Biogeographic characterisation of blue whale song worldwide: using song to identify populations

MARK A. MCDONALD*, SARAH L. MESNICK+# AND JOHN A. HILDEBRAND**

Contact e-mail: mark@whaleacoustics.com

ABSTRACT

Blue whale songs provide a measure for characterising worldwide blue whale population structure. 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. The nine song types can be divided into those containing only simple tonal components (high latitude North Pacific, North Atlantic and Southern Ocean song types), those comprised of complex pulsed units in addition to the tonal components (Pacific Ocean margin song types from California, Chile and New Zealand), and those which have the greatest complexity of all and the longest cycling times (Indian Ocean song types from Sri Lanka, Fremantle and Diego Garcia). We suggest that temporally stable differences in song provide another characteristic for comparison with genetic and morphological data when defining blue whale populations. Furthermore, as Mellinger and Barlow (2003) recommend, when there is a lack of other data or lack of clarity in other data sets, evidence of distinct differences in songs between areas should be used as a provisional hypothesis about population structure when making management decisions. Worldwide study is needed to better understand the various populations and subspecies within species like the blue whale that have large geographic distributions and have both migrating and resident populations.

KEYWORDS: BLUE WHALE; ACOUSTICS; VOCALISATION; COMMUNICATION; DISTRIBUTION; TAXONOMY; EVOLUTION; GENETICS

INTRODUCTION

Traditional studies based on external morphology, osteology and results of ongoing genetic analyses, have not produced an accurate picture of blue whale (*Balaenoptera musculus*) population structure or phylogeography (e.g. Reeves *et al.*, 1998). Collecting samples is not only logistically and geographically challenging, it is also difficult to obtain enough samples to have sufficient power to detect structure. In addition, over the ecological time scales relevant for management, traditional markers may fail to detect population structure because they may evolve too slowly and may not reflect present day movement and association patterns. Biochemical analyses of pollutants or the fatty acid signatures in blubber may better reflect the recent past. Here, we examine another line of evidence, acoustic characters, and blue whale song in particular, which provide a potentially rich source of data which can help delimit the population structure of blue whales worldwide (Cummings and Thompson, 1977; Thompson *et al.*, 1979; Edds, 1982; Stafford *et al.*, 1999a; Mellinger and Clark, 2003). Song types may be a useful indicator of population identity because they are likely to reflect present day movement and association patterns. Regional differences in song provide hypotheses of structure to be compared with genetic and morphological data when defining blue whale populations (e.g. Gilpatrick *et al.*, 1997; Le Duc *et al.*, 2003; Conway, 2005). Moreover, acoustic recording of songs offers a relatively cost-effective means of obtaining samples of sufficient size for population structure analyses.

The production of high intensity, low frequency, long duration acoustic calls is a trait common to blue whales worldwide (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). Although the function of song is unknown (see below), it is safe to assume that these are social signals used by the animals themselves to mediate social interactions and maintain associations between interacting animals. 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.

BACKGROUND

Blue whale subspecies and populations

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). Changes in population boundaries or other adjustments in population structure may be responding to recovery from these depletions and other environmental and anthropogenic changes, over the post-whaling era. However, despite considerable effort by the Scientific Committee of the IWC, the systematics of blue whales remains problematic. This uncertainty, in turn, hinders efforts to effectively monitor and manage blue whale populations at global and regional scales. Currently, blue whales are divided into four subspecies based on morphologic and geographic distinctions (Rice, 1998) and these have been further subdivided into populations for cetacean management and endangered species recovery plans (Gambell, 1979; Donovan, 1991; Reeves *et al.*, 1998). However, the subspecies and population divisions are poorly understood and the distinctions among them are vague beyond their presumed geographical separation (Reeves *et al.*, 2004). *B.m. musculus* includes all blue whales in the

* *Whale Acoustics, 11430 Rist Canyon Rd., Bellvue, CO 80512, USA.*
+ *Southwest Fisheries Science Center, NOAA Fisheries, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA.*
# *Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, UCSD, La Jolla, CA 92093-0202, USA.*
** *Marine Physical Laboratory, Scripps Institution of Oceanography, UCSD, La Jolla, CA 92093-0205, USA.*

Northern Hemisphere. In the North Atlantic, eastern and western subdivisions were recognised, while in the North Pacific as many as five population subdivisions were thought to exist. *B.m. intermedia* is the high latitude Southern Ocean and Antarctic waters blue whale. Whaling data suggest discrete feeding stocks, and consistent with these, the International Whaling Commission has assigned six stock areas in the Southern Ocean (Donovan, 1991). *B.m. brevicauda*, the pygmy blue whale, is distributed in sub-Antarctic waters of the Indo-Pacific Ocean and south-eastern Atlantic Ocean (Zemsky and Sazhinov, 1994; Kato *et al.*, 2002; IWC, 2003, pp.264-5). *B.m. indica* is from the northern Indian Ocean. Unfortunately, the utility and validity of these subspecies descriptions is uncertain because osteological studies have been based on only a few specimens (Omura *et al.*, 1970) and external measurement comparisons often yield equivocal or even contradictory results (Gilpatrick *et al.*, 1997). Additional lines of evidence can improve taxonomy and population designations (Reeves *et al.*, 2004).

Blue whale song

Blue whale calls are among the most powerful (188dB_{RMS} re: 1μPa @ 1m) and lowest frequency (16-100Hz) sounds made by any animal (Cummings and Thompson, 1971; McDonald *et al.*, 2001). Singing is the behaviour during which a limited number of stereotypic sound types are produced in regular succession and form a recognisable pattern in time. Calling is the behaviour in which individual, transient sounds are produced at irregular intervals or as call and counter-call between two or more individuals. Blue whale calls are often downswept tones (80-30Hz) of moderate duration (2-5s), with seasonally variable occurrence (Thompson *et al.*, 1996; McDonald *et al.*, 2001). It is not our intent to completely describe the acoustic repertoire of blue whales worldwide, but only to describe the sounds which are known to be used in blue whale song. The acoustic repertoire includes calls which are never seen in song and song units which are sometimes used alone, apparently as calls.

The songs are divided into units, which are continuous segments of sound, and phrases, which are repeated combinations of units (Payne and McVay, 1971; Mellinger and Clark, 2003). Blue whale call units are classified as primarily pulsed or tonal. A unit boundary is defined here as any abrupt change in call character (frequency, sweep rate or modulation rate) regardless of whether there is a pause between units. This usage differs slightly from that of Payne and McVay (1971) in that their definition classifies a new sound as a subunit if there is no pause to separate it. Their definition is problematic because, in blue whale song, certain sounds are sometimes separated by a pause, yet sounds are used with the same syntax, regardless of the presence of a pause. Overall, blue whale song is much less complex than humpback whale (*Megaptera novaeangliae*) song, requiring less nomenclature and making it possible to represent all the basic song units in spectrograms, rather than only representative phrases as is normally done for humpback whale song. One to five call units are combined to produce a phrase and a song is composed of many repeated phrases, each made up of only these units. Breaks in the song typically coincide with respiration, but the songs themselves may continue for many hours or even days (Cummings and Thompson, 1971; McDonald *et al.*, 2001; Clark and Ellison, 2004). The units are sometimes combined in different sequences, these apparently having rules or syntax, by which only certain 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.

