Aquatic Mammals 2018, *44*(4), 357-366, DOI 10.1578/AM.44.4.2018.357

Short Note

"Northern" Form Short-Finned Pilot Whales (*Globicephala macrorhynchus*) Inhabit the Eastern Tropical Pacific Ocean

Susan J. Chivers,[1] Wayne L. Perryman,[1] Morgan S. Lynn,[1] Kristi West,[2] and Robert L. Brownell, Jr.[1]

[1]*Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA*
E-mail: susan.chivers@noaa.gov
[2]*Department of Human Nutrition, Food and Animal Science, College of Tropical Agriculture and Human Resources, Agricultural Sciences 216, 1955 East-West Road, University of Hawai'i at Manoa, Honolulu, HI 96822, USA*

Morphology is the basis for species recognition in most animal groups, including cetaceans. Interspecific differences in characters provide clues to the evolutionary and ecological processes that shape species, while intraspecific variation reveals unique adaptations that have evolved among populations throughout a species' range. Most cetaceans are inherently difficult to study due to their wide-ranging, pelagic lifestyles, and morphological studies have been primarily limited to species hunted or by-caught. However, the development of molecular genetic markers combined with the development of projectile biopsy techniques to non-lethally sample animals in the wild (Palsbøll et al., 1991) has provided new insights about taxonomy, including revealing previously unidentified geographic forms (e.g., Foote et al., 2011), subspecies (e.g., Viaud-Martinez et al., 2008), and species (e.g., Dalebout et al., 2002), as well as evidence of intraspecific population structure. While important for cetacean taxonomy, the interpretation of molecular genetic variability in the absence of morphological data can be difficult (Schwartz & Boness, 2017; Taylor et al., 2017). Evidence of geographic concordance in morphological characters (phenotype) and genetic markers (genotype) provides the strongest support for taxonomic status.

The short-finned pilot whale (*Globicephala macrorhynchus*; Gray, 1846) is broadly distributed throughout temperate and tropical waters of all ocean basins (Olson, 2009; Taylor et al., 2011). In the North Pacific, two geographic forms of short-finned pilot whale (SFPW) have been described off Japan: (1) the "northern" and (2) "southern" forms. The forms differ ecologically, morphologically, genetically, and acoustically. Ecologically, the northern form inhabits cool temperate waters characteristic of the oceanic waters off Japan's northern archipelago, and the southern form inhabits warm temperate waters off the coast of southern Japan (Kasuya et al., 1988). The common names ascribed to the forms reflect this difference in their distribution off Japan. Morphologically, the northern form is notably larger than the southern form. Northern form females average approximately a meter larger, while males are about 2 m larger. Melon shape and color pattern also differ between the forms (Kasuya et al., 1988; Miyazaki & Amano, 1994). Genetically, the degree of genetic differentiation evident between the two forms supports the morphological and ecological differences distinguishing them (Wada, 1988; Oremus et al., 2009; Van Cise et al., 2016). Acoustically, significant differentiation in call characteristics have been documented from recordings of the northern form in the eastern North Pacific (ENP) and the southern form around Hawai'i (Van Cise et al., 2017). While individual metrics suggest the forms may warrant recognition as subspecies, the lack of regional support from multiple metrics and of data from much of their worldwide range has hampered further revisions to their taxonomy.

Morphological evidence confirming the distribution of the two forms across the North Pacific is limited, with morphological data available from relatively few SFPW specimens collected in coastal waters of the ENP, western North Pacific (WNP), and Hawai'i. To date, the known range of the southern form is in the WNP from southern Japan (Kasuya et al., 1988) south to the Philippines (Chen et al., 2014) and east to Hawai'i (Mazzuca et al., 1999), while that of the northern form extends across the North Pacific from the north cold-temperate waters off Japan (i.e., north of 35º N) to the cold-temperate waters of the California Current (Appendix 1 in Perrin & Reilly, 1984; Heyning et al., 1994; Bernard & Reilly, 1999). However, SFPWs are distributed throughout the ENP and occupy both coastal and pelagic waters of the California Current Ecosystem and the eastern tropical Pacific (ETP) (Wade & Gerrodette, 1993; Barlow & Forney, 2007; Hamilton et al., 2009). The morphological form(s) inhabiting the ETP is unknown.

