, 1985). In order for a dominance hierarchy to exist, one of three conditions must be met. There must be individual specific information in the song and a humpback must be capable of associating differences in the song with competitive abilities for all individuals in the entire population. This seems unlikely, given that the entire song is be replaced with new material every few years (Payne and Payne, 1985). Signature whistles, which do carry individual specific information, are stereotyped and maintained throughout an animals life (Tyack, 1986). Alternatively, humpbacks could travel in large groups within the population, so that encounter rate is great enough to maintain dominance relationships. None of the studies published on individual association patterns support such an idea (Gabriele, 1992) Finally, the duration of such dominance relationships may be short-lived and not formed into a stable hierarchy at all. This last alternative seems possible.

Observations of males approaching singers are often characterized as short-lived and agonistic (Tyack, 1981; Darling, 1983). Similar agonistic behavior has been observed in surface active groups composed solely of males (Clapham et al., 1992). These surface

active groups typically consist of multiple males competing for reproductive access to females(Tyack and Whitehead, 1983; Baker and Herman, 1984a),

Though any or all of the above functions may be operating, the complexity of humpback song would appear to be the result of strong sexual selection (Tyack, 1981). Fitness indicator models of sexual selection (e.g., Clutton-Brock and Albon, 1979) propose that variation in a trait (in this case, song) reliably indicates the possession of heritable fitness-enhancing genes. If a component of song serves as a fitness indicator, then females should choose males on the basis of that component.

Underwater Acoustics

Because much of the work discussed here revolves around underwater sound, it is useful to review the major concepts and applications concerning sound underwater. Sound is a propagating sequence of high and low pressure zones, typically produced by a vibrating surface. When the surface moves outward, a compressive wave is created, and when it reverses direction a low pressure (rarefaction) occurs. Very close to the sound source, the particles of the transmitting medium are physically displaced. This defines the near field around the sound projector. There is a transition zone between the far and near fields. The medium particles experience no net movement in the far field (Urick, 1983). Most sound measurements are made in the far field, because the near field is very small (circa 0.5-2.0 meters) and close to the sound source.

It is typical to assume that there is a point source for sound, which radiates uniformly from that point. At increasing ranges from the source, the sound pressure level will be lower. The decrease in sound pressure is described as the transmission loss. In an unbounded medium, transmission loss can be calculated from simple spherical spreading (Urick, 1983). This is referred to as 20*log(range) or "20 log r" transmission loss. If a sound is produced in a bounded layer then it will experience cylindrical spreading, or 10 log r spreading. These generalizations survive until they encounter the real world.

In a real setting, sound waves radiate from the source and encounter layers of differing density. Differences in density, such as a thermocline, will cause sound waves to refract. This explains the deep sound layer, which is a sound velocity minimum. The deep sound layer is found at approximately 800 meters depth near Hawai'i. Warmer water (faster) above the layer causes sound waves to refract back into the layer. Water below the layer under more pressure, which likewise causes an increase in sound velocity, refracting waves upwards. Sound waves radiating at the proper angle will be trapped in the deep sound layer.

When sound waves encounter discontinuous acoustic velocity differences, such as the ocean bottom or surface, they are reflected or absorbed. The angle of incidence and the surface texture and composition affect how or if a wave will be reflected or absorbed. There are a number of models that predict transmission loss, given specific parameters (Harrison, 1989). These work well for deep water situations. In shallow water, there are semi-empirical models that one can use (Marsh and Schulkin, 1962). However, the best approach is direct measurement of the study area.

One particularly difficult aspect of sound measurement is defining measures of amplitude. There are numerous definitions and variations of the term decibel. A decibel is a ratio of pressures (force/area) or intensities (energy/time). It is always the ratio of a measured sound pressure or intensity over a reference (fixed) sound pressure or intensity. These are defined as:

$$dB = 10[\log(\text{Intensity}/\text{Reference Intensity})] \text{ or}$$

$$dB = 20[\log(\text{Pressure}/\text{Reference Pressure})]$$

Most sound levels are measured as sound pressure levels. Measurements in air typically use the 20 μPa reference level while the current underwater sound reference level currently in use is 1 μPa.

Since there are multiple reference levels, it is important to always specify the reference level when providing a dB value. If a source level is being described, it is necessary to state the range as well. Finally, it is important to state the bandwidth over which the sound measurement was taken. Bandwidths can range from spectrum level (1 Hz wide) to 1/3 octave, 1 octave or 'broadband' (typically 20 Hz-20 kHz) measurements. For white noise (constant energy distribution in the frequency domain), the dB level will increase as one increases the bandwidth of the measurement, because more energy is being integrated into the measurement. The relationship:

$$dB = SPL + 10[\log(\text{bandwidth})]$$

provides the value for different bandwidths, where SPL refers to sound pressure level.

Research Questions

The ultimate goal of unraveling the mating system of humpback whales remains distant. The questions asked here represent pieces of the puzzle. Past observations have raised questions, suggestions and hypotheses to be addressed. Most previous studies have relied upon observations of single pods or visual observations of a number of pods in visual range of an elevated shore station. Such work has provided much information, but has not been successful at answering the questions of the function of song.

Several hypotheses concerning song and song function will be addressed in this dissertation. The first is the effect of song upon the spacing of singers. Next, inter-individual variation in song structure will be examined. Finally, an estimate of the acoustic response threshold of whales will be attempted.

Tyack (1983) suggested that humpback song may function to maintain spacing between singing whales. Determining the location and movement patterns of multiple singers simultaneously would allow an examination of the distribution pattern and their movements relative to each other. This should reveal the effect of singers upon each other. This is addressed in chapter 3.

Song has been proposed to function intrasexually as well. If the signal is to carry any information other than location and species identity, there must be differences between individuals. While there have been references to inter-individual differences in song (Payne and McVay, 1971) they have never been quantified. Establishing the levels of difference between individual whales would remove uncertainty in our understanding of whale song and could represent a strong step forward in defining the function of whale song. The issue of individual differences is addressed in chapter 4.

As with variation in song structure, the issue of amplitude of the song has been poorly addressed. Differences in the amplitude of other species signals have been implied as an important cue in female choice of mates (Clutton-Brock and Albon, 1979). The one existing estimate of whale song amplitude is 155.4 dB re 1 μPa at 1 m (Levenson, 1972). This estimate is probably low, based upon empirical comparisons of calibrated loudspeakers and free-ranging singing whales. By locating whales and recording their calls, one can get absolute sound pressure levels and examine the variability in these measurements. Differences in song amplitudes between whales could be related to fitness. This issue is addressed in Chapter 4.

These issues all deal with the production of song and other vocalizations. The other end of the auditory system is hearing. This issue has become important in relation to management of human waterborne actives including boating, shipping and acoustic oceanography. Only one dedicated acoustical study has been conducted with humpback (Malme et al, 1985). Industrial noise was broadcast to humpback whales in Alaska. There was no perceived reaction or change in behavior to these stimuli. Therefore, there are no data on the auditory response thresholds of humpbacks. Experiments conducted with gray and bowhead whales suggest a disturbance threshold of 116-124 dB (Malme et al., 1983; Malme et al., 1984; Richardson et al., 1990).

Playback experiments with a variety of biological and non-biological sounds produced reactions that are clear indicators of detection and reaction (Mobley et al., 1988). These trials can be examined to determine at what received level whales react to these stimuli. It is likely that biological stimuli have a lower response threshold that non-biological stimuli and thus better approximate the detection threshold. This issue is presented in chapter 5.

Chapter 2
General Methods for Data Collection
OVERVIEW

Three seasons of field data were collected from 1989 to 1991. Each field season spanned early January to early April. Most data were collected from a site referred to as "Old Ruins." Old Ruins (20° 05' 00", 155° 41' 48") is located five kilometers NNW of Kawaihae harbor on the Big Island of Hawai'i . The shore station was established at a vantage point 65.6 meters above sea level. There is an approximately 180° view of Kawaihae Bay from the shore station. The shore stations are shown in figure 2.1.

The playback data reported in Chapter five were gathered from both the Big Island and Maui. The Maui shore stations were Pu'u Olai (20° 48' 19", 156° 37' 18") in the Makena district and Kilea pu'u (20° 38' 22", 156° 27' 08") one kilometer inshore from Olowalu point. Pu'u Olai was 143 m high with an approximately 270° view, The Kilea pu'u at Olowalu was 79 meters high and had an approximately 180° view.

An array of three hydrophones was installed approximately 250 meters offshore. The array consisted of three separate sonobuoys moored in 30-35 meters of water. Each sonobuoy had the hydrophone element anchored near the bottom and a cable that connected the hydrophone to the buoy. Each buoy contained an FM transmitter that radioed data to a receiver and data recorder on shore. Acoustic data were collected, when conditions allowed, from morning through the afternoon (typically ~0900 to ~ 1600).
Visual observation sessions were begun when whales were sighted and continued until they left the area or observation conditions (i.e. Beaufort sea state or surface glare) did not allow accurate observation. During an observation session the behavior and movement patterns of whales and vessels were recorded. Whale behavior was observed with binoculars and recorded along with the time of occurrence. Positions were visually determined using a theodolite to measure the angles of declination and bearing. These

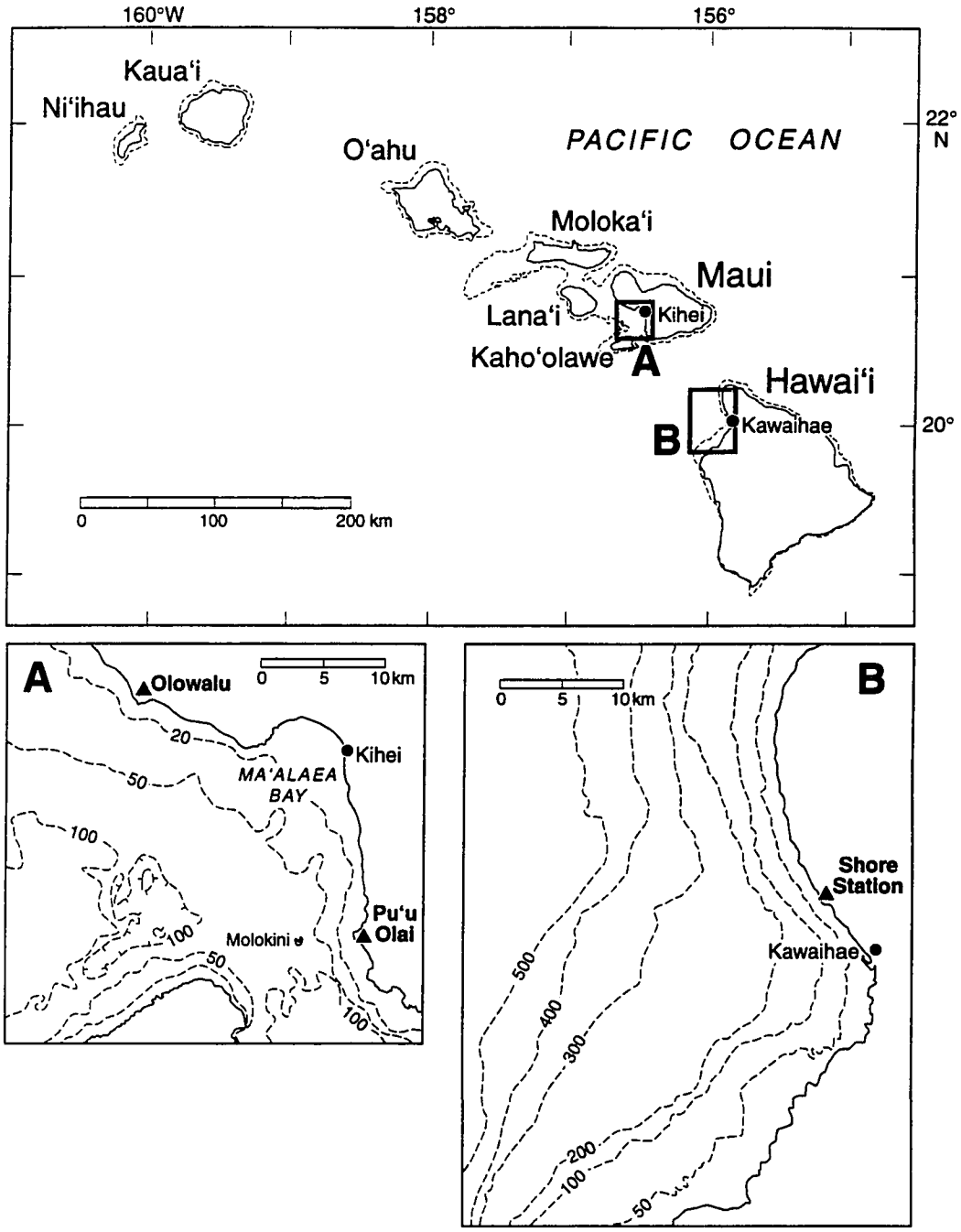

Figure 2.1
Study Area
Area A describes the area surrounding Pu'u Olai and Olowalu on Maui. These areas were used for some of the playback trials described in Chapter 5. Area B in the Kawaihae Bay region where most of the work in this dissertation was conducted.

angles were later converted to Cartesian coordinates. These coordinates were used to construct whale and vessel movement tracks.

Visual Behavioral Observation

The height of the shore station allowed long-range observation of multiple pods, and behavioral observations from shore do not influence the behavior of the whales (Würsig et al., 1990). A maximum range of six kilometers was determined to be the greatest distance that whale behavior could be described accurately. The main goal of the experiment was to describe the interactions of singers with other whales. Therefore a non-focal behavioral observation scheme was used. This procedure sacrificed detailed information on one pod so that information on all pods visible to the observer could be collected. A non-focal ethogram was created to describe behavioral states of pods (Table 2.1). The minimum information collected on each pod included the time that the pod surfaced, its behavioral state and the time that it dove. When possible, individual behaviors were collected. These behaviors were described with a standard ethogram developed previously (Appendix 1; Baker and Herman, 1982).

When whales were sighted, an observation session would begin. Whale behavior was always the first item recorded during an observation session. The theodolite operator would then begin fixing all whales and vessels in the area. The behavioral observer viewed the area with the naked eye or with 7x35 Nikon or 7x50 Bushnell binoculars. The behavioral observer described the behaviors as three-digit codes. The first digit represented the pod number. The final two digits described a behavior or behavioral state (e,g. 112 = pod 1 blow). The behavioral recorder entered these codes into a computer, which time-stamped the entries. Two computer systems were used for this purpose during the study. In 1989, we used a Tandy TRS-80 Model 100. This computer ran a data recording program named Behav.BA. In 1990 and 1991, we used a Toshiba T-1000

running TRSBeast. TRSBeast was able to perform all the tasks of the previous system and had the added ability to use function keys as toggle switches for pod surfacings and dives.

Once initiated, observation sessions continued while observation conditions allowed and while whales remained within visual range. This design was used to maximize the amount of information collected, as opposed to fixed length observations as used in previous studies (Mobley and Herman, 1985; Bauer, 1986). Previous studies with fixed observation lengths were designed for statistical analysis of their observations. These studies were more exploratory rather than for testing specific hypotheses. The unlimited observation time allowed for the possibility of capturing both the interaction of interest and its antecedent conditions.

Visual Theodolite Tracking

Theodolite tracking has been used previously in the study of movements and behaviors of a number of cetacean species, including bottlenose dolphins (Würsig and Würsig, 1979), gray whales (Malme et al., 1983), right whales (Clark and Clark, 1980), and humpback whales (Mobley et al., 1988). The speed and direction of movement of vessels or whales were calculated from a series of positions over time. Positions were determined by measuring the horizontal and vertical angles between the shore station and the whale. These are polar coordinates. The azimuth (bearing) is measured directly and distance is calculated from the angle of declination.

A Topcon DT-20 was used in 1989 and a Leitz DT-5 was used in 1990 and 1991. The Topcon was accurate to 20 seconds of arc while the Leitz was accurate to 10 seconds. The theodolite stations were the same in all years. The altitude of Old Ruins was determined to be 65.6 meters. The theodolite was always used with a wooden tripod and the reference marker for relative bearing angles was the day marker (navigational aid) at Malae Point, approximately 2 kilometers north of Old Ruins. The reference angle between

Malae Point, Old Ruins and True North was 19° 40'. The vertical angle was zeroed referenced to gravity, so that 0° was vertical and 90° was horizontal.

Theodolite "fixes" include the time and the two measured angles. A fix was taken by placing the cross-hairs in the theodolite telescope upon the waterline of a vessel or whale and recording the time and angles. The theodolite can measure the position of a target with a range accuracy of ± 1 m at 1 km and ± 90 m at 10 km (Bauer, 1986). The vertical and horizontal angles of the fix were later converted to x-y coordinates.

In 1989, fixes were recorded by hand onto a form and later entered into a computer using SightlogPC, a custom program to enter and store theodolite data. In 1990, fixes were recorded electronically using a cable connecting the theodolite data port to the serial port of a Tandy TRS-80 Model 100 computer running Theo.BA, a program written to store the theodolite data to a file. In all years, theodolite data files were converted from angles to X-Y data by another program, SightstatPC. The main algorithm concerns the conversion of measured relative bearing angles to compass bearings relative to true north, and the calculation of range from the angle of declination, accounting for the curve of the earth.

Fluke Identification Photography

Whales were photographed opportunistically throughout the study. Recognition of a whale as an individual is made possible by comparing the distinctive coloration patterns found on the ventral side of the tail flukes (Katona et al., 1979).

Two vessels were used to obtain photographs: a 17' Boston Whaler and a 16' Zodiac Mk III GT. Canon AE-1 and A-1 cameras with motor drives or power winders and 300 mm f/5.6 telephoto lenses were used with Kodak Tri-X, TMax 400 or Ilford XP1 black and white film. Vessels followed behind or to the side of pods and approached to photograph the flukes of the whales as the whales dove. Descriptive data was recorded on pod master data sheets and entered into a daily log. Individual photographs were selected from contact sheets, and 3x5 inch prints were made. These prints were matched against the

University of Hawai'i photographic database (Perry et al., 1988). When the animal was matched against another whale in the catalog, it was said to be identified. Examination of the individual whale's resighting history can reveal the sex of the whale (Glockner, 1983; Glockner and Venus, 1983). Behavioral and social indications of sex include the presence of a calf, which identifies the adult as a mother. Observations of the individual singing or escorting indicate that the whale is male (Lambertsen et al., 1988; Clapham et al., 1992; Medrano et al., in press). Such information can be used in interpreting behavioral interactions between whales.

Acoustic Location

Physical Description of the Array

A linear three-element hydrophone array was used. The array was 2.1 km long in 1989 and 2.4 km long in 1990. Each element was a moored buoy. Mooring sites for the buoys were in 25 meters of water the first year and 30 meters of water the following years. Moorings were installed by SCUBA divers into sand patches to prevent damage to coral reefs. The positions were also chosen so that the buoys would have line of sight for transmissions to the shore station. The geometric positions of the hydrophones were determined (estimated error = $\pm$ 3-4 m) with a theodolite.

Each element consisted of a sonobuoy constructed of a ballasted PVC shell containing a Johnson gel-cell battery pack, a Sippican, Inc. FM transmitter, a Tandy VHF 20-176 antenna and a connector for the hydrophone cable. The buoy was moored in approximately 30 m of water. As shown in Figure 2.2, the mooring rig consisted of 1 or 2 Danforth-type or treble hook anchors connected to two meters of 3/8" chain that then connected to a 6.1 meter line running along the bottom. This line was shackled to one or two 45 kilogram cement blocks. A 45.7 meter surface line ran from these blocks to the sonobuoy. The concrete blocks were initially intended to prevent surface action from lifting the anchor. However, the concrete weights proved to be the most effective anchor.

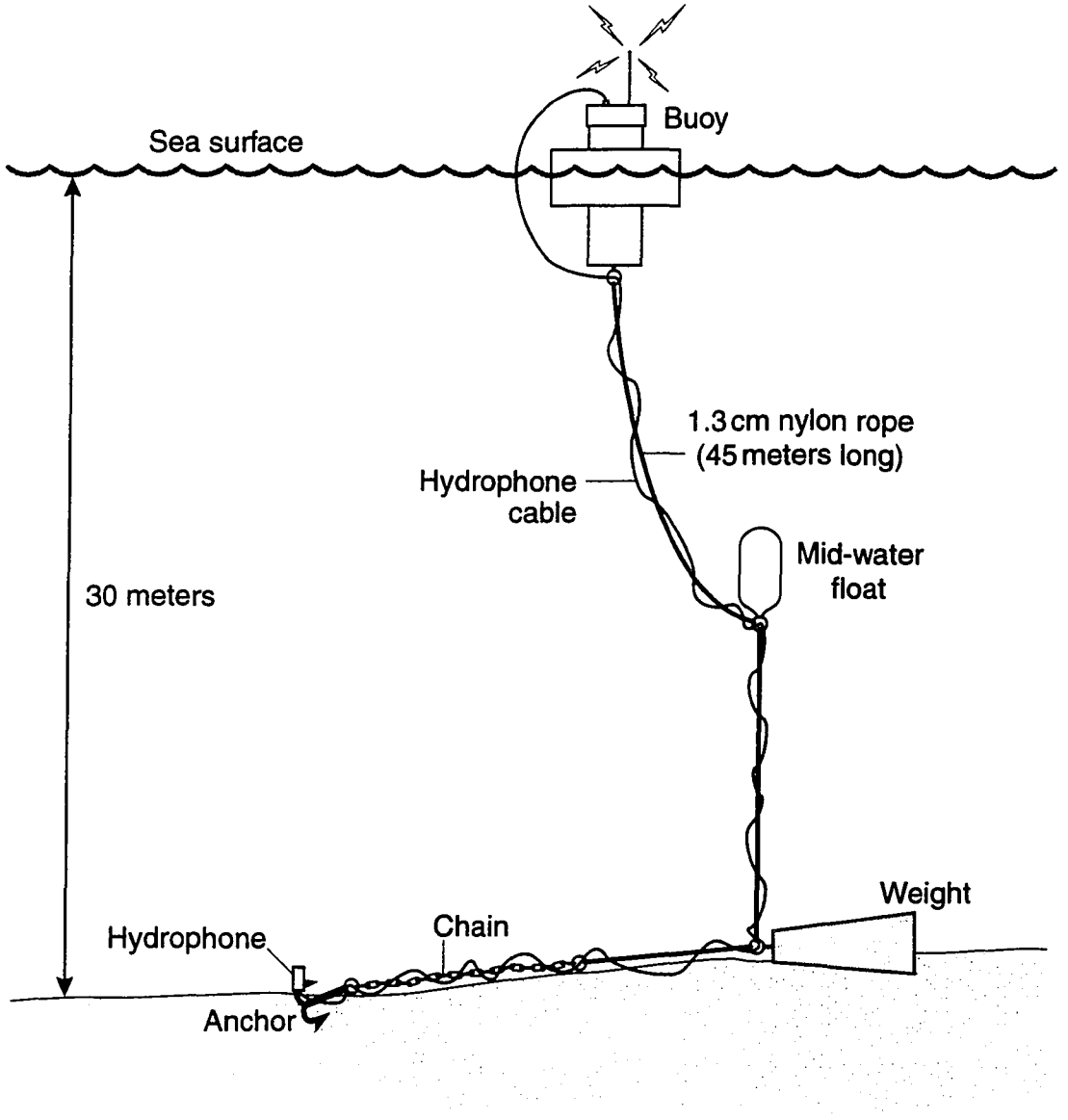

Figure 2.2
Buoy Rig
A sonobuoy mooring rig is depicted. The locations of the hydrophone, physical mooring components, and surface buoy are shown. The signal from the hydrophone entered the top of the buoy, which contained a batterey and an FM transmitter that radioed the signal to shore.

The hydrophone cable exited the top of the buoy, ran along its side and attached to the mooring line below the buoy. The cable ran down the mooring line. Once it reached the concrete blocks, it continued out to the anchor. In 1989, the hydrophone element was suspended in the water column with a small float approximately 3 m above the bottom. Water-current induced cable fluttering caused us to move the hydrophone element for the 1990 season, when it was tie-wrapped to an upright anchor-tine, eliminating the cable flutter.

Signal Transmission

Sounds received at the hydrophones were carried by the cable to the FM transmitter, which transmitted them a four-channel receiver onshore. The recording level was adjusted in 10 dB steps with a custom built multi-channel audio monitoring system. Data were recorded with a TEAC R-61D cassette tape recorder using Ampex normal bias cassettes. The data recording system was similar to that described by Clark et al. (1986a). Tapes were made throughout the day, while the station was manned.

Signal Acquisition and Location Method

To calculate the location of a whale, the array geometry, speed of sound and differences in arrival times must be known. The first two variables have been discussed. Arrival times were calculated using two different sound analysis workstations based upon a DEC PDP-11/23 and an Apple Macintosh Quadra 800. The DEC PDP-11/23 computer ran Whale software (Clark, Ellison and Beeman, 1986a). The multichannel tapes are played back on a TEAC R-61D connected to Frequency Devices 901 anti-aliasing filters that then connect to an ADAC analog to digital converter in the PDP-11. The signal from each channel is stored separately in a circular buffer. The operator listens to the tape and when selecting a signal to localize, hits the return key to acquire the sound in the buffer.

The Whale program then generates and displays a sonogram for each channel. Sonograms were produced by a series of 100 Fast Fourier Transforms (FFTs). The FFTs

are displayed sequentially along the time axis and the strength of each frequency band was represented as brightness on the screen (see figures 4.1-4.3). Spectrograms had a frame size of 256 ms and a FFT size was 256 points. The overlap was 99% and a rectangular window was used.

