Geographic variation in external morphology of North Pacific and Southern Hemisphere blue whales (*Balaenoptera musculus*)

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ABSTRACT

Geographic variations in size and proportions of blue whales (*Balaenoptera musculus*) were investigated using length data acquired from whaling records and aerial photogrammetric surveys. Results showed that blue whales found in the eastern Pacific off Central and North America are significantly shorter (by approximately 2m) than blue whales found at higher latitudes in the North Pacific. Results support the occurrence of a morphologically distinct eastern North Pacific (ENP) blue whale population which migrates in spring/summer from warm waters off Central America and Mexico to temperate feeding grounds along the west coast of North America. Southern Hemisphere blue whales sampled with vertical aerial photogrammetry off northern Peru and the Galapagos Islands were similar in size to the ENP blue whales. However, the population affinity of these southern blue whales remains uncertain. No length data were available for blue whales formerly captured off southern Japan and Korea. Nonetheless, a history of diminishing fishery catches and a lack of any recent sightings suggests that these whales were members of a geographic population that is now severely depleted or extinct. Based on comparisons of total length, length of rostrum and length of tail region, ENP blue whales were found to be morphologically similar to the 'pygmy' blue whale (*B.m. brevicauda*) described from the Kerguelen Island region of the southern Indian Ocean. 'Antarctic' blue whales (*B.m. intermedia*) from the Southern Ocean were found to be statistically significantly larger than their conspecifics at high latitudes in the North Pacific. These results support the hypotheses that blue whales that migrate from warm seas to cold feeding grounds in high latitudes are larger than those whose distributions are limited to low and mid-latitudes. Differences in morphology may reflect selective pressure on populations to adapt physiologically to energy demands associated with different migration, environmental and ecological regimes. As some of the results come from populations located far apart in different oceans, questions remain concerning the continuity of populations within and among ocean basins. Consequently, research using fishery data and approaches such as photogrammetry, telemetry, acoustics and molecular genetic analysis should be continued to better understand the worldwide blue whale population structure.

KEYWORDS: BLUE WHALE; DISTRIBUTION; MORPHOMETRICS; PHOTOGRAMMETRY; PHOTOGRAPHY; SOUTHERN HEMISPHERE; WHALING-HISTORICAL; PHOTO-ID; SURVEY-AERIAL; MIGRATION; PACIFIC OCEAN; SOUTHERN OCEAN

INTRODUCTION

Despite extensive commercial exploitation, blue whales (*Balaenoptera musculus* Linnaeus, 1758) are still found in all major oceans. However, their population structure remains for the most part uncertain. Blue whales typically migrate in summer from tropical and sub-tropical waters to productive upwelling coastal and shelf waters at higher latitudes where they congregate and feed primarily on euphasiid shrimps or krill (Croll *et al*., 2000). Commercial whalers targeted these feeding areas as blue whales were predictably found there in large numbers. Blue whales were hunted primarily for the market value of their oil. Since they are fast swimming and sink when killed, they were hunted in large numbers only once steam catcher boats and explosive harpoons had been developed in the late 19th Century; extensive overexploitation belatedly led to complete protection by the International Whaling Commission in the mid 20th Century although illegal Soviet whaling continued for some time after that (e.g. Donovan, 2007). Mate *et al*. (1999) estimated roughly 15,000 blue whales remained in the world's oceans. This number represents a small fraction of global abundance prior to exploitation. For example, in the Southern Ocean, Antarctic blue whales (*B.m. intermedia*) were the most abundant population in the world prior to modern whaling. During the 20th Century approximately 333,000 Antarctic blue whales were taken commercially. The size of this population in 1998 was estimated by Branch (2007) to be 2,280 (95%CI 1,150-4,500) or a mere 0.37-2.2% of their estimated original abundance (202,000-311,000) prior to commercial whaling

Since the cessation of commercial whaling of blue whales, research and conservation efforts have focused on assessing the status of biologically unique geographic populations (Donovan, 1991; Hucke-Gaete *et al*., 2004; NMFS, 1998; Sears, 2002) or on the Antarctic blue whales as a whole (Branch, 2007; Branch *et al*., 2004), although there is almost certainly more than one population and perhaps as many as six (e.g. Donovan, 1991).

According to Rice (1998) three diagnosable blue whale subspecific names are recognised. The 'Antarctic' (also sometimes known as the 'true') blue whale, *B.m. intermedia* (Burmeister, 1871) occurs in the Southern Hemisphere and is the largest form. It migrates to the Antarctic Zone during the austral summer (e.g. Williams and Donovan, 2007). Blue whales found at high latitudes during summer in the North Atlantic and North Pacific have been named *B.m. musculus* (Linnaeus, 1758). Although *B.m. musculus* was described from the North Atlantic, blue whales in the North Pacific were assumed to be similar based on limited visual observations and some comparative length data. The smallest or 'pygmy' blue whale, *B.m. brevicauda* was described by Ichihara (1966) from fishery specimens taken near Kerguelen Island in the southern Indian Ocean. Pygmy blue whales are thought to be widely distributed in sub-Antarctic waters of the Indian Ocean (typically north of the Antarctic convergence) and they probably extend into regions of the southeast Atlantic, southwest and southeast Pacific (Branch *et al*., 2007; Gill, 2002; Rice, 1998). It may also be that the blue whales sighted near the Maldives, Sri Lanka and within the Arabian Sea are pygmy blue whales (Anderson, 2005; Zemsky and Sazhinov, 1982). A fourth subspecific name (*B.m. indicas*, Blythe, 1859) has sometimes been used in reference to blue whales from the northern Indian Ocean but the biological features that apparently distinguish these whales from the other blue whale subspecies are undocumented (Rice, 1998). At present, all blue whale sub-species designations are considered to be provisional pending more detailed information on the morphology, genetics, geographic range and ecology of these populations (NMFS, 1998; Rice, 1998).

North Pacific Ocean

Historical records and recent information point to several geographic populations of blue whales for the North Pacific. In the 1600s, blue whales were killed with hand-held harpoons in the coastal waters of southern Japan (Kashahara, 1950; Omura, 1986). In the 1900s, this fishery became modernised with motorboats and mounted harpoon guns and increased fishing effort; consequently blue whale catches increased in waters between southern Japan and Korea. By 1950, overexploitation had brought the blue whale in the region to commercial extinction and recently there have been no confirmed sightings of blue whales in these waters despite some 50 years of little or no exploitation (Kato *et al*., 2005; Matsuura, 1935; Omura, 1950; Tago, 1922). It thus seems likely that the blue whales formerly found in waters south of Korea, into the Sea of Japan and along the coast of southern Japan (and perhaps including the Kuril Islands and Kamchatka – see below) comprised a separate geographic population that remains severely depleted if not extinct (T. Kasuya, pers. comm.).

