

SC/68A/SH/15

Further analyses to separate pygmy blue whale catches by population

Branch, Monnahan, Sirovic, Balcazar, Barlow, Cerchio, Double, Gavrilov, Gedamke, Hodge, Jenner et al.



INTERNATIONAL
WHALING COMMISSION

Further analyses to separate pygmy blue whale catches by population

TREVOR A. BRANCH¹, COLE C. MONNAHAN¹, ANA ŠIROVIĆ², NAYSA BALCAZAR³, DAWN BARLOW⁴, SALVATORE CERCHIO⁵, MICHAEL DOUBLE⁶, ALEXANDER GAVRILOV⁷, JASON GEDAMKE⁸, KRISTIN HODGE⁹, CURT JENNER¹⁰, ROBERT MCCAULEY⁷, JENNIFER MIKSIS-OLDS¹¹, FLORE SAMARAN¹², FANNIE SHABANGU^{13,14}, KATE STAFFORD¹⁵, KAROLIN THOMISCH¹⁶, LEIGH TORRES⁴, JOY TRIPOVICH¹⁷

ABSTRACT

There are widely recognized to be at least four clearly distinct populations of pygmy blue whales found respectively in the northern Indian Ocean (NIO, Sri Lanka to the central Indian Ocean), south-western Indian Ocean (SWIO, Madagascar to Kerguelen), south-eastern Indian Ocean (SEIO, Australia to Indonesia), and south-western Pacific Ocean (SWPO, New Zealand). This classification is based on catch locations and four song types associated with each pygmy blue whale population. A putative fifth song type has been proposed from recordings off Oman and north-western Madagascar and dubbed the Oman blue whale. Here we focus on the four well recognized blue whale populations, and use acoustic song location data to separate catches, providing population-specific catch time series for each populations. Scattered pygmy blue whale catches were taken at Durban ($n = 4$, SWIO); the west coast of Australia ($n = 33$, SEIO); east coast of Australia ($n = 1$, 1954, SWPO); in New Zealand and eastern Australia ($n = 127$, 1912-13, SWPO); and in pelagic expeditions off Kerguelen Island ($n = 125$, largely 1929/30), and in the southern Indian Ocean in 1934/35 ($n = 13$), 1935/36 ($n = 1$), 1937/38 ($n = 1$) and 1961/62 ($n = 2$). However, the vast majority of pygmy blue whale catches were caught by Japanese expeditions ($n = 2578$, nearly all in 1959/60–1963/64) in the southern Indian Ocean; and Soviet expeditions ($n = 9299$, nearly all in 1962/63–1971/72) that whaled in the northern and southern Indian Oceans and eastward into New Zealand waters. Here we define the region inhabited by pygmy blue whales, based on catch length frequencies, and then separate blue whale catches within this region among the four populations using song types, satellite tag data, and fetal lengths. Fetal lengths in Soviet catches demonstrate that blue whales off southern Somalia (south of 2°N) have similar conception dates to blue whales in the Southern Hemisphere, but those north of 9°N and off India (north of 4°N) have aseasonal or out-of-phase reproduction, suggesting that SWIO (or Oman) blue whales extend to 2°N, further

¹ School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA, email: tbranch@uw.edu

² Department of Marine Biology, Texas A&M University Galveston, Galveston, TX 77553, USA

³ COPAS Sur-Austral, University of Concepcion, Barrio Universitario s/n, Concepción 4030000, Chile

⁴ Marine Mammal Institute, Department of Fisheries and Wildlife, Oregon State University, Newport, OR 97365, USA

⁵ Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA 02110, USA

⁶ Australian Marine Mammal Centre, Australian Antarctic Division, 203 Channel Hwy, Kingston, TAS 7050, Australia

⁷ Centre for Marine Science and Technology, Curtin University, GPO Box U1987, Perth, Western Australia 6845, Australia

⁸ NOAA Fisheries Office of Science & Technology, Ocean Acoustics Program, 1315 East West Highway, Silver Spring, MD 20910, USA

⁹ Bioacoustics Research Program, Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA

¹⁰ Centre for Whale Research (WA) Inc., PO Box 1622, Fremantle, Western Australia 6959, Australia

¹¹ Center for Acoustics Research and Education, University of New Hampshire, 24 Colovos Road, Durham, New Hampshire 03824, USA

¹² ENSTA Bretagne, UMR CNRS 6285 Lab-STICC 29806 Brest Cedex 9, France

¹³ Fisheries Management, Department of Agriculture, Forestry and Fisheries, Foreshore, Cape Town, South Africa

¹⁴ Mammal Research Institute Whale Unit, University of Pretoria, c/o 16 Ebor Road, Wynberg, 7800, South Africa

¹⁵ Applied Physics Laboratory, University of Washington, 1013 NE 40th Street, Seattle, Washington 98105, USA

¹⁶ Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Ocean Acoustics Lab, Klusmannstr. 3d, 27570 Bremerhaven, Germany

¹⁷ Evolution & Ecology Research Centre, School of BEES, University of New South Wales, Biological Sciences Building (D26), Randwick, Sydney, New South Wales 2052, Australia

north than previously assumed. A surface fitted to the locations of different blue whale songs was used to estimate the proportions of each population throughout the range of pygmy blue whales, and to split the pelagic catches by population. Estimated total catches for each of the four pygmy blue whale populations were 1796 (NIO), 7674 (SWIO), 2310 (SEIO), and 404 (SWPO), with 97.6% of the overall total of 12,184 coming during 1959/60 to 1971/72.

INTRODUCTION

A major stumbling block in assessing the status of pygmy blue whales is that there is population structure, but no reliable method to geographically separate these populations using biological data or genetics. Based on long-term generally stable song types (with slight drift over time), pygmy blue whales can be separated into at least four populations: northern Indian Ocean (NIO) including Sri Lanka and Oman; south-western Indian Ocean (SWIO) including Madagascar; south-eastern Indian Ocean (SEIO) including western and southern Australia and Indonesia; and south-western Pacific Ocean (SWPO) from New Zealand to Tonga. An additional putative song type recorded off Oman and north-western Madagascar suggests the possibility of a fifth, poorly-studied and previously unrecognized “Oman” blue whale population (Cerchio et al. 2018). There is mitochondrial DNA differentiation between the SWPO and other blue whale populations, including the SEIO population; furthermore the SWPO population has much lower genetic diversity than other blue whale populations (Barlow et al. 2018). However, genetic samples are not available from a broad enough set of locations to be used to separate historical pygmy blue whale populations.

It has been suggested that the NIO population has a breeding season six months out of phase of the Southern Hemisphere pygmy blue whale population (Mikhalev 2000), which we examine in more depth here. In addition, length at maturity for female blue whales is slightly shorter (by 0.5-0.6 m) for the NIO population, but this difference is small compared to the 4.2 m longer length at maturity for Antarctic blue whales (Branch & Mikhalev 2008).

Previous blue whale catch time series were developed for Antarctic blue whales (Branch et al. 2004), for pygmy vs. Antarctic vs. North Pacific vs. North Atlantic (Branch et al. 2008), and for eastern North Pacific vs. western and central North Pacific populations (Monnahan et al. 2014). Here we use methods similar to those developed by Monnahan et al. (2014) to separate the four populations of pygmy blue whales. The basic idea is to gather data about the proportion of each song type that is heard on passive acoustic recorders at different locations, and then fit a spatial smoother to the data separately for each population, to predict the probability that each is detected at a location, and then calculate the proportions of each population at a given latitude and longitude. The task at hand in the Indian Ocean is tricky because of the misreporting of the Soviet expeditions during the era that they targeted pygmy blue whales. While much of the data have since been recovered, individual catch locations are not available for all catches, which required adjustments.

METHODS

Defining pygmy blue whale boundaries: At the time when pygmy blue whales were caught (November to March), the vast majority of Antarctic blue whales are found in the Southern Ocean. To separate pelagic catches of the two subspecies, length frequencies of all blue whales, and of sexually mature female blue whales, were plotted by latitude and longitude bands to determine where to separate catches. These data came from the IWC’s individual catch database. Mixture models of the lengths of mature females previously found that 99.9% of pelagic catches north of 52°S and east of 35°E were pygmy blue whales (Branch et al. 2007a); the current analysis was used to further refine the western and southern boundaries for pygmy blue whales based on recorded lengths of both sexually mature females and all catches combined.

Land stations: Whaling was conducted from a variety of land stations in more northerly latitudes (north of 40°S) in the Southern Hemisphere, but no land stations were based in the northern Indian Ocean. Catches from each land station were examined to determine whether the catches were pygmy or Antarctic blue whales. Catches were assigned to Antarctic blue whales if a substantial portion of the whales were longer than 24.2 m (79.3 ft), which is the maximum observed length of pygmy blue whales (Omura 1984). Length frequencies of sexually mature females were also examined, since the length at which 50% of females are sexually mature is 23.4 m (76.8 ft) for Antarctic blue whales and 19.2 m (63.0 ft) for pygmy blue whales (Branch & Mikhalev 2008), thus sexually mature blue whales shorter than about 22 m (72 ft) are highly likely to be pygmy blue whales. The seasonal timing of catches was another important indicator: land station catches in the austral winter (May-September) were likely to be Antarctic blue whales; while land station catches peaking in the austral summer (December-March) were likely to be

pygmy blue whales, since Antarctic blue whales are generally south of 60°S during these months (Branch et al. 2007b). Note that to partially correct for whaling effort, monthly blue whale catches were also plotted as a proportion of all whale catches by month. Annual trends in blue whale catches also supply one final piece of evidence: Antarctic blue whales declined to 0.5% of pre-whaling numbers by 1963 (Branch et al. 2004), while substantial whaling on pygmy blue whales only started in 1959/60 from Japanese pelagic fleets, and in 1962/63 from Soviet pelagic fleets. Thus if annual catches (or blue whale catches as a percent of all whale catches) declined by 90-99% by the late 1950s, they would almost certainly be Antarctic blue whale catches rather than pygmy blue whale catches.

A standardized set of plots that tested each of these metrics was created for each land station in the Southern Hemisphere (map of catches, length frequencies, sexually mature female length frequencies, catches by month, catches by year, length of mature females by day of the year), and used to assign catches to either pygmy or Antarctic blue whales. If the catches were determined to be pygmy blue whales, land station catches were assigned 100% to the single population (NIO, SWIO, SEIO, SWPO) with the highest proportion of acoustic calls nearest to the land station, since land stations were each surrounded by a single song type.

Pelagic whaling: Two methods were conducted to estimate pygmy blue whale catches based on the IWC's annual catch database, and individual catch database. The annual catch database has reliable totals of blue whale catches for each expedition by whaling season ("expedition-season"). It should be noted that the season year is listed as the start year of a Southern Hemisphere whaling season, thus 1960 would be the 1960/61 season from 1 July 1960 to 30 June 1961, whereas for land stations 1960 would refer to the austral winter year from 1 January to 31 December 1960. In the annual catch database, notes for each expedition-season often include how many pygmy blue whales were caught, and how many "true" (i.e. Antarctic) blue whales were caught. Thus one estimate of total pygmy blue whale catches comes from adding up the totals in each of these notes.

A second estimate of pygmy blue whale catches comes from allocating blue whale catches in the IWC's individual catch database to pygmy blue whales if they fell within the boundaries of the pygmy blue whale region as outlined above. All blue whales caught in this region, which was a complex polygon largely 30°E to 180° and north of 52°S, were assumed to be pygmy blue whales, except for those that were longer than 24.2 m (79.4 ft) that were likely Antarctic blue whales. Previous analyses of the lengths of sexually mature females (Branch et al. 2007a), relationship between ovarian corpora accumulation against length (Branch et al. 2009), and length at sexual maturity (Branch & Mikhalev 2008) together provide evidence that 99.9% of blue whales caught in this general region were pygmy blue whales.

A third source of information comes from total blue whale catches from Japanese and Soviet pelagic expeditions in seasons when they concentrated on pygmy blue whales. For the Japanese fleets, 98.6% of 2579 catches listed as pygmy blue whales were caught in 1959/60 to 1962/63, plus 31 in 1963/64, 3 under special permit in 1966/67, and 2 under special permit in 1969/70. The Japanese fleets targeting pygmy blue whales were the *Tonan Maru*, *Tonan Maru II*, *Tonan Maru III*, *Nisshin Maru*, *Nisshin Maru II*, *Nisshin Maru III*, *Kinjo Maru*, *Kyokuyo Maru II*, and *Kyokuyo Maru III*. The Soviet fleets known to be targeting pygmy blue whales were the *Slava* (1962/63-1965/66), *Sovetskaya Ukraina* (1962/63-1972/73), *Yuri Dolgoruky* (1962/63-1969/70, plus 3 in pygmy locations in 1961/62), and *Sovetskaya Rossia* (1963/64-1972/73).

Cross-checks were made between each of these methods to highlight expedition-seasons in which many blue whales were listed in the annual catch database, but no or relatively few pygmy blue whales were noted in the notes of the annual catch database; to highlight expedition-seasons where substantially more blue whales were caught inside the pygmy blue whale boundaries than are listed in the notes of the annual catch database; and to highlight expedition-seasons where the annual catch database noted pygmy blue whale catches, but the individual catch database did not include any catch locations for those catches, thus making it difficult to separate catches among the four pygmy blue whale populations. Of note here is that Soviet expeditions are well known to have misreported catch locations, seasons, and species during the period of whaling on pygmy blue whales, and not all of the corrected individual catch locations have been recovered and included in the individual catch database (Yablokov 1994, Zemsky et al. 1995, Mikhalev 1996, Zemsky et al. 1996, Mikhalev 1997, Yablokov et al. 1998, Mikhalev 1999, Mikhalev 2000, Yablokov & Zemsky 2000, Mikhalev & Gill 2002).

Passive acoustic data for spatial models: For pelagic catches, the primary data used to separate pygmy blue whale catches into each of the four populations were songs recorded using passive acoustics (Table 1). Data were obtained from a number of compilations of acoustic song locations (McDonald et al. 2006, Branch et al. 2007b, Miller et al. 2014, Širović et al. 2018) from published papers found through a literature search, and from unpublished and

submitted data provided by a wide variety of researchers. In most cases, the underlying data were obtained directly from the authors, although in a few instances the data were read from figures or tables in published papers. Data were obtained in a format allowing for spatial models to be fitted to data from each month of the year for future refinements of this analysis, although the analysis presented here combines all data regardless of month. Data comprised the location, month, year, type of time unit analysed (individual days, or individual hours), number of time units examined, and number of time units with song types attributed to each of the four populations (NIO, SWIO, SEIO, SWPO), in addition to Antarctic blue whales. Some data sources only examined the data for song type from particular populations, requiring a judgement call as to whether the detections should be recorded as a zero (absence of the population) or as “not available” (NA) for the other populations. The NA data would be omitted when predicting spatial surfaces for the non-recorded populations. This issue was handled by asking the original authors whether they would have noticed song type from other populations in their data (zeros are true zeros), or whether they never looked extensively enough for other song types (zeros are converted to NAs). Two data points far outside the region considered to be inhabited by pygmy blue whales were excluded; these were NIO songs from hydrophones deployed in the south-eastern Atlantic Ocean off northern Angola (~6°S 12°E), which were heard for three hours on both hydrophones (Cerchio et al. 2010). These locations proved influential in spatial model fitting since they were so far from all other NIO song locations.