The signal is selected by inputting the time and frequency range that encompasses the signal in all three channels. This procedure reduces the amount of data to be cross-correlated and removes noise from the signal. A cross-correlation algorithm was used to measure the differences in arrival times of each signal. Cross-correlation is a technique that correlates both numerical matrices that represent the two sounds being compared. The procedure begins with a minimal (~1%) overlap of the two matrices, the end of the first matrix overlapping the beginning of the second. A spearman correlation coefficient is then calculated of the overlap area. The overlap is then increased by a small increment and the correlation repeated. The resulting function is the correlation values plotted against overlap. The peak in the correlation function represents the best agreement between the two matrices. The time offset value at the peak is the delay in arrival times.

The Apple Macintosh system was composed of the Macintosh with two Cornell expansion boards. The first is the Dare board, which is a digital signal processing board. The second is a Mallard board, which is an interface to control a TEAC RD-130T or RD-135T digital data recorder,. The TEAC uses standard digital audio tape (DAT). The earlier analog recordings were re-recorded onto DAT for use with the Macintosh system. The digitized signals were acquired and processed at Cornell Laboratory of Ornithology's Bioacoustics Research Program facility using a customized signal processing workstation operating an advanced version of Canary software (Charif et al., 1993). This signal processing package acquires and analyzes sound samples. As the tape is played into the Macintosh system, it produces sonograms of the sounds being input. The window displayed 30 seconds of sound at the 4.0 kHz sampling rate.

Signals were selected with this system by stopping the playback and highlighting the sonographic representation of the sound with the mouse. These signals were then exported to a standard Canary file. The highlighted window can be moved independently in each channel to select just the signal with a minimum of nearby noise. The exported Canary file can be filtered to eliminate energy at frequencies above and below the signal that might affect the cross-correlation. The cross-correlation procedure in Canary measured the same difference in arrival times as the DEC system.

A three-element array produces three time delays (1-2, 1-3, 2-3). Each of these time delays can be used to generate a hyperbolic pointing line. The whale could be anywhere along this hyperbola. When three hyperbolae are generated, the intersection represents the location of the whale (see Figure 2.3). There is a possible ambiguity in location since the hyperbolae extend to both sides of the array. This ambiguity is resolved by locating the array close to the shoreline. Further details of the location algorithm are given by Ellison et al. (1986). With this procedure, sounds from many different animals can be located, even when several were vocalizing simultaneously (Clark et al., 1986; Frankel et al., 1989).

Calibration

Two procedures were used to calibrate the array. Sound playback calibration confirmed the speed of sound in water in Kawaihae Bay. The accuracy of the acoustic location method was determined by comparing the positions of visually fixed singers with their acoustically computed locations.

Theodolite fixes were use to determine the location and distance between the three hydrophone array elements. The Boston Whaler was positioned near one buoy of the array and a U.S. Naval Research Laboratory J-9 underwater transducer was lowered to seven meters depth. A Marantz PDM-430 tape deck was connected to a preamplifier and an AB Systems amplifier that powered the J-9. This system was used to broadcast a 100-300 Hz

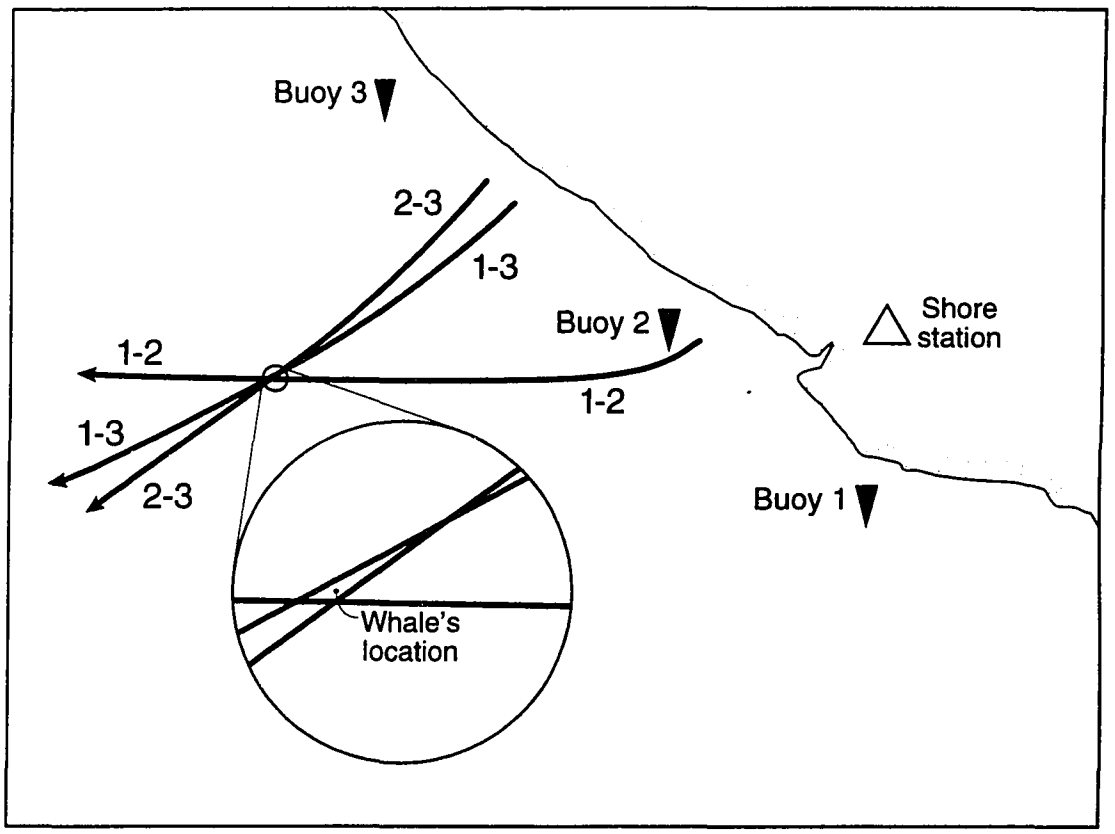

Figure 2.3
Intersection of Three Parabolic Lines.
Differences in arrival times of a whale's signal at a pair of hydrophones can be used to produce hyperbolic pointing lines. The intersection of the three hyperbolic pointing lines represents the location of the whale.

frequency sweep. This sound was recorded on both the near buoy and the next buoy in the array. Recordings of these calibration sessions were later analyzed to determine the time delay between the two buoys. The distances between each pair of buoys was divided by the time delays to give the speed of sound in water.

The reliability of the acoustic location method was determined by comparing acoustically and visually determined locations of singers. Acoustic and visual tracks of two singers were compared at ranges of 3-4 kilometers. The discrepancy between the two techniques was 0.7 degrees for bearing and 3% for range.

There is some error in both the visual and acoustic techniques. The bearing accuracy of the theodolite is largely unaffected by range, but is subject to operator initialization error (i.e., not leveling the instrument correctly). Theodolite range accuracy decreases with increasing range because of the decreasing declination angle. This error is small. A worst case scenario, assuming a one-meter swell and a possible +/-10" error in measurement, produced a total range error estimate of 70 meters at a range of 6 kilometers. In most situations, the error would be less.

Acoustic location errors are estimated by the length (parallel to the bearing) and width (perpindicular to the bearng) of the triangle formed by intersecting hyperbolic pointing lines. The length of the triangle represents the range error and the width represents the bearing error. In general, bearing error remains reasonably low at distances up to 20 km. The range estimate becomes unreliable at distances greater than four times the overall length of the array (Carter, 1987).

ANALYSIS

The acoustic location analysis produced a dataset of x - y coordinates and time of occurrence, similar to the theodolite data. Acoustic locations were plotted to visually check the assignment of individual locations to whales. Whales that were repeatedly located at ranges greater than 10 km with the same bearing were represented by the single location

with the smallest range. Thus, these whales are represented by a single point, with the minimum calculated range. These locations were only used in the depth preference analysis. Singers with calculated ranges of more than 20 km were deleted from the analysis. Specific analyses of these data varied with each project and are reported individually in chapters 3-5.

Sound Propagation

In any acoustic study it is important to understand the transmission loss in the study area. The propagation of sound in shallow water is a complex phenomenon. The seafloor and the surface both serve as wave scatterers and reflectors. Their contribution as a scatterer or reflector is dependent upon bottom composition and sea state. Flat seas and hard flat bottoms are excellent sound reflectors while sandy bottoms and stormy sea surfaces are poor sound reflectors.

These factors make it difficult to predict the transmission of sound in shallow water. There are semi-empirical equations for predicting transmission loss under these conditions (Marsh and Schulkin, 1962). Empirical determination is a far more accurate way to assess transmission loss.

A calibration experiment was conducted in 1989. Frequency sweeps were played back from a vessel to the array to verify the speed of sound and to examine transmission loss. Sinusoidal frequency sweeps from 100 to 300 to 100 Hz were used as the signal because they produce accurate cross-correlation functions. The difference in arrival times were determined by cross-correlation. The distance between hydrophones was divided by this time to determine the speed of sound in water.

The vessel's position was measured by theodolite during each broadcast. The ranges from the vessel to the hydrophone were then determined. Playbacks were conducted at various ranges and bearings from the three-element array. Playbacks were conducted on two different days (9 February 1989 and 11 March 1989) and were recorded with shore

based equipment with a step attenuator (Clark et al., 1986). The sea state during these calibration experiments was between a Beaufort 2 and 3. Similar conditions were present during all of the observations reported here.

The analog recordings were re-recorded onto a TEAC RD-135T DAT deck in 4 channel mode. The digitized signals were acquired using a custom version of CANARY software. A 4.0 kHz sampling rate was used. Sonograms were made of the signals with an analysis bandwidth of 21.48 Hz. The peak amplitude of the 300 Hz band was measured from the sonogram. The measurements were adjusted according to the recording gain. The resulting amplitudes were plotted against the range between the playback vessel and the receiving buoy, producing an empirical transmission loss curve for Kawaihae Bay.

This curve was compared to a curve derived from the Marsh and Schulkin semi-empirical model described in Urick (1983). This model has three different transmission loss (TL) equations for different water and layer depths and operating ranges. The comparison of the range and the calculated value H determines which equation is appropriate.

$$H = \text{sqrt}\ [\ 1/8(D + L)]$$

Where D is water depth in feet, L is the layer depth in feet and H is in kiloyards. A water and sound layer depth of 75 m were used. The value of H determined by these variables was 7.8 km. Because the ranges that we were operating in were less than that, the shallow water equation for transmission loss in dB was used.

$$TL = 20 \log r + \alpha r + 60 - k_L$$

where r is range in kiloyards, α is the absorption coefficient, and k_L is the "near-field anomaly." The α value used was 0.1 and the k_L value was 6.1, which represents a rocky bottom with a sea state of 2.

Table 2.1

The behavioral states of all visible pods were described for each surface sequence of that pod with the following definitions. Whale speeds included in these definitions were estimated in the field.

Stationary:	Behavior characterized by little or no movement between blows and divetimes less than 5 minutes
Singer-like:	Behavior characterized by little or no movement by a single whale with divetimes greater than 10 minutes
Slow swimming:	pods of any size moving at 1-2 km/h or less.
Typical swimming:	Pods swimming between 2 and 6 km/h.
Rapid swimming:	pods of any size moving at 6 km/h or more, including those whales which produce bow waves.
Low level agonism:	Behavior including bubbling, low intensity headlunges.
High level agonism:	Behavior including inflated and strenuous headlunges, striking another whale with any body part, or peduncle slaps
Affiliations and disaffiliations	Joining or leaving a pod.
Movement changes:	Obvious changes in speed and direction.
Respiration:	The time of surfacing and submergence. In the absence of a fluke up dive, dives were defined as any submergence longer than 60 seconds.
Aerial behaviors:	Aerial behaviors without defined function, including pectoral fin slaps, fluke slaps, breaches, unidentified splash/leap, head slaps

Chapter 3
Habitat Utilization and Social Interactions
INTRODUCTION

Song is primarily produced in the wintering grounds, but is occasionally heard in the late fall in high latitudes or along the migratory route (McSweeney et al., 1989; Clapham and Mattila, 1990). The common occurrence of song within a presumed reproductive context supports the idea that singing is a component of the humpback mating system. Some investigators have proposed that the broadcast of song may be a sexual advertisement to females (Payne and McVay, 1971; Winn and Winn, 1978; Tyack, 1981). Song may also establish or maintain space between potentially competing males, (Winn and Winn, 1978; Tyack, 1981; Mobley et al., 1988). Baker and Herman (1984) proposed that song may also serve to synchronize ovulation in females. Playback experiments and natural observations have shown that very few whales approach the playback of song (Tyack, 1981; Tyack, 1983; Mobley et al., 1988). Although song may advertise the presence of a male, it does not appear to attract other whales.

Previous attempts to address these questions have utilized visual observations or analyses of recordings of individual whales (Tyack, 1981; Mobley et al., 1988). The acoustic location procedure employed in this study records the vocalizations and directly determines the locations of the vocalizing whales. When used in combination with visual tracking, acoustic location allows simultaneous observation of whale surface behavior, movement patterns, vocalizations and social affiliations. The combined acoustic and visual techniques provide the opportunity to observe whale behavior both underwater and at the surface, potentially offering new insights into the social behavior of humpbacks.

Several whale and dolphin species have previously been studied with acoustic location techniques (Watkins and Schevill, 1972; Watkins, 1974; Norris and Dohl, 1980;

Clark, 1983; Clark et al., 1986a). For example, acoustic location has revealed that bowhead whales travel under the ice and are often further offshore than originally believed, at distances where they can be heard but not seen (Clark et al., 1986a; Clark and Ellison, 1988). Additionally, through the application of passive acoustics arrays, the population size of the Bering-Chukchi-Beaufort stock of bowheads has been shown to be much larger than indicated by earlier visual censuses (Zeh et al., 1993). Acoustic tracking of bowheads also revealed that these animals produce calls that may help them navigate through the ice (Ellison et al., 1987; George et al., 1989). Finally, acoustic locations have shown that bowhead singers have two distinct 'voices,' which indicates that bowheads either sing in closely spaced pairs or that a single bowhead produces two harmonically unrelated sounds simultaneously (Clark et al., 1990).

In this paper, I report on the use of passive acoustic location techniques in combination with more traditional visual techniques to study humpback whale behavior on the wintering grounds of Hawai'i.

METHODS

Overview

This research represents the synthesis of data from several techniques: shore-based passive acoustic location (Clark et al., 1986b), visual observation and theodolite tracking (Tyack, 1981). The three shore-based techniques were conducted simultaneously and were described in Chapter 2. Observations were conducted from 0800 to 1700 daily, when weather and ocean conditions permitted.

Analysis

The acoustic location analysis produced a dataset of x - y coordinates and time of occurrence, similar to theodolite data. These locations were plotted to visually check the assignment of individual locations to whales. The initial individual assignment was based upon the similarity of bearings, ranges and difference-in-arrival times.

Singers up to 20 km from the shore station were used to examine spatial distribution. Singers at ranges of less than 10 km were represented by the mean of all the acoustically determined locations. Singers located at ranges from 10 - 20 km were represented by the location with the shortest range. Locations were converted to latitude and longitude and compared to a database of the bathymetry of Kawaihae Bay. The depth of water at each singer position was determined from the bathymetry database and the mean and median depth values were calculated.

Inter-individual separation was measured for singers at ranges less than 10 km. Pairs were examined for the first hour that they both were tracked. The data were divided into 20 minute time bins or segments. The mean position for each whale was calculated from all its locations for each time segment. The separation between all combinations of pairs of singers was calculated for each time segment. Separation between each pair of singers was plotted against time. Initial and final separation for each pair was measured. Change-in-separation was regressed against initial separation. The relative bearing from one singer to another was also measured. Four relative bearing classes were used: toward (315°-45°), parallel (45°-135°), away (135°-225°) and anti-parallel (225°-315°). The distribution of angles was examined with a chi-square test (Zar, 1974). The expected values used were the sample size divided by 4, so the test examined for departure from random relative orientation.

Whale speed was calculated for all singers within 10 km of the shore station. A speed estimate from acoustic data was determined by the dividing the total distance covered by the total time elapsed. This probably produced a slight underestimate, but most singer tracks were nearly linear. A different technique was used with the visual data. The weighted mean and the median value were calculated from each individual leg. These were weighted by the elapsed time between locations, so that the shorter, more error prone legs would contribute less to the value. Legs shorter than 90 seconds were eliminated.

RESULTS

Combined visual and acoustic data were collected during January through March in 1989 and 1990. A total of seventy-six visual observation sessions were conducted, and 280 hours of acoustic recordings were made. Forty-five hours of acoustic data were analyzed for acoustic locations, and a total of 62 singers were located.

Spatial Distribution and Water Depth

Figure 3.1 shows the spatial distribution of all 62 singers located during the study. As shown in Figure 3.1, singers were found in water depths ranging from 10.4 fathoms (19 m) to 305 fathoms (558 m). The mean water depth was 126 fathoms (230 m), the median water depth of singers was 109 fathoms (199 m) and the standard deviation was 72.98 fathoms or 133.5 m (N=62). Singers were located from 400 m to 12.9 km from the shoreline. The mean offshore distance was 4.44 km (S.D. = 3.03) and the median distance was 3.76 km.

Although whales were found throughout the bay, their distribution did not appear random. As shown in Figure 3.1, a 120° sector was drawn over the study area, representing the theoretical range of operation of the array, or the "arena." The centerline in the middle of the arena was perpendicular to the axis of the array. The sector was divided with radii of 8.66, 12.25 and 15 km., which subdivided the arena into six equal areas of 39.2 km^2. A few whales had mean locations just outside these areas, and were included in the nearest section. Comparing the two sections closest to shore showed 15 singers in the northern sector and 16 in the southern. Thus there was no north-south difference in distribution in the nearshore area. The mid-range sections had five singers north and 13 to the south. Finally, in the furthest offshore area, there were none to the north and 13 to the south. It is relevant to note the higher proportion of shallow water in the southern portion of the arena. Thirty-one of the 62 singers located were offshore of the 100 fathom isobath.

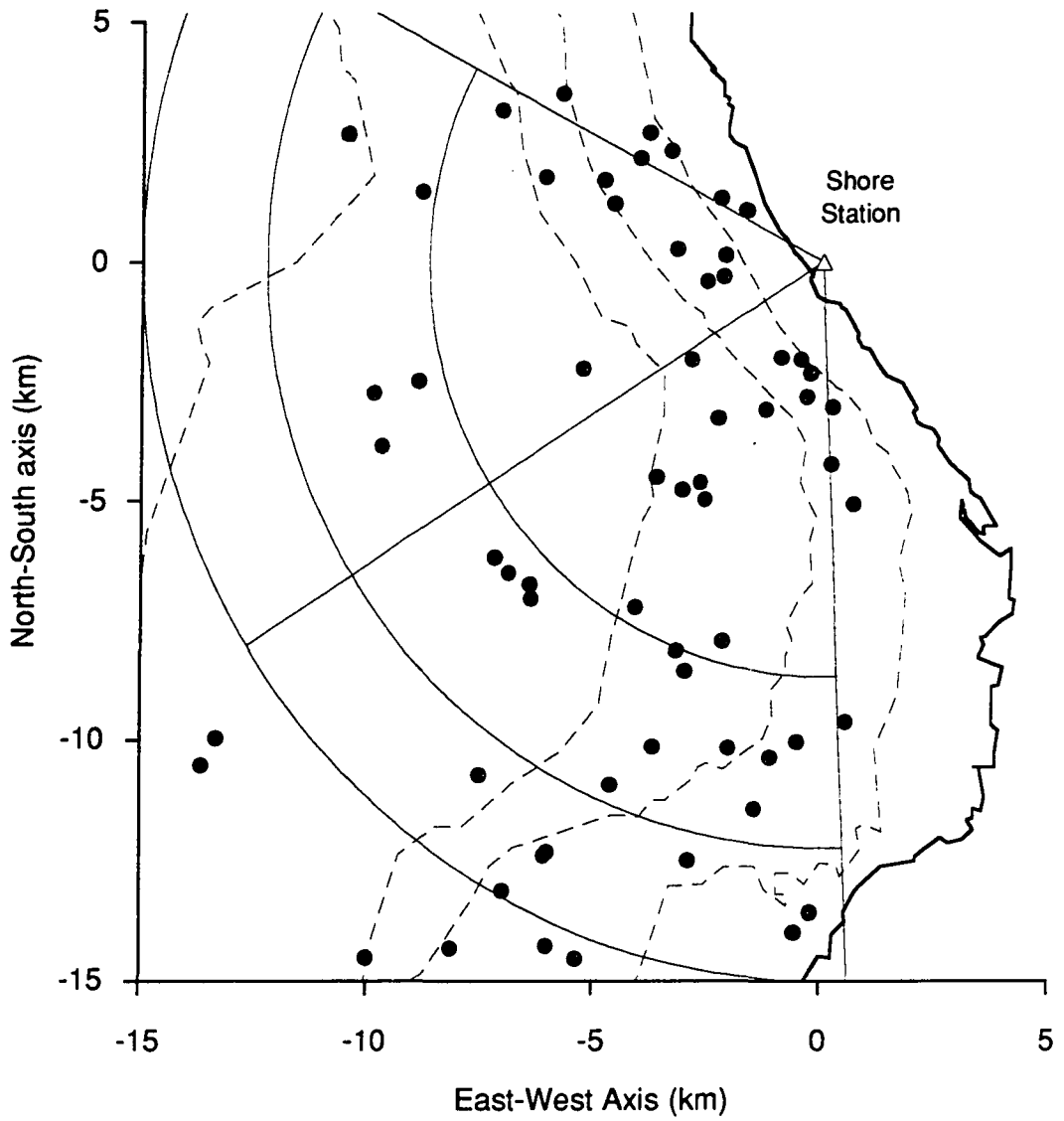

Figure 3.1
Mean Location of Singers

The three radii correspond to 8.6, 12.6 and 15 km, dividing the area into six equal area sections. The dots indicate the mean positions of the 62 singers located in the study

The circular sector representing the arena had a total area of 235 km^2. The amount of area within the 100 fathom contour was 50 km^2 and the remaining offshore area was 185 km^2. Thus the density of whales in the nearshore area was higher than the offshore area (0.62 singers/km^2 v. 0.17 singers/km^2). It is important to remember that this figure is a collection of locations, so these density figures are only for comparison of onshore v. offshore habitat utilization. While most singers are located near shore, there are a substantial number of singers in the offshore, deep water environment. Singers in very deep water are presumably in a different acoustic environment than shallow water singers. Important acoustic differences may include transmission loss, ambient noise and signal degradation.

Inter - Individual Separation

Separation distances between 19 singers forming 21 pairs were judged sufficiently reliable to analyze. All separations are based upon the first hour that the pair of whales was tracked. The mean initial separation was 6.6 km (S.D. = 2.9) with a median value of 6.0 km. Change-in-separation between singers was regressed against their initial separation. Figure 3.2 shows that there were more movements away from another singer than toward (10 v. 6). And that approaches did not occur at ranges less than 4 km. One pair maintained a 2 km separation. Increases in distance began at 3 km. There was a negative relationship between change-in-separation and initial separation [$F(1,19) = 5.683$, $p < 0.05$] Singers closer to another were more likely to move away and those further away were more likely to approach. The general pattern is that singers are more likely to move away from another singer. This is supported by the relative bearing data shown in Table 1. Fifteen singers were oriented away from singers as opposed to four that were oriented toward another singer. This was significantly different from random orientation (Chi-square (3) = 11.41, $p < 0.01$).

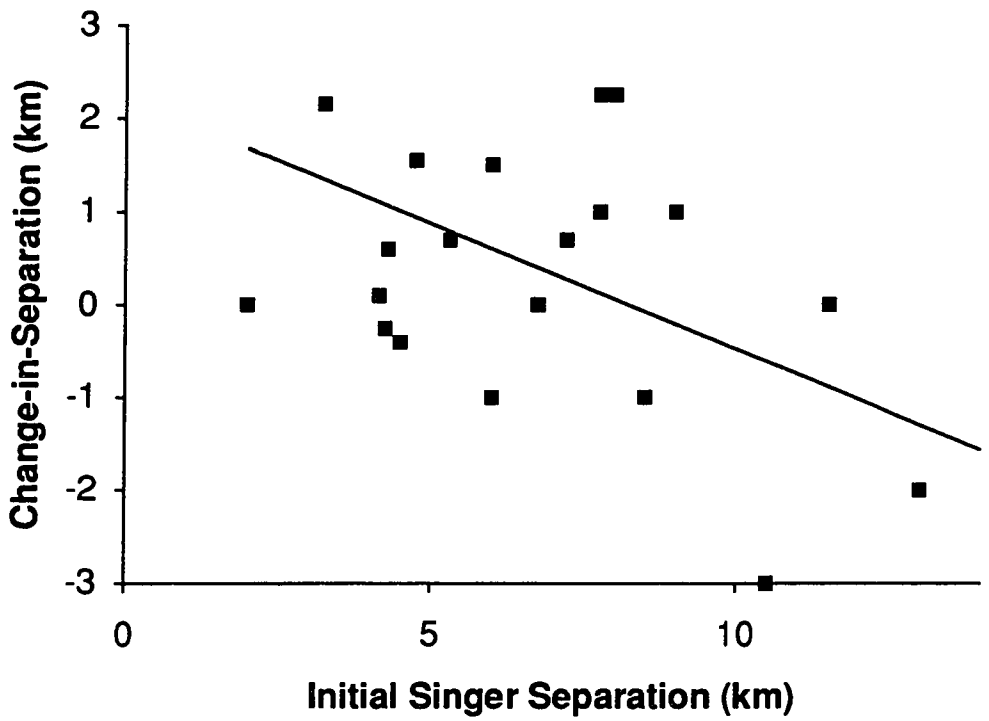

Figure 3.2
Inter-Individual Spacing

The change-in-separation between singers over a one hour period as a function of their inital separation. Note that no decrease in separation occur at ranges of less than 4 kilometers.

