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A COMPARATIVE ANALYSIS OF HUMPBACK WHALE SONGS RECORDED IN PELAGIC WATERS OF THE EASTERN NORTH PACIFIC: PRELIMINARY FINDINGS AND IMPLICATIONS FOR DISCERNING MIGRATORY ROUTES AND ASSESSING BREEDING STOCK IDENTITY

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A comparative analysis of humpback whale songs recorded in pelagic waters of the eastern North Pacific:

preliminary findings and implications for discerning migratory routes and assessing breeding stock identity

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ABSTRACT

A comparative analysis of humpback whale (*Megaptera novaeangliae*) songs recorded in the eastern North Pacific was performed in order to assess the feasibility of using songs to determine the stock and breeding area identity of migrating whales. Acoustic recordings were made in spring 1997 throughout temperate and subtropical waters of the eastern North Pacific during a marine mammal research cruise (SWAPS) and at the Revillagigedo Archipelago, Mexico during a separate investigation of humpback whales. Songs were analyzed from samples recorded at three distinct pelagic regions of the SWAPS cruise: 1) approximately 2000 km NNE of Hawaii; 2) approximately 1200 km west of San Francisco, California; and 3) approximately 1400 km west of San Diego, CA. These samples were compared to songs recorded during a coincident period at Socorro Island, a humpback whale breeding area in the Mexican Pacific. More than 400 phrases were extracted, qualitatively categorized, and compared. Nine unique phrase types were identified from the Mexican sample of which eight were also identified from the two pelagic samples recorded off California. Reliable comparisons among the four regions sampled were problematic, primarily due to the poor quality of most recordings made during the SWAPS cruise. For future work, we recommend a dedicated effort to obtain high quality recordings of songs for all geographic areas to be compared. Furthermore, songs from respective breeding areas should be characterized quantitatively *before* proceeding with comparative analyses. In the near future, rapid advances in digital signal processing technology and worldwide deployments of acoustic monitoring equipment should make it more practical to use songs as an indicator of stock and breeding area identity. However, at present there other more efficient and reliable methods of accomplishing these goals.

INTRODUCTION

Studying marine mammals in the wild is inherently difficult, especially for those populations with pelagic distributions. Traditional techniques usually require directly observing or collecting samples from animals. Any techniques that allow data to be collected remotely can be quite advantageous. Many species of marine mammals produce acoustic signals in order to communicate with others or sense the environment. Humpback whales (*Megaptera novaeangliae*) are well known for their loud, repetitious songs produced during the winter/spring breeding season and during migration (Payne & McVay, 1971; Matilla *et al.* 1987; McSweeney *et al.* 1989; Clapham & Matilla, 1990; Norris *et al.* 1999). Humpback whale songs, an acoustic reproductive display, probably include information about the identity, gender, reproductive status, and other characteristics that are important for assessing a potential mate or deterring competitors. If the features encoding this information can be identified, they can be used by researchers to obtain important information about the characteristics of an individual, group, or a population of whales from remotely recorded sounds.

During Spring 1997 a research cruise was conducted to assess sperm whale abundance and population structure (SWAPS) in the central and eastern North Pacific. During this cruise, numerous singing humpback whales were detected in pelagic waters using passive acoustic techniques (Norris *et al.* 1999). Of particular interest were songs that were detected and recorded from two distinct regions approximately 1000 and 1500 km west of central (i.e. San Francisco) and southern (i.e. San Diego) California, and a third area 2000 km NNE of the Hawaiian Islands. Norris *et al.* (1999) suggested that the animals off California may have been migrating from low latitude breeding areas in Mexico (e.g. the Revillagigedo Islands), to high latitude feeding areas in the central and western North Pacific and Bering Sea. Because none of these animals were detected visually, traditional techniques (e.g. analyses of identification photographs and biopsies) could not be used to assess their population characteristics. Thus, the only remaining possibility was to analyze recordings of humpback whale songs to determine if they could be used to associate these animals with a particular breeding area.

Songs of closely related species of katydids, crickets and frogs are known to be important for species identification, particularly for sympatric populations (Anderson, 1994). In these organisms, song characteristics are innately determined. However, in many higher vertebrates, including most birds and mammals, at least some characteristics of songs are "inherited" via cultural transmission (Guinee *et al.* 1983; Payne & Payne, 1985; Catchpole & Slater, 1995; Payne, 1996). In several species of cetaceans, researchers have determined a strong correlation between certain characteristics of "vocalizations" and population structure. For example, certain characteristics of whistles from bottlenose dolphins (*Tursiops truncatus*) (Ding, 1995), "calls" from killer whales (*Orcinus orca*)(Ford, 1991; Ford & Fisher, 1982), and "codas" from sperm whales (*Physeter macrocephalus*) (Weilgart & Whitehead, 1997; Whitehead *et al.* 1998), have been determined to be good indicators of social and/or population structure in each of these species.

Previously, songs of humpback whales recorded from disparate geographic regions have been used as indicators of "stocks" (Winn *et al.* 1981; Payne and Guinee,

1983) [1]. In these studies, researchers determined that humpback whales which breed in the same ocean basin sing the same "version" of song, whereas those in separate (e.g. North Pacific, South Pacific, and North Atlantic) ocean basin sing different songs (Winn *et al.* 1981; Payne and Guinee, 1983; Dawbin & Eyre, 1991). This synchronization of song occurs despite the fact that, for any particular population, the current version of song changes continuously throughout the breeding season (Payne *et al.* 1983). Interestingly this synchronized progressive change occurs for animals in separate breeding areas within the population even though some areas may be isolated acoustically from each other (i.e. it is unlikely that whales can directly hear each across geographically separate breeding areas). For example in several studies conducted in the North Pacific, researchers determined that songs recorded during the same breeding season at three separate humpback whale breeding areas (Hawaii, Mexico and Japan) were found to share most, if not all, themes (Payne and Guinee, 1983; Helweg *et al.* 1992; Cerchio, 1993).

Populations of humpback whales have been proposed worldwide based exclusively on song characteristics (Winn *et al.* 1981; Payne and Guinee, 1983; Dawbin & Eyre, 1991) even though a definitive relationship between song structure and population structure has not been proven. In general, however, the results of those studies correspond well to designations of humpback whale stocks determined using more traditional methods of stock assessment (Chittleborough, 1965; Nishiwaki, 1966; Rice, 1978; Baker *et al.* 1986, 1993, 1994; Katona and Beard, 1990, 1991; Calambokidis *et al.* 1997). To date, songs of humpback whales have not been used to determine population structure *within* an ocean basin population. The possibility of doing this depends on whether or not reliable and detectable differences exist between songs from different breeding areas.

Cerchio *et al.* (in press) examined geographic variation in songs recorded from Mexico and Hawaii during the same breeding seasons. Their results indicated that most song components changed both within and between areas in similar ways, while only a few variables remained the same, or changed differently. Although they stated that "local dialects" were not found, subtle but significant, differences were detected in a few song variables between the two breeding areas. Cerchio (1993) suggested that the differences between the two regions could be due to time lags in the cultural transmission of changes in songs between the two breeding areas. In other words, it would take some time for the changes that occur in a given area to be "transported" and then incorporated into songs of animals from a different area. The biological significance of these subtle differences in songs and their relationship, if any, to population structure in humpback whales has yet to be determined.

