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EVALUATION OF HUMPBACK WHALES WINTERING IN CENTRAL AMERICA AND SOUTHERN MEXICO AS A DEMOGRAPHICALLY INDEPENDENT POPULATION

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Evaluation of Humpback Whales Wintering in Central America and Southern Mexico as a Demographically Independent Population

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U.S. DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

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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*), however this document considers evidence for a case where the DPS contains only a single DIP. This putative DIP is composed of the animals that winter in the waters offshore of Central America, nearly all of whom spend summers off of the U.S. west coast, called the CentAm/SMex-CA/OR/WA unit. A status review conducted in 2015 concluded that, based on genetics and movement data, this group of animals met the criteria of a DPS) (Bettridge *et al.* 2015), and they were subsequently listed as an endangered DPS under the Endangered Species Act (ESA).

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.

For the CentAm/SMex-CA/OR/WA unit, there are robust data consistent with demographic independence for two strong lines of evidence: genetics and movements. There are no lines of evidence to suggest that further DIPs exist within this unit.

Data collected since a 2015 status review (Bettridge *et al.* 2015) indicate that the wintering area for the Central American DPS extends into southern Mexico. Few data were available from the Pacific coast of southern Mexico at the time of the status review and the resulting description of the DPS (2016). However, 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 unit (Audley *et al.* 2016, García Chavez *et al*. 2016a,b, García Chavez *et al*. 2017, Steiger *et al*. 2017, García Chavez *et al*. 2018, Auladell Quitana *et al*. 2019, Ramirez *et al*. 2019, Ortega-Ortiz *et al*. 2021). Some whales photographed in the area between Bahia 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 2020-2022, the extent of the geographic range of the MMex-CA/OR/WA unit should be reconsidered in the near future.
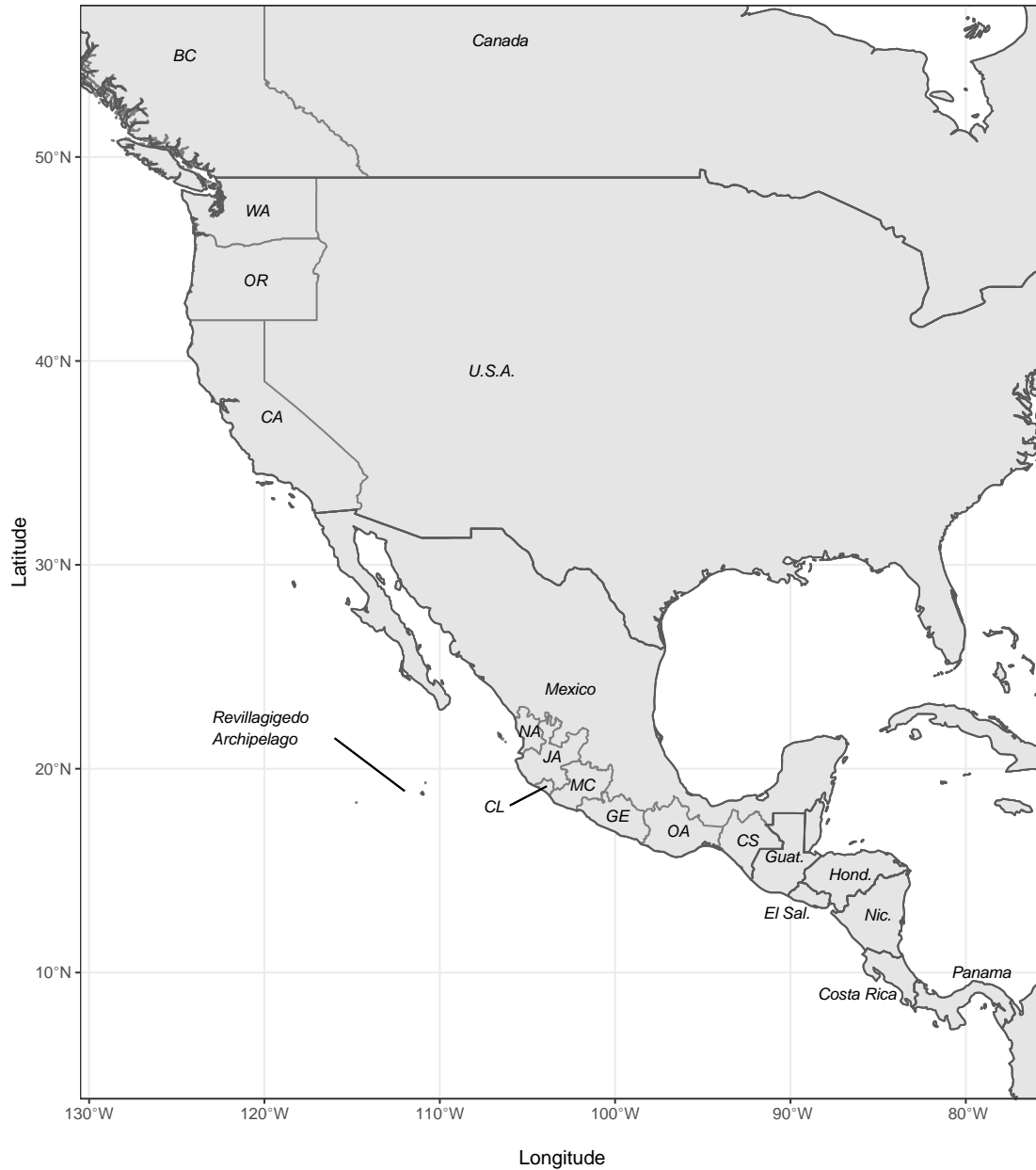
Figure 1. Map of placenames referenced in the text. The CentAm/SMex wintering ground extends north at least through Guerrero (GE), with animals sometimes sighted as far north as Michoacán (MC) and Colima (CL). Country and state names abbreviations from north to south are: BC = British Columbia, WA = 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.