Conversion of acoustic data to a common unit of time: The spatial models require both a measure of acoustic effort (time units examined) and prevalence of song type (proportion of time units with song). However, data were coded in two different time units: days and hours, with somewhat more records available in hourly format. Since the proportion of days with songs will always be higher than the finer-resolution proportion of hours with songs, it is necessary to convert these data into a common time unit. For this purpose, fine-scale data (sub-hourly) were made available for a large dataset from around Australia by authors A.G. and R.M., grouped into individual months, and then each month of data was converted into both proportion of hours with songs, and proportion of days with songs. A variety of models were fit to the resulting data, predicting proportion of hours with songs from proportion of days with songs, assuming binomial likelihood, and minimizing the resulting negative log likelihood. The only acceptable model prediction came from the cumulative distribution function of a beta distribution, with the two parameters α and β of the beta distribution estimated. The resulting model predictions were used to convert proportion of days with songs into proportion of hours with songs for all datasets with day units; and the number of days was multiplied by 24 to obtain the number of hours.

Fetal length data for spatial models: Northern Indian Ocean blue whales have a breeding season that is reported to be six months out of phase of that for Southern Hemisphere blue whales (Mikhalev 2000, p. 151). This source states that both early stage and late stage fetuses are recorded in November-December, when Southern Hemisphere blue whales have small fetuses, and therefore breeding is either shifted by 6 months, or there are two peaks of reproduction in these pygmy blue whales, one corresponding to the Southern Hemisphere reproductive cycle, and the other similar to reproduction in the Northern Hemisphere. Mikhalev (2000) concluded that northern Indian Ocean blue whales are restricted to the waters north of 5°S. We reanalysed the Soviet fetal length data, using data for 470 blue whales, transcribed by K. Stafford (pers. comm.) from Yablokov & Zemsky (2000), examining at which latitude the breeding period shifts, to determine at which latitude the populations of SWIO and NIO blue whales can be divided. Based on these analyses (see Results), we added three data points to the data fitted by the spatial models, each equivalent to 90 days (2160 hours) of acoustic data. Two data points were assigned to the NIO population (1440 hours NIO song detected, 0 hours SWIO song detected) in the centre of the two catch locations displaying aseasonal reproduction (at 10.38°N 52°E and 9°N 71°E); and one data point was assigned to the SWIO population (1440 hours SWIO song detected, 0 hours NIO song detected) in the center of the catches with Southern Hemisphere seasonal reproduction (at 1.2°S 53°E).

Satellite tag data for spatial models: Positions from satellite tags on blue whales off south-west Australia (SEIO population) were obtained from Double et al. (2014). These were added to the data fitted by the spatial models, by treating each satellite tag position as equivalent to one hour of acoustic data with a detection of SEIO song type, and NA values for the other populations.

Spatial model fitting: We assumed for each population that occupancy is a smooth, continuous surface that varies in space only, and not by month or year. We fit binomial generalized linear models independently for each stock to the data, using latitude and longitude as predictors. These models predict a probability of being observed at a location for each population. We also considered two extensions with additional flexibility (Monnahan et al. 2014): non-parametric smoothers, which allow for a more flexible shape of the distribution based on the data; and a beta-binomial distribution, which allows for an overdispersion parameter to be estimated in addition to the probability of

occurrence. The binomial model expects independent events for data, but with acoustic recordings there is often temporal dependence because, for instance, a whale is likely to be heard on many consecutive hours of recordings. We fit our models using the GAMLSS framework (Rigby & Stasinopoulos 2005), which allows for beta-binomial estimation and non-parametric smoothers. Thus for each population we fit four models comprising the combinations of binomial vs. beta-binomial and parametric vs. non-parametric smoothers. AIC was used to select the best model for each stock (Burnham & Anderson 2002).

Catch assignments to each population: The selected model for each population predicts the probability of detecting a song from each population at a given location for one unit of effort (one hour). We assume these reflect the probability of occurrence of the whole population, even though it is thought that songs are produced only by males (e.g. Oleson et al. 2007), and their production may vary by month of the year (e.g. Samaran et al. 2013). From these probabilities we calculated the probability of detecting each of the four populations at a location by dividing the probabilities by their total. Thus, if detection probabilities were 1.00, 0.50, 0.50 and 0.001 then the probability a catch belongs to a population would be 0.62, 0.31, 0.06 and 0.00. This calculation makes two key assumptions: (1) each population sings at the same rates, and (2) recent acoustic detections mirror the historical distribution of each population during the period of whaling. While simple, this approach provides a more objective way for acoustic detections to inform population structure than attempting to draw hard boundary lines between populations that, based on the acoustic data, clearly overlap. In the present iteration, uncertainty in the model estimates is not calculated, but is planned to be estimated in the future by bootstrapping the data and explicitly testing sensitivities regarding biological assumptions of singing behaviour, as done for catch separation in the North Pacific (Monnahan et al. 2014).

RESULTS

Fetal length analysis: Soviet fetal length data are available for November from three main areas in and around the northern Indian Ocean (rectangles in Fig. 1), but few data are available for November from other areas (red circles in Fig. 1). The lengths of pregnant females in these three areas were all 18.5-23.5 m long (Fig. 2), typical of pygmy blue whales, but the fetal length distributions differed dramatically: those caught at 3°S-2°N off central Somalia had a unimodal fetal length peak at 1.5-2.0 m, while those caught at 7-19°N off northern Somalia, Yemen, and Oman had fetal lengths spread from 0-7.0 m, as did those in the central Arabian Sea (4-11°N) (Fig. 2). These data suggest that blue whales in these regions have some kind of mixture of a breeding season that is six months out of phase with blue whales in the Southern Hemisphere, and year-round breeding. Furthermore, these data provide evidence that SWIO blue whales are found as far north as 2°N, rather than the 5°S suggested by Mikhalev (2000).

Satellite tag data: Data from SEIO blue whales showed consistent movements among western Australia and Indonesia, and the region south of Perth Canyon (Double et al. 2014).

Defining pygmy blue whale boundaries for catches: Pygmy blue whales were assumed to have a maximum length of 24.2 m (79.3 ft) (Omura 1984). Length frequencies of all catches combined show a clear separation of lengths in pelagic catches, with catches south of 52°S all including substantial numbers of whales greater than 80 ft, while those in the Indian Ocean north of 52°S are nearly all shorter than 80 ft (Fig. 3). An even more marked geographic separation is seen in the lengths of sexually mature females, although there are fewer length data available for this group (Fig. 4). Zooming in on the region of overlap between Antarctic and pygmy blue whales (Fig. 5-6) reveals that it is too simplistic to assert that all blue whales north of 52°S are pygmy blue whales, and all those south of 52°S are Antarctic blue whales. Instead, there is a slightly different southernmost latitude for pygmy blue whales depending on longitude (Figs. 3-7):

- West of 20°E: no (or virtually no) pygmy blue whales caught in pelagic catches; substantial Antarctic blue whales caught south of 51°S.
- 20°-30°E: pygmy blue whales caught north of 46°S, scattered Antarctic blue whale catches 47-51°S, substantial Antarctic blue whale catches south of 52°S.
- 30-70°E: pygmy blue whales caught north of 52°S, Antarctic blue whales south of 52°S, with a gap in catches at 52-54°S and 50-70°E.
- 70-80°E: pygmy blue whales caught north of 53°S, Antarctic blue whales south of 54°S.
- 80-180°E: pygmy blue whales caught north of 40-45°S, Antarctic blue whales south of 58°S (Fig. 7).
- There were no pygmy blue whale catches from 180° eastwards to 20°E.

These exploratory results were used to divide pelagic catches between pygmy and Antarctic catches, with pygmy blue whales assumed to comprise none of the catches west of 20°E, but 100% of catches north of 46°S (20-30°E), north of 52°S (30-70°E), north of 53°S (70-80°E), and north of 52°S (80°E-180°), as shown in Fig. 7. Exceptions were made for catches longer than 79.3 ft, in these areas, which were assumed to be Antarctic blue whales.

Land stations: a brief description of the blue whale catch characteristics at each land station is given here, together with the determination of how catches were assigned to subspecies (three are assumed: Antarctic, pygmy, and SEPO) or pygmy blue whale population (NIO, SWIO, SEIO, SWPO). The locations of key whaling stations are shown on Fig. 7.

Peru: catches were highest in November-March, were nearly all caught in 1936 and 1937, and showed lengths typical of SEPO blue whales (Branch et al. 2007a). These were considered to be SEPO blue whales.

Chile: catches increased over time, peaking in 1965, and remained high as a percentage of all species. Catches were primarily in austral summer months (November to April), and showed lengths typical of SEPO blue whales (Branch et al. 2007a). These were considered to be SEPO blue whales.

Galapagos: catches peaked in September, were caught in only two years (1926, 1954) and displayed small lengths. Only two sexually mature females were recorded (<60 ft) which is anomalously small even for pygmy blue whales. These data are more ambiguous, but were considered to be SEPO blue whales.

Falkland Islands, South Georgia, South Shetland, South Orkneys: catches here were all south of 52°S in the Antarctic, declined precipitously to near zero by mid-century, had catches which peaked in November to February, and displayed lengths typical of Antarctic blue whales. In the earlier years up to 1929, a larger portion of sexually mature females were recorded between 60 and 75 ft, but these early data were also characterized by high proportions of rounding to the nearest 5 ft or 10 ft (also noted in Branch et al. 2007a), reports of dubious recording practices, and a lack of standardized length measurement techniques. Previous analyses of lengths of sexually mature females had estimated up to 8-10% were pygmy blue whales in these early years but only 1.9% in later years (Branch et al. 2007a). Since carefully standardized measurements found no small sexually mature females (Mackintosh & Wheeler 1929) and defined South Georgia as part of the canonical region inhabited by Antarctic blue whales, all of these catches were considered to be Antarctic blue whales.

Brazil: only two blue whales were caught from land stations, in June and September, and their lengths (65-70 ft) and unknown maturity status preclude assignment to subspecies. In addition, a 23.1 m female that stranded in 1992 could not be assigned to Antarctic or pygmy blue whales (Dalla Rosa & Secchi 1997), although this would be longer than almost all pygmy blue whales. Given the months, the location far to the east of SEPO blue whales, and far to the west of pygmy blue whales, these were assumed to be Antarctic blue whales, while admitting the data are ambiguous.

West coast of Africa: Saldanha Bay, Hangklip, Namibia, Angola, and Congo: catches peaked in July to September, declined to around 1% of original catch levels, and all sexually mature females were typical of Antarctic blue whale sizes. Substantial portions of all catches were longer than 79 ft, but many more small individuals were caught in all of these land stations than elsewhere, especially in Angola where the modal length was just 60 ft. At Saldanha Bay, an extensive study revealed that the smaller individuals were sexually immature, and that the lengths and bodily proportions were the same as the Antarctic blue whales caught at South Georgia (Mackintosh & Wheeler 1929). Only one individual was caught in Congo, and was in poor condition. Previous analysis of the lengths of sexually mature females indicated that 0.6-10.7% (95% CIs) of these catches could be pygmy blue whales after dubious lengths from early Hangklip catches were removed, but was based on a small sample of sexually mature females ($n = 56$) (Branch et al. 2007a). All of these catches were therefore assigned to Antarctic blue whales.

Durban: at least one pygmy blue whale was caught by the companies operating out of Durban: a 66 ft pregnant female caught on 21 September 1963, with a note that “this appears to be the first record of this [sub]species at Durban” (Gambell 1964). Catch indicators point toward Antarctic blue whales dominating at this location: blue whale catches declined from 10-20% of all species in 1918-1932 to <2% from 1946 onwards; catches peaked in May to August; and substantial proportions of blue whales were longer than 24.2 m (79.3 ft). Only 14 sexually mature females were noted in the records, and 10 were typical of lengths for Antarctic blue whales. However, after 1937, although catches were still taken in June to August, fewer catches exceeded 24.2 m (9% instead of 24%), and all three sexually mature females were short (65, 66, 72 ft), including the previously noted pygmy blue whale catch (Gambell 1964). Catch per unit effort data here declined to 2.8% of the level in 1920-28 (Best 2003) instead of the 0.3% expected if these later catches were Antarctic blue whales (Branch et al. 2007b). Thus some of these later blue

whale catches may have been pygmy blue whales. More work is needed to reconcile these conflicting data. For example, if 10% of all catches after World War II were pygmy blue whales, then 18 pygmy blue whales would have been caught out of Durban out of a total of 176. We decided to assign all Durban catches to Antarctic blue whales, except for four short sexually mature females that were assigned to SWIO pygmy blue whales: 72 ft (12 July 1924), 72 ft (22 April 1937), 66 ft (21 Sept 1963), and 65 ft (3 May 1965).

West coast of Australia (Carnarvon, Point Cloates): scattered blue whale catches (22 in total) were made here in most years that these land stations were open (1925-28, 1956-63), but humpback whales comprised the majority of the catches. Nearly all catches of other whales were in June to September, but blue whales were mainly caught in May, September, and October, and were thus unlikely to be Antarctic blue whales. Little decline in blue whale catches was apparent over time (2.3/yr in 1925-28, 1.6/yr in 1956-63). Blue whales caught were typical lengths for pygmy blue whales (58-76 ft) except for one 84 ft individual caught on 1 October 1926, which was a mother accompanied by a calf. Two other sexually mature females (both pregnant) were 66 and 72 ft long. In addition, five blue whales caught at Carnarvon are noted as being pygmy blue whales in the IWC's annual catch records (4 in 1962, 1 in 1963). Blue whales caught at these land stations were therefore assigned to the SEIO pygmy blue whale population except for the single long whale caught in 1926, which is assumed to be an Antarctic blue whale.

West coast of Australia (Albany and Vasco da Gama): four blue whales were caught at Vasco da Gama during 1912-14 (individual information only available for one), and eight blue whales were caught at Albany (1959-60). All catches were in May or June, and were small (62-70 ft), including one small pregnant female (66 ft 2 in). One blue whale stranded dead at Albany (May 1973) and was processed for oil, but is excluded here since it was not a catch. Blue whale catches at these locations were all assigned to SEIO pygmy blue whales.

