BIOGEOGRAPHIC CHARACTERIZATION OF BLUE WHALE SONG WORLDWIDE: USING SONG TO IDENTIFY POPULATIONS

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ABSTRACT

Blue whale songs provide a new means for characterizing blue whale population structure worldwide. These songs are divided into nine regional types, which maintain a stable character. Five of the nine song types have been recorded over time spans greater than 30 years showing no significant change in character. We suggest that distinct differences in song provide another data set for comparison with genetic and morphological data when defining blue whale populations. Furthermore, we recommend that when there is a lack of other data, or lack of clarity in other data sets, evidence of distinct differences in songs between areas be used as the provisional population structure when making management decisions. Worldwide study is needed to better understand the various populations (subspecies) within species like the blue whale that have large geographic distributions and have both migrating and resident populations. The song types we propose here can be used to test various phylogeographic hypotheses with other datasets (bones, external measurements, genetics, parasites, etc.).

INTRODUCTION

A trait common to blue whales worldwide is the production of high intensity, low frequency, long duration acoustic calls (e.g. Cummings and Thompson, 1971). These calls often form repetitive multi-part songs, which have been documented to be constant in character over decadal time scales (c.f. Thompson, 1965; McDonald *et al.*, 2001). This paper reports on the characteristics, geographic range and seasonality of blue whale songs worldwide. We describe nine distinctive regional types of songs, which are produced with stereotyped character in distinct geographic regions with distinct oceanographic characteristics. The study of blue whale song provides new data to help delimit the population structure of blue whales worldwide. We suggest that distinct differences in song provide another data set for comparison with genetic and morphological data when defining blue whale populations as songs reflect interacting groups of animals, and thus are also likely to be good indicators of population identity.

BACKGROUND

Blue whale acoustic repertoire

Blue whale calls are among the highest intensity (188 dB_{RMS} re: 1µPa @ 1m) and lowest frequency (16-100Hz) sounds made by any animal (Cummings and Thompson, 1971; McDonald *et al.*, 2001). These calls are often made in regular succession and form a recognizable pattern in time, which we call song. The songs are divided into units, which are continuous segments of sound, and phrases, which are repeated combinations of units. Blue whale songs do not appear to contain themes, or repeated sets of phrases, as found in humpback whale song (Payne and McVay, 1971). Blue whale call units are classified as primarily pulsed or tonal. We define a unit boundary as any abrupt change in call character (frequency, sweep rate or modulation rate) regardless of whether there is a pause between units. From one to five call units are combined to produce a phrase, and a song is composed of many repeated phrases. Breaks in the song occur for respiration, but otherwise the songs may continue for hours or days. The units are sometimes combined in different sequences, these apparently having rules or syntax, by which only some combinations are allowed. When units are combined in more than a single sequence we refer to this as mixed mode phrasing. When only one sequence has been observed we refer to this as single mode phrasing.

In addition to the songs reported here, blue whales produce calls in irregular patterns or as call and counter-call between two or more individuals. These calls are often downswept tones (80-30 Hz) of moderate duration (2-5 sec), with seasonally variable occurrence (Thompson *et al*., 1996; McDonald *et al*., 2001). To the best of our knowledge, these downswept calls have a consistent character worldwide, although further research may reveal regional variations in their character or usage.

Although definitions vary for song, terminology should not obscure the importance of acoustics as a tool in population identification for blue whales. In fact, we do not really care what you call it (call it "gazingas" if you want) our objective is to highlight the value of acoustic information as a tool in marine mammal conservation and management.

Acoustic communication: function, variability, flexibility and potential evolutionary consequences

The precise function of blue whale song, as with other mysticete songs, is not well understood. Social functions proposed for mysticete calls (calls in this case referring to all types of msyticete vocalizations, including song) include foraging, mating and parental behavior, long range contact, assembly, sexual advertisement (male-male or male-female), greeting, spacing, threat and individual identification (Dudzinski *et al*., 2002). However, only rarely has a specific call been associated with a given behavioral event. Regarding mysticete song specifically, in species such as humpbacks and fin whales, the evidence to date indicates that only males sing (Croll et al., 2002, Darling and Bérubé 2001). Much of the speculation on the function of song in these species has revolved around whether singing functions in territorial defense or mate selection but these hypotheses are being called into question by additional research (Darling 2002, Darling and Bérubé 2001, Tyack 2000).

In blue whales, it is known that male blue whales produce song (McDonald *et al*., 2001), but it remains unknown if female blue whales also sing. Animals vocalize throughout the year with peaks from midsummer into winter (Burtenshaw *et al,* 2003; Širović *et al*., 2003). Field observations suggest that singers are solitary animals (Calambokidis, pers. comm.). Diel chorusing at dusk and dawn increases the number of singers during these time periods (Thompson, 1965). When singing blue whales have been tracked, either visually or acoustically, they swim at 2-10 km/hr while producing songs (Kibblewhite, 1967; Northrop, 1971; McDonald *et al*., 1995; Thode *et al*., 2000; McDonald *et al*., 2001). Blue whale songs can be detected for hundreds, and under optimal conditions, thousands of kilometers (Stafford et al., 1998). Such sounds are ideal for communication between individuals of a widely dispersed and nomadic species. During a single season, the fundamental frequency components of a song type are precisely synchronized within a population of singers. For this reason, social integration may be a key function of blue whale song, that is, the song may allow two or more whales to integrate their activities.

Blue whale songs are known to be variable, but individual variability within a song type is much less than that which distinguishes song types. Variability within a song type has been shown to be useful to distinguish between individual whales off California over the hours long time periods during which whales were observed (McDonald *et. al*, 2001). Individual signature information in blue whale song has been reported for many days in North Atlantic blue whales (Clark, 1995). The utility of these relatively subtle individual variations to further subdivide blue whale populations acoustically remains a topic for further research.

