Evaluation of the Western North Pacific Distinct Population Segment of Humpback Whales as Units under the Marine Mammal Protection Act

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Pacific Islands Fisheries Science Center

NOAA Technical Memorandum NMFS-PIFSC-124
https://doi.org/10.25923/n5p9-4m02

February 2022

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February 2022

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Recommended citation

Oleson EM, Wade PR, Young NC. 2022. Evaluation of the western North Pacific distinct population segment of humpback whales as units under the Marine Mammal Protection Act. U.S. Dept. of Commerce, NOAA Technical Memorandum NMFS-PIFSC-124, 27 p. doi:10.25923/n5p9-4m02

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Executive Summary

The Guidelines for Preparing Stock Assessment Reports Pursuant to the 1994 Amendments to the Marine Mammal Protection Act (MMPA) specify that a stock under the MMPA should identify a demographically independent population (DIP). Considerable new data suggest the existence of potential DIPs within the Western North Pacific (WNP) distinct population segment (DPS) of the North Pacific subspecies of humpback whales (*Megaptera novaeangliae kuzira*). Animals that winter near Pacific island nations off the Asian continent, including the Philippines and Japan, and other unidentified breeding areas in the western North Pacific, and summer off of Russia and in U.S waters surrounding the central and western Aleutian Islands together are listed under the Endangered Species Act (ESA) as the WNP DPS. However, even at the time of listing, this group was considered to comprise two discrete units, those wintering in the Philippines and Okinawa and those wintering in an as-yet unidentified location (or locations) in the western North Pacific. New data collected since the 2015 status review of humpback whales under the ESA (Bettridge et al. 2015) suggest that the wintering area for the WNP DPS extends into the U.S. territory of Guam and the Commonwealth of the Northern Mariana Islands (CNMI) (together referred to as the Mariana Archipelago or Marianas). No data were available from the Mariana Archipelago at the time of the status review and the description of the DPS. However, genetic and movement data collected in the Marianas, as well as in other Asian wintering grounds and Russian feeding grounds in recent years suggest that individuals in the Marianas are part of the WNP DPS, as presently designated, likely representing one portion of the 'unidentified breeding area' described in the status review and ESA listing.

Martien et al. (2019) identify three Lines of Evidence (LoE) for delineating DIPs considered to be "strong" – movements, genetics, and morphology. Robust data from a single strong LoE are sufficient to meet the DIP definition, where 'robust data' means that there has been appropriate evaluation of all relevant factors (e.g., age and sex difference, sample size, analytical methods, etc.) such that the observed difference that indicates demographic independence is real, not a sampling or analytical artifact. For the WNP DPS, there are reasonable data to indicate the presence of multiple DIPs and to delineate discrete wintering aggregations. One aggregation winters in the waters around the Philippines and Okinawa, as well as other similar habitats along the Ryukyu Archipelago (including Amami Oshima), and summers off mainland Russia, particularly off of Kamchatka. The second aggregation winters around the Mariana Archipelago, Ogasawara and additional as-yet unidentified areas, and summers off the Commander Islands and the northern portion of the Russian feeding area. The available movement and genetic data strongly support the separation of these two wintering aggregations. It is possible that these groups contain multiple DIPs, as is the case for the humpback whales utilizing the Hawai'i and Mexico wintering grounds (Martien et al. 2021, Wade et al. 2021), but the available data and analyses are not sufficient to evaluate that possibility at this time. We therefore focus on summarizing and evaluating the data that support separation of these wintering grounds as separate units. For consistency with the Hawai'i and Mexico cases, we refer to these wintering aggregations as the Philippines/Okinawa-Northern Pacific (Phil/Ok-NorthPac) unit and the Mariana Islands/Ogasawara-Northern Pacific (MI/Og-NorthPac) unit.

The recent expansion of humpback whale research off Japan, the Marianas, and in Russian waters continues to reveal new information and refine existing understanding of the linkages

between specific wintering and feeding areas. These research efforts may produce data soon that will enable the delineation of DIPs within the Phil/Ok-NorthPac and/or MI/Og-NorthPac groups. Exploration of other humpback whale wintering, migratory, or feeding habitats off China, Korea, throughout the Sea of Japan and the Sea of Okhotsk, led by historic catch records that demonstrate these areas as habitat previously occupied by humpback whales, may be required before the structure of this DPS can be fully resolved.

Introduction

Most humpback whales occupy relatively coastal habitats for most of the year, which makes obtaining both biopsy samples and photographic identification of their flukes possible. Between 2004 and 2006, a basin-wide study took place on nearly all North Pacific summer and winter areas (Calambokidis et al. 2008, Barlow et al. 2011, Baker et al. 2013, Wade 2021). The study, known as SPLASH (Structure, Population Levels, And Status of Humpbacks), produced substantial photographic and genetic data regarding the population structure of North Pacific humpback whales. The SPLASH study obtained data in nearly every region within the North Pacific in both summer feeding areas and wintering areas, so results regarding the population structure of North Pacific humpbacks are considered robust. Note that the SPLASH study referred to the wintering areas as breeding grounds. However, due to uncertainty regarding the fraction of breeding that actually takes place there, we henceforth refer to them as wintering areas.