East coast of Australia (Tangalooma): one sexually mature female (66 ft 10 in) was captured on 11 June 1954 at Tangalooma on Moreton Island near Brisbane (27.2°S 153.4°E), and is assigned to the SWPO pygmy blue whale population.

East coast of Australia to New Zealand: The factory ship *Loch Tay* operated by the Australia Co caught 33 blue whales in 1912 and 93 blue whales in 1913, operating in New Zealand waters and the south coast of New South Wales (Southland Times, 11 December 1913). In addition, one blue whale was caught by the company *New Zealand Wh* in Rakiura and Prince George. Individual locations and lengths are not available for these catches, all of which were assigned to SWPO pygmy blues.

Pelagic expeditions: pelagic catches were listed as under "SH" and included catches up to the northern Indian Ocean. There are four groupings of pelagic pygmy blue whale catches: catches around Kerguelen Islands (that did not include data for individual whales); scattered catches within the pygmy region for which location and length data are available; directed catches by Japanese expeditions, for which individual data are available; and directed catches by Soviet expeditions, for which individual data are missing for a few expedition-season combinations. Each category is dealt with in a manner tailored to data availability.

Kerguelen Islands: 125 blue whales were caught off Kerguelen by three expeditions: the *A/S Kerguelen* ($n = 8$ in 1908/09, $n = 1$ in 1909/10), the *Mangoro* ($n = 3$, 1909/10), and the *Radioliene* ($n = 113$, 1929/30). These are assumed to be pygmy blue whales since they come from 47-53°S and 67-73°E, which is well within the boundaries of pygmy blue whales. Ichihara (1966) reports the 113 blue whales as being likely pygmy blue whales, but says the season was 1928/29; however the IWC database states these catches were July-Nov 1929, and hence in the 1929/30 season. Apportionment to each population was based on the assumption that these catches came from the center of the IWC region for Kerguelen (50°S 70°E).

Scattered catches: occasional pelagic expeditions ventured into the pygmy blue whale region (Fig. 8), headlined by the 1934/35 season when Norwegian expeditions caught 13 blue whales: *Solglimt* caught 2, *Skytteren* caught 10, and Sir James Clark Ross caught 1. In addition, *Skytteren* caught 1 additional blue whale the following season; the South African expedition *UniWaleCo* caught 1 blue whale in 1937/38; and the *Willem Barendsz* (Netherlands) caught 2 blue whales in 1961/62. Individual catch locations were used to apportion these catches to pygmy blue whale populations (Fig. 8).

Japanese expeditions: pelagic whaling by the Japanese on pygmy blue whales started in 1959/60 and essentially ended in 1962/63 except for the following catches in the pygmy blue whale region: *Kyokuyo Maru III* in 1963/64 ($n = 27$) and in 1966/67 ($n = 3$, by special permit); and by *Nisshin Maru* in 1969/70 ($n = 2$, by special permit). The cessation of whaling on pygmy blue whales was driven by assessments in the International Whaling Commission suggesting that the catch level was not sustainable, in addition to the pending ban on catching blue whales in the

Southern Hemisphere, for which an exception had been made for pygmy blue whales in region 0-80°E and 40-54°S. Japanese pygmy blue whale catches were confined to this region for all expeditions and seasons (Fig. 9). There is a very close correspondence in all years and expeditions between the total catch noted as pygmy blue whale in the annual catch summaries, and the total catch from the individual catch records inside the pygmy blue whale. For most expedition-seasons, these match exactly, and any differences are only 1 or 2 whales per year. However, catch locations reported to the IWC were rounded to the nearest whole degree. For Japanese whaling, annual catch summaries are the most accurate estimate of total pygmy blue whale catches, and the individual catch locations were used to assign catches to each of the individual pygmy blue whale populations.

Soviet expeditions: the primary period of Soviet whaling on pygmy blue whales was 1962/63 to 1971/72, with the exception of 3 blue whales caught by *Yuri Dolgoruky* in 1961/62, and 2 caught by each of *Sovetskaya Ukraina* and *Sovetskaya Rossia* in 1972/73, which was the season that international observers were first introduced to the Soviet fleet (Fig. 10). Pygmy blue whale catches halted for most fleets in 1972/73 and for all fleets in 1973/74. For most expedition-seasons, the number of pygmy blue whales in the annual catch record notes matches closely (mean of annual/individual = 1.02) to the number of catches with individual locations inside the pygmy blue whale region, but the discrepancies are greater than for the Japanese expeditions. In addition, three expeditions listed as being SH pelagic (i.e. all whaling south of 0°) have zero individual catch locations: *Yuri Dolgoruky* in 1967/68 (7 pygmy blue whales and 43 total blue whales in annual catch data); *Sovetskaya Rossia* in 1965/66 (88 pygmy blue whales, 93 total blue whales); and *Sovetskaya Rossia* in 1968/69 (94 pygmy blue whales, 113 total blue whales). For expedition-seasons with individual catch locations, the proportion belonging to each pygmy blue whale population was calculated, and then multiplied by the total catch of pygmy blue whales noted in the annual catch database. For the three expedition-seasons with no individual catch locations, the proportions in the previous and following season from the same expedition were averaged, and applied to the total catch of pygmy blue whales noted in the annual catch database. If information becomes available on where whaling was likely conducted in these three expedition-seasons, catches could be more realistically separated.

Conversion of acoustic data to a common unit of time: the best model fit to predict proportion of hours with songs from proportion of days with songs, was the cumulative distribution function of a beta distribution with $\alpha = 0.9533$ and $\beta = 0.1771$ (Fig. 11).

Acoustic data: acoustic records (supplemented by three points based on fetal length data in the NW Indian Ocean, and by satellite tag data), showed clear spatial separation in songs made by the four pygmy blue whale populations (Fig. 12). The NIO type songs were recorded in the northern Indian Ocean, although three locations south of 34°S recorded these songs together with SWIO and SEIO songs. The intrusion of NIO blue whales into the central and southern Indian Ocean is the most interesting feature of the acoustic data. The SWIO songs were recorded around Madagascar stretching east to 75°E where they overlapped with SEIO songs, especially south of 30°S. SEIO songs were recorded throughout north-western, western and southern Australian waters, with occasional songs on the east coast of Australia, and also stretched west to waters almost directly south of Madagascar in waters south of 40°S. The SWPO songs were confined to waters from 145°E to 174°W from Tasmania to New Zealand, the east coast of Australia, and near Tonga at 174°W.

Spatial model fitting: In general, additional complexity was favoured by AIC, but some versions of the GAMLSS models failed to converge, likely due to overparameterization relative to the information contained in the data. These models were discarded and only those which converged were used in AIC selection (Table 2). The best fitting models showed predicted surfaces (probability of detecting whales of each population) that largely matched expectations (Fig. 13), and are converted in Fig. 14 to the proportion of each population in each region (if a blue whale was detected, this is the probability that it should be assigned to each population). The NIO population was predominantly in the northern Indian Ocean, although with substantial probabilities in the central Indian Ocean and even in the southern Indian Ocean, as the model fitted to the three locations in the southern Indian Ocean where NIO songs were recorded. The SWIO population was predicted to occur only in the south-western Indian Ocean. The SEIO population was predicted to occur around Australia except for the east coast, into Indonesian waters, and westwards and southwards to about 50°S and 70°E, with some probability of being further westward. Of interest here is that sightings of blue whales around the Solomon Islands in Aug-Oct 1957 (Ohsumi & Shigemune 1993, Branch et al. 2007b) are predicted to be at the boundary between fitted surfaces for the SEIO and SWPO populations. The SWPO population was confined to the region around New Zealand, from Tasmania to the east coast of Australia, northwards to the equator, and southwards toward the Antarctic. The largest area of overlap among the populations was in the southern Indian Ocean around 30°S and 75°E where the NIO, SWIO, and SEIO

populations all were predicted to occur with some probability, as has been noted in previous papers examining their songs (Samaran et al. 2013).

Catch assignments to each population

Land stations: catches at land stations were assigned to the population with highest probability near to the land station, with little ambiguity given the fitted model surface: pygmy blue whale catches at Durban were assigned to SWIO; west coast Australia catches were assigned to SEIO, and the east Australia catch was assigned to SWPO. Catches from the expedition operating from Australia to New Zealand (no recorded catch locations) were also assigned to SWPO. In total, 0 were assigned to NIO, 4 to SWIO, 33 to SEIO, and 128 to SWPO (Table 3).

Kerguelen Islands and scattered pelagic catches: catches were assigned based on the predicted proportions at 50°S 70°E, namely 7% NIO, 87% SWIO, 5% SEIO, and 0% SWPO (Table 3). Scattered pelagic catches were assigned to populations based on the predicted proportions at the respective catch locations. For expedition-seasons with a single catch, the highest proportion was used in the assignment. In total, 142 pygmy blue whale catches were identified, of which 113 were caught by Radioliene at Kerguelen in 1929/30. Of these catches, 11 were NIO, 125 SWIO, 6 SEIO and 0 SWPO (Table 3).

Japanese pelagic catches: the IWC's annual catch database notes 2578 pygmy blue whales from Japanese expeditions (Table 5), which compares to 2569 inside the pygmy region from the individual catch database. For each expedition-season combination, the summed predicted proportions for each population were applied to the total pygmy blue whale catch listed in the notes to assign annual catches by expedition and season, to the pygmy blue whale populations. Some notes follow for further investigation.

- 1) 1963/64 two pygmy blue whales caught by *Tonan Maru* but with no individual locations within the pygmy region were assigned to SWIO since most Japanese catches came from this population.
- 2) 1963/64 one pygmy blue whale caught by *Tonan Maru II* but no location was recorded; this was assigned to SWIO.
- 3) Slight rounding adjustments are made to ensure the totals equal the listed total for each expedition and season.

Overall, the allocation method estimates that Japanese expeditions caught predominantly from the SWIO population (2428 out of 2578), with additional catches from the SEIO (45) and NIO (105), but none from the SWPO population (Table 5). It should be noted that although the Japanese catches were all south of 40°S and west of 80°E, this region is predicted by the model to be an area of overlap for the SWIO, SEIO, and NIO populations (Fig. 13-15).

Soviet pelagic catches: Soviet catch data required more finesse to reconcile individual catch data with annual summaries of total catch. In some cases, annually recorded pygmy blue whale catches were smaller than the individual blue whale catches within the pygmy blue whale region: *Slava* in 1964/65 0 vs. 784, *Slava* in 1965/66 0 vs. 447, *Sovetskaya Ukraina* in 1962/63 0 vs. 7; Yuri Dolgoruky in 1963/64 503 vs. 578; and *Sovetskaya Rossia* in 1967/68 19 vs. 26. In these cases the higher individual catch totals were taken to be more accurate and supplanted the lower annual catch totals.

For other expedition-season combinations, pygmy blue whale catches were noted, but no individual catch data are available, for instance *Yuri Dolgoruky* caught 7 pygmy blue whales in 1967/68, and 88 in 1965/66; while *Sovetskaya Rossia* caught 94 in 1968/69. For these cases, the proportions in adjacent seasons were used to assign these catches to pygmy blue whale populations.

The total Soviet catches were 9299 (Table 6), with substantial catches coming from the SWIO (5117) and SEIO (2226), as well as a large proportion of all catches from the NIO (1680) and SWPO (276).

Total catches from all sources combined: Summing up catches of pygmy blue whales from land stations and pelagic whaling operations (Table 7), we found 1796 catches from NIO, 7674 from SWIO, 2310 from SEIO and 404 from SWPO, for a grand total of 12,184 pygmy blue whale catches.

DISCUSSION

The catch separation presented here is the first attempt at separating pygmy blue whale populations, and reveals that the whaling impacts differed greatly among the populations, with 19-fold greater catches coming from the SWIO population than from the SWPO population. Even with total catches of 12,184, these numbers are still dwarfed by the estimated 345,775 Antarctic blue whales caught by whalers (Branch et al. 2008). Total numbers for pygmy blue whales here are lower than the 13,022 estimated previously (Branch et al. 2008), largely because that estimate

assumed that 3.9% of blue whales caught on the west coast of Africa were pygmy blue whales and 30-50% of the Durban catches were pygmy blue whales. A reanalysis of the data finds little evidence for substantial pygmy blue whale catches at either of these locations, or outside the region considered here to be that inhabited by pygmy blue whales (Fig. 7). Papers based on length frequencies of sexually mature females (Branch et al. 2007a) and corpora counts in ovaries (Branch et al. 2009) concluded that only 0.8% and 0.1% respectively of blue whales south of 52°S are pygmy blue whales.

The current analysis improves on the previous analysis using acoustic data (Branch et al. 2018). Previously the spatial model was fit to proportions of whale songs at each location, which resulted in a statistically problematic likelihood surface. Here we compiled the underlying data for the number of hours (or days) of acoustic recordings examined, and the number of hours (or days) in which whale songs of each type were recorded, thus individual surfaces to be predicted for the probability of occurrence of each population in each region. In addition, the data compiled here are by month, and thus it should be possible in the future to extend the analysis by fitting monthly surfaces to reveal movement pathways for each blue whale population, and thus also obtain more accurate catch separation. At a minimum, future efforts will focus on the period when most of the pelagic whaling was undertaken (mostly November in NIO, Jan-March in southern locations). Of great importance is a planned analysis of the uncertainty around the time series of catches presented here. The time series here is the best estimate (mean) of the model surface. It does not take into account uncertainty due to unknown catch locations, uncertainty due to the probabilistic assignments of individual catches to each population, or uncertainty in the shape of the fitted spatial models. A bootstrapping analysis similar to that conducted in Monnahan et al. (2014) would be an obvious first step at accounting the last source of uncertainty.

Nevertheless, the analysis here is a key step in assessing the current status of these four populations. Partial abundance estimates are available for the NIO, SWIO, and SEIO populations; and preliminary abundance estimate is available for SWPO blue whales (Barlow et al. 2018). Population assessment models could be run that combine the catch estimates here with abundance estimates to assess minimum abundance over time, as done for Chilean blue whales (Williams et al. 2011). In addition, the spatial model also allow for a statistical method to extrapolate survey abundance estimates conducted in small areas, such as the one on SWIO blue whales south of Madagascar (Best et al. 2003), to the whole area inhabited by each population, since the spatial models predict probability of occurrence in space for each population separately.