A distinguishing feature of blue whale song is the apparent constancy of the song types over time. In contrast, another cetacean to produce song is the better-studied humpback whale. An important difference between blue whale song and the better-studied humpback song, or bird song, is the apparent lack of mutation in blue whale song over decades of observation. Blue whale song appears to be copied nearly perfectly across generational boundaries. In some bird species there is flexibility in song type, where an individual may change song type to match a local dialect or successfully breed while singing a different song (Payne, 1996). In humpbacks, a similar phenomenon is known to occur where a single singer arriving from a different population apparently caused an entire population to switch to the new song (Noad *et al*., 2000). The dramatic changes in humpback song from month-to-month and from year-to-year combined with the much more complex form of humpback song (Payne *et al*., 1983) serves to caution against analogies with blue whale song.

The evolutionary consequences of variation in vocalizations are profound. In numerous birds, vocalizations are the predominant means by which individuals communicate; conspecifics recognize each other by their voices and vocal differences among species are among the most powerful isolating mechanisms known (Irwin 1996). Regional variation, or dialects, is well known in birds and it not uncommon for song to be a powerful isolating mechanism among populations as well (Irwin, 1996). Likewise, in whales, songs types are likely to be under strong selection for effective communication, because effective communication is expected to confer an advantage in access to resources or mates. Song is also likely to be specialized to be informative, efficient, and adapted for transmission in particular environments (Dudzinski, 2002). Consequently, song may diverge between populations occupying different environments. If only males produce songs, song may also function as a reproductive isolating mechanism, accelerating diversification among populations (West-Eberhard, 1983; Irwin 1996). The result is differentiation into acoustic stocks based on geographic variation of song types. Species and/or populations of birds (Martens, 1996), insects (Wells and Henry, 1998), amphibians (Ryan, 1990), and primates (tamarins; Maeda and Masataka, 1987) including humans (Barbujani, 1991) are sometimes defined primarily on acoustic characterization, sometimes without morphological differences.

BIOGEOGRAPHIC VARIATION

Blue whale song can be separated into nine types each of which we associate predominantly with a geographic region. (See Table 1 for a listing of source data.) The best known songs are from the Pacific Ocean, which has four song types. The Indian Ocean, though poorly studied, has at least three song types, whereas, the Atlantic Ocean and Southern Ocean each have a single song type. We assume additional song types remain to be discovered. For instance, no recordings are available for the South Atlantic, where blue whales are undoubtedly present. Locations for all known blue whale recordings are shown in Figure 1, the locations being numbered corresponding to the song type listed in table 1. Stability of the song character is illustrated in Figure 2 for song type 3 over a 33 year time span. Changes in song character through time are small relative to differences between song types, the common change being a slow and regular drift in the frequency of the tonal components. Spectrogram displays of each song type are grouped into three figures, the first two (Figures 2 and 3) are grouped based on similarity of character, while Figure 4 illustrates the Northern Indian Ocean types which do not readily group with the others in call character.

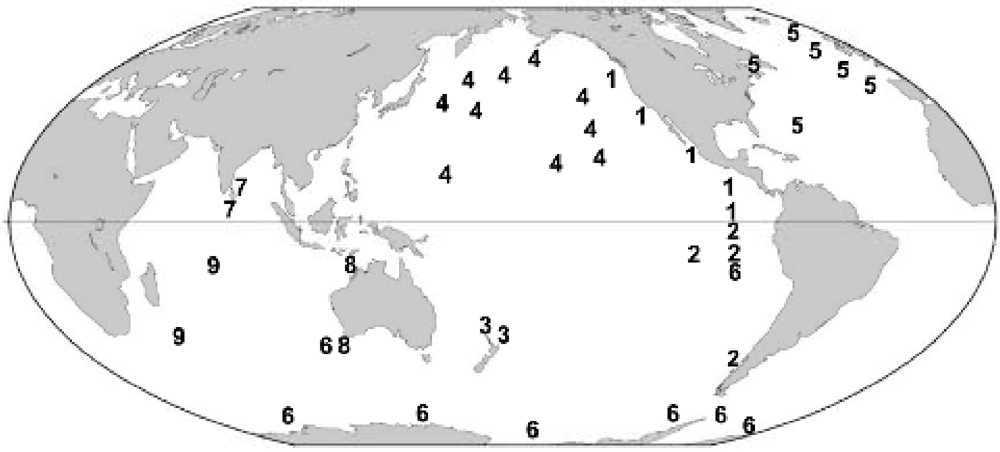

FIGURE 1. Distribution of blue whale song, classified into nine regional types (numbers). See Table 1 for regional designations.

Table 1. Blue whale song type by region. The type locality and type reference refer to the best/first/most complete published reference for each song type. Song character is stable over the known time spans, listed as the year of the first and the most recent recordings known.

Type	Time Span	Region (Abbreviation)	Type Locality	Type Reference
1	1963-2003	Northeast Pacific (NEP)	California	McDonald *et al*., 2001
2	1970-1997	Southeast Pacific (SEP)	Isla Guafo, Chile	Cummings &Thompson, 1971
3	1964-1997	Southwest Pacific (SWP)	New Zealand	Kibblewhite, 1967
4	1967-1997	North Pacific (NP)	Aleutian	Stafford *et al*. 2001
5	1959-2001	North Atlantic (NA)	Eastern N. Atlant.	Clark and Charif, 1998
6	1997-2003	Southern Ocean (SO)	West Ant. Penins.	Širović *et al*. 2003
7	1984-2002	North Indian (NI)	Sri Lanka	Alling *et al*., 1991
8	1993-2000	Southeast Indian (SEI)	Fremantle	McCauley, 2000
9	2002	Southwest Indian (SWI)	Diego Garcia	This Paper