Blue whales were hunted in other regions of the North Pacific starting in the 1800s. By 1920 shore-based catcher boats were taking blue whales on both sides of the Pacific (Tønnessen and Johnsen, 1982). Over time, the North Pacific fishery extended from Taiwan to Kamchatka, along the Aleutian Islands to the Gulf of Alaska, into pelagic waters and south along the Baja California peninsula (Miyazaki, 1952; Reeves *et al*., 1985; Rice, 1963; 1974; Sakiura *et al*., 1953; Tomilin, 1957). Based on an apparent hiatus (at 50°N, 175°E; Fig. 1) in the catch distribution along with results from tagging studies, several authors have proposed that blue whales found on summer feeding grounds off northern Japan, the Kuril Islands and Kamchatka comprised a western stock that was geographically separate from a central stock in the North Pacific (Ivashin and Rovnin, 1967; Nishiwaki, 1966; Ohsumi and Masaki, 1975; Omura and Ohsumi, 1964)[1]. The western stock was thought to migrate in winter to waters as far south as Taiwan, while the central stock was thought to winter in waters north of the Hawaiian Islands (Berzin and Vladimirov, 1981; Northrop *et al*., 1971; Thompson and Friedl, 1982). The proposed central stock was also exploited during summer on feeding grounds extending from the central and eastern Aleutian Islands to the coast of British Columbia, Canada (Rice, 1992).

Results from distribution, photo-identification and acoustic studies suggest the occurrence of an eastern North Pacific (ENP) population of blue whales. Results from mark-recapture and line-transect studies conducted in waters off Baja California, California, Oregon and Washington (during summer and autumn) provide a seasonal population size at between 2,000 and 3,000 blue whales (Calambokidis and Barlow, 2004). Areas of concentration include the Costa Rican Dome (CRD, an upwelled oceanographic feature located approximately 300-400km west of Central America), the Gulf of California and the Pacific waters of Baja California and California (Fiedler, 2002; Reilly and Thayer, 1990; Rice, 1992). Blue whales have been sighted at the CRD year round; it is not known if some of these whales represent a non-migratory segment of the ENP population (perhaps sexually immature individuals that have yet to join the migratory breeding groups) or if they are members of a Southern Hemisphere population (Reilly and Thayer, 1990). Mother and calf pairs inhabit the Gulf of California and the CRD and it is likely that both regions serve as important breeding and calving habitats (Gendron, 2002; Pitman *et al*., 2007). ENP blue whales migrate in summer from Central American and Mexican waters to feeding grounds off California (Calambokidis *et al*., 1990; Mate *et al*., 1999). During this season, most of the population appears to be off central California (in productive upwelling waters between the California Channel Islands and Monterey Bay); but photographic matches of California blue whales off Canada and Alaska show that at least some individuals migrate beyond California to feeding areas between Vancouver Island, Canada and the Gulf of Alaska (Burtenshaw *et al*., 2004; Calambokidis *et al*., 1998; McDonald *et al*., 1995; Stafford and Fox, 1995). Furthermore, two different blue whale acoustic signals have been recorded off British Columbia and Alaska: a two-part signal (frequency <20Hz) associated with the ENP blue whales; and a signal of slightly higher frequency (>20Hz) associated with blue whales in the central and western regions of the North Pacific (referred to as a single 'western North Pacific' population based on acoustic studies by Stafford and Fox (1998)). These data suggest that the ENP population may be more widely distributed than was previously thought. It also implies that two migratory populations share habitat between Oregon and Alaska during the summer and autumn. ENP blue whales return to the eastern tropical Pacific (ETP) during the autumn and winter and, based on the distribution of sighting data, there is some speculation that a portion of the population migrates south of the Equator to the productive waters of the Peru Current (Reilly and Thayer, 1990).

Southern Hemisphere

Distribution and acoustic studies suggest that the region extending south from the Equator to northern Peru and west of the Galapagos Islands may be habitat (at least seasonally) for blue whales from at least two different populations (McDonald *et al*., 2006). One population, studied near the Galapagos Islands, is thought to be related to the Antarctic blue whale and migrates during the austral spring to feeding grounds close to Antarctica (Palacios, 1999; Stafford *et al*., 2004). Whales from the other population are believed to be similar in external morphology to the Indian Ocean pygmy blue whale, but their migration patterns remain unclear (Donovan, 1984). Therefore, it is not known if these whales are part of the ENP blue whale population, comprise a separate northeastern South Pacific (NESP) population or are associated with the blue whales recently discovered off southern Chile (Branch *et al*., 2007; Cabrera *et al*., 2006; Hucke-Gaete *et al*., 2006).

Ichihara (1966) described blue whales taken near Kerguelen Island in the southern Indian Ocean as pygmy blue whales. He documented their smaller size relative to the Antarctic blue whales that were taken during summer at higher latitudes in the Southern Hemisphere (Ichihara, 1975; Mackintosh and Wheeler, 1929); (Fig. 2). In a comparative study of blue whale genotypes using mitochondrial(mt) DNA, LeDuc *et al*. (2007) found a small but consistent difference in alleles between Antarctic and pygmy blue whales in the Southern Hemisphere. They also found that

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[1] Tomilin (1957), Berzin and Rovnin (1966) and Ohsumi and Wada (1972) referred to blue whales in the western North Pacific as an 'Asiatic' stock while those from the central and eastern North Pacific were called an 'American' stock.