Evidence from studies of vocal behaviors in other cetaceans indicates that even minor differences in socially or reproductively related vocalizations may be indicative of real differences in population and/or social structure among groups of animals (Ford, 1991; Whitehead *et al.* 1998). It may be possible to determine if subtle differences in humpback whale song structure is a reliable indicator of population structure using photographic identification or genetic methods. Regardless of the outcome of such comparisons, if there are reliably detectable differences in songs from discrete breeding

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1 In these studies the term "stock" implied reproductively isolated populations, however, in this report we use the term "population" is used to indicate this (also see "definition of terms" in Methods).

areas within a population, then it should be possible to use such differences to determine which breeding area that a migrating animal, or group of animals, was associated with most recently (i.e. breeding area identity), and thus its most recent point of departure.

The main goals of this study were:

1.) To qualitatively characterize humpback whale songs recorded from migrating animals at three distinct pelagic regions and compare them to songs recorded from two breeding areas (Hawaii and Mexico).
2.) To assess the feasibility of examining songs from migrating animals to determine their most recent association with a breeding area and/or most recent departure point.
3.) To provide a review and recommendations regarding:
    a.) methods of analyzing and comparing songs from different areas;
    b.) choice of song variables for future comparative analyses;
    c.) acoustic recording and analysis techniques.

Definition of terms

Population versus stock: Because there is no consensus among biologists for the definitions of *population* and *stock*, these terms are often used interchangeably. For the purposes of this report, we use the term *population* to describe a group of animals that interbreed. In the case of humpback whales, a *population* usually refers to all animals that occur within an ocean basin (e.g. the North Pacific, the North Atlantic, the South Pacific). Some ocean basins, however, may include more than one population (e.g. the Indian Ocean). We use the term *stock* to refer a sub-set of animals within a population that have a detectable degree of segregation within the geographic boundaries of that population. For example, several "feeding stocks" have been identified for North Pacific and North Atlantic humpback whales (Baker *et al.* 1986, 1990; Katona & Beard, 1990). In the North Pacific, several distinct areas have been identified where singers and reproductively active females congregate (e.g. Japan, Hawaii, and Mexico). In the North Atlantic, the Caribbean Sea contains most of the known humpback whale breeding areas (usually islands and offshore banks). The degree of segregation and assortative mating at discrete breeding areas within an ocean basin is not well known, but is currently being investigated (Cerchio, pers. comm).

Humpback whale song: The songs of humpback whales consist of patterns of sounds that are repeated rhythmically. Humpback whale song structure has been described in great detail (Payne and McVay, 1971; Winn & Winn, 1978; Payne *et al.* 1983). As with most types of song, the structural organization of humpback whale song is hierarchical. Units (analogous to notes in human music) occur at the lowest level, followed by phrases, themes, songs, and song sessions at the highest level. The general organization of humpback whale song is graphically illustrated in Figure 1.

Dialects and geographic variation: Other authors have incorrectly used the term *dialect* to refer to humpback whale songs from different populations (Winn *et al.* 1981; for a review of this issue see Conner, 1980). To avoid such confusion, we instead use the terms *macro-geographic* and *micro-geographic variation* (Mundinger, 1982). In our study, macro-geographic variation is used to refer to differences in the acoustic structure of songs from separate populations (e.g. different phrase types in songs from different ocean basins). Micro-geographic variation is used to refer to the usually more subtle differences in song structure that occur within a population (e.g. differences in unit structure in songs from the same ocean basin).

METHODS

Pelagic recordings

Recordings of humpback whale songs were made in the temperate eastern North Pacific during a marine mammal survey from 6 March to 10 June 1997 aboard the NOAA R/V McArthur, a 52 meter oceanographic research ship (Fig. 2). Two recording systems were used: a towed hydrophone array system, and a sonobuoy/receiver system. Recordings made from these systems will be hereafter referred to as the "pelagic sample".

The towed hydrophone array and data acquisition system is described in detail elsewhere (Barlow, 1997; Norris *et al.* 1999). This acoustic system was capable of recording the entire bandwidth of humpback whale sounds (~ 40 Hz – 20 kHz; Norris, 1995), although noise from the ship sometimes caused masking (interference) in the low frequency band (up to 100 Hz). Signals from two of the five hydrophones on the towed array were recorded continuously onto audio DAT using a two-channel Sony DAT Walkman recorder (models TCD-D8 or TCD-D7).

Sonobuoys (type 57A) were deployed non-randomly on most days when the ship was in transit and during encounters with large cetaceans (including humpback whales). The sonobuoy receiving and recording system is described in detail elsewhere (Norris *et al.* 1999). Sonobuoy hydrophones were deployed at a depth of 122 m. Signals from sonobuoys were recorded for at least 40 minutes or until the signal-to-noise level degraded to an unacceptable quality.

Mexican recordings

Songs from humpback whales were recorded at Socorro Island (18° 40'N, 111°00'W), a breeding area in Mexico (Mexican sample) that is part of the Revillagigedo Archipelago. Recordings of songs were made from a small inflatable vessel that was maneuvered within one hundred meters of the singing animal before a recording session was initiated. The recording system consisted of a "dipping" hydrophone (a modified sonobuoy hydrophone connected to coaxial cable) powered by an external DC power source. Hydrophone signals were recorded using a professional model portable cassette recorder (Sony TCD-5M). The frequency response of this system was generally flat (± 5dB) from approximately 50 Hz to 16 kHz. Singing animals usually were located visually, either before, or at some point during the recording (for a description of the techniques used see Norris, 1995). If possible, a photograph of the fluke was taken to identify the singing animal. Photographs were used to assess if independent samples (i.e. different animals) were recorded.

Signal analysis

All recordings were played back from a DAT or audio-cassette player into a Macintosh computer and digitized using Sound Edit software (Ver. 96, Syntrillium Software Corp.). Recordings made from the towed array were hi-pass filtered using a variable, band-pass, active filter (HP Krohn-Hite model 3202) set at 200 Hz to reduce signal saturation that can occur at low frequencies (mostly due to array flow noise). Segments of signals from two to eight minutes in duration were acquired at a 22.2 kHz sample rate (11.1 kHz bandwidth) and saved in *.PCM wave format. Spectrograms of each of these file were printed for easy reviewing. Two consecutive phrases of each unique phrase type were extracted from each "parent" sound file and saved as separate files using either Sound Impression (Ver. 3.7) or Cool Edit (Ver. 97) sound editing software. Spectrograms (2048 point FFT/5.4 Hz frequency resolution, Hamming analysis window) were made of each file using Gram (Ver. 4.1.2) software. Hard copies of extracted phrases were printed for qualitative analyses and comparisons.