One limitation to our approach is the availability of acoustic data, and whether the available data are representative of the distribution of all populations in the assessed regions. As a prime example, the authors are aware of reports and data available for a putative fifth song type in the Indian Ocean that is also thought to be made by (pygmy) blue whales, recorded primarily off Oman from November to June, but also sparsely off north-western Madagascar during April and May (Cerchio et al. 2018), and in at least one other location in equatorial Indian Ocean waters. This has been dubbed the “Oman” blue whale song type, and may complicate our analysis and substantially alter our conclusions if it does in fact represent a previously unrecognized population of blue whales. Notably, these songs were recorded most extensively off Oman, but also in the southern catch area with fetal length distributions more typical of Southern Hemisphere blue whales. It should be noted that there is limited acoustic monitoring effort in the westernmost reaches north of the equator in the Indian Ocean, with only the shallow-water deployments which detected the Oman song type at a position on the edge of the shelf break. Thus it seems possible, if not likely, that the northern Indian Ocean may comprise two separate blue whale populations: one that sings the “Sri Lanka” song type and referred to here as NIO blue whales, and a second that sings the Oman song type and represents a population of blue whales in the western Arabian Sea, ranging down the western edge of the Indian Ocean. In future refinements that include this song type, we suspect that many of the catches currently allocated to the NIO population, and some allocated to the SWIO population, may shift to the new population, altering our conclusions on the impacts of whaling.

ACKNOWLEDGEMENTS

The manuscript benefited from extensive discussion about population boundaries with Bob Brownell and Pete Gill. The authors thank Abigail Alling, Dana Brodie, and Mark McDonald for assistance with data. Note that due to a lack of time before the meeting, coauthors had little time to review the manuscript; and any errors and omissions are therefore the sole responsibility of the lead author, T.A.B.

REFERENCES

Alling A, Dorsey EM, Gordon JCD (1991) Blue whales (*Balaenoptera musculus*) off the Northeast coast of Sri Lanka: distribution, feeding and individual identification. UNEP Marine Mammal Technical Report 3:247-258

- Balcazar NE, Klinck H, Nieukirk SL, Mellinger DK, Klinck K, Dziak RP, Rogers TL (2017) Using calls as an indicator for Antarctic blue whale occurrence and distribution across the southwest Pacific and southeast Indian Oceans. *Marine Mammal Science* 33:172-186
- Balcazar NE, Tripovich JS, Klinck H, Nieukirk SL, Mellinger DK, Dziak RP, Rogers TL (2015) Calls reveal population structure of blue whales across the southeast Indian Ocean and southwest Pacific Ocean. *Journal of Mammalogy* 96:1184-1193
- Barlow DR, Torres LG, Hodge KB, Steel D, Baker CS, Chandler TE, Bott N, Constantine R, Double MC, Gill P, Glasgow D, Hamner RM, Lilley C, Ogle M, Olson PA, Peters C, Stockin KA, Tessaglia-Hymes CT, Klinck H (2018) Documentation of a New Zealand blue whale population based on multiple lines of evidence. *Endangered Species Research* 36:27-40
- Best PB (2003) How low did they go? An historical comparison of indices of abundance for some baleen whales on the Durban whaling ground. IWC paper SC/55/SH18
- Best PB, Rademeyer RA, Burton C, Ljungblad D, Sekiguchi K, Shimada H, Thiele D, Reeb D, Butterworth DS (2003) The abundance of blue whales on the Madagascar Plateau, December 1996. *Journal of Cetacean Research and Management* 5:253-260
- Branch TA, Abubaker EMN, Mkango S, Butterworth DS (2007a) Separating southern blue whale subspecies based on length frequencies of sexually mature females. *Marine Mammal Science* 23:803-833
- Branch TA, Allison C, Mikhalev YA, Tormosov D, Brownell Jr RL (2008) Historical catch series for Antarctic and pygmy blue whales. IWC paper SC/60/SH9
- Branch TA, Matsuoka K, Miyashita T (2004) Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Marine Mammal Science* 20:726-754
- Branch TA, Mikhalev YA (2008) Regional differences in length at sexual maturity for female blue whales based on recovered Soviet whaling data. *Marine Mammal Science* 24:690-703
- Branch TA, Mikhalev YA, Kato H (2009) Separating pygmy and Antarctic blue whales using long-forgotten ovarian data. *Marine Mammal Science* 25:833-854
- Branch TA, Monnahan CC, Širović A (2018) Separating pygmy blue whale catches by population. IWC paper SC/67B/SH23. 23pp
- Branch TA, Stafford KM, Palacios DM, Allison C, Bannister JL, Burton CLK, Cabrera E, Carlson CA, Galletti Vernazzani B, Gill PC, Hucke-Gaete R, Jenner KCS, Jenner M-NM, Matsuoka K, Mikhalev YA, Miyashita T, Morrice MG, Nishiwaki S, Sturrock VJ, Tormosov D, Anderson RC, Baker AN, Best PB, Borsa P, Brownell Jr RL, Childerhouse S, Findlay KP, Gerrodette T, Ilangakoon AD, Joergensen M, Kahn B, Ljungblad DK, Maughan B, McCauley RD, McKay S, Norris TF, Oman Whale and Dolphin Research Group, Rankin S, Samaran F, Thiele D, Van Waerebeek K, Warneke RM (2007b) Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean. *Mammal Review* 37:116-175
- Brodie DC, Dunn RA (2015) Low frequency baleen whale calls detected on ocean-bottom seismometers in the Lau basin, southwest Pacific Ocean. *Journal of the Acoustical Society of America* 137:53-62
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference, Vol Springer, Berlin, Heidelberg, New York
- Cerchio S, Collins T, Mashburn S, Clark C, Rosenbaum H (2010) Acoustic evidence of blue whales and other baleen whale vocalizations off northern Angola. IWC paper SC/62/SH13. 8 pp.
- Cerchio S, Willson A, Muirhead C, Al Harthi S, Baldwin R, Cholewiak D, Collins T, G M, Rasoloarijao T, Willson MS (2018) A new baleen whale song type described for the Western Indian Ocean off Oman and northwest Madagascar. IWC Paper SC/67B/SH/24 Rev1. 7 pp.
- Dalla Rosa L, Secchi ER (1997) Stranding of a blue whale (*Balaenoptera musculus*) in southern Brazil: 'true' or pygmy? Report of the International Whaling Commission 47:425-430
- Double MC, Andrews-Goff V, Jenner KCS, Jenner M-N, Laverick SM, Branch TA, Gales NJ (2014) Migratory movements of pygmy blue whales (*Balaenoptera musculus brevicauda*) between Australia and Indonesia as revealed by satellite telemetry. *PLoS One* 9:e93578
- Dréo R, Bouffaut L, Leroy E, Barruol G, Samaran F (2018) Baleen whale distribution and seasonal occurrence revealed by an ocean bottom seismometer network in the western Indian Ocean. *Deep-Sea Research II* doi: 10.1016/j.dsr2.2018.04.005
- Gambell R (1964) A pygmy blue whale at Durban. *Norsk Hvalfangst-Tidende* 53:66-68
- Garcia-Rojas MI, Jenner KCS, Gill PC, Jenner M-NM, Sutton AL, McCauley RD (2018) Environmental evidence for a pygmy blue whale aggregation area in the Subtropical Convergence Zone south of Australia. *Marine Mammal Science* 34:901-923

- Gavrilov AN, McCauley RD (2013) Acoustic detection and long-term monitoring of pygmy blue whales over the continental slope in southwest Australia. *Journal of the Acoustical Society of America* 134:2505-2513
- Gavrilov AN, McCauley RD, Gedamke J (2012) Steady inter and intra-annual decrease in the vocalization frequency of Antarctic blue whales. *Journal of the Acoustical Society of America* 131:4476-4480
- Gavrilov AN, McCauley RD, Paskos G, Goncharov A (2018) Southbound migration corridor of pygmy blue whales off the northwest coast of Australia based on data from ocean bottom seismographs. *JASA Express Letters* 144(4):EL281-EL285
- Gedamke J, Gales N, Hildebrand J, Wiggins S (2007) Seasonal occurrence of low frequency whale vocalisations across eastern Antarctic and southern Australian waters, February 2004 to February 2007. IWC paper SC/59/SH5. 11pp
- Gedamke J, Robinson SM (2010) Acoustic survey for marine mammal occurrence and distribution off East Antarctica (30-80°E) in January-February 2006. *Deep-Sea Research II* 57:968-981
- Ichihara T (1966) The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. In: Norris KS (ed) *Whales, dolphins, and porpoises*. University of California Press, Berkeley and Los Angeles, p 79-111
- Kibblewhite AC, Denham RN, Barnes DJ (1967) Unusual low-frequency signals observed in New Zealand waters. *Journal of the Acoustical Society of America* 41:644-655
- Ljungblad DK, Clark CW, 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. Report of the International Whaling Commission 48:439-442
- Ljungblad DK, Stafford KM, Shimada H, Matsuoka K (1997) Sounds attributed to blue whales recorded off the southwest coast of Australia in December 1995. Report of the International Whaling Commission 47:435-439
- Mackintosh NA, Wheeler JFG (1929) Southern blue and fin whales. *Discovery Reports* 1:257-540
- McCauley RD, Gavrilov AN, Jolliffe CD, Ward RD, Gill PC (2018) Pygmy blue and Antarctic blue whale presence, distribution and population parameters in southern Australia based on passive acoustics. *Deep-Sea Research I* doi: 10.1016/j.dsr.2018.09.006
- McDonald MA (2006) An acoustic survey of baleen whales off Great Barrier Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 40:519-529
- McDonald MA, Hildebrand JA, Mesnick SL (2006) Biogeographic characterization of blue whale song worldwide: using song to identify populations. *Journal of Cetacean Research and Management* 8:55-65
- Mikhalev YA (1996) Pygmy blue whales of the northern-western Indian Ocean. IWC paper SC/48/SH30:30pp
- Mikhalev YA (1997) Additional information about the catches of Soviet whaling fleet *Sovetskaya Ukraina*. Report of the International Whaling Commission 47:147-150
- Mikhalev YA (1999) Biological characteristics of blue whales taken during the first cruises of the whaling fleet *Slava*. IWC paper SC/51/CAWS41:16pp
- Mikhalev YA (2000) Whaling in the Arabian Sea by the whaling fleets *Slava* and *Sovetskaya Ukraina*. In: Yablokov AV, Zemsky VA (eds) *Soviet Whaling Data (1949-1979)*. Center for Russian Environmental Policy Marine Mammal Council, Moscow, p 141-181
- Mikhalev YA, Gill P (2002) Biological characteristics of pygmy blue whales taken in the Great Australian Bight during 1964/65 Antarctic whaling season. IWC paper SC/54/IA24:6pp
- Miksis-Olds JL, Nieukirk SL, Harris DV (2018) Two unit analysis of Sri Lankan pygmy blue whale song over a decade. *Journal of the Acoustical Society of America* 144:3618-3626
- Miller BS, Collins K, Barlow J, Calderan S, Leaper R, McDonald M, Ensor P, Olson PA, Olavarria C, Double MC (2014) Blue whale vocalizations recorded around New Zealand: 1964–2013. *Journal of the Acoustical Society of America* 135:1616-1623
- Monnahan CC, Branch TA, Stafford KM, Ivashchenko YV, Oleson EM (2014) Estimating historical eastern North Pacific blue whale catches using spatial calling patterns. *PLoS One* 9:e98974
- Ohsumi S, Shigemune H (1993) A sightings survey of larger whales in lower latitudinal waters of the Pacific in austral winter, with special reference to the blue whale. IWC paper SC/Oc93/BW WP 6:23pp
- Oleson EM, Calambokidis J, Burgess WC, McDonald MA, LeDuc CA, Hildebrand JA (2007) Behavioral context of call production by eastern North Pacific blue whales. *Marine Ecology Progress Series* 330:269-284
- Omura H (1984) Measurements of body proportions of the pygmy blue whale, left by the late Dr. Tadayoshi Ichihara. *Scientific Reports of the Whales Research Institute* 35:199-203
- Pangerc T (2010) Baleen whale acoustic presence around South Georgia. University of East Anglia

- Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location, scale and shape. *Journal of the Royal Statistical Society C-Applied Statistics* 54:507-544
- Samaran F, Stafford KM, Branch TA, Gedamke J, Royer J-Y, Dziak RP, Guinet C (2013) Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. *PLoS One* 8:e71561
- Shabangu FW, Findlay KP, Yemane D, Stafford KM, van den Berg M, Blows B, Andrew RK (2019) Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa. *Journal of Marine Systems* 190:25-39
- Shabangu FW, Yemane D, Stafford KM, Ensor P, Findlay KP (2017) Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. *PLoS One* 12:e0172705
- Širović A, Branch T, Brownell Jr RL, Buchan S, Cerchio S, Findlay K, Lang A, Miller B, Olson P, Rogers TL, Samaran F, Suydam R (2018) Blue whale song occurrence in the Southern Hemisphere. IWC Paper SC/67b/SH11. 12pp.
- Širović A, Hildebrand JA, Thiele D (2006) Baleen whales in the Scotia Sea during January and February 2003. *Journal of Cetacean Research and Management* 8:161-171
- Širović A, Hildebrand JA, Wiggins SM, McDonald MA, Moore SE, Thiele D (2004) Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep-Sea Research II* 51:2327-2344
- Širović A, Hildebrand JA, Wiggins SM, Thiele D (2009) Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. *Marine Mammal Science* 25:125-136
- Stafford KM, Chapp E, Bohnenstiehl DR, Tolstoy M (2011) Seasonal detection of three types of “pygmy” blue whale calls in the Indian Ocean. *Marine Mammal Science* 27:828-840
- Thomisch K (2017) Distribution patterns and migratory behavior of Antarctic blue whales, Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany
- Thomisch K, Boebel O, Clark CW, Hagen W, Spiesecke S, Zitterbart DP, Van Opzeeland I (2016) Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea. *Endangered Species Research* 30:239-253
- Tripovich JS, Klinck H, Nieukirk SL, Adams T, Mellinger DK, Balcazar NE, Klinck K, Hall EJS, Rogers TL (2015) Temporal segregation of the Australian and Antarctic blue whale call types (*Balaenoptera musculus* spp.). *Journal of Mammalogy* 96:603-610
- Williams R, Hedley S, Branch TA, Bravington M, Zerbini AN, Findlay K (2011) Chilean blue whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species. *Conservation Biology* 25:526-535
- Yablokov AV (1994) Validity of whaling data. *Nature* 367:108
- Yablokov AV, Zemsky VA (2000) Size and sex composition of embryos of whales caught in the Southern Hemisphere. *Soviet Whaling Data (1949-1979)*. Appendix I., Vol. Center for Russian Environmental Policy, Marine Mammal Council, Moscow
- Yablokov AV, Zemsky VA, Mikhalev YA, Tormosov VV, Berzin AA (1998) Data on Soviet whaling in the Antarctic in 1947-1972 (population aspects). *Russian Journal of Ecology* 29:38-42
- Zemsky VA, Berzin AA, Mikhalev YA, Tormosov DD (1995) Soviet Antarctic pelagic whaling after WWII: review of actual catch data. *Report of the International Whaling Commission* 45:131-135
- Zemsky VA, Mikhalev YA, Berzin AA (1996) Supplementary information about Soviet whaling in the Southern Hemisphere. *Report of the International Whaling Commission* 46:131-138

