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Little evidence for interchange between north-east Pacific and southeast Pacific blue whale populations despite morphological similarities

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ABSTRACT

Population structure and relationships are examined here between blue whales in the north-east Pacific Ocean (NEPO) and south-east Pacific Ocean (SEPO). The two populations have similar total lengths, lengths of sexually mature females, and tail length as a proportion of total length, and these features distinguish them from the western and central North Pacific, Antarctic, and pygmy blue whale populations. However, available data from catches, sightings, surveys, satellite tags, acoustics, and genetics all provide strong and coherent evidence for a division between the two populations at 2°N to 6°N, albeit with rare vagrants that may briefly move from one region into the other.

INTRODUCTION

Blue whales globally are divided into at least ten populations, largely on the basis of unique songs that are identifiable over periods of decades (McDonald et al. 2006, Širović et al. 2017, Širović et al. 2018, Branch et al. 2021), albeit with a declining frequency over time (McDonald et al. 2009, Gavrilov et al. 2012, Leroy et al. 2018, Malige et al. 2020). There is much more debate over the validity of the subspecies of blue whales that are currently recognized by the Committee on Taxonomy for the Society for Marine Mammalogy, which currently comprise northern blue whales, Antarctic blue whales, pygmy blue whales, and northern Indian Ocean blue whales (Committee on Taxonomy 2020), but do not classify south-east Pacific blue whales into any subspecies. In the Pacific Ocean there are generally recognized to be four populations: the central and western North Pacific Ocean (CWNPO), north-east Pacific Ocean (NEPO, California and Mexico), south-west Pacific Ocean (SWPO, New Zealand), and south-east Pacific Ocean (SEPO, southern Chile to Galapagos). While the CWNPO and NEPO populations have some spatial overlap in acoustic song and catches (Monnahan et al. 2014), the SWPO and SEPO populations have been considered to be quite geographically separate from other blue whale populations, except for seasonal overlap with Antarctic blue whales in the austral winter months (Barlow et al. 2018, Buchan et al. 2018, Branch et al. 2021).

In 2020, the Scientific Committee (SC) of the International Whaling Commission noted that a recent study (LeDuc et al. 2017) suggested some genetic interchange between NEPO and SEPO blue whales in the low-latitude wintering grounds in the Eastern Tropical Pacific. The SC requested comparisons of catch length data and analysis of mitochondrial DNA between these two populations. Here I address the request for a comparison of the catch length data between NEPO and SEPO populations. In addition, I present a brief review of other relevant sources of information informing possible interchange between the NEPO and SEPO populations.

METHODS

Catch data

Historical catches with individual location data were extracted from the IWC database v. 7.1 (Allison 2020) and plotted for the regions around the SEPO population (Fig. 1). In addition, the annual catch summaries in the IWC database were examined to identify blue whale catches in pelagic expeditions and land stations in the possible area of overlap (eastern Pacific Ocean between 20°N and 10°S), that do not have individual location data.

Surveys and sightings

The Southwest Fisheries Science Center conducted a series of surveys for marine mammals in the Eastern Tropical Pacific ending in 2005 (Reilly and Thayer 1990, Hamilton et al. 2009), with good coverage between approximately 35°N and 15°S. These data were examined for evidence of separation between NEPO and SEPO populations.

Acoustic information

Blue whale populations are distinguishable by the repeated songs produced by each population, thought to be made exclusively by males and to have a role in reproduction. NEPO and SEPO blue whales have distinct song types that are recorded in different regions. Data from published studies on the songs of the two populations were reviewed.

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Satellite tag data

Satellite tags have been deployed on more than 100 NEPO blue whales tagged in Californian waters (Mate et al. 1999, Bailey et al. 2009, Abrahms et al. 2019, Palacios et al. 2019). For the SEPO population, 10 blue whales were tagged off southern Chile of which 5 underwent long-distant migrations (Hucke-Gaete et al. 2018).