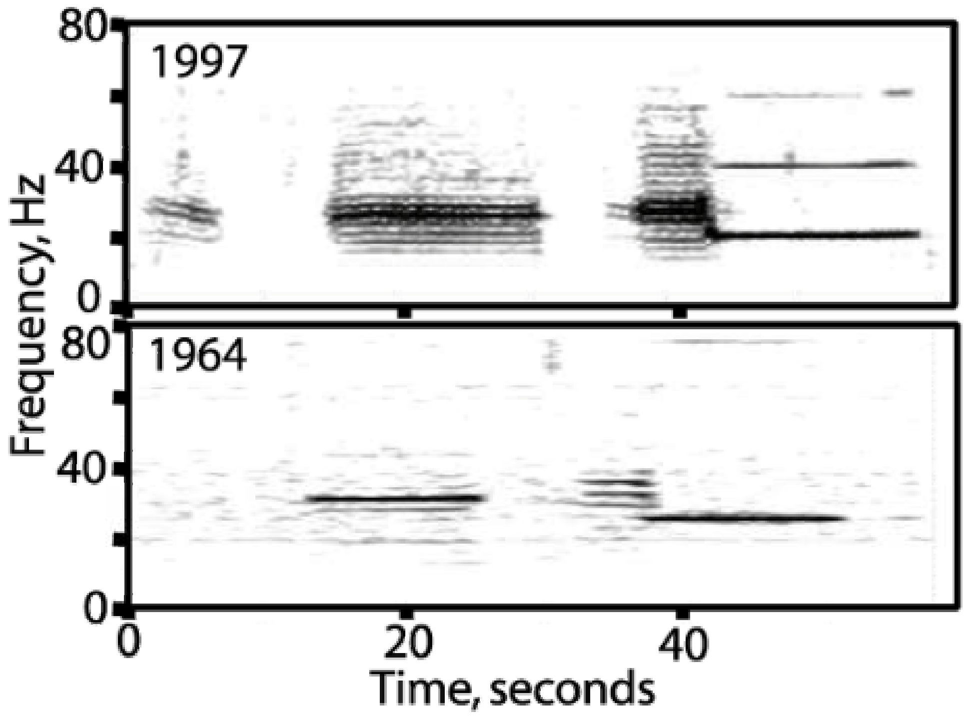

FIGURE 2. Recordings from New Zealand illustrate the stable character of the blue whale song in this region over a 33 year time period. The apparent lack of the first song unit in the 1964 recording may be due to poorer signal to noise ratio in that recording. All song types for which long time spans of recording are available show some frequency drift through time, but only minor change in character.

Northeast Pacific

Blue whale songs have been recorded off the coast of California since 1963 (Thompson, 1965), the northeast Pacific song being the best documented for any worldwide. The character of this song has remained stable over the past four decades. This song has two call units (Figure 3a, Table 2). The first unit (A) is pulsed with multiple, time-offset non-harmonic components. The second unit (B) is tonal, with a series of harmonically related higher frequencies. Single mode (ABABAB or ABBBABBB) phrasing is common, with the A unit always initiating the song sequence.

The geographic range for the Northeast Pacific blue whale song (type 1 in Figure 1) is primarily along the west coast of North and Central America. The type locality is off the coast of California, where these calls have been well described (Thompson, 1965; Rivers, 1997; Stafford *et al*., 2001; McDonald *et al*., 2001). In the northern part of this region, off the coast of Washington, Oregon and British Columbia, they are heard seasonally, beginning in the summer and continuing into the fall and early winter (Stafford *et al*., 2001, Burtenshaw *et al*., 2003). In the south of their range, at the Costa Rica Dome region and in the Gulf of California, calls from these whales are present year-round, but with a peak occurrence in the winter and spring (Thompson *et al*., 1987; Stafford *et al*., 1999a). This pattern suggests a seasonal movement with a spring peak presence in the Costa Rica Dome region, and fall peak presence off the California coast and points further north, substantiated by photo-identification studies (Calambokidis *et al*., 1999) and satellite tagging (Mate *et al*., 1999). These calls also have been heard further offshore, where they mix with the North Pacific song type (Stafford *et al*., 2001).

Southeast Pacific Ocean

Southeast Pacific blue whale song has been described off the west coast of South America (Cummings and Thompson, 1971; Stafford *et al*., 1999b), maintaining the same character for 27 years. This song contains three pulsed call units, closely spaced in time and with a total duration of 37 seconds (Figure 3b, Table 2). The call units are repeated about every 100 seconds, with single mode phrasing (ABCABC).

The southeast Pacific blue whale song (type 2 in Figure 1) is observed along the west coast of South America and adjacent offshore waters, with the type locality in the Isla Guafo region of southern Chile (Cummings and Thompson, 1971). In the northern part of the range, off the coast of Peru, the songs are recorded year-round, but in greater numbers during the austral fall and winter (March-August) (Stafford *et al*., 1999b). In the south of their range, the song has been heard in the summer (Cummings and Thompson, 1971). These data suggest a seasonal movement with a winter peak presence in tropical waters, and summer peak presence further south. Sightings and whaling data confirm blue whale presence in southern Chile year-round (Tønnessen and Johnsen, 1982; Aguayo-Lobo *et al*., 1998; Findlay *et al*., 1998).

