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Evaluation of Mexico Distinct Population Segment of Humpback Whales as units under the Marine Mammal Protection Act

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Executive Summary

The Guidelines for Preparing Stock Assessment Reports Pursuant to the 1994 Amendments to the Marine Mammal Protection Act specify that a stock under the Act should, whenever possible, comprise a demographically independent population (DIP). Considerable new data suggest the existence of potential DIPs within some distinct population segments (DPSs) of the North Pacific subspecies of humpback whales (*Megaptera novaeangliae kuzira*). One putative DIP is composed of whales that winter in the waters off mainland Mexico (MMex) and summer off of the contiguous U.S. west coast (referred to here as the MMex-CA/OR/WA unit). The Mexico DPS also includes whales that winter in mainland Mexico and the Revillagigedo Archipelago and that feed in more northerly waters (mainly in Alaska and to a lesser extent in Russia). We refer to these whales as the Mexico-Northern Pacific unit (Mex-NPac). We consider whether there are data to suggest that these Mex-NPac whales represent a single or multiple DIPs, and if so whether there are adequate data to delineate them.

Martien *et al.* (2019) identify three ‘strong’ lines of evidence for delineating DIPs – movements, genetics, and morphology. Robust data from a single strong line of evidence 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 is real, not a sampling or analytical artifact.

The MMex-CA/OR/WA unit has robust data consistent with demographic independence for two strong lines of evidence: genetics and movements. The MMex-CA/OR/WA whales meet the DIP definition. There are no lines of evidence to suggest that further DIPs exist within this unit.

NMFS conducted a status review of humpback whales in 2015 that resulted in the identification of 14 DPSs of humpback whales. These include the Mexico DPS and the Central America DPS, which overlap to some extent on the feeding grounds along the U.S West Coast (Bettridge *et al.* 2015). Few data were available from the Pacific coast of southern Mexico at the time of the status review to include within the assessment and resulting description of the two DPSs (81 Federal Register 62660; September 3, 2016). Data collected since the 2015 status review indicate that the wintering area for the Central America DPS extends into southern Mexico. For example, genetic and movement data collected in recent years suggest that individuals that winter along the Pacific coast of southern Mexico off the states of Oaxaca and Guerrero (Figure 1) are likely part of the Central America DPS instead of the Mexico DPS, and therefore also part of the CentAm/SMex-CA/OR/WA unit¹ (Castillejos-Moguel 2015, Audley *et al.* 2016, García Chavez *et al.* 2016a,b, García Chavez *et al.* 2017, Steiger *et al.* 2017, García Chavez *et al.* 2018, López-Aquino *et al.* 2018, Auladell Quintana *et al.* 2019, Ramirez *et al.* 2019, Ortega-Ortiz *et al.* 2021). Some whales photographed in the area between Bahía Banderas off the state of Nayarit and the northern border of the state of Guerrero have been matched to the CentAm/SMex-CA/OR/WA unit, while others have matched to whales photographed to the north along the mainland within the range of the Mexico DPS. The proportion of whales in the area between Nayarit and Guerrero that belong to the MMex-CA/OR/WA unit may vary among years, and with substantially more effort in this area being made in 2014-2022, the extent of the geographic range of the MMex-CA/OR/WA and CentAm/SMex-CA/OR/WA units should be reconsidered in the near future.

¹ The CentAm/SMex-CA/OR/WA unit is a DIP comprised of the animals that winter off the coasts of Central America and southern Mexico and feed off the coasts of California, Oregon, and Washington. Information supporting the delineation of the CentAm/SMex-CA/OR/WA unit can be found in Taylor *et al.* (2021).

Available movement data are consistent with the existence of multiple DIPs within Mex-NPac. However, the photographic data have not been stratified in the way required to formally evaluate additional putative DIPs. Thus, for the Mexico DPS, there is evidence to delineate one DIP (MMex-CA/OR/WA) but insufficient analyses (and perhaps data) to resolve the multiple DIPs within the Mex-NPac unit.