Mark-recapture information

Photo-id catalogues are available for NEPO and SEPO blue whales, with many resightings both within and among years (e.g., Calambokidis et al. 2009, Torres-Florez et al. 2015, Galletti Vernazzani et al. 2017), including one with an additional genetic mark-recapture record (Torres-Florez et al. 2015). Discovery-type marks were only deployed and retrieved in the northern parts of the North Pacific (S. Mizroch in Branch et al. 2019) and do not provide any insights into links between NEPO and SEPO blue whales.

Genetic analysis of population structure

Two studies have been conducted on the relationship between SEPO blue whales and other blue whale populations, but only the later study compared the genetics of NEPO and SEPO blue whales (LeDuc et al. 2007, LeDuc et al. 2017). Further analysis is ongoing. One additional study examined relations among Antarctic, southern Chile, northern Chile, and Eastern Tropical Pacific samples (Torres-Florez et al. 2014).

Morphometric data

To compare length frequencies between the NEPO and SEPO populations, data on length, sex, location, and maturity status were extracted from the IWC individual catch database (Allison 2020). The SEPO population is considered to be geographically discrete, and catches from 2°N–50°S and 69–120°W were assigned to this population. For NEPO blue whale, there is spatial overlap with the central and western North Pacific (CWNPO) population, and catches of the two populations were previously separated using spatial models fitted to song distribution (Monnahan et al. 2014). More precise locations of some catches in the western regions are now available in the IWC database, and the most likely dividing line between the two populations is always west of 133°W albeit with some monthly variability (Monnahan et al. 2014). Therefore, all catches within 15–60°N and 104–133°W were considered to belong to the NEPO population, while recognizing that additional catches west of this region would also likely be NEPO blue whales.

More detailed morphometric data were reviewed from additional sources: fluke-to-anus and snout-to-eye measurements from 60 SEPO blue whales caught off Chile in the 1960s (Pastene et al. 2020); measurements of the rostral length (snout-to-blowhole for 51 NEPO and 5 SEPO blue whales), and tail length (edge of dorsal fin to fluke notch for 63 NEPO and 3 SEPO blue whales) (Gilpatrick and Perryman 2008); two studies using hexacopters on SEPO blue whales off southern Chile measuring 22 whales (Durban et al. 2016), and 15 whales (Leslie et al. 2020) respectively; and aerial photogrammetry on 82 whales from a Cessna 182 aircraft on NEPO blue whales in the Gulf of California (Ortega-Ortiz et al. 2018).

RESULTS

Catch data

There were no catches with individual locations between the equator and 22°N (Fig. 1), or with annual summaries between 2°N and 22°N. Annual catch summaries included catches listed as occurring in Chile/Peru/Ecuador, and in Mexico, but from none of the interspersed countries in Central or South America. Catches in Mexico, which recorded 1072 blue whale catches, were all by Norwegian expeditions 1913-1935 except for one US expedition in 1929. Catches in Chile/Peru/Ecuador (554 blue whales) were by four Norwegian expeditions in 1912-1915. One of these expeditions is listed as "Capella 1, Gorgona, Columbia" (two blue whales, 1914), which likely refers to an island off Colombia at 2°N 78°E. Another expedition is the only season of the infamous *Olympic Challenger* owned by Aristoteles Onassis (Anon 1956b, a, Barthelmess et al. 1997) that recorded blue whale catches: 287 caught during 29 August to 14 November 1954. The *Olympic Challenger* blue whale catches were taken south of the equator and west of the Galapagos Islands: 0-8°S and 93-98°W, and contravened international regulations by taking whales below legal minimum sizes, and during closed seasons (Tønnessen and Johnsen 1982, Barthelmess et al. 1997). However, no length data are available in the IWC database for these catches.