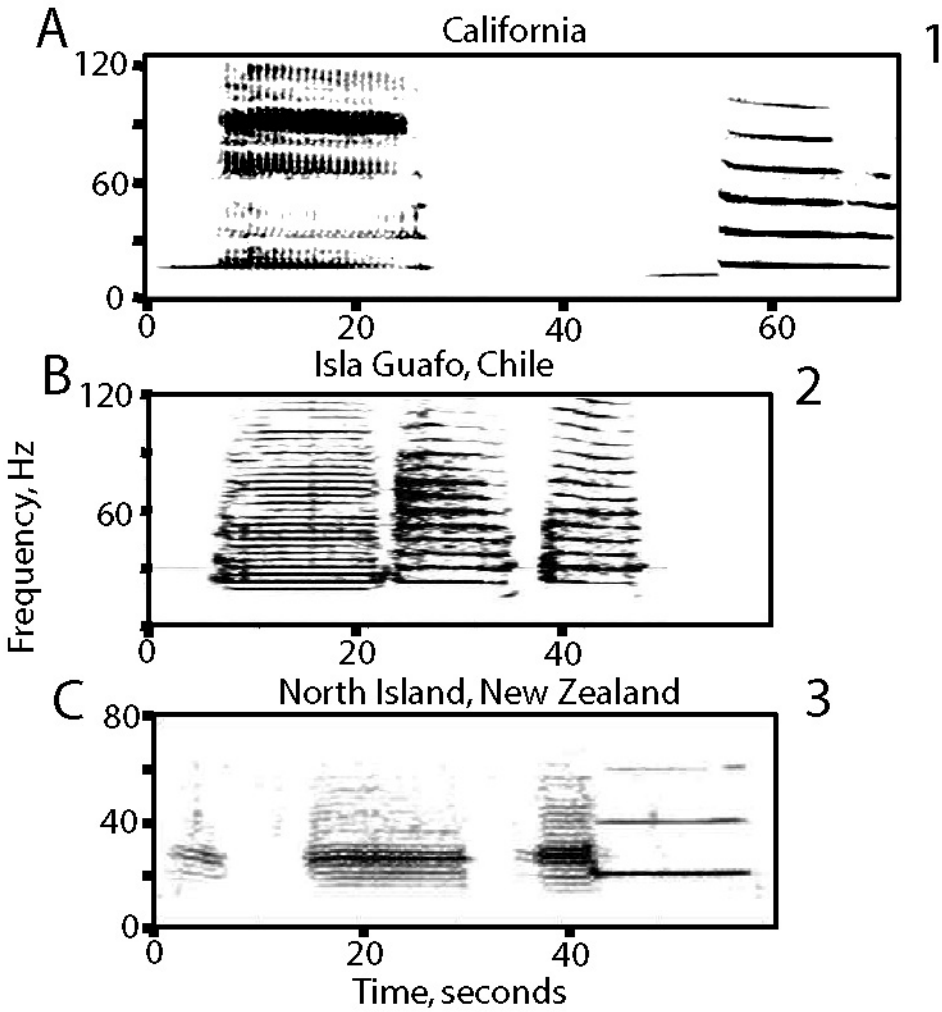

Figure 3. Blue whale songs for: (A) Northeast Pacific – California, recorded June 2001 near San Clemente Island, California, this being the highest signal to noise ratio recording available, (B) Southeast Pacific – Chile, recorded May 1970 near Isla Guafo, Chile, (Cummings and Thompson, 1971). Spectrogram produced from archival tape in Hubbs SeaWorld Sound Library, and (C) Southwest Pacific – New Zealand, recorded December 1997 near Great Barrier Island, New Zealand. Recording from the Center for Monitoring Research collected as part of the Comprehensive Test Ban Treaty. The recording shown here has higher signal to noise ratio than the type recording, though song character is the same.

Southwest Pacific Ocean

Southwest Pacific blue whale song has been recorded off North Island, New Zealand (Kibblewhite *et al*., 1967), with no change in character over the 33 year time span between recordings. This song consists of three pulsed call units (A, B, C) followed by a tonal call unit (D), with a total duration of about 55 seconds (Figure 3c, Table 2). The first pulsed unit (A) has lesser amplitude than the following units (B and C). The call units are repeated about every 108 seconds, with single mode phrasing (ABCDABCD). This song has been recorded in waters off North Island, New Zealand: twice near Three Kings Island (Kibblewhite, 1967), and four times near Great Barrier Island, scattered throughout the year (author's unpublished data).

North Pacific Ocean

North Pacific blue whale song, first reported from Midway Island recordings made in 1968 (Northrop *et al*., 1971), consists of 2-4 tonal units with frequencies near 20 Hz (Figure 4a and 4b, Table 2). Six different call units have been reported, with varying usage over the North Pacific (e.g. Stafford *et al*. 2001), suggesting that it may be possible to break this song region into finer subdivisions. The call units typically last for 5-20 seconds. Figure 4a shows representative calls recorded near Midway Island (Northrop *et al*., 1971). The call units are repeated about every 85-95 seconds, with single mode phrasing (ABABAB). Figure 4b shows song recorded near Wake Island (author's unpublished data) with three tonal units (A, B, C). The phrasing of the Wake Island call is single mode, with a repeated second unit (ABBCABBC). Other variants for the North Pacific blue whale song type have been reported by Stafford *et al*. (2001).

The range for the North Pacific blue whale song type (Type 4 in Figure 1) is primarily from the Aleutian Islands, stretching to about 40 °N (Moore *et al*., 2002). Lesser numbers of calls are heard as far south as Hawaii and Wake Island (Watkins *et al*., 2000; Stafford *et al*., 2001). In the Aleutians region, these songs are abundant in the summer and fall, and are detected nearly every hour on fixed hydrophones. Aleutian calling is diminished during the winter and is nearly absent in the spring. This pattern suggests a strong seasonal movement with summer and fall spent at high latitude and spring spent at lower latitudes.