Introduction

Most humpback whales occupy relatively coastal habitats for most of the year, which makes obtaining both genetic 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 2017, 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. It was the largest study of its kind for large whales, with over 400 researchers, and was designed such that areas throughout the range of north Pacific humpbacks were relatively equally represented with strong sampling (Calambokidis *et al.* 2008). 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) and identified 14 distinct population segments (DPSs) under the Endangered Species Act (ESA) (81 FR 62260; September 8, 2016). One of the DPSs that was identified by Bettridge *et al.* (2015) is the Mexico DPS, which is listed as threatened under the ESA. This DPS is described as whales that winter along the Pacific coast of mainland Mexico (MMex) and in the Revillagigedo Archipelago and transit through the Baja California Peninsula coast (Figure 1). The Mexico DPS feeds across a broad geographic range from California to the Kamchatka Peninsula, with concentrations in the California-Oregon, northern Washington-southern British Columbia, northern and western Gulf of Alaska and Bering Sea feeding grounds, though the feeding ground destinations differ between animals that winter off mainland Mexico versus Revillagigedo (Calambokidis *et al.* 2008, Wade 2017, Titova *et al.* 2018, 2019). This DPS was determined to be discrete based on re-sight data as well as findings of significant genetic differentiation between it and other populations in the North Pacific. The status review (Bettridge *et al.* 2015) noted that Revillagigedo differed in both movements from photographic identification and genetics from mainland Mexico but at a level deemed insufficient to meet the criteria to be separate DPSs under the ESA. Revillagigedo differ significantly from mainland Mexico using mitochondrial DNA (mtDNA) ($\Phi_{st} = 0.03$) and 10 microsatellites for nuclear DNA ($F_{st} = 0.0023$), but these differences were less than comparisons between the Mexico strata and Central America or Hawaii (Baker *et al.* 2013). Martínez-Aguilar (2011) examined photographs taken between 1986 and 2006 and estimated the matching rate between mainland Mexico and Revillagigedo at 3.6% using the entire pool of individuals

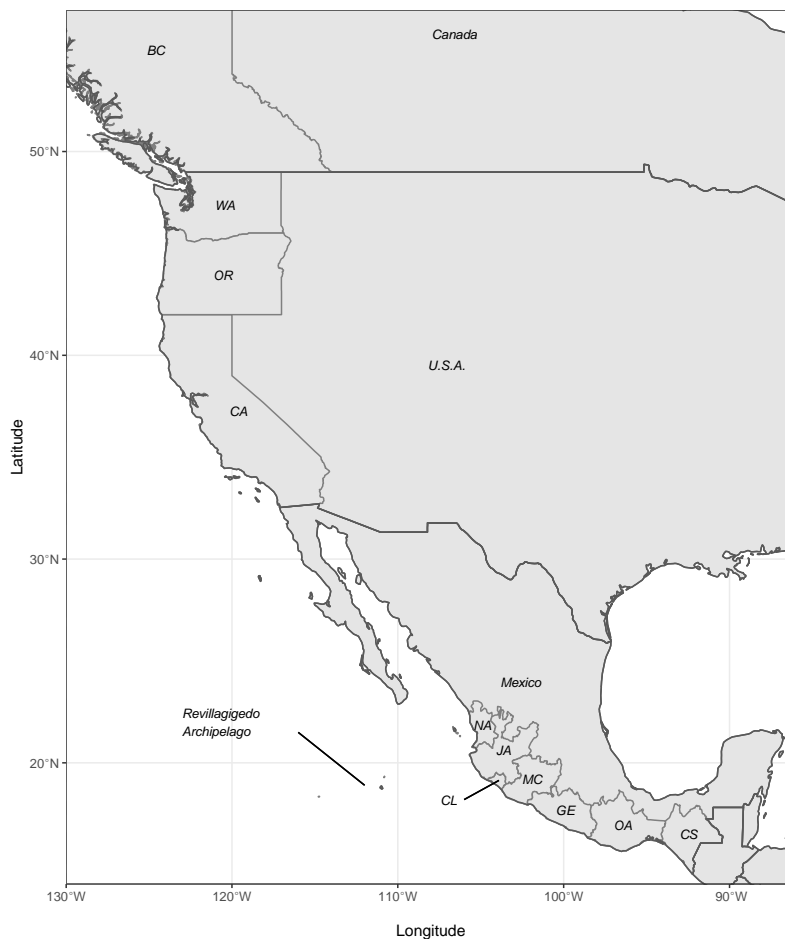
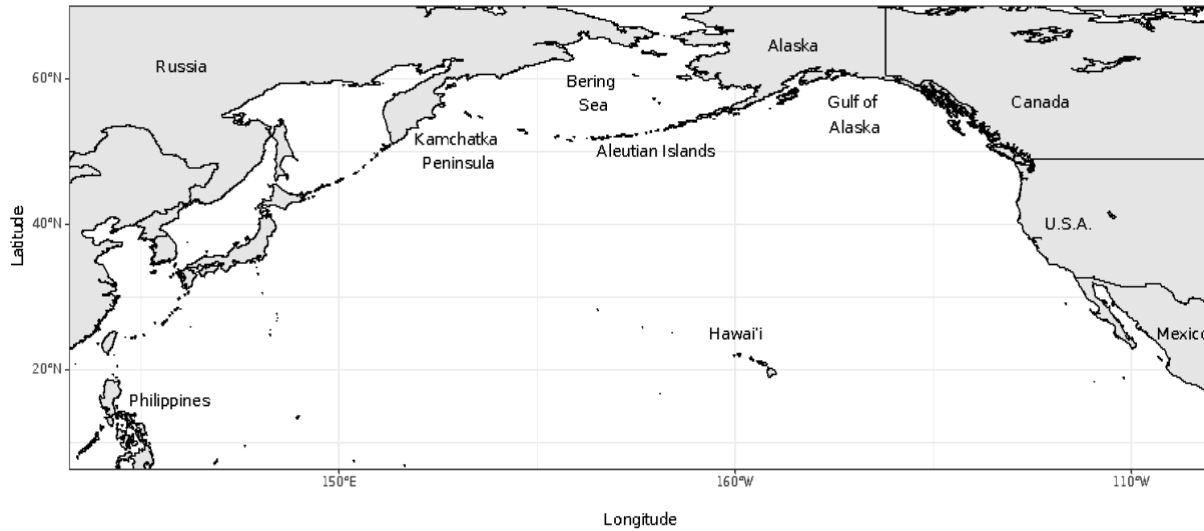