Surveys and sightings

The Southwest Fisheries Science Center surveys found clusters of blue whales off Mexico, the Costa Rica Dome (~10°N 92°W), and spread out south of the Equator with a concentration west of the Galapagos Islands (Reilly and Thayer 1990), with no sightings between 2°N and 6°N despite extensive search effort (Fig. 2). Spatial smoothing models identify three regions of higher blue whale sightings in these surveys: off Mexico, the Costa Rica Dome, and west of the Galapagos (Yuan et al. 2017). Additional sightings of SEPO blue whales have also been recorded around the Galapagos

Islands, coastal Ecuador, Peru and other locations south of the equator (Donovan 1984, Palacios 1999, Branch et al. 2007b, Félix et al. 2007).

Acoustic information

The songs of NEPO blue whales are primarily heard off Mexico, California, Oregon, Washington, and northwards to the Gulf of Alaska (Stafford et al. 1999a, 2001, Stafford 2003, Oleson et al. 2007a, Oleson et al. 2007b, Stafford et al. 2007, Stafford et al. 2009, Monnahan et al. 2014, Širović et al. 2015, Širović et al. 2017). Songs of SEPO blue whales, which come in two forms, SEP1 and SEP2 (Buchan et al. 2014), have been recorded in southern and northern Chile, and both forms link Chile to the southern portion of the eastern tropical Pacific (Buchan et al. 2010, Buchan et al. 2014, Buchan et al. 2015, Malige et al. 2020, Patris et al. 2020).

In the region between NEPO and SEPO blue whales, the most useful source of information comes from an array of six hydrophones in a grid at 8°N, 0°, and 8°S latitude and 95°W and 110°W longitude (Stafford et al. 1999b). NEPO song was detected in the north-easternmost hydrophone (8°N 95°W) on 50% of hours examined, at 0°N 95°W on 5% of hours, and at the other hydrophones in less than 1% of hours (Stafford et al. 1999b). SEP1 and SEP2 song was detected most frequently at 8°S 95°W (20% of hours) and 0°S 95°W (11% of hours), and at other hydrophones in less than 1% of hours examined (Stafford et al. 1999b, Buchan et al. 2015). In addition, there were also five individual detections of the Central and Western North Pacific (CWNPO) population on various hydrophones (Stafford et al. 1999b). There was a clear seasonal separation between NEPO and SEPO song types, with NEPO song being recorded in the northern winter months, and SEPO song being recorded primarily in the southern winter months on these hydrophones. In addition, information from the migratory endpoints and seasonality of NEPO and SEPO blue whales illustrates that there is a six-month offset in overall occurrence and occupancy in the ETP by these two populations (Stafford et al. 1999a, Buchan et al. 2015). Overall, therefore, these data support a spatial separation between NEPO and SEPO song between 0° and 8°N, with a clear seasonal separation.

However, it should be noted that two vagrant song detections have been reported for SEPO blue whales: off South Georgia on one occasion (Pangerc 2010), and off southern California on one occasion (A. Širović, pers. comm. 16 April 2021), both presumably from a single stray individual. Similar vagrants have been reported for other blue whale populations, for example central Indian Ocean ("Sri Lanka") blue whales have been detected off Angola (Cerchio et al. 2010), Antarctic blue whales north of the equator in the Atlantic Ocean (Samaran et al. 2017), and south-east Indian Ocean song off New Zealand (D. Barlow pers. comm. in Branch et al. 2021) and Chile (Buchan et al. 2020).

Satellite tag data

Most NEPO blue whales move annually between California to Mexico or to an aggregation area west of the Costa Rica Dome at 6–12°N 90–105°W (Bailey et al. 2009). In these areas, they display extensive area-restricted search behavior, indicating feeding locations. Occasionally, NEPO blue whales undergo meandering migrations far offshore and into the waters of Washington, British Columbia, and the Gulf of Alaska, and in the course of these excursions, one individual ventured to a southernmost position of about 4°N 115°W (Bailey et al. 2009).