The objectives of this study are to identify the morphological form(s) of SFPWs inhabiting the ETP, including the Gulf of California, and to provide confirmation of the form(s) occupying the ENP and Hawai'i. Our findings will contribute to a review of SFPW taxonomy by providing additional data about geographic concordance of phenotype and genotype in the ENP. Although Van Cise et al. (2016) recommended re-adopting the original historic Japanese names, *Shiho* and *Naisa*, for the northern and southern forms, respectively, the use of these names has not been universally adopted, and they are not currently used in Japan (Amano, 2009). Herein, we refer to the forms using the original common names ascribed to them to facilitate recognition of their relative geographic distributions in the North Pacific.

Two datasets were assembled to characterize ENP SFPW body size. In the first, standard total body length (TL) measurements (Norris, 1961) of stranded and live-captured SFPWs sampled off the west coast of the U.S. (hereafter referred to as the California Current) and Hawai'i between 1940 and 2017 were compiled. In the second, body size was measured from vertical aerial photographs taken during ETP research cruises conducted between 1988 and 2003 (Figure 1). Hereafter, we refer to these as the "specimen" and "photographic" datasets, respectively.

The photographic dataset was assembled from vertical aerial photographs taken using a military reconnaissance camera mounted below a Hughes 500D helicopter launched from the National Oceanic and Atmospheric Administration (NOAA) research vessel *David Starr Jordan*. Kodak Aerial Plus X black and white film was used to ensure high-resolution photographs were obtained. The photographs were taken opportunistically during research surveys designed to estimate the abundance of small dolphin populations in the ETP (e.g., Holt & Sexton, 1989; Wade & Gerrodette, 1993; Barlow et al., 1998; Kinzey et al., 2000). The field sampling and processing methods for photographs of SFPWs analyzed for this study follow those of prior studies (Perryman & Lynn, 1993, 1994; Perryman & Westlake, 1998; Cramer et al., 2008), and we present only a summary of the methodology herein.

SFPWs swimming parallel to and near the surface were measured from the tip of the rostrum, or melon for SFPWs, to the trailing edge of the flukes (see Figure 2 in Perryman & Lynn, 1993). This differs from the standard TL defined in Norris (1961) as measured from the tip of the rostrum to the fluke notch. This difference would

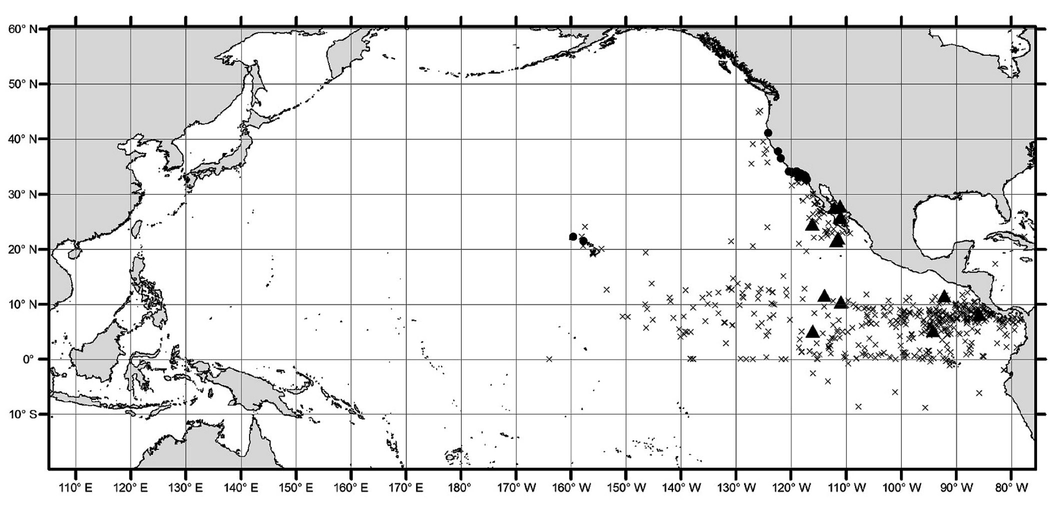

Figure 1. Geographic collection locations for the specimen (dots) and photographic (triangles) data assembled for this study. Sightings of short-finned pilot whales (SFPWs; *Globicephala macrorhynchus*) (crosses) made during research vessel cruises in the eastern North Pacific (ENP) document their distribution within the study area (Hamilton et al., 2009).

be expected to result in longer body size measurements equivalent to the depth of the fluke notch, but the difference is negligible due to the swimming behavior of the animals. Body size data obtained from vertical aerial photographs have been validated for use in morphological studies using the same equipment and field sampling techniques used here (Perryman & Lynn, 1993, 1994; Perryman & Westlake, 1998). While SFPWs are much larger than the small delphinids studied by Perryman & Lynn (1993, 1994) and Perryman & Westlake (1998), the difference between specimen and photographic length measurements of SFPWs is expected to be negligible as has been demonstrated for photographic body size data of killer whales (Pitman et al., 2007). Thus, we use TL to refer to photographic measurements as well as those of specimens.