Song comparisons

Recording sessions from both the Mexican and pelagic samples were separated into two time-periods: 1.) 03/10 to 3/15 and 2.) 04/09 to 04/30). Recordings were selected from the Mexican sample by comparing dates so that they corresponded closely in time with the dates of recordings from the pelagic sample. The pelagic samples were categorized into three geographic regions: 1.) approximately 2000 km NW of Hawaii; 2.) approximately 1400 km west of southern California, and 3.) approximately 1200 km west of central California (i.e. a few hundred kilometers north of region 2; Fig. 2). These three regions represented the main discrete regions where humpback whale detections were clustered temporally and spatially (see Norris et al. 1999). Spectrograms of phrases from the Mexican sample were examined and compared visually, then placed into groups representing similar phrase types. All classifications were determined qualitatively. Phrases from the pelagic sample were examined visually and classified into groups corresponding to the Mexican phrase types that already had been identified. If the phrase could not be matched to any of the existing groups, a new category was created.

Assessment of variability for variables

The general variability of humpback whale song components was assessed by compiling results from previous studies conducted in the central and eastern North Pacific (Cerchio, 1993; Frankel, 1994; Norris, 1995). The methods of recording and analysis in those studies were similar to our study. The relative variability of different categories of song variables was evaluated by compiling and summarizing quantitative measures (e.g. S.D.'s S.E.'s and C.V.'s) and qualitative measures (e.g. error bars on graphs) of variability for data presented in these studies (appendices I-III).

RESULTS

Approximately eight hours of songs were analyzed from eleven recording sessions for all regions sampled. Over 200 sound files containing phrases were extracted, processed, and qualitatively compared (Table 1). Nine unique phrase types were identified from five recording sessions analyzed for the Mexican sample (Table 2). When these were compared to the six pelagic recordings sessions, eight phrase types were determined to be "shared." There were no additional phrase types identified in the pelagic sample that were not also identified in the Mexican sample. Half (three of six) of the pelagic recordings consisted of poor quality (i.e. low signal/noise; S:N) levels, so that only one or no phrase type could be identified. A single pelagic sample recording session (TCII-10 4/29) contained one third (three of nine) of all the shared phrase types identified for the pelagic sample (Table 2). In fact, this was the only high-quality recording from the pelagic sample. The disparity in recording quality between the Mexican and pelagic samples is quite apparent when examining representative spectrograms for each (Fig. 3).

The recordings made from Socorro Island, Mexico were of recording quality (i.e. high S:N). There were two phrase types (1 & 2) with sub-phrases (1A-1B and 2A-2B) that were only slight variants of each other. Although these categories could have been combined, it would have had little effect on the overall results. Only one phrase type (2C) was not identified in both time-periods (Table 2). Most (eight of nine) identified phrase types were shared among all recording sessions with the single exception of recording session SC13A (04/09/97). In recording session SC13A (04/09/97) almost half (four of nine) of the identified phrase types did not occur. The animal recorded in this session had unusual song and respiration patterns, which some researchers define as "aberrant" (Frumhoff, 1983).

DISCUSSION

The results of song comparisons between the Mexican sample and pelagic samples are difficult to interpret because in half (three of six) of the recording sessions from the pelagic samples only one or no phrase types could be identified. In general, the low occurrence of shared phrase types between the two samples can be attributed directly to the poor quality of most recording sessions from the pelagic sample[2]. Reasons for the relatively poor quality of pelagic recordings and recommendations for correcting this problem are discussed later.

The relatively high recording quality of the Mexican sample made identification and within sample comparisons of phrase types much easier than for the pelagic sample. Of the nine phrase types identified, eight were shared among most (4 of 5) of the five Mexican recording sessions. In the remaining recording session (SC13A; 04/09/97) four of the nine identified phrase types were not present. Further analysis of songs from this session, and the respiratory behavior of the associated singer, revealed that this animal had atypical song and respiration patterns, possibly an indication of an "aberrant singer" (Frumhoff, 1983). Several hypotheses have been proposed regarding the function and circumstances relating to aberrant song (Darling et al. 1999; Zoidis, 1999). However, at present there is insufficient information to verify any single hypothesis.

2 This is not meant to imply that better quality recordings would have resulted in more shared phrase types, rather that more phrase types would have been identifiable.

Phrase type 2C was present in Mexican samples SC3A (03/11/97) and SC3B (03/11/97) but was not identified during recordings later in study period (Table 2). This phrase occurred infrequently (i.e. had few repetitions) in the song sessions in which it occurred, and may have been in the process of becoming extinct (Payne *et al.* 1983). Interestingly, this phrase also was identified in the pelagic sample from a recording session (TCII-10; 4/29/97) made late in the season several hundred miles off the coast of central California. The significance of this finding is difficult to interpret without a sample from the Hawaiian breeding area for comparison. For example, if the end-of-the-season extinction of phrase 2C is representative of the Mexican sample, and this phrase occurred frequently in late season recordings from Hawaiian animals, it might indicate a stronger association of the pelagic animals with the Hawaiian breeding area than with the Mexican area. However, definitively reaching any such conclusion from the limited sample in this study would be unwarranted.

One important consideration when comparing songs from different geographic regions is the time-period in which recordings were made. It is well documented that humpback whale songs evolve rapidly (Payne *et al.* 1983; Payne & Payne, 1985). In fact, the songs change so quickly that the song of an individual will be more like the current songs of its neighbors than its own song from a few seasons, or even months, earlier (Guinee *et al.* 1983). Differences in songs recorded more than two to three weeks apart are likely the result of the evolution (i.e. progressive change) of song over time, rather than due to differences between geographic regions. Therefore, it is critical that all songs used for geographical comparisons are recorded during coincident periods, preferably no more than two weeks apart. In our study, the last two recording sessions from the pelagic sample (TCII-10, 04/29 and TCII-16, 04/29) were recorded almost 2 weeks later than the last Mexican session (because these were the last recordings available from Mexico). Although this situation would be difficult to avoid whenever comparing songs from migrating animals, the time-lag could have introduced some bias.

There were some recordings of songs made from the R/V McArthur, near Hawaii, but these were limited in duration, had low S:N, or perhaps more importantly were recorded at different time periods than the other samples. Because of these problems, a representative sample of songs from Hawaii was not analyzed. Unfortunately, this precluded an assessment of the breeding area identity for the only pelagic recording session that had good recording quality.

To reliably compare songs from geographic areas requires high quality recordings from all regions sampled. The quality of recordings from the two samples in this study varied greatly. Pelagic samples generally were limited to a frequency band from approximately 200 Hz to 800Hz. The limited bandwidth was due to masking from ship and flow noise for low frequencies and frequency dependent attenuation due to absorption and scattering for the higher frequencies. However, recordings from the Mexican sample were analyzable for the entire 5 kHz bandwidth used in this study. This was because these recording were made close to the singer (usually < 100 m) and there were few sources of loud noise nearby. The disparity in recording quality for the different recording techniques used is readily apparent when comparing representative spectrograms (Fig. 3). In the future, if humpback whale song recordings needed for comparative purposes are made from a large research vessel, techniques must be used that maximize the S:N over the bandwidth of interest.

Recommendations for song recording techniques

The most effective way to record high S:N and maximize the effective bandwidth of songs is to position the hydrophone(s) as close as possible to the animal while maximizing the distance to any noise sources (e.g. motoring vessels). At least 500 m should be maintained between the hydrophone and noisy vessels (including the research vessel). If moving vessels are unavoidable, the hydrophone should be located so the vessels is oriented stern aspect and heading away. One effective method of working from a large research vessel is to use small "runner" boats (e.g. inflatable boats) to approach singing animals and deploy a "dipping" hydrophone or sonobuoy nearby. Alternatively, sonobuoys can be deployed from the main vessel. Sonobuoys should be positioned as close as possible to stationary animals and, if possible, slightly ahead of traveling animals. Hydrophones should deployed to at least 20m depth to reduce surface effects.