Following the SPLASH study, the National Marine Fisheries Service (NMFS) conducted a worldwide status review of humpback whales (Bettridge et al. 2015). Based on information presented in the status review report and other factors, NMFS which identified 14 Distinct Population Segments (DPSs) under the Endangered Species Act (ESA) (81 FR 62660; September 3, 2016). One of these, the Western North Pacific (WNP) DPS is listed as endangered under the ESA. This DPS is described as those whales that breed off Okinawa, the Philippines, and another unidentified breeding area (inferred from sightings of whales in the Aleutian Islands area feeding grounds) and those whales transiting the Ogasawara area. Whales in the WNP DPS migrate to feeding grounds in the northern Pacific, primarily off the Russian coast, but also to feeding grounds in the western and central Aleutian Islands (81 FR 62260, September 8, 2016). The WNP DPS combines the Okinawa/Philippines and a Second West Pacific DPS defined in Bettridge et al. (2015). The status review team considered those whales that winter off Okinawa and the Philippines to be discrete from those that winter in other, unidentified locations in the western North Pacific (discussed in Calambokidis et al. 2008), but with a similar migratory pathway past Ogasawara, where whales from both populations are observed. While the status review team concluded there was sufficient evidence to support the existence of two discrete population segments in this region, uncertainty on the location of the unknown breeding grounds and the common migratory habitat off Ogasawara led NMFS to combine these populations into a single DPS in the listing decision.

Since the SPLASH study, considerably more data have been collected that further our understanding of humpback whale population structure in the Pacific. Significant additional photographic catalog matching has been undertaken among photo contributors in the western Pacific wintering and feeding areas, research in Russian feeding areas has expanded substantially, and a new study has been initiated in the Mariana Archipelago that has confirmed the occurrence of humpback whales in that region. These new data and analyses are relevant to consideration of finer population structure within the WNP DPS.

NMFS' Guidelines for Preparing Stock Assessment Reports Pursuant to the 1994 Amendments to the MMPA specify that a stock under the MMPA should identify a demographically independent population (DIP), where 'demographic independence' is to mean that

> *…the population dynamics of the affected group is more a consequence of births and deaths within the group (internal dynamics) rather than immigration or emigration (external dynamics). Thus, the exchange of individuals between population stocks is not great enough to prevent the depletion of one of the populations as a result of increased mortality or lower birth rates* (NMFS 2016).

Humpback whale stocks in the North Pacific are delineated at large geographically defined scales with names referring to feeding grounds (for example, the California/Oregon/Washington stock). However, it has long been recognized that, in most cases, feeding ground aggregations do not represent DIPs. Rather, they comprise animals from multiple wintering grounds and, therefore, different DPSs. Martien et al. (2020) suggest that humpback research and management should focus on 'migratory whale herds,' which are defined as groups of animals that share the same feeding ground and wintering ground. Recruitment into a herd is almost entirely through maternally directed learning of the migratory destinations. Available photographic and genetic data show strong fidelity of animals to a given feeding and wintering ground, and therefore to a herd, suggesting very little dispersal (permanent movement of animals) between herds. If dispersal between herds is low enough to render them demographically independent, a migratory whale herd is a special case of a DIP.

Migratory whale herds interbreed with other herds to varying extents, and therefore are not reproductively isolated. However, interbreeding among herds only results in the exchange of genetic material between them, not an exchange of animals. It therefore has no impact on the demography of either herd. Because gene flow (the transfer of genetic material between groups through interbreeding) can occur without dispersal (the transfer of individuals between groups), reproductive isolation is neither required nor expected between stocks under the MMPA (Eagle et al. 2008, Moore and Merrick 2011, Martien et al. 2019).

The NMFS policy on stock designation under the MMPA (NMFS 2019) indicates that stocks should generally be composed of a single demographically independent population (DIP), although it notes that in some situations it may be impractical to manage DIPs as stocks. One such exception is when DPSs are designated under the ESA; however, the policy notes that even within that case, separate DIPs within the DPS may warrant recognition as stocks under the MMPA. At present, the WNP DPS and the Western North Pacific stock under MMPA are aligned, with recognition that whales from Hawai'i and Mexico may also occur on Russian and other western North Pacific feeding grounds used by WNP DPS whales (Muto et al. 2020). Similarly, there is overlap of WNP whales into the Gulf of Alaska and Bering Sea regions largely used by the Central North Pacific stock (largely the Hawai'i DPS) and whales from the Mexico DPS. However, the WNP stock assessment does not address new data that may support finer structure within the DPS. This report is intended to document and discuss the data and analyses available or required to correctly define one or more DIPs within the WNP DPS, given the guidance offered within the DIP Delineation Handbook (Martien et al. 2019). Specifically, the Handbook identifies three strong lines of evidence (LoEs) for inferring demographic independence- movements, genetics and morphology. Robust data from a single strong LoE are sufficient to delineate a DIP, where 'robust data' means that there has been appropriate evaluation of all relevant factors (e.g., age and sex difference, sample size, analytical methods, etc.) such that the observed difference that indicates demographic independence is real, not a sampling or analytical artifact. We summarize the data available for WNP humpback whale genetics and movements below. No data allowing meaningful morphological comparisons are available within the North Pacific humpback whale subspecies. Although the WNP DPS and stock likely comprise at least two DIPs, at present there is insufficient data to assess population abundance, range, and threats for the DIPs separately.

Lines of Evidence for Demographic Independence

Movements

Strong fidelity to both feeding and wintering areas has been observed in North Pacific humpback whales, but movements between feeding and wintering areas are often complex and varied (Calambokidis et al. 2008; Barlow et al. 2011). An overall pattern of migration has recently emerged. Asia and Central America are the dominant wintering areas for humpback whales that migrate to feeding areas in lower latitudes and more coastal areas on each side of the Pacific Ocean, such as California and Russia. The Revillagigedo Archipelago and Hawaiian Islands are the primary winter migratory destinations for humpback whales that feed in the more central and higher latitude areas (Calambokidis et al. 2008). However, there are exceptions to this pattern, and it seems that complex population structure and strong site fidelity coexist with lesser known, but potentially high, levels of plasticity in the movements of humpback whales (Salden et al. 1999).