The photographic dataset is comprised of TLs obtained from individual SFPWs measured from the original film negatives. All measurements were converted to true length using the focal length of the camera lens and distance from the camera to the SFPWs, which was determined by the helicopter's radar altimeter calibrated by photographing and measuring objects of known size.

The life stage of SFPWs measured in photographs was classified as adult female–calf pairs, calves, or unidentified; males and females could not be distinguished. Adult female–calf pairs were identified by evaluating (1) the close proximity of two SFPWs swimming together relative to others in the school, (2) the size of the smaller whale relative to the adult's length, and (3) the position of the smaller whale relative to the adult. Small SFPWs swimming in calf position with an adult-sized whale were classified as "calves." The adult-sized whale was assumed to be the adult female that gave birth to the calf, and we refer to these SFPWs as "adult females." Additional "calves" were identified by their small size. All other SFPWs measured were classified as "unidentified," which includes all juvenile and adult males and females.

All data were reviewed for quality prior to finalizing the datasets for analyses. During review of the photographic data, one adult female–calf pair fell well outside the range of measurements for other adult females and calves (i.e., > 500 cm and < 400 cm, respectively; Figure 2). Because photographs are a snapshot in time of animals swimming, classification errors can occur when just by

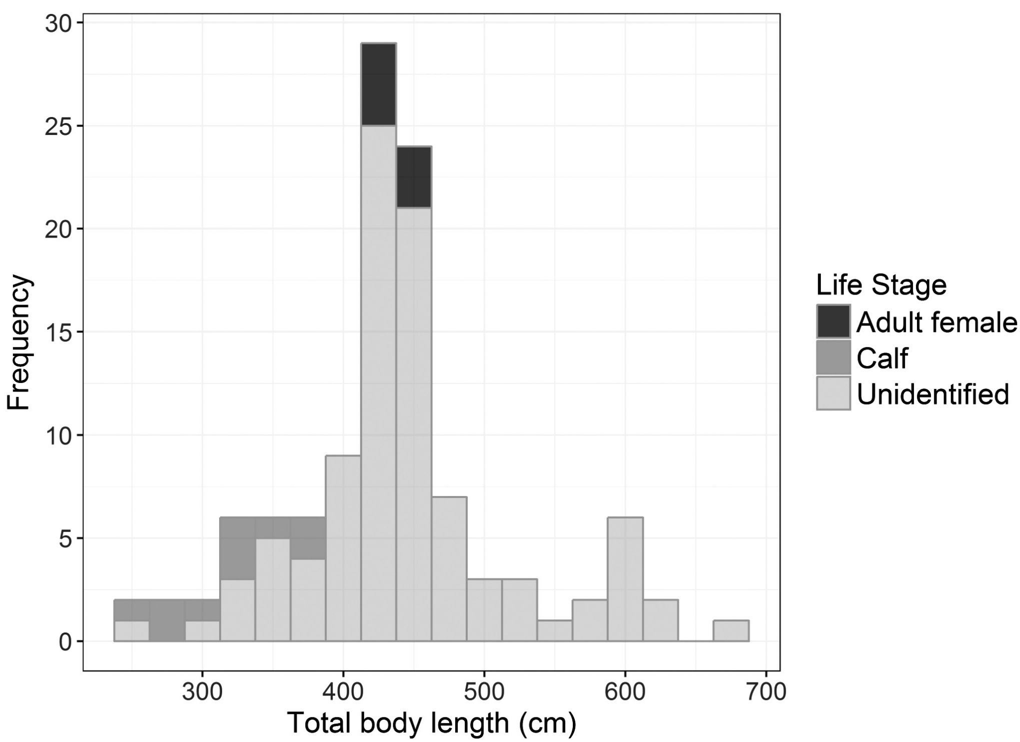

Figure 2. Total body length distribution of eastern tropical Pacific (ETP) SFPWs measured in vertical aerial photographs ($N = 111$) by life stage (see text for explanation)

chance a large and small animal are photographed in adult–calf position. As described above, adult female–calf pairs are identified by position and proximity of a small, calf-sized individual swimming next to an adult-sized animal, and errors can only be identified by size anomalies. In our case, the exception was a 618 cm "adult female" and a 442 cm "calf." Both animals were reclassified as "unidentified" for analyses.