The function of blue whale song

The function of blue whale song, as with other mysticete songs, is not well understood. Social functions proposed for mysticete calls (calls in this case refers to all types of mysticete vocalisations, including song) include foraging, mating and parental behaviour, long range contact, assembly, sexual advertisement (male-male or male-female), greeting, spacing, threat, individual identification and sensing of the environment (Tyack, 1999; Tyack, 2000; Clark and Ellison, 2004). However, only rarely has a specific call been associated with a given behavioural event. Regarding mysticete song specifically, in species such as humpback and fin whales, the evidence to date indicates that only males sing (Watkins, 1981; Darling and Berube, 2001; Croll *et al.*, 2002). Much of the prevailing speculation on the function of song in these species has revolved around if, and how, singing functions as a mating display (Payne and McVay, 1971; Tyack, 2000; Darling and Berube, 2001; Croll *et al.*, 2002; Darling, 2002) but recent data indicate that males also sing during migration and on feeding grounds, suggesting that there is much yet to learn about the function of song (Norris *et al.*, 1999; Clark and Clapham, 2004).

In blue whales, it is known that males sing (McDonald *et al.*, 2001), but it remains unknown if females also sing. Animals vocalise throughout the year with peaks from midsummer into winter (Burtenshaw *et al.*, 2004; Širović *et al.*, 2004). Field observations suggest that singers are solitary animals (Calambokidis, pers. comm.). Diel chorusing at dusk and dawn increases the number of singers during these periods (Thompson, 1965) and tracking, either visually or acoustically has shown that blue whales swim at 2-10km hr^{-1} while producing songs (Kibblewhite *et al.*, 1967; Northrop *et al.*, 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 kilometres (Stafford *et al.*, 1998).

Individual, temporal and spatial variation in blue whale song

From personal observation based on the data presented below, the songs of individual blue whales are known to be variable, but individual variability within a song type is much less than that which distinguishes among song types. Variability within a song type has been shown to be useful to distinguish between individual whales off California over the 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 for North Atlantic blue whales (Clark, 1995). More work is needed to determine if and how individuals vary their calls spatially, seasonally or functionally and whether individual whales ever change song type (Stafford and Moore, 2005). The utility of relatively subtle individual variation to further subdivide blue whale populations acoustically remains a topic for further research.

Regional and spatial variation in blue whale song is among the better documented of the baleen whale songs, although the data have yet to be compiled on a global scale. Previous studies have used the characteristics of vocalisations to determine the seasonal presence and movement of blue whales through a region (e.g. Clark, 1995; Stafford *et al.*, 1999a; Moore *et al.*, 2002), including the possibility of populations mixing within a region (Stafford *et al.*, 2001) and have used differences in blue whale song to identify populations and to distinguish populations from neighbouring ones (e.g. northeastern vs northwestern Pacific (Stafford *et al.*, 2001; Moore *et al.*, 2002) and Antarctic versus others (Stafford *et al.*, 2004)). For the global comparison described below we build upon the excellent work in these previous studies.

The case of using vocalisations as a proxy for population identity

In many species, vocalisations are the predominant means by which individuals communicate; species-level and regional variation is well known and song can be a powerful isolating mechanism among taxa (Marler, 1957; West-Eberhard, 1983; Slabberkoorn and Smith, 2002). Due to recent advances in bioacoustics, vocal differentiation has become increasingly important in the taxonomy of many terrestrial species and the structure of vocalisations is becoming common in the descriptions of populations and closely related species of birds (Baptista, 1975; Catchpole and Slater, 1995; Martens, 1996; Wright, 1996; Irwin *et al.*, 2001b), mammals (Maeda and Matasaka, 1987; Gautier, 1988; Bearder, 1999; Kingston and Rossiter, 2004; Siemers and Schnitzler, 2004), amphibians (Ryan, 1990) and insects (Wells and Henry, 1998; Gray and Cade, 2000). Acoustic characteristics may be the key distinguishing feature used in the identification of otherwise 'cryptic' taxa (e.g. nocturnal primates, Anderson *et al.*, 2000; green warblers, Irwin *et al.*, 2001a), resulting in significant increases in diversity (Price, 1996; Bearder, 1999).

While regional diversity in vocalisations is well-known, some researchers regard vocal displays as too ephemeral and too influenced by ecological (e.g. habitat matching) and social (including learning, imitation and mating with individuals singing other songs) factors to be useful in elucidating genetic relationships (Harvey and Pagel, 1991; but see Wimberger and de Queiroz, 1996). In birds, the relationship between song dialects and population structure show conflicting results (reviewed in Catchpole and Slater (1995) and Slabberkoorn and Smith (2002)). Some studies find little evidence of genetic differentiation (Fleischer and Rothstein, 1988; Wright and Wilkinson, 2001) while others show a strong correlation between dialects and genetic variation (MacDougall-Shackleton and MacDougall-Shackleton, 2001) sometimes indicating higher level divergence (Irwin *et al.*, 2001a). Several factors contribute to these differences, including the social function and the timing of vocal learning relative to dispersal (Wright and Wilkinson, 2001). In addition, genetic subdivisions may exist but go undetected (Bossart and Pashley Powell, 1998; Taylor and Dizon, 1996; 1999), or differences in song features across different populations may have occurred too recently to be detected genetically (Hatch and Clark, 2004).

Cetacean biologists have long noted the potential utility of whale songs as an indicator of biologically meaningful stocks for blue whales (Cummings and Thompson, 1971; Edds, 1982), humpback whales (Payne and Guinee, 1983; Cerchio *et al.*, 2001), fin whales (Thompson *et al.*, 1992; Hatch and Clark, 2004) and Bryde's whales (Oleson *et al.*, 2003). Geographic variation of non-song calls is also known in killer whales (Ford, 1991) and sperm whales (Weilgart and Whitehead, 1997). Mellinger and Barlow (2003) recently reviewed intraspecific acoustic structure in cetaceans with notations on temporal stability and its utility for stock assessment. Hatch and Clark (2004) examined the concordance between fin whale song and genetic divergence among eleven geographic regions in the North Atlantic and North Pacific Oceans. They found that acoustic differences were not correlated with estimates of genetic divergence among regions, and suggested that the patterns of acoustic dissimilarity may reflect demographic discontinuities in behaviour and/or movement that are too recent to be reflected genetically, but that exist on the shorter time scales relevant to management (i.e. decadal time) scales. As a more complete understanding of the acoustic repertoire of each whale species is acquired, we may be able to distinguish regionally distinctive sounds from those common throughout the species' range in these and other species and to test these acoustic patterns for concordance with patterns of morphological and genetic variation.

Biogeographic characterisation of blue whale song worldwide

The objective of this paper is to describe blue whale song on a worldwide scale. The approach used intentionally simplifies since the focus is to look for big picture patterns and gross differences among regions, while for many biologists, the focus is on the subtleties of natural variation, as these may provide clues to the underlying behavioural, demographic and evolutionary processes. Much additional research is needed to more fully describe the individual, temporal, seasonal and microgeographic variability of the acoustic repertoire of blue whales. The intriguing exceptions to the rules may indicate there is more to the story than that provided here, but the objective here is to highlight the value of acoustic information as a tool in marine mammal conservation and management.

METHODS

Recordings and spectrograms of blue whale songs from publicly available literature, from recordings offered by colleagues and from our own research have been reviewed. From these data, spectrograms have been studied from as few as 10 songs for some of the least well known Indian Ocean song types to as many as 100,000 songs for the northeast Pacific where millions of song recordings are now available. A typical acoustic encounter with a singing blue whale resulted in recording about twenty songs before either the whale stops singing or the signal to noise ratio becomes undesirably low, thus the number of whale encounters examined scales more or less by a factor of twenty fewer. It was possible to compare songs between regions as the differences were apparent visually in the spectrograms. A typical song phrase or in some cases several phrases for each song type are presented, representing nearly all the well known song units. Undoubtedly, detailed study will reveal additional, less common units, for some song types. To investigate temporal variation within a region, as many as 15 different years of recordings from the Northeastern Pacific song were looked at and as few as two different years of recordings for the Indian Ocean song types. For this study, 'acoustic-types' were established for each of the geographic regions described with the acoustic measures above, much as morphologists identify 'morpho-types' when a new species is described.