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 Central America DPS, which is listed as endangered under the ESA. This DPS is composed of whales that winter along the Pacific coast of Costa Rica, Panama, Guatemala, El Salvador, Honduras and Nicaragua (and likely southern coastal Mexico, see later discussion) (Figure 1). Whales from this wintering ground feed almost exclusively offshore of California and Oregon in the eastern Pacific, with only a few individuals identified in the northern Washington/southern British Columbia (WA/SBC) feeding grounds (Figure 5, Calambokidis *et al.* 2017). The Central America DPS was determined to be discrete based on photographic re-sighting data, as well as findings of significant genetic differentiation between it and other populations in the North Pacific (F_{st} = 0.081, Φ_{st} = 0.087 comparing the Central America and the mainland Mexico strata, Baker *et al.* 2013). The status review (Bettridge *et al.* 2015) concluded that the wintering ground (and presumed breeding ground) of this DPS occupies a unique ecological setting, and its primary feeding ground is in a different marine ecosystem from most other humpback populations. Bettridge *et al.* (2015) therefore decided that loss of this population would also result in a significant gap in the range of the species.

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 Quitana *et al.* 2019, Ramirez *et al.* 2019, Ortega-Ortiz *et al.* 2021). 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 how the proportion of whales from the Central America wintering aggregation decreases going from southern California towards Washington (Calambokidis *et al.* 2017).

NMFS' Guidelines for Preparing Stock Assessment Reports Pursuant to the 1994 Amendments to the 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, it has long been recognized that, in most cases, feeding ground aggregations do not represent DIPs. Rather, they comprise groups of 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 (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 whether human-caused mortality is excessive.

The policy on stock designation (NMFS 2019) suggests high priority should be given for possible stock revisions for a number of conditions. The humpback whales that winter off of Central America and

southern Mexico 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 Mexican DPS and Hawaiian DPS) making it incompatible with 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 the animals that winter off of Central America and southern Mexico and feed off of the U.S. west coast as a DIP. We refer to this putative DIP as the CentAm/SMex-CA/OR/WA unit. 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.

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).

Based on SPLASH data, the Central America wintering area encompasses the areas offshore of the western coasts of Costa Rica, Panama, Guatemala, El Salvador, Honduras, and Nicaragua (Calambokidis *et al.*, 2008, Rasmussen *et al.*, 2002). However, the SPLASH study collected very little data from southern Mexico, although at least six photo-IDs were collected in south of Bahia Banderas and were treated as mainland Mexico samples in SPLASH, and later examination of these photo-Ids indicated four of the six photos matched to the U.S. west coast and one matched to Costa Rica (Cascadia, Unpublished data). Photo-identification data collected in this region in recent years suggests that the Central America wintering area likely extends into the southern Mexican coast (Dobson *et al.* 2015, Calambokidis *et al.* 2017, Ramirez *et al.* 2019, Auladell Quintana *et al.* 2019, Ramirez Barragan *et al.* 2018).

The SPLASH study (Calambokidis *et al.* 2008) found that 26 of 29 photographic matches between Central America and any feeding ground were to CA/OR, with the remaining 3 matches to WA/SBC. However, these matches were not corrected for effort, which was relatively low for Central America. After correcting for effort, Wade (2017) estimated that 93% of humpback whales from Central America migrate to the CA/OR feeding area, with the remaining individuals migrating to WA/SBC. A larger

photographic dataset for the U.S. west coast that dates through 2016 suggests a clinal distribution of the CentAm/SMex group, where matches were highest between the U.S./Mexico border and Monterey Bay (see Figure 5, Calambokidis *et al.*, 2017). Notably, the proportion of humpback whales from the Central America strata north of Oregon was lower in Calambokidis *et al.* (2017) than indicated by the model using SPLASH data (Wade 2017). The inter-year photographic identification match rate of humpback whales within California between 1986 and 1992 was estimated to be 88% (Calambokidis *et al.*, 1996). Similarly, Wade's (2017) analysis indicated that individuals showed strong site fidelity, returning to the same feeding and wintering area each year.

