Spatial patterns in the migratory destinations of humpback whales (Megaptera novaeangliae) encountered in Canadian Pacific waters, based on photo-identification data and ocean basin-wide collaboration

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SPATIAL PATTERNS IN THE MIGRATORY DESTINATIONS OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) ENCOUNTERED IN CANADIAN PACIFIC WATERS, BASED ON PHOTO-IDENTIFICATION DATA AND OCEAN BASIN-WIDE COLLABORATION

by

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ABSTRACT

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Current knowledge of the abundance, movements, and population structure of humpback whales (*Megaptera novaeangliae*) at the scale of the entire North Pacific Ocean is based primarily on data collected during and prior to 2004-06. In recent years, new technology and international collaboration among research groups across the North Pacific have enabled comparison of photographic identification (photo-identification) images at an unprecedented scale, and the development of a more comprehensive data set than was previously possible. Using photo-identification data from all known humpback whale wintering areas, we sought to determine spatial patterns in the migratory destinations of humpback whales encountered in Canadian Pacific waters. Two methods were used to predict the spatially-varying probability of an individual humpback whale being matched to Hawaiian or Mexican wintering areas, based on the locations of encounters of the individual in Canadian Pacific waters. Results of both methods predicted that as the latitude of encounters increased in Canadian Pacific waters, a lower proportion of individuals were matched to Mexico, and a higher proportion to Hawaii. These results provide insights into the population structure of humpback whales in Canadian Pacific waters and how anthropogenic threats may affect whales that migrate to each of these areas differently.

RÉSUMÉ

McMillan, C.J., Ford, J.K.B., Cheeseman, T., Calambokidis, J., Audley, K., Birdsall, C., Byington, J.K., Currie, J., Darling, J.D., De Weerdt, J., Doe, N., Doniol-Valcroze, T., Dracott, K., Finn, R., Frisch-Jordán, A., Gabriele, C., Goodwin, B., Hildering, J., Jones, M., Lyman, E., Malleson, M., Martinez Loustalot, P., Pack, A.A., Quintana-Rizzo, E., Ransome, N., Shaw, T.J.H., Stack, S., Urbán R., J., Wray, J., Wright, B.M., and Yano, K.M. 2023. Spatial patterns in the migratory destinations of humpback whales (*Megaptera novaeangliae*) encountered in Canadian Pacific waters, based on photo-identification data and ocean basin-wide collaboration. Can. Tech. Rep. Fish. Aquat. Sci. 3519: v + 27 p.

Les connaissances actuelles sur l'abondance, les déplacements et la structure des populations de rorquals à bosse (*Megaptera novaeangliae*) à l'échelle de l'océan Pacifique Nord tout entier reposent principalement sur des données recueillies pendant et avant la période 2004-06. Ces dernières années, de nouvelles technologies et une vaste collaboration internationale entre les groupes de recherche du Pacifique Nord ont permis la comparaison d'images d'identification photographique (photo-identification) à un degré sans précédent ainsi que le développement d'un ensemble de données plus complet que jamais auparavant. À l'aide de données de photo-identification de toutes les aires d'hivernage connues, nous avons cherché à déterminer les patrons spatiaux des destinations migratoires des rorquals à bosse rencontrées dans les eaux canadiennes du Pacifique. Deux méthodes ont été utilisées pour prédire la manière dont varie, spatialement, la probabilité qu'un rorqual à bosse donné soit apparié aux aires d'hivernage hawaïennes ou mexicaines, en fonction des lieux de rencontre de l'individu dans les eaux canadiennes du Pacifique. Les résultats des deux méthodes ont prédit qu'à mesure que la latitude des positions augmentait dans les eaux canadiennes du Pacifique, une proportion plus faible d'individus était appariée au Mexique et une proportion plus élevée à Hawaï. Ces résultats donnent un aperçu de la structure de population des rorquals à bosse dans les eaux canadiennes du Pacifique et de la manière dont les menaces anthropiques pourraient affecter différemment les baleines qui migrent vers chacune de ces zones.

1 INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a wide-ranging marine species that undertakes long distance migrations between winter breeding grounds in tropical or subtropical waters, and summer feeding grounds in higher latitude areas. In the North Pacific Ocean, these migrations cross international boundaries, with at least ten different countries having jurisdiction over the known feeding and/or wintering areas. Obtaining abundance estimates and population structure information at the scale required for effective conservation and management of the growing population of North Pacific humpback whales thus tends to require large data sets and international collaboration among research groups.