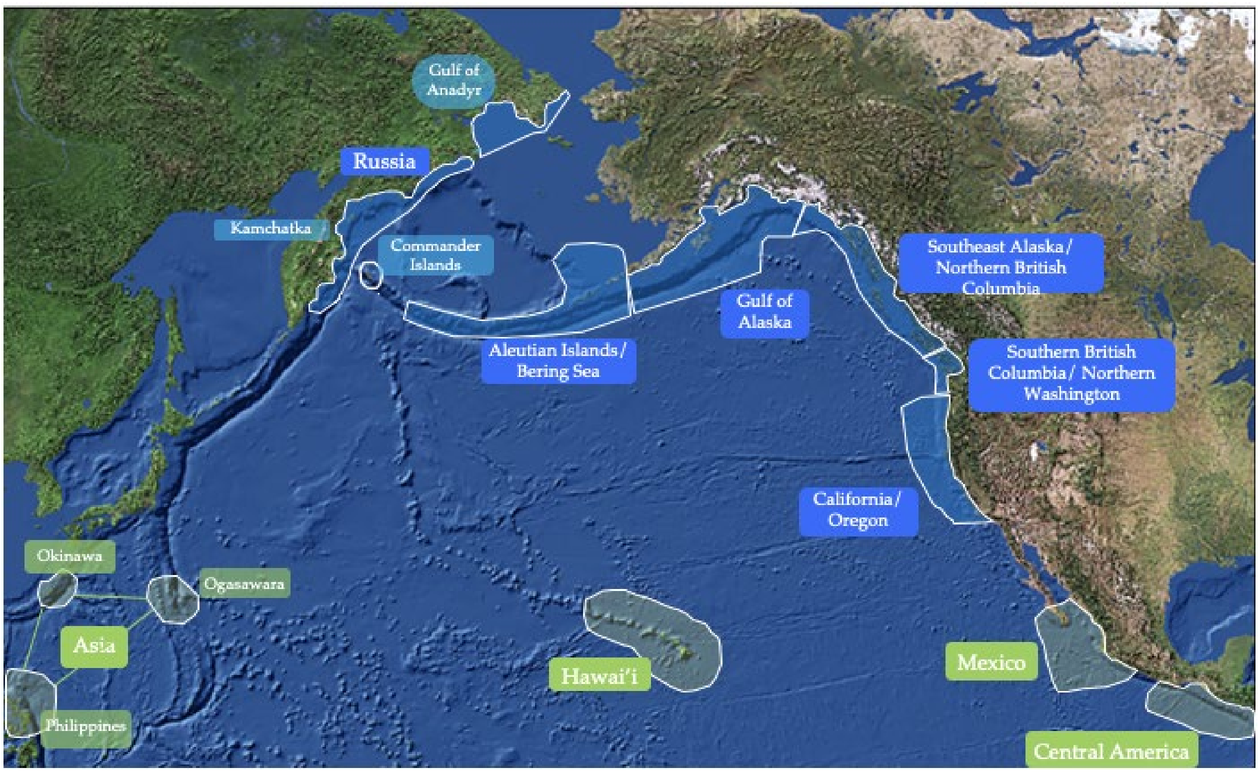

Figure 1. Winter (green) and summer (blue) areas sampled as part of SPLASH. Labels represent the regional Strata used in Wade (2017, 2021), where the Gulf of Anadyr and Commander Islands are part of the Aleutian Islands and Bering Sea stratum in Wade (2017), and reassigned to the Russia stratum in Wade (2021). The polygons roughly enclose where survey effort occurred for each area.

Whaling records and historical sightings of humpback whales suggested Asian wintering areas extend across a broad region of the western North Pacific, from the South China Sea to the Philippines, and including the waters around Japan, the Korean Peninsula, the Mariana

Archipelago, and the Marshall Islands (Rice 1998). Three wintering areas within the western North Pacific with ongoing humpback whale research efforts were included within the SPLASH study, including the Babuyan Islands in the Philippines, and two regions of Japan, the mainland and offshore waters around Okinawa (Ryukyu Islands) and three island areas within Ogasawara (Bonin Islands) (Calambokidis et al. 2008). SPLASH did not include sampling effort within other historical wintering areas in the western Pacific.

Prior to SPLASH there was documented exchange of individual humpback whales between Okinawa and Ogasawara (Darling and Mori 1993), and as part of SPLASH movements of individuals between Ogasawara, Okinawa, and the Philippines were observed (Table 1, Calambokidis et al. 2008). Genetic data available at the time of the status review indicated that whales in Okinawa were not significantly different in their mitochondrial DNA (mtDNA) or nuclear DNA (nDNA) from those sampled in the Philippines (Baker et al. 2013). This pooled group differed substantially from whales sampled off Ogasawara and from all other feeding and wintering grounds included in the SPLASH study (Baker et al. 2013). Together, the movement and genetic data suggested that the Ogasawara area is both a wintering area and a migratory area for whales from Okinawa and the Philippines, as well as from other unsampled regions.

Table 1. Photographic identification matches between wintering areas within the Western North Pacific Distinct Population Segment. SPLASH matches (2004−2006, Calambokidis et al. 2008) are shown at the top of the table, with the values on the diagonal representing the number of unique identifications from the specific wintering area over the course of the SPLASH effort. Matches from more recent published studies are shown below, with citation in parentheses. When available, the sex of matched individuals is provided in parentheses. The number of unique identifications from new studies is shown on the diagonal.

SPLASH	Philippines	Okinawa	Ogasawara	Mariana Archipelago	Other North Pacific breeding areas
Philippines	77	5	5	NA	1 (Hawai‘i)
Okinawa		215	10	NA	0
Ogasawara			294	NA	1 (Hawai‘i)
Other published comparisons					
Okinawa (Acebes et al. 2021)	100 (26F, 41M)	1445	-	-	-
Ogasawara (Nakagun et al. 2020)	86 (14F, 40M)	-	1389	-	-
Mariana Archipelago (Hill et al. 2020)	1 (1 M)	4 (3M, 1U)	7 (3F, 2M, 2U)	31	0

M = male, F = female, U = unknown sex.