Table 3.1
Relative Singer Bearings

The table shows the distribution of relative angles between singers. The distribution was significantly different from random [Chi-Square = 11.41 ($p < 0.01$)] indicating that singers predominately orient and move away from other singers.

Relative Bearing	N
Toward (315°-45°)	4
Parallel (45°-135°)	4
Away (135°-225°)	15
Anti-parallel (225°-315°)	6

Moving Singers

Several singers were moving while singing. The speeds of singers located within 10 km of the shore station were calculated from the first and last acoustic location of each singer. This was done to minimize the effect of error in position measurement. Thirty-one singers were used to produce acoustically derived speeds with a mean of 1.6 km/h (S.D. = 1.03) and a median value of 1.2 km/h. Swimming speeds were also estimated from the visual data. Median and means weighted by the time interval between successive locations were calculated. Time was used as a weighting factor because short legs tend to have a greater percentage of measurement error. Speeds derived from visual data were higher than those from the acoustic tracks. The median speed was 1.4 km/h and the weighted mean was 1.8 km/h (N = 12 whales).

It is possible that some of the observed movements of singers may have been the result of passively drifting with the current. Shallow current meters (< 20m deep) placed nearby reported a median current speed of 1.13 km/h (NODC database). Direct

observation of the currents showed that they were primarily parallel to shore. Nevertheless, other singers showed clear signs of actively swimming. On several occasions, singing whales were observed to transit the hydrophone array quickly. These whales were probably singing and swimming. Other singers were observed moving with other whales. Four singers were tracked simultaneously on March 24, 1990 (Figure 3.3). One of the singers (pod C) first swam parallel to the shore and then moved directly offshore. Current flow in the area is primarily tidal and parallel to the coastline, both northerly and southerly. Since this track is perpendicular to current flow for at least a portion of the track, it seems likely that the moving singers were actively swimming rather than passively drifting in the current. Furthermore, on the same day, two singers in relatively close proximity were tracked simultaneously moving in opposite directions: Pod B was tracked moving north and pod D was moving south. Therefore not all singer movement can be passive drifting with the current.

Singing was occasionally observed in multiple adult pods. Of the 71 pods that included a singer, one was a dyad, two were in trios, and one was a pod of four animals. The 71 pods include the 62 observed from shore and nine singers observed only from the boat. These observations mirror those of Tyack (1981) who found 91 lone singers, three in dyads, one in a trio and no instances of a singer in a group of four whales.

Case Studies of Social Interactions

The first observation describes a singer's approach and affiliation with a singleton. At 12:50 on February 26, 1989, we sighted a single whale (pod 4) when it breached while swimming north along the coast from the southern portion of the array (Figure 3.4). It was first visually positioned at 13:13. This whale breached again and performed a series of flukeslaps at 13:20. At 13:36, another whale joined pod 4, and they swam northwest until 13:55, when only one whale was seen again. This whale was tracked until 14:46. This appeared to be a routine affiliation between two adults. When the

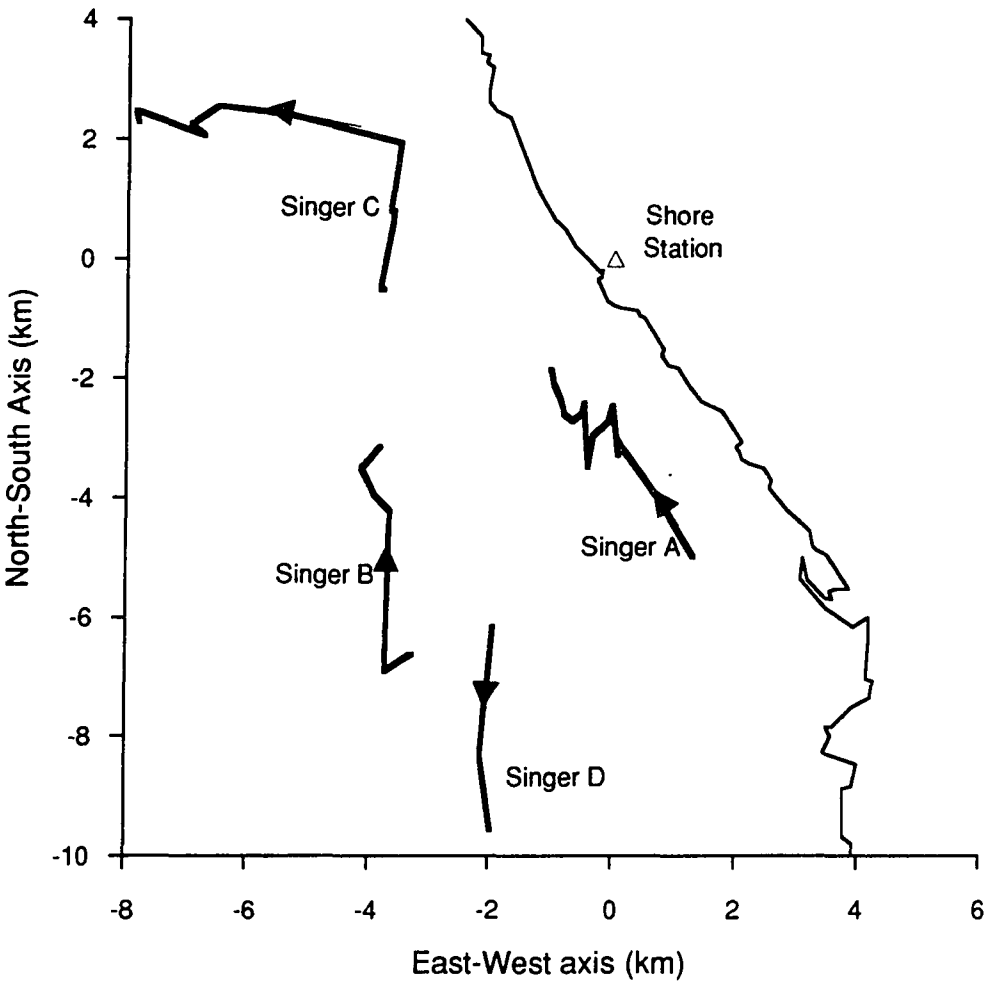

Figure 3.3
Four Simultaneously Moving Singers

Four singers are simultaneously moving in different directions.
The implication is that some singers are actively swimming while singing.

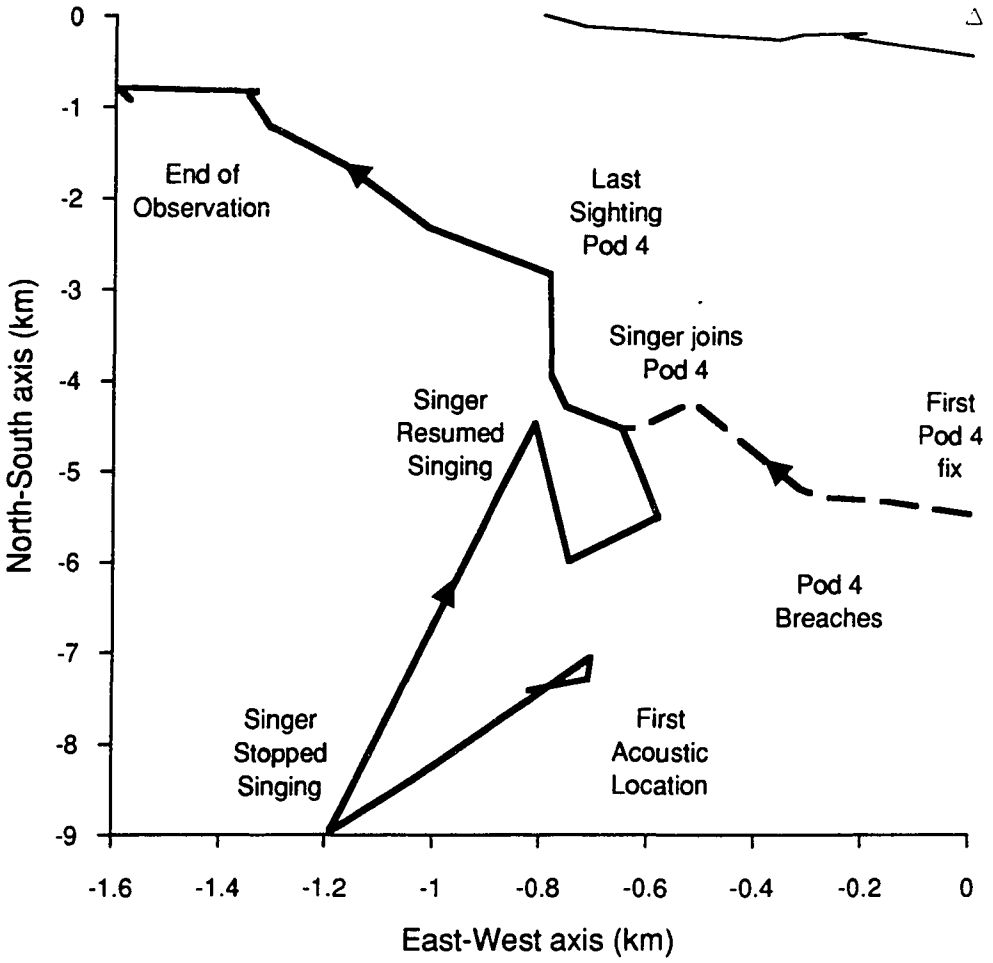

Figure 3.4
Affiliation of a Singer with another Whale

The singer is shown approaching and affilating with Pod 4.

acoustic location data were added to the visual data, an entirely different picture emerged: A relatively stationary singer was detected acoustically at 11:40. It stopped singing at 12:44 for fourteen minutes, and it resumed at 12:58 while swimming at 3.6 km/h. Pod 4 breached (13:20) as the singer approached. The acoustic data indicated that it was the singer that joined with pod 4 at 13:36. The singer continued to sing for the short duration of their affiliation, which apparently ended by 13:55. The then solitary singer was tracked visually and acoustically as it swam along the coastline.

This example demonstrates how the combination of acoustic and visual data produces a more complete description of a social interaction; in this case a singer joining a lone adult and continuing to sing. This type of interaction has not been reported previously.

On March 8, 1989, a single whale affiliated with a singer (Figure 3.5). The singer (pod 1) was sighted to the south of the shore station at 10:20, swimming north along the coastline while singing. Meanwhile, another singleton (pod 2) was approaching from the north. The two whales joined at 10:58, and the singer continued to sing as they swam north until 11:28. They then reversed course 180 degrees and swam southeast together. They disaffiliated at 12:02. Pod 1, the singer, continued south until 12:11 and then turned and rapidly swam north, resuming its northerly travel. Pod 1 continued to sing throughout the affiliation. Pod 2 was last seen heading north and away from pod 1, when it was lost from view. Similar to the previous description, this observation presents an example of a singer affiliating with an adult and continuing to sing.

While pod 1 continued to sing throughout the course of the affiliation, it did not sing continuously. On two occasions the pod was closely approached by vessels. In both cases the singer stopped singing for a short period of time (< 15 min.), indicating that vessel approach may affect singing.

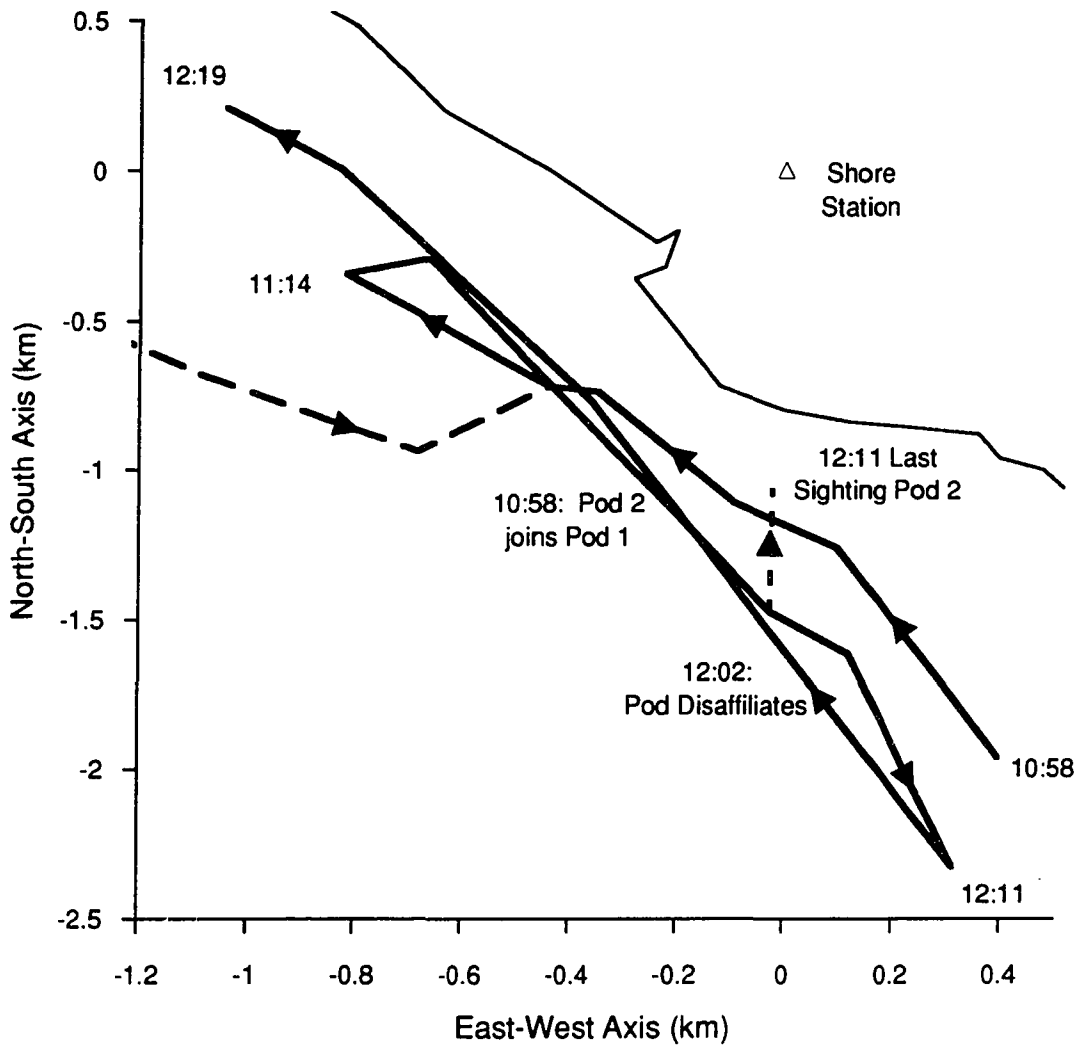

Figure 3.5
A Whale Approaches and Affiliates with a Singer

A whale is shown to approach and affiliate with a singer

Non-vocal Acoustic Communication

On January 21, 1989, two singing whales were heard when only two hydrophones were operating. One whales was north of the array and the other was to the south. Neither whale was seen. Suddenly, a whale breached north of the observation station and both whales stopped singing almost immediately. After about 1-2 minutes, the southern singer resumed singing, followed by the northern singer 30 seconds later. It is not known if the whale that breached was one of the singers. Additionally, on February 26 (Figure 3.4), pod 4 breached before and during the approach of the singer. It is possible that the observed changes in behavior were in response to the acoustic signal of the breaches.

DISCUSSION

The combination of acoustic location and visual tracking methods has revealed several interesting social interactions between singers and other pods that could not have been observed using either method alone. Acoustic location data not only enhance but alter the conclusions that would have been reached from purely visual observation. The results suggest the need to revise the traditional interpretations of singing humpback whales as obtained from visual observations alone.

Habitat Utilization

Humpbacks are a coastal species while on their wintering grounds(Herman and Antinoja, 1977). Their distribution has been described as restricted to shallow water within the 100 fathom contour line (Herman and Antinoja 1977; (Chittleborough, 1953; Winn et al., 1975). Forsyth et al. (1991) found that whales in the Penguin Bank and Maui regions were located in a mean depth of 51.4 fathoms. Recent aerial survey data showed that 74% of all pods were seen in waters less than 100 fathoms (Mobley et al. 1994). This generalization may hold for many age and sex classes; however, the distribution of singers off the Kohala coast of the Big Island appears to differ from the generalized pattern.

Singers were found throughout the bay. No dense aggregation of whale locations were observed. Singers were located at least 12.9 km offshore and in water up to 300 fathoms deep. The measurable offshore distance is limited by the functional range of the hydrophone array (Carter, 1987). Many whales were heard during the analysis at calculated distances of greater than 20 km on offshore bearings from the array. While these whales cannot the accurately located, it does suggest that singing whales may be found further offshore than 12.9 km. Fifty percent (31/62) of singers were located in water deeper than 100 fathoms. This is a significant depature from expected frequencies if 74% of all pods are found within the 100 fathom contour ($\chi^2(1)=18.57$, $p < 0.05$). This indicates that while singers are found close to shore, there is a higher proportion of singers found in deep water than other classes of whales.

While an equal number of singers were found within and outside of the 100 fathom isobath, the densities were not equal. The area of water with depths < 100 fathoms that was covered by the array was 50 km^2. The offshore area was 185 km^2. Converting to densities, the shallow water was 0.62 singers/km^2 compared to 0.17 singers/km^2 for the offshore area. This represents preferential usage of the shallower waters by singers. Such a preferences also explains the greater number of singers located in the southern portion of the arena, as the amount o shallow water is greater in the southern portion of the arena. Furthermore, when examining only the nearest two sub-regions of the array, the numbers of singers was almost equal and the depth distribution in these two areas are similar. It appears that the nearshore preference of humpbacks whales does apply to singers as well, but not absolutely. Although the density of offshore singers was less, half of the singers were located outside the 100 fathom isobath.

Such an onshore-offshore range in distribution opens the possibility that differing oceanographic and acoustic conditions may affect the choice of singing locations. Offshore singing locations provide improved acoustic propagation conditions, due to the deep water

and lack of physical obstructions that absorb sound. However, the factors that determine which area is preferable may be social rather than oceanographic. Pods with a calf are found significantly closer to shore than pods without calves (Smultea, 1992). Mothers with calves do mate post-partum, but the percentage is small (Chittleborough, 1958). Most likely, mature females without calves represent better mating prospects. Mature females, probably estrous or pre-estrous can be reliably found in large surface-active or competitive pods (Clapham et al., 1992). These pods are found further offshore than mothers and calves. Therefore, it might be argued that the region frequented by mature females without calves represents the prime singing areas, and that these areas off the Island of Hawai'i are several kilometers offshore.

Swimming Singers

Singing humpbacks have been most often described as lone and stationary or slowly moving (Payne and McVay, 1971; Winn and Winn, 1978; Tyack, 1981). While some moving singers have been observed (Tyack, 1981; Baker and Herman, 1984) it seemed that these were unusual examples. This impression may be due to difficulties in identifying singers from small boats, which are overcome with a directional hydrophone (Winn and Winn, 1978) or a hydrophone array. The mean singer speeds reported here are low, with a large portion of animals moving at speeds low enough to be considered stationary or drifting with the current. However, there are a few examples of singers moving at high rates of speed.

Bauer (1986) found that the average speed of singers was 3.86 km/h based upon visual tracking alone. This speed is confounded since Bauer combined 'suspected' singers, animals that displayed 'singer-like' behavior, such as long down times and limited movement between surfacings, with singers confirmed by monitoring hydrophones deployed from boats. This inclusion may have biased the speed value downward since 'suspected singers' were always nearly stationary. The discrepancy between the speeds

determined by Bauer (1986) and ours may be due to one or more factors. Difference in study region may contribute to the observed speed differences; Bauer's data were collected off Maui. The Maui region typically has a greater whale density, which may affect the behavior of singers. The difference in speeds may be an artifact (Bauer, pers. comm.). In producing acoustic tracks, many individual locations are averaged and locations with apparent erroneous ranges are discarded. The net effect is one of smoothing the path of the singer. This smoothing will reduce the length of the path, and reduce the calculated speed. Bauer's visual data were error-checked and obviously erroneous fixes were discarded, but there may be less net smoothing in visual tracks compared to acoustic tracks. Finally, the most likely scenario is that some of the whales initially described as singers stopped singing and began swimming or increased speed. Non-singing singletons had a mean speed of 4.62 km/h. The standard deviation for singers was greater than non-singers (2.89 v. 1.95). Furthermore the maximum singer speed recorded was 11.07 km/h v 8.09 km/h for non singers.

Observations with the hydrophone array have demonstrated that whales may behave as singers and not sing. As an example, one whale observed less than 1 km from the shore station had 18 minute downtimes, usually blew four times per surfacing, and surfaced in nearly the same location each time. Experienced observers were nearly certain that this whale was singing. However, when the hydrophones were switched on, no song was heard. The whale continued the same behavioral pattern for over an hour after the hydrophones were activated and no singing was heard during that time.

The presence of moving singers indicates that the singing display can be spatially dynamic, although the potential significance of moving versus stationary singers has not been resolved.

Aerial Behaviors

Aerial behaviors of one pod sometimes precede changes in the behavior of other pods. In one observation, a breach was immediately followed by cessation of singing by two animals, suggesting that at least one of the singers detected the sound of the breach and altered its behavior in response. This suggests that the sound of aerial behaviors can intentionally or unintentionally convey information to other whales. It is unlikely that aerial behaviors function exclusively as acoustic signals, given the energetic cost of aerial behaviors compared to vocally produced signals. Furthermore, many examples produce very little sound. Nevertheless, reception of the sound of an aerial behavior such as a breach may indicate the breaching animal's location and perhaps its behavioral state.

Inter - Individual Separation

The data presented support the hypothesis that one function of humpback whale song is to maintain spacing between individuals. The orientation data show that singers tend to avoid one another at all ranges. Singers did not orient and move toward another at distances < 4 km, although there was one pair that maintained a 2 km separation. Singers oriented and moved away from other singers at distances of 3 km and greater. It is possible that the spacing may be different on other islands, which have different population densities or ambient noise levels. This would certainly seem to be the case in the Caribbean, where singers are reported to be 100-300 m apart with a mean density of 0.3 whales/km^2 (Whitehead, 1981). This is compared to a maximum density of 0.045 whales/km^2 off Maui (Whitehead, 1981). The maximum density determined by visual means on Hawai'i was 0.035 whales/km^2, similar to the figure for Maui. Given the much higher population density on Silver Bank than in Hawai'i, a density dependence upon spacing seems likely. This is supported by observation of two singers separated by ~500 meters off Kauai during the seasonal peak in abundance (Cerchio pers. comm.).

One question is: if singers less than 4 km away are usually moving away, how did they get to be within 4 km of another singer? The most likely answer is that one male closes range while one or both are silent. After both are singing, they may increase their spacing in response to the other. Alternatively, it is possible that a singer may be displaced from its location by another singer. Active displacement of a singer by another whale has been observed, following an affiliation of the two whales (Tyack, 1981).

Winn and Winn (1978) noted that the separation between singers varied between 1 and 40 km, apparently depending upon local population density. These estimates were based upon the sequential rather than simultaneous detection of singers, which reduces their accuracy. Tyack (1981) rarely observed singers closer than 5 km of each other during his studies off Maui. Both Winn and Winn (1978) and Tyack (1981) suggested that song might function in maintaining that spacing. Winn and Winn (1978) also suggested that song production may allow females to localize displaying males. Tyack (1981) proposed that song facilitates affiliation, at least by advertising location. On the basis of these studies and additional playback experiments, Frankel (1987) proposed that males sing songs with messages to both sexes. The inter-sexual message is one of advertisement: singing conveys location, and an indication of reproductive fitness. The intrasexual message is to 'stay away'; that is, to maintain the spacing between individual singers. The spacing between singers presumably increases the ability of females to localize displaying males. The ability to locate sound sources has been demonstrated in humpback whales (Tyack, 1983; Mobley et al., 1988).

Social Interactions

Previous descriptions of affiliations of singers with other pods found that singing stopped when the singer joined a pod (Tyack 1981). Observations in which singing continues after affiliation are difficult to interpret, since the gender of the second whale is uncertain. However, they are similar to observations of singing escorts accompanying

mothers and calves (Baker and Herman, 1984). Singing in both of these contexts may represent a component of courtship.

However, affiliations involving singers tend to be short-lived, leaving the possibility that singers may be affiliating with other males. If singers are broadcasting individual-specific information in the song, then males as well as females should be able to assess the singer. These affiliations could be between males of approximately equal fitness. Such affiliations may represent one male attempting to displace another male from the area. However, it is doubtful that such displacements would result in the formation of a dominance hierarchy (Darling, 1983) because the degree of movement of individuals between different islands (Cerchio et al., 1991) and the impermanence of whale social affiliations in the wintering grounds (Mobley and Herman, 1985) probably does not allow sufficient time for such a hierarchy to develop or have much utility.

In summary, singers have been shown to utilize the habitat differently than other classes of whales. Their distribution is further offshore than other classes, although the density of whales within the 100 fathom isobath were higher than those offshore. The observed speeds of singers were lower than those off Maui, suggesting regional differences in singer behavior. Whales were observed to be singing while after affiliating with another whale. Earlier observations suggested that singers stopped when they joined another whale (Tyack 1981). Singing before and after an affiliation is consistent with the observations of singing in pods consisting of multiple adults. Sizes of pods containing singers observed off Hawai'i were similar to those reported off Maui (Tyack 1981). In conclusion, the behavioral role of the singer has been refined and enlarged.