There were 111 SFPWs ($N = 7$ adult females, 10 calves, and 94 unidentified to life stage; Figure 2) measured in photographs. Because relatively little is known about SFPWs in the Gulf of California, an ecologically important area for marine mammals (Rosales-Nanduca et al., 2011), we compared the non-calf TL distribution of the unidentified life stage category sampled in the pelagic ETP ($N = 54$) to those sampled in the Gulf of California ($N = 30$) before proceeding with analyses. No significant difference in the TL distributions from the two areas was detected (Student's t test: $t = 1.69$, $df = 80.23$, $p = 0.09$), and we analyzed all of the photographic data as representative of the ETP. The unidentified life stage portion of the photographic dataset ($N = 94$) was further restricted to SFPWs > 400 cm to provide comparable summary statistics for both datasets (see definition of non-calf specimens in the following paragraph). The summary data include the mean and range of TLs for non-calves ($N = 77$) as well as asymptotic length estimated as the mean of the 90th percentile of the distribution (Barlow & Boveng, 1991) to characterize adult body size (Table 1). Both the maximum and 90th percentile TL for the photographic data are interpreted as characterizing the body size of adult male SFPWs because males are approximately 30% longer than females (see Appendix 1 in Perrin & Reilly, 1984).

We compiled TL for 89 specimens ($N = 46$ females, 35 males, and 8 of indeterminable sex; Figure 3). The specimen data included date and location of sampling. Too few specimens had sexual maturity determined to provide sufficient data to characterize the TL distributions by maturity state. Therefore, we summarized TL for non-calves by sex and region: the California Current and the Hawaiian Islands (Table 1). For the California Current, non-calves are those > 400 cm (see Appendix 1 in Perrin & Reilly, 1984); and for the Hawaiian Islands, > 200 cm (Jefferson et al., 1993). The summary includes the mean and range of TL, and asymptotic length is estimated as the mean of the 90th percentile of the distribution (Barlow & Boveng, 1991).

The TL characteristics of non-calves in the specimen and photographic data from the California Current and ETP are consistent with those in the published literature (Table 2) for northern form SFPWs, which range from 390 to 510 cm for females and from 560 to 720 cm for males (Kasuya & Tai, 1993). These results, therefore, confirm the northern form inhabits the California Current and provide the first morphological evidence that the northern form inhabits the ETP. Similarly, the specimen data from Hawai'i are consistent with those of southern form SFPWs (Table 1), which range from 316 to 405 cm for females and from 422 to 525 cm for males (Kasuya & Tai, 1993). These data are also consistent with the published data for specimens collected from Hawai'i between 1957 and 1998 confirming the southern form occurs around Hawai'i (Mazzuca et al., 1999).

The TL data we present from the ETP confirms concordance between phenotype (i.e., body size) and genotype in the ETP where northern form genotypes were detected but the phenotype was

Table 1. Standard total body length (TL) characteristics for male and female short-finned pilot whales (SFPWs; *Globicephala macrorhynchus*) sampled from three regions within the eastern North Pacific: the California Current, the eastern tropical Pacific (ETP), and the Hawaiian Islands. Specimen TL data are summarized by region: the California Current and Hawaiian Islands for non-calves. However, only photographic data are available for the ETP, and those data only provide a maximum size for males and mean size for adult females (see text for explanation). Asymptotic TL was not estimated if $N < 10$. Summary statistics not available are indicated by "NA."