RESULTS

Blue whale song can be categorised into nine types, each of which was associated predominantly with a geographic region (see Table 1 for a listing of source data). The best known songs were from the Pacific Ocean, which had four song types. The Indian Ocean, although poorly studied, had at least three song types, whereas the Atlantic Ocean and Southern Ocean each had a single song type. Additional song types may remain undiscovered, for instance, no recordings are available for the South Atlantic. Locations for all known blue whale recordings are shown in Fig. 1, the locations being numbered corresponding to the song type listed in Table 1. Stability of the song character is illustrated in Fig. 2. 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 (Figs 2 and 3) are grouped based on similarity of character, while Fig. 4 illustrates the Northern Indian Ocean types which do not readily group with the others in call 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 (Fig. 3A). 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 Fig. 1) is primarily along the west coast of North and Central America. The type 1 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 autumn and early winter (Stafford *et al.*, 2001; Stafford, 2003; Burtenshaw *et al.*, 2004). 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.*, 1996; 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; Stafford, 2003).

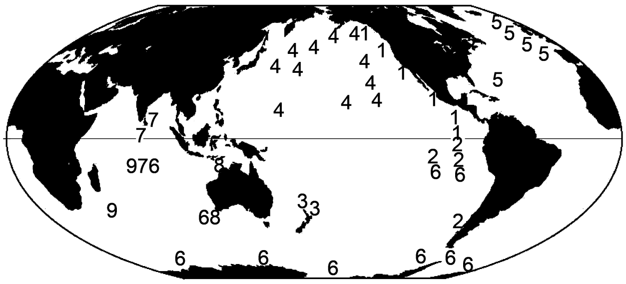

Fig. 1. Distribution of blue whale song, classified into nine regional types (numbers). See Table 1 for regional designations.

Southeast Pacific

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, with a total duration of 37 seconds (Fig. 3B). The call units are repeated about every 100 seconds, with single mode phrasing (ABCABC).

The southeast Pacific blue whale song (type 2 in Fig. 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 (Tonnessen and Johnsen, 1982; Aguayo-Lobo *et al.*, 1998; Findlay *et al.*, 1998). A variant of this song has been detected on the Eastern Tropical Pacific hydrophones south of the equator (Stafford *et al.*, 1999b). This song (Fig. 3C) consists of four pulsive units, making it more similar to the Isla Guafo song type than the New Zealand song type, although it is somewhat intermediate in character. As more data becomes available, it may be appropriate to categorise this variant as a separate song type.

Southwest Pacific

Southwest Pacific blue whale song has been recorded off North Island, New Zealand (Kibblewhite *et al.*, 1967), with no apparent change in character over the 33 year time span between recordings (Fig. 2, Fig. 3D). This song consists of three pulsed call units (A, B, C) followed by a tonal call unit

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 available. See the text for the time span references.

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 and Thompson (1971)
3	1964-1997	Southwest Pacific (SWP)	New Zealand	Kibblewhite *et al*, (1967)
4	1967-1997	North Pacific (NP)	Aleutian Islands	Stafford *et al.* (2001)
5	1959-2001	North Atlantic (NA)	Eastern north Atlantic	Clark and Charif (1998)
6	1997-2003	Southern Ocean (SO)	W. Antarctic Peninsula	Širović *et al.* (2004)
7	1984-2002	North Indian (NI)	Sri Lanka	Alling *et al.* (1991)
8	1993-2000	Southeast Indian (SEI)	Fremantle	McCauley *et al.* (2000)
9	2002	Southwest Indian (SWI)	Diego Garcia	This paper

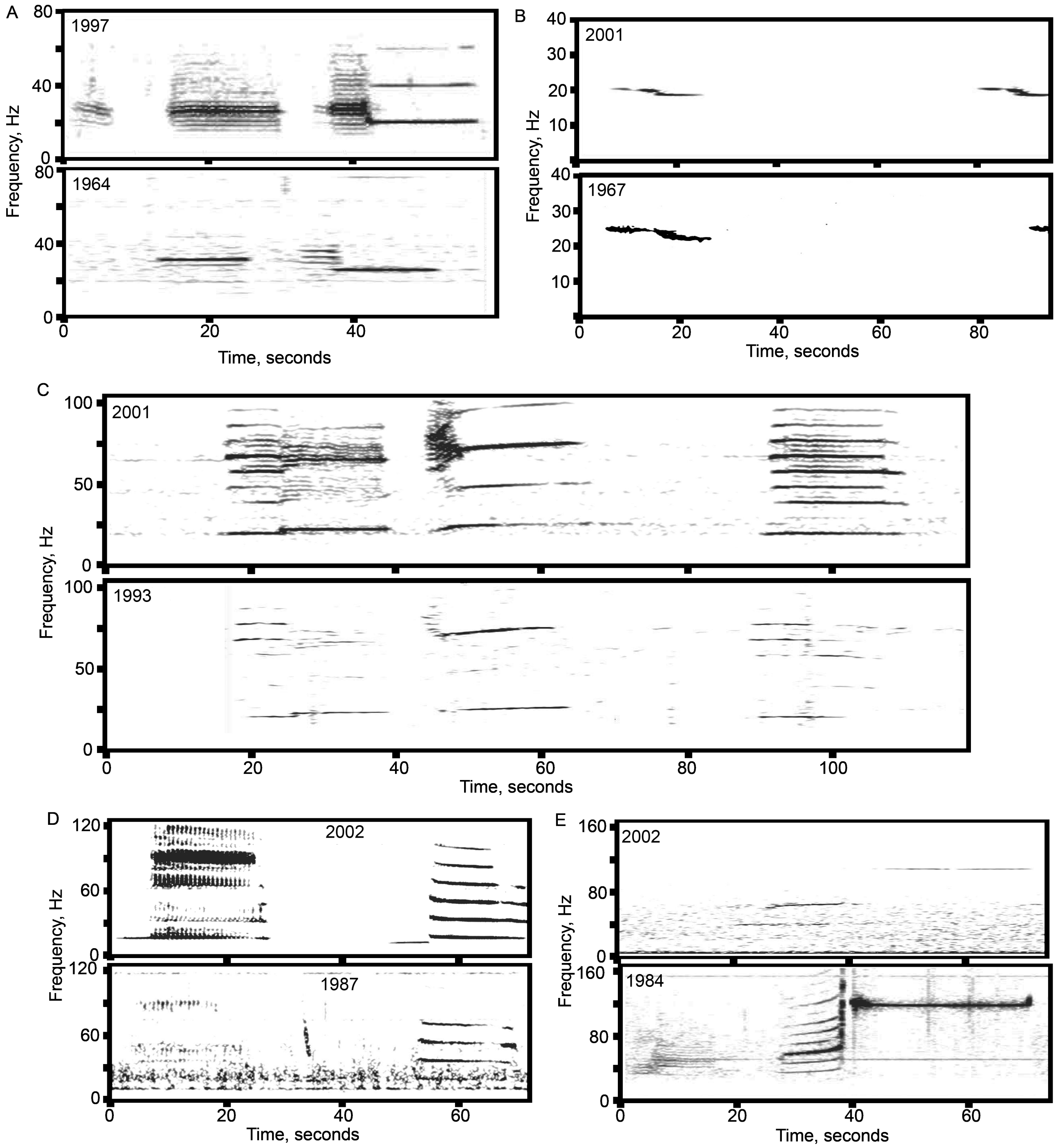

Fig. 2. Recordings from New Zealand (A), the Central North Pacific (B), Australia (C), the Northeast Pacific (D) and North Indian Ocean (E) illustrate the stable character of the blue whale song over long time periods. All song types for which long time spans of recording are available show some frequency drift through time, but only minor change in character. These examples were chosen because recordings over a significant time span were available to the authors in raw form, and not because these song types are more stable than the others. The stability of song character in the other types and for longer time spans in these types is available to various degrees in copyrighted spectrograms and/or written descriptions. The missing first units in the 1964 New Zealand example and 2002 Sri Lanka example are probably due to lower signal to noise ratio, rather than a change in the song.