Chapter 4
Variation in Structure and Amplitude of Humpback Whale Song Units
INTRODUCTION

Many species from a wide variety of taxa sing during reproductive periods, from crickets (Arak and Eriksson, 1992) to gibbons (Mitani, 1988). Most of the singing species are birds and there has been a sizable amount of work done on birdsong. The question most often asked about such songs is what functions do they serve? Songs can frequently serve multiple functions. Most hypotheses center around 1) attraction of mates or 2) stimulating females to reproductive condition, or 3) driving other males from the singer's territory (Kroodsma and Byers, 1991) .

Bird song has been shown to be attractive to females by comparing the song output of unpaired and paired males. Unpaired males sang far more than those with mates, indicating that song was used to attract females (Wasserman, 1977). Males may stop singing altogether once there is a female has been attracted to their territory (Catchpole, 1973). Finally, playback experiments with bird songs have shown that nestboxes with speakers playing conspecific song attracted more females than those that were silent (Eriksson and Wallin, 1986)

Song may also function to stimulate females into reproductive condition. Male northern mockingbirds increase their singing at the start of each nesting attempt during the season, suggesting that male song stimulates the female to initiate the next clutch (Logan, 1983). Laboratory experiments have shown that precopulatory calls or songs can increase the female solicitation rate or nest building activities (Brockaway, 1965; Hinde and Steele, 1976).

The effects of song on territorial defense have been long studied. One of the most common experiment is the 'speaker replacement' procedure, in which a male is removed

from its territory and replaced with a speaker that produces the male's song. Such experiments have shown that song itself can deter male intrusion into the territory (Falls, 1988). Most convincing have been the male manipulation studies. When the singing ability of sparrows was removed by puncturing their air sacs, they were delayed in acquiring territories and had difficulty in maintaining them. The males' ability to acquire and maintain territories returned when the air sacs healed (McDonald, 1989).

Recent investigations into song in other species such as frogs and birds have focused upon the evolutionary pathways that led to the observed female preference patterns and mate choice mechanisms (Searcy and Andersson, 1986), because those preferences have already been well established. In humpback whales we have yet to describe the mate choice mechanisms. The study of variation in song represents the beginnings of the development of testable hypotheses of how song can function in mate choice.

The critical factor in determining a signal's function an evaluation of the listener response (McGregor, 1991). Many studies have examined how variation in a signal influences its effectiveness. Such factors include repertoire size (Searcy and Andersson, 1992), calling rate (Clutton-Brock and Albon, 1979; McComb, 1991), fundamental frequency (Robertson, 1986a), signal structure (Bauer and Nagl, 1992; Cate, 1992) and amplitude (Ryan, 1988).

The effect of variation in calls is usually addressed by measuring the reactions of the receivers. Examples include higher rates of solicitation display by females in response to larger repertoire sizes (Catchpole, 1980). Male frogs that produced lower pitched calls have increased ability to defend their territory (Robertson, 1986b).

It is uncertain how female preferences actually affect reproductive success. In most of the repertoire-size experiments, the effect of the repertoire size is typically removed once the effect of territory or male experience is controlled (Kroodsma and Byers, 1991). Similarly, Telford et al. (1989) found that females exhibited preferences for lower

fundamental frequency calls only in small chorus sizes, smaller than occur naturally. These negative results are not absolute, however. McComb (1991) found that females were attracted to higher rates of roaring in red deer. Variation in the calling rate of male mouse lemurs has been correlated with reproductive success (Zimmerman and Lerch, 1993). Mate choice based upon phenotypic characters (size) has been shown to affect allele frequency in swordtail fish (Ryan et al., 1990). These studies support the hypothesis that variation in advertisement calls can affect the reproductive success of the caller.

The study of humpback song has concentrated upon several areas: description of its acoustic structure (Payne and Payne, 1985), correlation of song production with reproductive behavior (Winn and Winn, 1978; Tyack, 1981), and the formation of hypotheses concerning song function (Frankel, 1987; Mobley et al., 1988). One component that has been implicitly stressed in the literature is the stereotypy of humpback song (Payne and Payne, 1985). However, during field observations with a hydrophone array (Figure 3.1) off the Island of Hawai'i, it became obvious that there was a great deal of variation in the structure of the songs.

Inter-individual variability has been noted previously, but not investigated. Payne and McVay (1971) stated that songs differed between repetitions and between individuals, but they did not pursue this subject. Later Payne and Payne (1985) stated that inter- and intra-individual variability existed, however it was "not as great as the variation between songs of consecutive years." Hafner et al. (1979) attempted to describe differences in the "cry" component between different singers. However their sample size was six whales distributed over three years. Only two whales were recorded and compared within a short period of time. Differences in the acoustic structure were noted, although they could be attributable to evolution in song structure in the population. An extreme form of variation has been documented. In a study of song 11.4% of whales were found to sing 'aberrant' songs (Frumhoff, 1983). Aberrant songs were defined as any song that lacks a

fundamental theme, which in turn was defined as any theme that appears in almost all songs over a number of years.

In 1989, the first year of the present study, the variability within and between the songs became obvious after a short period of listening. The question that remained concerned the distribution of the variation: Was the variation between singers greater than that within the songs of one singer?

Additionally, analysis of humpback song has largely taken place at the thematic level or higher (Payne and Payne, 1985). Only recently have unit or note scale analyses been feasible thanks to advances in signal-processing capability. It seemed plausible that variation could exist at this level, where factors such as frequency, signal duration and relative amplitude could be measured. Signal variability might be correlated with variation in physiological parameters, and could be used by other whales to assess the singer, as has been shown in other species.

METHODS

One fundamental characteristic of humpback song is the evolution of song structure over time (Payne and McVay, 1971; Payne and Payne, 1985). Examination of 1989 song structure during the data analysis for chapter 3 found that it took at least a month for perceptible changes to occur in the structure of song (personal observation). In order to limit or remove any effects of this trend, the data were selected from a one-week period from February 21 to February 28, 1989. It was believed that the evolution of song structure within this short period would be minimal.

Eleven singers were examined during the six days of the seven day sampling period. Whales recorded simultaneously or on the same day at different locations were clearly different animals. It was assumed that whales recorded on different days were different animals. This assumption is based upon the low probability of an animal being in the same general area on successive days. This is shown by the low rate of photographic

resights of singers within years. An examination of the Kewalo Basin Marine Mammal Laboratory fluke database revealed 66 individually identified singers, photographed between 1980 and 1991. Of these 66, five (7.6%) were resighted between years and three (4.6%) were resighted within years as singers. Two singers (3.0%) was re-sighted on the same day. On the basis of on these resight rates, there is a probability of 0.046 that one of the whales was recorded twice on different days. Even allowing that photographic sampling could underestimate the probability of re-recording, it seems unlikely that more than one singer was re-recorded.

The 68 analog tapes made during this period were originally recorded in the field with a TEAC R-61D data recorder onto 45 minute normal bias analog cassettes. These cassettes were replayed on the R-61D and re-recorded with a TEAC RD-130T digital data recorder. Two analog tapes easily fit onto the 2-hour digital audio tapes (DAT) used by the RD-130T.

The data were acquired with the Macintosh based workstation described in Chapter two. Each tape was played and examined for the presence of whales singing. Whales were selected for measurement if the signal to noise ratio exceeded 20 dB. Once a whale was selected, its song was monitored for at least four repetitions.

The whale's song was sampled with six different units from three different themes. These themes were chosen because they were almost always present in an individual song. These themes are referred to as fundamental themes (Payne and Payne, 1985). The themes selected were themes 2,3 and 4, as shown in Figures 4.1-4.3.

Theme one is also referred to as a 'ratchet.' This theme is typically sung as the whale approaches the surface and while on the surface. As the whale dives, it typically begins to sing the theme two. Theme two consisted of only two units in 1989. Unit 1 was either a long, low, slow frequency downsweep, or a pair of two monotonic tones in the

same frequency range. This was followed by 3-4 repetitions of unit 2, which were sharp frequency upsweeps, typically from 200-800 Hz.

Theme three unit one is typically a downward sweep from 250 to 100 Hz. The unit sometimes begins with a sharp sweep up from 100 Hz to 250 Hz, followed by the nearly ever-present 250 to 100 Hz moderate downsweep. The second unit is usually a downsweep from 400 to 200 Hz. The contour of this unit is extremely variable.

Theme four consisted of two units. The first unit was a single or pair of long amplitude modulated pulses, approximately two seconds in duration. After a 1-2 second pause, there are two units with a sharp, almost immediate jump in frequency from < 100 Hz to 1-1.5 kHz. The unit then frequency modulates around the original frequency at the end of the upsweep. The first of these two units is usually longer than the second.

Sampling Technique

Whales that were loud and distinct were acoustically located. All songs that met the criterion of signal/noise ratio were selected for sampling. Sampling typically began after the occurrence of theme 1, the "ratchet," which typically indicated the occurrence of a respiratory surfacing and the "beginning" of the song. After the ratchet and the typical period of silence, the whale would begin vocalizing theme 2. Since the vocalizations began quietly, the first occurrence of theme 2 was not sampled. Sampling began on the second or third occurrence, when the whale was vocalizing at full amplitude. This was indicated by the first clear occurrence of unit 1. That example of unit 1 would be sampled, as would the first following occurrence of unit 2. This pair and the next three pairs of units 1 and 2 were sampled. Early observation suggested that unit 2 of theme 2 was particularly variable in bandwidth and the lowest frequency of the unit. An additional four examples were therefore sampled from the next four repetitions of theme 2. Since Unit 1 showed much less variability, its sample size was not increased. Both units of theme 2 were sampled at a rate of 4 kHz.

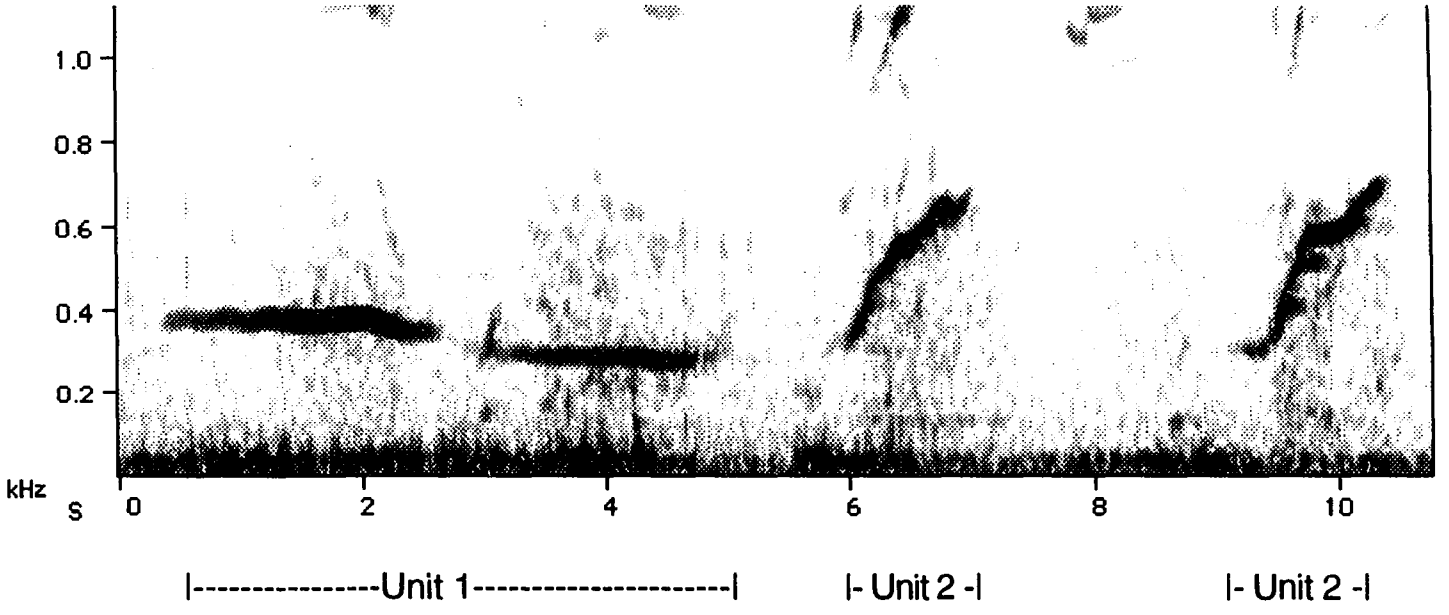

Figure 4.1
Spectrogram of Theme 2

Theme 2 is shown and Units 1 and 2 are delineated. Unit 1 is a gradually descending frequency downsweep and Unit 2 is a sharp frequency upsweep.

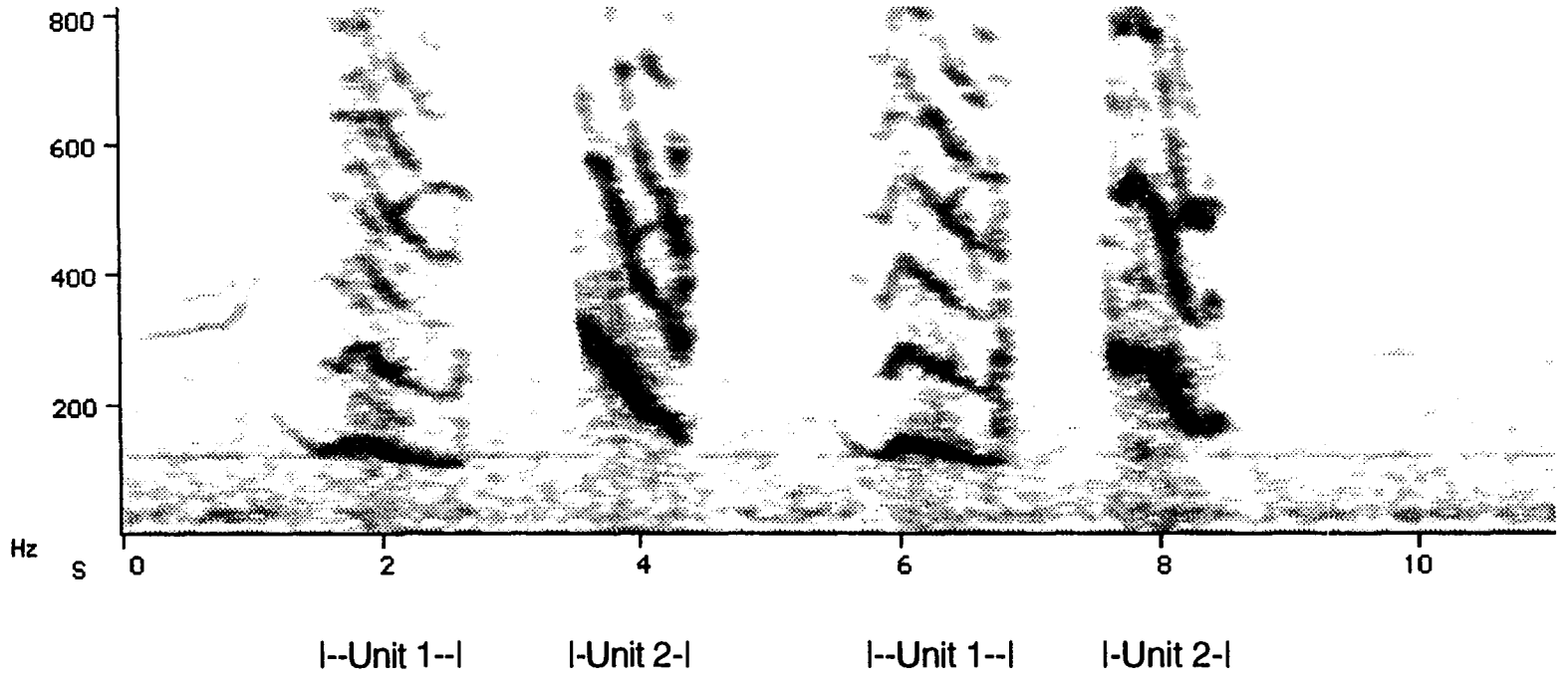

Figure 4.2
Spectrogram of Theme 3

The spectrogram of theme 3 is shown. Two repetitions of themes 1 and 2 are depcited.

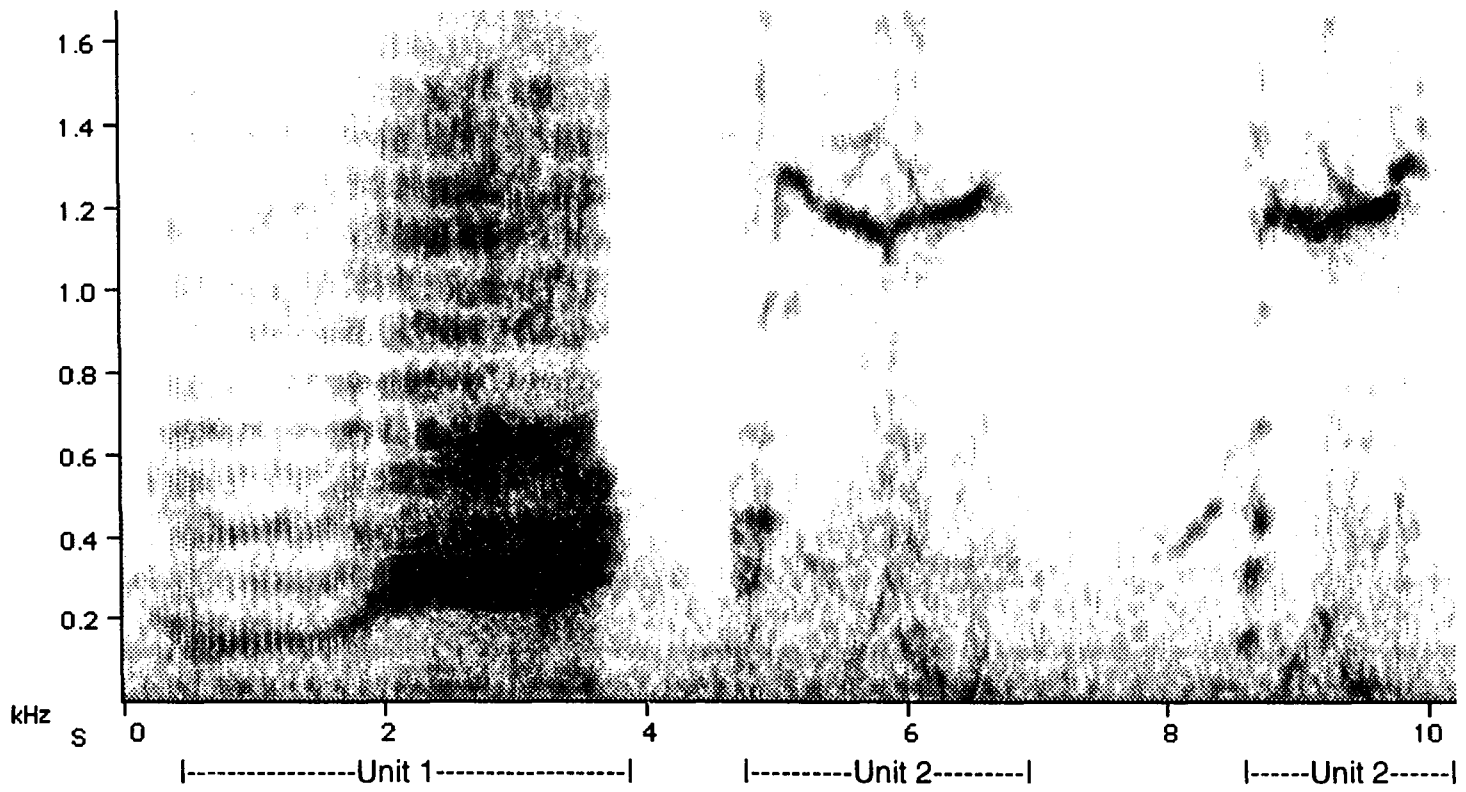

Figure 4.3
Spectrogram of Theme 4

The spectrogram of Theme 4 is shown. The blank space between units 1 and 2 has abeen compressed for this figure

Theme 3 had the first pair of units 1 and 2 from the first four phrases sampled. These signals were acquired with a sampling rate of 2 kHz. Their low frequency allowed the lower sampling rate, reducing storage requirements.

Theme 4 was sampled at 4 kHz, due to its high frequency range. The first four complete occurrences of theme 4 were sampled. Unit 1 was acquired separately. The two occurrences of unit 2 were first acquired in a single computer file and later separated for analysis.

An analysis log was kept while sound files were acquired. The variables recorded included the date, time, theme, unit, song number, sequence of production, the number of units per phrase and the channel that had the clearest representation of the sound ("best channel").

Once the samples were all acquired, spectrograms were made for each file. Since each file had three representations of the sound, the channel indicated as best channel in the analysis log was used for the spectrogram. The spectrograms all had the same parameters to allow comparison. These parameters are listed in Appendix 2.

Feature Analysis

Spectrograms were displayed on a 19" monitor. The signal file was displayed with its total file length and a frequency range suitable to measure the signal of choice (i.e., 1 kHz for Theme 2, Unit 2). These display parameters are listed in Appendix 2. The signal was "rubber-banded," a technique of drawing a highlighted box around the signal, that encompasses the entire frequency range and duration. These measurements were first recorded in the Canary Datalog, and later exported to an Excel spreadsheet.

These measures were then imported into SAS. A mean was taken of all the measures (e.g., duration, bandwidth) for each song unit within each song. Thus there was a 6 unit by 4 songs factorial design, where all the factors varied within the subject. Song features were examined separately with a repeated measures ANOVA design. A significant

difference reported by these tests would indicate that there are significant differences in the song features between whales (Cody and Smith, 1991).

The repeated measures test was complemented by univariate ANOVAs for each measure on each factor. The number of tests (24) raises the issue of increased probability of a type 1 experimental error. However these tests would only be conducted following a significant finding of the inclusive model, and are therefore protected.

Amplitude Analysis

Estimates of humpback song source levels were calculated for the same song samples referred to above. The peak amplitude was measured in the Canary program. The received sound level at the hydrophone was calculated by adding measuring signal gain for the recording system. Source levels were estimated using an empirically-based transmission loss curve.

The amplitudes of the same song samples acquired for feature analysis were also recorded in the database to allow source level calculation. The Canary program was configured to record the peak amplitude of each signal when the other measurements were made. The peak amplitude was recorded rather than amplitude at a fixed frequency per unit, because it was expected that the frequencies of the units could differ between samples, and a fixed frequency sampling might produce an artifactual difference between samples.

The received levels at the hydrophone were calculated from the transfer functions for each component of the recording system. Transfer functions describe the effect of a component on the signal strength, i.e. the magnitude and direction of the change. The hydrophones were all calibrated at -169 dB sensitivity. The transmitter and receiver combinations had a 38 dB gain in signal strength. Recording levels were adjusted in 10 dB increments with a step attenuator. Finally, the R-61D analog tape deck had 0 dB gain.

A 1 V (peak to peak) calibration tone was recorded on the beginning of every tape. This calibration tone was defined to be 0 dB. The Canary output was referenced to this level.

Mean received levels were calculated for each theme and unit for each song repetition. Therefore each whale had a maximum of 24 received level estimates. Each of these was converted to source levels by adding the transmission loss (TL) for the acoustically determined distance between the whale and the receiving hydrophones. Transmission loss for Kawaihae Bay was estimated using the equation:

$$TL = 17.61[\log(\text{range})]$$

Because this portion of the calculation is range dependent, an error in range or transmission loss calculations could have produced differences between whales at different ranges that actually had the same source level. Therefore, calculated source levels were regressed against range, to see if range could account for any observed differences. A non-significant regression should be an indication that no major range or transmission loss error had occurred.

Source levels were then tested with an analysis of variance (ANOVA). The ANOVA tested the null hypotheses that there no differences between singers and between repetitions of song by the same singer. A post hoc analysis was used to partition the whales into statistically significantly different groups.

RESULTS

Sample Whales and Locations

Eleven whales were sampled on six of the seven day sampling period. Two whales were sampled on February 21, 1989. Samples were taken from these whales simultaneously at different locations, so they were clearly different whales. Three whales were sampled on February 22, 1989. One (22E) was sampled from 11:32 to 12:27 and the other whales on that day were sampled approximately 12 hours later. There was a 30

minute interval between these two samples, but the whales were at very different bearings (346° v. ~ 180°), making it very unlikely that a whale would move ten or more kilometers in 30 minutes and then resume singing. Two whales were sampled on February 26, 1989. There was a 1.5 hour interval between the samples of singer A and singer B. However, singer A was located at 300° and remained stationary for the entire duration of its sample, whereas singer B was very near shore and moving north along the coast for the duration of its sample. The remaining whales were the only singers sampled on the days of February 23, 25, 27 and 28.

Song Features

The song feature data were first examined with an omnibus repeated measures ANOVA. The results are presented in Table 4-1. The first source of variance examined was the within-whale effect. This represents the measures across the four songs of each animal. This source of variance was not significant ($p > 0.05$) for the four measures of bandwidth, duration, lowest frequency and frequency of peak amplitude. This indicates that there was no significant variation from song to song within the same whale. When the song unit effect was examined between whales, significant ($p < 0.05$) variation was found on all four measures. This indicates that there are differences on the four measures between different whales. The interaction of within and between whale variance was tested in the omnibus repeated measures test, and found to be non significant ($p > 0.05$). This indicates that the observed differences are apparently randomly spaced between the whales.

Table 4.1
Repeated Measures Omnibus Tests

The Omnibus tests are tests of differences between whales. The significant result of the variable 'Song Unit' indicates that statistically significant differences are found between whales on all four variables tested. The lack of a significant 'Song' effect shows that there is no significant changes from song to song and the interaction was also not significant.