	Male				Female			
Region	Sample size (*N*)	Mean (SE)	Range	Asymptotic	Sample size (*N*)	Mean (SE)	Range	Asymptotic
California Current	8	530.3 (28.0)	419-670	NA	23	440.3 (3.7)	403-480	471.7
Eastern tropical Pacific	77	Max: 685.7	NA	619.4	7	432.9 (6.4)	414-460	NA
Hawaiian Islands	9	444.3 (8.9)	329-550	NA	5	350.9 (12.0)	285.8-411.0	NA

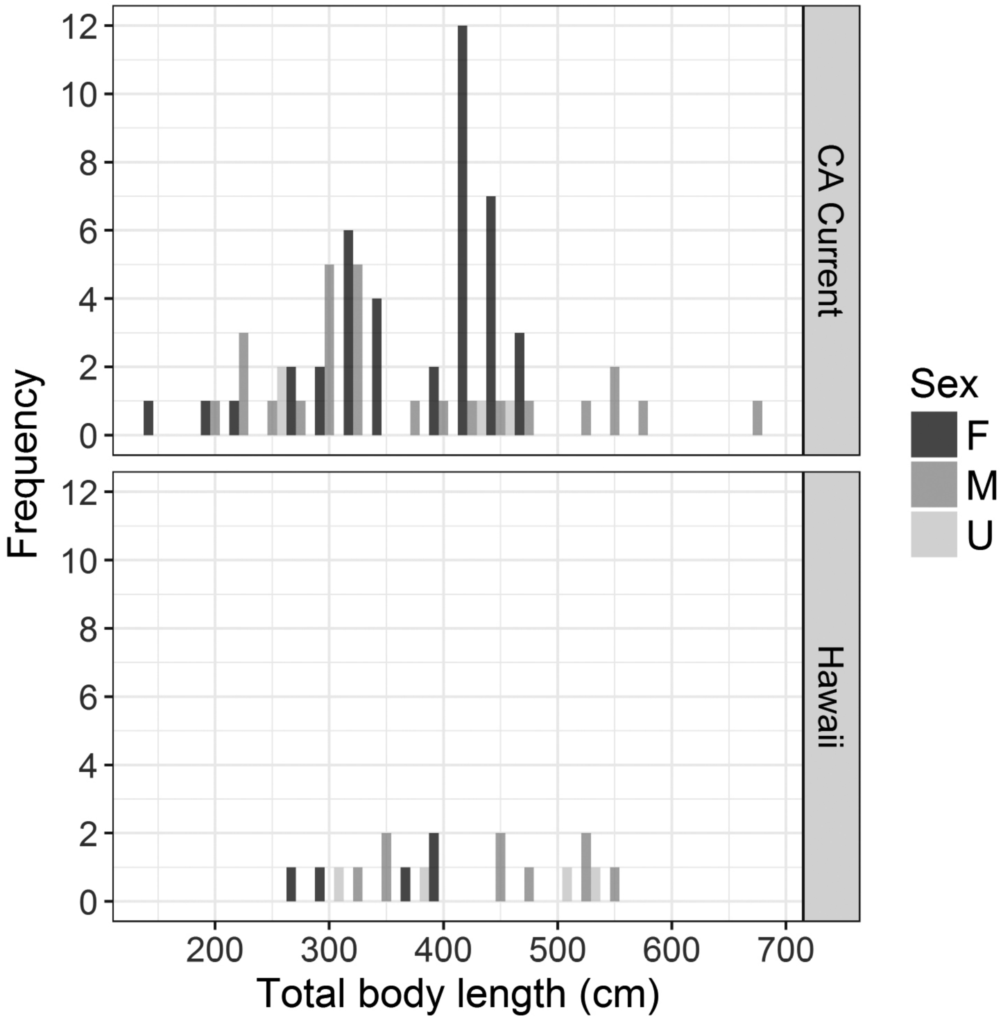

Figure 3. Total body length distribution of specimens collected in the California (CA) Current and around Hawai'i (N = 89) by sex: F = Female, M = Male, and U = Undetermined.

unknown (Van Cise et al., 2016). This concordance allows us to refine the known distribution of northern form SFPWs in the ENP to extend south from the temperate waters of the California Current through the ETP to Peru (Figure 4). While this latitudinal range includes tropical waters, at-sea sightings in the ETP reveal that SFPWs are not found in the warmest, shallowest thermocline waters characteristic of the ETP core habitat where the tuna–dolphin association is strongest, but, rather, they occupy deeper thermocline waters, which are warm but relatively cooler than the core area (Ballance et al., 2006; Fiedler & Talley, 2006; Hamilton et al., 2009; Scott et al., 2012). This apparent hiatus in distribution is consistent with existing information of their preferred habitat of warm, deep waters off the continental shelf (Taylor et al., 2011). Evidence of southern form SFPWs occupying Hawaiian waters suggests that in the central Pacific, the southern limit of the northern form is north and east of the Hawaiian Islands. Limited morphological and genetic data combined with few at-sea sightings in the oligotrophic waters to the west of the ETP preclude identifying a boundary between the forms with certainty.