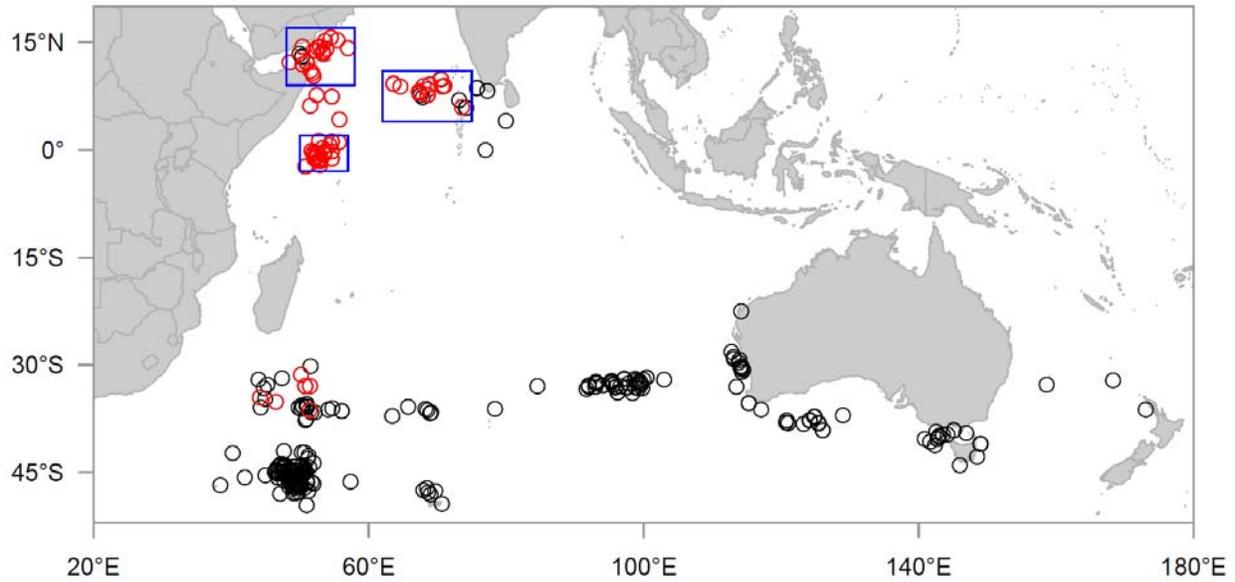


Fig. 1. Locations of fetal length data from the Soviet expeditions (black circles), highlighting those collected in three main areas (rectangles). Catches in November are in red.

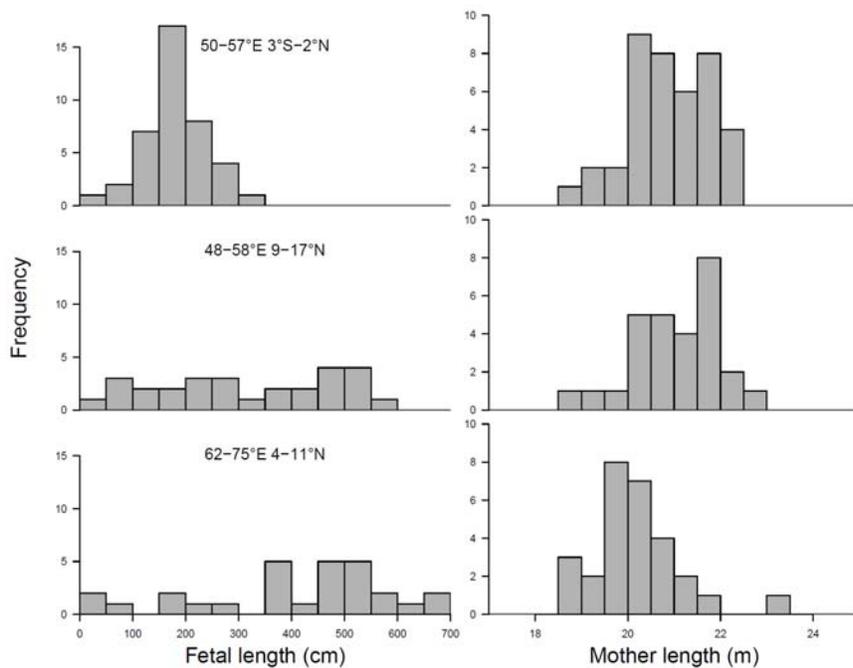


Fig. 2. Fetal lengths (left) and maternal lengths (right) for whales caught during November in Soviet expeditions in the three rectangles depicted in Fig. 1, showing a broad distribution of fetal lengths in the two northernmost clusters of catches, compared to the unimodal distribution in the more southern cluster.

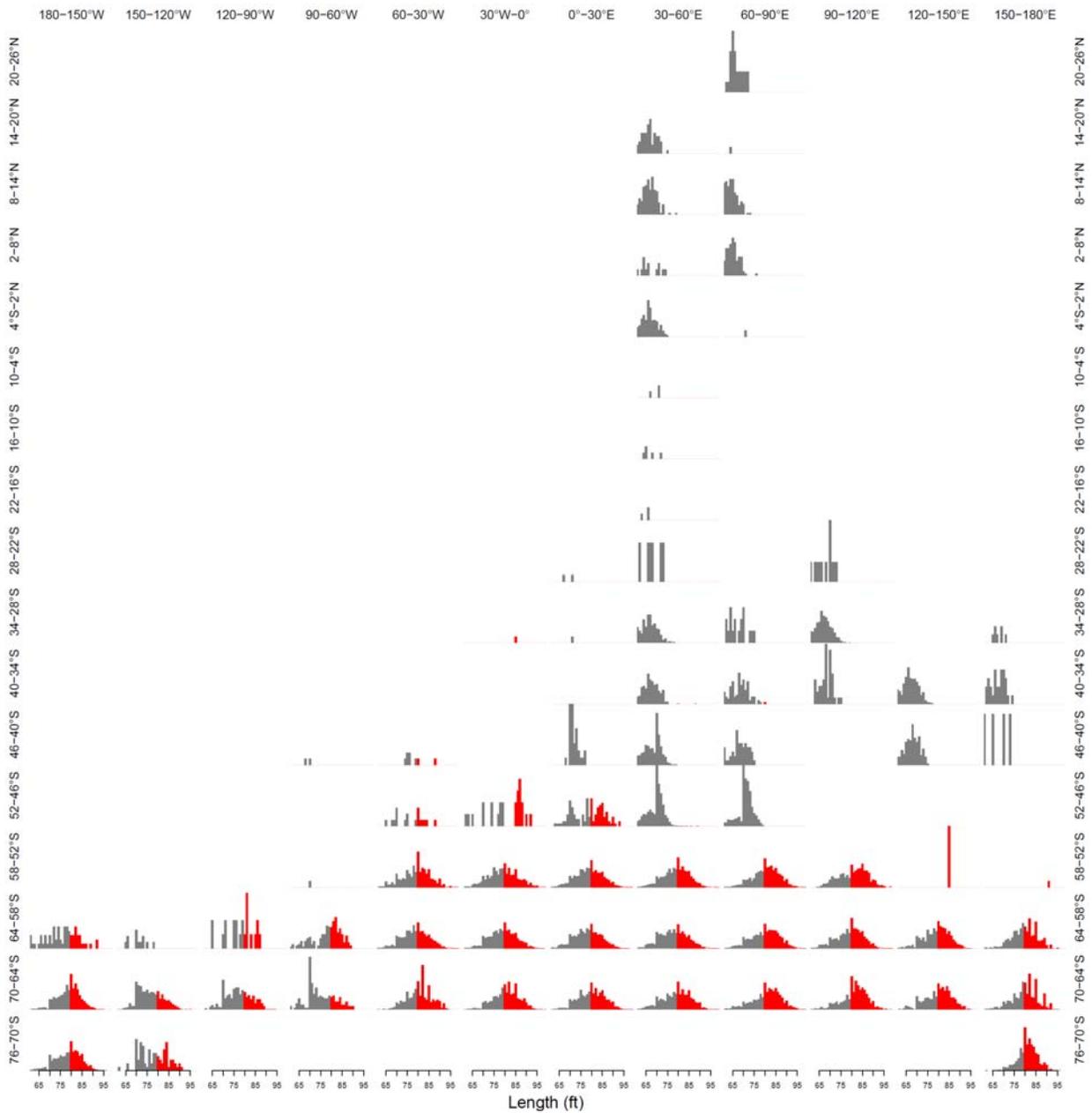


Fig. 3. Length frequencies of blue whale catches (**both sexes combined**) in the Southern Hemisphere and northern Indian Ocean, in bins of 30° longitude and 6° latitude. Red indicates lengths ≥ 80 ft, i.e. longer than the maximum pygmy blue whale length.

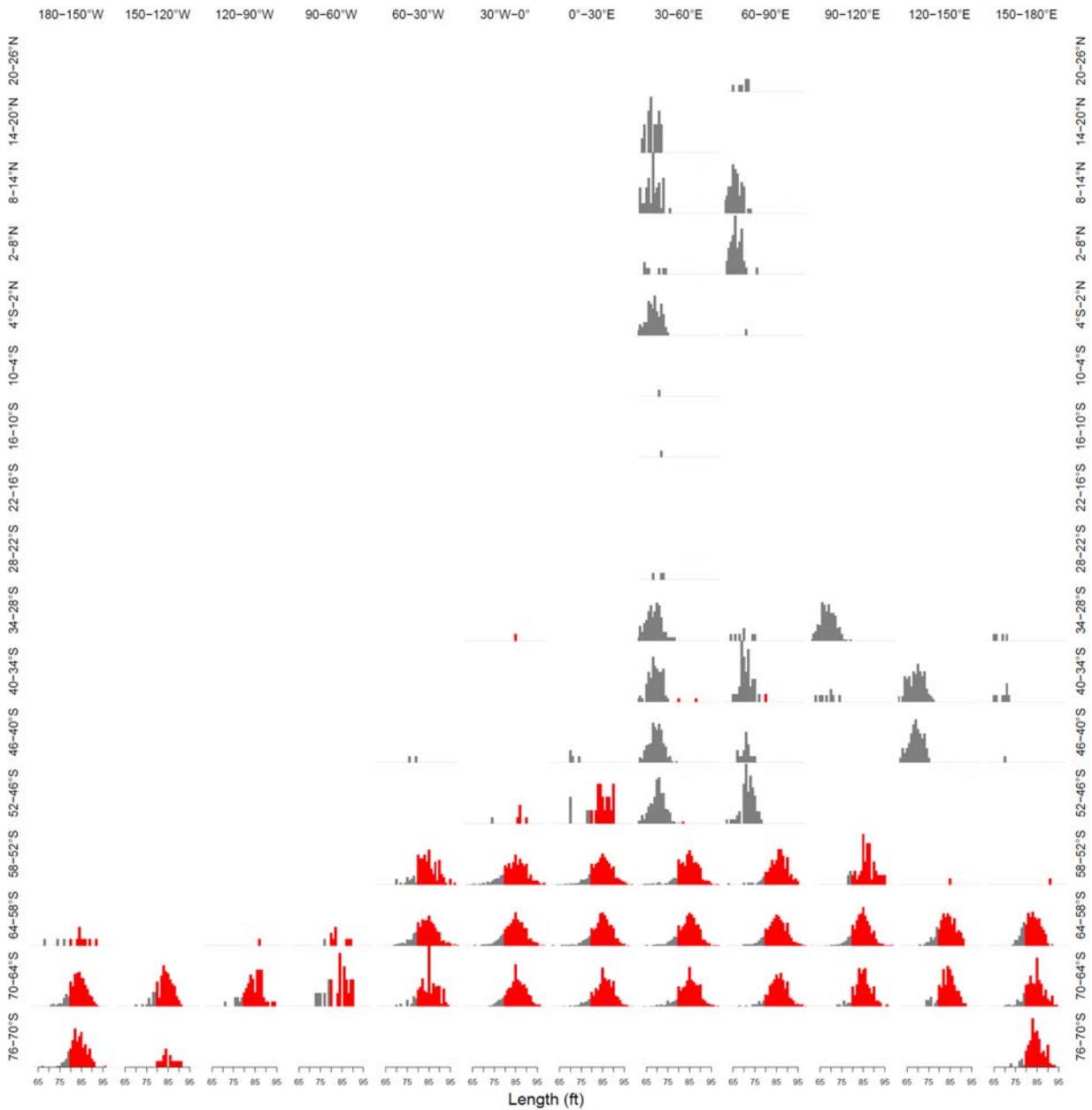


Fig. 4. Length frequencies of **sexually mature female blue whales** in the Southern Hemisphere and northern Indian Ocean, in bins of 30° longitude and 6° latitude. Red indicates lengths ≥ 80 ft, i.e. longer than the maximum pygmy blue whale length.