Variable	Song	Song Unit	Interaction
Bandwidth	F(3/18)=1.68 p=0.2066	F(5/30)=9.99 p=0.0001	F(15/90)=1.30 p=0.2205
Duration	F(3/18)=0.81 p=0.5067	F(5/30)=149.86 p=0.0001	F(15/90)=1.10 p=0.3672
Frequency of Peak Amplitude	F(3/18)=2.22 p=0.1208	F(5/30)=261.56 p=0.0001	F(15/90)=0.48 p=0.9449
Lowest Frequency	F(3/18)=1.14 p=0.3596	F(5/30)=393.99 p=0.0001	F(15/90)=0.79 p=0.6830

These significant differences where further investigated with univariate ANOVAs. Because the distribution of variables was not normal, these parametric ANOVAS were supplemented with non-parametric Kruskall-Wallis tests. Both the univariate ANOVA tests and the non-parametric results are summarized in Table 4.2 and the complete data are presented in Table 4.3. The overall pattern is that variable of subject was significant, song was not, and the interaction was not significant. There are a few deviations from this pattern. These tests also indicate that the songs of different whales are significantly different in structure. The conclusion that the songs of a whale do not change with repetitions is supported by non-significance of the song variable. The interaction term was typically significant, indicating that the songs of different whales changed in different patterns, rather than a linear shift relative to another whale. This can be seen in Figures 4.4 through 4.9, which show the mean and standard deviation of each measure for each whale and song unit.

Table 4.2
Summary of Univariate Song Feature Tests

This table summarizes the results of the 24 individual univariate tests for each of the six units and four variables. In 22 of 24 cases, the variable 'subject' was significant, again showing that measurable differences between whales are present. The variable 'song' was typically not significant, showing that there is no variation between songs of the same whale. Interactions at this level were significant, indicating that the patterns of differences were not linear between whales.

Bandwidth				Duration			
Unit	Subject	Song	Interact	Unit	Subject	Song	Interact
1	*	NS	*	1	*	NS	*
2	*	NS	*	2	*	NS	*
3	*	NS	*	3	*	*	*
4	*	NS	*	4	NS	NS	*
5	*	NS	*	5	*	NS	NS
6	*	NS	*	6	NS	NS	NS

Frequency of Peak Amplitude				Lowest Frequency			
Unit	Subject	Song	Interact	Unit	Subject	Song	Interact
1	*	NS	NS	1	*	*	*
2	*	NS	*	2	*	*	*
3	*	*	*	3	*	NS	*
4	*	NS	*	4	*	NS	*
5	*	NS	*	5	*	NS	*
6	*	*	*	6	*	*	*

Twenty-three of the twenty-four non-parametric tests indicated significant differences. All twenty-three of the corresponding parametric tests showed significant ($p < 0.05$) differences as well. The one non-parametric test that reported no difference was duration of song unit 6. The parametric test for this analysis also reported no difference.

Song Amplitude

The mean source spectrum level was 152 dB re 1μPa^2/Hz. The average bandwidth of the units was 175 Hz. Therefore the average source level was 174 dB re 1μPa. The measures of source level were then checked for normality of distribution, using SAS PROC univariate. The test indicated that the distribution was not significantly different from normal ($W= 0.9377$, $p =.0865$). The analysis was therefore continued.

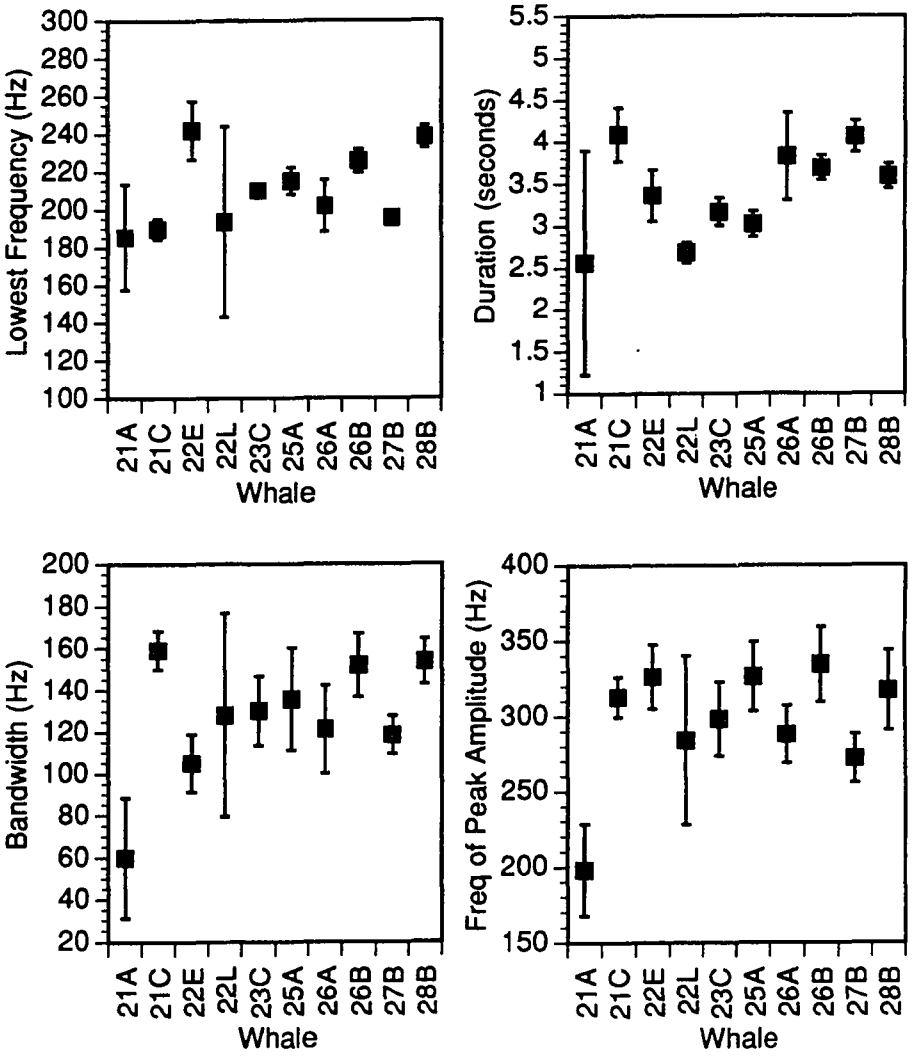

Figure 4.4
Theme 2 Unit 1 Features

Each Whale's score for the Lowest Frequency, Unit Duration, Bandwidth, and the Frequency of Peak Amplitude for Theme 2 Unit 1 are shown.

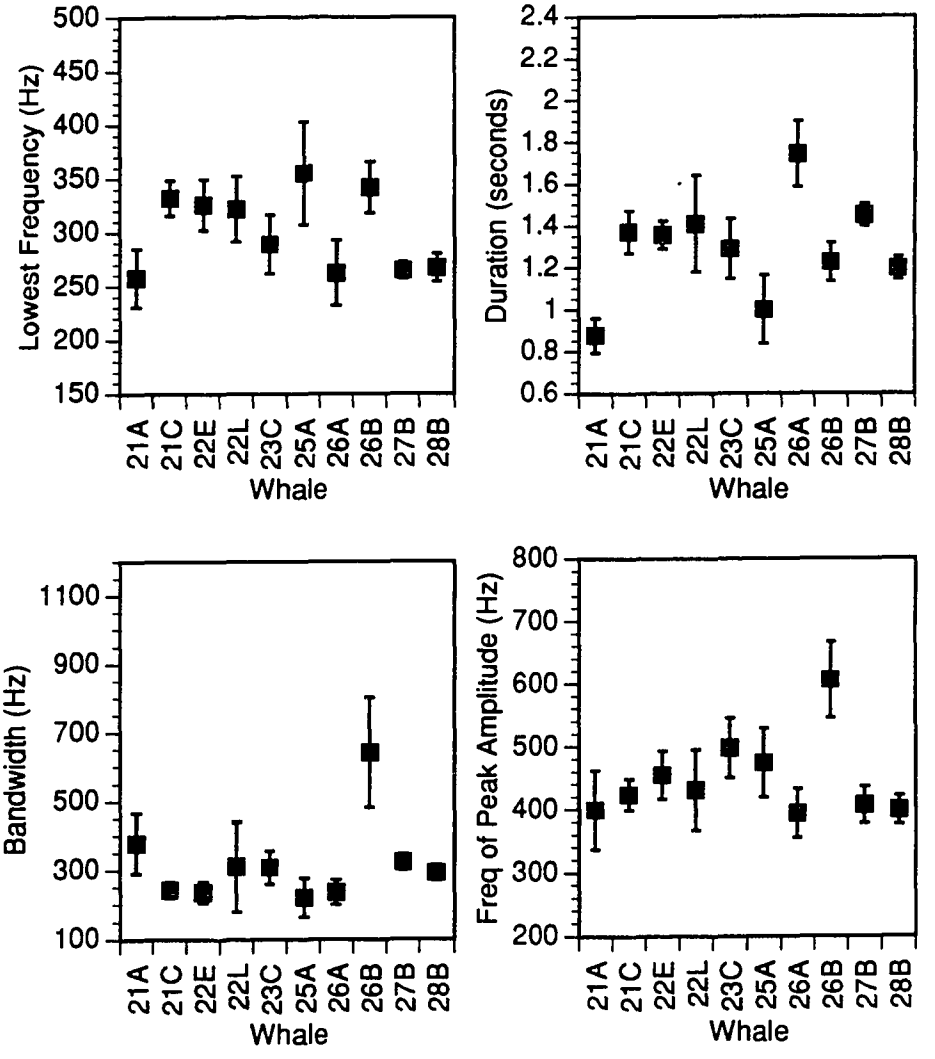

Figure 4.5
Theme 2 Unit 2 Features

Each Whale's score for the Lowest Frequency, Unit Duration, Bandwidth and the Frequency of Peak Amplitude for Theme 2 Unit 2 are shown.

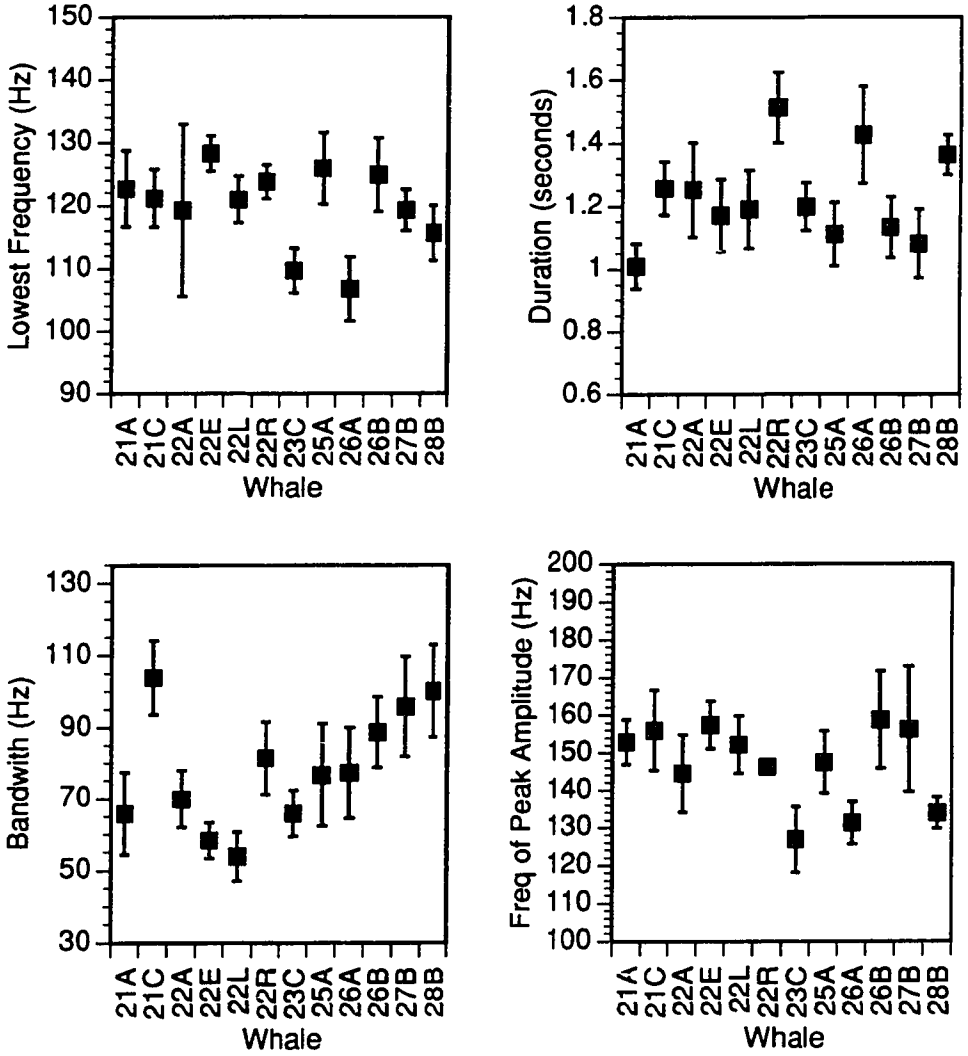

Figure 4.6
Theme 3 Unit 1 Features

Each Whale's score for the Lowest Frequency, Unit Duration, Bandwidth and the Frequency of Peak Amplitude for Theme 3 Unit 1 are shown.

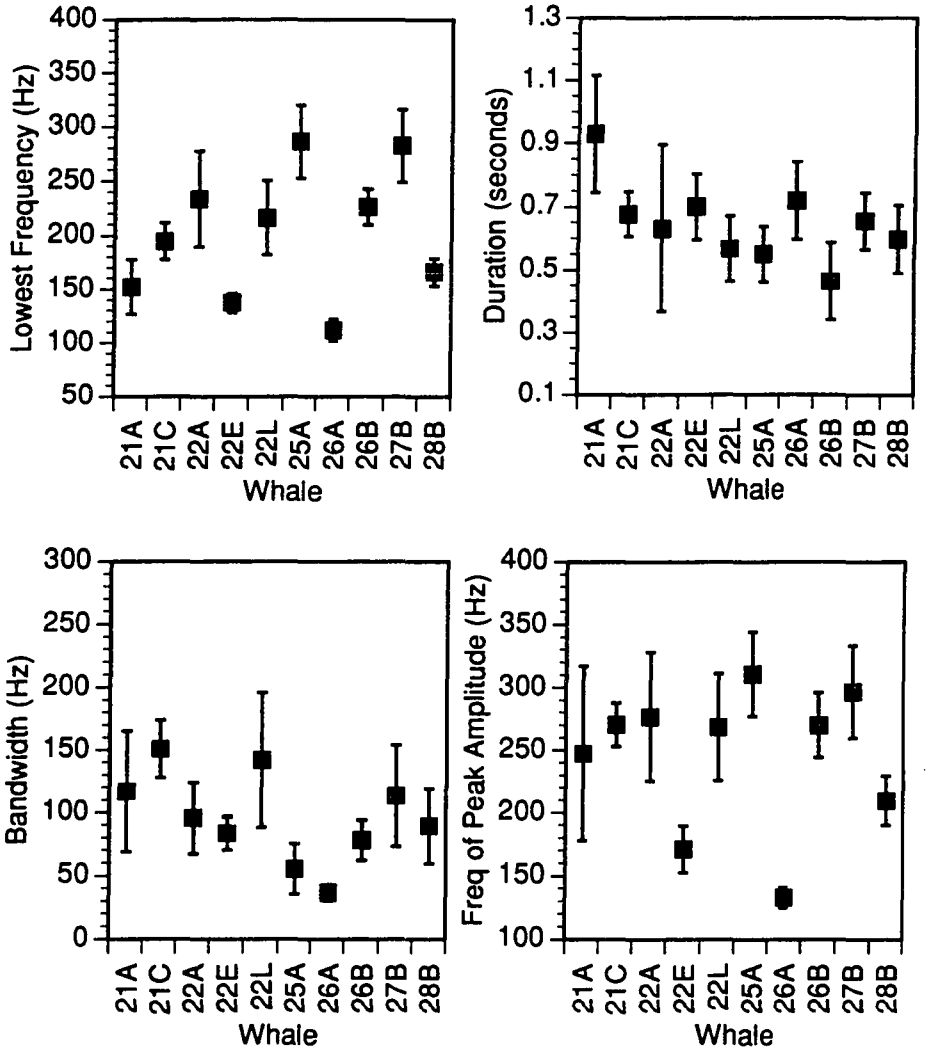

Figure 4.7
Theme 3 Unit 2 Features

Each Whale's score for the Lowest Frequency, Unit Duration, Bandwidth, and the Frequency of Peak Ampliutde for Theme 3 Unit 2 are shown

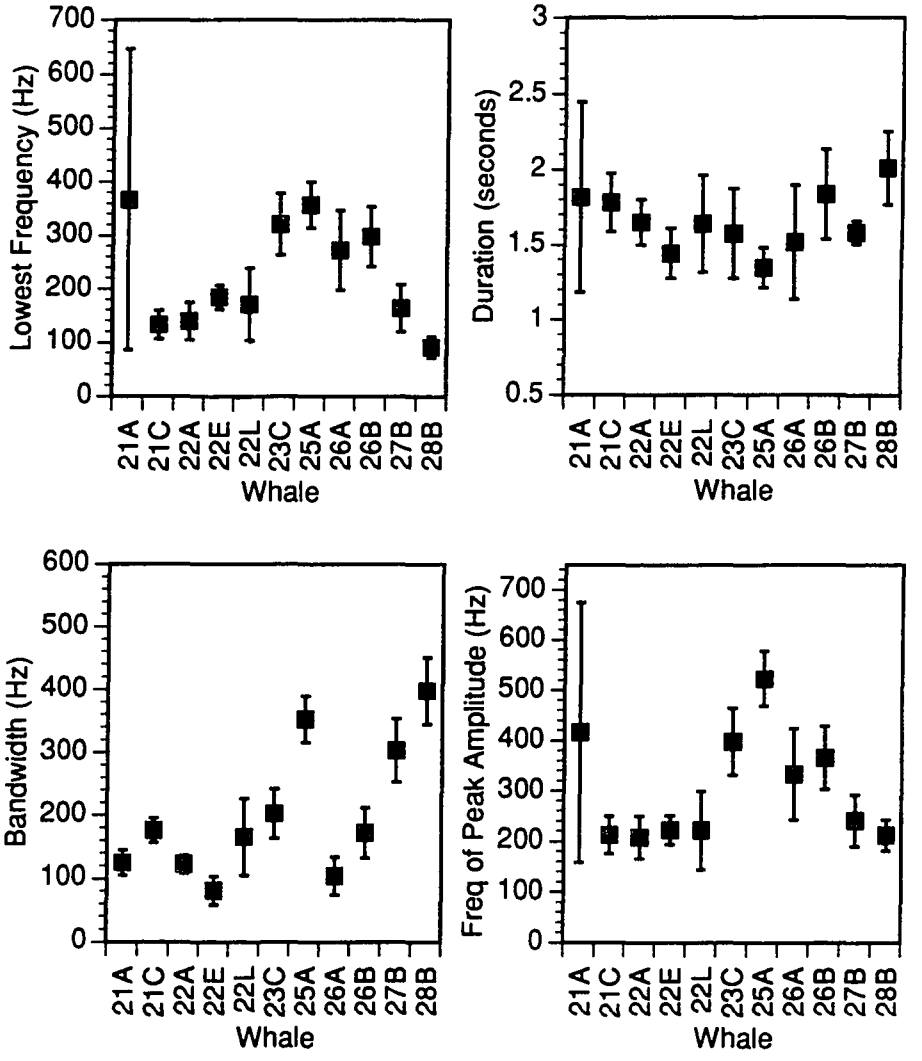

Figure 4.8
Theme 4 Unit 1 Features

Each Whale's score for the Lowest Frequency, Unit Duration, Bandwidth and the Frequency of Peak Amplitude for Theme 4 Unit 1 are shown

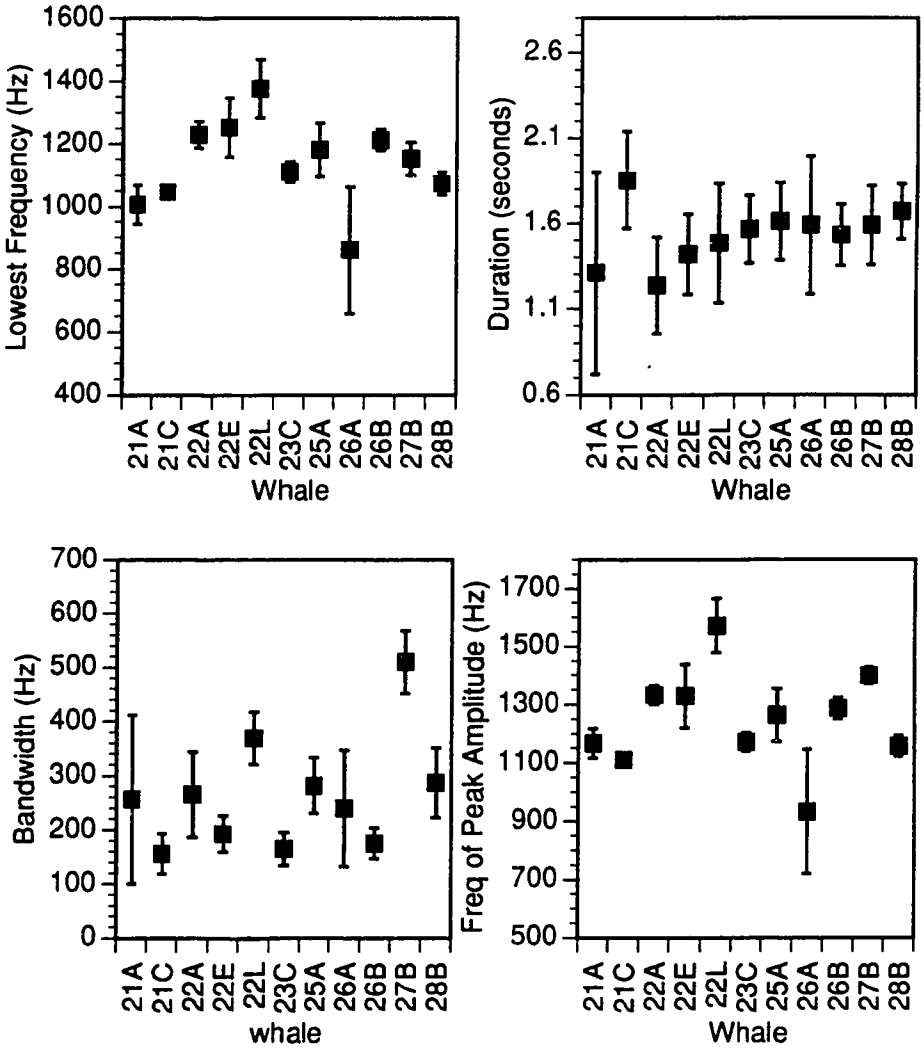

Figure 4.9
Theme 4 Unit 2 Features

Each Whale's score for the Lowest Frequency, Unit Duration, Bandwidth, and the Frequency of Peak Amplitude for Theme 4 Unit 2 are shown

Source levels were calculated for the whales. Figure 4.10 shows the regression of source level onto range. This proved to be non-significant [$F(1,29) = 1.14$; $p = 0.295$] with an extremely low r^2 (0.038), indicating that range between the array and the whale had no significant affect upon the calculation of source level. This indicates that the source levels were not an artifact of calculation.

The hypothesis that there were no differences in song amplitude was tested with an ANOVA. The test indicated that there were significant [$F(8;17)=6.39$, $p < 0.001$] differences between individual whales tested.

DISCUSSION

The results indicate that differences between individuals were found on every variable measured, and that the differences within individual's songs were not significantly different. It is possible that the observed differences may be due to song structure evolution. The short sampling period was chosen to reduce this possibility, but it could not eliminate it. However, some of the whales sampled on the same day are significantly different from each other. Therefore it is likely that the significant differences between whales indicate that there are measurable differences between the songs of different whales.

Lowest fundamental frequency is negatively correlated with body size in some anurans and is used by female frogs in making mate choices (Ryan, 1980). However, in adult mammals of the same sex, body size and fundamental frequencies do not seem to be related (Gunter and Manning, 1982). Frequency differences have been noted between male and female mammals (Monsen and Engebretson, 1977), and between adult and juvenile mammals (McGlone, 1966). If these findings apply to humpback whales, then the differences in the lowest frequency of whale calls are probably attributable to our recording adult and sub-adult singers.