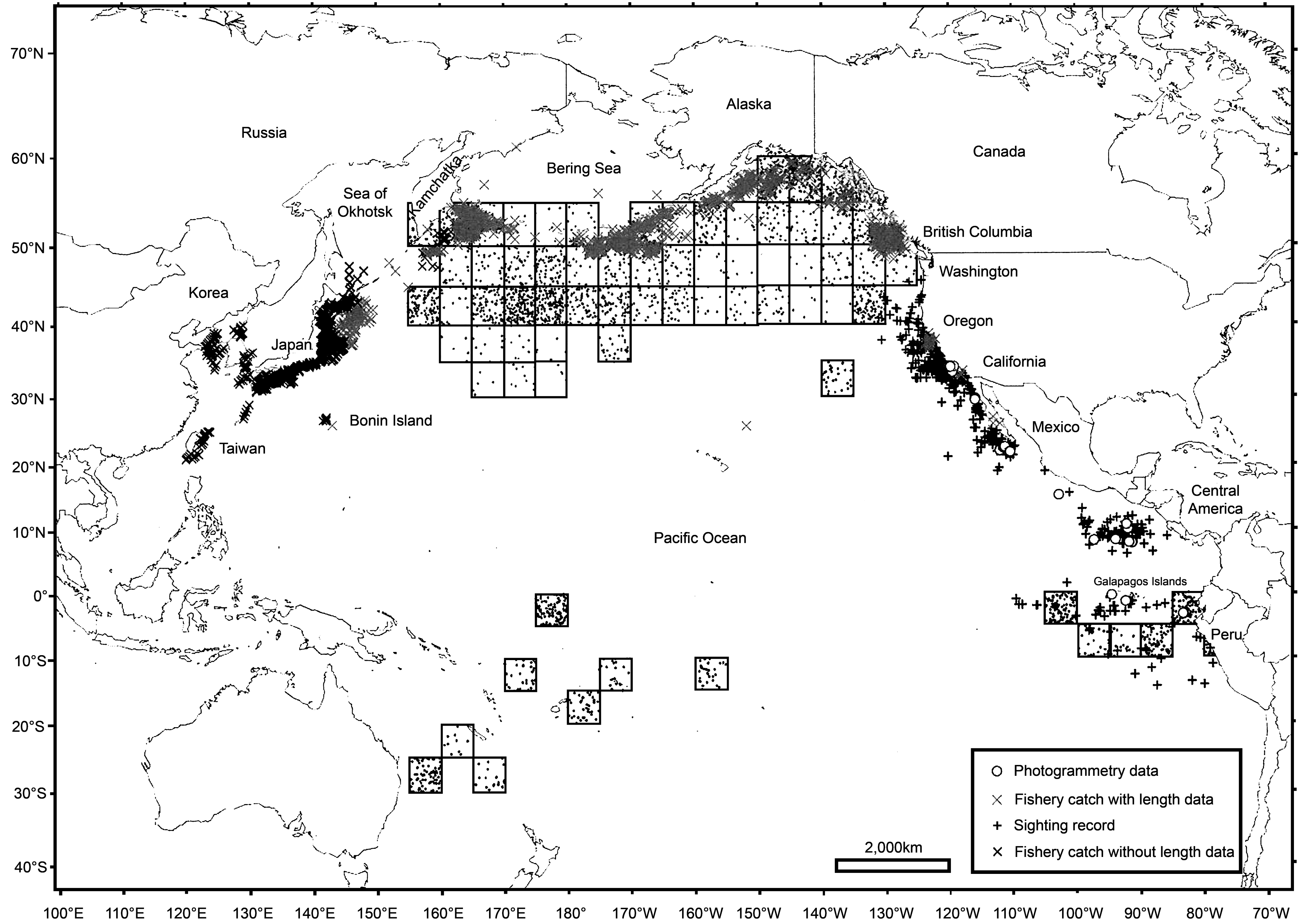

Fig. 1. Distribution of blue whales in the Pacific Ocean (north of 15°S in coastal areas of the eastern Pacific and north of 40°S in coastal areas of the western Pacific). Unpublished fishery records (with TL data) provided by the IWC and the Suzzalo Library, Univ. Of Washington. Published fishery records from near the Kuril and Commander Islands are from Sakiura *et al.* (1953). Sighting data from Matsuura (1935), Kasahara (1950), Berzin and Rovnin (1966), Berzin (1978), Berzin and Vladimirov (1981), Reilly and Thayer (1990), Fujise et al. (1995), Barlow *et al.* (1995) and NOAA, SWFSC and NMML data. Black dots within squares represent the minimum number of blue whale sightings made within 5°×5° survey grids by Japanese catcher boats (Miyashita *et al.*, 1995).

blue whales off southwestern Australia and southern Chile (both populations assumed to be pygmy blue whales) differed from each other genetically as much as they do from the Antarctic blue whale. Although positive identification of the pygmy blue whale at sea is difficult, adults appear shorter, are more 'tadpole' shaped and have a shorter tail-stock when compared to the more streamlined Antarctic blue whale (Ichihara, 1981; Kato *et al.*, 1995). There are also differences between sub-species in the morphology of the blowhole (Kato *et al.*, 2002). Additionally, the range distributions of both types are believed to overlap during the austral winter when they both occupy tropical and temperate waters of the southern Indian Ocean (Kato *et al.*, 1995). Later, during the austral spring and summer, Antarctic blue whales undergo extensive migrations to cold, productive feeding grounds near Antarctica, while pygmy blue whales are generally more restricted and move to sub-Antarctic waters north of 55°S (or the Antarctic Convergence).

Objectives

This paper examines geographic variation in blue whale length data (acquired from vertical aerial photographs and selective whaling records from the Pacific, Indian and Southern Oceans) to assess population structure of North Pacific blue whales and to investigate and discuss relationships between Pacific blue whales and the Antarctic and pygmy blue whale sub-species described from the Southern Hemisphere. Current and historical information on fishery effects, blue whale acoustics and the geographic distributions of populations are also utilised in this study.

MATERIALS AND METHODS

Aerial photogrammetry

Vertical aerial photographs of blue whales were taken in the eastern Pacific between California and northern Peru during summer and autumn between 1994 and 2003 (Fig. 1). Photographs were taken with a vertically mounted 127mm

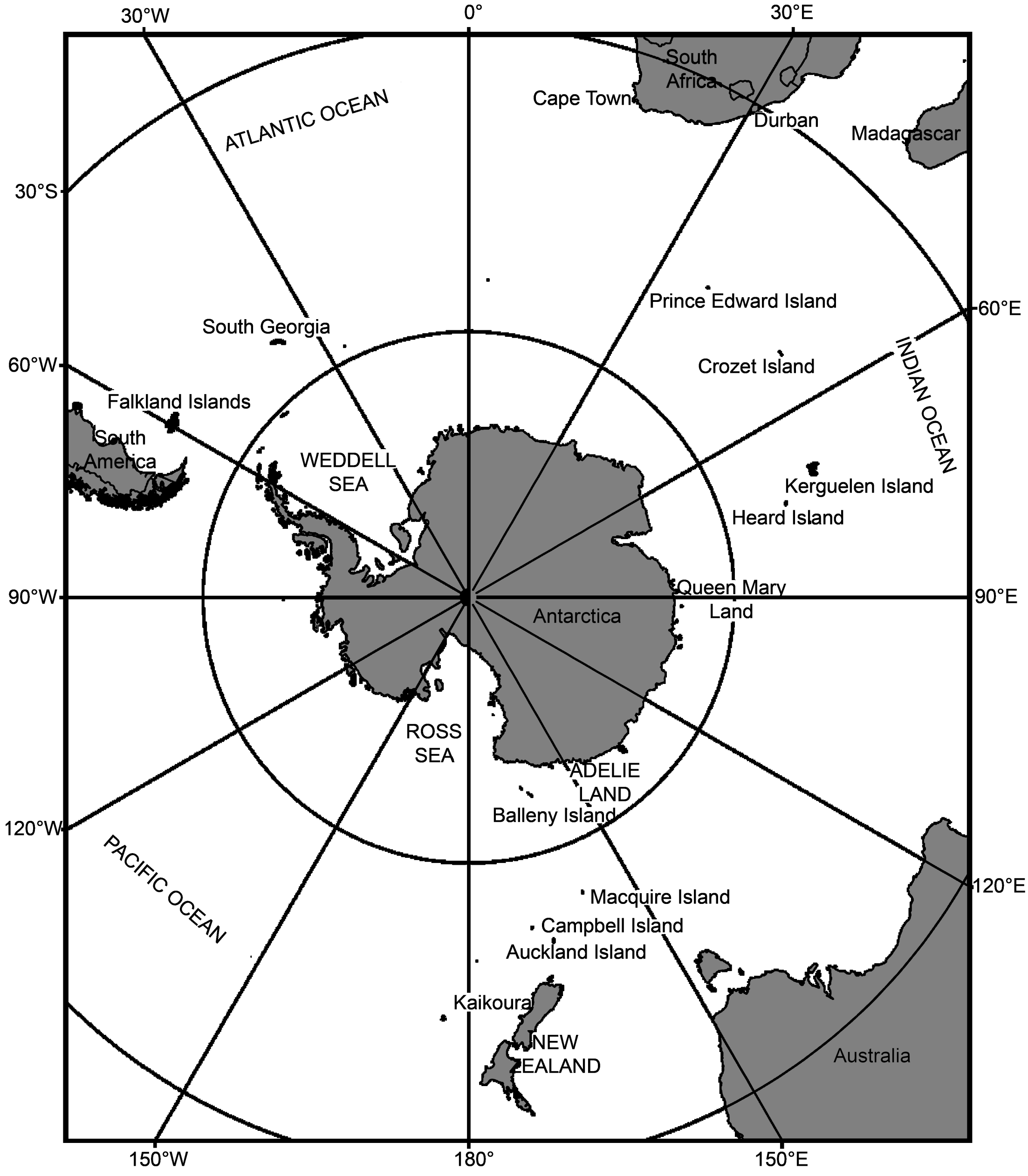

Fig. 2. Southern Hemisphere whaling grounds. For this report, length data for Antarctic blue whales were recorded from whales landed at South Georgia Island in the South Atlantic Ocean (Mackintosh and Wheeler, 1929). Length data for pygmy blue whales were recorded during factory ship operations in the Kerguelen Island region of the Southern Indian Ocean (Ichihara, 1966).