Figure 1. Maps of placenames referenced in the text. The MMex wintering ground is concentrated off the coasts of Nayarit (NA) and Jalisco (JA), with animals sometimes sighted as far south as Colima (CL) and Michoacán (MC). Country and state names abbreviations from north to south are: BC = British Columbia, WA = Washington state, OR = Oregon, CA = California, U.S.A. = United States of America, NA = Nayarit, JA = Jalisco, CL = Colima, MC = Michoacán, GE = Guerrero, OA = Oaxaca, CS = Chiapas, Guat. = Guatemala, El Sal. = El Salvador, Hond. = Honduras, and Nic. = Nicaragua.

Since the SPLASH study, considerably more data have been collected that further our understanding of humpback whale population structure in the Pacific. Field efforts off of both California/Oregon/Washington (CA/OR/WA) and mainland Mexico have resulted in dramatic increases in the numbers of photographs and genetic samples (Henry *et al.* 2020, Calambokidis *et al.* 2017, Audley *et al.* 2016, García Chavez *et al.* 2016a,b, García Chavez *et al.* 2017, García Chavez *et al.* 2018, Auladell Quintana *et al.* 2019, Ramirez *et al.* 2019, Ortega-Ortiz *et al.* 2021, Castillejos-Moguel 2015, López-Aquino *et al.* 2018). A new effort that uses contributions from both researchers and citizens (Happywhale, Cheeseman *et al.* in press) has produced many more matches of humpback whales and their associated movements in recent years. A new automated matching algorithm implemented by Happywhale has also improved matching between all photographs, including those from the earlier SPLASH efforts. These new data are used to improve the understanding of the population structure and migratory patterns of whales in these regions (Calambokidis *et al.* 2017).

NMFS' 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 comprise 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 currently designated at large geographically defined scales with names referring to feeding grounds (for example, the California/Oregon/Washington stock). However, these feeding ground aggregations do not represent DIPs. Rather, they comprise animals originating from multiple wintering grounds, which NMFS has recognized as different DPSs under the ESA. 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 (summarized below) 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 term 'herd' has been used in the literature to refer to different types of animal groups. The use of the term here does not imply that large groups of whales migrate in tight formation, as is seen in some ungulates nor does it imply strong social cohesion within herds, as is seen, for example, in elephant herds. While there is typically strong site fidelity to both feeding and wintering areas for humpbacks, the location of these areas may shift in years with unusual environmental conditions.

Management under the MMPA requires an abundance estimate for the stock. Estimating abundance and subsequent assessment, management, and conservation of a stock requires being able to delineate DIPs, typically by placing geographical boundaries. It is clear that such boundaries do not represent, in most cases, physical impediments to movement. For most DIPs there will be movements across the boundaries used to delineate them. Such movement could result from annual environmental changes that cause individuals to shift their preferred feeding or wintering area to improve their condition and maximize fitness. Even in typical conditions, there will be individual differences in the strength of site fidelity that results in some whales exploring far outside the range typical for its DIP. Such movements, be they individual or resulting from environmental changes, do not negate that fidelity to core regions is the rule, not the exception. It is this very fidelity to both feeding and wintering areas that generates the strong patterns seen in both photographic identification and genetic data over multiple years. Placing boundaries seeks to achieve the best management for the DIP by resulting in abundance estimates that, on average, are accurate and will result in overall management objectives being achieved when determining the impact of human-caused mortality.

The policy on stock designation (NMFS 2019) suggests high priority should be given for possible stock revisions for a number of conditions. The units considered here meet these conditions: 1) DPSs for the species to which the stock belongs have recently been recognized under the ESA, and 2) new data, analyses or other information for the stock have become available. The California-Oregon-Washington stock, as currently defined in the Pacific Stock Assessment Report, comprises individuals from multiple DPSs (all of the Central America DPS and parts of the Mexico DPS and Hawai'i DPS) making it incompatible with stock designation policy described in NMFS (2019).