Additionally, the geographic concordance in phenotype and genotype in the ETP supports rejecting the current working hypothesis that pilot whale distributions are correlated with sea surface

Table 2. Review of worldwide phenotypic and genotypic data for distribution of northern (N) and southern (S) forms of short-finned pilot whales. **Notes:** MSE = mass stranding event; sample sizes are listed in the "References" column when sex-specific sample size was not available; maximum total body length is listed in the male total length column when sex was not specified; and a question mark (?) indicates uncertainty in our ability to unequivocally designate geographic form from the data presented.

Location	Female total length (cm)	*N*	Male total length (cm)	*N*	References	Total length	Color phenotype	Skull morphology	Oremus et al. (2009) genetics	Van Cise et al. (2016) genetics
Japan northern	390-510		560-720		Kasuya & Tai, 1993	N	N	N	N	N
California	396-480		Max: 590		Perrin & Reilly, 1984	N	N	N	N	N
	463		610		Heyning et al., 1994	N				
	461		660		Sinclair, 1992	N				
	403-480	23	419-670	8	This study	N				
	Max: 483	21	Max: 470	6	Hall et al., 1971	N				
	Max: 424		Max: 556		Norris & Prescott, 1961	N				
	Max: 480	4			Harrison et al., 1972	N				
Eastern Tropical Pacific	414-460	7	Max: 686	77	This study	N				N
Gulf of California	451-471	4	538-664	6	G. Gomez, pers. comm.[1]	N				
Peru	Max: 550		Max: 720		Reyes Robles, 2009	N	N	N		N
Japan southern	316-405		422-525		Kasuya & Tai, 1993	S	S	S	S	S
Taiwan	322-415	4	495-511	3	Chen et al., 2014	S	S			
Hawai‘i			Max: 519		MSEs, *N* = 60; Mazzuca et al., 1999	S	S	S		S
	286-411	5	329-550	9	This study	S	S			?
South Pacific	Max: 464	10	Max: 589	10	Scott, 1942	S	S	S	S	S
Indian Ocean	425-550	31	475-575	39	Alagarswami et al., 1973	?	S	S		?
	339-510	14	306-555	13	Raghunathan et al., 2013	S	S	S		?
			Max: 500		P. Jayasankar, pers comm.[2]	S	S	S		?
NW Atlantic	293-397	77	468-535	10	Mead & Potter, 1987	S	S	S		?
	390-400		510-520		*N* = 135; Irvine et al., 1979	S				
	197-387	23	156-506	8	Hohn et al., 2006	S				
NE Atlantic (e.g., Spain)	357-450	6	345-427	4	Gonzalez & Lopez, 2000	S	S	S		

[1] G. Gomez, Baja California, Mexico. Stranding of 27 SFPWs on 14 May 2016 at Punta Bufeo, Sea of Cortez, Baja California, Mexico.
[2] P. Jayasankar, Bhubaneswar, India. Stranding of 73 SFPWs in 12 January 2016 at Tuticorin, Tamil Nadu, India.