(D), with a total duration of about 55 seconds (Fig. 3C). The first pulsed unit (A) has lesser amplitude than the following units (B and C). The call units are repeated approximately 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 *et al.*, 1967) and on four occasions near Great Barrier Island, scattered throughout the year (author's unpublished data).

North Pacific

North Pacific blue whale song, first reported from Midway Island recordings made in 1967 (Northrop *et al.*, 1971), consists of 2-4 tonal units with frequencies near 20Hz (Fig. 4A and 4B). 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. Fig. 4A shows representative calls

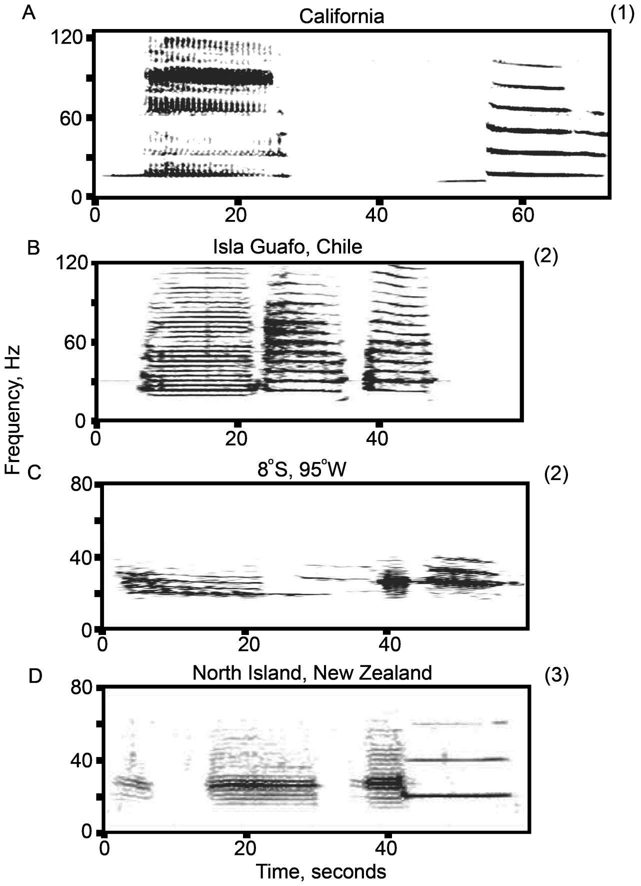

Fig. 3. Blue whale songs for: (A) Northeast Pacific – California, recorded June 2001 near San Clemente Island, California, (B) Southeast Pacific – Chile, recorded May 1970 near Isla Guafo, Chile, (Cummings and Thompson, 1971). Spectrogram produced from archival tape in Hubbs SeaWorld Sound Library, (C) 8°S 95°W – recorded 1996 (Stafford *et al.*, 1999b) and (D) Southwest Pacific – New Zealand, recorded December 1997 near Great Barrier Island, New Zealand. Recording from the Centre for Monitoring Research collected as part of the Comprehensive Test Ban Treaty. The numbers in brackets refer to song types.

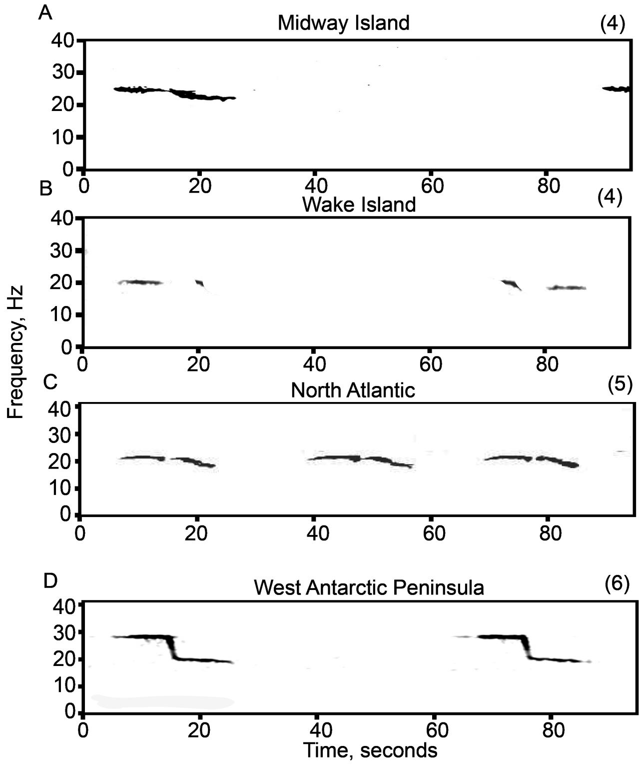

Fig. 4. Blue whale songs for (A) North Pacific – Midway Island, recorded on December 1967 near Midway Island (Northrop *et al.*, 1971). Spectrogram produced from archival tape in Hubbs SeaWorld Sound Library, (B) North Pacific – Wake Island, recorded January 1997 from the Wake Island MILS hydrophone array. Data provided by the Centre 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), and (D) Southern Ocean – West Antarctic Peninsula, recorded February 2002 at 66°S, 71°W off Adelaide Island (Širović *et al.*, 2004). The numbers in brackets refer to song types.

recorded near Midway Island (Northrop *et al.*, 1971). The call units are repeated about every 85-95 seconds, with single mode phrasing (ABABAB). Fig. 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 Table 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.

North Atlantic

North Atlantic blue whale song was first described in detail for the St. Lawrence River Estuary (Edds, 1982), consisting of a single tonal unit near 19Hz (Fig. 4C), although descriptions date back to 1959 (Weston and Black, 1965). The most thorough description of this song type is found in Mellinger and Clark (2003). Each phrase consists of two units, although there is sometimes no gap between the two units as is the case in Fig. 4C. The first unit is of nearly constant frequency, with a duration of about 8 seconds, while the second unit sweeps down having a duration of about 11 seconds (Mellinger and Clark, 2003).

The range for the North Atlantic blue whale song (Type 5 in Table 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 from offshore Antarctica (Ljungblad *et al.*, 1998; Matsuoka *et al.*, 2000; Širović *et al.*, 2004). The song consists of three tonal units with frequencies near 20Hz (Fig. 4D). 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 in Table 1). A year-round presence is documented from fixed hydrophones deployed near the West Antarctic Peninsula (Širović *et al.*, 2004). The Southern Ocean blue whale song has also been recorded at tropical latitudes during the southern winter (Stafford *et al.*, 2004).

North Indian

North Indian Ocean blue whale song is best known offshore from Sri Lanka (Alling and Payne, 1987; Alling *et al.*, 1991). The song consists of four units, three pulsive and one tonal (Fig. 5A). The call units are repeated about every 210 seconds, with single mode phrasing (ABCDABCD).