format reconnaissance camera. Off California, photographs were taken from a twin-engine *Partenavia* aircraft; south of California, aerial photographs were taken from an *MD* 500 helicopter stationed aboard the NOAA research ship *David Starr Jordan*. Blue whale photographs were taken from altitudes ranging from 122-183m (400-600ft). Aircraft ground speed averaged 213km hr^{-1} (100 knots). The camera had a fixed 152mm (6") lens and featured 'forward-motion-compensation' (FMC) whereby the film in the camera was advanced along a stationary platen (while the shutter was open) at the same rate and direction as the image recorded by the camera (Cox, 1992; Smith, 1968). FMC eliminates the potential loss of image resolution due to the forward movement of the aircraft. Images were photographed with *Kodak* Plus-X Aerecon II (3404) black and white film and *Kodak* Aerochrome MS 2448 film. The cycle rate of the camera was adjusted to provide 80% overlap between adjacent photograph frames; this provided four separate photographs of individual whales from each photographic pass. As each photograph was taken, a computer-based data acquisition system recorded GPS latitude and longitude, altitude and time. The altitude reading for each photo-frame was recorded from a *Honeywell* AA-300 radar altimeter.

To check for bias in the recorded altitude data (A_r), known-size calibration targets were placed at the sea surface and photographed from various altitudes (between 107-229m, or 350-750ft). 'True' altitudes for photographs of the calibration targets were calculated (eq. 1) from the scale factor relationship (see Ghosh, 1988; Gilpatrick, 1996)

$$A_t = (I/O) * F \qquad (1)$$

where:

A_t = estimated 'true' altitude (in metres);
I = known length of the calibration targets (in metres);
O = measurement of the calibration target (in metres) in the photograph (measuring instrument described below); and
F = camera focal length (= 152.4mm or 6").

Altitude data calculated from the calibration target measurements were then compared with the altimeter readings recorded (A_r) with each target photograph. A consistent bias in A_r was found and because of this linear regression coefficients (eq. 2 below), describing the relationship of 'true' altitude against radar altimeter readings, were applied to calculate a corrected altitude (A_c) for each blue whale photograph used in this report.

$$A_c = (A_r) * 0.988 - 4.731\text{m} \qquad (r^2 = 0.996) \qquad (2)$$

Blue whales were measured from photographic transparencies using a personal computer based video imaging and measurement system (Gilpatrick and Lynn, 1994).

Total length (TL) was measured only when the tip of the rostrum and the tail fluke notch were visible and the whale's body appeared straight and oriented parallel to the sea surface (Fig. 3). For images in which the dorsal fin was also visible, the distance from the trailing edge of the dorsal fin to the base of the fluke notch (DF-FLK) was measured. Rostral length (RL) was measured from mid-point in the blow-hole to tip of rostrum. Image measurements were converted to estimated 'true' lengths by use of the scale factor equation:

$$I = (A/F)\ O \qquad (3)$$

where A = altitude from which the photograph was taken (metres), F = focal length of the camera lens, O = measurement of the object (whale) in the photograph (metres), and I = estimated 'true' length of the measured image (whale).

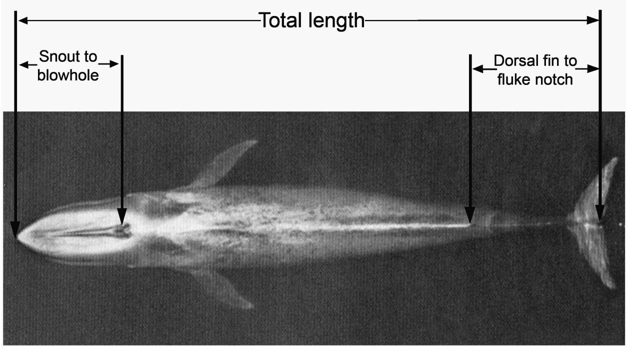

Fig. 3. Vertical aerial photograph of a blue whale taken off Santa Rosa Island, California on 6 September 1995. Arrows depict photogrammetric length measurements taken for this report. Unique colour and mottling patterns found on the anterio-dorsum region were used to identify and catalogue individual blue whales. Total length for this whale (no. BM135) estimated at 22.02m; rostral length (snout to centre of blowhole was 4.24m; tail-stock length (dorsal fin to fluke notch) was 4.58m.

To ensure that the photogrammetric length sample was not biased by the introduction of duplicate length measurements for individual whales, photo-prints for each blue whale image were made. From this print set, individual blue whales were identified based on unique colour mottling and pigmentation patterns and distinctive scars. The search for unique colour and scar patterns was focused on the anterior-dorsal region of the whale from the tip of the snout back to about 1/3 of the total body length (Fig. 3). This region was concentrated on because it was visible with good resolution in the majority (76%) of the prints. Once an individual blue whale was identified, it was assigned a unique catalogue number and for all photographs length and location data associated with the whale were filed with the catalogue number. Since this method provided replicates data on the TL of individual whales, it was possible to compute the coefficient of variation (CV) values to assess the precision of the photogrammetric system (Table 1).

Fishery records with length data

North Pacific Ocean

Catch records containing length data for 2,340 North Pacific blue whales were reviewed. The data were recorded during commercial whaling operations conducted from 1924 to 1965 by the USA, Norway, Japan and Canada. Most of these records were reported to the Bureau of International Whaling Statistics (BIWS) in Norway and then sent to the IWC (IWC, 1950; IWS, 1954). Records included information on catch dates and localities, TL, sex and pregnancy status of females. The study also included data published by Sakiura *et al.* (1953) for 55 blue whales taken near the Kuril and Commander Islands and 117 unpublished records for blue whales landed at whaling stations in British Columbia, Canada (archived at the Suzzallo Library, University of Washington). Length data recorded for 103 blue whales taken in the ENP fishery (off California and Baja California Sur, Mexico) were compared with the photogrammetric length sample (see earlier) using a *t*-test (a =0.05).

Catch records from the former USSR were not included because of known reporting irregularities in the Southern Hemisphere blue whale fishery. These irregularities may have carried over to data reported in the North Pacific fishery as well (Yablokov, 1994).

Table 1

Precision of photogrammetrically derived morphometric data for blue whales photographed with aerial cameras in the eastern North Pacific. Coefficient of variation (CV) values and 95% confidence limits (95%CL) were calculated for individual blue whales having three or more replicate length measurements (taken independently from separate photographs).

Morphometric variable	Mean value (m) [1]	Ave. %CV [2]	Range %CV [3]	Ave. 95%CL [4]	Range 95%CL[5]
Total length (TL)	20.90 (*n*=141)	1.29	0.02-3.64	±0.32m	± (0.003m-0.98m)
Rostral length (RL)	3.70 (*n*=108)	3.78	0.10- 9.80	±0.17m	± (0.005m-0.52m)
Tail length (DF-FLK)	4.72 (*n*=75)	4.00	0.66-7.31	±0.22m	± (0.02m-0.45m)

[1]Mean value for sampled variable (m). [2]Average %CV for replicate measures. [3]Range of %CV values for sampled variable. [4]Average 95%CL for replicate measurements done on individual whales (m). [5]Range of 95%CL values for replicate measures done on individual whales (m).