Building on the connections between Japanese wintering areas and the Philippines observed during SPLASH, several other new studies provide greater insight into the connectivity of these regions. Acebes et al. (2021) identified 100 whales (of a total catalog of 230 whales from the

Philippines) seen in both the Philippines and Okinawa (n = 1,445), including 8 whales seen in both regions in the same year. Nakagun et al. (2020) compared the Philippines catalog with one of two catalogs available for Ogasawara (n = 1,389), finding 86 matches, supporting the SPLASH findings that whales that are seen in the Philippines use and transit past Ogasawara, while a much larger cohort of whales in the Japanese wintering area either stays in Ogasawara or transit from there to other wintering areas. Kobayashi et al. (in review) found high interchange between whales photographed at Amami Oshima and Okinawa (both within the Ryukyu Archipelago), and relatively lower interchange rates between both Ryukyu locations and Ogasawara, further establishing the that whales wintering within the Ryukyu Archipelago and the Philippines represent an Asian wintering aggregation.

New field efforts in the Mariana Archipelago have revealed that this region also represents a present wintering area for humpback whales and that there are connections between whales found there and those in other WNP wintering and feeding areas (Table 1). Hill et al. (2020) reported that among 31 individuals within the Mariana fluke ID catalog, 10 had been seen in other WNP wintering areas, including 7 matches to Ogasawara, 4 to Okinawa, and 1 to the Philippines (Table 1). They further found 3 individuals that had been identified on feeding grounds near the Commander Islands, but no matches to catalogs for the Chukotka and Kamchatka Peninsulas or elsewhere along the Russian mainland. Although sex is known for only 7 of the 11 animals matched among feeding and wintering areas, of those whales seen in both the Marianas and in the Philippines or Okinawa (n = 5), four were male, and one was of unknown sex. Three female whales were seen in both the Marianas and Ogasawara wintering areas.

The SPLASH effort also was the beginning of what have become regular annual surveys in Russian feeding grounds, carried out by the Russian Cetacean Habitat Project. The substantial increase in survey effort and number of identified whales within the broader Russian Far East, together with continued research efforts and catalog comparisons with research groups working in the Philippines, Japan, and now the Mariana Archipelago, has resulted in substantial additional information about movements, site fidelity, and linkages between specific feeding and breeding grounds in the WNP (matches summarized in Table 2).

Titova et al. (2018) compared 1,459 whales in Russian waters with 4,525 whales identified on all breeding areas during SPLASH, as well as expanded catalogs from the Philippines (2000−2006) and Okinawa (1989−2006). This effort was then further expanded in Titova et al. (2019a) using 435 additional new whales identified in 2015−2017 and including a ninth region within the Russian Far East (eastern Chukotka, or the Senyavin Strait), resulting in 24 new matches to feeding and breeding ground catalogs (included in Table 2). The combined efforts revealed 176 matches between feeding and breeding grounds, representing 10% of all humpbacks in the Russian catalog. Whales from Okinawa and the Philippines (combined) were seen at all Russian feeding areas except eastern Chukotka and western Kamchatka (Figure 2, Table 1), though the sampling effort off western Kamchatka has been very small (only 6 whales identified to date). Whales from Ogasawara were seen between the Gulf of Anadyr and eastern Kamchatka, except off the Koryak coast, though only 4 whales have been identified from the later region.