The North Indian Ocean blue whale song (Type 7 in Table 1) is reported from the near-shore waters of Sri Lanka, (Alling and Payne, 1987; Alling *et al.*, 1991), where it was recorded on two consecutive seasons, both in the spring, and the whales are reported to be present between January and May. It is also known of from deep ocean hydrophones near Diego Garcia (Tolstoy and Bohnenstiehl, 2002; Maya Tolstoy, pers. comm.).

Southeast Indian

The southeast Indian Ocean blue whale song (Type 8 in Table 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; 2001). These songs were heard in the southern summer and autumn (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 (Fig. 5B). The call units are repeated about every 180 seconds, with single mode phrasing (ABCDEABCDE).

Southwest Indian

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 Madagascan songs consist of four call units with a total duration of about 60 seconds (Fig. 5C). 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 (Fig. 5D). The call units are repeated every 200 seconds, with single mode phrasing (ABCDEABCDE).

The southwest Indian Ocean blue whale song (Type 9 in Table 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. A seasonality analysis of the Diego Garcia song is in progress (Maya Tolstoy, pers. comm.).

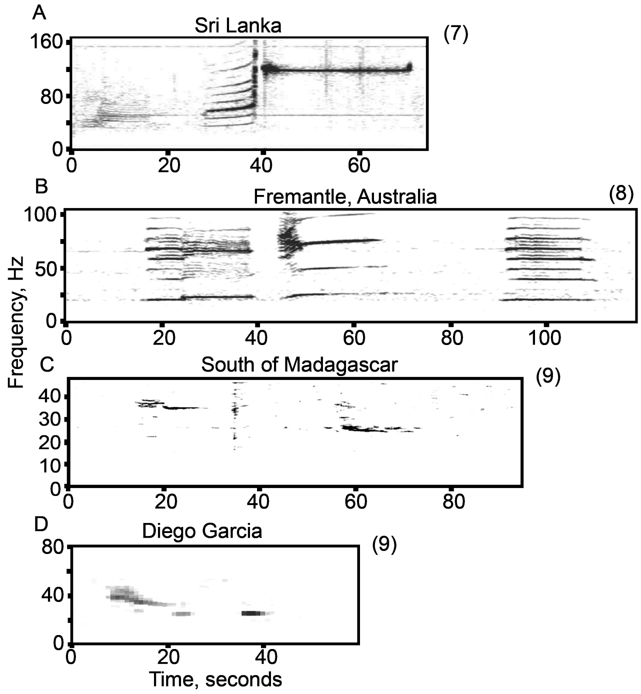

Fig. 5. Blue whale songs for: (A) North Indian Ocean – Sri Lanka, recorded April, 1984 within 5 miles of the entrance to Trincomalee Harbour (Alling and Payne, 1987). Spectrogram produced from archival tape at the British Library, Natural Sound Archive, London, (B) Southeast Indian Ocean – Fremantle, recorded west of Perth, Australia (courtesy of R. McCauley), (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 Organisation. The numbers in brackets refer to song types.

DISCUSSION

Acoustic identification of regional differences

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. 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. Gilpatrick *et al.*, 1997; LeDuc *et al.*, 2003; Conway, 2005). As Mellinger and Barlow (2003) recommend, in regions where data are lacking, or resolution of traditional markers is insufficient, distinct differences in songs between areas may be used as evidence for provisional population structure in management decisions. For these reasons, we provisionally recommend nine acoustic populations of blue whales worldwide.

Blue whale song may be grouped into three categories based on their similar characteristics. 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; Fig. 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 (102-118s). High latitude North Pacific, North Atlantic, and Southern Ocean songs (Type 4, 5 and 6; Fig. 4A, C, D) have a simple character, with only tonal call units lacking harmonics, and a short cycle time (35-90s). Indian Ocean songs (Type 7, 8 and 9; Fig. 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 210s).

Acoustic characteristics are increasingly being investigated as cost-effective means of obtaining data with which to determine population identity and structure (Mellinger and Barlow, 2003). The recording of sound at sea also offers a relatively fast and efficient means of gathering information on marine mammal populations remotely and in difficult visual or sea conditions and locations (e.g. Širović *et al.*, 2004). Furthermore, because vocalisations may evolve more rapidly than traditional markers, such as genetic or morphological characteristics, acoustic recordings may be particularly useful in detecting cryptic, insipient and sibling cetacean populations and/or species.

These data and those from other recent studies provide a growing body of evidence that geographic differences in whale songs can provide useful information for discovering and determining population boundaries (Fig. 6). As noted above, a recent study of the acoustics of fin whales (Hatch and Clark, 2004) showed that fin whale song varied significantly among regions in two ocean basins, although the differences were not reflected in genetic differentiation, suggesting that the patterns of acoustic dissimilarity may represent recent discontinuities in movement/behaviour that exist on the shorter time scales relevant to management. Recent studies of the acoustics of minke whales suggest a simple downswept call is used across geographic regions (Edds-Walton, 2000; Schevill and Watkins, 1972), but a complex song-like vocalisation often referred to as the 'star-wars', 'thump-train' or 'boing' sound is regionally distinctive (Gedamke *et al.*, 2001; Mellinger *et al.*, 2000; Jay Barlow, pers. comm.; Wenz, 1964; Thompson and Friedl, 1982; author's unpublished data). For minke whales, the limited data available are consistent with the hypothesis that the complex sound appears to be produced only during the breeding season, while the simple sounds are produced throughout the year.

Understanding the regional variation, function and significance of differences among blue whale songs requires a variety of approaches. Future work is likely to include a quantitative analysis of the differences within and between call types to better quantify the categories suggested here and help distinguish the variants in a more quantifiable way. Such analysis would likely parameterise the start frequency, end frequency, duration and gap for each unit of a song and apply statistical methods such as used by Anderson *et al.* (2000). For the better studied songs such as the northeast Pacific, there are millions of calls recorded to which such a system could be applied, while other regions such as the Indian Ocean need more data to meaningfully measure the variation within the song types for comparison to other types. Future work is also needed to tease apart the various historical, ecological, morphological and behavioural factors that influence these geographic patterns while investigation into the relative complexity of blue whale calls may provide insights into the differences in the intensity of selection and density of individuals among regions as predicted by studies of birds (Catchpole, 1980; Price, 1998; Kroodsma, 1983). Ultimately, the goal is to understand the potential significance of acoustic differences in the evolution of blue whale populations; if it is a part of their systematics, it should be a part of ours.

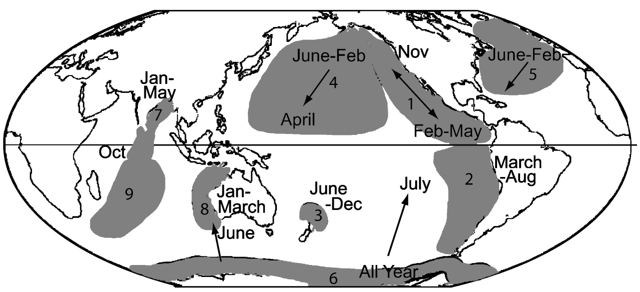

Fig. 6. Blue whale residence and population divisions suggested from their song types. Arrows indicate the direction of seasonal movements.

CONCLUSIONS

Blue whale songs provide a new means for characterising blue whale population structure worldwide. Song types may be a useful indicator of population identity because they are social signals, which are likely to reflect present day movement and association patterns. 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. We provisionally recommend nine acoustic populations for management.