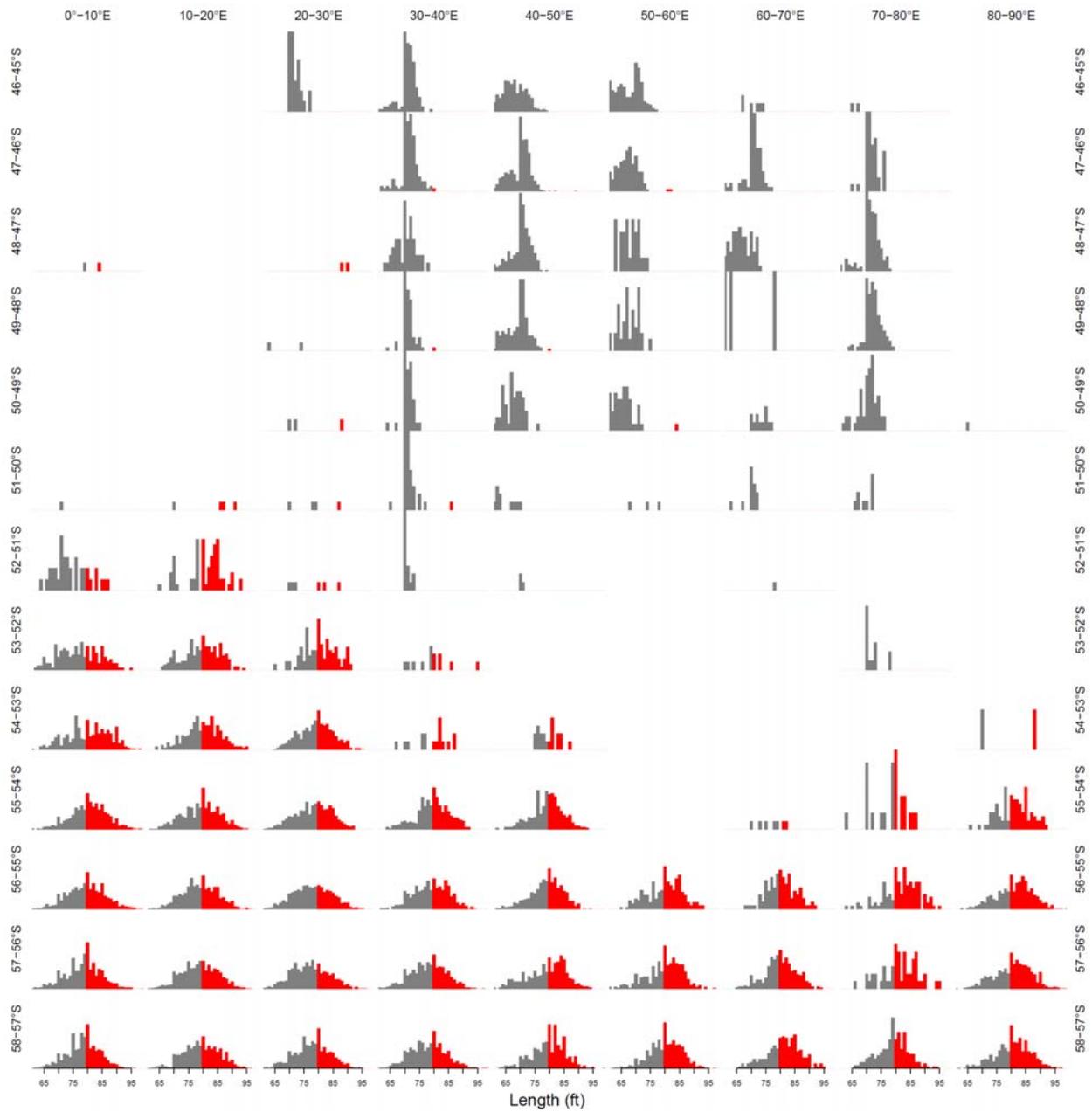


Fig. 5. Zoomed in length frequencies of blue whale catches (**both sexes combined**) in the region of overlap between Antarctic and pygmy blue whales (45-58°S 0-90°E), in bins of 10° longitude and 1° latitude. Red indicates lengths ≥ 80 ft, i.e. longer than the maximum pygmy blue whale length.

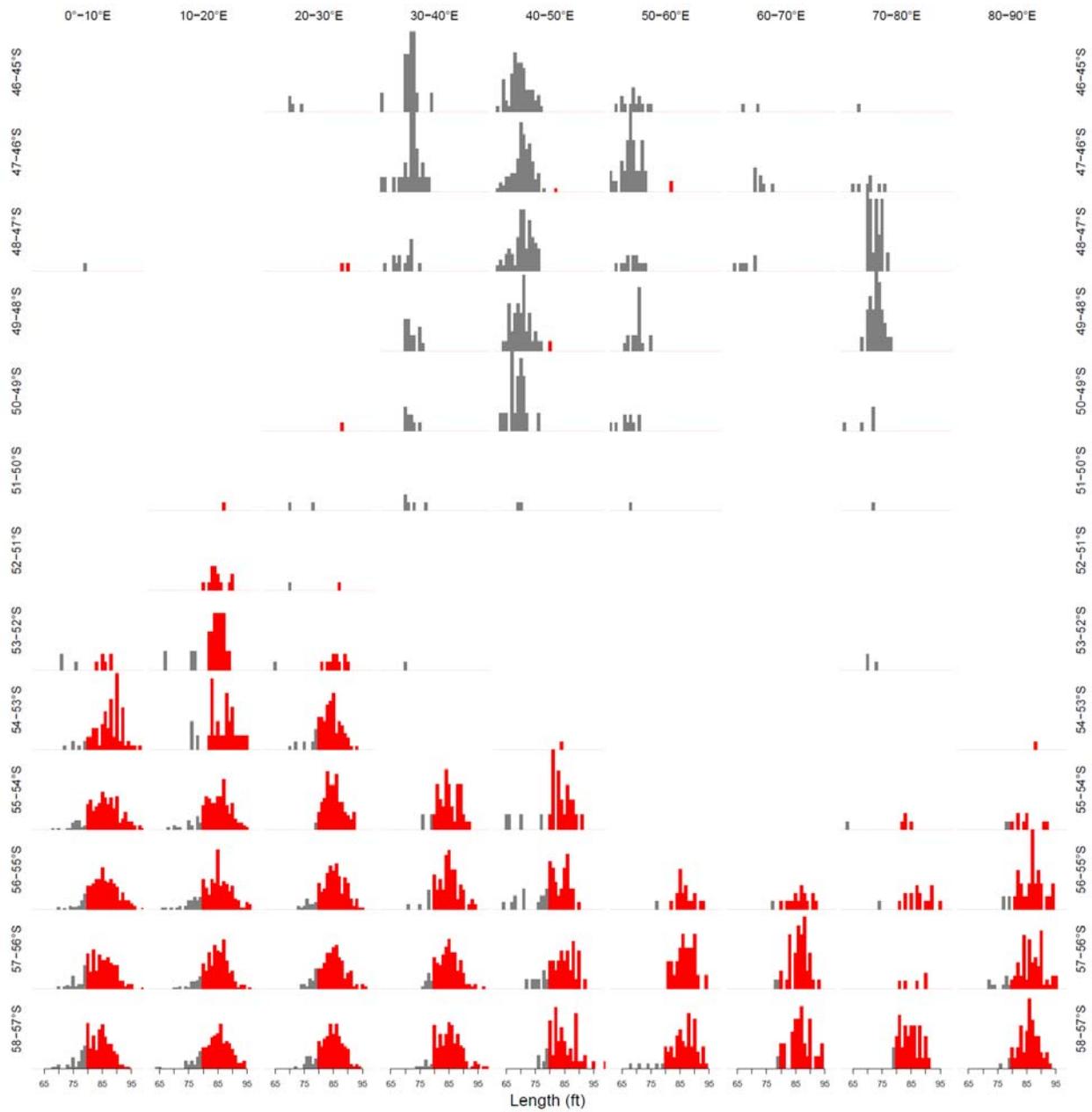


Fig. 6. Zoomed in length frequencies of **sexually mature female blue whale** catches in the region of overlap between Antarctic and pygmy blue whales (**45-58°S 0-90°E**), in bins of **10° longitude** and **1° latitude**. Red indicates lengths ≥ 80 ft, i.e. longer than the maximum pygmy blue whale length.

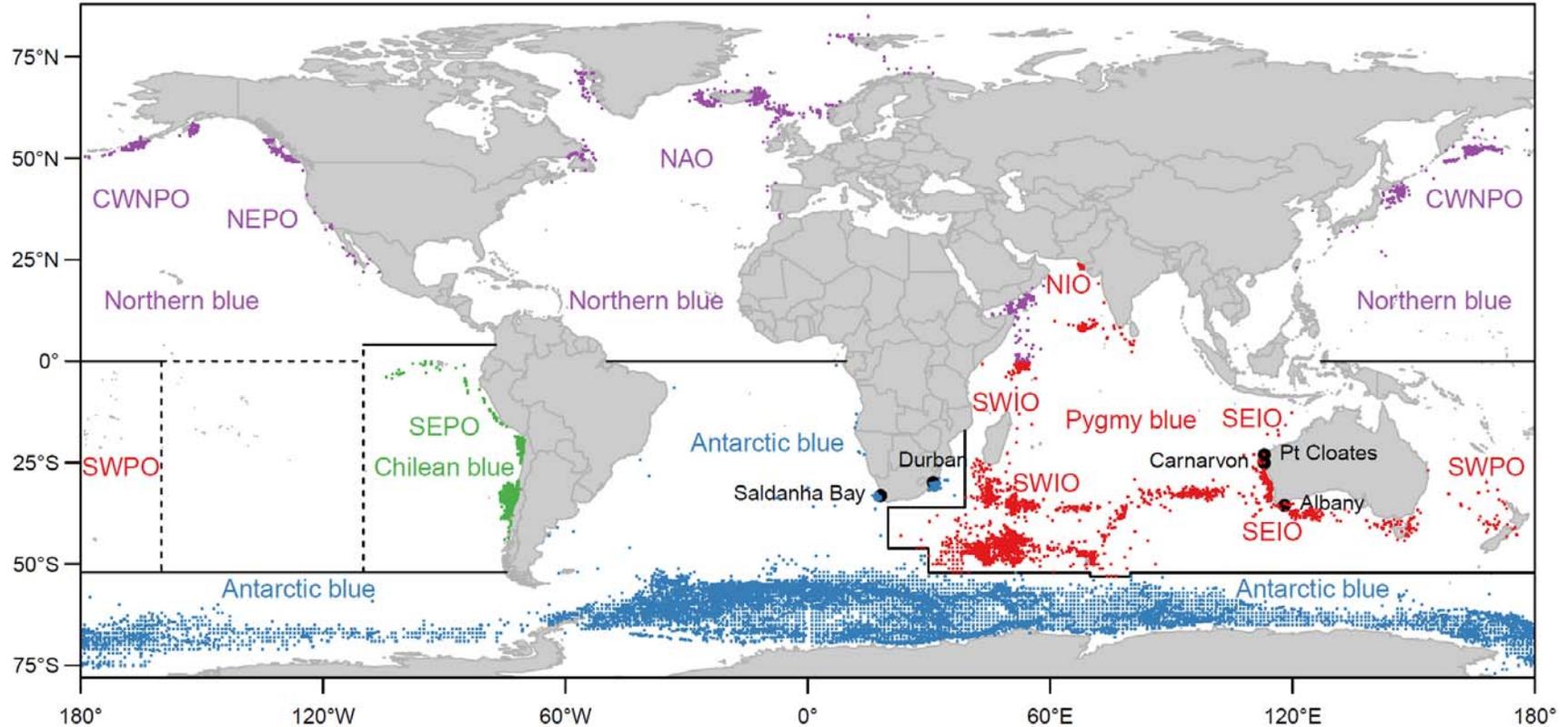


Fig. 7. Global blue whale catches of each of the four generally accepted subspecies (northern blue, Chilean blue, Antarctic blue, and pygmy blue), showing assumed boundaries in black used to enclose catches of each. Dashed boundaries enclose an area in the South Pacific with no known blue whale data. Individual populations are shown by acronyms for pygmy blue whales: northern Indian Ocean (NIO, Sri Lanka), south-west IO (SWIO, Madagascar), south-east IO (SEIO, Australia/Indonesia), south-west Pacific Ocean (SWPO, New Zealand); Chilean blue whales (SEPO); northern blue whales: north-east PO (NEPO, California/Mexico), central and western north PO (CWNPO, Japan to Gulf of Alaska), north Atlantic Ocean (NAO). Selected land stations are labelled.

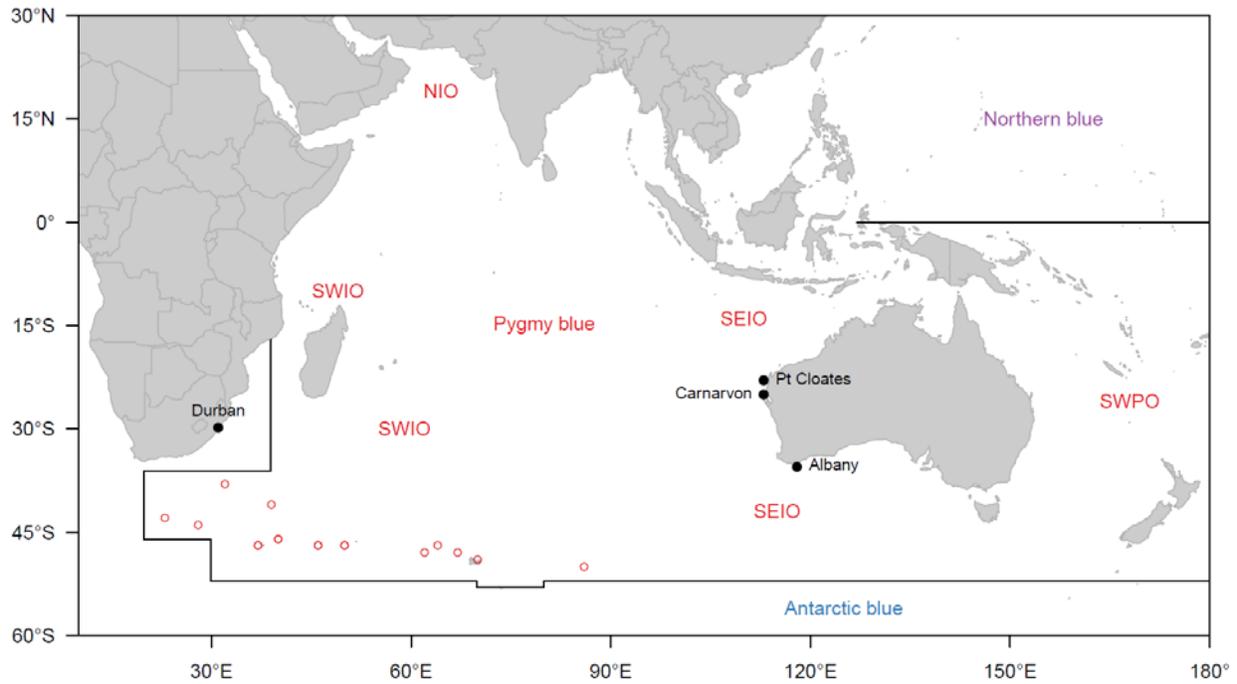


Fig. 8. Locations of assumed pygmy blue whale catches from pelagic expeditions excluding Japanese and Soviet expeditions.