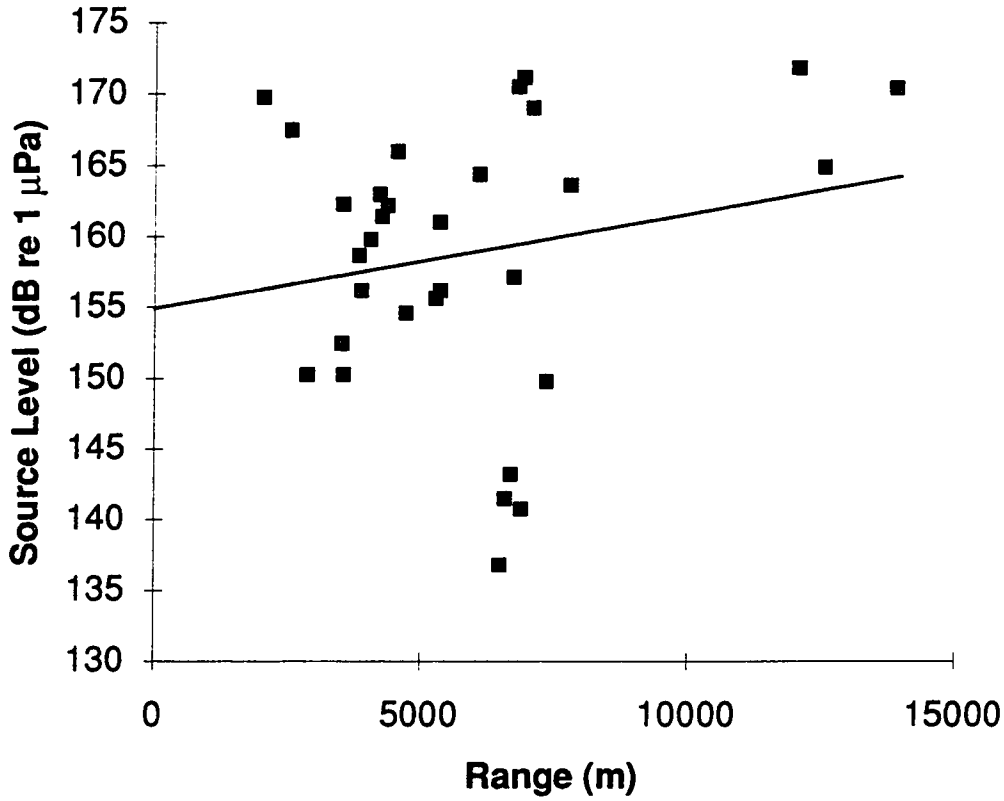

Figure 4.10
Source Level v. Range

The near zero regression coefficient (0.00066) shows that the differences observed in source levels are not due to errors in range or transmission loss measurements

Longer call duration was more attractive to female gray tree frogs (Klump and Gerhardt, 1987) and Pacific tree frogs (Whitney and Krebs, 1975). Increased signal duration, has been related to increased energetic output in anurans (Taigen and Wells, 1984). Increased energetic cost of a signal appears to be a feature generally attractive to females in male display calls. The variation in the duration and amplitude of humpback song units suggests that this parameter could be used by other whales to assess the singer. However, song production in humpbacks may represent a much smaller portion of the energy budget than in these much smaller species. A calculated estimate of the energetic cost of singing for 24 hours was only 700 calories, a vanishingly small portion of the total daily energy expenditure (Helweg et al., 1992).

Additional parameters that increase call attractiveness in other species include intensity, the number of components, and rate of production (Ryan, 1988). Roaring rate has been shown to affect female preference in red deer (McComb, 1991) indicating that vocal characteristics can influence mate choice in mammals.

The conclusion is that there are real, measurable differences in the songs of different whales at the level of the song unit. These differences were a necessary requirement for the validity of current arguments concerning the functions of song, based upon the listener's assessment of song quality. Specifically, the hypotheses that females are obtaining information about the singer through the song, or that other males may be assessing the physical ability of the males through song quality can now be considered more seriously.

Song is probably a multi-function display, with inter- and intra-sexual functions. Bird songs have been shown to possess both of these functions (Searcy and Yasukawa, 1990). This dual functionality is based upon the ability of song to convey information about the individual to the listener, not just position and species identity.

Size in many frog species contributes to success in male-male contests and this is reflected in their vocalizations (Arak, 1983; Robertson, 1986b). Many anuran species show variation in the fundamental frequency of their calls, and this is typically inversely correlated with male size (Robertson, 1986b). Thus males can assess another male's size, and therefore fighting ability, from its vocalizations. This may be inevitable in anurans, because vocal cord size increases with body size (Martin and Mitchell, 1975)

Variation in signal structure also occurs in intra-sexual signals. The song of sedge warblers is continually altered in new combinations of song types. Female preference for elaborate songs was shown in the earlier pairing of males with the most elaborate songs (Catchpole, 1980). These findings were confirmed with laboratory studies using estradiol implanted females (Catchpole et al., 1984). Further work with the polygynous great reed warbler demonstrated that males with larger song repertoires attracted more females and produced more young (Catchpole et al., 1985; Catchpole, 1986).

Song literature in these species is now focusing on how these preferences and social mechanisms evolved. In humpbacks we are now just establishing that there is a basis for female preference or for male assessment. There are two possible next steps.

There has been a recent basin-scale research project in the Atlantic, called Years of the North Atlantic Humpback (YONAH)(Clapham et al., 1992; Clapham et al., 1993). This project was an attempt to photographically identify and genetically sample as much of the population as possible. If enough of the population has been genetically sampled, it may be possible, after extensive lab work, to DNA-fingerprint enough animals to build paternal reproductive histories. This may allow a measure of the variance in individual male reproductive success, which is a critical parameter.

Given that such an accomplishment is possible, then recordings made currently of identified singers would allow an eventual comparison of song characteristics and reproductive success. This is one approach that would allow testing of the hypothesis that

song features are used by females, and that there are female preferences for certain features. We do not know which, if any, of these variable song features are used.

The second approach that could shed light upon this issue is another song playback experiment. This has been attempted twice. Tyack (1983) presented song and social sounds to humpbacks in Hawai'i. He reported a very strong charge response to social sounds and no charging response to song. Mobley et al. (1988) played song and other vocalizations to humpbacks. They described rapid approach responses to several vocalizations; primarily feeding call and social sounds, and to a lesser extent, synthetic sounds and song.

One overriding factor in both studies was signal reproduction quality. Tyack (1983) calibrated his equipment informally, adjusting the output gain until the sounds was qualitatively the same as an equidistant singer. Mobley et al. (1988) calibrated all of their sound stimuli to a broadband average output of 163 dB re 1 μPa at 1 m. However their system had a flat (+/-3 dB) response from 100 Hz to 10 kHz. There was low-frequency rolloff below 100 Hz. This may well represent a significant difference between their song playbacks and real singers.

The playback paradigm is a powerful one and has been used to great effect with other species (Kroodsma, 1990). Playback experiments with humpback song may still yield results, if the quality of the sound projection equipment is improved. Malme et al. (1985) used an array of sound projectors to achieve a frequency range of 32 Hz to 20 kHz. A similar system used for song playbacks has the potential to elicit response from females. Song could be presented at different amplitudes and perhaps with modifications to the signal, as has been done with bird song playbacks (Emlen, 1972). Any such attempt must include both genetic sampling and photographic identification to verify the sex of the subjects.

Despite the limitations of the completed playback experiments, they have provided information about reactions to song. Tyack (1983) reported that fourteen of sixteen whales moved away from playback of song. Similarly, Baker and Herman (1984) reported that in seven playbacks of song, all animals either did not respond or moved away. In one example, an escort appeared to 'herd' the mother and calf away from the song playback.

Two of Tyack's (1983) sixteen subjects approached, but did not charge the song playback. Mobley et al. (1988) reported a single rapid approach to playback of 1981 song (then four years old). A significant decrease in whale- vessel distance was demonstrated for 1981 song, but not current song. This indicates that outdated song was an overall attractive stimulus (Frankel, 1987).

The group that approached that playback of song was composed of three adults of unknown sex. Most pods composed only of adults are pods of mixed sex (Clapham, 1993). Assuming for a moment that this pod was one female and two males, the female could have been attracted to the old, now novel, song. Song structure slowly evolves, and there is some evidence in frogs for female preference for novelty (Rand et al., 1992). Alternatively, the pod could have been three males, that approached either out of 'curiosity' or as a challenge to the unusual singer. Birds are more likely to respond to a 'stranger' than a previously encountered 'neighbor' (Brooks and Falls, 1975). This could also be consistent with the reported approach of whales to synthetic sounds.

Observations of whales approaching singers are few, but they do occur (Tyack, 1981; Darling, 1983; Medrano et al., in press). Tyack described unknown sex animals approaching singers. Darling (1983) reported males approaching singers, and Medrano et al. (in press) reported females approaching singers. So while these interactions do not occur frequently, whales do respond to and interact with real singers.

Two of the most prominent hypotheses of the function of humpback whale song are that it serves to maintain spacing between males (Tyack, 1981; Frankel et al., 1991) and

that it is an advertisement directed toward females (Payne and McVay, 1971; Winn and Winn, 1978; Tyack, 1981). Implicit in these hypotheses is the assumption that individual specific information is encoded into the signals. The results presented in this chapter have demonstrated systematically measurable differences in the unit structure of individual humpback song. It is necessary for such differences to exist between the songs of different singers in order for these and other hypotheses to be plausible.

Table 4.3
F-Scores, Degrees of Freedom and Probabilities for Univariate Tests

The F-scores and associated probabilities for the tests summarized in Table 4.2 are shown.

Bandwidth F-Ratios				
Song Unit	Subject	Song	Interaction	Non-parametric
1	F(9/90)=8.77 p=0.0001	F(4/90)=2.45 p > 0.24	F(25/90)=2.55 p = 0.0007	$\chi^2(9)$=41.22 p=0.0001
2	F(9/172)=16.36 p=0.0001	F(4/172)=2.00 p=0.10	F(26/172)=5.68 p=0.0001	$\chi^2(9)$=49.94 p=0.0001
3	F(11/139)=9.8 p=0.0001	F(5/139)=1.59 p=0.17	F(33/139)=1.98 p=0.003	$\chi^2(11)$=69.58 p=0.0001
4	F(9/74)=6.23 p=0.0001	F(4/74)=0.28 p=0.89	F(23/74)=3.73 p=0.0001	$\chi^2(9)$=36.60 p=0.0001
5	F(10/222)=26.56 p=0.0001	F(3/222)=0.94 p=0.42	F(21/222)=2.60 p=0.0003	$\chi^2(10)$=135.97 p=0.0001
6	F(10/227)=19.67 p=0.0001	F(3/227)=2.63 p=0.0510	F(19/227)=3.01 p=0.0001	$\chi^2(10)$=99.69 p=0.0001

Duration F-Ratios				
Song Unit	Subject	Song	Interaction	Non-parametric
1	F(9/90)=5.12 p=0.0001	F(4/90)=1.91 p > 0.12	F(25/90)=1.92 p = 0.0137	$\chi^2(9)$=52.37 p=0.0001
2	F(9/172)=18.87 p=0.0001	F(4/172)=1.95 p=0.1041	F(26/172)=2.74 p=0.0001	$\chi^2(9)$=79.20 p=0.0001
3	F(11/139)=7.14 p=0.0001	F(5/139)=5.04 p=0.0003	F(33/139)=2.06 p=0.0020	$\chi^2(11)$=52.86 p=0.0001
4	F(9/74)=1.96 p=0.0568	F(4/74)=2.44 p=0.0539	F(23/74)=1,82 p=0.0286	$\chi^2(9)$=22.80 p=0.0067
5	F(10/222)=3.30 p=0.0005	F(3/222)=0.78 p=0.5040	F(21/222)=0.99 p=0.4797	$\chi^2(10)$=27.61 p=0.0021
6	F(10/227)=1.11 p=0.3582	F(3/227)=1.89 p=0.1326	F(19/227)=1.43 p=0.1135	$\chi^2(10)$=14.39 p=0.1561

Table 4.3 (Continued)
F-Scores, Degrees of Freedom and Probabilities for Univariate Tests

Frequency of Peak Amplitude F-Ratios				
Song Unit	Subject	Song	Interaction	Non-parametric
1	F(9/90)=6.89 p=0.0001	F(4/90)=2.08 p > 0.0895	F(25/90)=1.44 p = 0.1079	$\chi^2(9)$=32.89 p=0.0001
2	F(9/172)=10.01 p=0.0001	F(4/172)=1.25 p=0.2901	F(26/172)=1.88 p=0.0093	$\chi^2(9)$=57.74 p=0.0001
3	F(11/139)=5.81 p=0.0001	F(5/139)=2.70 p=0.0232	F(33/139)=2.33 p=0.0004	$\chi^2(11)$=58.12 p=0.0001
4	F(9/74)=8.82 p=0.0001	F(4/74)=0.54 p=0.7044	F(23/74)=3.17 p=0.0001	$\chi^2(9)$=48.31 p=0.0001
5	F(10/222)=17.62 p=0.0001	F(3/222)=0.44 p=0.7279	F(21/222)=3.04 p=0.0001	$\chi^2(10)$=88.28 p=0.0001
6	F(10/227)=32.88 p=0.0001	F(3/227)=13.96 p=0.0001	F(19/227)=10.85 p=0.0001	$\chi^2(10)$=132.57 p=0.0001

Lowest Frequency F-Ratios				
Song Unit	Subject	Song	Interaction	Non-parametric
1	F(9/90)=13.46 p=0.0001	F(4/90)=1.56 p = 1917	F(25/90)=1.85 p = 0.0192	$\chi^2(9)$=77.64 p=0.0001
2	F(9/172)=10.06 p=0.0001	F(4/172)=4.28 p=0.0025	F(26/172)=1.83 p=0.0122	$\chi^2(9)$=75.48 p=0.0001
3	F(11/139)=9.53 p=0.0001	F(5/139)=4.22 p=0.0013	F(33/139)=6.65 p=0.0001	$\chi^2(11)$=57.59 p=0.0001
4	F(9/74)=17.07 p=0.0001	F(4/74)=0.63 p=0.6397	F(23/74)=3.27 p=0.0001	$\chi^2(9)$=63.61 p=0.0001
5	F(10/222)=17.93 p=0.0001	F(3/222)=0.25 p=0.8638	F(21/222)=2.78 p=0.0001	$\chi^2(10)$=112.07 p=0.0001
6	F(10/227)=15.52 p=0.0001	F(3/227)=10.18 p=0.0001	F(19/227)=7.77 p=0.0001	$\chi^2(10)$=87.69 p=0.0001

Chapter Five
Behavioral Response Thresholds to Playback of Biological Signals
INTRODUCTION

Past estimates of auditory detection thresholds for cetaceans have been limited to captive odontocetes using psychophysical experimental methods (Johnson, 1967; Hall and Johnson, 1972; Thomas et al., 1988; Au, 1990) or cortical/brainstem evoked-potential techniques (Bibikov, 1992; Johnson, 1992). Similar studies with large whales are lacking due mainly to methodological restrictions imposed by their size. Recent investigations of the auditory capabilities of free-ranging mysticetes have been motivated by concerns for the possibly disturbing effects of anthropogenic low frequency sounds (i.e., less than 100 Hz) (Green et al., 1994) and by interest in developing acoustic safeguards to reduce fish net entanglements (e.g., Lien et al., 1992; Lien et al., 1990; Todd et al., 1992). One response threshold has been defined as the received level at which 50% of individual whales altered their course during migration (Malme et al., 1983). Using this criterion, responses have been found for received levels of 115-124 dB re 1 μPa for gray whales, *Eschrichtius robustus* (Malme et al., 1984) bowhead whales, *Balaena mysticetus* (Richardson et al., 1991; Richardson and Malme, 1993) and humpback whales, *Megaptera novaeangliae* (Malme et al., 1985). These investigations have all used anthropogenic noise, including air gun blasts, noise from oil and gas industrial operations, and vessel noise. Typically, the studies were motivated by the needs of maritime industry to determine the impact of coastal ocean-based operations, so the types of signals chosen were largely constrained to those as noted.

One exception was reported by Dahlheim and Ljungblad (1990) who exposed gray whales to pure tone signals varying between 200 and 2500 Hz, and source levels varying between 70 and 142 dB re 1 μPa at 1 m. Signals were one second in duration.

The authors reported startle responses and changes in direction and/or transit speed in response to signals between levels of 95 dB re 1 μPa (at 800 Hz) and 142 dB re 1 μPa (1800 Hz), with the majority of responses occurring between 108 dB re 1 μPa (1000 Hz) and 135 dB re 1 μPa (1500 Hz). The exact range to the animal was not included in the analysis and the reported levels were source levels rather than received levels. The authors estimated an approximate 13 dB transmission loss at a range of 20 m using a simple spherical spreading model.

Although it is important to know the received levels at which whales respond to anthropogenic noise, such levels would be more meaningful if the lower limits of detection were also known. Our approach represents two departures from past studies using anthropogenic sound: a) like Dalheim and Ljungblad (1990) we found clear behavioral responses to sound playback, but we additionally calculated received levels based on known ranges to the animals. The furthest ranges at which such responses occur are arguably closer to limits of detection; and b) we used playbacks of socially meaningful sounds, rather than anthropogenic sounds.

The proposal to use responses to biological sounds to estimate response threshold is based on the assumption that whales are likely to respond to biologically meaningful signals at levels approaching detection threshold. If this assumption is not valid, then the results obtained would serve as an upper bound of the estimates of response threshold. Most mysticete species produce sounds that are likely used for social communication, among other possible functions (Watkins and Wartzok, 1985; see review in Clark, 1990; Herman and Tavolga, 1980). Playback experiments have presented recordings of biological signals to mysticete species and produced observable behavioral responses such as approach and avoidance (Clark and Clark, 1980; Cummings and Thompson, 1971; Malme et al., 1983; Tyack, 1983).

The playback studies described here were conducted during the 1985 and 1986 winter seasons in Hawaiian waters, as reported earlier (Mobley et al., 1988). Three different biological recordings and two control stimuli were presented to humpback whales. The most dramatic behavioral response of humpbacks to the playback of sound stimuli was the "rapid approach response." This term describes the approach of whales to within 50 m or less of the playback vessel after the presentation of the sound stimulus. Whales that responded in this manner typically approached at higher than baseline speeds. These results have been re-analyzed in light of subsequent measurements of sound transmission loss in one of the two study areas that permitted the estimation of received sound levels in trials that produced a rapid approach response.

We utilized this rapid approach response as an unambiguous indication of detection and response, and estimated the received levels that evoked such responses. To do so, we computed an empirically based transmission loss curve and calculated the received levels of the stimulus playback at the whale's position when sound transmission began.

METHODS

Description of Playback Studies

A detailed description of procedures used in the playback studies described here may be found in Mobley et al. (1988). Briefly, the playback system used a Navy J-11 transducer whose output was standardized at a broadband source level of 163 dB re 1 μPa at 1 m for all sound types (bandwidth was approximately 30 Hz-20 kHz). The transducer was deployed at a depth of 7 m in water ranging from 100 to 500 m deep (Mean = 290 m, S.D. = 130 m). Acoustic velocity profiles conducted nearby in the upper 75 m of the water column indicated a uniform acoustic velocity field. Recordings of three natural sounds of humpback whales were used for playback experiments: (1) a feeding call recorded during the summer season, (2) social sounds and (3) winter song. Synthetic

sound was also used, consisting of a continuously frequency-modulated signal varying between 10 Hz and 1.4 kHz. Sonograms of these signals were presented in Mobley et al. (1988) and their characteristics are shown in Table 5.1

Table 5.1

Sound conditions used during playback studies

A listing of the sound stimuli used in the playback experiment. The approximate bandwidth and social context are given.

Principal sound	Bandwidth	Social context
Feeding call	400-550 Hz	made by single presumed female during lunge-feeding episode; recorded in southeastern Alaska (Baker, 1985)
Social sounds	200 Hz-3.0 kHz	large surface active pod; presumed to be multiple males competing for access to single female (Silber, 1986)
Winter song	50 Hz-10 kHz	produced by single male; may function as an intra- and/or inter-sexual display (see review in Helweg et al., 1992)
Synthetic sound.	10 Hz-1.4 kHz	(produced by waveform generator)
Blank tape		(used as control condition)

Playback trials were conducted off the northwest coast of the island of Hawaii in Kawaihae Bay and off the south shore of Maui (see Figure 3.1). The vessel was between 0.5 and 3.5 km offshore during the trials (mean = 1.1 km, S.D. = 0.8 km).

The sounds were presented in a randomized schedule and included a blank tape control condition to control for observer effect. A shore-based team visually observed each trial and remained blind to sound condition. The shore team used 7x35 binoculars to observe behavior, and followed whales and vessels with a theodolite to determine

whale and vessel positions. The theoretical error of the theodolite is < 1% of the range of the measurement. Empirical measurements of range error at ranges < 6 km were also < 1%.

An A-B design was used, where the "A" phase was a 20 minute baseline period and "B" was a 20 minute presentation of the sound stimulus. The playback vessel was maneuvered into the path or proximity of the whales prior to the beginning of the trial so that the whales would be within the range of the transducer at the beginning of playback.

Description of Transmission Loss Calibration Study

Two methods were used to estimate transmission loss: empirical measurements of calibration sounds and theoretical calculations from established equations. The sound propagation characteristics of Kawaihae Bay were examined empirically by broadcasting frequency-modulated sweeps (100-300-100 Hz) to a three-element hydrophone array. A Marantz PMD-430 cassette tape deck played the signal into a pre-amplifier and a Tandy equalizer. An AB Systems amplifier powered a Navy J-9 transducer deployed at 7 m depth. The frequency sweeps were broadcast at various ranges and bearings from the hydrophone array on two different days (9 Feb. 1989 and 11 March 1989). The transmissions were recorded with the array. Each element of the array radio-transmitted its signal to a shore-based receiver connected to a TEAC R-61D four-channel analog tape recorder. The recording gain was adjusted with a step attenuator in 10 dB increments (Clark et al., 1986). The frequency response of the array was flat from 100 Hz to 5 kHz.

The analog recordings were re-recorded with a TEAC RD-135T digital audio tape (DAT) deck in four-channel mode. The digitized signals were acquired and processed at Cornell Laboratory of Ornithology's Bioacoustics Research Program facility using a customized signal processing workstation operating an advanced version of Canary software (Charif et al., 1993). This signal processing package acquires and analyzes

sound samples. A 4 kHz/channel sampling rate was used. The received level at 300 Hz was measured from sonograms of the received frequency sweeps. The analysis bandwidth was 24.18 Hz. The peak amplitude at 300 Hz was used because the signal-to-noise ratio was best at this frequency. The empirical transmission loss curve is therefore based upon transmission at 300 Hz. The transmission characteristics of other frequencies are assumed to be similar since the frequency range was small.

The closest amplitude measurement during calibration was 22 m. The source level of the projector was estimated by adding 26 dB (20 log (22)) to the measurement taken at 22m. The amplitude measurements were corrected for the hydrophone sensitivity, the transmitter and receiver gain, and pre-amp gain to produce the estimated received level. These resulting amplitudes were plotted against the range between the playback vessel and the receiving hydrophone array element, producing an empirical transmission loss curve for Kawaihae Bay. A logarithmic curve was fit to the empirical transmission data to produce an empirical transmission loss curve. The standard error of the spreading term was calculated. The 95% confidence limits of the transmission loss curve were calculated by increasing and decreasing the spreading term by twice its standard error and recalculating the curve.

This curve was compared to a theoretical curve derived from the Marsh and Schulkin (1962) semi-empirical model, as described in Urick (1983). Parameters of this model were set according to conditions at the time of the calibration broadcasts as follows: The model has three different transmission loss (TL) equations for different water and sound layer depths and operating ranges. The comparison of the range and the calculated value H determines which equation is appropriate.

$$H = \text{sqrt}\,[\ 1/8(D + L)]$$

Where D is water depth in feet, L is the layer depth in feet and H is in kiloyards. The mean water depth for all trials of 951 ft (290 m) was used along with a sound layer depth

of 246 feet (75m) which corresponds to the depth of the thermocline. The value of H determined by these variables was 12.2 kyds (11.2 km). When the transmission range is less than the calculated value of H, then the shallow water equation is used to calculate transmission loss (TL):

$$TL = 20 \log r + \alpha r + 60 - k_L$$

where r is range in kiloyards, α is the absorption coefficient, and k_L is the "near-field anomaly." The α value used was 0.1 and the k_L value was 6.1, which represents a rocky bottom with a sea state of 2, typical experimental conditions.

Calculation of received levels of playback trials

Whale movement patterns during experiments that evoked rapid approaches were plotted and the separation between the whale and vessel at the onset of playback was calculated. This separation distance was used with the transmission loss curve was used to generate transmission losses. Broadband received sound levels were calculated by subtracting the estimated transmission loss from the 163 dB broadband source level.

Thirteen of the 24 analyzed playback experiments were conducted in Kawaihae Bay and remaining 11 off Maui. The transmission characteristics off Maui are likely similar at short ranges to those found in Kawaihae Bay, as the operating depth and bottom topography were similar.