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REFERENCES

Aguayo-Lobo, A., Navarro, D.T. and Ramirez, J.A. 1998. Marine mammals of Chile. I. Cetacea. *Ser. Cient.* INACH 48:19-159.

Alling, A. and Payne, R. 1987. Songs of Indian Ocean blue whales, *Balaenoptera musculus*. (unpublished) [Available from the lead author). 11pp.

Alling, A., Dorsey, E.M. and Gordon, J.C.D. 1991. Blue whales *Balaenoptera musculus* off the northeast coast of Sri Lanka: Distribution, feeding and individual identification. *UNEP Mar. Mamm. Tech. Rep.* 3:247-58.

Anderson, J.J., Ambrose, L., Bearder, S.K., Dixson, A.F. and Pullen, S. 2000. Within-species variation in the vocalizations and handpad morphology of southern lesser galagos, *Galago moholi*: a comparison with *G. senegalensis*. *Int. J. Primatol.* 21(3):537-55.

Baptista, L.F. 1975. Song dialects and demes in sedentary populations of the white-crowned sparrow, *Zonotrichia leucophphrys nuttalli*. *Univ. Calif. Publ. Zool.* 105:1-52.

Bearder, S. 1999. Physical and social diversity among nocturnal primates: a new view based on long term research. *Primates* 40(10):267-82.

Bossart, J.L. and Pashley Powell, D. 1998. Genetic estimates of population structure and gene flow: limitations, lessons and new directions. *Trends Ecol. Evol.* 13:202-6.

Burtenshaw, J.C., Oleson, E.M., Hildebrand, J.A., McDonald, M.A., Andrew, R.K., Howe, B.M. and Mercer, J.A. 2004. Acoustic and satellite remote sensing of blue whale seasonality and habitat in the northeast Pacific. *Deep Sea Research* II(51):967-86.

Calambokidis, J., Chandler, T., Rasmussen, K., Steiger, G.H. and Schlender, L. 1999. Humpback and blue whale photo-identification research off California, Oregon and Washington in 1998. Final report to Southwest Fisheries Science Center, Olympic Coast National Marine Sanctuary, University of California at Santa Cruz, and Cornell University. 36pp. [Available from J. Calambokidis, e-mail: *Calambokidis@CascadiaResearch.org*].

Catchpole, C.K. 1980. Sexual selection and the evolution of complex song among European warblers of the genus *Acrocephalus*. *Behaviour* 74:149-66.

Catchpole, C.K. and Slater, P.J.B. 1995. *Bird Song: Biological Themes and Variations*. Cambridge University Press, Cambridge. 256pp.

Cerchio, S., Jacobsen, J.K. and Norris, T.N. 2001. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Anim. Behav.* 62:313-29.

Clapham, P.J. and Baker, C.S. 2001. Modern whaling. pp. 1328-32. *In:* W.F. Perrin, B. Würsig and J.G.M. Thewissen (eds.) *Encylopedia of Marine Mammals*. Academic Press, New York.

Clark, C.W. 1995. Report of the Scientific Committee, Annex M. Matters arising out of the discussion of blue whales. Annex M1. Application of US Navy underwater hydrophone arrays for scientific research on whales. *Rep. int. Whal. Commn* 45:210-2.

Clark, C.W. 1996. Whales '93: Hot Tracks and Greatest Hits, Blue Whales '93, Fin Whales '93, North Atlantic Minke Whales '93, North Atlantic. A seven-CD set. Cornell Laboratory of Ornithology, Bioacoustics Research Programme, 159 Sapsucker Woods Rd., Ithaca NY, 14850, USA.

Clark, C.W. and Charif, R.A. 1998. Acoustic monitoring of large whales to the west of Britain and Ireland using bottom-mounted hydrophone arrays, October 1996 – September 1997. *JNCC Report* 281 25 pp.

Clark, C.W. and Clapham, P.J. 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. *Proc. R. Soc. Lond. Ser. B.* 271:1051-7.

Clark, C.W. and Ellison, W.T. 2004. Potential use of low frequency sounds by baleen whales for probing the environment: evidence from models and empirical measurements. pp. 564-89. *In:* J. Thomas, C. Moss and M. Vater (eds.) *Echolocation in Bats and Dolphins*. University of Chicago Press, Chicago.

Conway, C.A. 2005. Global population structure of blue whales, *Balaenoptera musculus spp.*, based on nuclear genetic variation. Ph.D. Thesis, University of California, Davis.

Croll, D.A., Clark, C.W., Acevedo, A., Tershy, B., Flores, S., Gedamke, J. and Urban, J. 2002. Only male fin whales sing loud songs. *Nature* 417:809.

Cummings, W.C. and Thompson, P.O. 1971. Underwater sounds from the blue whale, *Balaenoptera musculus*. *J. Acoust. Soc. Am.* 50:1193-8.

Cummings, W.C. and Thompson, P.O. 1977. Long 20-Hz sounds from blue whales in the Northeast Pacific. Second Conference on the Biology of Marine Mammals, December 12-15, San Diego, CA [Abstract] p.73.

Darling, J. 2002. Song. pp. 1124-6. *In:* W.F. Perrin, B. Wursig and J.G.M. Thewissen (eds.) *Encyclopedia of Marine Mammals*. Academic Press, San Diego.

Darling, J.D. and Berube, M. 2001. Interactions of singing humpback whales with other males. *Mar. Mammal Sci.* 17(3):570-84.

Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn* (special issue) 13:39-68.

Edds, P.L. 1982. Vocalisations of the blue whale, *Balaenoptera musculus* in the St. Lawrence River. *J. Mammal.* 63:345-7.

Edds-Walton, P.L. 2000. Vocalizations of minke whales *Balaenoptera acutorostrata* in the St. Lawrence estuary. *Bioacoustics* 11:31-50.

Findlay, K., Pitman, R., Tsurui, T., Sakai, K., Ensor, P., Iwakami, H., Ljungblad, D., Shimada, H., Thiele, D., Van Waerebeek, K., Hucke-Gaete, R. and Sanino-Vattier, G.P. 1998. 1997/1998 IWC-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) blue whale cruise, Chile. Paper SC/50/Rep2 presented to the IWC Scientific Committee April 1998 (unpublished). 39pp. [Paper available from the Office of this Journal].

Fleischer, R.C. and Rothstein, S.I. 1988. Known secondary contact and rapid gene flow among subspecies and dialects in the brown-headed cowbird. *Evolution* 42(6):1146-58.

Ford, J.K.B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Can. J. Zool.* 69(6):1454-83.

Gambell, R. 1979. The Blue Whale. *Biologist* 26(5):209-15.

Gautier, J.P. 1988. Interspecific affinities among guenons as deduced from vocalizations. *In:* A. Gautier-Hion, F. Bourliere, J.P. Gautier and J. Kingdon (eds.) *A Primate Radiation: Evolutionary Biology of the African Guenons*. Cambridge University Press, Cambridge.

Gedamke, J., Costa, D.P. and Dunstan, A. 2001. Localization and visual verification of a complex minke whale vocalization. *J. Acoust. Soc. Am.* 109(6):3038-47.

Gilpatrick, J.W., Jr., Perryman, W.L., Brownell Jr., R.L., Lynn, M.S. and DeAngelis, M.L. 1997. Geographical variation in North Pacific and Southern hemisphere blue whales (*Balaenoptera musculus*). Paper SC/49/O9 presented to the IWC Scientific Committee, September 1997, Bournemouth (unpublished). 33pp. [Paper available from the Office of this Journal].