Martien *et al.* (2019) identify three strong Lines of Evidence (LoE) 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 below the movements and genetic data that are available for delineating DIPs within the Mexico DPS. Within each LoE we consider both data on demographic independence and on geographic range. Data allowing meaningful morphological comparisons are unavailable within the North Pacific humpback whale subspecies. We examine one putative DIP that is composed of whales that winter in the waters off mainland Mexico (MMex) and summer off of the contiguous U.S. west coast (referred to here as the MMex-CA/OR/WA unit). We also consider whether there are data to suggest that the whales that winter off of mainland Mexico and the Revillagigedo Archipelago and that feed in more northerly waters (mainly in Alaska and to a lesser extent in Russia) represent multiple DIPs, and if so whether there are adequate data to delineate them. We refer to these Mexico DPS whales that feed further north and west of the MMex-CA/OR/WA unit as the Mexico-Northern Pacific (Mex-NPac) unit.

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, Ramirez *et al.* 2019, Ramirez Barragan *et al.* 2018). An overall pattern of migration has recently emerged. Whales wintering in the southern-most areas, like the Philippines and Central America, migrate to feeding areas at the western and southeastern ends (respectively) of the north Pacific feeding grounds (Steiger *et al.* 2017). 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 (from Washington state to the Bering Sea; Calambokidis *et al.* 2008).

The Mexico DPS wintering area exists in the Revillagigedo Archipelago and off mainland Mexico (Calambokidis *et al.* 2008, Martínez-Aguilar 2011, Bettridge *et al.* 2015). At the time the DPS was described, the data examined did not include the southern coast of Mexico separately, which likely is part of the Central America DPS (Castillejos-Moguel 2015, Dobson *et al.* 2019, Steiger *et al.* 2017, Ramirez *et al.* 2019, Calambokidis *et al.* 2017, Taylor *et al.* 2021).

Within the Mexico DPS, the proportion of whales migrating to California, Oregon, Washington, and southern British Columbia (CA/OR/WA/SBC) differed according to whether the wintering area was mainland Mexico or Revillagigedo. There were 167 matches of whales from mainland Mexico to a feeding ground. Of those, 119 were found in CA/OR/WA/SBC and the remainder were from Southeast Alaska through the Bering Sea. The largest number of matches were to the area between the Gulf of the Farallones and Oregon, with few matches to Washington and southern British Columbia (see Figure 5, Calambokidis *et al.* 2017, Steiger *et al.* 2017). Wade (2017) estimated that over 80% of whales that winter in mainland Mexico migrate to CA/OR (77.5%) and WA/SBC (4.3%; Table 1).

*Table 1. Movement probabilities between the two Mexico DPS wintering areas (mainland Mexico and Revillagigedo Archipelago) to five U.S. west coast, British Columbia, and Alaska feeding grounds, based on SPLASH data (extracted from Wade *et al.* 2017, Table 4). Abbreviations are as follows: GOA-Gulf of Alaska, SE-Southeast Alaska, NBC-Northern British Columbia, WA-Washington, SBC-Southern British Columbia, CA-California, OR-Oregon.*

| Area moving from | Area moving to | | | | | |
|------------------|----------------|--------------------------|-------|--------------|--------|-------|
| | Kamchatka | Aleutians/ Bering Sea | GOA | SEAK/ NBC | WA/SBC | CA/OR |
| Revillagigedo | 0.000 | 0.803 | 0.163 | 0.023 | 0.011 | 0.000 |
| Mainland Mexico | 0.000 | 0.135 | 0.034 | 0.012 | 0.043 | 0.775 |

In contrast, humpback whales from Revillagigedo were found to migrate almost exclusively to feeding grounds in the Gulf of Alaska and Bering Sea (Table 1; Calambokidis *et al.* 2008, González-Peral, 2011, Urbán *et al.* 2017, Wade 2017). Of 87 matches from Revillagigedo to feeding grounds, there were no matches to CA/OR and only 2 matches to WA/SBC. Wade (2017) estimated movement probabilities from Revillagigedo to the Aleutian/Bering strata as 0.803, to Gulf of Alaska at 0.163, and 0 to OR/CA strata

(Table 1). More recent data (Calambokidis *et al.* 2017) compare the CA/OR/WA/SBC area to the wintering areas and find some matches between Revillagigedo and OR/WA/SBC, with a few matches to California. Because there are no recent comparisons with feeding grounds further to the north, it remains unclear whether these more recently matched individuals represent a substantial proportion of whales from the Revillagigedo wintering area or could even be whales destined to move further north. Therefore, there may be some overlap between the Revillagigedo whales and the contiguous U.S. feeding destinations.