Following severe depletion by industrial whaling until 1965, humpback whale populations in many areas have been increasing. As of 2006, the abundance of North Pacific humpback whales was growing at an annual estimated rate of 8% (Barlow et al. 2011). However, despite this high overall rate of increase, there is evidence of variability in growth rates among subsets of the North Pacific humpback whale population (Calambokidis and Barlow 2020). Management and stock delineation of humpback whales throughout the North Pacific Ocean also vary among nations. In Canadian Pacific waters, North Pacific humpback whales are currently considered to be a single population, listed as Special Concern under Canada's Species at Risk Act (SARA). In adjacent United States waters, however, humpback whales in the North Pacific Ocean are managed as four Distinct Population Segments (DPS), based on the wintering grounds where they have been sighted. Humpback whales that breed in Central American and Western Pacific waters are listed as Endangered under the U.S. Endangered Species Act (ESA), while humpback whales that breed in the waters off Mexico are listed as Threatened, and those that breed around the Hawaiian Islands are considered Not at Risk (NOAA 2016).

The North Pacific-wide SPLASH (Structure of Populations, Levels of Abundance, and Status of Humpbacks) project was conducted in 2004-2006 and involved the participation of over 400 researchers from ten countries (Calambokidis et al. 2008). Photographic identification (hereafter referred to as photo-identification) and genetic data were collected from all known feeding and wintering areas for humpback whales in the North Pacific (Calambokidis et al. 2008) and led to ocean basin-wide abundance estimates based on mark-recapture models, as well as an assessment of population structure based primarily on analysis of mitochondrial DNA (mtDNA; Baker et al. 2013). Abundance was estimated at 21,808 (CV = 0.04) whales for the North Pacific (Barlow et al. 2011), while abundance in coastal portions of Canadian Pacific waters was estimated at 2,145 whales (Rambeau 2008). Results from genetic analyses indicated significant differences in mtDNA haplotype frequencies among the four known wintering areas (Baker et al. 2013).

Analyses conducted using the SPLASH data set considered Canadian Pacific waters to comprise portions of two different humpback whale feeding areas. Humpback whales documented south of approximately 50 degrees latitude were included in the Southern British Columbia/Northern Washington (SBC/NWA) feeding group, while whales sighted north of 50 degrees were considered part of the Northern British Columbia/ Southeastern Alaska (NBC/SEAK) feeding group (e.g., Calambokidis et al. 2008, Barlow et al. 2011, Baker et al. 2013). Of the 116 individual humpback whales that were documented in NBC during SPLASH and matched to at least one wintering area, the vast majority (85%) were matched to Hawaii, while the remainder were matched to Mexico (Calambokidis et al. 2008). The 55 individuals documented in SBC/NWA during SPLASH and matched to at least one wintering area were more varied in their migratory destinations, with 36% matched to Hawaii, 58% matched to Mexico, and 5% matched to Central America (Calambokidis et al. 2008).

Since the completion of data collection for SPLASH, there have been significant changes in humpback whale abundance and distribution in many areas off the west coast of Canada. For example, during line-transect surveys conducted in 2004, no humpback whales were seen in the southern Salish Sea (Williams and Thomas 2007); however, recent dedicated and opportunistic efforts have indicated the presence of humpback whales in this area during all seasons (Miller 2020, McMillan et al. 2022). Due in part to the recent return of humpback whales to areas including the Salish Sea, as well as effort by dedicated research groups, tourism operators, and citizen scientists, extensive photo-identification data sets now exist for areas from which very little data were available for the SPLASH project.

Concurrently, technological advances have provided the opportunity for much more efficient large-scale collaboration than was possible during the SPLASH study. The automated image recognition platform “Happywhale” has facilitated the comparison of very large data sets for humpback whale photo-identification with error rates of only 1-3% (i.e., exceeding the accuracy of manual matching of identification photographs; Cheeseman et al. 2021). SPLASH was one of the largest international collaborative projects ever conducted for a whale population, resulting in a data set composed of 18,469 encounters of 7,640 individual humpback whales (Calambokidis et al. 2008, Cheeseman et al. in review). In comparison, as of 2021, the “Happywhale” data set consisted of 157,379 encounters of 27,956 individual humpback whales, contributed by 43 research groups and thousands of public contributors throughout the North Pacific Ocean (Cheeseman et al. in review).