Gray, D.A. and Cade, W.H. 2000. Sexual selection and speciation in field crickets. *Proc. Natl. Acad. Sci. USA* 97(26):14449-54.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, UK. 248pp.

Hatch, L.T. and Clark, C.W. 2004. Acoustic differentiation between fin whales in both the North Atlantic and North Pacific Oceans, and integration with genetic estimates of divergence. Paper SC/56/SD6 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 37pp. [Paper available from the Office of this Journal].

International Whaling Commission. 2003. Report of the Scientific Committee. Annex G. Report of the Sub-Committee on the Comprehensive Assessment of Whale Stocks – In-Depth Assessments. *J. Cetacean Res. Manage. (Suppl.)* 5:248-92.

Irwin, D.E., Alstrom, P., Olsson, U. and Benowitz-Fredericks, Z.M. 2001a. Cryptic species in the Genus *Phylloscopus* (Old World leaf warblers). *Ibis* 143:233-47.

Irwin, D.E., Bensch, S. and Price, T.D. 2001b. Speciation in a ring. *Nature* 409:333-7.

Kato, H., Honno, Y., Yoshida, H., Kojima, E., Nomura, A. and Okamura, H. 2002. Further developments on morphological and behavioural key for sub-species discrimination in southern blue whales, analyses from data through 1995/96 to 2001/02 SOWER cruises. Paper SC/54/IA8 presented to the IWC Scientific Committee, April 2002, Shimonoseki, Japan (unpublished). [Paper available from the Office of this Journal].

Kibblewhite, A.C., Denham, R.N. and Barnes, D.J. 1967. Unusual low-frequency signals observed in New Zealand waters. *J. Acoust. Soc. Am.* 41:644-55.

Kingston, T. and Rossiter, S.J. 2004. Harmonic-hopping in Wallacea's bats. *Nature* 429:654-7.

Kroodsma, D.E. 1983. The ecology of avian vocal learning. *Biosci.* 33:165-71.

LeDuc, R.G., Dizon, A.E., Goto, M., Pastene, L.A., Kato, H. and Brownell, R.L. 2003. Patterns of genetic variation in Southern Hemisphere blue whales. Paper SC/55/SH9 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 8pp. [Paper available from the Office of this Journal].

Ljungblad, D.K., Clark, C.W. and Shimada, H. 1998. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded off Antarctica. *Rep. int. Whal. Commn* 48:439-42.

MacDougall-Shackleton, E.A. and MacDougall-Shackleton, S.A. 2001. Culture and genetic evolution in mountain white-crowned sparrows: song dialects are associated with population structure. *Evolution* 55:2568-75.

Maeda, T. and Matasaka, N. 1987. Locale-specific vocal behaviour of the tamarin (*Saguinus l. labiatus*). *Ethology* 75:25-30.

Marler, P. 1957. Species distinctiveness in the communication signals of birds. *Behaviour* 2:13-9.

Martens, J. 1996. Vocalizations and speciation of palearctic birds. pp. 221-40. *In:* D.E. Kroodsma and E.H. Miller (eds.) *Ecology and Evolution of Acoustic Communication in Birds*. Cornell University Press, Ithaca.

Mate, B.R., Lagerquist, B.A. and Calambokidis, J. 1999. Movements of North Pacific blue whales during the feeding season off Southern California and their southern fall migration. *Mar. Mammal Sci.* 15(4):1246-57.

Matsuoka, K., Murase, H., Nishiwaki, S., Fukuchi, T. and Shimada, H. 2000. Development of a retrievable sonobuoy system for whale sounds recording in polar region. Paper SC/52/O7 presented to the IWC Scientific Committee, June 2000, in Adelaide, Australia (unpublished). 7pp. [Paper available from the Office of this Journal].

McCauley, R.D., Jenner, C., Bannister, J.L., Cato, D.H. and Duncan, A. 2000. Blue whale calling in the Rottnest trench, Western Australia, and low frequency sea noise. Paper presented at the Australian Acoustical Society Conference, Joondalup, Australia, November 2000. [Available from: *GeneralSecretary@acoustics.asa.au*].

McCauley, R.D., Jenner, C., Bannister, J.L., Burton, C.L.K., Cato, D.H. and Duncan, A. 2001. Blue whale calling in the Rottnest Trench – 2000, western Australia. Report R2001-6, Centre for Marine Science and Technology, Curtin University of Technology, Perth, Western Australia. 56pp.

McDonald, M.A., Hildebrand, J.A. and Webb, S.C. 1995. Blue and fin whales observed on a seafloor array in the northeast Pacific. *J. Acoust. Soc. Am.* 98(2):712-21.

McDonald, M.A., Calambokidis, J., Teranishi, A.M. and Hildebrand, J.A. 2001. The acoustic calls of blue whales off California with gender data. *J. Acoust. Soc. Am.* 109(4):1728-35.

Mellinger, D.K. and Barlow, J. 2003. Future directions for acoustic marine mammal surveys: stock assessment and habitat use. NOAA OAR Special Report, NOAA/PMEL Contribution 2557. 37pp. [Available from NOAA Pacific Environmental Laboratory].

Mellinger, D.K. and Clark, C.W. 2003. Blue whale (*Balaenoptera musculus*) sounds from the North Atlantic. *J. Acoust. Soc. Am.* 114(2):1108-19.

Mellinger, D.K., Carson, C.D. and Clark, C. 2000. Characteristics of minke whale (*Balaenoptera acutorostrata*) pulse trains recorded near Puerto Rico. *Mar. Mammal Sci.* 16(4):739-56.

Moore, S.E., Watkins, W.A., Daher, M.A., Davies, J.R. and Dahlheim, M.E. 2002. Blue whale habitat associations in the northwest Pacific: analysis of remotely-sensed data using a Geographic Information System. *Oceanography* 15(3):20-5.

Norris, T.F., McDonald, M. and Barlow, J. 1999. Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *J. Acoust. Soc. Am.* 106(1):506-14.

Northrop, J., Cummings, W.C. and Morrison, M.F. 1971. Underwater 20-Hz signals recorded near Midway Island. *J. Acoust. Soc. Am.* 49:1909-10.

Oleson, E.M., Barlow, J., Gordon, J., Rankin, S. and Hildebrand, J.A. 2003. Low frequency calls of Bryde's whales. *Mar. Mammal Sci.* 19(2):407-19.

Omura, H., Ichihara, T. and Kasuya, T. 1970. Osteology of pygmy blue whale with additional information on external and other characteristics. *Sci. Rep. Whales Res. Inst., Tokyo* 22:1-27.

Payne, R. and Guinee, L.N. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of 'stocks'. pp. 333-58. *In:* R. Payne (ed.) *Communication and Behavior of Whales*. AAAS Selected Symposium 76. Westview Press, Colorado. xii+643pp.

Payne, R. and McVay, S. 1971. Songs of humpback whales. *Science* 173:585-97.

Price, T. 1996. Exploding species. *Trends Ecol. Evol.* 11(8):314-5.

Price, T. 1998. Sexual selection and natural selection in bird speciation. *Philos. Trans. R. Soc. Lond.* B 353:251-60.

Reeves, R.R., Clapham, P.J., Brownell, R.L. and Silber, G.K. 1998. Recovery Plan for the blue whale (*Balaenoptera musculus*). Office of Protected Resources, National Marine Fisheries Service, Silver Spring, MD 20910. 42pp.

Reeves, R.R., Perrin, W.F., Taylor, B.L., Baker, C.S. and Mesnick, S.L. 2004. Report of the workshop on shortcomings of cetacean taxonomy in relation to needs of conservation and management, April 30-May 2, 2004, La Jolla, California, USA. *NOAA Technical Memorandum NMFS* NOAA-TM-NMFS-SWFSC-363:94pp.