Locations of animals can be determined in near real-time using a variety of acoustic techniques that can provide estimates of bearing and range. For example, bearings can be obtained from a towed hydrophone array signals by using differences in time-of-arrival (Barlow, 1997) or by beamforming (Thode et al. 2000). Alternatively, omni-directional and DIFAR (directional) sonobuoys (D'Spain *et al.* 1991, 1992) can be deployed from a survey ship. If a towed hydrophone array is used, towing the array deep, slow, and as far behind the ship as practical will produce the best results. The quality and length of recordings can be maximized by locating the singing animal using an array and recording nearby using a sonobuoy or dipping hydrophone.

Humpback whales songs as indicators of population structure

Songs of humpback whales have been compared among and within geographic regions to assess stocks in the North Atlantic (Winn *et al.* 1981; Mattila *et al.* 1987), North Pacific (Winn *et al.* 1981; Payne & Guinee, 1983; McSweeney *et al.* 1989; Helweg et. al. 1992), the South Pacific (Winn *et al.* 1981), and the eastern and western coasts of Australia (Cato, 1991; Dawbin and Eyre, 1991). Some of these studies were compromised by small sample sizes or problems related to non-concurrent recording periods. In general, however, results from all of these studies were consistent with more traditional assessments of humpback whale populations (i.e. different populations exist in different ocean basins).

More recently, researchers have examined detailed differences of songs between different breeding areas within the same population (e.g. Hawaii and the Revillagigedo Islands; Cerchio 1993; Cerchio *et al.* in press). A review of Cerchio's (1993) study reveals small but statistically significant differences for 11 of 47 song variables in one "recording period"[3] and 14 of 47 in another. Variables in which significant differences existed between Mexico and Hawaiian breeding areas, and the relative variability of different families of song variables are summarized for this study in Appendix I. From this summary, it is apparent that there is no single variable "family" (e.g. phrase structure) in which a majority of variables were different between breeding areas. Relative

3 In Cerchio's study "recording period" indicated recordings made during a coincident three week period.

variability in the "unit and phrase structure" variable family was less than that of other families, and included several variables with significant differences (Appendices I & II).

Investigators of killer whales and sperm whales have determined a correlation between genetic population structure and vocalization characteristics (Hoelzel & Dover, 1991; Ford, 1991; Whitehead *et al.* 1998). In these studies, differences in the repertoires of acoustic vocalizations were considered to be the most reliable indicator of differences in population structure. Differences in humpback whale population structure between Hawaii and Mexico have been detected using a variety of non-acoustic methods. It seems reasonable that song differences among breeding areas could be used as an indicator of population structure within the North Pacific population of humpback whales. First, however, it will be necessary to more precisely determine the rules of progressive change and obtain a better understanding the relationship between subtle differences in songs and population structure.

Population structure in North Pacific humpback whales

Evidence from photographic identification and genetic studies of humpback whales in the North Pacific indicate that significant population structure exists at discrete feeding areas in northern latitudes, and to a lesser degree at Mexican and Hawaiian breeding areas (Darling, and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.* 1986; Calambokidis *et al.* 1996, 1997). Baker *et al.* (1990, 1993 & 1994) examined humpback whale mitochondrial and nuclear DNA from feeding and breeding areas in the eastern and central North Pacific and found substantial genetic structure among disparate geographical regions. In fact, sufficient differences were found in the genetic structure of mitochondrial DNA for whales from Mexico (and associated California feeding areas) and Hawaii (and associated SE-central Alaska feeding areas) to warrant dividing the North Pacific population of humpback whales into at least these two main breeding/feeding stocks (Baker *et al.* 1994). A third breeding area in the southern Japanese Islands of Ryukyo and Bonin has been identified from whaling and photographic identification data (Nishiwaki, 1959, 1966; Darling & Mori, 1993), however, this population remains relatively unstudied. A preliminary comparison of photographic identification samples indicated limited interchange between Japanese whales and central and eastern North Pacific breeding and feeding areas (Calambokidis *et al.* 1997). The population structure of humpback whales in Japanese waters has not yet been examined.

Although there are differences in genetic structure and song structure for humpback whales from Mexican and Hawaiian breeding areas, at present there is no evidence to demonstrate a direct relationship between the two. In fact, detailed analyses of songs (beyond a comparison of "shared phrase types" commonly used by others) by Cerchio *et al.* (in press) revealed only subtle differences between the two areas. They suggested the possibility that the differences in song structure detected between Hawaii and Socorro Island might be due to time lags in transmission of song changes across large geographic areas. They hypothesized that, these differences would eventually disappear, due to the continuously evolving nature of the songs. However, it is possible that new differences are constantly arising and disappearing such that persistent differences between breeding areas exist at any given point in time. Long-term studies comparing songs from different breeding areas will be necessary to elucidate these issues.

Bird song

Birds songs are probably the best terrestrial corollary, in terms of song structure and function, to humpback whales songs. Unfortunately, there is no consensus among scientists regarding the relationship between song structure and population structure. Baker (1975, 1982) has argued that a relationship exists between micro-geographic variation in songs (i.e. dialects) and genetic structure for sparrow (*Zonotrichia sp.*) populations. He proposed that song dialects reduce gene-flow between populations because they facilitate non-random mating. However, Zinc and Barrowclough (1984) re-analyzed Baker's data and their findings led them to question the Baker's statistical methods and his resulting finding that "dialect populations" (i.e. populations with different song dialects) showed significant genetic differentiation. Others also have failed to find a significant relationship between micro-geographic variation and allozyme variation (Lougheed & Handford, 1992) or mitochondrial DNA variation in sparrow song (Lougheed *et al.* 1993). Finally, a review of numerous bird song studies by Payne (1996) did not reveal any compelling evidence that genes and songs co-evolve in most species of birds. Thus, Payne concluded that there is little evidence to support the prediction that bird populations with different song traditions (e.g. dialects or micro-geographic variation) are genetically different.

Regardless of whether or not a relationship exists between genetic structure and song structure in humpback whales, subtle differences in songs have been demonstrated between at least two breeding areas in the same ocean basin population (Cerchio, 1993). Furthermore, others have demonstrated that animals which are in immediate acoustic contact with each other converge on a similar song type (Guinee *et al.* 1983; Payne & Guinee, 1983). Thus, by simply comparing songs from an "unknown" animal to songs from known breeding areas it should be possible to determine the breeding area that the animal was associated with most recently. For example, songs recorded from animals migrating to feeding areas from breeding areas could be compared to songs recorded late in the season from different breeding areas. Such an analysis could provide valuable information about breeding area "identity" and migration routes for animals acoustically detected and recorded in pelagic waters.