RESULTS

Transmission Loss Measurements

Figure 5.1 shows the empirical measurements of the received level of a 24 Hz band centered at 300 Hz of the frequency sweeps plotted against range between the broadcasting vessel and the receiving hydrophones. A logarithmic curve of the form **TL = - a[log(range)]** was fit to the data. The resulting equation was:

$$TL = -\ 17.61\ (+/-2.38)[\log(Range)]\ dB$$

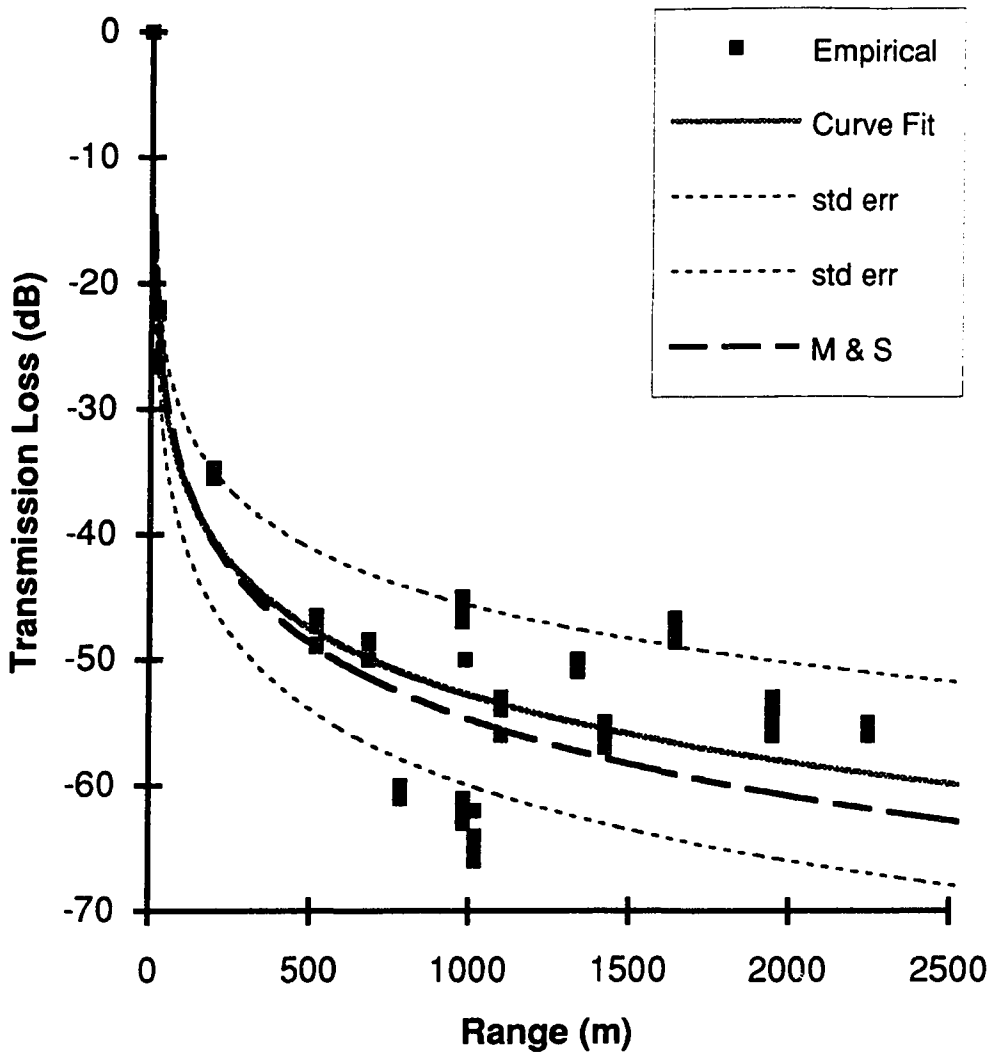

Figure 5.1
Kawaihae Bay Transmission Loss

Two curves are shown the logarithmic curve fitted to the empirical data with its error range and the Marsh and Schulkin curve. There is strong agreement between these two curves.

The r^2 for this equation was 0.74. The spreading term of 17.61 had a standard error of 1.19. The 95% confidence limit of the spreading term was taken as +/- twice the value of the standard error. This equation was used to estimate received levels of playback trials by using the range from the whale to the vessel at the time of onset of playback.

The Marsh and Schulkin curve for shallow water was also plotted (Figure 5.1). The shape of the curve fitted to the empirical data and the theoretical curve shows remarkable agreement. The difference in transmission loss between the empirical and Marsh and Schulkin curve was 1.8 dB at the mean responding range of 928 m and 3 dB at the maximum range of 2807 m.

The ambient noise was measured from the same sound samples used to determine received levels. Ambient noise was measured between successive frequency sweeps, when the sweeps were not being broadcast. The mean spectrum ambient noise level measured at 400 Hz was 64 dB re $1\mu Pa^2/Hz$. The integrated value over the 0-2000 Hz band was 99 dB re 1 μPa.

Playback Experiment Results

A total of 143 playback trials were conducted. Twenty-seven of these trials produced rapid approach responses. Most of the responses were to the feeding call; (21.6% of the pods that were tracked within 3 km of the vessel approached the vessel) and social sounds (8.3% of the pods approached). The conditions of synthetic sounds and song elicited approach responses in 4.1% and 3.4% of the pods tracked, respectively. Theodolite data were available for 24 of the 27 observed rapid approach responses. Only trials that included theodolite data were used in the analysis.

Analyses of covariance (ANCOVA) were conducted to test if sound condition affected the separation between whale and vessel. The mean separation during the playback phase was used as the dependent variable and the mean separation during the

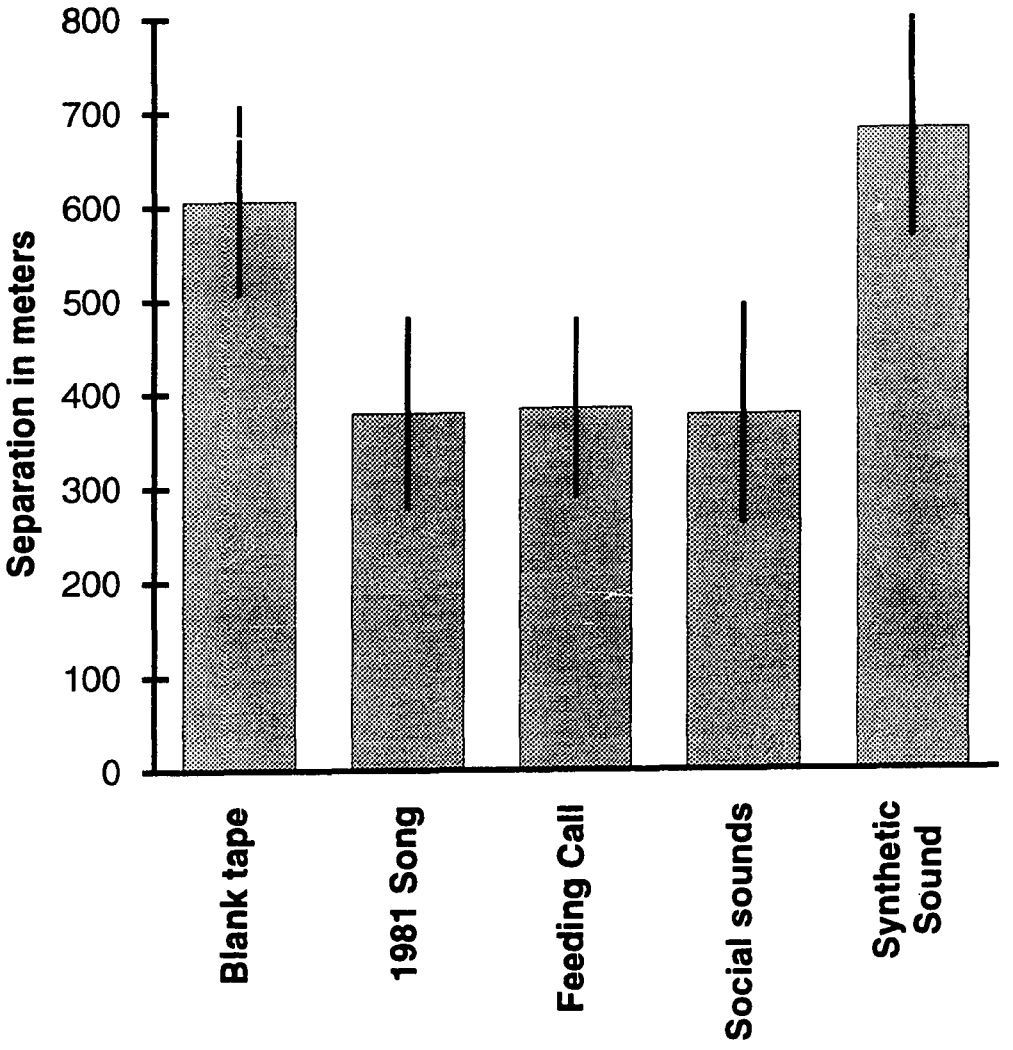

Figure 5.2
Whale-Vessel Separation

The least square means for whale-vessel separation shown. Significantly closer approach is seen in response to feeding call, social sounds and 1981 song.

baseline period was used as the covariate. This procedure controlled for variability due to initial distance. Responses to experimental conditions were compared with blank tape control.

Sound playback condition was found to significantly affect the separation between the playback vessel and the whale [$F(5,401) = 2.94$ $p < .05$]. As shown in Figure 5.2, post-hoc comparisons found that playback of feeding call, social sounds or outdated song produced significantly smaller separation distances ($p < 0.05$).

Whale speed was also examined with a similar Analysis of Covariance. Three sound playback conditions were found to significantly affect whale speed [$F(5,330) = 4.04$, $p < .05$]. Figure 5.3 shows that significantly higher ($p < 0.05$) whale speeds were observed following playback of feeding call, social sounds or synthetic sound than playback of the other sound types.

These analyses showed that playback of feeding call or social sounds produced changes in both separation and whale speed, indicating the ability of these sounds to alter whale behavior. Outdated (1981) song resulted in changes in separation but not whale speed. Synthetic sounds resulted in a change in speed, but not separation.

The statistical evidence demonstrates the strength of the sound stimuli to affect whale behavior in general. Further, some trials elicited a rapid approach response that was an unambiguous indication of sound detection by the whale. This response could be used to determine a received level at which humpback whales respond. Only approximately 8% of all pods tracked within 3 km of the sound projector showed the rapid approach response (27 out of 338). The distances between the whale and the playback vessel were calculated at the onset of playback for all rapid approach sessions that had theodolite data. The median distance was 686 m with a maximum range of 2085 m. Estimated received levels were then calculated using the logarithmic curve fit to the

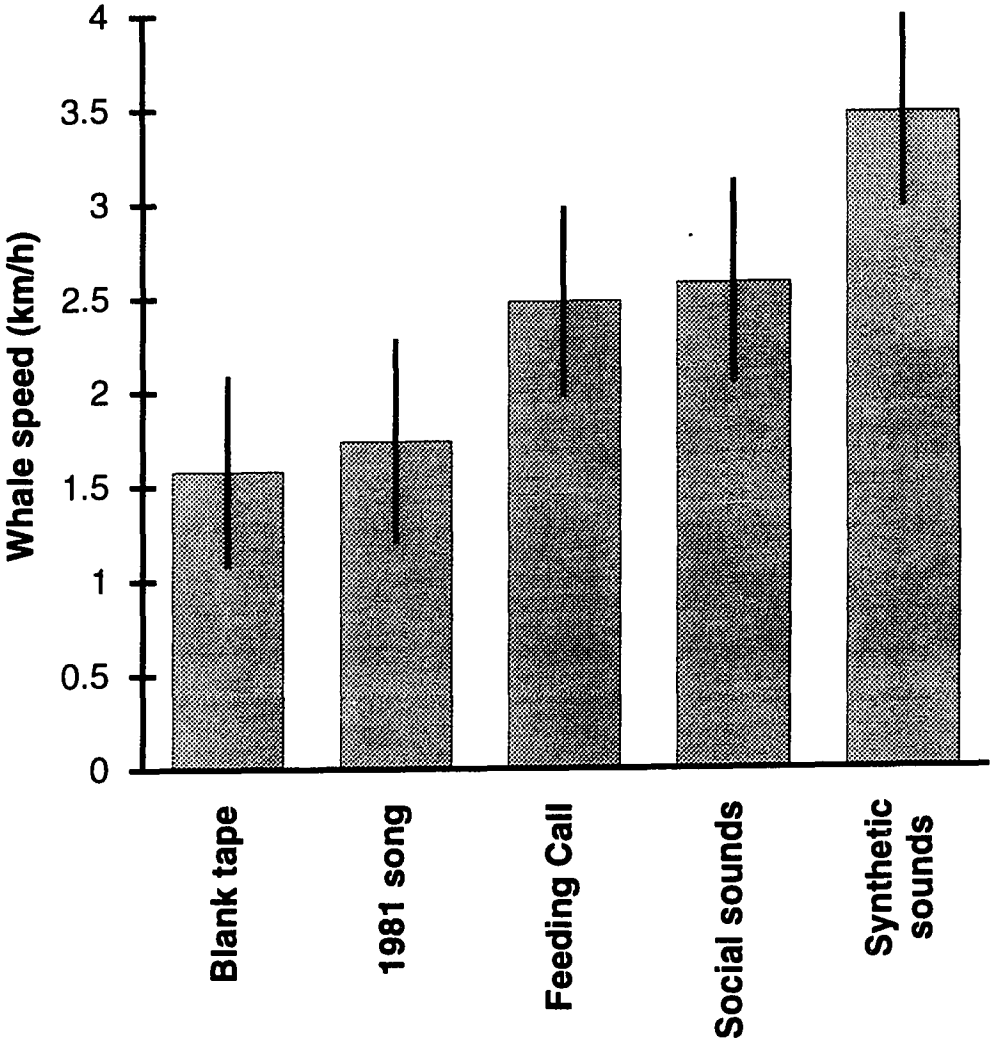

Figure 5.3
Whale Speed

The least square means for whale speed are shown. Significantly higher whale speeds can be seen following presentation of feeding call, social sounds and synthetic sounds.

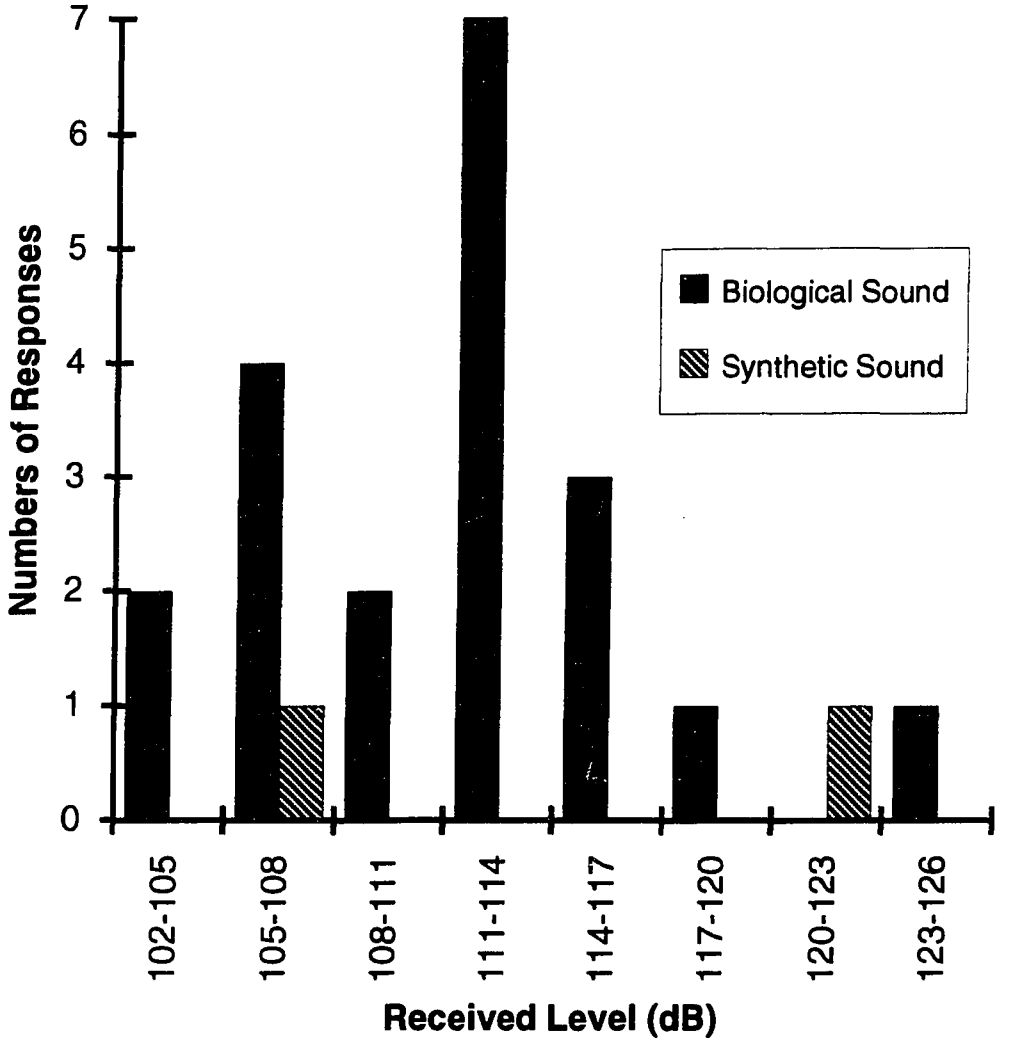

Figure 5.4
Distribution of Rapid Approach Responses by Received Level

The distribution of responses is shown as a function of receved level. The lowest level that produced a response was 102 dB (with a signal-to-noise ratio of 16 dB).

empirical data (Figure 5.1). Figure 5.4 shows the numbers of responses by condition as a function of received level.

Received Sound Pressure Levels

Table 5.2 lists the estimates of received level, based upon the separation distance at onset of playback. The reported received levels represent the mean of the levels determined from the empirical transmission loss curve. The lowest received level estimate for a trial inducing a response was for a feeding call trial: 103 dB (95% confidence limits = +/-8.2). Trials that used a biological stimulus (feeding call, outdated song, social sounds) had a median response level of 113 (+/-6.7) dB. Estimated median received levels for the synthetic sound trials were 113 (+/-6.7) dB (N=2), with a minimum level of 106 (+/-7.6) dB.

Table 5.2

Calculated Received Levels from Playback Trials that Resulted in Rapid Approach Responses (dB re 1 μPa)

Received levels for both biological and synthetic sounds were estimated with the separation distance between the whale and sound projector at the onset of playback. Minimum received levels were 102 dB re 1 μPa for biological and 106 dB for synthetic. Only trials with supporting theodolite data are included.

	Biological Sound	**Synthetic Sound**
Mean	113.3	113.3
Std Deviation	7.5	9.9
Median	112.7	113.3
Minimum	102.2	106.3
Maximum	131.9	120.
N	22	2

Feeding call had a measured bandwidth of 150 Hz. Thus the broadband minimum response level of 102 dB would have a spectrum level of 80 dB re 1 $\mu Pa^2/Hz$. Ambient noise in the 400-550 Hz band was 64 dB re 1 $\mu Pa^2/Hz$, therefore noise in the same band as feed call would have a broadband level of 86 dB re 1μPa. Thus both broadband and spectrum level Signal-to-noise ratios can be estimated. Both the broadband value (102 dB-86 dB) and spectrum level (80 dB-64 dB) signal-to-noise ratios were 16 dB.

DISCUSSION

The use of biologically meaningful sounds in these playback studies represents an important departure from past studies investigating the auditory sensitivity of free-ranging whales. The rapid approach response provides a clear behavioral marker of detection. The received levels can then be estimated from the range between the sound source and the whale. Analysis of the rapid approach results shows that humpback whales could detect and respond to conspecific sound as low as 102 dB. The median received level was 113 dB. Synthetic sounds elicited a response at a minimum level of 106 dB, with a median level of 113 dB (based on only two instances of approach, in the latter case). These levels are all lower than the 115-124 dB range reported by previous authors (e.g., Malme et al., 1984; Richardson et al., 1991; Richardson and Malme, 1993; Malme, et al., 1985). However all of these studies used a different method to determine response. The 115-124 dB range represents estimated received levels at which 50% of the observed whales changed behavior by avoiding the sound source, whereas in our case, we are reporting estimated received levels for only those pods that approached the source. This produces a conservative estimate, as whales could have detected the signal but did not respond or did not approach the vessel closely enough to be observed as a rapid approach response.

The minimum response levels of 102-106 dB reported here are similar to those obtained by Dahlheim and Ljungblad (1990) for gray whales. The gray whale study used

one-second duration pure-tone stimuli designed to produce an unmistakable indication of detection (startle response). Our results of similar received levels obtained using biologically meaningful sound suggest that the use of such sounds may allow for estimation of the behavioral threshold without using aversive stimuli.

Three of the four sound conditions used in the studies described here (all but synthetic sound) were recordings of humpback whale vocalizations. Two of these vocalizations, feeding call and social sounds, were shown to be attractive to a substantial portion of whales within 3 km of the source, as evidenced by the rapid approach response. Since these studies took place in the context of the winter breeding season, the behavioral responses to these sounds are presumably related to reproduction. Mobley et al. (1988) suggested that the whales who approached the vessel during playback were predominantly males who were responding to the implied presence of a female. This was proposed because the feeding call is believed to have been produced by a female (Baker, 1985), and social sounds are typically produced in surface-active groups typically containing multiple males and a single female (Clapham et al., 1992; Medrano et al., in press). This suggestion was supported by the observation of a singing whale (male) approaching the playback vessel, and the fact that cows with calf never approached. Additionally, no escorts (males accompanying cow and calf pods) approached the source, which would be expected since they were already paired with a female. According to this model, the feeding call should be highest in attractiveness, since it is believed to be made by a female, who may or may not be alone. Social sounds should be next in attractiveness, since they imply the presence of a female, but one who is already accompanied by a group of competing males. Winter song should be lowest in attractiveness, since it implies the presence of a single male. This model does not explain, however, why synthetic sound and winter song should produce several approaches each.

It is conceivable that whales are more predisposed to respond to socially meaningful sounds than to anthropogenic noise. Modern signal detection theory maintains that a response to a stimulus is a combination of sensory impressions and decision processes (Kantowitz and Roediger, 1984). The latter, in part, are based on motivational factors in the form of cost/benefit analysis. If a socially meaningful sound (e.g., feeding call or social sounds) is presented in the context of the winter breeding season, then one would expect a heightened readiness to respond if that sound class is relevant to reproduction. That whales are responsive to biological sounds is further supported by the avoidance reactions of gray whales to orca "scream" playbacks (Cummings and Thompson, 1971; Malme et al., 1983).

The lowest measured spectrum level signal-to-noise ratio in this study was 16 dB. The response of gray whales to orca "screams" can occur at received levels circa 0 dB S/N ratios in the loudest 1/3 octave band (Malme et al., 1983). Assuming that the detection thresholds of humpbacks are similar to gray whales, then our results are probably the lowest that we could measure, rather than the minimum response threshold. The most distant rapid approach response occurred at a range of 2.8 km and we only considered whales within 3 km. Source levels for the experiment were maximized to approximate those source levels described for humpback whale song (Levenson, 1972). The original purpose of the experiment was to investigate the social functions of these signals rather than test for minimum levels of detection (Mobley et al, 1988). Repetition of the experiment with source levels circa 140 dB, for example, would reduce the received level to 79 dB at a range of 3 km. This closer range would be sufficient to permit whales that detect the signal to approach close enough to be classified as an instance of rapid approach. Using lower source levels in this fashion could potentially provide a better estimate of detection threshold.

In summary, sound playback has proven to be a useful paradigm for investigating the functions of animal vocalizations. Playback studies using cetacean subjects have demonstrated clear behavioral responses, primarily in the form of attraction, to conspecific vocalizations (e.g., Clark and Clark, 1980, for right whales; Morgan, 1979, for beluga whales; and Tyack, 1983; Mobley et al., 1988, for humpback whales).

We are proposing that future attempts to assay the acoustic sensitivity of whales be expanded to include responsiveness to conspecific vocalizations in addition to anthropogenic noise. The rapid approach response described here for humpback whales is an example of a clear indicator of acoustic detection that can be used to estimate received levels as a response threshold. Such techniques currently represent the only feasible method of determining such thresholds in free-ranging cetaceans.

Chapter 6
Synthesis and Summary

The previous chapters have introduced the topic of humpback whale reproduction and discussed findings about behavioral and ecological components of the mating system. Clutton-Brock (1989) stated that mammalian mating systems arise as a result of the mating strategies used by individuals. This chapter will synthesize some of the findings reported in this dissertation with previous work to provide a comprehensive description of humpback whale mating strategies and how they contribute to the mating system as it is exhibited in Hawaiian waters.

Because our level of understanding is still focused on describing the mating strategies and mating system, most of the explanations offered will be at a proximal level. Selection pressures that might have driven the evolution of the observed behaviors will receive less attention, because the proximal mechanisms are not yet well defined.

As described earlier, the operational sex ratio of humpbacks is skewed; there are more reproductively active males than females (Baker et al., 1987; Clapham and Mayo, 1987; Herman and Tavolga, 1980). This has apparently resulted in two male reproductive strategies: singing and physical competition. Males can switch roles from singer to escort and back (Tyack, 1981; Baker and Herman, 1984a). Males in surface active groups appear to compete for reproductive access to females. Once the other males have left the pod or been forced out, the lone remaining escort presumably mates with the female, although this has not been observed. It is unknown if the female simply accepts the 'winner' of such competition or if she exerts active choice in this situation. This could be accomplished via influencing the competition or by rejecting the 'winner.'

In a review of mammalian mating systems Clutton-Brock (1989) proposed that variation in male mating behavior is determined by four characteristics. These are the effectiveness of male parental care, the defensibility of female ranges and core areas, the

size and stability of female groups, and the density and distribution of females in space. In the case of humpbacks, males do not provide parental care. Females appear to range over a large area on the breeding grounds, and these ranges cannot be controlled by the males. Female humpbacks do not appear to group together, and may avoid other females (Herman and Tavolga, 1980; Tyack, 1982). The final factor considered by Clutton-Brock (1989) is that of female distribution. This can be approached on a number of different spatial scales; i.e. within the waters adjoining a portion of an island, within the waters adjoining all of the islands of Hawai'i, or within the North Pacific. It is reasonable to decide which scale to use based upon what an individual male humpback will experience, i.e., the local or near an island scale. On such a scale, females are considered to be solitary and unpredictably distributed. The model then predicts roving males defending individual females. This certainly matches much of the observations of humpback behavior. Thus the mating system of humpbacks is probably female defense polygyny or promiscuity. It is unknown if females mate more than once, but it is possible, given the short-term affiliation of pod members (Mobley and Herman, 1985; Tyack and Whitehead, 1983).

Early observation of singers in Hawai'i led to the suggestion that song may function in maintaining spacing between singers. This was based on the observation that singers were never closer than 5-10 km (Tyack, 1981). The results presented in chapter 3 support that observation. The average separation between singers was 6.6 kilometers and the median distance was 6.0 kilometers. Examining the change in separation over one hour compared to the initial distance between singers shows a clear trend for singers located closer than 4.5 kilometers apart to move away from one another.