The objectives of this report are to update the state of knowledge and identify current data gaps regarding the migratory destinations of humpback whales in Canadian Pacific waters, and to identify how the spatial distribution of photo-identification efforts and humpback whales may affect North Pacific-wide abundance estimates. This information is relevant to several initiatives. Planning is underway to use the collaborative ocean basin-wide data set and a mark-recapture approach to produce updated abundance estimates for humpback whales in the North Pacific Ocean (SPLASH-2). Additionally, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) conducted an updated assessment of the status of humpback whales in Canadian Pacific waters in late 2022, and a Management Plan for the North Pacific humpback whale in Canada is currently in development by Fisheries and Oceans Canada’s Species at Risk Program.

2 METHODS

Humpback whale photo-identification data were collected during dedicated and opportunistic effort conducted by researchers and citizen scientists throughout the North Pacific Ocean between 1985 and May 2022. See Cheeseman et al. (in review) for details about the “Happywhale” data set and the extensive collaboration and effort that has led to the compilation and maintenance of these data. Table 1 summarizes the major data contributors to the current analyses.

An encounter was defined as a single sighting of an individual humpback whale, recorded on a specific day at a specific location (Cheeseman et al. in review). Encounters used in the analyses included, at a minimum, a fluke photograph of the individual humpback whale or positive identification based on identification photographs and confirmed by an experienced observer, encounter date, and encounter location. Fluke photographs were compared to the North Pacific-wide data set using the “Happywhale” photo-identification algorithm (Cheeseman et al. 2021, Cheeseman et al. in review). All matches made by the automated “Happywhale” algorithm were confirmed by an experienced human matcher to rule out false positives.

Given the opportunistic nature of the encounters contributed to the “Happywhale” data set, we evaluated these photo-identification encounters for how well they covered the estimated summer distribution of humpback whales in Canadian Pacific waters, i.e. whether there were areas where aggregations of humpback whales were predicted but for which there was little to no photo-identification effort. We compared the distribution of photo-identification encounters to spatially explicit predictions of humpback whale density produced by Wright et al. (2021). Wright et al. (2021) divided Canadian Pacific waters into three strata (see Figures 4 - 6) and used sightings data from ship-based systematic line-transect visual surveys conducted in 2018 and a density surface modeling approach to predict the summer (July-August) abundance of humpback whales per 25 km^2 grid cell in each of the strata. Abundance estimates were generated using a distance sampling approach; identification photographs were not collected during sightings (Wright et al. 2021). Using the same 5 x 5 km grid as Wright et al. (2021), we plotted the proportion of photo-identification encounters that occurred within each grid cell by dividing the number of encounters in that grid cell by the sum of all encounters in the relevant stratum. Similarly, we calculated the proportion of estimated humpback whale abundance per cell (from the 2018 surveys) by dividing the estimated abundance in each grid cell as predicted by the Wright et al. (2021) analysis by the total estimated abundance in its stratum. We then calculated the difference between the proportion of photo-identification effort and the proportion of humpback whale estimated abundance in each grid cell to highlight areas that were over- and under-represented in the photo-identification data set.

Individual humpback whales were grouped based on the wintering area(s) to which they were matched (i.e., Hawaii, Mexico, Central America, Japan, and all potential combinations of these). Sighting histories of whales matched to each of these wintering areas were determined based on data contributed to and maintained by “Happywhale”, including data from throughout Canadian Pacific waters, and from all wintering areas. Where possible, sex was determined based on: 1) DNA collected from biopsy or sloughed skin samples, and analyzed by one of the collaborators; or 2) in the case of females, confirmed sightings of an adult whale with a dependent calf.

Two different methods were used to determine which of the two primary migratory destinations (Hawaii and Mexico) humpback whales were more likely to migrate to, based on the locations of encounters of these individuals in Canadian Pacific waters. Generalized linear models (family: binomial, link: logit) were used to assess whether latitude is a significant predictor of a humpback whale being sighted in each of the two wintering areas, compared to a null model. To address the bias that could result from including an uneven number of encounters of each whale in these analyses, only one encounter per individual in Canadian Pacific waters was used in the models. For individuals that were encountered more than once in Canadian Pacific waters anytime during the study period, all encounters in these waters were plotted, and one encounter per individual was selected for inclusion in the models. Where possible (i.e. in the case of individuals with an odd number of encounters), the encounter with the median latitude in Canadian Pacific waters was used. For individuals with an even number of encounters, one of the two encounters closest to the mean latitude of each individual’s encounters was randomly selected. Model results were compared using Akaike Information Criterion (AIC) scores, and by considering the p-values associated with model parameters.