In the western Pacific, TL data were available from fisheries, which operated off northern Japan and the Hokkaido region, Kamchatka and the western Aleutians. TL data were also available for five blue whales landed in the western Bering Sea. Unfortunately, length data for blue whales landed at shore stations in Korea, southern Japan and the Kuril Islands have probably been misplaced (T. Kasuya, pers. comm.). In the northeast Pacific, length data were available from all major fishing areas (Fig.1).

Southern Indian and Atlantic Oceans

For Antarctic blue whales, complete external measurements and information on sex and length at onset of maturity were obtained from 536 catch records collected between 1925-27 at Grytviken, South Georgia Island (Fig. 2). This whaling station operated in the South Atlantic from 1904-65 (Gambell, 1993). Grytviken was (and remains) under British sovereignty but Norwegian workers largely staffed the whaling operations. All biological data were recorded and published by Mackintosh and Wheeler (1929). For the pygmy blue whale, external measurements, sex and female pregnancy status were published for 62 whales landed in 1960 aboard Japanese factory ships in the Kerguelen Island area. The data were analysed by Ichihara (1961; 1966) and individual records were later published by Omura (1984).

Analysis of variance in external morphology of geographic populations

With the exception of the photogrammetric length sample collected from south of the Equator (NESP), geographic differences in blue whale morphology were tested using analysis of variance (ANOVA). The NESP sample was omitted from the statistical model due to the small number of adults (*n*=6) sampled in this region. However, these length data are presented and compared with the morphology data recorded from the other geographic populations and the potential relatedness of the NESP whales to the other populations is discussed (Table 2).

TL data collected from aerial photographs and the various whaling operations in the North Pacific, Southern and Indian Oceans were plotted independently to investigate *a priori* assumptions of normality (Sokal and Rohlf, 1981). The frequency distributions of total body lengths (male and female samples combined) from the above regions were found to contain a large sample of adult and sub-adult whales and an additional smaller sample of calves and/or juvenile animals (see Fig. 4). To help remove the bias introduced by the variable number of smaller whales measured in the different geographic regions, the length frequency distributions were truncated so that primarily adult and near-adult sized whales would represent geographic samples used in statistical analyses. For Pacific blue whales and the Kerguelen pygmy blue whales, whales smaller than 19.5m were eliminated from the data sets. For Antarctic blue whales from the Southern Ocean, whales smaller than 21.5m in TL were eliminated from the data sets used for statistical analyses.

Length data from the North Pacific were stratified into western, central and ENP (photogrammetric sample ranging from California to Central America) areas (Fig. 1). These divisions were based on breaks in the catch distribution and the results of tagging and photo-ID studies (as discussed above). Prior to ANOVA, length data for the different geographic populations were tested for normality using a cumulative-frequency distribution function. As such, an idealised, normally distributed data set was generated for each of our geographic length samples (Anon., 1992; Zar, 1984). These distributions were modelled based on means and standard deviation values of the respective blue whale length samples. A non-parametric Mann-Whitney U statistic was then used to test for differences between the geographic length samples and data formulated from the normal distribution function (Zar, 1984). After ANOVA, pair-wise comparisons of population length samples were tested using Scheffe’s tests (Sokal and Rohlf, 1981). Tests were performed at a significance level of *a* =0.05.

The above analyses were repeated using a more standardised data subset limited to the size class of sexually mature females. For these analyses, pygmy and North Pacific blue whales that were recorded as ‘pregnant’ during whaling operation were selected. For the eastern Pacific region, whales (cows) that were photographed in close association with a calf were selected. The unique, close association between cows and calves has been documented for many cetaceans (Norris and Prescott, 1961; Wells and Scott, 1990) and this behaviour has been used to identify cow-calf pairs in several other population studies (Perryman and Lynn, 1993; 1994; Sumich, 1984; Whitehead and Payne, 1981). For Antarctic blue whales landed at South Georgia, mature females were determined as those examined with at least one ovarian *corpus luteum* present (Mackintosh and Wheeler, 1929). With the exception of South Georgia, all TL samples of sexually mature females were probably biased slightly towards larger females. That is, samples did not account for females that were sexually mature (i.e. *corpus luteum* present) but which had not yet become pregnant (Lockyer, 1984). These females would typically be younger and consequently smaller in size (Gilpatrick, pers. obs.).

Published external measurements (expressed as a percentage of TL) suggested that RL is similar for Southern Hemisphere pygmy and Antarctic blue whales (Ichihara, 1963; 1966; Mackintosh and Wheeler, 1929; Omura *et al*., 1970) and that the length of the tail region is relatively smaller in pygmy blue whales. Although Ichihara (1961) measured the distance from anus to fluke notch to compare

Table 2

Mean total length (TL), rostral length (RL) and tail length (DF-FLK) with standard deviation (SD) values for blue whales sampled in the various study areas. RL and DF-FLK values are reported as proportional to the TL of the whale.

	Males and females		Sexually mature females		Rostral length (RL) (proportional to TL)		Tail length (DF-FLK) (proportional to TL)	
Geographic regions	Mean TL	SD	Mean TL	SD	Mean %	SD	Mean %	SD
Antarctic blue whale (*B.m. intermedia*), South Georgia Island, (whales ≥21.5m)	24.6m (n=374)	1.5	25.5m (n=111)	1.2	18.1% (n=27)	1.3	24.2% (n=285)	1.3
WN Pacific, (whales ≥19.5m)	23.3m (n=268)	0.9	24.1m (n=31)	1.0				
Central N Pacific, (whales ≥19.5m)	23.3m (n=1,390)	1.3	24.1m (n=207)	1.1				
EN Pacific (ENP), (whales ≥19.5m)	21.7m (n=144)	1.1	22.1m (n=14)	0.9	17.7% (n=51)	1.3	22.2% (n=63)	1.2
NE South Pacific (NESP), (whales ≥19.5m	21.4m (n=6)	0.9	22.4m (n=2)	0.9	17.1% (n=5)	0.7	22.5% (n=3)	1.2
Pygmy blue whale (*B.m. brevicauda*), Kerguelen Island (whales ≥19.5m)	21.7m (n=55)	0.9	21.7m (n=7)	0.7	18.1% (n=38)	1.3	22.1% (n=30)	1.3

differences in lengths of the tail region, other published data indicate that an alternative character could also be used to demonstrate size differences in the tail region. Measurements made from the posterior edge of the dorsal fin to the base of the fluke notch (DF-FLK) revealed that the dorsal tail region was about 2% shorter in the pygmy blue when compared with the Antarctic form (Mackintosh and Wheeler, 1929; Omura, 1984; Omura *et al*., 1970). RL and DF-FLK were readily available in our blue whale aerial photographs. Consequently, these characters (expressed as a percentage of TL) were used and tested for proportional differences in lengths of rostrum and dorsal tail regions among ENP, pygmy and Antarctic blue whales. To avoid biases attributable to changes in body proportions with increased body length, statistical analyses were limited to larger blue whales assumed sexually mature or very close to maturity (≥19.5m TL for North Pacific and pygmy; ≥21.5m TL for Antarctic blue whales). ANOVA and *post hoc* Scheffe's tests were conducted at a =0.05.