The coasts around the southern part of the Baja Peninsula provide a great deal of photographic identification and genetic data (Calambokidis *et al.* 2017). While there have been many photographic matches between the Baja coast and wintering areas further south, including the Revillagigedo Archipelago, the Mexico mainland, and areas occupied by the Central America DPS, there are also many whales that have only been identified and sampled off the Baja coast. However, it is plausible that these 'Baja-only' whales were sighted during their migration and have simply not yet been photographed or sampled at their wintering destinations. Therefore, it remains unknown whether the Baja Peninsula is a wintering destination for some humpback whales. Data from this area are complex to analyze because this area is within the migration corridor for multiple wintering areas. If there are whales with a winter destination of coastal Baja, they are not considered in this document to be part of the MMex-CA/OR/WA unit.

Results from the SPLASH study (Calambokidis *et al.* 2008) provide strong evidence that whales have strong site fidelity to feeding grounds. The inter-year photographic identification match rate of humpback whales within California was found to be 88% (Calambokidis *et al.*, 1996). When examining interchange among feeding areas based on sightings in 2004 and 2005, there were 47 matches within CA/OR and only 1 match from CA/OR to WA/SBC (the neighboring area). Of mainland Mexico whales sighted in more northerly feeding destinations (i.e., northern British Columbia and Alaska), none were seen in the following year in either CA/OR or WA/SBC. These data are not consistent with a hypothesis that whales from mainland Mexico switch feeding destinations between the more northerly and more southerly feeding grounds. The extensive photographic identification matching that was basin-wide from SPLASH therefore provides robust data supporting the MMex-CA/OR/WA whales as a DIP.

There are fewer data available for delineating DIPs within the Mexico DPS animals that migrate to feeding areas north of southern British Columbia. The northern feeding grounds with appreciable effort from SPLASH and relatively high matches with Mexico are the Bering Sea, the western Gulf of Alaska, the northern Gulf of Alaska, and southeast Alaska/northern British Columbia (Table 2 based on data in Table 10 in Calambokidis *et al.* 2008, González-Peral 2011, Urbán *et al.* 2017). Research conducted subsequent to SPLASH has identified 13 matches between the Mexico DPS and the Commander Islands (Titova *et al.* 2018, 2019). However, the available data do not allow for robust conclusions regarding the proportion of Mexico DPS animals that migrate to the Commander Islands nor whether that proportion differs substantially between mainland Mexico and Revillagigedo.

The SPLASH data revealed only 14 photographic matches between the mainland Mexico and Revillagigedo wintering areas, indicating strong site fidelity to these wintering areas. Similarly, inter-year matches among Alaska feeding areas (Table 3) are consistent with strong site fidelity to feeding areas. Estimates of movement probabilities to the Alaska feeding areas differ substantially between mainland Mexico and Revillagigedo. For instance, approximately 80% of whales that winter in the Revillagigedo

migrate to the Aleutian Islands/Bering Sea, while less than 14% of the whales that winter in mainland Mexico migrate to the Aleutian Islands/Bering Sea feeding ground (Wade 2017).

Table 2. Photographic identification matches made between wintering areas (columns) and feeding areas (rows) between uniquely identified whales pooling over years of the SPLASH study, 2004-2006 (taken from Table 10, Calambokidis et al. 2008). The numbers in the shaded gray fields give the number of unique identifications within each stratum. Abbreviations are as follows: WGOA-Western Gulf of Alaska, NGOA-Northern Gulf of Alaska, SEAK/NBC-southeast Alaska/northern British Columbia, Rev-Revillagigedo Archipelago, MMex-mainland Mexico (mostly near Bahia Banderas). Note that SEAK and NBC were summarized separately in Calambokidis et al. 2008 but are now consider to comprise a single feeding aggregation.

| Region | | Rev | MMex |
|----------|------------------------|-----|------|
| | Unique identifications | 562 | 690 |
| Bering | 491 | 11 | 11 |
| WGOA | 301 | 13 | 4 |
| NGOA | 1038 | 44 | 21 |
| SEAK/NBC | 1708 | 17 | 8 |

Table 3. Interchange between feeding areas based on sightings in 2004 (rows) and 2005 (columns). Taken from Calambokidis et al. 2008, Table 8. Abbreviations as in Table 2 except 'Aleut' is the abbreviation of Aleutian Islands.

| Region | Bering | WGOA | NGOA | SEAK | NBC |
|--------------|--------|------|------|------|-----|
| Aleut-Bering | 41 | 0 | 0 | 0 | 0 |
| WGOA | 0 | 33 | 1 | 0 | 0 |
| NGOA | 0 | 6 | 119 | 1 | 0 |
| SEAK | 0 | 1 | 4 | 175 | 16 |
| NBC | 0 | 0 | 1 | 13 | 74 |

Taken together, it is extremely unlikely that whales mix across either the wintering areas or the feeding areas such that humpback whales that migrate to the various Alaska and Russia feeding grounds comprise a single DIP, or that whales that utilize the two Mexico wintering grounds (i.e., mainland Mexico and Revillagigedo) occur in the same DIP. Consider, for example, the Bering Sea strata, which has no matches to either Gulf of Alaska area. It does, however, have matches from both wintering areas of Mexico. While it is marginally plausible that a single herd uses this area to feed and migrates to either wintering area without preference, that scenario is unlikely because there are few whales that are seen in both wintering areas (Table 3, and the 3% matching rate estimates in Martínez-Aguilar 2011). It is more plausible that there is one DIP that migrates from mainland Mexico to the Bering strata and another that migrates from Revillagigedo to the Bering strata. Similarly, there are likely separate mainland Mexico and Revillagigedo herds at other northern feeding grounds. However, data have not yet been stratified and analyzed by herds, which makes descriptions of putative DIPs within the Mex-NPac unit not possible at this time based on movement data.