The spatially-varying probability of a whale sighted in Canadian Pacific waters being matched to either Hawaiian or Mexican wintering areas was also assessed using point pattern analysis (see Velázquez et al. 2016). A minimum bounding box was created around the geographic extent of the encounters of individual whales in Canadian Pacific waters matched to one of these two wintering areas (see Figure 10). A multitype point pattern data set was then created within this bounding box using the “spatstat” package in R (ver. 3.0-2; Baddeley et al. 2022), in which one encounter (as determined above) of each individual humpback whale in Canadian Pacific waters was “marked” (classified) by the breeding ground to which the individual was matched. The spatially varying probability (*p*) that a point at location *u* belongs to type *j* was then estimated using Nadaraya-Watson type kernel regression. This method uses each data point, along with surrounding data points, to estimate a locally weighted average (or in this case, a probability), using a Gaussian kernel as a weighting function (Baddeley and Turner 2005, Baddeley et al. 2015). The probability of a humpback whale at each location being matched to Hawaii or Mexico ($p_j(u)$) was estimated and plotted for each pixel in a fine-scale grid (in this case, a 128 x 128 pixel array). Note that probabilities in a given location did not always sum to one (i.e. *p*(Mexico) did not always equal 1-*p*(Hawaii)) because of the presence of individuals that were matched to more than one wintering area, and of individuals matched to a wintering area other than Hawaii or Mexico. Optimal bandwidth (i.e., the width of the kernel) was selected based on cross-validation.

3 RESULTS

The dedicated and opportunistic photo-identification effort conducted throughout Canadian Pacific waters resulted in 35,872 encounters of 3,376 individual humpback whales, collected between 1985 and May 2022. Encounters occurred primarily in coastal waters, with particularly intensive effort off northeastern Vancouver Island, in the waters around Gil Island, and in the Salish Sea (Figure 1). Most photo-identification data were collected in the years during and following the SPLASH project (2004-05 in the feeding areas; Figure 2) and during the months of June to October (Figure 3). The cumulative number of individuals identified in Canadian Pacific waters increased slowly until 2003, then grew quickly during the 2004 - 2005 SPLASH project and continued to increase rapidly until 2009 (Figure 2). The cumulative number of unique individuals increased more slowly from 2009 – 2015, and then began growing rapidly again, corresponding with the initiation of the “Happywhale” platform in 2015. The number of unique individuals appeared to level off as of 2020, though it should be noted that a substantial portion of research organizations’ data from 2020-2021 has not yet been processed and added to “Happywhale”, and most of the 2022 feeding season data were not included.

There were several areas where predicted abundance of humpback whales based on line-transect surveys and density surface modelling was high, but little to no photo-identification data had been collected. In the North Coast portion of the Canadian Pacific, parts of Queen Charlotte Sound had predicted densities of over three individuals per 25 km^2, yet no encounters from these grid cells are included in the “Happywhale” data set (Figure 4). Similarly, in the Offshore area, waters off northwestern Vancouver Island had predicted densities as high as six individuals per 25 km^2; however, very little photo-identification data were collected in this area (Figure 5). In the Salish Sea, there were a relatively high number of encounters in the waters south of Victoria, but fewer encounters in western Juan de Fuca Strait, where predicted density was over two individuals per 25 km^2 (Figure 6).

A total of 1,835 unique individual humpback whales documented in Canadian Pacific waters were matched to at least one wintering area. Of these, 1,176 individuals (64.1 %) were matched to Hawaii only, 608 (33.1 %) were matched to Mexico only, and three (0.2 %) were matched to Central America only. In addition, 37 individuals (2.0 %) were sighted in both Mexico and Hawaii, and 10 (0.5 %) were matched to both Mexico and Central America. No individuals in the available data set were matched to Japan.