One assumption of this type of analysis is that limited acoustic contact occurs among animals from other breeding areas during the breeding season and during migration. Norris *et al.* (1999) speculated that humpback whale migration routes from central and eastern North Pacific breeding areas to feeding areas cross in northern latitudes, allowing the possibility for exchange of song information (and thus synchronization of song changes). Evidence from photographic identification studies indicates limited exchange of animals between disparate breeding grounds (Darling and Cerchio, 1993; Darling and McSweeney, 1985). The effects of even limited interchange of singers on song structure are uncertain but potentially significant (Noad *et al.* 2000) and should be investigated further.

To test for differences in songs sampled from different areas, the appropriate song variables must be selected for analysis. Selecting acoustic variables with an appropriate level of variability is necessary so that differences can be discerned at the spatial scale of interest. Fortunately, sufficient information exists about variability of humpback whale song components to make informed decisions about which variables to analyze for a within ocean-basin song comparison. Furthermore, existing data may indicate which "families" of song variables have the least variability and, thus, will be the best variables to examine for detecting subtle differences among breeding areas (Cerchio, 1993).

In Cerchio's (1993) study, the differences detected in songs between the Hawaiian and Mexican breeding areas were very subtle (i.e. small effect size). In order to statistically detect subtle differences either a relatively large sample size is necessary (a difficult criteria to meet for most marine mammal studies), or alternatively, the variability of a small sample must be low. We have summarized the relative variability of several categories of song variables from three previous studies of humpback whale songs conducted in the North Pacific (Cerchio, 1993; Frankel, 1994; Norris, 1995; Appendices I-III). Examination of this summary does not reveal any "family" of variables that are characterized by low variability yet *consistently* exhibits differences between breeding areas. However, there are some families of variables that consistently have low variability, are simple to measure, and *occasionally* exhibited differences between the two breeding areas. Based on these considerations, unit morphology (time and frequency characteristics of units), phrase structure (number and proportion of units in a phrase), and song duration (related to the total number of phrase repetitions) are recommended as variable choices for future quantitative analysis. Unfortunately in our study, the poor recording quality of the pelagic samples resulted in song units that were degraded or undetectable. Also, pelagic recording sessions were much shorter in duration than those from the Mexican sample. This made reliable measurement of most of these variables difficult, if not impossible. In the future, as powerful digital-signal-processing techniques become readily available, it may be possible to easily measure other variables that either provide more detailed information about song structure (e.g. harmonic structure), or are not as susceptible to effects of low S:N (e.g. rhythmic patterning of signals).

Methods of song comparisons and analysis

There are numerous approaches that can be used for comparative song analyses. One simple approach would be to assess the probability that songs from an "unknown" animal were associated with a given population of singers. To do this requires several steps. First, the populations of singers (e.g. breading areas) that the unknown sample will be compared with must be thoroughly characterized. For example, the probability of occurrence of specific song features in each population can be determined by qualitative assessment of the absence or presence of specific themes and units. Using a combination of several independent variables, each of which occurs with different proportions in each of the populations, it should be possible to calculate the probability that the unknown sample is associated with any population (i.e. area) of singers.

Another approach is the use of multivariate statistical techniques. As researchers use a wider g range of variables to examine the relationship between animal vocalizations and population structure multivariate statistics becoming more important. There are numerous multivariate analyses that are commonly used to do this, such as: multivariate analysis of variance (MANOVA), principle component analysis (PCA), multiple linear regression, and discriminant analysis (DA) among others. A detailed discussion of these techniques is beyond the scope of this paper (but see Sparling and Williams, 1978, for a useful review re: analysis of avian vocalizations).

In numerous studies of cetacean vocal behaviors, multivariate techniques have been used to differentiate groups of animals using a suite of acoustic variables. For example: Payne and Guinee (1983) used DA on 14 variables of humpback whale songs to discriminate between different years and ocean basins; Weilgart and Whitehead (1997) used K-means cluster analysis to categorize sperm whale codas based on the number of clicks and click patterning; Whitehead *et al.* (1998) used non-metric multi-dimensional scaling plots, and PCA of correlation matrices to examine the relationships among dialects, fluke marks and genetics in a study to determine population structure for South Pacific sperm whales; and McCowen *et al.* (1998) used PCA to isolate acoustic variables from an original set of 38 variables characterizing bottlenose dolphin (*Tursiops truncatus*) whistles. Step-wise discriminant analysis were then applied to the PCA factor scores to determine the most important whistle variables for distinguishing among groups of animals. One drawback of most multivariate techniques is that they are very labor-intensive because they require (usually manual) measurement of many acoustic variables.

Recently, computer-based neural networks (NN) and automatic classification algorithms have been used for classification of bio-acoustic signals (Potter *et al.* 1994). These algorithms are gaining popularity due to their effectiveness in reducing large volumes of acoustic data through automated detection, classification, and categorization of digital signals. Most of these techniques are not based upon traditional statistical methods and some methods (e.g. multi-layer perceptron based NN) have been criticized because of the ambiguities inherent when determining the criteria that are used for classification or analysis. Such issues can be problematic when interpreting the results of NN outputs. However, one type of NN, the Elliptical Basis Function (EBF), provides information on the feature space (e.g. time-frequency distribution) used in the decision making process (Brotherton *et al.* 1998). EBF's may provide an acceptable alternative for the analysis of bio-acoustic signals in the future.

Summary and Conclusions

It is possible that songs can be used as indicators of stock structure or breeding area association for humpback whales within an ocean basin population. However, for this technique to be used reliably, a better understanding of the rules of song change and their function will be necessary. The advantages of acoustic techniques include the ability to collect samples remotely and the possibility to characterize a group of animals from only one or a few individuals. Of course, the latter possibility relies on certain assumptions whose validity still needs to be assessed for humpback whales (e.g. song differences reflect population structure differences).

Future effort should be directed at determining the function and rules of progressive changes in humpback whale songs and relating differences in songs to differences in genetic structure, social structure, and reproductive success of singers. For any comparative effort, songs should be recorded at different breeding areas during coincident periods and characterized quantitatively. Furthermore, the appropriate techniques need to be used so that high-quality signals can be obtained. In the very near future, advances in computing power will result in more sophisticated and efficient signal processing and analyses. Additionally, hydrophone array deployments are being planned or are already deployed for numerous sites across the world's oceans in order to collect acoustic data for a variety of applications (McDonald and Fox, 1999). If these facilities and their associated resources are made accessible to marine mammal researchers (e.g. Stafford *et al.* 1999), then in the near future, it seems likely that songs will be used to assess certain aspects of population structure in humpback whales.

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Table 1. Summary of humpback whale song recordings for “Mexican” and “pelagic” samples.