Fewer long-distance satellite tracks (n = 5) are available for SEPO blue whales tagged in southern Chile (Hucke-Gaete et al. 2018), but all consistently show movement northwards, with three heading to waters just south of the Galapagos Islands (2–5°S 83–93°W) and one to the Bauer Basin with a northernmost location of 5°S 104°W (Hucke-Gaete et al. 2018).

Mark-recapture information

An extensive photographic catalogue of more than 2000 individual NEPO blue whales, largely off California (Calambokidis et al. 1990, Calambokidis and Barlow 2004, Calambokidis et al. 2009, Douglas et al. 2015), and 650 individuals in the Gulf of California (Gendron and Ugalde de la Cruz 2012), reveals similar patterns of movement to those seen in the satellite tag data: multiple photographic recaptures linking blue whales sighted in the Gulf of Alaska and off British Columbia to those seen off California; and links between California, the Gulf of California, and the Costa Rica Rome. One blue whale was photographed in both the Costa Rica Dome and the Galapagos Islands, which is the only known trans-equatorial movement between NEPO and SEPO (Douglas et al. 2015).

For SEPO blue whales, one match was made between the Galapagos (1°S 92°W) and southern Chile (44°S 74°W), confirmed both photographically and genetically (Torres-Florez et al. 2015).

Genetic analysis of population structure

Samples taken from southern Chile, the southern Indian Ocean (pygmy blue whales), and the Antarctic, were all highly significantly different from each other, providing as much support for SEPO blue whales being a subspecies, as for pygmy blue whales (LeDuc et al. 2007).

A microsatellite and mtDNA genetic study conducted on NEPO and SEPO blue whales concluded that NEPO blue whales are linked to the Costa Rica Dome region, while SEPO blue whales favor waters off Peru and Ecuador (LeDuc et al. 2017). The authors also propose that the range of SEPO blue whales extends to the Costa Rica Dome and the eastern North Pacific. Sample locations were given as eastern North Pacific ($n = 51$), eastern South Pacific ($n = 66$), and eastern Tropical Pacific (ETP, $n = 46$). The ETP samples were further divided into northern (nETP, $n = 21$) and southern (sETP, $n = 25$) groupings, that were separated by a gap in samples at 0–7°N (LeDuc et al. 2017). Blue whales in the nETP were genetically similar to NEPO blue whales ($p = 0.25$), and those in the sETP were genetically similar to SEPO blue whales ($p = 0.82$), but the sETP and nETP groupings were genetically different ($p = 0.015$), as were the NEPO and SEPO samples ($p < 0.0001$). Therefore, these data provide strong evidence for a separation between NEPO and SEPO populations at 0–7°N. However, individual whales sampled in the nETP and sETP could not be uniquely assigned to their respective populations since samples in the NEPO, ETP, and SEPO share some haplotypes. As a result, individuals samples in the nETP had an average assignment probability of 0.707 to the NEPO population, while those in the sETP had an average assignment probability of 0.677 to the SEPO population (LeDuc et al. 2017).

Additional results found no genetic differentiation between southern Chile, northern Chile, and the sETP, although all were significantly different from Antarctic samples (Torres-Florez et al. 2014). The sETP samples in this study ($n = 25$) were all taken east, west, or south of the Galapagos, with none taken north of the equator (Torres-Florez et al. 2014).

Morphometric data

Gilpatrick and Perryman (2008) were the first to suggest that NEPO and SEPO blue whales are similar in external morphology, based on a mixture of whaling data and aerial photogrammetry from northern Peru, the Galapagos Islands, California, and the Gulf of California. After excluding blue whales shorter than 19.5 m, they concluded that Antarctic blue whales were the longest, followed by WCNPO blue whales, but that NEPO, SEPO, and pygmy blue whales had similar total lengths. Longer lengths for WCNPO than for NEPO blue whales were also found after catches were separated between these two populations (Monnahan et al. 2014). Gilpatrick and Perryman (2008) also reported that the tail region was a similar proportion of total length for NEPO, SEPO, and pygmy blue whales, and all of these populations were smaller than for Antarctic blue whales.