Humpbacks matched to Hawaii, Mexico, or both, were encountered at all latitudes within Canadian Pacific waters (Figure 7). However, the results of each of the analyses conducted indicate that there is a latitudinal gradient in the proportion of individuals matched to each wintering area. Mean latitude of sightings of individuals matched to Hawaii only was 51.13°N (SE = 0.012), while mean latitude of sightings of individuals matched to Mexico only was 49.76°N (SE = 0.025, Figure 8). Mean latitude for individuals matched to both Hawaii and Mexico was 50.24° N (SE = 0.034). Latitude was a significant predictor of the estimated probability of an individual whale being sighted in Hawaii or Mexico. The predicted probability of individuals being matched to Hawaii increased with increasing latitude (coefficient estimate: 0.501, SE = 0.028, $p < 0.0001$; Figure 9a), while the predicted probability of individuals being matched to Mexico decreased with increasing latitude (coefficient estimate = -0.479, SE = 0.027, $p < 0.0001$; Figure 9b).

When estimated using nonparametric kernel smoothing, the spatially-varying probability of a whale sighted in Canadian Pacific waters migrating to each wintering area showed a similar gradient, with the probability of being matched to Hawaii increasing with latitude and the probability of being matched to Mexico decreasing with latitude (Figure 10). Predicted probability of an individual being matched to Mexico was highest off southwestern Vancouver Island and lowest in the northern portion of Canadian Pacific waters. Sample size was not large enough to predict the spatially-varying estimated probability of an individual being matched to both Hawaii and Mexico. Of the 37 individuals matched to both Hawaii and Mexico, 16 are male while the sexes of the other 21 are unknown.

Apart from a single encounter that took place off southern Haida Gwaii, all individuals matched to Central America were documented south of 49.3° N latitude while in Canadian Pacific waters (Figure 11). Though only 13 individuals known from Canadian Pacific waters were matched to Central America; seven of these showed inter-annual site fidelity to southwestern Vancouver Island, including four individuals (BCX0010, BCX0411, BCZ0075, and BCZ0131) whose sighting histories in the southern portions of Canadian Pacific waters span 23 or more years (Table 2). Ten of the 13 individuals matched to Central America were also matched to Mexican wintering areas, while the other three whales were matched to Central America only. Of the three individuals that were matched to Central America only, one is female, while the other two are of unknown sex.

4 DISCUSSION

Our analyses provide evidence of a latitudinal gradient in the proportion of whales in Canadian Pacific waters that migrate to Hawaii versus Mexico. The data set maintained by “Happywhale” provides a new opportunity to collaborate with research groups across the North Pacific Ocean at an unprecedented scale and has been invaluable in providing insight into the migratory destinations of humpback whales that feed in Canadian Pacific waters. The results of these analyses can help to inform future research efforts, as well as how to interpret and support international collaborative projects.

4.1 IMPACTS OF GEOGRAPHICAL AND TEMPORAL INCONSISTENCIES IN EFFORT

Figures 4 to 6 illustrate the portions of Canadian Pacific waters where predicted humpback abundance is high based on density surface modeling of sightings from line-transect surveys, but where very little photo-identification effort has been conducted to date. It should be noted that the predicted humpback abundances are based on data collected during a single set of surveys in one season and year (summer 2018); thus, model results do not reflect the seasonal or annual variability in whale distribution and may over- or under-estimate humpback density in some areas. Nevertheless, it is clear based on the encounter data that effort post-SPLASH has been primarily focused on coastal areas where research groups and tourism operators are based, and thus the more inaccessible and remote parts of the coast, some of which are predicted to have high humpback whale densities at least during summer, are under-represented in the current data set. This heterogeneity in sampling effort indicates that capture probabilities may differ among humpbacks in Canadian Pacific waters, i.e., that individuals that exhibit site fidelity to well-sampled areas are more likely to be captured (and re-captured) than individuals that tend to feed in less well-sampled areas. This has the potential to negatively bias abundance estimates if this data set is used in mark-recapture methods.

Effort was also inconsistent temporally, both within and between years. The majority of annual encounters were from July – September (Figure 3), and there was a much higher number of encounters in 2015 – 2019 than in previous years (Figure 2). This likely contributed to the higher number of "new" individuals documented during 2015 - 2019 (Figure 2) and could lead to overestimation of the recent population growth rate of humpback whales in Canadian Pacific waters.

Previous humpback whale abundance estimates based on mark-recapture analysis have used various methods to minimize the effect of biases associated with inconsistent sampling effort. For example, Barlow et al. (2011) used a simulation modeling approach to determine and correct for violations of the assumptions of mark-recapture models when applied to the SPLASH data, including the assumption of equal capture probability. Recent estimates from the United States West Coast have used adapted versions of classic mark-recapture models that allow capture probabilities to vary in space and time (Calambokidis and Barlow 2020). Additionally, it could be argued that individuals missed in feeding areas due to inconsistent sampling effort are likely captured on their wintering grounds, or vice-versa. However, there are still limitations in the state of knowledge regarding the intra- and inter-annual site fidelity of individual humpback whales, and thus the extent to which these biases may affect abundance estimates.