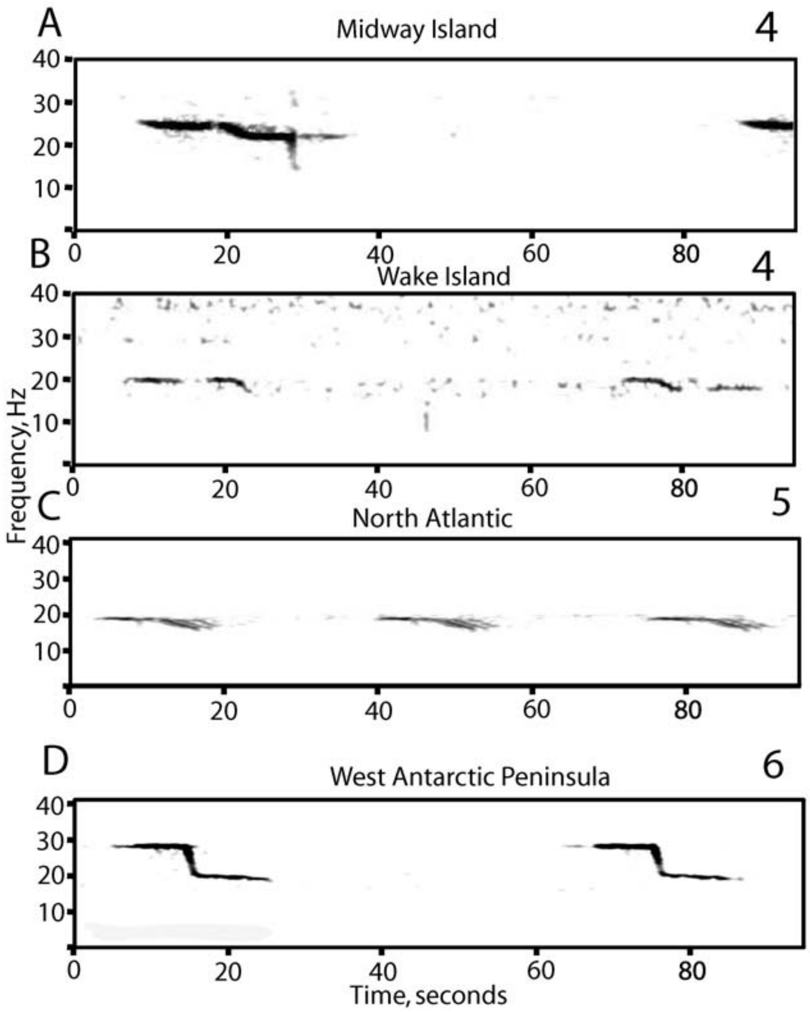

Figure 4. Blue whale songs for (A) North Pacific – Midway Island, recorded on December 1967 near Midway Island (Northrop *et al*., 1971). Spectrogram produced from archival tape in Hubbs SeaWorld Sound Library, (B) North Pacific – Wake Island, recorded January 1997 from the Wake Island Mils hydrophone array. Data provided by the Center for Monitoring Research, (C) North Atlantic, recorded in 1993 in the northeast Atlantic between Iceland and Spain. Data from the Integrated Undersea Surveillance System (Clark, 1996) is used here as the type locality recordings are not available, and (D) Southern Ocean – West Antarctic Peninsula, recorded February 2002 at 66˚S, 71˚W off Adelaide Island (Širović *et al.*, 2003) selected for best signal to noise ratio.

North Atlantic Ocean

North Atlantic blue whale song was first described in detail in the St. Lawrence River Estuary (Edds, 1982) as consisting of a single tonal unit near 19 Hz (Figure 4c, Table 2), although descriptions date back to 1959 (Weston and Black, 1965). The call unit lasts for about 17 seconds and repeats every 35-60 seconds.

The range for the North Atlantic blue whale song (Type 5 in Figure 1) stretches from the Arctic Ocean south to at least 35°N. Off the coast of Great Britain it is reported year-round (Clark and Charif, 1998). Using military hydrophone arrays, a singing blue whale was shown to move along a northeast-southwest track in the western north Atlantic during February – March 1993 (Clark, 1995). The probable pattern for North Atlantic blue whale song is year-round residence at high latitude, with some seasonal movement to lower latitudes during spring.

Southern Ocean
Southern Ocean blue whale song recently has been reported offshore from Antarctica (Ljungblad *et al*., 1998; Matsuoka *et al.*, 2000; Širović *et al.*, 2003). The song consists of three tonal units with frequencies near 20 Hz (Figure 4d, Table 2). The phrase is repeated about every 65 seconds, typically with single mode phrasing (ABCABC), although mixed mode phrasing also has been observed.

The reported locations for Southern Ocean blue whale song recording suggest a circumpolar distribution around the Antarctic Continent (Type 6 Figure 1). A year-round presence is documented from fixed hydrophones deployed near the West Antarctic Peninsula (Širović *et al.*, 2003). The Southern Ocean blue whale song has also been recorded at tropical latitudes, off the coast of Peru, during July (Stafford *et al.*, 1999b) and off the Southwest coast of Australia in June (Maya Tolstoy, pers. comm.), suggesting some movement to lower latitudes during the southern winter.

North Indian Ocean

North Indian Ocean blue whale song is reported offshore from Sri Lanka (Alling and Payne, 1988; Alling *et al.*, 1991). The song consists of four units, three pulsive and one tonal (Figure 5a, Table 2). The call units are repeated about every 210 seconds, with single mode phrasing (ABCDABCD).

The North Indian Ocean blue whale song (Type 7 Figure 1) is reported from the near-shore waters of Sri Lanka, (Alling and Payne, 1988; Alling *et al.*, 1991). It was recorded on two consecutive seasons, both in the spring, and the whales are reported to be present between January and May.