	Tape/CD ID #	Location	Date	Recording methods	Archival media	Recording quality	Phrases extracted	Total time
M								
E	SC3A	Socorro	03/11/97	omni h-phone	cassette	Exc.	19	0:37
X	SC3B	Socorro	03/14/97	omni h-phone	cassette	Exc.	18	0:42
I	SC13A	Socorro	04/09/97	omni h-phone	cassette	Exc.	19	0:45
C	JJ18A/B	Socorro	04/12/97	omni h-phone	cassette	Exc.	21	0:55
O	JJ19A	Socorro	04/14/97	omni h-phone	cassette	Exc.	30	0:58
P								
E	TA4	off S.CAL	03/12/97	Towed-array	DAT(Sony)	Fair	13	0:44
L	MMCD#1	off S.CAL	03/12/97	Sonobuoy	DAT->CD	Poor	19	0:24
A	MMCD#3	NW of HI	04/14/97	Sonobuoy	DAT->CD	Poor	6	0:24
G	TCII-7	NW of HI	04/15/97	Sonobuoy	DAT (TEAC)	Poor	32	1:01
I	TCII-10	off C.CAL	04/29/97	Sonobuoy	DAT (TEAC)	Good	23	0:42
C	TCII-16	off C.CAL	04/30/97	Sonobuoy	DAT(TEAC)	Poor	10	0:20
TOTAL							210	7:53

Table 2. Summary of phrase types identified from Mexican and pelagic samples. Large X denotes that numerous (>2) songs contained that phrase type. Small x denotes that few songs (≤2) contained that phrase type. Dashed lines (---) denote that this phrase type did not occur in the recording, but would have been identifiable if it did. An asterisk (*) denotes possibly aberrant song (Frumhoff, 1983). Blanks indicate that a phrase type was not detected but might have occurred in a song session (i.e. these were poor quality recordings). The poor quality of several recordings (e.g. MCD-3, TCII-7 and TCII-16) limited the ability to reliably identify numerous phrase types and made meaningful comparisons of samples problematic.

SAMPLE	**Mexican Sample**					**Pelagic Sample**					
LOCATION	Socorro Island, Revillagigedo Archipelago					off Southern CA		NW of Hawaii		off Central CA	
SESSION	SC3A	SC3B	SC13A*	JJ18A/B	JJ19A	TA-4	MCD-1	MCD-3	TCII-7	TCII-10	TCII-16
DATE	03/11	03/14	04/09	04/12	04/14	03/12	03/12	04/14	04/15	04/29	04/30
Phrase 1A	X	x	X	x	X	X	X	x		X	x
Phrase 1B	X	X	X	X	X					X	
Phrase 2A	X	x	X	X	X	x	X			X	
Phrase 2B	X	X	X	X	X	X	X			X	
Phrase 2C	X	x	---	---	---					X	
Phrase 3	X	X	x	X	X		x			X	
Phrase 4A	x	x	---	x	X					---	
Phrase 4B	X	X	---	X	X					X	
Phrase 4C	x	x	---	x	X		x			---	

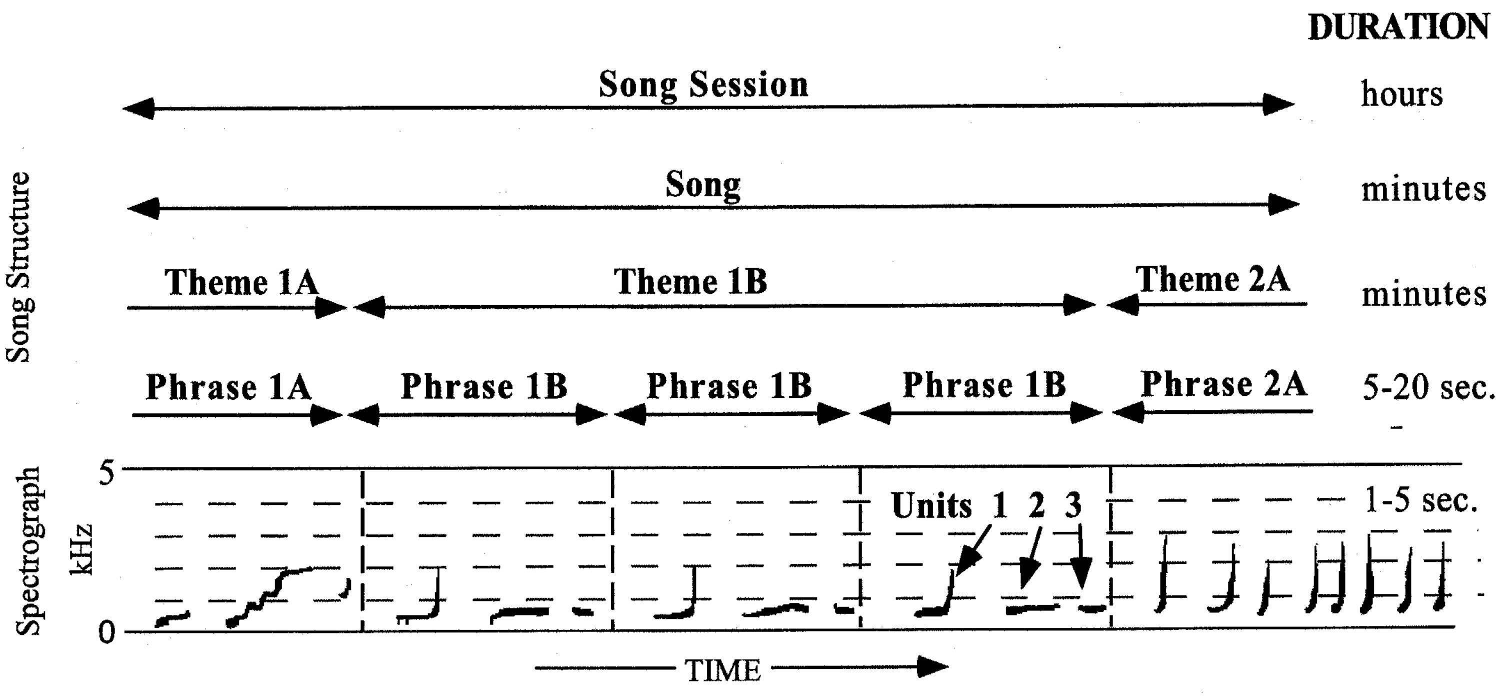

Figure 1. Structure and organization of humpback whale song. Song components are organized hierarchically from the most basic (bottom) to the most complex (top). Three phrase types are represented in the tracing of a spectrograph of the song at very bottom. Phrases are categorized based on qualitative similarities in patterns of units. Representative durations of each song component are presented at far right (layout from Payne et al. 1983).