North Pacific humpback whales are known to show strong, maternally-directed site fidelity to their feeding grounds, both within and between years (e.g., Calambokidis et al. 1996, Rambeau 2008, Gabriele et al. 2017, Witteveen et al. 2017, Wray et al. 2020). However, long distance re-sights between feeding areas have been documented. For example, during SPLASH, the vast majority of re-sightings of individuals within and among years were in the same or adjacent feeding areas, but one individual sighted in Northern British Columbia (NBC) in 2004 was documented in the northern Gulf of Alaska in 2005 (Calambokidis et al. 2008). In Canadian Pacific waters, it is unknown to what extent the individual humpbacks that comprise the large aggregations sighted during line-transect surveys in remote areas like northwestern Vancouver Island and Queen Charlotte Sound may have been identified on other parts of the coast. Efforts to collect and match identification photographs from these under-represented areas would provide insight into the impact that heterogeneous sampling effort has had on our understanding of humpback whale abundance, distribution, and population structure in Canadian Pacific waters.

4.2 DELINEATION OF NORTHERN AND SOUTHERN FEEDING AREAS

Results of both methods to estimate the spatially-varying probability of individual humpback whales being matched to Hawaiian vs. Mexican wintering areas provided evidence of a lower proportion of individuals being matched to Mexico, and a higher proportion to Hawaii, with the latter increasing with latitude. However, there is no obvious latitude at which a strict delineation between a southern British Columbia (SBC) and NBC feeding area can be identified. This is consistent with results based on data from up to 2007, which indicated that resights of humpback whales that have been encountered at above 54 degrees latitude decreased linearly with each 0.5 degree toward the south (Rambeau 2008). Analyses to date have generally considered either 50 degrees latitude, or the northern end of Vancouver Island, to be the delineation between the NBC and SBC feeding areas. However, the results herein indicate that a more appropriate method of dividing the NBC and SBC feeding areas may be to base this on a quantified gradient of probability of migration to each wintering area, rather than on a single threshold latitude.

Although there is no clear delineation of distinct northern and southern feeding areas within Canadian Pacific waters, the latitudinal gradient in the proportion of individuals matched to each wintering area means that there is likely to be variation in the threats faced by whales that migrate to each of these areas. For example, the marine heatwave that began in 2014 appeared to have primarily impacted humpback whales off NBC and SEAK (i.e., whales more likely to breed in Hawaiian waters), with individuals in these areas showing declines in abundance, survival, and calving rates (Gabriele et al. 2022). It could thus be expected that climate change may represent a greater and more immediate impact on whales that breed in Hawaii than in other areas because of their spatial patterns when present in Canadian waters, and recent research has provided some evidence of such impacts. Mother-calf encounters off Maui dropped by 76.5% between 2013 and 2018 (Cartwright et al. 2019), while data from a long-term shore-based study provided evidence that birth rate and abundance of whales in Hawaii decreased significantly with warmer waters in feeding grounds during previous feeding seasons (Frankel et al. 2021). The long-term impacts of marine heatwaves and climate change, as well as the role that density dependence may have played in the observed results, are poorly understood.

Although large vessel traffic is increasing throughout Canadian Pacific waters, the waters of the southern Salish Sea and off southwestern Vancouver Island account for more than 50% of the total shipping traffic nationally (Simard et al. 2014), and traffic in this area is expected to increase significantly in future years (National Energy Board 2019). The waters off southwestern Vancouver Island have been identified as an area of high relative risk of a lethal collision between a vessel and a humpback whale (Nichol et al. 2017). Over half of the humpback whales sighted off southwestern Vancouver Island were matched to Mexican and/or Central American wintering grounds, and whales that migrate to these areas are considered Threatened and Endangered, respectively, under the U.S. ESA. Vessel strikes may thus pose an increased risk to humpback whales that comprise more vulnerable portions of the North Pacific population.