Southeast Indian Ocean

The southeast Indian Ocean blue whale song (Type 8 in Figure 1) has been observed in waters off northern and southwestern Australia, in the Timor Sea (Lindsay Hall, pers. comm.) and near Fremantle (McCauley *et al.*, 2000; McCauley *et al.*, 2001). These songs were heard in the southern summer and fall (January-March), although data are not available for other seasons. This song contains four pulsed call units and one tonal call unit, with a total duration of about 120 seconds (Figure 5b, Table 2). The call units are repeated about every 180 seconds, with single mode phrasing (ABCDEABCDE).

Southwest Indian Ocean

The southwest Indian Ocean blue whale song has been recorded south of Madagascar (Ljungblad *et al.*, 1998) and on a fixed hydrophone array south of Diego Garcia Island. The Madagascar songs consist of four call units with a total duration of about 60 seconds (Figure 5c, Table 2). The call units are repeated about every 90-100 seconds, with single mode phrasing (ABCDABCD). The Diego Garcia variant of this song consists of five units, two pulsive and three tonal (Figure 5d, Table 2). The call units are repeated every 200 seconds, with single mode phrasing (ABCDEABCDE).

The southwest Indian Ocean blue whale song (Type 9 in Figure 1) has been observed south of Madagascar, at 32°S (Ljungblad *et al.*, 1998). The songs were heard in the southern summer (December) on two successive years. No data are available for other seasons. The Diego Garcia song is known from a single recording made in October.

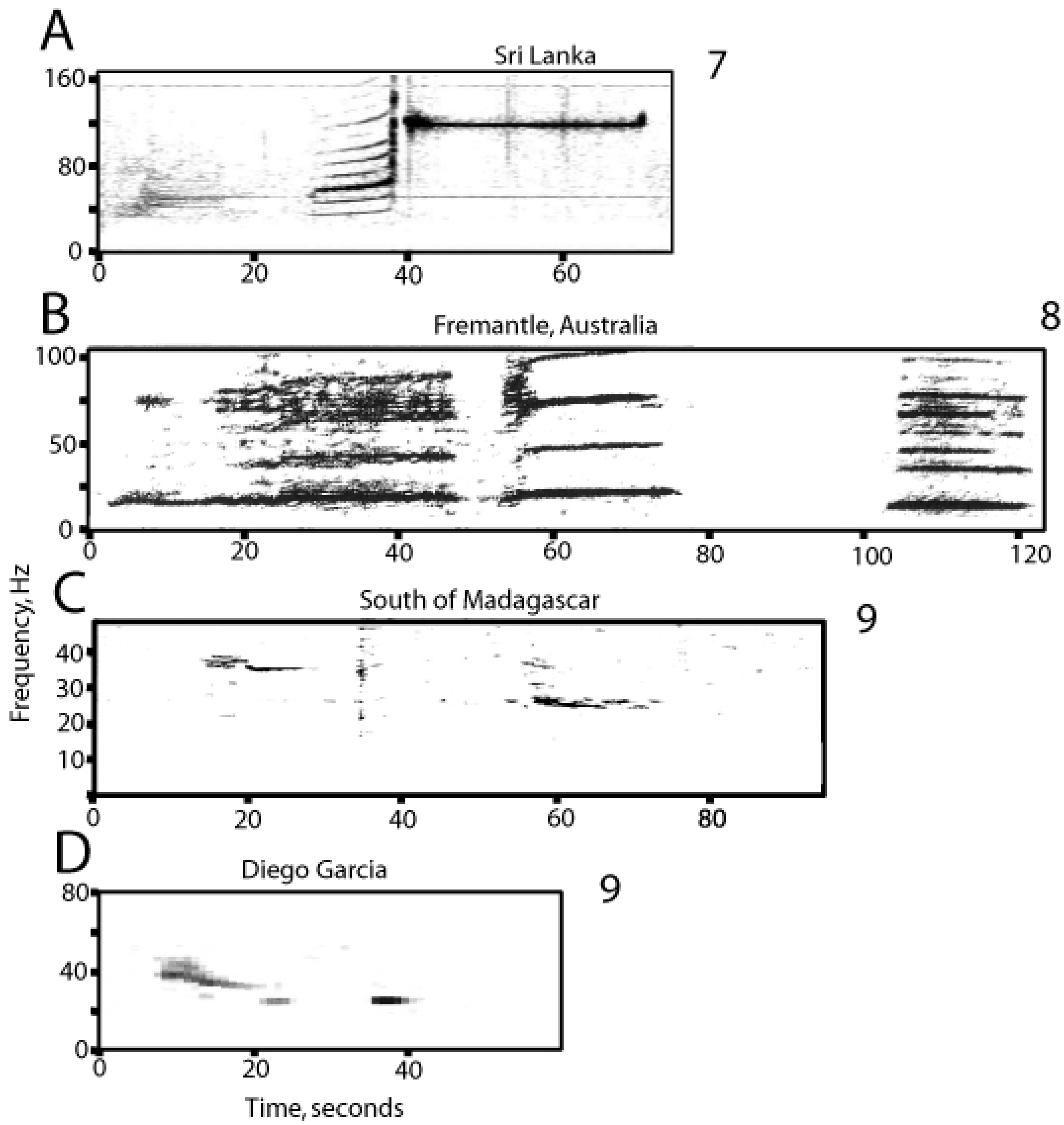

Figure 5. Blue whale songs for: (A) North Indian Ocean – Sri Lanka, recorded April, 1984 within 5 miles of the entrance to Trincomalee Harbor (Alling and Payne, 1988). Spectrogram produced from archival tape at the British Library, Natural Sound Archive, London, (B) Southeast Indian Ocean – Fremantle, recorded March 2000 in the Rottnest Trench, west of Perth, Australia (after McCauley 2001), (C) Southwest Indian Ocean – Madagascar, recorded December 1996, south of the Madagascar Plateau (after Ljungblad *et al.*, 1998), and (D) Southwest Indian Ocean – Diego Garcia, recorded October 2000, south of Diego Garcia, by the Comprehensive Test Ban Treaty Organization.