RESULTS

Aerial photogrammetry of eastern North Pacific blue whales

External morphology data were acquired for 170 blue whales from vertical aerial photographs taken in the eastern Pacific between California and northern Peru. Total body length (for whales north of the equator) averaged 20.9m (n=158; range: 14.5-24.5m). TL data were precise and averaged 1.29% CV. Average values and precision of morphometric variables are summarised in Table 1.

Eastern North Pacific fishery and photogrammetry data

When the mean TL of blue whales taken in the ENP blue whale fishery (off California and Baja California, Mexico) was compared with the ENP photogrammetric sample no significant difference was found (t-test; p=0.151). When this test was repeated using a sub-sample of total lengths comprised of adult females, no differences were detected between length frequency distributions acquired from the fishery records and those determined from aerial photogrammetry (p=0.3324). Since the photogrammetric length sample was larger (n=170) and appeared more normally distributed than the fishery sample (n=103), the ENP blue whale photogrammetry length data was used for subsequent parametric tests of geographic variation.

Analysis of variance in geographic populations

The Mann-Whitney U statistic found no significant differences (p value range: 0.345-0.965) between the geographic TL samples and the normally distributed length frequencies. ANOVA revealed significant differences in length frequency distributions among the study areas (p<0.0001; Fig. 5). Sheffe's *post hoc* tests demonstrated that Antarctic blue whales from the Southern Ocean were the largest whales sampled (p<0.0001). In the North Pacific, whales from the western and central regions were similar in TL (p=0.9961) and were significantly larger than those from the ENP and pygmy blue whale populations (p<0.0001). In addition, ENP and pygmy blue whales were similar in TL (p >0.9999).

A similar pattern of geographic variation was observed when the above statistical comparisons were repeated, but the tests were limited to TL subsamples comprised of sexually mature females (Fig. 5; Table 2). The largest females were from the Antarctic blue whale population (p<0.0001). Females from the western and central North Pacific regions were similar in size (p>0.999). The smallest females were the ENP and pygmy blue whales; these geographically separate groups were also similar in TL (p=*0*.9637).

ANOVA showed no significant differences in RL among Antarctic, pygmy and ENP blue whales (F=1.35; p=0.2643; df=2, 113; Fig. 6). However, the size of the tail region (DF-FLK) differed significantly among these groups (F=87.300; p<0.0001; df =2, 375). DF-FLK in the Antarctic blue whale is significantly longer than in the ENP and pygmy blue whales (Sheffe's test: p<0.0001). For ENP and pygmy blue whales, measurements of the DF-FLK were found to be similar (p=0.9233). For the Antarctic blue whale, the length of the DF-FLK averaged 24.2% of the whales' TL; for ENP and pygmy blue whales, this measurement averaged about 22.2 % of total body length (Fig. 6).

TL, RL and DF-FLK measurements for the NESP blue whale sample were similar on average with the morphological values estimated for the ENP and pygmy blue whale populations (Table 2).

DISCUSSION

The results presented here are consistent with earlier findings. Antarctic blue whales from the Southern Ocean are significantly larger (Figs 4 and 5) than their high-latitude conspecifics in the North Pacific Ocean (Ichihara, 1966;

Rice, 1977). Pygmy blue whales from the Kerguelen Island area of the southern Indian Ocean are significantly shorter in TL and have proportionally shorter tail sections (DF-FLK) than do Antarctic blue whales. No significant differences were found between pygmy and Antarctic blue whales in proportional estimates of RL. These results support the previous findings of Ichihara (1966) and Omura *et al.* (1970).

Morphometric data were not available for blue whales captured during the early 1900s off southern Japan and Korea. Nonetheless, a history of diminishing fishery catches and a lack of recent sightings support the premise that these whales were members of a separate North Pacific population that is now severely depleted or extirpated.

No significant difference was found in TL frequency distributions of catch data for whales from the western and central regions of the North Pacific (Figs 4 and 5). Although a gap in the distribution of fishery catches (at 50°N, 175°E; Fig. 1) and results from limited tagging studies suggest that there may be two separate populations, sightings recorded from Japanese whale catcher vessels show a near continuous historical distribution of blue whales across these regions (Miyashita *et al.*, 1995). Furthermore, acoustic monitoring indicates no difference in call patterns emitted between blue whales in the western and central regions of the North Pacific. Additionally, these call patterns are acoustically distinguishable from the patterns emitted by the ENP blue whales (Rankin *et al.*, 2005; Stafford *et al.*, 2001). Although these data suggest that blue whales in the western and central North Pacific comprise one population, additional work is needed to further resolve the population biology and migratory behaviour of blue whales in this broad and oceanographically diverse region. A similar size between geographic populations may correlate with similarities in ecology and migratory habits (Brodie, 1975) and it is feasible that different populations overlap geographically while on feeding grounds. Additional research may prove difficult as population numbers remain very low due to overexpoitation (Forney and Brownell, 1996).

ENP blue whales are significantly shorter (by approximately 2m) than those from western and central regions of the North Pacific (Figs 4 and 5; Table 2). These results provide strong evidence that the blue whales that migrate between Central America, Mexico and the west coast of the United States and Canada are morphologically distinct and are therefore a discrete population in the North Pacific. Additionally, based on comparisons of external morphology, they appear to be similar to the pygmy blue whale described from the Kerguelen Island area of the southern Indian Ocean. Studies on the movements and feeding of these whales also suggest that they are ecologically distinct in the North Pacific. They migrate in pelagic waters and most sightings occur along coastal shelf and slope areas between Central and North America (Fig. 1); (Reilly and Thayer, 1990; Rice, 1992). During spring and summer they migrate primarily to upwelled areas with high euphasiid biomass along the coast of California (Fiedler *et al.*, 1997), then in late summer/autumn some individuals migrate south while others exploit a secondary foraging area with high productivity off Vancouver Island (Burtenshaw *et al.*, 2004). During the southerly migration, ENP blue whales linger and forage (presumably on krill) in productive pelagic areas associated with shelf breaks and hydrographic fronts along the California and Baja California coasts (i.e. pelagic regions of the California Channel Islands and the Baja California Frontal System; Mate *et al.* (1999)). These productive regions appear to be feeding waypoints or