4.3 HUMPBACK WHALES MATCHED TO BOTH HAWAII AND MEXICO

A total of 37 individual whales sighted in Canadian Pacific waters were matched to both Hawaiian and Mexican wintering areas. It has long been known that there is some movement of whales between wintering areas; for example, a humpback whale photographed in Hawaiian waters in 1977 was documented off Mexico in 1979 (Darling and Jurasz 1983). During SPLASH, 17 of the 2,317 individuals sighted in Hawaii were also documented in Mexico (Calambokidis et al. 2008). More recently, at least two individuals have been documented in both Hawaii and Mexico during the same wintering season (Darling et al. 2022). Baker et al. (2013) provided evidence of male-biased gene flow, which is supported by the current photo-identification data set. Of the 37 whales documented in Canadian Pacific waters and matched to both Hawaii and Mexico, 16 are male and the sex of the other 21 individuals is unknown; none of these individuals are known to be female.

4.4 HUMPBACK WHALES MATCHED TO OTHER BREEDING AREAS

In the current data set, there were no matches between Canadian Pacific waters and western Pacific wintering areas (i.e., Japan). However, one individual sighted off Japan in 1990 and 1991 was sighted off the west coast of Vancouver Island in 1991 and in Japan again in 1993 (Darling et al. 1996), and multiple individuals have been sighted in the waters off both Hawaii and Japan (Darling and Cerchio 1993, Salden et al. 1999). At the time of compilation of the current data set, data from post-SPLASH years were not available from the western Pacific; thus, the absence of matches to Japan may reflect a paucity of data, rather than evidence that migration to this area from Canadian Pacific waters is very rare. Ongoing efforts by the North Pacific-wide collaboration to compile existing data will provide further insight into the number of individuals that have migrated between Canadian Pacific and western Pacific waters.

Humpback whales that breed in Central American waters are the most genetically distinct from other wintering areas, exhibiting haplotypes not found in any other wintering area (Baker et al. 2013). However, the majority (76%) of individual humpback whales sighted in Canadian Pacific waters that were documented in Central America were also matched to areas in Mexico (Figure 11). It is possible that some of these individuals were photographed as they were migrating past Mexico to or from their Central American breeding grounds. Baja California, in particular, is an area where whales from coastal and offshore Mexico tend to mix during their migrations north or south, which is reflected in this area having the highest haplotype diversity of any of the feeding or wintering areas during SPLASH (Baker et al. 2013). However, the high proportion of individuals sighted in both Central America and Mexico is also consistent with the evolving state of knowledge about the Central America DPS. At the time of its designation under the ESA, the Central America DPS was composed of the individuals that migrate to the Pacific coast of Central America between Panama and Guatamala (Curtis et al. 2022). However, until 2010, there were very limited photo-identification data available from southern Mexico, thus individuals that migrate to this area were not assigned to any DPS (Martinez-Loustalot et al. 2021, Curtis et al. 2022). It is now recognized that the Central American wintering area extends into southern Mexico, with recent abundance estimates for the Central American wintering area considering various potential northern limits for this subunit of whales, all of which include southern Mexican waters (Curtis et al. 2022). It would be beneficial for future analyses of migratory destinations of humpback whales sighted in Canadian Pacific waters to consider how varying the northern boundary of the “Central America” wintering area impacts our understanding of the proportion of humpback whales that migrate to each wintering area.

Except for a single encounter, humpback whales in Canadian Pacific waters that have been matched to Central American wintering areas have been exclusively documented off southwestern Vancouver Island. Many of these individuals exhibited long-term site fidelity to the waters off southwestern Vancouver Island and thus spend significant periods of time in areas with intensive vessel traffic. Humpback whales matched to Central American wintering areas have been documented in the waters off southwestern Vancouver Island in all months of the year, other than April and May. Recent measures aimed at reducing the threats of vessel strikes and disturbance to southern resident killer whales off southern Vancouver Island, including mandatory avoidance zones and vessel slowdown areas, have the potential to benefit humpback whales in this area as well; however, most of these measures are only in effect from June to November annually (Government of Canada 2022).

4.5 CONCLUSIONS

The results presented herein provide insight into the population structure of humpback whales in Canadian Pacific waters, as well as direction for future research efforts. Our analyses indicate that there is a latitudinal gradient in the proportion of humpback whales in Canadian Pacific waters matched to the two primary wintering areas, Hawaii and Mexico; however, that no specific division between the northern and southern feeding areas within these waters can be delineated. Collection and analysis of additional photo-identification data and genetic samples from under-represented areas, including the waters off northwestern Vancouver Island and in Queen Charlotte Sound, are required for a more fulsome understanding of the population structure of humpbacks in Canadian Pacific waters. Although currently managed as a single population under Canada’s Species at Risk Act, there is evidence that more vulnerable portions of this population (i.e. those that breed off Central America and Mexico) may be more susceptible to threats, including vessel strikes, that primarily impact the waters off southern British Columbia.