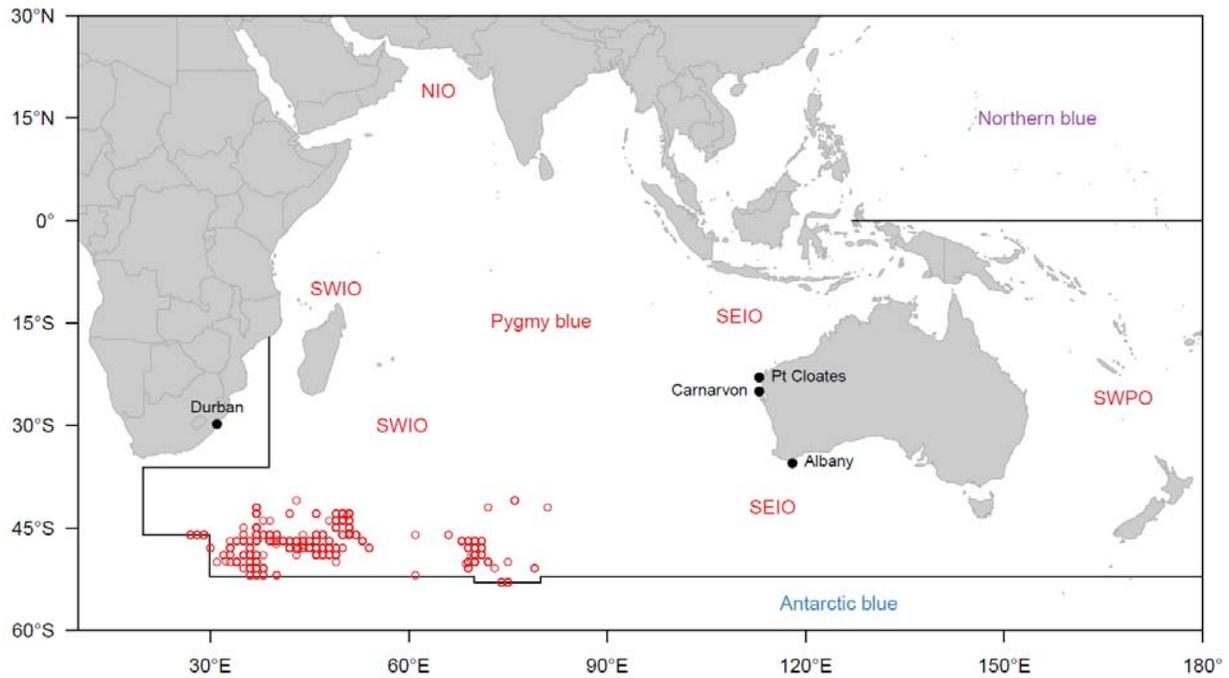


Fig. 9. Locations of pygmy blue whale catches by Japanese expeditions, almost all 1959/60 to 1963/64.

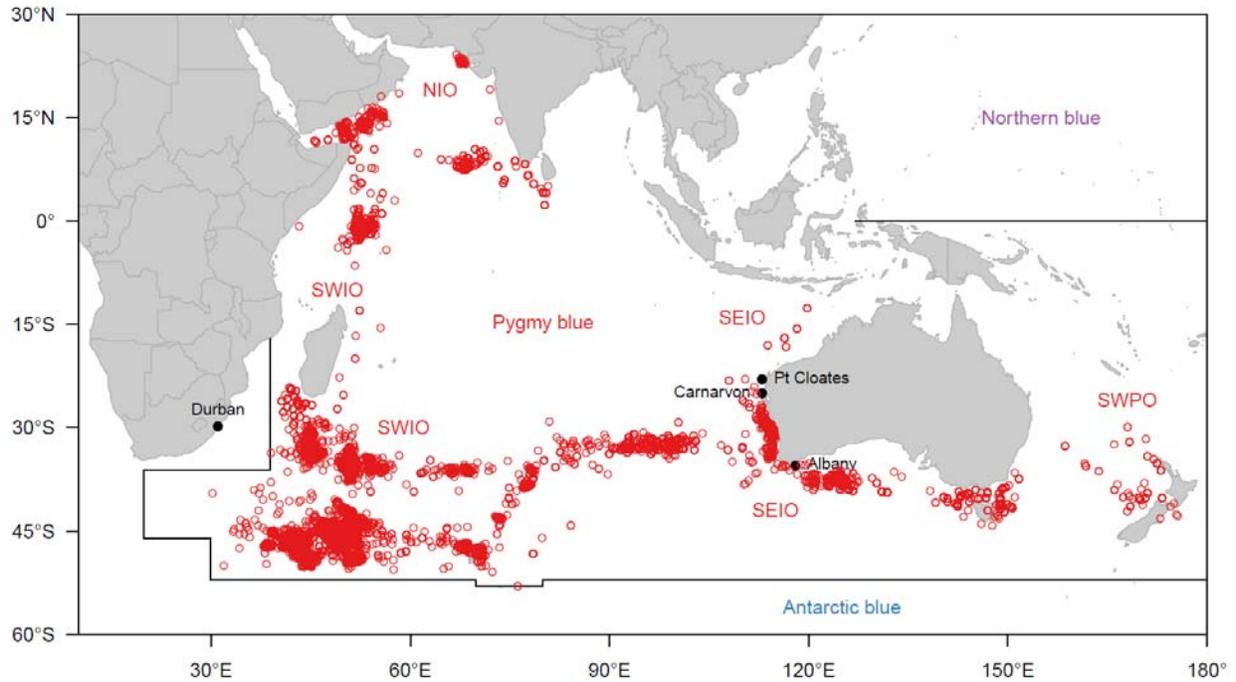


Fig. 10. Locations of pygmy blue whale catches by Soviet expeditions, almost all 1962/63 to 1971/72.

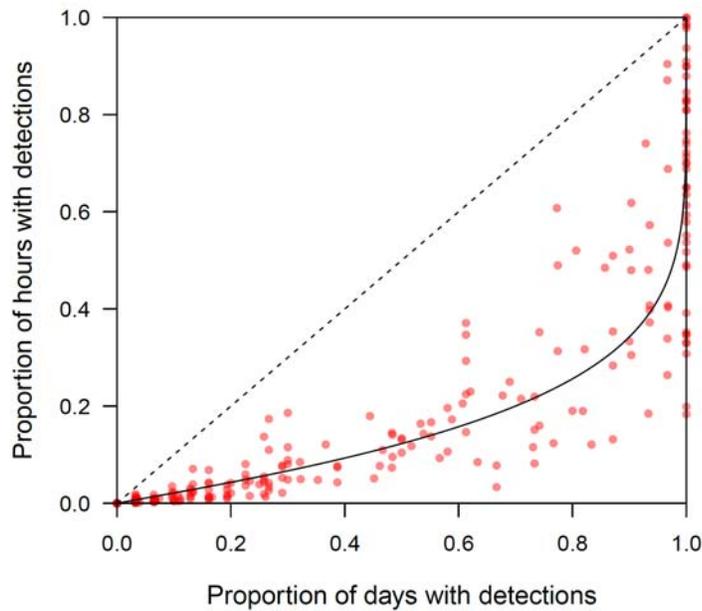


Fig. 11. Curve used to convert daily acoustic data to hourly acoustic data. Many of the acoustic data were provided in the form of number of days examined and number of days with detections of each song type; while other data were in the form of number of hours examined and number of hours with song detections. Each red point is one month of data where both proportion of hours with calls and proportion of days with calls is plotted. The fitted curve (solid black line) is the best fitted curve, which was the cumulative distribution function of a beta distribution with $\alpha = 0.9533$ and $\beta = 0.1771$, fitted by minimizing the negative log likelihood, assuming binomial likelihood.

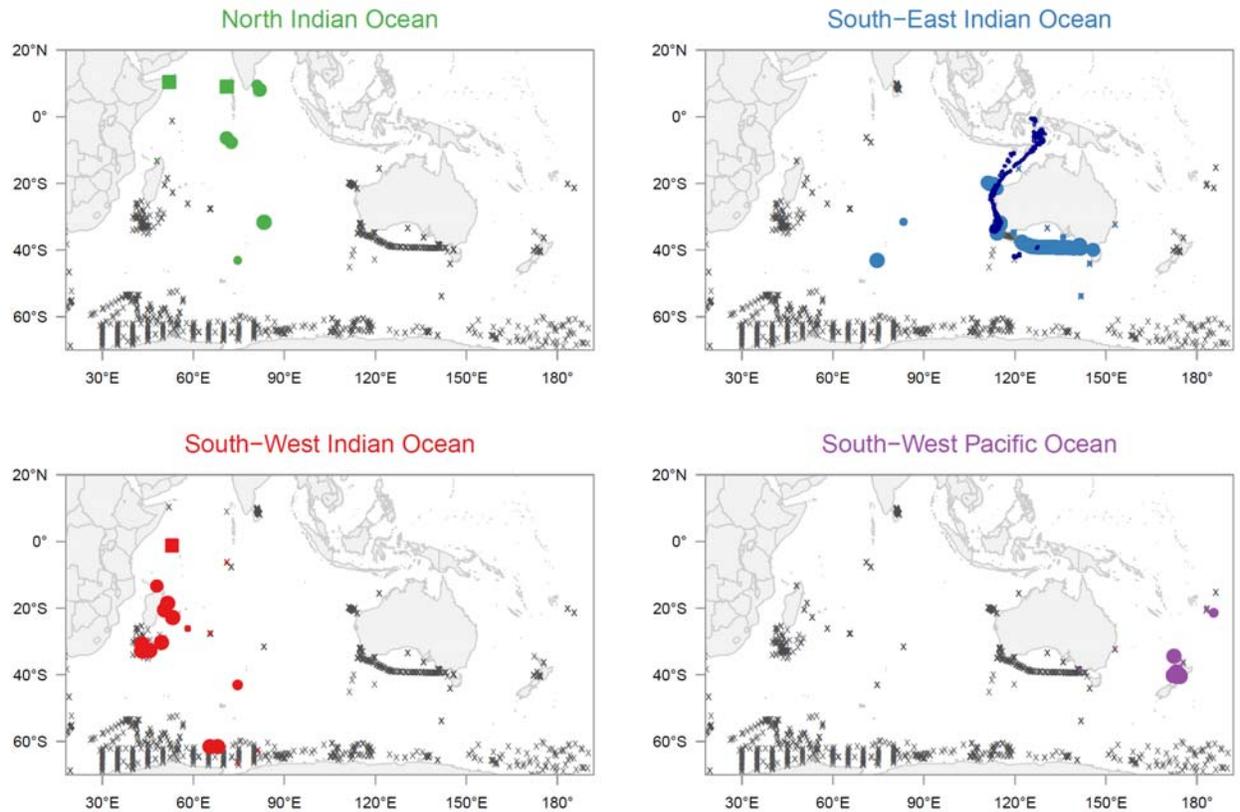


Fig. 12. Data used to separate pygmy blue whale populations. Nearly all of the data are acoustic positions (x = no detections; solid circles proportional to proportion of hours with each song type); except for the small dark-blue points in South-East Indian Ocean that are satellite tag locations from Double et al. (2014), and the squares which represent information derived from fetal length distributions. Since circles are solid, and one circle is plotted for each month with data, the circles depict the highest monthly proportions recorded at each location.

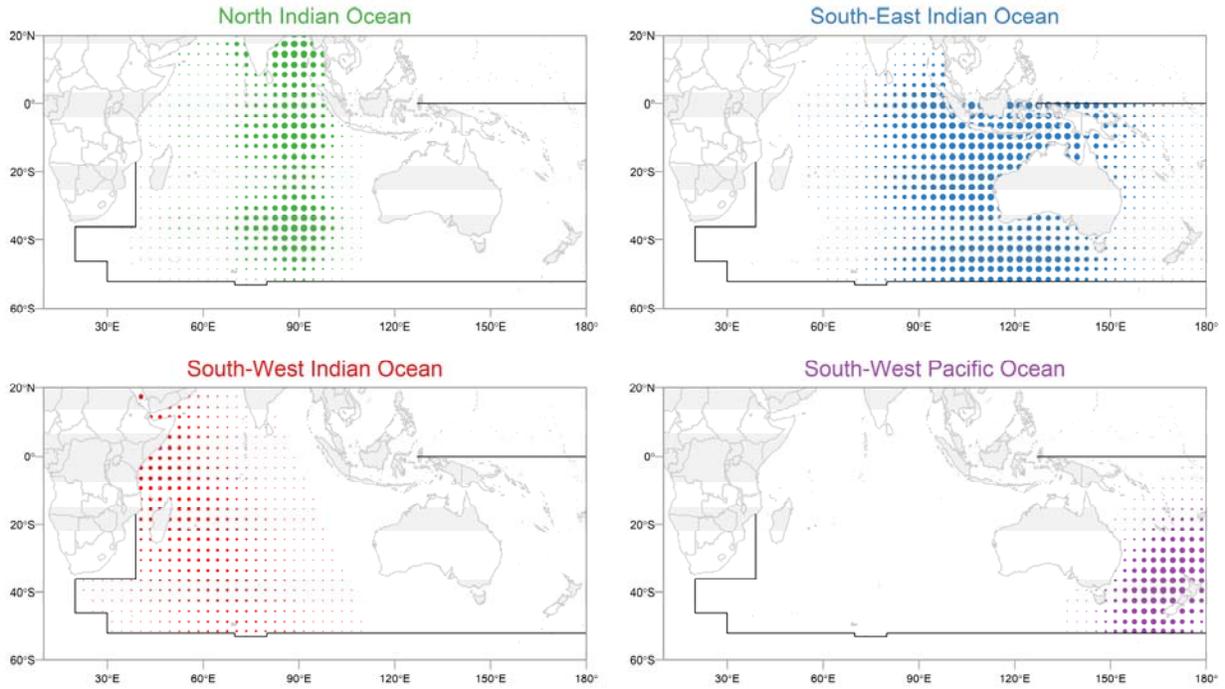


Fig. 13. Best-fitting spatial models for each population, showing the predicted probability of detecting a blue whale from that population at each position. These probabilities are obtained independently for each population, and thus could all be zero or one at a given location.