Rice, D.W. 1998. *Marine Mammals of the World. Systematics and Distribution.* Special Publication No. 4. The Society for Marine Mammalogy, Allen Press Inc., Lawrence, Kansas. v-ix+231pp.

Rivers, J.A. 1997. Blue whale (*Balaenoptera musculus*), vocalizations from the waters off central California. *Mar. Mammal Sci.* 13:186-95.

Ryan, M.J. 1990. Signals, species and sexual selection. *Am. Sci.* 78:46-52.

Schevill, W.E. and Watkins, W.A. 1972. Intense low-frequency sounds from an Antarctic minke whale, *Balaenoptera acutorostrata*. *Breviora* 388:1-8.

Siemers, B.M. and Schnitzler, H.U. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* 429:657-61.

Širović, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E. and Thiele, D. 2004. Seasonality of blue and fin whale calls west of the Antarctic Peninsula. *Deep Sea Research* II(51):2327-44.

Slabberkoorn, H. and Smith, T.B. 2002. Bird song, ecology and speciation. *Philos. Trans. R. Soc. Lond.* B 357:493-503.

Stafford, K.M. 2003. Two types of blue whale calls recorded in the Gulf of Alaska. *Mar. Mammal Sci.* 19(4):682-93.

Stafford, K.M. and Moore, S.E. 2005. Atypical calling by a blue whale in the Gulf of Alaska. *J. Acoust. Soc. Am.* 117(5):2724-7.

Stafford, K.M., Fox, C.G. and Clark, D.S. 1998. Long-range acoustic detection and localization of blue whale calls in the Northeast Pacific Ocean. *J. Acoust. Soc. Am.* 104:3616-25.

Stafford, K.M., Nieukirk, S.L. and Fox, C.G. 1999a. An acoustic link between blue whales in the eastern tropial Pacific and the northeast Pacific. *Mar. Mammal Sci.* 15(4):1258-68.

Stafford, K.M., Nieukirk, S.L. and Fox, C.G. 1999b. Low-frequency whale sounds recorded on hydrophones moored in the eastern tropical Pacific. *J. Acoust. Soc. Am.* 106:3687-98.

Stafford, K.M., Nieukirk, S.L. and Fox, C.G. 2001. Geographic and seasonal variation of blue whale calls in the North Pacific. *J. Cetacean Res. Manage.* 3(1):65-76.

Stafford, K.M., Bohnenstiehl, D.R., Tolstoy, M., Chapp, E., Mellinger, D.K. and Moore, S.E. 2004. Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. *Deep Sea Research* Part 1(51):1337-46.

Taylor, B.L. and Dizon, A.E. 1996. The need to estimate power to link genetics and demography for conservation. *Conserv. Biol.* 10(2):661-4.

Taylor, B.L. and Dizon, A.E. 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. *Mol. Ecol.* 8:S11-6.

Thode, A.M., D'Spain, G.L. and Kuperman, W.A. 2000. Matched-field processing, geoacoustic inversion, and source signature recovery of blue whale vocalizations. *J. Acoust. Soc. Am.* 107:1286-300.

Thompson, P.O. 1965. Marine biological sound west of San Clemente Island: diurnal distributions and effects on ambient noise level during July 1963. US Navy Electronics Laboratory Report 1290, San Diego, California. 42pp.

Thompson, P.O. and Friedl, W.A. 1982. A long term study of low frequency sounds from several species of whales off Oahu, Hawaii. *Cetology* 45:1-19.

Thompson, P.O., Findley, L. and Vidal, O. 1992. 20-Hz pulses and other vocalisations of fin whales, *Balaenoptera physalus*, in the Gulf of California, Mexico. *J. Acoust. Soc. Am.* 92(6):3051-7.

Thompson, P.O., Findley, L.T., Vidal, O. and Cummings, W.C. 1996. Underwater sounds of blue whales, *Balaenoptera musculus*, in the Gulf of California, Mexico. *Mar. Mammal Sci.* 12(2):288-92.

Thompson, T.J., Winn, H.E. and Perkins, P.J. 1979. Mysticete sounds. pp. 403-31. *In:* H.E. Winn and B.L. Olla (eds.) *Behavior of Marine Animals*. Vol. 3. *Cetaceans*. Plenum Press, New York and London. i-xix+438pp.

Tolstoy, M. and Bohnenstiehl, D.R. 2002. Analysis of hydroacoustic signals in the Indian Ocean. pp. 666-75. *In: Proceedings of the 24th Seismic Research Review, Nuclear Explosion Monitoring: Innovation and Integration, Sept. 17-19, 2002, Ponte Vedre Beach Florida*. Los Alamos National Laboratory.

Tonnessen, J.N. and Johnsen, A.O. 1982. *The History of Modern Whaling*. C. Hurst & Co., London. i-xx+798pp.

Tyack, P.L. 1999. Communication and cognition. pp. 287-323. *In:* J.E. Reynolds III and S.A. Rommel (eds.) *Biology of Marine Mammals*. Smithsonian Institution Press, London.

Tyack, P.L. 2000. Functional aspects of cetacean communication. pp. 270-307. *In:* J. Mann (ed.) *Cetacean Societies: Field studies of dolphins and whales*. University of Chicago Press, Chicago.

Watkins, W.A. 1981. Activities and underwater sounds of finback whales (*Balaenoptera physalus*). *Sci. Rep. Whales Res. Inst., Tokyo* 33:83-117.

Watkins, W.A., Daher, M.A., Reppucci, G.M., George, J.E., Martin, D.L., DiMarzio, N.A. and Gannon, D.P. 2000. Seasonality and distribution of whale calls in the North Pacific. *Oceanography* 13:62-7.

Weilgart, L. and Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* 40:277-85.

Wells, M.M. and Henry, C.S. 1998. Songs, reproductive isolation and speciation in cryptic species of insects: a case study using green lacewings. pp. 217-33. *In:* D. Howard and S. Berlocher (eds.) *Endless Forms: Species and Speciation*. Oxford University Press, New York.

Wenz, G.M. 1964. Curious noises and the sonic environment in the ocean. pp. 101-19. *In:* W.N. Tavolga (ed.) Vol. Vol. 1. *Marine Bio-Acoustics*. Pergamon Press, Oxford.

West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.* 58:155-83.

Weston, D.E. and Black, R.I. 1965. Some unusual low-frequency biological noises underwater. *Deep-Sea Res.* 12:295-8.

Wimberger, P.H. and de Queiroz, A. 1996. Comparing behavioural and morphological characters as indicators of phylogeny. pp. 206-33. *In:* E. Martins (ed.) *Phylogenies and the Comparative Method in Animal Behavior*. Oxford University Press, Oxford.

Wright, T.F. 1996. Regional dialects in the contact call of a parrot. *Proc. Royal Soc., Biol. Sci.* 263:867-72.

Wright, T.F. and Wilkinson, G.S. 2001. Population genetic structure and vocal dialects in an amazon parrot. *Proc. Royal Soc., Biol. Sci.* 268:609-16.

Zemsky, V.A. and Sazhinov, E.G. 1994. Distribution and current abundance of the pygmy blue whales. SWFSC Admin. Rep. No. LJ-94-02:17pp. [Originally in Russian with English summary. Translated in 1994 as above from Àrsen'ev',V.A.(ed). 1982, Marine Mammals: Collected Papers', VNIRO, Moscow. 53-70p.].

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