Genetics

The Mexico DPS includes animals from both Revillagigedo Archipelago and mainland Mexico because the status review concluded that genetic and movement data were not sufficiently strong to meet the DPS criteria (Bettridge *et al.* 2015) for each area. However, these differences warrant re-examination when considering whether these different wintering areas or groups within them meet the DIP definition. Baker *et al.* (2013) found significant genetic differences when comparing mtDNA control region sequences between the mainland Mexico and the Revillagigedo Archipelago when using Φ_{ST} ($p < 0.05$) but not when using F_{ST} . However, González-Peral (2011) did find significant differences using F_{ST} and a greater sample size from the full three years of SPLASH data. Φ_{ST} uses genetic distances and accounts for within-stratum diversity, while F_{ST} uses frequency differences and does not account for within-stratum diversity, resulting in a negative bias in estimates of divergence (Meirmans and Hedrick 2011). Baker *et al.* (2013) also found statistically significant differentiation ($p < 0.05$) between Revillagigedo Archipelago and mainland Mexico using nuclear data (10 microsatellites). Because the genetic differences between Revillagigedo Archipelago and mainland Mexico are small, they were deemed not of the evolutionary level expected for a DPS. However, such differences would be consistent with evidence used to delineate DIPs, between which magnitudes of differentiation are expected to be smaller (O’Corry-Crowe *et al.* 2003, Martien *et al.* 2014, Taylor *et al.* 2010).

Baker *et al.* (2013) did not find significant nuclear differences between Central America and mainland Mexico, though the small number of loci and small sample size from mainland Mexico limited statistical power. It is interesting to note that the route to and from Central America passes by the mainland Mexico wintering area but is more remote from the Revillagigedo Archipelago. Breeding during migration could therefore explain the lack of nuclear differentiation between Central America and mainland Mexico. However, further research is necessary to evaluate this possibility.

Reproductive isolation is not necessary to delineate a DIP. Thus, the MMex-CA/OR/WA unit can still constitute a DIP even if some interbreeding occurs between it and other whales from Mexico or Central America DPSs. Whales from the MMex-CA/OR/WA unit can mate with each other, and hence meet the MMPA definition of a stock as ‘interbreeding when mature’. Since migratory whale herds migrate between common wintering and feeding areas, these units can interbreed when mature. However, they could also mate with other whales should mating occur during migration when whales from different migratory whale herds are mixed. It is also worth noting the MMPA stocks are defined as those occurring within waters under the jurisdiction of the United States, which often are the summering areas for migratory cetaceans. For some cetaceans, notably several stocks of beluga whales (see Beaufort Sea stock of beluga whales in Muto *et al.* 2020), the wintering area is not well known and yet the stocks have been designated based upon the best available scientific information and are managed by the United States under the MMPA.

The Baker *et al.* (2013) analyses pooled samples within feeding areas (where the MMex-CA/OR/WA animals mix with animals that winter off of Central America/southern Mexico) and in wintering areas (where whales from MMex-CA/OR/WA mix with Mexico DPS animals that feed off of northern British Columbia and Alaska). Consequently, Baker *et al.* (2013) do not present any analyses relevant to evaluating the DIP status of MMex-CA/OR/WA.

A new genetic analysis by Martien *et al.* (2020) directly addresses this question by stratifying samples into migratory herds. Martien *et al.* (2020) sequenced the mitogenomes of animals sampled off of California-Oregon that had been photographically identified on the mainland Mexico wintering ground. They refer to these samples as the MMex-CA/OR herd. There were no samples analyzed from Washington, so the Martien *et al.* (2020) herd name differs from the potential MMex-CA/OR/WA DIP discussed elsewhere in this document. They compared the MMex-CA/OR herd sample (n=50) to all animals sampled off of mainland Mexico (n=62), which includes members of the MMex-CA/OR/WA herd and all other herds that winter off mainland Mexico, regardless of their feeding ground affiliation. They found significant differentiation between the MMex-CA/OR herd and the mainland Mexico wintering ground ($\Phi_{st} = 0.044$, $p = 0.039$) that were comparable to the difference between the Central America DPS and MMex-CA/OR ($\Phi_{st} = 0.044$, $p = 0.035$), confirming that the MMex-CA/OR herd is not a random selection from its wintering ground (Table 4). The comparable levels of differentiation with the Central America DPS strongly suggest that the MMex-CA/OR unit is demographically independent with internal recruitment far more important to maintaining the unit than immigration.