Song # Loc	Units Total# Tonal# Pulse#	Unit A F T P	G	Unit B F T P	G	Unit C F T P	G	Unit D F T P	G	Unit E F T P	Call Cyc. Time	Resp. Time	Dive Time
1 NEP	2 1 1	16- 88 19 1.2	28	18- 15 19 0							118	160	660
2 SEP	3 0 3	20- 32 13- 15 3.8	0- 2	20- 31 9-10 7.7	2- 4	20- 31 8-9 7.7					102	178	798
3 SWP	4 1 3	18- 35 6 2.6	10	18- 35 13 2.6	10	18- 35 6 2.6	0	20 12 0			108	220	730
4 NP Mid way	2 2 0	25 12 0	0	25- 23 12 0							90	249	990
4 NP Wake	3 3 0	22 10 0	5	22- 18 3 0	50	22- 18 3 0	5	18 10 0			90	245	720
5 NA	1 1 0	19- 18 17 0									35- 60	--	--
6 SO	3 3 0	28 10 0	0	28- 20 1 0	0	20- 19 10 0					65	180	--
7 NI	4 1 3	60- 100 12 3.6	12	50- 150 11 13	1	130- 110 29 0	49	35- 93 9 19			210	153	--
8 SEI	5 1 4	15- 80 20 1.6	0	15- 80 22 2	5	15- 80 2 2	0	20- 26 23 0	23	20- 100 20 8	198	--	--
9 SWI Mada	4 2 2	36- 42 5-8 1	0	26 10- 12 0	25	28- 15 1-2 0	0	27 15- 20 1			100	--	--
9 SWI DG	5 3 2	42 3 5	0	42- 30 5 10	0	33- 30 6 0	0	25 4 0	12	25 5 0	200	--	--

F = frequency (Hz), T = unit time (sec), P = pulse rate (1/sec), G = inter-unit gap (sec)

Table 2. Blue whale song unit characteristics by region. The typical blue whale song phrase consists of three call units, of which one or two are pulsed and one or two are tonal. The call unit average duration is 11 sec. The phrase repetition rate averages 118 sec. Only about one-third of the song cycle is spent calling, with quiet periods occurring between units and between phrases. The gap between call units is highly variable but averages 16 sec. Pauses in the song cycle occur for respiration, lasting about 3 minutes. The time between respiration periods is 11 to 22 minutes.

DISCUSSION

Acoustic Identification of Regional Differences

Several other populations of marine mammals also demonstrate regional acoustic differences, including killer whales, sperm whales, Bryde's whales, humpbacks, and fin whales (Ford, 1991; Weilgart and Whitehead, 1997; Oleson *et al*., 2003; Thompson *et al*., 1992; Rendell and Whitehead 2003), among others. Please refer to Table 1 in Mellinger and Barlow (2003) for a more complete listing with notation on temporal stability and whether there is known geographic structure from other markers. As a more complete understanding of the acoustic repertoire of each whale species is acquired, we will likely be able to distinguish regionally distinctive sounds from those common throughout the species. Recent study of the acoustics of minke whales suggests a simple downswept call is used across geographic regions, but a complex song-like vocalization variously referred to as the star-wars, thump-train and boing sound is geographically distinctive (Gedamke *et al*., 2001; Mellinger *et al*., 2000; Jay Barlow, pers. comm.; Wenz, 1964 ; Thompson and Friedl, 1982). In minke whales the complex sound appears to be produced only during the breeding season while the simple sounds are produced throughout the year. Acoustic characters are increasingly being investigated as a cost-effective means of population identity and structure (Mellinger and Barlow 2003). Moreover, over the ecological time scales relevant for management methods of determining population identity may fail to detect structure because traditional markers, such as morphology or genetics, are slow to evolve and may not reflect present day movement and association patterns and, in addition, samples are difficult to obtain. In contrast, songs are social signals. The animals themselves can be safely assumed to use these signals to mediate social interactions and to maintain associations between interacting individuals. Acoustics also offers a relatively a fast and efficient means of gathering information on marine mammal populations remotely and in difficult visual or sea conditions and locations.

Blue whale song types can be helpful in defining population boundaries. There are distinct differences, outlined above, between songs recorded in different regions. We have identified nine acoustic types, many of which are known to have remained stable for decades (Table 2). These results suggest that there are at least nine distinct populations of blue whales worldwide, with the possibility of more as acoustic data are collected in unstudied areas. These distinct differences between areas provide another data set for comparison with genetic and morphological data when defining blue whale populations (e.g., Le Duc et al. 2003). As Mellinger and Barlow (2003) recommend, in regions where there is a lack of data, or lack of resolution using traditional markers, evidence of distinct differences in songs between areas be used as the provisional population structure when making management decisions. For these reasons, we provisionally recommend nine acoustic populations of blue whales worldwide.

Song Type Groups

Blue whale song may be grouped into three categories based on similarity of character. Song types bordering the Pacific Ocean, which may be grouped together due to common characteristics, are: California, Chile and New Zealand (type 1, 2, and 3; Figure 3A, B, C). These songs have the following characteristics: (1) pulsed call units, (2) when present, tonal call units contain higher harmonics, and (3) song cycle times of intermediate length (102-118 sec). High latitude North Pacific, North Atlantic, and Southern Ocean songs (type 4, 5 and 6; Figure 4A, C, D) have a simple character, with only tonal call units lacking harmonics, and a short cycle time (35-90 sec). Indian Ocean songs (type 7, 8, and 9; Figure 5A, B, C, D) have the highest level of complexity. There are similarities in the structure of the Fremantle song (type 8) and Sri Lanka song (type 7). They have a comparable number, type, and ordering of call units, with long song cycle times (198 and 210 sec).