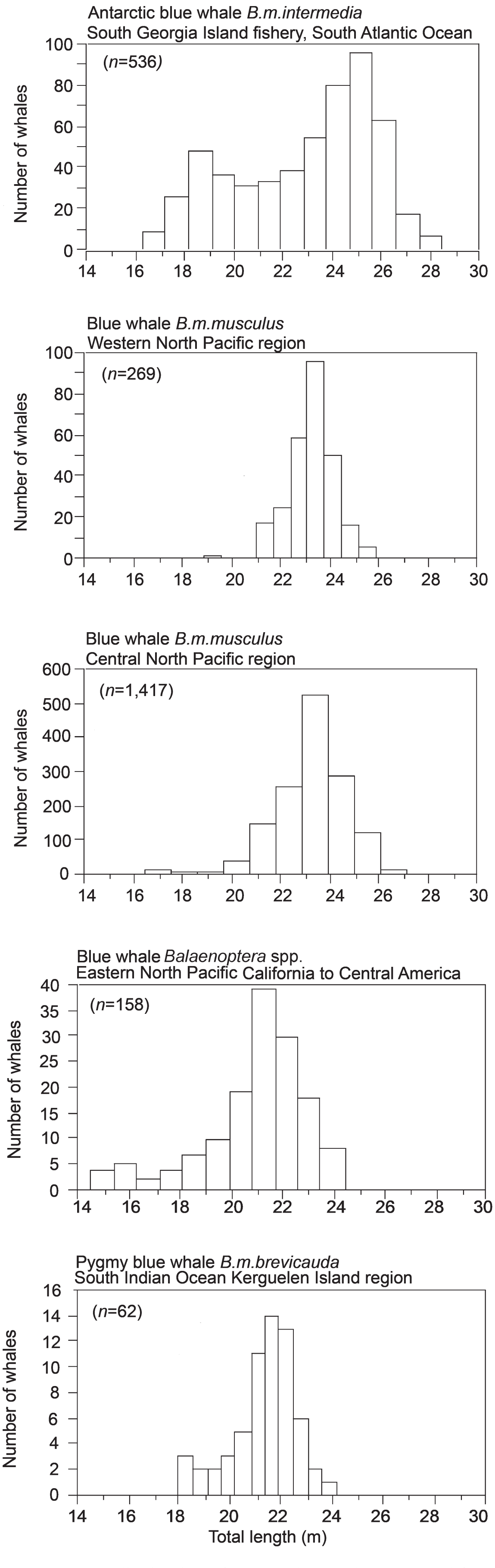

Fig. 4. Frequency distribution of total body length (males and females) for the Antarctic and pygmy blue whale subspecies from the Southern Hemisphere and blue whales from three regions of the North Pacific. Total length (TL) data for whales from the Eastern North Pacific are from aerial photogrammetry. TL data for whales from other geographic regions were acquired from fishery records.

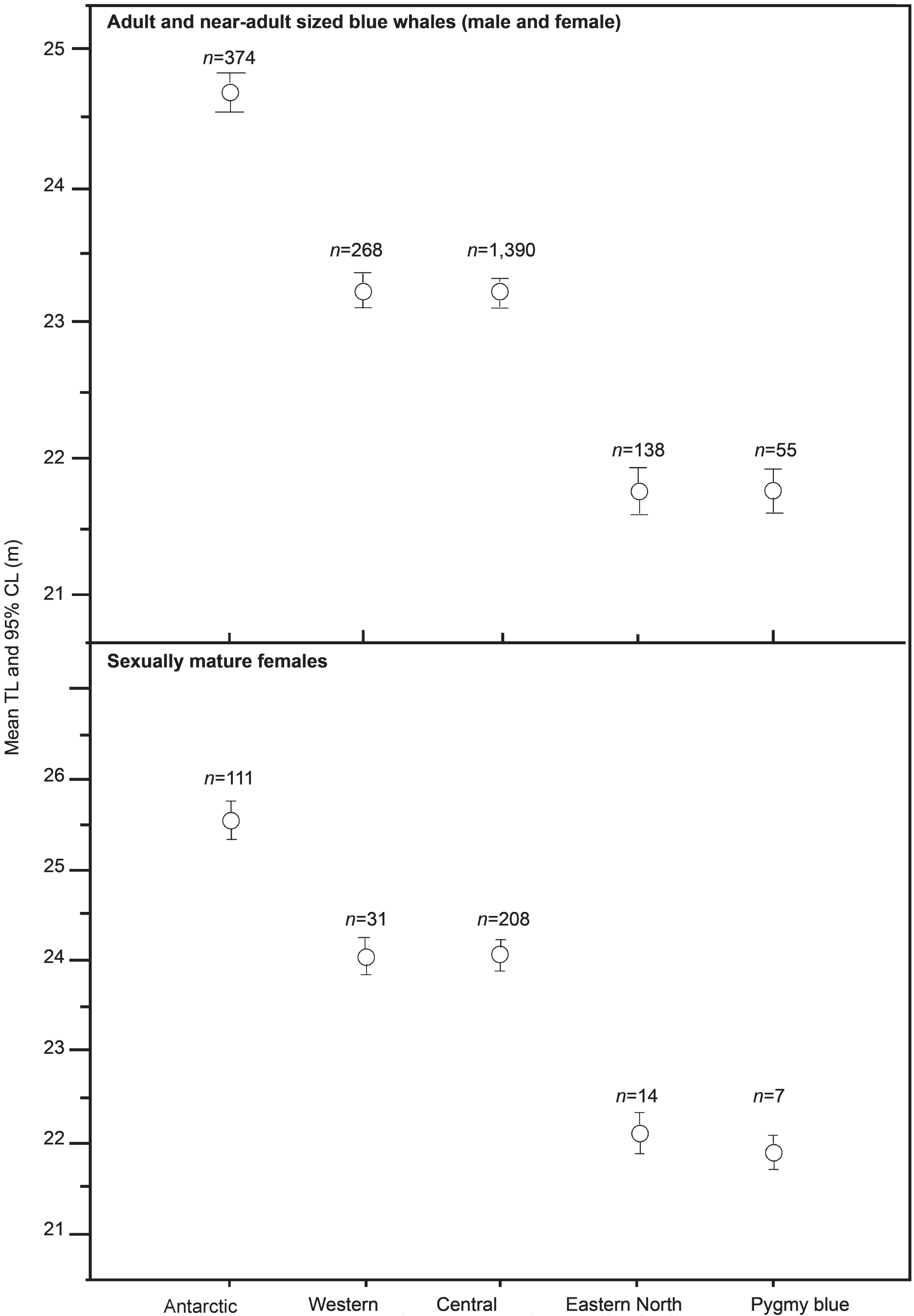

Fig. 5. Mean TL with 95% CL for adult and near-adult sized blue whales (top) and sexually mature females (bottom). For statistical analyses of TL samples which included both males and females (top), with the exception of Antarctic blue whales, geographic length samples were truncated at 19.5m in order to remove the variable number of smaller whales measured in the different regions. Because Antarctic blue whales mature at a greater size when compared to blue whales from the other study areas, Antarctic blue whales smaller than 21.5m TL were eliminated from the data sets used for statistical analyses.

'stepping stones' used during their migration (Etnoyer *et al.*, 2004). Feeding has also been observed during winter in the Gulf of California and CRD (Gendron, 1992). Thus, feeding in this population appears to occur year-round (Croll *et al.*, 1995; Gendron, 1992; 1995; Rice, 1992; Sears, 1987; 1990). In contrast, whales from the western and central regions of the North Pacific are thought to migrate farther offshore and move during summer from the tropical or sub-tropical waters where they breed, to cold, highly productive, feeding areas at high latitudes (Reilly and Thayer, 1990). However, acoustic monitoring indicates that some North Pacific blue whales remain at high latitudes during winter, where they