However, additional catch data found strong differences between pygmy blue whales and the NEPO and SEPO blue whales. Notably, mature female SEPO catches were intermediate in length compared to pygmy or Antarctic blue whales (Branch et al. 2007a). Furthermore, fluke-anus measurements as a proportion of total length were significantly different between SEPO and pygmy blue whales, but not between SEPO and Antarctic blue whales (Pastene et al. 2020). Aerial photogrammetry of blue whales in the Gulf of California also confirmed that the tail region of NEPO blue whales is significantly greater than for pygmy blue whales, but similar to SEPO blue whales (Ortega-Ortiz et al. 2018).

Recent drone-based measurements in southern Chile (Durban et al. 2016) also found two females accompanied by calves (22.2 m and 22.7 m), and body lengths in general that were longer by 0.9 m than expected for pygmy blue whales and shorter by 2.7 m than expected for Antarctic blue whales (Durban et al. 2016, Leslie et al. 2020). Relative tail length of SEPO blue whales was similar to Antarctic blue whales but significantly longer than for pygmy blue whales (Leslie et al. 2020).

Length distributions from whaling data for NEPO and SEPO blue whales (Fig. 3) corroborate the findings of Gilpatrick and Perryman (2008) that total lengths of NEPO and SEPO blue whales are similar, both for all whales combined and for sexually mature females. A statistical comparison is complicated by substantial evidence of "whale stretching", where undersized blue whales were reported at exactly the legal minimum length, which was either 65 ft in earlier years for shore stations, or 70 ft in later years for all whaling operations (Branch et al. 2007a, Pastene et al. 2020); and in addition there are peaks in the length frequencies at regular intervals for NEPO catches that suggest a substantial proportion of recorded lengths were rounded to 5-ft or 1-m intervals, as has been noted for catches in other regions (Branch et al. 2007a).

DISCUSSION

There is little evidence for interchange between the NEPO and SEPO blue whale populations. Catches, sightings, and surveys all find a gap in distribution of blue whales between 2°N and 6°N, which corresponds with the data from satellite tags and photographic mark-recapture evidence showing virtually no whales from either population cross this latitudinal zone just north of the equator. Blue whales sampled in the Eastern Tropical Pacific north of 7°N are genetically similar to NEPO blue whales, while those sampled just south of 0° are genetically similar to SEPO blue whales (LeDuc et al. 2017). Songs of the NEPO blue whales, which can sometimes be heard over considerable distances, were commonly detected at 8°N (50% of hours), but rarely (5%) at 0°N and almost never (<1%) at 8°S; conversely, SEPO song was heard primarily at 8°S (20% of hours) and 0°S (11%) but almost never at 8°N (Stafford et al. 1999b).

Counterbalancing this narrative, is the fact that NEPO and SEPO blue whales share some haplotypes (LeDuc et al. 2017), have similar total lengths both for all individuals and sexually mature females, and their tail regions are a similar proportion of total both length, and longer than for pygmy blue whales. Indeed, the similarity in lengths between NEPO and SEPO blue whales, is comparable to the similarity in lengths of mature females, and the length at maturity of females among regions inhabited by different pygmy blue whale populations in the Indian Ocean (Branch et al. 2007a, Branch and Mikhalev 2008).