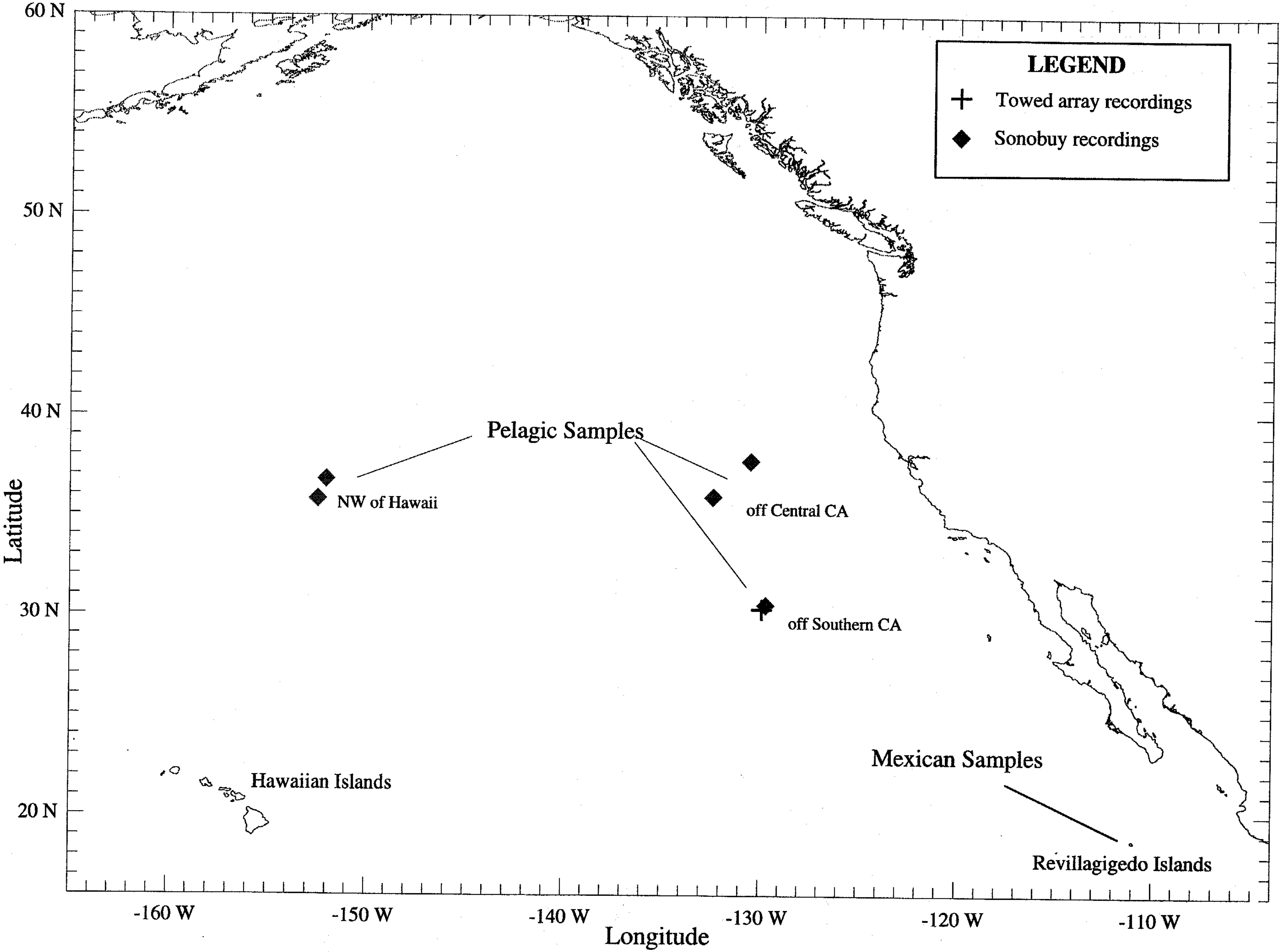

Figure 2. Locations of recordings (from Table 2) used in the analyses. Entire Mexican sample was recorded near Socorro Island.

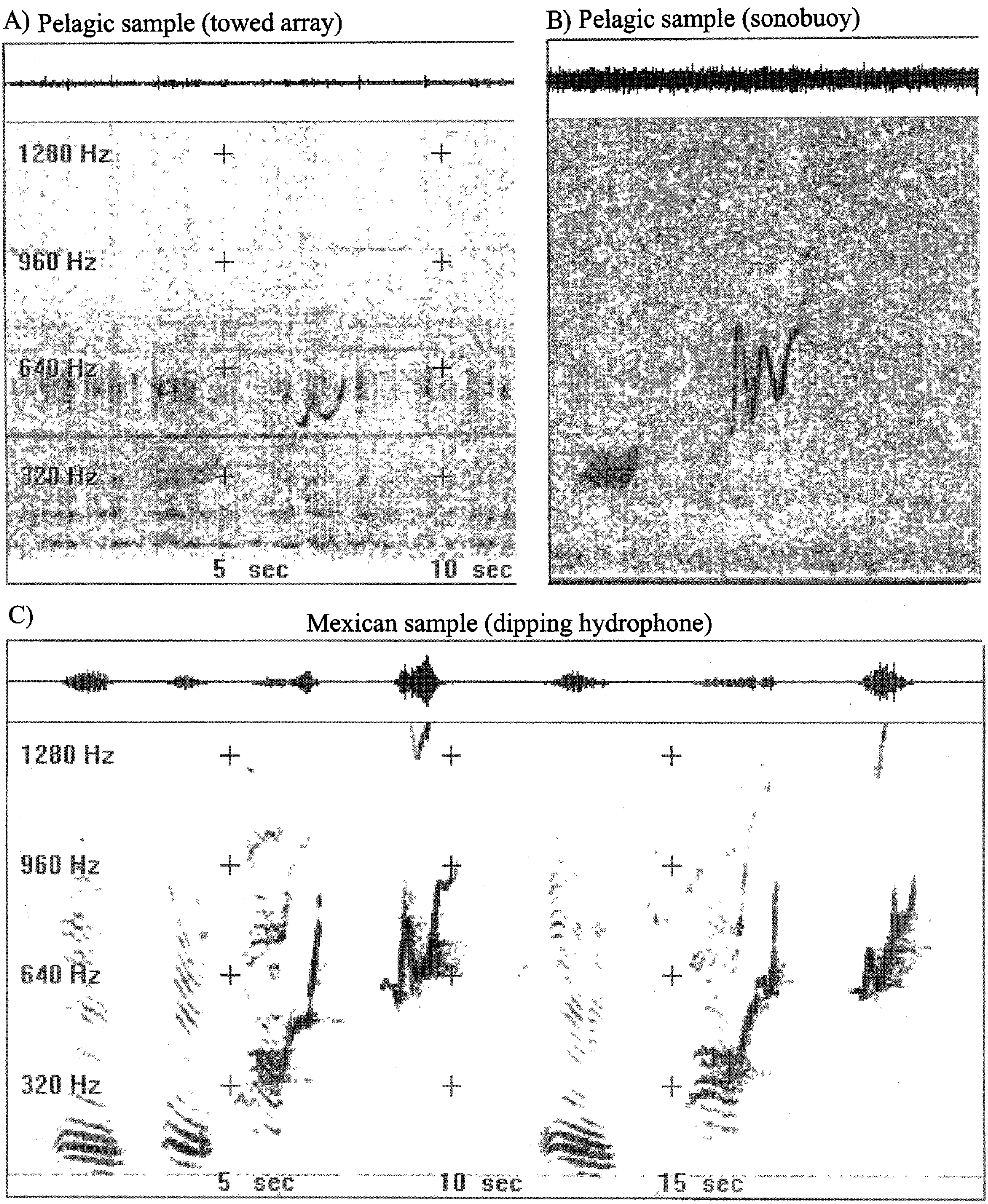

Figure 3. Spectrograms of the same phrase type recorded from three different recording systems. Differences in signal quality are evident when comparing recordings from: A) a towed-array (HP filtered at 200 Hz), B) a sonobuoy, and C) a "dipping" hydrophone deployed from a small inflatable boat. (all spectrograms settings: 2048 pt FFT, 5.4 Hz filter b-w, 40 msec time res.)