Table 4. Pairwise estimates of genetic differentiation between two CA/OR herds and the mainland Mexico wintering aggregation. All tests are based on mitochondrial sequence data. P-values are based on 10,000 permutations. Taken from Martien *et al.* 2020.

| Strata | Φ_{ST} | p-value |
|---|-------------|--------------|
| Herd comparisons | | |
| CentAm-CA/OR (n=65) v. MMex-CA/OR (n=50) | 0.044 | 0.035 |
| Herd vs. wintering aggregation comparison | | |
| MMex-CA/OR (n=50) v. MMex wintering ground (n=62) | 0.044 | 0.039 |
| CentAm-CA/OR (n=65) v. MMex wintering ground (n=62) | 0.192 | 0.001 |

Differentiation between the MMex-CA/OR strata in Martien *et al.* 2020 and the Revillagigedo strata from Baker *et al.* 2013 was strong ($F_{st} = 0.0422$, $p = 0.002$, $\Phi_{st} = 0.1594$, $p < 0.001$). The high Φ_{ST} value between MMex-CA/OR and Revillagigedo strata reflects the frequency differences between the distantly related A-haplotypes (that make up over half the Revillagigedo strata and are uncommon in the MMex-CA/OR strata) and F-haplotypes (that are common in the MMex-CA/OR strata and uncommon in the Revillagigedo strata). Recall that Baker *et al.* (2013) found only small significant genetic differences between the mainland Mexico and the Revillagigedo Archipelago when using Φ_{ST} ($\Phi_{ST} = 0.030$, $p < 0.05$) but not when using F_{ST} ($F_{ST} = 0.004$, $p > 0.05$). These results confirm that the animals from mainland Mexico that are not part of the MMex-CA/OR/WA herd and therefore migrate to more northerly feeding grounds are more similar in genetic make-up to the Revillagigedo whales with similar feeding destinations than they are to the MMex-CA/OR/WA herd.

The strict maternal inheritance mode of mitochondrial DNA makes it particularly useful for assessing demographic independence (Martien *et al.* 2019). The statistically significant mitochondrial differentiation between the MMex-CA/OR/WA unit and all other groups to which it has been compared provides strong evidence of demographic independence (Martien *et al.* 2019). Many DIPs have been designated as stocks based on significant differences in mtDNA control region data. For example, all

beluga whale stocks use such genetic differentiation as a major component of the evidence for being DIPs and wintering areas for these DIPs are not even known (O’Corry-Crowe *et al.* 1997). Similarly, many harbor seal and harbor porpoise DIP delineations are based strongly on mtDNA data (O’Corry-Crowe *et al.* 2003, Morin *et al.* 2021). Thus, use of these data for the MMex-CA/OR/WA unit is consistent with these results as sufficient for finding this group to be demographically independent.

Strata for genetic comparisons within Mex-NPac unit all involve a mixture of different DPSs on the feeding grounds. Within the wintering areas, there has been no attempt to identify genetic samples within mainland Mexico and the Revillagigedo Archipelago that have photographs in both the wintering and northern summering areas. Thus, data from this LoE have not been stratified and analyzed in a way that allows evaluating any potential DIPs within Mex-NPac.

Geographic range

The MMex-CA/OR/WA whales range from the Mexico mainland through Washington state, with some animals found in southern British Columbia. Photo-identification based movement data available through 2018 suggest that the wintering range of the Central America DPS extends from Panama northward into waters off the southern coast of Mexico. Castillejos-Moguel (2015) found that interchange indices for whales photographed off the coast of Oaxaca were highest with Guerrero and Costa Rica, intermediate for Bahía de Banderas and the Baja California Peninsula, and lowest with Revillagigedo. Martinez-Loustalot *et al.* (2019) found that whales photographed in the states of Guerrero and Oaxaca have a high interchange index (0.83) with each other and a much lower interchange index to other wintering areas in Mexico (with the next highest value of 0.17 to the state of Colima to the north). Dobson *et al.* (2015) matched 60% (40/72) of whales photographed in Guerrero to destinations on the contiguous U.S. west coast; 13 were previously sighted off Central America and 6 off mainland Mexico. Recently collected genetic data also indicate that the animals that winter off of southern Mexico are more genetically similar to the Central America DPS than to the Mexico DPS. Animals sampled off of Guerrero and Oaxaca ($n = 51$) do not differ significantly in their mtDNA from the Central America strata from Baker *et al.* 2013 ($F_{ST} = 0.0114$, p -value > 0.05), but do differ significantly from the Mexico strata ($F_{ST} = 0.062$, p -value < 0.05) (Martinez-Loustalot *et al.* 2019). Similarly, there are significant differences between Martinez-Loustalot *et al.*’s Guerrero/Oaxaca stratum and the MMex-CA/OR stratum in Martien *et al.* (2020) ($F_{ST} = 0.033$, p -value = 0.021).