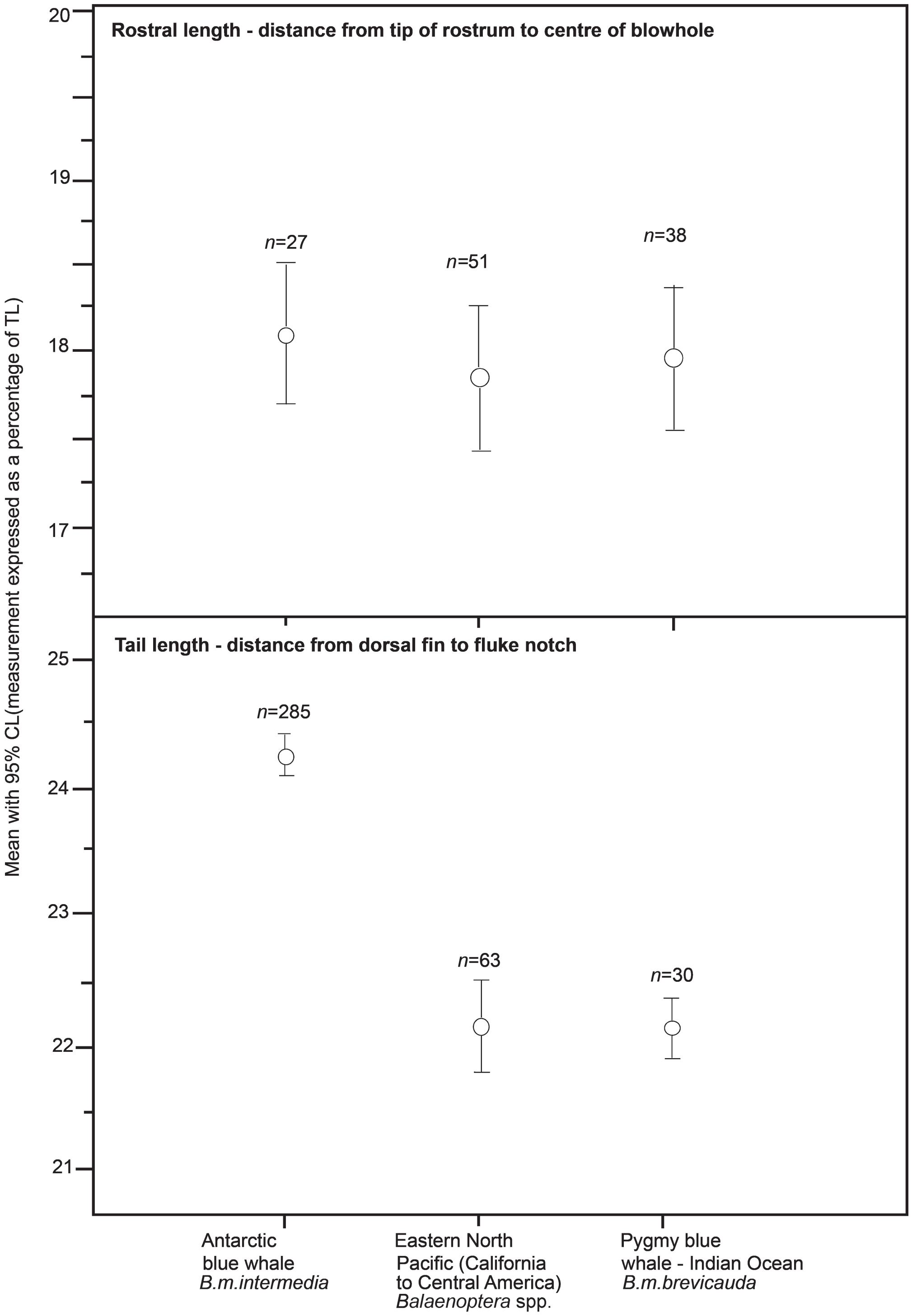

Fig. 6. Mean with 95% CL for measurements of rostrum (top) and distance from dorsal fin to fluke notch (bottom) expressed as a percentage of the whale's total length. To avoid biases attributable to changes in body proportions with increased body length, statistical analyses were limited to larger blue whales (≤19.5m TL for North Pacific and pygmy; ≤21.5m TL for Antarctic blue whales).

are found in association with topographical features such as the continental slope of Kamchatka, the Emperor Seamounts and the Aleutian Island chain (Moore *et al*., 2002).

The photogrammetric sample from the NESP (Table 2) indicates that these whales may be similar in morphology to both the ENP and the Kerguelen pygmy blue whales, but a larger photogrammetric sample is needed to confirm this. In support of these findings, blue whales sighted in coastal waters off Ecuador, northern Peru and Chile (at 33°S) have been described visually as the 'pygmy-type' (Aguayo L, 1974; Clarke *et al*., 1978; Donovan, 1984) but the population identity of these whales needs further investigation as noted by those authors. Branch *et al*. (2007) examined catch data from southern Chile and found that the average TL was intermediate between that of the Antarctic and pygmy blues. Our NESP length sample falls within the lower range of the TLs published for these Chilean whales. Thus, there is a possibility that the blue whales photographed off northern South America may be associated with the Chilean whales. In support of this, McDonald *et al*.

(2006) found that blue whales ranging north from southern Chile to the Equator produced a unique song pattern that was different from the songs produced by the ENP and Antarctic blue whales. Additionally, blue whales tagged near Chiloe Island in southern Chile were tracked north via satellite to productive upwelled waters associated with the Nazca Ridge (B. Mate, unpubl. data). This indicates that the blue whales off southern Chile migrate north to at least 25°S (off northern Chile) and thus, raises speculation as to whether or not the Chilean whales are migrating further north to the NESP area. For proper management, the relationship of these NESP whales to the Chilean blue whales discovered near the Gulf of Corcovado in Chile should be further investigated (Hucke-Gaete *et al*., 2004).

Another possibility, based on seasonal patterns in sighting records, is that the NESP whales migrate north of the Equator to the CRD, where they forage on krill and coincide temporally with a segment of the ENP blue whale population (Reilly and Thayer, 1990). Relative to this, it is interesting to note that Berzin (1978) observed blue whales off the Galapagos Islands and Costa Rica and later reported they were all pygmy blue whales and that they comprised a geographically continuous 'Galapagos biostock'.

The results presented here support the idea that blue whales, which migrate to cold waters at high latitudes, achieve a greater size than those whose movements are limited to low and mid-latitudes (Brodie, 1977). The reasons for this remain uncertain. Differences in body morphology may reflect selective pressure on these populations to adapt physiologically to energy demands associated with differences in migration, environment and ecology. Mayr (1969) suggested that increased body size for *Balaenoptera* in Antarctic waters was due to a selective pressure to minimise thermal stress. He agreed with Bergmann (1847) and proposed that large rorquals are able to conserve energy in cold waters because their bodies have a relatively small surface-to-volume ratio. Brodie (1975; 1977) posited that selection for large body size in high latitude fin and blue whales enables them to store abundant lipids during restricted summer feeding seasons. These energy reserves, in turn, are utilised during extensive migrations into warm waters where whales breed but do not feed (Lindstedt and Boyce, 1985). Omura *et al*. (1970) noted that Indian Ocean pygmy blue whales were noticeably heavier in body weight when compared to Antarctic blue whales of the same length. However, the weight differences were attributable to a heavier gastrointestinal tract for the pygmy blue whales and not to differences in fat, bone or muscle mass. This, they speculated, probably reflects an evolutionary adaptation stemming from differences in foraging ecology between the two sub-species.

In this report, some of the comparative morphological data came from populations that are located far apart in separate ocean basins. In addition, much of the information concerning the distribution of pygmy-type blue whales stems from unconfirmed sightings and fishery records which may be subject to sampling biases (Branch *et al*., 2007; Donovan, 1984; Eyre, 1995; Fujise *et al*., 1995; Ichihara, 1981). Therefore, questions remain concerning the taxonomic status of certain geographic populations and their range distributions in the Atlantic, Pacific and Indian Oceans. Because of this, additional work using methods such as photogrammetry, telemetry, acoustics and molecular genetic analysis should be continued to gain a better understanding of the global structure of blue whale populations.

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