Appendix I. Relative variability of song variables (summarized from Cerchio, 1993). To simplify comparisons, variables are grouped into families of similar variables. **Boldfaced** variables indicate low variability and significant (or nearly significant) differences between Hawaiian and Mexican breeding areas. At least two complete songs from a minimum of five animals were analyzed for each location and period. Periods 1 and 2 correspond to the beginning and end of the breeding season, respectively. Mean C.V.'s were calculated by averaging C.V.'s across periods and locations for each variable type.

#	**Variable Type**	**Variability**	**Significant diff.'s**		**Coeffecients of variation**				
		(low,med.,hi)	Hawaii & Mexico		Hawaii		Mexico		Mean
			Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	All
Phrase & Song Durations									
C1	Phrs.Dur R	l			0.21	0.19	0.22	0.19	0.20
C2	**Phrs.Dur RT**	**l**	x	x	**0.18**	**0.21**	**0.24**	**0.20**	**0.21**
C3	Phrs.Dur 1A	l			0.07	0.06	0.09	0.08	0.08
C4	Phrs.Dur 1B	l			0.05	0.05	0.07	0.05	0.06
C5	Phrs.Dur 2A	l			0.07	0.09	0.09	0.10	0.09
C6	Phrs.Dur 2B	l			0.11	0.08	0.09	0.10	0.10
C7	**Phrs.Dur 3B**	**l**	(x)	(x)	**0.06**	**0.09**	**0.07**	**0.09**	**0.08**
C8	**SongDurAll**	**l**	x	x	**0.39**	**0.17**	**0.31**	**0.14**	**0.25**
C9	**SongDurTypical**	**l**	(x)	(x)	**0.17**	**0.10**	**0.22**	**0.14**	**0.16**
# of Phrase Repetitions per Song									
C12	**PhraseRep R**	**l**	x	x	**0.12**	**0.12**	**0.21**	**0.21**	**0.17**
C13	PhraseRep 1	m	----	----	0.43	0.30	0.43	0.20	0.34
C14	PhraseRep 1A	m-h			0.50	0.40	0.62	0.31	0.46
C15	PhraseRep 1B	m-h		x	0.65	0.37	0.50	0.46	0.49
C16	PhraseRep 2A	m			0.40	0.41	0.43	0.51	0.44
C17	PhraseRep 2B	m			0.33	0.31	0.43	0.29	0.35
C18	PhraseRep 3B	m			0.52	0.41	0.50	0.35	0.44
Unit Structure									
C19	**UnitDur 1A-u2**	**m**	x	(x)	**0.27**	**0.23**	**0.31**	**0.24**	**0.27**
C23	**UnitDur 1B-u2**	**l**	x	x	**0.19**	**0.18**	**0.23**	**0.19**	**0.20**
C27	UnitDur 2A-u1	m			0.13	0.16	0.14	0.11	0.14
C31	UnitDur 2A-u2	l			0.18	0.17	0.15	0.15	0.16
C20	UnitSlope 1A-u2	h			0.52	0.78	0.40	0.58	0.56
C24	**UnitSlope 1B-u2**	**m**	x	x	**0.52**	**0.28**	**0.42**	**0.34**	**0.38**
C28	UnitSlope 2A-u1	m			0.30	0.31	0.36	0.20	0.29
C32	UnitSlope 2A-u2	m			0.39	0.29	0.31	0.21	0.30
C21	BeginFreq 1B-u2	m			0.25	0.28	0.21	0.14	0.22
C25	**BeginFreq 2A-u1**	**l**	(x)	x	**0.13**	**0.09**	**0.07**	**0.06**	**0.09**
C29	BeginFreq 2A-u2	l			0.15	0.08	0.08	0.07	0.09
C22	**UnitHzRange1Bu2**	**m**		x	**0.47**	**0.42**	**0.40**	**0.26**	**0.38**
C26	UnitHzRange2Au1	m			0.28	0.17	0.25	0.17	0.21
C30	UnitHzRange2Au2	l-m			0.37	0.19	0.27	0.16	0.24
Phrase Structure									
C33	# Units/Phrs RT	m			0.27	0.29	0.29	0.35	0.30
C34	**# Units/Phrs 1A**	**l**		x	**0.14**	**0.23**	**0.18**	**0.14**	**0.17**
C35	# Units/Phrs 1B	l			0.17	0.23	0.12	0.06	0.14
C36	# Units/Phrs 2As2	l			0.24	0.19	0.18	0.27	0.22
C37	# Units/Phrs 3Bs1	l			0.19	0.09	0.17	0.13	0.14
Theme and Song Structure									
C11	**Phrs3BMaxFreq**	**l-m**	(x)	(x)	**0.26**	**0.26**	**0.25**	**0.22**	**0.25**
C10	**Theme1AMaxFreq**	**l-m**	x	x	**0.47**	**0.21**	**0.36**	**0.25**	**0.32**

Appendix II. Relative measures of song variability from Norris (1995). Songs were recorded from 9 animals during 1991 and 1992 off Kauai, Hawaii.

	Variable Type	Unit/Phrase	Variability	S.E.	Mean	Mean/S.E.
N1	Unit Duration	U1	l	0.20	2.14	0.09
N2	Unit Duration	U2	l	0.15	1.86	0.08
N3	Inter-unit Dur	U1-U2	l	0.09	1.98	0.05
N4	Phrase Duration	1B	l	0.47	11.06	0.04
N5	Theme Duration	1B	m	19.90	160	0.12
N6	Song		l	72.43	774	0.09
N7	Frequency Min.	U1	l	4.80	121	0.04
N8	Frequency Min.	U2	l	12.00	223	0.05
N9	Frequency Avg	U1	l	4.00	145	0.03
N10	Frequency Max	U2	h	113	498	0.23
N11	# units/phrs	1B	l	0.12	3.04	0.04
N12	# phrase/theme	1B	m	2.20	14.80	0.15

Appendix III. Relative measures of song variability from Frankel (1994). Variability was assessed qualitatively from error bars on bar graphs for each variable. Songs were recorded off the Big Island, Hawaii from 1989 to 1991.

	Variable Type	Unit/Phrase	Variability
F1	Frequency Min.	Them2U1	l
F5	Frequency Min.	Them2U2	l
F9	Frequency Min.	Them3U1	l
F13	Frequency Min.	Them3U2	l
F17	Frequency Min.	Them4U1	l
F21	Frequency Min.	Them4U2	l
F2	Unit Duration	Them2U2	l
F6	Unit Duration	Them2U2	l
F10	Unit Duration	Them3U1	l
F14	Unit Duration	Them3U2	l-m
F18	Unit Duration	Them4U1	l-m
F22	Unit Duration	Them4U2	l-m
F3	Unit Bandwidth	Them2U3	m
F7	Unit Bandwidth	Them2U2	l-m
F11	Unit Bandwidth	Them3U1	l-m
F15	Unit Bandwidth	Them3U2	l-m
F23	Unit Bandwidth	Them4U2	l
F19	Unit Bandwidth	Them4U1	l
F4	FreqPeakAmpl	Them2U5	l-m
F8	FreqPeakAmpl	Them2U2	l
F12	FreqPeakAmpl	Them3U1	l
F16	FreqPeakAmpl	Them3U2	l-m
F20	FreqPeakAmpl	Them4U1	l
F24	FreqPeakAmpl	Them4U2	l

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