In addition, on at least two occasions, a blue whale has been reported moving from one population to the other: a photographic match between the NEPO area of the Costa Rica Dome and the SEPO region of the Galapagos Islands (Douglas et al. 2015); and the detection of SEPO song off California (A. Širović, pers. comm.). Satellite tags and photographic mark-recapture also show that individual NEPO blue whales occasionally travel many thousands of kilometers away from standard migration routes, including to the Gulf of Alaska, towards Hawaii, and far west of the Costa Rica Dome (Bailey et al. 2009, Calambokidis et al. 2009). Rare vagrant blue whales have also been reported from other blue whale populations: Antarctic blue whales north of the equator in the Atlantic Ocean (Samaran et al. 2017, Samaran et al. 2019), south-east Indian Ocean (SEIO, Australia/Indonesia) blue whale songs off New Zealand (D. Barlow, pers. comm.) and the Philippines (Acebes et al. 2021), SEPO blue whale calls at South Georgia (Pangerc 2010), and central Indian Ocean (Sri Lanka) songs off Angola (Cerchio et al. 2010). In nearly all of these cases, a single vagrant blue whale likely was, or could have been, responsible for the out-of-normal-range detection of song, tag, or photographed whale.

Overall, despite the morphological similarities between NEPO and SEPO blue whales, I conclude that NEPO and SEPO blue whales are geographically, acoustically, and genetically separated, with a gap between 2°N and 6°N. Since songs are produced by males only and are thought to have a reproductive function, the fact that the two populations have distinct song types should also maintain reproductive isolation on the rare occasions when vagrants move from one population into the distribution of the other.

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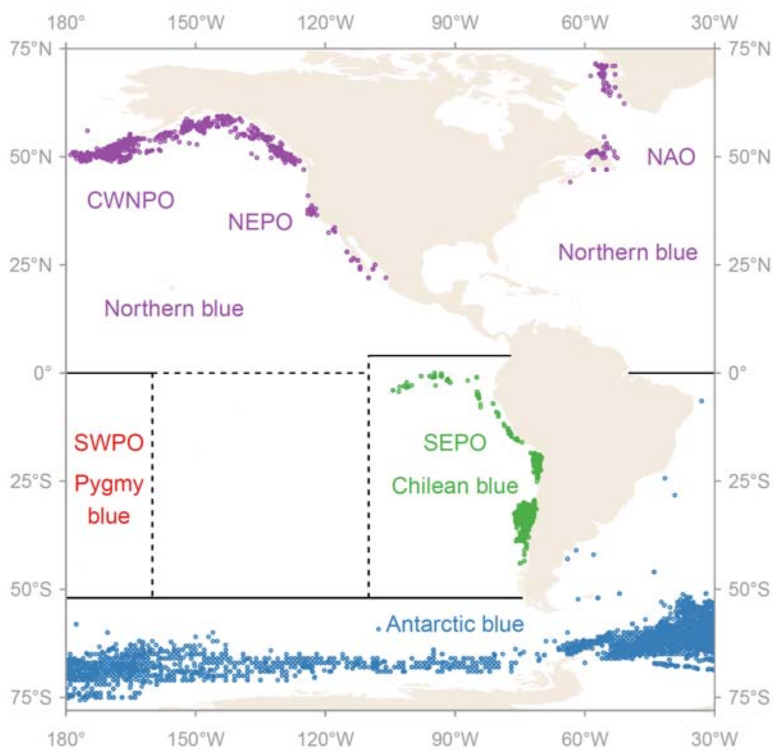

Fig. 1. Blue whale catches with recorded position data, showing distinct gaps between NEPO, SEPO, and Antarctic blue whales. Source of data: IWC database 7.1 (Allison 2020).