Phylogeographic Patterns and Processes

It is tempting to consider that blue whale songs contain historical information, information that can be used to infer taxonomic relationships among blue whale populations. However, the difficulty of teasing apart historical, environmental and behavioral components of vocalizations has discouraged cetacean biologists from using acoustic characters for studying the evolution of populations and species groups. For instance, the acoustic properties of the ocean (sound speed profile, bathymetry) and ecological factors (ambient noise) can shape vocalizations so that distantly related populations in the same habitat may sound more similar than closely related populations in different habitats. McCracken and Sheldon (1997) note, for example, that the vocalizations of terrestrial species inhabiting dense vegetation tend to have lower frequencies and narrower frequency ranges than those that inhabit open areas because the longer wavelengths propagate energy more efficiently through vegetation than shorter wavelengths. In addition, because vocalizations are signals, we expect them to vary according to the intensity of selection on vocal characters among populations (Price, 1998). The use of vocalizations for phylogenetic reconstruction may be further confounded by individual behavioral flexibility, learning, and cultural evolution (Rendell and Whitehead, 2001; Noad *et al*., 2000; Deecke *et al*., 2000). Thus, different song types may be similar by convergent evolution or chance, rather than by shared ancestry. While these problems make systematics difficult, they are simply homoplasy, the parallel evolution of identical character states, which can potentially affect any type of character used in phylogenetic reconstruction (McCracken and Sheldon, 1997; Irwin, 1996).

The pattern of similarity among the song types suggests various phylogeographic patterns based on the acoustic properties of the songs and the habitats in which they are found. We present three of them for heuristic purposes and to encourage further research to test the various evolutionary processes at work. The first, antitropical model, describes geographic distributions in which related taxa are found in regions on opposite sides of the warm equatorial waters; such distributions are a prominent feature of several cetacean clades (Rice, 1998). Blue whales in polar waters share simple tonal songs (Figure 4). This pattern can be explained by shared common ancestry and subsequent antitropical divergence or, alternatively, by convergence (e.g., due to the acoustic properties of polar waters that may select for songs with tonal characteristics or similarities in the demographics of blue whale populations that inhabit polar waters), for example. Likewise, blue whales in Chile and California share similar song types (Figure 3); shared ancestry and subsequent antitropical divergence is one of the hypotheses that may explain this pattern. The second, ocean basin/ocean margin model, describes geographic distributions in which simple tonal songs are found in the interior of the basin and songs which contain complex pulsed units are found along the basin margins. This ocean basin/ocean margin pattern can be observed in the North Pacific (Figure 6). The pattern may be the result of an ancestral blue whale population that subsequently radiated into ocean basin and ocean margin habitats, the different song types reflecting the different signaling environments in the two habitats. The third (complexity) model is not a hypothesis of taxonomic relationships but rather one that incorporates the influence of demography and the intensity of selection on the evolution of signal characters. This model is based on the observation that, in birds, stronger selection tends to increase song complexity (Price, 1998). Thus, the relative complexity of the Sri Lanka song type may be explained by taking into account not only the various factors mentioned above, but also the observation that this may be an isolated population under stronger social/sexual selection than populations with simpler songs. These various patterns and processes can be tested when demographic as well genetic and morphological data with which to reconstruct blue whale phylogenetic relationships become available.

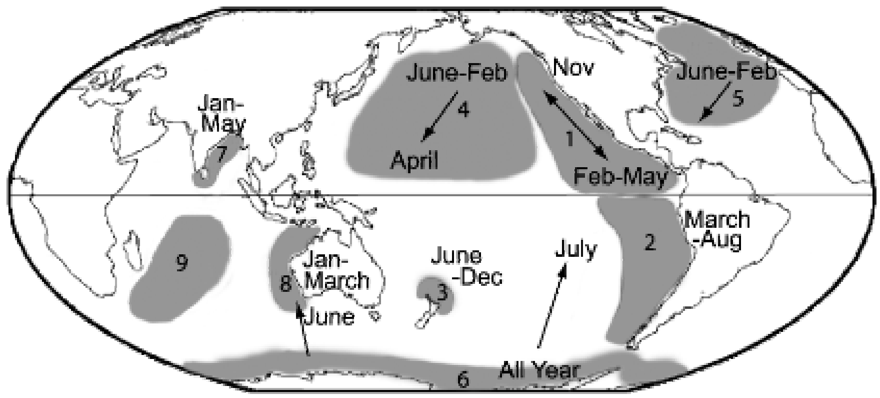

Figure 6. Blue whale residence and population divisions suggested from their song types. Arrows indicate the direction of seasonal movements.

CONCLUSION

Song types may be a useful indicator of population identity because they are social signals that evolve more rapidly than genetic or morphologic traits. Commercial whaling harvested more than 360,000 blue whales, primarily in the Southern Ocean, but with significant numbers from almost every part of the world's oceans (Clapham and Baker, 2001). Stock changes or other adjustments in population structure may be responding to these changes over the post-whaling time scale. These rapid changes in population structure may escape detection by genetic or morphologic means which are slow to evolve, but may be reflected in songs which can rapidly change.

Blue whale songs provide a new means for characterizing blue whale population structure worldwide and also suggest various phylogeographic patterns and evolutionary processes, which can be tested against non-acoustic data. Recent advances in technology make the collection and analysis of long-term acoustic records practical, even for remote regions of the world's oceans and at moderate costs. The availability of these data will enhance the potential for blue whale song to play a key role in describing population structure worldwide. Provisionally, we recommend nine acoustic populations for management. To be risk adverse, it is prudent to listen to what the whales are saying.

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