The critical parameter for determining demographic independence is the balance between internal and external recruitment into the group. Though this balance cannot be quantitatively evaluated based on the available movement data, the high site fidelity exhibited by Central America humpback whales to both their wintering and feeding areas is suggests that dispersal between it and other DPSs is low enough to render the CentAm/SMex-CA/OR/WA unit demographically independent.

Genetics

Using samples collected during SPLASH, Baker *et al.* (2013) analyzed genetic variation in a large (n = 2,193) sample of whales from 8 wintering and 10 feeding regions within the North Pacific, including Central America. Overall, the level of genetic divergence among wintering areas at the mtDNA control region was substantial (Φ_{ST} = 0.093). Pairwise estimates of divergence among wintering areas were very high for Hawaii vs Central America, for example. The wintering areas when all compared together (i.e. presuming panmixia within the North Pacific) were less strongly (but still significantly) differentiated at 10 nuclear microsatellite loci (F_{ST} = 0.006). Differentiation at nuclear loci is expected to be one quarter of that for the mtDNA control region, on average, due to differences in the ploidy and inheritance mode between the nuclear and mitochondrial genomes (Wright 1965, Larsson *et al.* 2009). However, the observed difference between the two marker types in this case is greater than the expected four-fold difference, which could suggest male mediated gene flow (Hedrick *et al.* 2007).

Baker *et al.* (2013) found significant genetic differences comparing mtDNA control region sequences from Central America animals to both the Mexican mainland and the Revillagigedos Islands (both included in the Mexico DPS). Martien *et al.* (2020) used full mitochondrial genome sequences and found that Central America animals differ significantly from the portion of the Mexico DPS with which it shares the CA/OR feeding ground. Baker *et al.* (2013) showed that haplotypic diversity was lower in the Central America stratum than in Mexico, which is consistent with the lower abundance estimates for that area compared with Mexico. Fifty additional genetic samples have been collected from Guerrero, southwest Pacific Mexico and analysis is pending.

Baker *et al.* (2013) did not find significant nuclear differences between the Central America and mainland Mexico samples but did find differences compared with the Revillagigedos. However, the small number of loci (10) used in the study and small sample size from mainland Mexico resulted in very low statistical power for detecting differentiation. It is interesting to note that a likely route to and from Central America passes by the mainland Mexico wintering area, but is more remote from the Revillagigedos Islands. 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 CentAm/SMex-CA/OR/WA unit can still constitute a DIP even if some interbreeding occurs between it and whales from the Mexico DPS. Whales from the CentAm/SMex-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 that 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 and are managed by the United States under the MMPA.

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 Central America wintering aggregation 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 evidence 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 (O'Corry-Crowe *et al.* 2003) and harbor porpoise (Morin *et al.* 2021) DIP delineations are based strongly on mtDNA data. Thus, use of these data for the CentAm/SMex-CA/OR/WA unit is consistent with past delineation of DIPs.

Geographic Range

Though the Central America DPS was described as occupying wintering areas off the Pacific coasts of Costa Rica, Panama, Guatemala, El Salvador, Honduras, and Nicaragua (Calambokidis *et al.*, 2008, Rasmussen *et al.*, 2002, Bettridge *et al.* 2015), photo-identification based movement data available through 2018 suggest that the wintering range extends from Panama northward into waters off the southern coast of Mexico. 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 in the states of Oaxaca and Guerrero are more genetically similar to the Central America DPS than to the Mexico DPS (Martínez -Loustalot *et al.* 2019). 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 winter range of the CentAm/SMex-CA/OR/WA unit extending northwards to include the states of Oaxaca and Guerrero, with some animals ranging even farther north (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.

The summer range of the DIP is almost exclusively off the coasts of California and Oregon, with fewer whales occurring as far north as Washington and occasionally in British Columbia. Surveys within these areas are useful for estimating the abundance of the DIP within these waters, taking into consideration available information on the mixing and proportions of whales from other wintering areas as well.

Conclusions

Robust data from two strong LoEs (movements and genetics) support a finding that the CentAm/SMex-CA/OR/WA unit of humpback whales meet the DIP definition. Similar to the findings of Bettridge *et al.* (2015), available lines of evidence demonstrate group fidelity to both winter and summer areas. Both photographic identification data and genetic data are consistent with this fidelity. There are no data to suggest further population structure within this unit. This DIP differs from the Central America DPS, as described in the listing of the DPS, in extending the wintering ground to the north based on data gathered in southern Mexico since the SPLASH effort.

Because the CentAm/SMex-CA/OR/WA DIP summers off the contiguous U.S. west coast, the entire DIP was surveyed in 2018 (Henry *et al.* 2020). It is anticipated that estimates can be made of abundances of DIPs that summer within this area 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. Human-caused mortality can also be assigned proportionately using these same data.

Acknowledgements

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