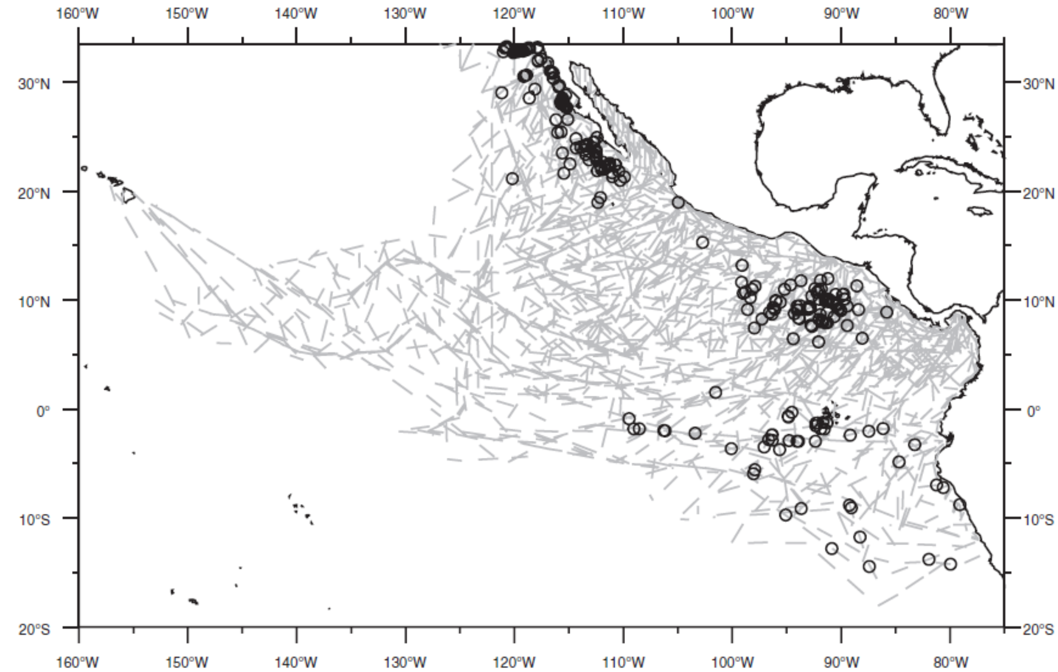

Fig. 2. Southwest Fisheries Science Center surveys between 1986 and 2006 in the eastern tropical Pacific (Hamilton et al. 2009). Grey lines indicate primary search effort, while circles show both on-effort and off-effort sightings of blue whales. Source: Branch et al. (2007b), based on data provided by T. Gerrodette.

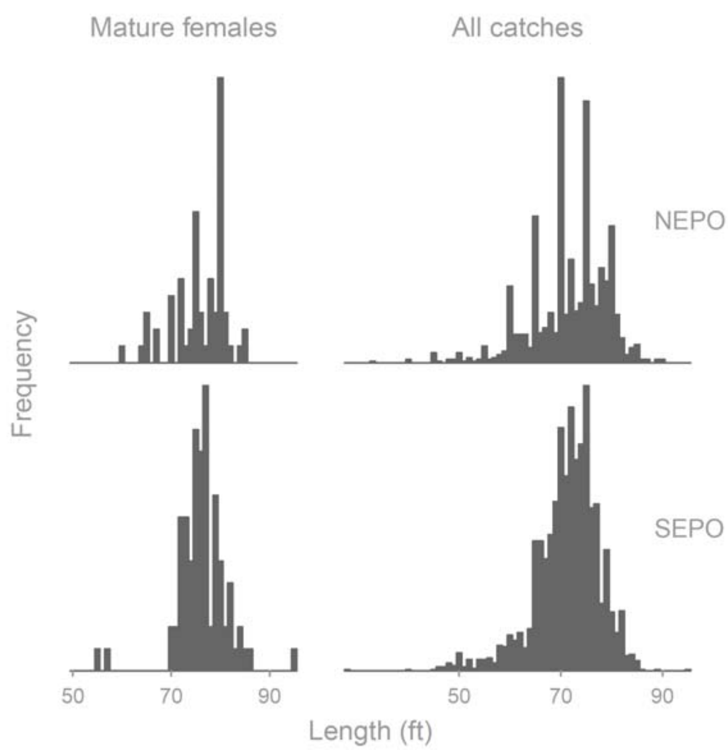

Fig. 3. Length frequencies in catches of mature females (left column) and all individuals (right column) for blue whales caught from catches assigned to the north-east Pacific Ocean (NEPO, top row) population, and from the south-east Pacific Ocean (SEPO, bottom row) population. Source of data: IWC database 7.1 (Allison 2020).