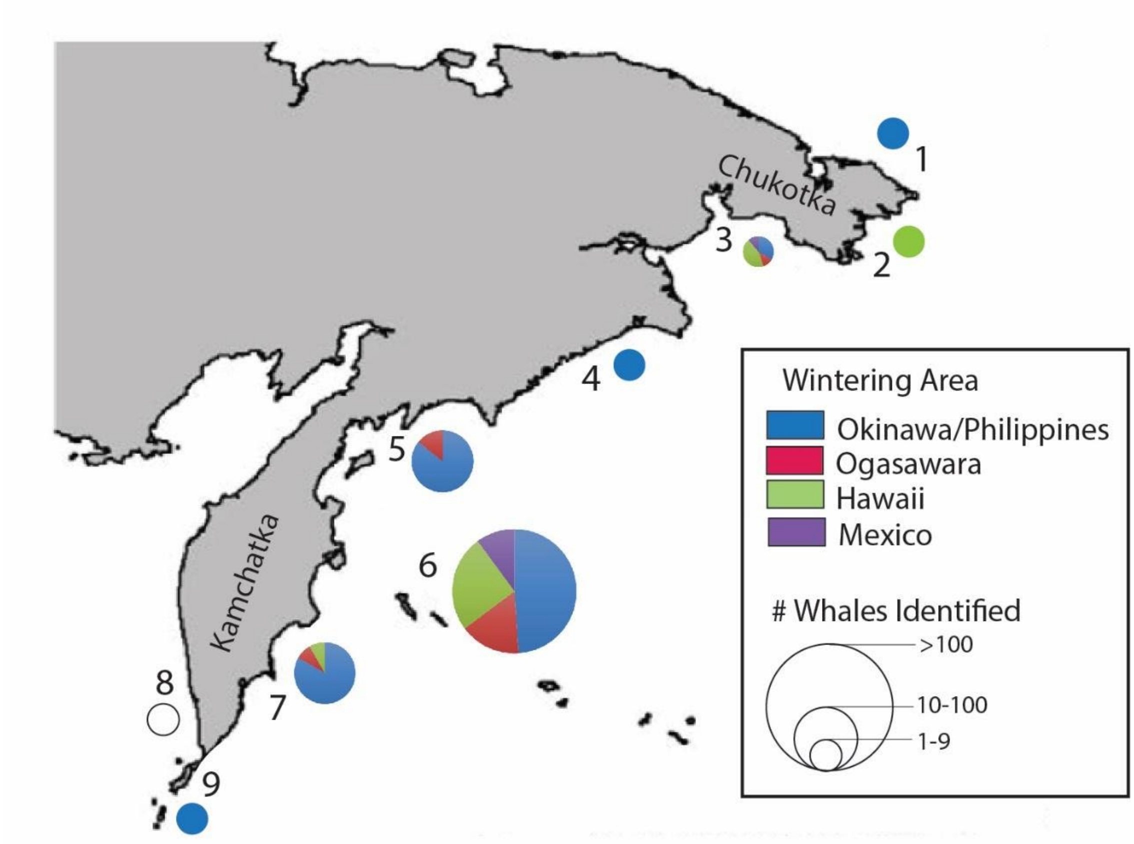

Figure 2. Re-created from data provided in Titova et al. (2019a) illustrating match rates between Russian feeding areas and North Pacific wintering areas for 2004–2017. The numbers on the map represent specific sampling areas: 1—Chukchi Sea, 2—Eastern Chukotka, 3—Anadyr Gulf, 4—Koryak coast, 5—Karaginsky Gulf, 6—Commander Islands, 7—eastern Kamchatka, 8—western Kamchatka coast, 9—northern Kuril Islands. There were no matches between western Kamchatka and the various wintering grounds.

The additional survey and photo-identification data from Russia provide a more detailed picture of the usage of feeding areas there by whales from various wintering region, though the conclusion are not significantly different than those arising from the SPLASH data alone. Eastern Kamchatka, the Karaginsky Gulf and Koryak coast collectively represent the Kamchatka stratum of various SPLASH analyses. New whale identifications and matches presented in Titova et al. (2019a) connect this region solely to Asian wintering areas, consistent with movement probabilities derived from SPLASH data sets in Wade (2017). New photo-identification data from eastern Chukotka/Senyavin Strait and the Anadyr Gulf (collectively called the Anadyr Gulf in SPLASH assessments) and Commander Islands (Titova et al. 2019a) connect 112 of a total 170 matched whales, or 65.9%, with Mexico and Hawaiʻi wintering areas (Table 2). These match rates are smaller than the movement probabilities from Russia to Asia (90.9%) for a larger Russia stratum presented in Wade (2021), although similar to a Bayesian optimized movement model derived from mtDNA frequencies developed by Lizewski et al. (2021), which estimated 68.6% of whales sampled on Russian feeding grounds originated from Asian wintering areas. Additional analyses will be required to develop movement probabilities that can incorporate new photo-ID data sets, particularly at the finer-scale required to assess the relative proportion of whales from various DPSs in specific Russian feeding areas.

Table 2. Number of photographic identification matches between Western North Pacific wintering areas and various North Pacific summer feeding areas. For each feeding area, the most recently reported catalog size (n) is provided after the area name. Within the body of the table, values in parentheses are those available from SPLASH (Table 1 of Wade et al. 2016). Titova et al. (2018, 2019a) included new data since SPLASH, with some regions represented at finer-scale. In particular, Kamchatka and the western Aleutian Islands (WAI) have been subdivided, with sub-regions indented below the SPLASH-defined region. Areas surveyed again since SPLASH are shown in italics, and new survey regions since SPLASH are in bold. Area abbreviations follow those designated during SPLASH: WAI = Western Aleutian Islands. EAI = Eastern Aleutian Islands. WGOA = Northern Gulf of Alaska. NGOA = Northern Gulf of Alaska.

Feeding Area	**Philippines**	**Okinawa**	**Ogasawara**	**Mariana Archipelago**	**HI / MX / CentAm**
Kamchatka	(5)	(14)	(7)		(0)
Koryak coast (n = 4)	0	2	0	0	0
Karaginsky Gulf (n = 111)	*10*	*21*	*5*	0	0
E. Kamchatka (n = 72)	*	*10**	*1*	0	*1 HI*
W. Kamchatka (n = 6)	*2^*	0	0	0	0
Commander Islands (n = 1,450)	*15*/(0)*	*68*/(0)*	*22/(1)*	*3*	*35/(2) HI, 13/(0) MX*
E. Chukotka / Senyavin Strait (n = 92)	**0**	**0**	**0**	**0**	**3 HI**
Gulf of Anadyr (n = 140)	*	3*/(1)	1		4/(3) HI, 1/(0) MX
Chukchi Sea (n = 24)		**1**			0
WAI		(1)		0	(2) HI
Kuril Islands (n = 20)	*1**	*2**	0	0	0
EAI				0	(2) HI
Bering Sea		(3)	(5)	0	(43) HI, (32) MX
WGOA			(2)	0	(26) HI, (24) MX
NGOA			(1)	0	(124) HI, (85) MX
E. North Pacific feeding areas	(0)	(0)	(0)	0	

HI = Hawai'i, MX = mainland Mexico and the Revillagigedos, CentAm = Central America

* Titova et al. (2019a) combined the Philippines and Okinawa breeding areas when matching with Russian feeding areas. The number of matches for the combined area is shown in the Okinawa column. Matches in the Philippines column are based on Titova et al. (2018).

^ These matches are not represented in Titova et al. (2019a). It is not clear whether the Titova et al. (2018) and SPLASH matches for this area were in error.

While low levels of inter-annual movements of individual whales between broadly defined feeding areas was not uncommon for some regions studied during SPLASH, there was not any documented exchange of whales observed off Russia or in the Aleutian Islands and Bering Sea. Some exchange was observed between the western and northern Gulf of Alaska between study years. Finer-scale examination of movements within the broadly defined Russian feeding ground also revealed no movements between the Commander Islands, Gulf of Anadyr, and the Kamchatka Peninsula (Calambokidis et al. 2008). However, more recent within-Russia evaluations, incorporating many additional years of survey and photo-ID effort, have revealed inter-annual movements among Russian feeding grounds (see Figure 2). The highest rate of interchange was observed between the Gulf of Anadyr and Chukchi Sea and between eastern Kamchatka and the Karaginsky Gulf, and the greatest number of individuals was resighted between the Commander Islands, eastern Kamchatka and Karaginsky Gulf (Titova et al. 2019a). Site fidelity on feeding grounds in Russian waters has only been examined for the Commander Islands, a region with several years of repeated survey effort. Within the Commander Islands, 28.9% of individuals were encountered in more than one year (Titova et al. 2018), with no significant differences in the return rate for different wintering grounds.