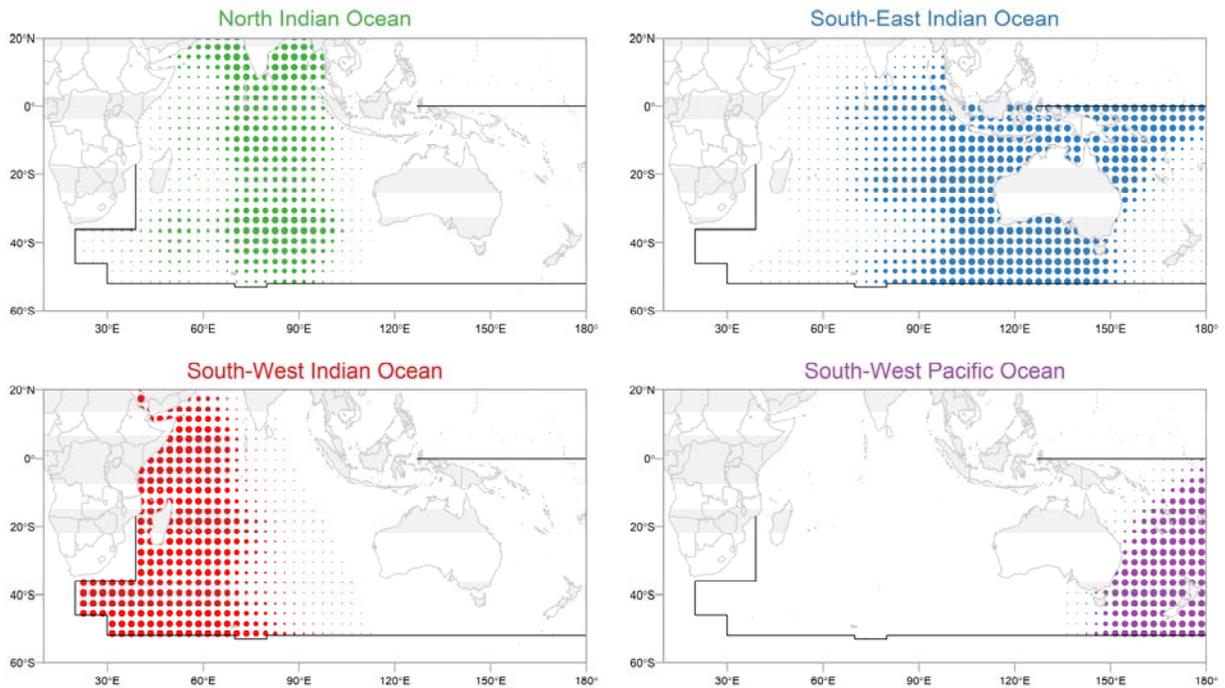


Fig. 14. Predicted probability at each location that a detected blue whale belongs to each of the four pygmy blue whale populations (sum of probabilities for each population at a location is one).

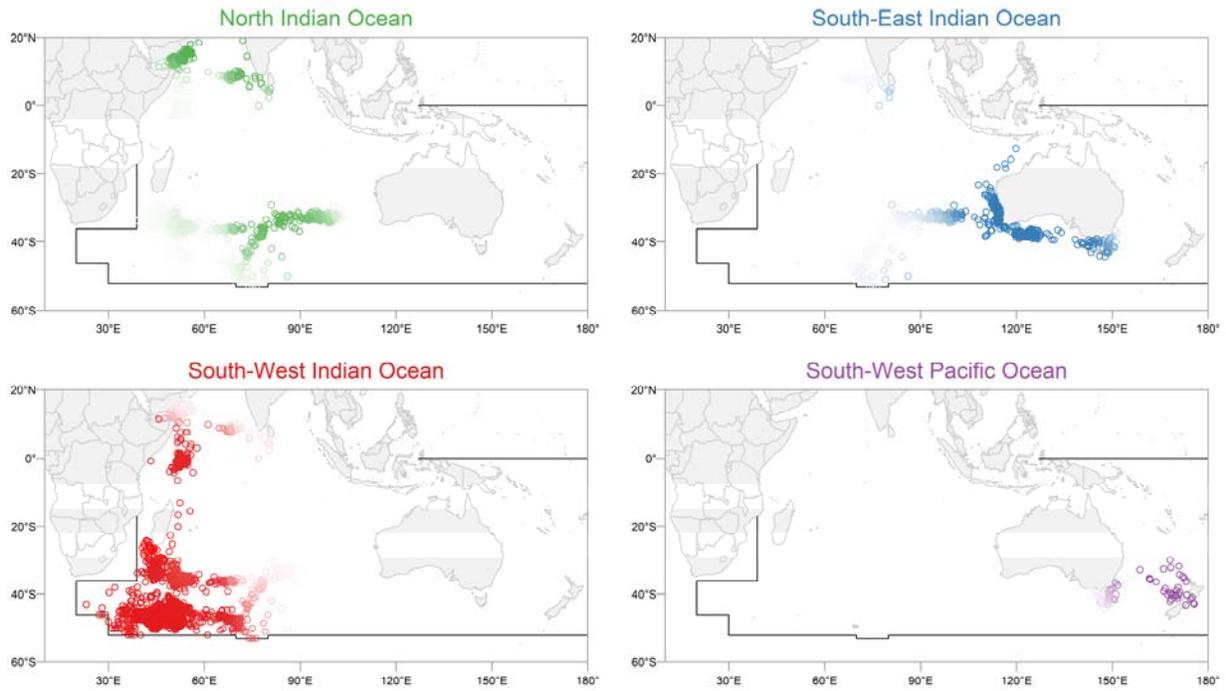


Fig. 15. For each pelagic catch, the probability the catch is assigned to each of the four pygmy blue whale populations. High color intensities represent high probabilities, while colors close to white have very low probabilities.

Table 1. Sources and summary of acoustic song type data used to separate the four populations.

Source	Time period	Latitudes	Longitudes	Type of data	Time examined
Alling et al. (1991)	1984-1984	8-11°N	80-82°E	Hours	563
Balcazar et al. (2015)	2009-2010	15-39°S	115°E-173°W	Days	1,316
Balcazar et al. (2017)	2009-2013	15-39°S	115°E-173°W	Days	2,889
Barlow et al. (2018)	2016	39-41°S	172-175°E	Days	1,607
Brodie and Dunn (2015)	2009-2010	20-22°S	174-177°W	Days	626
Cerchio et al. (2010)	2008	6-7°S	12-13°E	Days	550
Cerchio et al. (2018)	2016-2017	13-14°S	48-49°E	Hours	7,776
Dréo et al. (2018)	2012-2013	18-31°S	49-66°E	Days	2,384
Garcia-Rojas et al. (2018)	2013	34-40°S	114-144°E	Hours	100
Gavrilov and McCauley (2013)	2002-2010	34-35°S	114-115°E	Hours	78,888
Gavrilov et al. (2012)	2002-2011	34-35°S	114-115°E	Hours	87,792
Gavrilov et al. (2018)	2014	19-21°S	111-113°E	Hours	2,688
Gedamke and Robinson (2010)	2006	59-71°S	29-81°E	Hours	145
Gedamke et al. (2007)	2004-2007	44-67°S	74-145°E	Days	900
Kibblewhite et al. (1967)	1964	34-35°S	172-173°E	Hours	1
Ljungblad et al. (1997)	1995	31-43°S	114-144°E	Hours	55
Ljungblad et al. (1998)	1996	25-35°S	40-51°E	Hours	52
McCauley et al. (2018)	2004-2017	15-40°S	113-146°E	Hours	124,310
McDonald (2006)	1997	36-37°S	175-176°E	Days	179
Miksis-Olds et al. (2018)	2002-2012	6-7°S	71-72°E	Hours	95,592
Pangerc (2010)	2006-2007	53-54°S	37-38°W	Days	60
Samaran et al. (2013)	2017	26-43°S	58-84°E	Days	1,095
Shabangu et al. (2017)	1997-2009	38-79°S	180°W-180°E	Hours	476
Shabangu et al. (2019)	2014-2015	34-35°S	17-18°E	Hours	5,056
Širović et al. (2004)	2001-2004	62-68°S	62-75°W	Days	4,190
Širović et al. (2006)	2003	52-63°S	26-57°E	Hours	107
Širović et al. (2009)	2003-2004	60-72°S	52°W, 70°E, 173°E	Days	520
Stafford et al. (2011)	2002-2003	6-35°S	71-115°E	Hours	45,240
Thomisch (2017)	2011-2013	20-21°S	5-6°E	Days	460
Thomisch et al. (2016)	2008-2013	59-69°S	27°W-0°	Days	5,157
Tripovich et al. (2015)	2009-2010	38-39°S	141-142°E	Hours	10,320

Table 2. Difference in AIC between the best model and all the other models for spatial model fits. GLM is generalized linear models that use quadratic parametric relationships, with and without an interaction term between longitude and latitude; GAM is generalized additive models that use non-parametric smoothers. Each is fitted with either binomial or beta-binomial likelihood. NA denotes a model that failed to converge. The best model (lowest AIC) was selected for spatial predictions.

Population	Binomial GLM	Binomial GAM	Beta-binomial GLM	Beta-binomial GAM	Beta-binomial GLM interaction
NIO	77,589.6	50,452.1	90.8	0.0	77.5
SWIO	57,951.7	37,061.9	28.6	4.0	0.0
SEIO	141,941.9	122,164.0	331.3	0.0	293.1
SWPO	39,074.9	1,155,123.2	0.9	NA	0.0

Table 3. Land station catches of pygmy blue whales, and their assignment to each of the four pygmy blue whale populations (see text for details)

Category	Exped. code	Region	1912	1913	1914	1924	1926	1927	1928	1937	1954	1958	1959	1960	1962	1963	1965	Total
SP	5035	LochTay	33	93														126
SP	5039	Rakiura Pr Gge	1															1
SP	4700	Tangalooma									1							1
IO	4680	Albany											6	2				8
IO	5030	Vasco da Gama	1	1	1													3
IO	4610	Point Cloates					5	3	1									9
IO	4650	Carnarvon										2	6		4	1		13
IO	4480 & 4490	Durban				1				1						1	1	4
		NIO																0
		SWIO				1				1						1	1	4
		SEIO	1	1	1		5	3	1			2	12	2	4	1		33
		SWPO	34	93							1							128
Grand total																		165

Table 4. Catches made around Kerguelen, and scattered pelagic catches through the years, and their assignment to the four pygmy blue whale populations (see text for details). These catches are listed under SH pelagic catches.

Fleet	Exp. code	Region	1908/09	1909/10	1929/30	1934/35	1935/36	1937/38	1961/62	Total
A/S Kerguelen	280	Kerguelen	8	1						9
Mangoro	5303	Kerguelen		3						3
Radioliene	5760	Kerguelen			113					113
Willem Barendsz	6282	SH pelagic							2	2
SirJamesClark Ross	5941	SH pelagic				1				1
Solglimt	5681	Antarctic				2				2
Skytteren	5710	Antarctic				10	1			11
UniWaleCo	6010	Antarctic						1		1
		NIO	1	1	8		1			11
		SWIO	7	3	99	13		1	2	125
		SEIO			6					6
		SWPO								
Total			8	4	113	13	1	1	2	142

Table 5. Catches made by Japanese expeditions, and their assignment to each of the pygmy blue whale populations. The three catches in 1966/67 and the two catches in 1969/70 were taken under Special Permit.

Fleet	Exp. code	Region	1959/60	1960/61	1961/62	1962/63	1963/64	1966/67	1969/70	Total
Tonan Maru	5981 & 5982	Antarctic & SH pelagic	9		25	45	2			81
Nisshin Maru	6062	Antarctic			5	102			2	109
Tonan Maru II	6131 & 6132	Antarctic & SH pelagic	10	311	9	49	1			380
Nisshin Maru II	6141	Antarctic	272	114	55	83				524
Kinjyo Maru	6410	Antarctic		273						273
Kyokuyo Maru II	6430 & 6431	Antarctic & SH pelagic	20	203	182	147				552
Kyokuyo Maru III	6450	SH pelagic		226	36	202	28	3		495
Nisshin Maru III	6480	Antarctic			78	86				164
		NIO	29	42	24	9		1		105
		SWIO	264	1066	358	705	31	2	2	2428
		SEIO	18	19	8					45
		SWPO								0
		Total	311	1127	390	714	31	3	2	2578

Table 6. Pygmy blue whale catches by Soviet fleets in the Antarctic, SH pelagic, and SH pelagic+ regions. The underlined numbers indicate years where individual catches are used in place of annual totals because the sum of the individual catches was higher. The bold numbers are years that are missing individual catch data, and hence only annual totals are available. In those years the catches were assigned to population using the average proportions in the year before and year after the missing data.

Fleet	Exp. code	1961/2	1962/3	1963/4	1964/5	1965/6	1966/7	1967/8	1968/9	1969/70	1970/1	1971/2	1972/3	Total
Slava	6301/2		189	243	<u>784</u>	<u>447</u>								1663
S. Ukraina	6440/1		<u>7</u>	14	1843	312	46	310	22	550	570	71	2	3747
Yuri Dolgoruky	6460/1	2	488	<u>578</u>	488			<u>7</u>	464	265				2292
S. Rossia	6490			510	7	88	157	<u>26</u>	94	68	192	453	2	1597
	NIO		32	195	992	198	57	19	23	43	113	8		1680
	SWIO	2	648	1076	643	347	2	309	479	685	515	409	2	5117
	SEIO		4	63	1420	283	105	11	70	150	30	90		2226
	SWPO			11	67	19	39	4	8	5	104	17	2	276
	Total	2	684	1345	3122	847	203	343	580	883	762	524	4	9299

Table 7. Total catches of pygmy blue whales separated by population and year.

Pelagic season	NIO	SWIO	SEIO	SWPO	Total	Pelagic season	NIO	SWIO	SEIO	SWPO	Total
1908/09	1	7			8	1941/42					0
1909/10	1	3			4	1942/43					0
1910/11					0	1943/44					0
1911/12					0	1944/45					0
1912/13			1	34	35	1945/46					0
1913/14			1	93	94	1946/47					0
1914/15			1		1	1947/48					0
1915/16					0	1948/49					0
1916/17					0	1949/50					0
1917/18					0	1950/51					0
1918/19					0	1951/52					0
1919/20					0	1952/53					0
1920/21					0	1953/54					0
1921/22					0	1954/55				1	1
1922/23					0	1955/56					0
1923/24					0	1956/58					0
1924/25		1			1	1957/59					0
1925/26					0	1958/59			2		2
1926/27			5		5	1959/60	29	264	30		323
1927/28			3		3	1960/61	42	1066	21		1,129
1928/29			1		1	1961/62	24	362	8		394
1929/30	8	99	6		113	1962/63	41	1353	8		1,402
1930/31					0	1963/64	195	1108	64	11	1,378
1931/32					0	1964/65	992	643	1420	67	3,122
1932/33					0	1965/66	198	348	283	19	848
1933/34					0	1966/67	58	4	105	39	206
1934/35		13			13	1967/68	19	309	11	4	343
1935/36	1				1	1968/69	23	479	70	8	580
1936/37					0	1969/70	43	687	150	5	885
1937/38		2			2	1970/71	113	515	30	104	762
1938/39					0	1971/72	8	409	90	17	524
1939/40					0	1972/73		2		2	4
1940/41					0	Total	1796	7674	2310	404	12,184