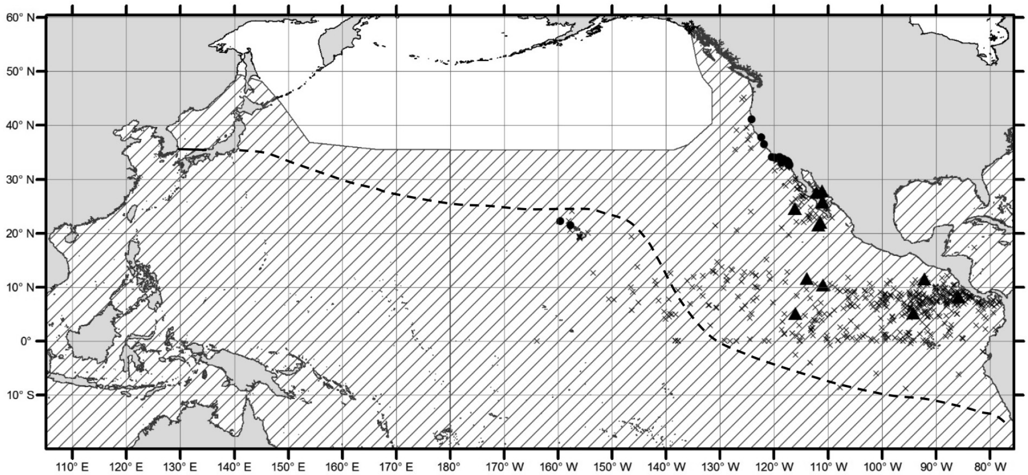

Figure 4. The distribution of northern and southern form SFPWs indicated by concordance of phenotype and genotype in the North Pacific revealed by our dataset (Table 1) and the published literature (Table 2). The northern form is distributed north of the proposed boundary (dashed line) shown here overlaid on the International Union for Conservation of Nature (2017) range map for SFPWs and sighting locations of the species, unidentified to form, within our ENP study area (Hamilton et al., 2009).

temperature (SST). Off Japan, the habitat preferences for the two forms of SFPWs are correlated with SST, and that relationship has been expected to hold throughout their range. That is, the northern form would inhabit cool temperate waters with the southern form inhabiting warm temperate and tropical waters throughout their range as they do off Japan (Kasuya et al., 1988). However, our data reveal that the distribution of the northern form extends through the ETP, which is not consistent with the working hypothesis; the southern form would be expected in the ETP. The apparent hiatus in their ETP distribution (i.e., east of 120° W between 10 and 20° N) suggests there may be separate populations in the region (Hamilton et al., 2009) and that population structure studies are needed.

On the other hand, the SST hypothesis remains consistent for the known distribution of long-finned pilot whales (*Globicephala melas*; Traill, 1809). In the North Atlantic, the long-finned pilot whale (*G. melas melas*) occurs in cold-temperate waters and has an antitropical distribution with the subspecies *G. m. edwardii*, which are found in cold-temperate waters in the southern hemisphere (Fraser, 1950; Davies, 1963). Along the west coast of South America, the cold Humboldt Current flows northward to approximately 4° S and then west to the Galapagos Islands, and long-finned pilot whales are associated with this water mass off Chile (True, 1903; Clarke et al., 1978). However, both long- and short-finned pilot whales occur in Peruvian waters. The long-finned subspecies is known from as far north as Bahia de Paracas (13° 52' S, 76° 16' W), and SFPWs are known from as far south as off Pacasmayo (07° 24' S, 79° 34' W) and Pucusana (12° 25' S, 76° 47' W) (Reyes Robles, 2009). In addition, one of us (RLB) examined a skull from a large male SFPW collected at Punta San Juan (15° 22' S), which extends the range of SFPWs farther south.

The distribution of the northern form SFPWs is dramatically different on the two sides of the North Pacific Ocean. They have a broader latitudinal distribution in the ENP than WNP. In the west, northern form SFPWs inhabit the productive Oyashio Current off Japan with a southern limit to their distribution of about 35° N. Other small cetacean species exhibit similar patterns, including Hubbs' beaked whale (*Mesoplodon carlhubbsi*), Stejneger's beaked whale (*M. stejnegeri*), and Baird's beaked whale (*Berardius bairdii*) (Mead, 1989; MacLeod et al., 2006). In the east, northern form SFPWs and these beaked whales occupy waters influenced by the California Current, which provides a larger area of high-productivity temperate habitat in the ENP than does the Oyashio Current in the WNP. The difference in habitat provided by the cool temperate Oyashio and California Currents likely supported larger populations in the east than west such that more north-south animal movement likely occurred during cool glacial periods, resulting in animals finding and occupying suitable habitat farther south in tropical latitudes and south of the equator. Like SFPWs, both Hubbs' and Baird's beaked whales have been sighted in the ENP and the WNP. The similarity in current day distribution patterns of these species suggests similar ecological processes influenced their evolution.

In summary, the new morphological data we present identifies northern form SFPWs in the ETP to support geographic concordance in phenotype and genotype there. Our findings allow us to refine the known distribution of the two forms (Figure 4) and to reject the hypothesis that their distributions are correlated with SST. In conjunction with previous studies of pilot whales, our results provide additional clues to the evolutionary processes influencing SFPWs, including the role of potential barriers limiting animal movements (e.g., ocean current boundaries and glacial periods). Our findings also provide additional support for the hypothesis that the northern and southern forms of SFPWs are likely different subspecies.

Acknowledgments

We thank the many field personnel who participated in stranding response along the U.S. West Coast and in the Hawaiian Islands as well as in field work to take the vertical aerial photographs. John Durban, Paula Olson, and two anonymous reviewers provided valuable comments to improve this paper.

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