Genetics

Samples collected during SPLASH provided the first indication of finer division within the western North Pacific feeding and wintering areas. Baker et al. (2013) reported significant differentiation in mtDNA haplotype frequencies between Ogasawara and both Okinawa ($F_{ST} = 0.059$, $p < 0.001$) and the Philippines ($F_{ST} = 0.068$, $p < 0.01$) (Table 3), leading to the conclusion that there are likely 2 WNP wintering units that overlap or mix in Ogasawara: one that winters in Okinawa and the Philippines and a second that winters in an unsampled region of the central or western Pacific (Bettridge et al. 2015).

Table 3. Pairwise comparisons of mtDNA haplotype frequencies between Western North Pacific wintering areas compiled from SPLASH (Baker et al. 2013), and with the addition of samples from the Mariana Archipelago (Hill et al. 2020). Values are FST with significant differences indicated in bold with *** p < 0.001, ** p < 0.01, * p < 0.05.

	Philippines	Okinawa	Ogasawara	Mariana Archipelago
Philippines	-			
Okinawa	0	-		
Ogasawara	**0.069 ****	**0.059 *****	-	
Marianas	**0.078 ***	**0.066 ***	0.351	-
Hawai‘i	**0.276 *****	**0.268 *****	**0.075 *****	**0.074 ****
Mexico−Revillagigedo	**0.103 ****	**0.040 *****	**0.075 *****	0.001
Mexico−Baja	**0.096 ****	**0.104 *****	0	0
Mexico−Mainland	**0.117 *****	**0.120 *****	**0.081 *****	0.005
Central America	**0.078 ***	**0.117 *****	**0.228 *****	**0.097 ****

Three genetic studies carried out since SPLASH have provided finer-scale examination of genetic connectivity between WNP feeding and wintering areas. Richard et al. (2018) examined finer-scale differences in humpback whale structuring on Russian feeding grounds through comparison of samples collected over an 8-year period in the Commander Islands and Karaginsky Gulf with the broader SPLASH data set. This analysis used standardized haplotypes definitions consistent with Baker et al. (2013) and did not report any new haplotypes, but also did not subdivide haplotypes A+ and A-, thereby limiting the resolution of their findings related to the A-type haplotypes. Their analysis indicated strong mtDNA differentiation between the Commanders and Karaginsky Gulf ($F_{ST} = 0.18$, $p < 0.001$), suggesting maternal fidelity to these separate feeding regions. They further found significant differentiation between whales sampled at the Commanders and all eastern feeding grounds (northern Gulf of Alaska to California/Oregon), but no differences between the Commanders and the western Gulf of Alaska and western Aleutians (Table 4). Samples from the Karaginsky Gulf were differentiated from all other feeding grounds, although weakly from the western Aleutians ($F_{ST} = 0.09$, $p > 0.05$, $phi_{ST} = 0.18$, $p < 0.05$). Comparisons to wintering grounds found differentiation between the Commanders and all wintering grounds except Mexico ($F_{ST} = 0.01$, $p > 0.05$ Mexico-Revillagigedo and Mexico-Mainland, $p < 0.05$ Mexico-Baja), while Karaginsky Gulf whales differed from all wintering grounds except the Philippines ($F_{ST} = 0.02$, $p > 0.05$), and with weak, but still significant differences with Okinawa ($F_{ST} = 0.02$, $p < 0.05$).

With a set of 68 samples from the Commander Islands, Karaginsky Gulf, and Senyavin Strait over 4 years, Filatova et al. (2019) found the same pattern as described by Richard et al. (2018) for the Commander Islands and Karaginsky Gulf. They further found weaker, but still significant differences in haplotype frequencies between the Senyavin Strait and both Russian feeding areas (Commanders $F_{ST} = 0.078$, $p < 0.01$, Karaginsky $F_{ST} = 0.173$, $p < 0.01$), as well all other North Pacific feeding areas other than the eastern or western Aleutians and western Gulf of Alaska. Wintering ground comparisons (Table 5) also followed the same pattern as Richard et al. (2018), with comparisons for the Senyavin Strait significantly differentiated from Okinawa ($F_{ST} = 0.113$, $p < 0.001$), Philippines ($F_{ST} = 0.108$, $p < 0.01$), Hawaiʻi ($F_{ST} = 0.088$, $p < 0.001$), and Central America ($F_{ST} = 0.057$, $p < 0.05$). All other comparisons to Ogasawara and three Mexican wintering grounds were not significantly different. Together the results of Filatova et al. (2019) suggest the Senyavin Strait feeding area is of mixed origin (Mexico and Ogasawara), in contrast to the photo-ID results of Titova et al. (2019a), which showed the only matches for this region (n = 3) were to Hawaiʻi whales.

Hill et al. (2020), using 24 samples from the Mariana Archipelago, examined mtDNA haplotype frequencies compared to the SPLASH data set (Baker et al. 2013). They found significant differences between Mariana whales and those from 4 wintering grounds (Philippines, Okinawa, Hawaiʻi, and Central America) and 5 feeding grounds (Bering Sea, northern Gulf of Alaska, southeast Alaska, northern British Columbia, and California/Oregon/Washington). There were no significant differences between Mariana whales and those sampled during SPLASH from Russia, the western Aleutians, or Ogasawara. Haplotype diversity of the Marianas whales ($h = 0.837$) is notably higher than SPLASH samples from Okinawa ($h = 0.655$) or the Philippines ($h = 0.628$) and quite similar to that of Ogasawara whales ($h = 0.865$) suggesting interchange between Ogasawara and the Marianas. They also reexamined differences in haplotype frequencies between the Karaginsky Gulf and Commander Islands portion of the Russian feeding areas following the additional samples provided through Richard et al. (2018). As in Richard et al. (2018), there were strong differences between the Karaginsky Gulf and all other wintering areas except for the Philippines. However, strikingly, while there was strong differentiation between whales sampled at the Commander Islands with all other WNP wintering grounds, comparison to Mariana whales showed near identity ($F_{ST} = 0.0000$, $p = 0.68$). The Commander Islands are known to be a feeding ground for Hawaiʻi and Mexico whales as well, and the lack of significant differences between the Marianas wintering area and all Mexican breeding areas (Table 3), may suggest some interbreeding on the feeding ground, or inadequate sample from the Marianas to detect differences between these groups.