Observations on Silver Bank in the Caribbean Sea have shown that singers are typically separated by 100-500 meters, rather than the several kilometers seen in Hawai'i (Whitehead, 1981). On occasion, singers in Hawai'i have been observed within 1 kilometer of another singer (Cerchio, pers. comm.). This occurred during the seasonal

peak in abundance, when the highest number of animals are present in the area. The density of humpbacks on Silver Bank is far greater than that of Hawai'i. This leads to the possibility that singing may indeed function in spacing animals, but that the distance between individuals is density-dependent. When there are more whales in a given area, less distance can be maintained between singers.

Singers have typically been described as lone, stationary males, who sing while in a "singing posture," that is head down, tail up at about 45°. A large number of whales sing in this fashion, but not all. Tyack (1981) described actively singing whales pursuing other whales at speeds up to 1.7 km/h (although not all singer speeds were reported). Bauer (1986) reported a mean singer speed of 3.86 km/h. This value could be biased by the inclusion of "suspected singers," animals that appeared to be singers but were not confirmed by boat observation. Speed values found here were lower than Bauer's (1986). The visual data gave a mean of 1.7 km/h and a median of 1.4 km/h. Acoustic data provided a mean value of 1.6 km/h with a median of 1.2 km/h. The acoustically derived speeds were calculated from first to last point, so they are probably underestimates. The clear picture is that the average singer speed was lower in Kawaihae Bay than that found off Maui. There were some individually high values in Kawaihae Bay, which appears to reflect a portion of the population that appears to be swimming actively while singing. Some of the perceived movement can be accounted for by singers drifting passively with the current, although Figure 3.3 showed four singers moving in three different directions simultaneously.

One question that follows from the consideration of moving singers is whether or not the differences in movement patterns while singing reflect any other parameter. For example, do certain age classes sing while swimming while others remain stationary? Are there differences in the songs of stationary and moving singers? What is the effect of the presence of other whales on singer movement?

One of the main variables describing the distribution of humpback whales has been their nearshore (within 100 fathom) preference (Herman and Antinoja, 1977; Herman et al., 1980; Chittleborough, 1953). This is supported by recent aerial observations showing the mean water depth in which whales were found was 51.4 fathoms off the four island region of Maui, Molokai, Lanai and Kaho'olawe (Forsyth et al., 1991). Furthermore, Mobley et al.,(1994) found that 74% of all whales were found within the 100 fathom isobath, despite the majority of observation effort being concentrated outside the 100 fathom isobath. All of these studies are visually based. Singers typically have long dive times of 15-25 minutes in length; so that they are less easily sighted on aerial surveys. Acoustic location removes that difficulty in tracking singers. The acoustic data from Kawaihae Bay show that singers were located up to 12.9 km offshore, in water as deep as 305 fathoms (558 meters). The median depth was 109 fathoms (199 meters). Of 62 singers tracked in this study, 31 were inside the 100 fathom contour and 31 were outside of it. Clearly, singers are not constrained within the 100 fathom isobath and were found throughout the bay.

Neither were singing whales distributed randomly with respect to depth. The overall density of singers within the 100 fathom contour was almost four times the offshore density (0.62 v.0.17). Therefore singers utilize the nearshore waters of Kawaihae Bay more heavily at the same time that a significant number of them are found offshore. What factors contribute to this pattern? Certainly there is potential for differences in acoustic propagation quality that could affect the propagation of the song. Nearshore areas offer the shallow bottom as a possible acoustic reflector. Other species use their environment to increase the amplitude of their display. Mole crickets dig burrows in the shape of acoustic horns and perch inside to amplify their signal (Forrest, pers. comm.). Alternatively, the deep water offers an environment free of obstacles to reflect and dissipate sound energy.

Whatever the trade-offs in better acoustic propagation characteristics, these are likely secondary to the distribution of females, the probable target of the song. Mothers and calves show a preference for shallow water (Glockner-Ferrari and Ferrari, 1990). Mothers with calves certainly attract the attention of a large number of escorts (Tyack and Whitehead, 1983; Baker and Herman, 1984; Mobley and Herman, 1985; Clapham et al., 1992; Medrano et al., in press). This attention is in spite of the low post-partum ovulation rate of 8.5% (Chittleborough, 1958). Certainly the distribution of 'adult females,' or reproductively active females without a calf, is important as well. Unfortunately, the specific distribution of adult females relative to all other whales is not well known. We can only rely on the shallow water tendency for all adults whales and the finding of equal mean depth preferences for pods with and without calves in the four-island and Penguin Bank regions (Forsyth et al., 1991). Future work combining photographic and genetic sexing techniques with GPS location technology can help to clarify the distribution of adult females. Based upon what we know about the distribution of females, it is likely that singers in Kawaihae Bay prefer shallow-water areas.

This raises the question of why singers are located offshore. If the nearshore areas are truly preferred, perhaps the offshore singers are younger males that are not able to vocally compete with older males. In territorial systems of songbirds, younger males typically occupy lower quality territories, assuming that they can maintain one at all (Payne, 1985). If this is the case then differences in the songs of inshore versus offshore singers may be detectable. Within males, the fundamental frequency of mammalian vocalizations typically varies between mature and juvenile animals (McGlone, 1966). Amplitude is another potential variable that might indicate fitness of the singers, although it was shown in chapter 4 that there was no relationship between range and amplitude. If such correlations between song structure and age or habitat usage exist, then song could be conveying this type of information about the singer to the listeners, both male and female.

Considering the listeners raises the issue of how other whales respond to the song. Tyack (1981) described the tendency for all classes of whales to avoid singers. However, this is not an absolute. Tyack (1981) reported a few instances of other whales approaching singers, including a mother and calf. Darling (1983) cites four approaches of other whales toward and affiliating with a singer. These whales turned out to be males. Medrano et al (in press) cited two instances of females (without calf) approaching singers, although they did not describe the behavior that took place during this approach. So while interactions with singers initiated by other whales are rare, they do occur. Tyack (1981) reported that 13 of 28 whales that stopped singing joined other whales. Most of these involved the whale stopping singing and pursuing another whale. In all of these cases the singer stopped singing before or as it joined the other whale(s). Therefore male-initiated interactions with other whales are fairly common, but they are rarely still singing when these interactions begin (but see chapter 3 for an example of a singer joining another whale and continuing to sing).

What can these interactions reveal about song function? The fact that both males and females interact with singers support the hypothesis that song has both intersexual and intrasexual functions. The main intersexual function is likely mate attraction. This fits well with similar models of function of bird songs used to attract females (Catchpole, 1987). Other proposed intersexual functions such as synchronization of ovulation may exist as well (Baker and Herman, 1984a) . The proposed mechanism of female attraction is that the displaying male broadcasts to the females. The information included in the song includes at minimum information about location and species. The inter-individual variation in song structure discussed earlier raises the possibility of individual-specific information being included in the song as well; Such information may be used by other whales to assess the fitness-related characteristics of the singer. Females swimming through an area with multiple singers would have the opportunity to assess them. If the female finds a song

attractive, indicating an attractive potential mate, she may approach and affiliate with that male or allow a pursuing singer to join.

Darling (1983) described the approach and interactions of lone adults with singers. He reported three categories of interactions. In the first type, the pair of whales would roll at the surface and slap their pectoral fins on the surface, and then swim off together. A second type of interaction is typified by the two whales affiliating for one surface sequence and then disaffiliating, with one or both then beginning to sing. Finally, the two whales might begin a sequence of aggressive behaviors. All of the lone adults that Darling (1983) sexed were male, however the number was not reported and it was not stated whether known males participated in each of the types of affiliations he described. Certainly the last two categories were the result of interacting males. Pods composed only of males have been seen to engage in agonistic or competitive behavior (Clapham et al., 1992). Tyack (1981) described an affiliation of two males that had been singing separately. Both these two animals swam off together for at least 30 minutes, but did not display surface behavior (e.g., flipper slapping).

These types of interactions are rare given the number of singers and non-singing males that are found during the mating season. Lone adults and singers have been observed to pass close by without interacting (Tyack, 1981). Why are these interactions rare? Darling (1983) suggested that male humpbacks form a dominance hierarchy. He proposed that aggressive contests were used to establish each individual's place in the dominance structure. Possibly the low incidence of agonistic encounters between males is due to a knowledge of their rank in a dominance hierarchy.

The difficulty with such an interpretation is that one basic component of the dominance hierarchy does not appear to apply to humpback whales. Members of a dominance hierarchy must interact on a frequent basis to maintain the hierarchy. Otherwise the changing status of each individual would eliminate, if not prevent, any dominance

structure. Humpback whales move throughout the island chain while in the breeding grounds (Cerchio et al., 1991). On average, 14% of humpback pods experience a change in membership each hour (Mobley and Herman, 1985). In conclusion, the transient nature of humpback whales social groups seems to rule out a dominance structure. Intersexual interactions and competition clearly occurs, but the formation of a dominance hierarchy seems improbable.

The first type of affiliation noted by Darling (1983), flipper slapping and then swimming together, could result from a female approaching and joining a singer. The lack of agonistic behavior and the longer duration of the affiliation are consistent with a male-female interaction.

The interactions of non-singing males with females also need to be considered. Surface active groups consisting of multiple males, presumably competing for reproductive access to females, have been described previously (Baker and Herman, 1984a; Tyack and Whitehead, 1983). The escorts in these groups have been identified as males (Clapham et al., 1992; Medrano et al., in press). Singers have been observed to stop singing and join these groups, and displaced escorts have been observed to begin singing (Tyack, 1981).

The typical behavioral pattern for males in these groups is to acquire and maintain the position of the primary escort, which is the animal that maintains the closest proximity to the female (Tyack and Whitehead, 1983; Baker and Herman, 1984). Multiple males have the same goal and the primary escort is replaced by a new animal every 8.5 hours, on average (Tyack and Whitehead, 1983). While not demonstrated, it is presumed that if a primary escort can displace other escorts out of the pod, then that male will at least have an increased probability of mating with the female. A stronger interpretation is that this may be a passive form of mate choice; the female accepts whatever male wins the contest.

Thus two male strategies have been discussed: singing and physical competition. These two strategies have been well known for years. Truly alternative strategies where

the reproductive value of each strategy are equal rarely occur (Partridge and Halliday, 1983). It is more likely that one of the strategies has a higher probability of successful reproduction than the other, but which one? I propose that physical competition is the preferred strategy. Singers have been observed to stop singing in order to join surface-active (or competitive) groups while escorts that have been displaced out of a surface-active group are observed to resume singing (Tyack, 1981).

Engaging in physical competition is characterized by large benefits and large costs. The primary benefit is the close physical proximity of a female. It has been suggested that these groups form around females that are in estrus (Baker and Herman, 1984a; Tyack and Whitehead, 1983). Thus the female at the center of the group may be reproductively active. The costs involved are long periods of swimming at greater than average speeds, the energy used to deliver physical blows to other escorts, and the potential for injury while competing. It is not unusual for an escort's leading edges of fins and the rostrum to be rubbed raw and one animal was observed to have blood flowing freely from a wound (Baker and Herman, 1984a).

Singing appears to have lower costs and lower benefits. Singing in birds and anurans is a very costly activity (Taigen and Wells, 1984) . However, it does not appear to be so in humpback whales. A calculation of energetic cost based upon the sound pressure output, and assuming a 1% conversion efficiency from chemical to sound energy, found that only 700 calories were needed to sing for 24 hours, a small fraction of any reasonable estimate of the resting metabolism (Helweg et al., 1992). These small costs may be balanced by the low rate of approach to singers by females.

What has been added to this framework is evidence for avoidance and perhaps spacing between singers, the wider range of behavioral contexts in which singing can occur, and the establishment of the existence of inter-individual differences in humpback song. The next step is to attempt a model of the male reproductive strategy. Much of this

model is based upon the assumption that both males and females are capable of receiving and utilizing the differences in an individual's songs. These differences may or may not indicate anything about the animal's fitness or ability. In either case, the existence and utilization of these differences is the important parameter. Whether or not these differences reflect the singer's fitness is more of a concern for understanding how the system evolved, not how it currently operates. The operational aspect is whether or not females use the differences in song in making reproductive choices.

For the purposes of this model, two classes of singer and song are considered and are summarized in Table 6.1. "Preferred" songs would have whatever feature is more attractive to females or more effective at maintaining spacing between singers or minimizing interference from other males. "Average" song and singer would represent the less attractive portion of the population in song attractiveness or effectiveness.

The first situation is a male alone. Whales with a "preferred" song should definitely sing. The cost is low, and with a high quality display, it may attract a female. Males with an "average" song should sing if the density of other whales is low. If the density is high, then that whale should not sing, relying instead upon active search or acoustic detection of surface active groups. Possible gustatory detection of estrus females cannot be ruled out. Dolphins, for example, appear to sample the excretory products of other pod members (Norris and Dohl, 1980).

If a female is detected, then both "preferred" and "average" singers should approach and affiliate with her. The "preferred" whale should sing while approaching because of its preferred song. An "average" male should approach silently. This might explain the low incidence of singing escorts, although it should also be considered that song may be sung only in a particular stage of courtship, which could also explain the low frequency of observation of singing escorts.

If a surface active group is detected, then it is logical to predict that both "preferred" and "average" singers should join the group. The probability is very high that the group contains a female. However, not all singers stop singing and join a surface active group (Tyack, 1981). This may be due to two factors. Surface active groups produced social sounds, which may function as acoustic threats (Silber, 1986; Mobley et al., 1988). Singers may be less motivated to join groups that produce such sounds. They may be able to assess the fitness and numbers of escorts in the pod. Silber (1986) concluded that most of the escorts produced social sounds, since the call rate increased with increasing pod size. It may not benefit singers to join large pods containing fit escorts. Males in surface-active groups have never been heard to sing.

The next situation to consider is single escorts in a mother, calf and escort pod, as first described by Herman and Antinoja (1977). Escorts are primarily observed as silent, while a small percentage have been observed singing while escorting (Baker and Herman, 1984a). Perhaps singing by escorts only occurs in the final stages of courtship. Alternatively, singers with a "preferred" song may sing to increase their chances of successful mating while those with average or less than average song remain silent. This also minimizes the risks inherent in physical competition. This hypothesis could be tested by sampling the song of singing escorts and comparing it to the songs of other singers that were recorded at the same time, to control for song structure evolution. The hypothesis would be supported if differences in lone singer and escort song were found.

If there are differences in the song, and if they reflect differences in the singers, then it is possible to predict where each class will be located. "Preferred" singers should be located in the nearshore waters, where most of the females are believed to be located. The "average" singers should be located further offshore, perhaps outside of the 100 fathom isobath. It may be possible to test for an association of song features with distance offshore. However, this simple model assumes a uniform or random distribution of

females. If females were clumped, then the distribution of singers will probably reflect that of the females.

Table 6.1
Model of Male Strategies

This Table shows the predicted responses of a "Preferred" and an "Average" male in different male social contexts

Male Context	"Preferred"	"Average"
Alone	Sing	Sing
Alone, detect S.A.G.*	Join	Sing
Escort	Sing	Don't Sing
Displaced from S.A.G.	sing/search	Sing
Alone and detect female	sing & approach	approach silent
Probable location	onshore/near females	offshore, away from females

*S.A.G. = Surface Active Group, in which physical competition typically occurs.

A critical consideration in this discussion is how females react to the various male strategies and behavior. Specifically, do females exert active mate choice? An absolute answer is not available, because mating has never been observed, so mate choice cannot yet be described. However, one can make predictions based upon what is known of the mating system. It has been argued that song complexity is the result of inter-sexual selection (Tyack, 1981). If so, then this implies that active female choice has occurred, as that is the mechanism of intersexual selection.

Presumably, all of the choices and strategies employed by both sexes have shaped humpback whale song. This display is notable for three components of its structure; its complexity, the seasonal change of its structure, and the convergence by all singers on a common version of song, even as it evolves. Female preferences has been shown in other species for greater song complexity. Catchpole (1980) found that male *Acrocephalus*

warblers with more elaborate songs were paired with females earlier. Additionally, male great reed warblers with larger song repertoire sizes attracted more females and produced more young (Catchpole, 1986; Catchpole et al., 1985).

One of the most difficult portions of song to explain is the slow change in structure (Guinee et al., 1983; Payne et al., 1983). Payne and Payne (1985) have raised the possibility that such change may serve an anti-habituation effect. This hypothesis is supported by analogy with results from the advertisement calls of frogs. Tungara frog calls have two components (Rand et al., 1992). The first, a "whine" is very constrained in acoustic structure and appears to function in species recognition. The second component, the "chuck," has a variable structure. Rand et al. (1992) demonstrated that variation in this call, even novelty, could increase its effectiveness at attracting females. This apparent female preference for novelty in Tungara frogs might operate in female humpbacks as well. A female humpback preference for novelty or innovation could explain the evolutionary nature of humpback song.

Another mechanism that might explain the evolution of song structure is modeled upon the behavior of indigo buntings. One-year-old males do not yet have adult plumage. Some of the yearlings mimic older adults. The mimics shown an increased reproductive success compared to non-mimicking immatures (Payne, 1982). This suggests that the evolution of song structure might result from younger males mimicking more mature males. Why the matures males would continue to innovate new structures remains unknown, although female preference for novelty would explain this.

Whatever sexual selection mechanism gave rise to the changing structure of song, it is almost certainly due to inter-sexual selection, as female preferences in other species appear to select for signal complexity (Baker et al., 1986). This is consistent with all models of sexual selection, i.e. runaway, sensory exploitation and good genes (Harvey and Bradbury, 1991).

The final quality of song that is puzzling is the convergence by all singers upon a common version of song, aside from the inter-individual variation. One possible explanation would be a exaggerated form of what is known as the "Honest convergence theory" (Rothstein and Fleischer, 1987) . This was described to explain the convergence of cowbirds on a common local dialect. Animals that move into the area begin to mimic and sing the local dialect. In this particular system, the ability to sing the local dialect indicated that the animal had been in the area for a substantial amount of time, and was therefore an older male. Male age was correlated with reproductive success, and females appeared to use the ability to sing the local dialect as an indicator of male age and made mate choices based on the criterion of local dialect production. It is possible that a similar system could have been in place in the evolutionary history of humpbacks, and that female preference for convergence has led to the entire ocean basin population converging on the same basic version of song, although regional differences are still found (Helweg et al, 1990).

Future Work

The biggest missing piece of the puzzle of the mating system is establishing variation in male mating success and identifying fathers. A unique opportunity to answer these questions is present in the data collected by the YONAH project. This project was a basin scale effort to collect photographic identification photographs and genetic samples from as much of the Northwest Atlantic Ocean population as possible. It is possible to determine parental lines and determine the variation in male reproductive success. If song was collected from sampled males, then it would be possible to correlate song variables with reproductive success. This would establish a reproductive fitness basis for possible female choice.

Appendix 1
Focal Animal Behavioral Ethogram

Respiration

1. No Blow Rise: animal comes to surface with no visible blow. Respiration is assumed.

2. Blow: animal comes to surface with visible blow.

3. Underwater Blow: exhalation of air under surface of water.

4. Linear Bubble Trail: Stream of bubbles released underwater while animal is swimming in a straight line.

Submergence

5. Fluke Down Dive: animal dives, arching peduncle but not throwing flukes into air. Usually medium to long dives.

6. Fluke Up Dive: animal dives, arching peduncle and throwing flukes into air. Usually long dives.

7. Slip Under: animal slips below surface without arching peduncle or lifting flukes. Usually short dives.

8. Unidentified Submergence: submergence was not observed, or was not one of the above.

Feeding (after Jurasz, 1979)

9. Lateral Lunge: animal lunges forward at surface, on side, with mouth open and ventral pleats greatly expanded.

10. Vertical Lunge: animal lunges up through surface vertically, with mouth open and ventral pleats greatly expanded.

11. Small Bubblenet: circular bubblenet less than one half a whalelength in diameter.

12. Large Bubblenet: circular bubblenet more than one half a whalelength in diameter.

13. Flick feed: animal flicks water forward with flukes, concentrating feed in front of it.

14. Other: other type of feeding behavior not included above.

Head behaviors

15. Headrise (Spyhop): animal rises head vertically out of water without open mouth or expanded pleats.

16. Inflated Headrise: animal rises head vertically out of water with mouth full of water and slightly open, and pleats slightly expanded. Water may be pouring out of corners of mouth.

17. Head Lunge: animal lunges forward through water at surface, dorsum up, and without open mouth or expanded pleats.

18. Inflated Head Lunge: animal lunges forward through water at surface, dorsum up, with mouth full of water and slightly open, and pleats slightly expanded. Water may be pouring out of corners of mouth.

19. Other: other head behavior not included above.

Leaping

20. Head Slap: animal rises head vertically out of water, and slaps it on the surface of the water.

21. Breach: animal leaps out of water, usually twisting in mi:air.

22. Unidentified Splash: large splash is observed, but the exact cause cannot be determined.

Fluke Behaviors

23. Fluke Extension: animal extends flukes out of water and holds for a few moments. Animal may or may not wave them.

24. Fluke Slap: animal extends flukes out of water, then slaps ventral surface of flukes on water.

25. Inverted Fluke Slap: animal extends flukes out of water, then slaps dorsal surface of flukes on water.

26. Peduncle Slap: animal extends caudal peduncle out of water, then slaps broad side on water.

27. Fluke Swish: animal swishes flukes back and forth at surface of water, or just below surface.

28. Lateral Display: one half of flukes extends through surface of water, usually with animal swimming on side. Often seen with Lateral Lunge.

29. Fluke Flick: animal flicks flukes at or just below surface, often arching peduncle, but is not feeding.

30. Other: other feeding behavior not included above.

Pectoral Fin Behaviors

31. Pectoral Fin Extension: animal extends one or both pectoral fins into air, and holds it/them there for a few moments. Animal may or may not wave them in air.

32. Pectoral Fin Slap: animal extends one pectoral fin into air and slaps the water's surface

33. Lateral Pectoral Fin Slap: animal is on its side at the surface; animal extends one pectoral fin into the air and slaps the water's surface

34. Ventral Pectoral Fin Slap: The animal is on its back at the surface; animal extends one pectoral fin into the air and slaps the water's surface

35. Rolling Pectoral Fin Slap: animal rolls at the surface back and forth, usually on back; extends then slaps the water first with one pectoral fin and then with the other

36. Other: other pectoral fin behavior not included above

Contactual Behavior

37. Touching with Fluke: one animal touches any part of another animal with its flukes.

38. Touching with Pectoral Fin: one animal touches any part of another animal with its pectoral fin.

39. Touching with Head: one animal touches any part of another animal with its head.

40. Other: one animal touches another part of another animal with any part of its own body other than those included above.

Affiliative/Disaffiliative behaviors.

41. Affiliation between pods: two or more pods or singletons join together to form one pod.

42. Pod Disaffiliation: pod splits into two or more pods or singletons.

43. Coalescence: animals within pod decrease inter-individual distance.

44. Dispersal: animals within pod increase inter-individual distance.

Agonistic Behaviors

45. Head Lunge Displacement: one animal displaces another by head lunging in the direction of, or in the path of, the other.

46. Striking: one animal forcefully strikes another with its head, flukes, caudal peduncle, pectoral fin, etc.

47. Jostling: animals jostle one another for position within the pod and/or relative to some resource.

48. Interposition: one animal moves into the path of another, blocking its movement.

49. Other: other agonistic behaviors not included above.

States And Changes of State

50. Change In Direction by More than 45 Degrees: pod diverts from previous path by 45 degrees or more.

51. Resting: animals(s) resting at surface; not swimming.

52. Moving: animals(s) moving at any rate.

53. Inverted Posture: animal is at surface with ventrum up.

54. Reinverts: animal is at surface and goes from inverted (ventrum up) to normal (dorsum up) position. Used only after Inverted Posture.

Whale States With Respect to Vessel

55. Whale Interposes Before Vessel: animal moves into position in front of vessel, placing itself between the vessel and other pod members.

56. Whale Lays Bubblescreen Before Vessel: animal swims in front of vessel, laying underwater bubble trail. Often crosses path of vessel.

57. Whale Charges Vessel: animal suddenly rushes toward vessel, at or just below surface of water.

58. Other: other vessel-directed behavior by animal not included above.

Appendix 2
Sonogram Parameters

Sound Sampling Parameters

Theme	Sampling Rate (kHz)
Theme 2 Unit 1	4
Theme 2 Unit 2	4
Theme 3 Unit 1	2
Theme 3 Unit 2	2
Theme 4 Unit 1	4
Theme 4 Unit 2	4

Sonogram Computation Parameters

	Theme 2 Unit 1	Theme 2 Unit 2	Theme 3 Unit 1	Theme 3 Unit 2	Theme 4 Unit 1	Theme 4 Unit 2
FFT Size (num. points)	1024	512	1024	1024	512	512
Filter Bandwidth (Hz)	31.72	31.72	24.20	24.20	31.72	31.72
Time Resolution (ms)	32	16	64	32	32	32
Overlap Percentage	75	87.5	75	87.5	75	75
Frequency Resolution (Hz)	3.906	7.812	1.953	1.953	3.906	3.906
Frame Size (points)	512	512	512	512	512	512
Window Function	Hamm-ing	Hamm-ing	Black-man	Black-man	Hamm-ing	Hamm-ing

Spectrogram Display Parameters

Theme	Display Range Hz
Theme 2 Unit 1	500
Theme 2 Unit 2	1000
Theme 3 Unit 1	500
Theme 3 Unit 2	500
Theme 4 Unit 1	1000
Theme 4 Unit 2	2000

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