Together, the photo-identification and genetic data are consistent with the southern range of the MMex-CA/OR/WA unit extending at least to the southern border of Jalisco, with some animals ranging as far south as Colima and Michoacán in some years (Castillejos-Moguel 2015, Dobson *et al.* 2015, Steiger *et al.* 2017, Ramirez *et al.* 2019, Ramirez Barragan *et al.* 2018, Ortega-Ortiz *et al.* 2021, Calambokidis *et al.* 2020). A review of fluke IDs ($N=525$) and genetic data ($N=50$) collected off the coast of Guerrero (2014-2021) is currently underway. Resighting rates, migration and site fidelity patterns along with a larger body of genetic samples will contribute to this review and should provide a more complete understanding of the wintering range of the DIP in the near future.

Whales migrate along the coastal corridor, so during migration periods MMex-CA/OR/WA whales would be mixed with the CentAm/SMex-CA/OR DIP and some of the whales from Mexico DPS destined for northern feeding areas. The summer feeding area for the MMex-CA/OR/WA DIP is off the coasts of California, Oregon, Washington (including inland waters) and southern British Columbia. The proportion

of whales that feed in southern British Columbia is small and hence using the US/Canada border for the purposes of estimating abundance for MMex-CA/OR/WA DIP should be sufficient to achieve management objectives. Note that the whales that belong to the Hawai'i DPS that feed in Washington waters are not considered part of the MMex-CA/OR/WA unit. Wade (2021) estimated that approximately 58% of the animals sighted off of CA/OR and 25% of the animals sighted off WA/SBC originated from the Mexico DPS, and that these animals represented approximately 21% and 3% of that DPS, respectively.

Movement data suggest that the Mex-NPac unit uses the wintering areas of the Revillagigedo Archipelago and the same areas of mainland Mexico as the MMex-CA/OR/WA DIP. Migratory habitats would include both coastal areas (for whales migrating from mainland Mexico to northern feeding areas) and offshore areas if whales from the Revillagigedo Archipelago use more direct routes to feeding areas like the Bering Sea strata. Although some recent data suggest some whales from the Revillagigedo Archipelago summer in southern feeding areas (OR/WA/BC; Calambokidis *et al.* 2017), the proportion there is currently unquantified. The SPLASH survey suggests that the greatest representation of Mex-NPac is within 3 strata in Alaska: the Aleutians/Bering Sea, western Gulf of Alaska, and northern Gulf of Alaska, although some whales from the Mexico DPS were matched to Southeast Alaska and Russia (Calambokidis *et al.* 2008, Urbán *et al.* 2017, Titova 2018 and 2019). Wade (2017) estimated that most animals from Revillagigedo migrate to either the Aleutian Islands/Bering Sea (80.3%) or Gulf of Alaska (16.3%), while most mainland Mexico animals that are not part of the MMex-CA/OR/WA DIP migrate to the Aleutian Islands/Bering Sea (13.5%). Recent analyses indicate that some animals from the Mex-NPac unit migrate to the Commander Islands (Titova *et al.* 2018, 2019), though it is unclear what fraction of the unit these animals represent. To be inclusive, the feeding area borders for the Mex-NPac unit should range from the border between Southeast Alaska and British Columbia to the Commander Islands. Future analyses that stratify the photo-identification data by herd and correct for effort could result in refinement of these borders.

Conclusions

Robust data from two strong LoEs (movements and genetics) support a finding that the MMex-CA/OR/WA unit of humpback whales meet the DIP definition, with levels of movement and genetic differentiation similar to those used to define DPSs. There are no data to suggest further population structure within this unit. While it is likely that multiple DIPs exist within the Mex-NPac unit given the photographic data suggesting strong fidelity to both feeding and wintering grounds, analyses (and perhaps data) are not sufficient to delineate DIPs within this unit.

Because the MMex-CA/OR/WA DIP summers off the contiguous US west coast, the entire DIP was surveyed in a 2018 survey (Henry *et al.* 2020). It is anticipated that using both the survey data (which includes photographic identification, biopsy sampling and environmental data) and a larger photographic identification time series that allows better assignment of individual whales to DIP, estimates can be made of abundances of DIPs that summer within this area. Human-caused mortality can also be assigned proportionately using the same data. A separate survey, also conducted in 2018, produced an abundance estimate for humpback whales off the coast of British Columbia, Canada (Wright *et al.* 2021). However, there have been no abundance estimates for humpback whales in Alaska since the SPLASH efforts nor has there been estimates since that time of the proportion of animals from different DPSs using different feeding areas.

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