Table 4. Pairwise comparisons of mtDNA haplotype frequencies between Western North Pacific feeding areas. Results are compiled from SPLASH (Baker et al. 2013) and recent finer-scale studies in Russian waters. Values are F_{ST} with significant differences indicated in bold with *** p < 0.001, ** p < 0.01, * p < 0.05. Feeding grounds east of the NGOA are not included as there is little evidence of substantial exchange of WNP DPS whales into those areas. The number of samples (n) from each area is indicated under the feeding ground with superscript reference to the cited work. Area abbreviations follow those designated during SPLASH: WAI = Western Aleutian Islands. EAI = Eastern Aleutian Islands. WGOA = Northern Gulf of Alaska. NGOA = Northern Gulf of Alaska, SEAK = Southeast Alaska, NBC = Northern British Columbia, SBC = Southern British Columbia, CA/OR/WA = US west coast states of California, Oregon, and Washington. "NA" within the body of the table indicates no genetic comparisons have been made.

	Senyavin Strait	**Karaginsky Gulf**		**Commander Islands**		**WAI**	**EAI**	**Bering Sea**	**WGOA**	**NGOA**
	n = 31 †	n = 68 ‡	n = 12 †	n = 102 ‡	n = 25 †	n = 8 §	n = 36 §	n = 114 §	n = 96 §	n = 233 §
Karaginsky Gulf	**0.173 ****	-	-			NA	NA	NA	NA	NA
Commander Islands	**0.078 ****	**0.18 *****	**0.277 *****	-	-	NA	NA	NA	NA	NA
WAI	0	0.09	**0.120 ***	0	0.053	-				
EAI	0.008	**0.22 *****	**0.228 *****	0.01	**0.039 ***	0	-			
Bering Sea	**0.032 ***	**0.22 *****	**0.230 *****	0.01	0.025	0	0	-		
WGOA	**0.014**	**0.16 *****	**0.147 *****	0	**0.049 ***	0	0.003	**0.023 ****	-	
NGOA	**0.058 ****	**0.33 *****	**0.272 *****	**0.04 *****	**0.069 ****	0.017	0.011	**0.039 *****	**0.027 ****	-

† Filatova et al. 2019, ‡ Richard et al. 2018, § Baker et al. 2013

Table 5. Pairwise comparisons of mtDNA haplotype frequencies between all feeding areas and Western North Pacific wintering areas. Results are compiled from SPLASH (Baker et al. 2013) and recent studies within Russian waters and the Mariana Archipelago. Values are F_{ST} with significant differences indicated in bold with *** p < 0.001, ** p < 0.01, * p < 0.05. The number of samples (n) from each area is indicated under the feeding ground with superscript reference to the cited work. Area abbreviations follow those designated during SPLASH: WAI = Western Aleutian Islands. EAI = Eastern Aleutian Islands. WGOA = Northern Gulf of Alaska. NGOA = Northern Gulf of Alaska, SEAK = Southeast Alaska, NBC = Northern British Columbia, SBC = Southern British Columbia, CA/OR/WA = US west coast states of California, Oregon, and Washington. 'NA' within the body of the table indicates no genetic comparisons have been made.

	Senyavin Strait	**Karaginsky Gulf**		**Commander Islands**		**Russia**	**WAI**	**EAI**	**Bering Sea**	**WGOA**	**NGOA**	**SEAK**	**NBC**	**SBC**	**CA/OR/WA**
	n = 31 †	n = 68 ‡	n = 12 †	n = 102 ‡	n = 25 †	n = 70 §	n = 8 §	n = 36 §	n = 114 §	n = 96 §	n = 233 §	n = 183 §	n = 104 §	n = 51 §	n = 123 §
Philippines	**0.108 ****	0.02	0	**0.16 *****	**0.207 *****	0.036	0.05	**0.159 *****	**0.165 *****	**0.094 ****	**0.218 *****	**0.474 *****	**0.406 *****	**0.166 *****	**0.123 *****
Okinawa	**0.113 *****	**0.02 ***	0.005	**0.15 *****	**0.199 *****	**0.035 ****	0.05	**0.173 *****	**0.166 *****	**0.100 *****	**0.217 *****	**0.434 *****	**0.373 *****	**0.169 *****	**0.152 *****
Ogasawara	0.006	**0.08 *****	**0.107 ****	**0.04 *****	**0.074 *****	**0.016 ***	0	**0.052 *****	**0.064 *****	**0.031 *****	**0.097 *****	**0.269 *****	**0.211 *****	**0.063 *****	**0.081 *****
Marianas n = 24 ††	NA	**0.114 ****	NA	0	NA	0	0	0.02	**0.034 ***	0	**0.042 ***	**0.231 *****	**0.164 *****	0.025	**0.082 *****

† Filatova et al. 2019, ‡ Richard et al. 2018, § Baker et al. 2013, †† Hill et al. 2020

Conclusions

Data from two strong LoEs (movements and genetics) suggest that the WNP DPS of humpback whales comprises multiple DIPs. This is not surprising given the evidence presented in the 2015 status review that suggested two populations occur in this region: one with wintering grounds around the Philippines and Okinawa and the other in an as-yet unsampled location, but with a common migratory pathway at Ogasawara. Data collected since SPLASH provide some additional detail on the migratory connections within this region, aiding further review of fine-scale structure.

At present, we can identify two units within the currently defined WNP DPS. The Phil/Ok-NorthPac unit winters near the Philippines and Okinawa, and elsewhere in the Ryukyu Archipelago, and summers primarily off the Russian mainland and Commander Islands. The MI/Og-NorthPac unit winters off the Mariana Archipelago, Ogasawara, and other unidentified areas and summers off the Commander Islands and other feeding grounds off the Russian coast in the Bering Sea. Each of these units likely contain more than one DIP, though the specific wintering-feeding area connections of the DIPs are difficult to define, particularly for the MI/Og-NorthPac unit. Genetic data suggest maternal fidelity to the three separate regions within the Russian Far East—the Commanders, Karaginsky Gulf, and the Senyavin Strait portion of the Chukotka Peninsula (Richard et al. 2018, Filatova et al. 2019), regions with adequate sample size to carry out such analyses. These studies and Hill et al. (2020) also suggest migratory connections between the Philippines and Karaginsky Gulf, and between the Marianas and Commanders Islands, providing some evidence for migratory groups between these destinations, but without sufficient samples in neighboring feeding areas to further refine the identification of DIPs. There remains significant uncertainty on the migratory affiliation of a large portion of the whales in Russian waters, with some regions along the mainland (primarily in the Senyavin Strait) and in the Commander Islands affiliated with Hawai‘i or Mexico wintering areas. SPLASH data and the analysis of Wade (2017, 2021) indicate that there are connections between the WNP DPS and feeding grounds in the Aleutians and GOA, though those connections cannot be further refined with the available datasets.

Photo-ID matches indicate that both WNP units use waters around Ogasawara during migration to northern feeding grounds. Whales photographed in Ogasawara have been seen along the Ryukyu Archipelago and in the Philippines (e.g., Calambokidis et al. 2008, Nakagun et al. 2020, Kobayashi et al. in review), and in the Marianas (Hill et al. 2020), such that the region is clearly a migratory pathway for whales from other wintering areas. Photo-ID results from Nakagun et al. (2020) and Kobayashi et al (in review), as well as previous work, suggest some whales remain in the Ogasawara region for sufficient duration to consider that their primary migratory destination. Genetic results to date suggest that within the WNP wintering areas, whales wintering near Ogasawara are most closely related to those sampled near the Marianas. There are several active collaborations underway among researchers in Japan examining connectivity among wintering areas there, including regions with less frequent observations, including near Tokyo and the Izu Islands (including Hachijo Jima), and the migratory corridor off Hokkaido. These investigations, together with comprehensive photo matching studies among wintering and feeding areas within the WNP, will aid in further evaluation of DIP structure and the placement of boundaries between the currently defined units. For example, the photographic match of one whale seen off Hokkaido and Okinawa in the same year (Mitani et al. 2020) and matches of three whales between the Philippines and Okinawa and the Kuril Islands (Titova et al. 2019a) suggests that at least a portion of the Phil/Ok-NorthPac unit whales may roughly follow the island chains between wintering and feeding grounds. The migratory pathway for MI/Og-NorthPac whales, other than past Ogasawara, cannot presently be assessed without additional photo-ID data or telemetry data.

A recent increase in survey effort and photo-ID collection for humpbacks in Russian waters has provided more refined assessments of migratory connectivity with specific feeding aggregations in this region. As survey and photo-ID efforts have expanded, the catalog has grown substantially and the overall match rate for the Russian Far East is now lower (10%, Titova et al. 2018, 2019a) than was reported from SPLASH (30%, Burdin 2010). Aside from recent efforts in Russian waters, there has not been substantial additional effort in the western Aleutians, Bering Sea, or western Gulf of Alaska, hindering more detailed examination of the extent of use of this region by Philippines/Okinawa whales versus those from more recently sampled Mariana waters.

There remain several regions within the WNP where additional surveys for humpback whales may help refine not only the structure of this DPS, but also the abundance of the component units or DIPs. Several regions historically known to be occupied by humpback whales have not been extensively studied in recent years, including the Hainan region of China (Swinhoe 1870), Taiwan (Acebes et al. 2007, Yu 2002), waters around the southern part of the Korean Peninsula (Brownell 1981, Brownell et al. 2000, Baker et al. 2006), the west coast of Japan, and the Marshall Islands (Kellogg 1929). Recent passive acoustic observations from the central and western Pacific indicate humpback whales are heard in open-ocean regions away from known migratory pathways during the breeding season (Klinck et al. 2016, Allen et al. 2021, Darling et al. 2021). While these passive acoustic observations do not suggest discovery of large aggregations offshore, they do provide evidence that humpback whale wintering grounds may be more dispersed than traditionally thought, and such dispersed wintering grounds may contribute to the large portion of unaffiliated whales on WNP feeding grounds. Acoustic recordings of full songs or song fragments heard on feeding grounds may help to elucidate wintering ground affiliation for whales in various Russian and Alaskan regions (e.g., Schall et al. 2021).

Because there is still considerable uncertainty in the migratory connections of the WNP units it is difficult to draw boundaries for either the Phil/Ok-NorthPac unit or the MI/Og-NorthPac unit or to assess abundance at the unit level. Abundance has been estimated for the entire Russian feeding area based on SPLASH data (Barlow et al. 2011, Wade 2021), as well as for smaller geographic strata or individual feeding aggregations in Russia (Titova et al. 2019b, Wade 2017), though these evaluations are incomplete and do not account for known feeding/wintering ground structuring. At present, survey coverage of the Mariana Archipelago is insufficient to estimate abundance for that region. Abundance of the Phil/Ok-NorthPac unit may be best assessed on the wintering grounds given the substantial mixing that is occurring between whales from a variety of migratory groups on the feeding grounds.

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