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7 TABLES & FIGURES

Table 1. Major data contributors (> 50 encounters included in the current analyses*). "Unique IDs" indicates the number of unique individual humpback whales documented by each organization and included in the current analyses. "Encounters" indicates the total number of encounters (i.e. a sighting of an individual humpback whale, recorded on a specific day at a specific location) from each organization included in the current analyses, while "Years" is the number of years from which these encounters were documented. "Org. Type" indicates each organization's primary focus, categorized as "Research" (directed humpback whale research) or "Tourism" (data collected opportunistically during wildlife tours).

Organization	Unique IDs	Encounters	Years	Org. Type
Pacific Canadian waters				
Fisheries and Oceans Canada	1655	4608	10	Research
Cascadia Research Collective	633	1187	31	Research
Marine Education and Research Society	529	17196	28	Research
Pacific Wildlife Foundation	490	728	25	Research
Humpback Whales of the Salish Sea	484	1618	18	Research
North Coast Cetacean Society	453	5494	17	Research
Ocean Wise Research Institute	276	1048	13	Research
Prince of Whales Whale Watching	223	634	15	Tourism
Port Angeles Whale Watch Co.	194	429	8	Tourism
Eagle Wing Tours	177	368	8	Tourism
Sooke Whale Watching	167	285	12	Tourism
Orca Spirit Adventures	137	261	5	Tourism
Juan de Fuca Express	122	133	12	Tourism
Bluewater Adventures	93	133	8	Tourism
Campbell River Whale Watching	81	272	11	Tourism
Ocean EcoVentures	56	83	6	Tourism
Maple Leaf Adventures	56	62	6	Tourism
Hawaii				
Pacific Whale Foundation	483	824	30	Research
Hawaii Marine Mammal Consortium	308	445	18	Research
Whale Trust	272	366	14	Research
Hawaiian Islands Humpback Whale National Marine	204	245	17	Research
Ultimate Whale Watch	159	188	7	Tourism
The Dolphin Institute	156	187	7	Research
Captain Steve's Rafting Adventures	89	97	15	Tourism
Atlantis Cruises	65	76	9	Tourism
Marine Mammal Research Program, University of Hawaii	49	56	1	Research
Blue Water Maui Charters	48	51	5	Tourism
Mexico				
Whale Watch Cabo	293	422	10	Tourism
ECOBAC	252	321	22	Research
Cabo Trek	199	254	9	Tourism
Programa de Investigacion de Mamiferos Marinos (UABCS)	173	220	14	Research
La Orca de Sayulita	168	266	10	Research
Vallarta Adventures	47	61	5	Tourism
Central America				
Cascadia Research Collective	6	9	4	Research
Simmons University	5	8	5	Research
Association ELI-S	3	3	2	Research

*Note that due to the limited data available from Central America, all organizations that contributed more than one encounter to the current analyses are included.

Table 2. Sighting histories of the 13 individual humpback whales documented in Canadian Pacific waters and Central American wintering areas.

Happywhale ID	Canada ID	First year in Canada	Most recent encounter in Canada	Years sighted in Canada	Months sighted in Canada	Sex	Other wintering areas?
725	BCY0798	2002	2002	1	June	Unknown	No
1070	BCX1528	2012	2012	1	August	Unknown	Mexico
1089	BCZ0131	1990	2016	11	June - November, January, February	Unknown	Mexico
4544	BCY0413	2004	2006	3	May, July, September, October	Male	Mexico
4931	BCY1131	2017	2018	2	June, October	Unknown	Mexico
5549	BCY0379	2004	2004	1	October	Unknown	Mexico
6628	BCZ0075	1996	2021	13	June - December	Male	Mexico
7090	BCY1081	2017	2018	2	August - October	Unknown	Mexico
16403	BCX0010	1991	2021	8	June - September	Unknown	Mexico
16744	BCX0411	1999	2021	7	June - September, November	Unknown	Mexico
21968	BCX0888	2005	2005	1	June	Unknown	Mexico
42690	BCY1128	2018	2018	1	October	Female	No
50366	BCY0825	2008	2008	1	August	Unknown	No

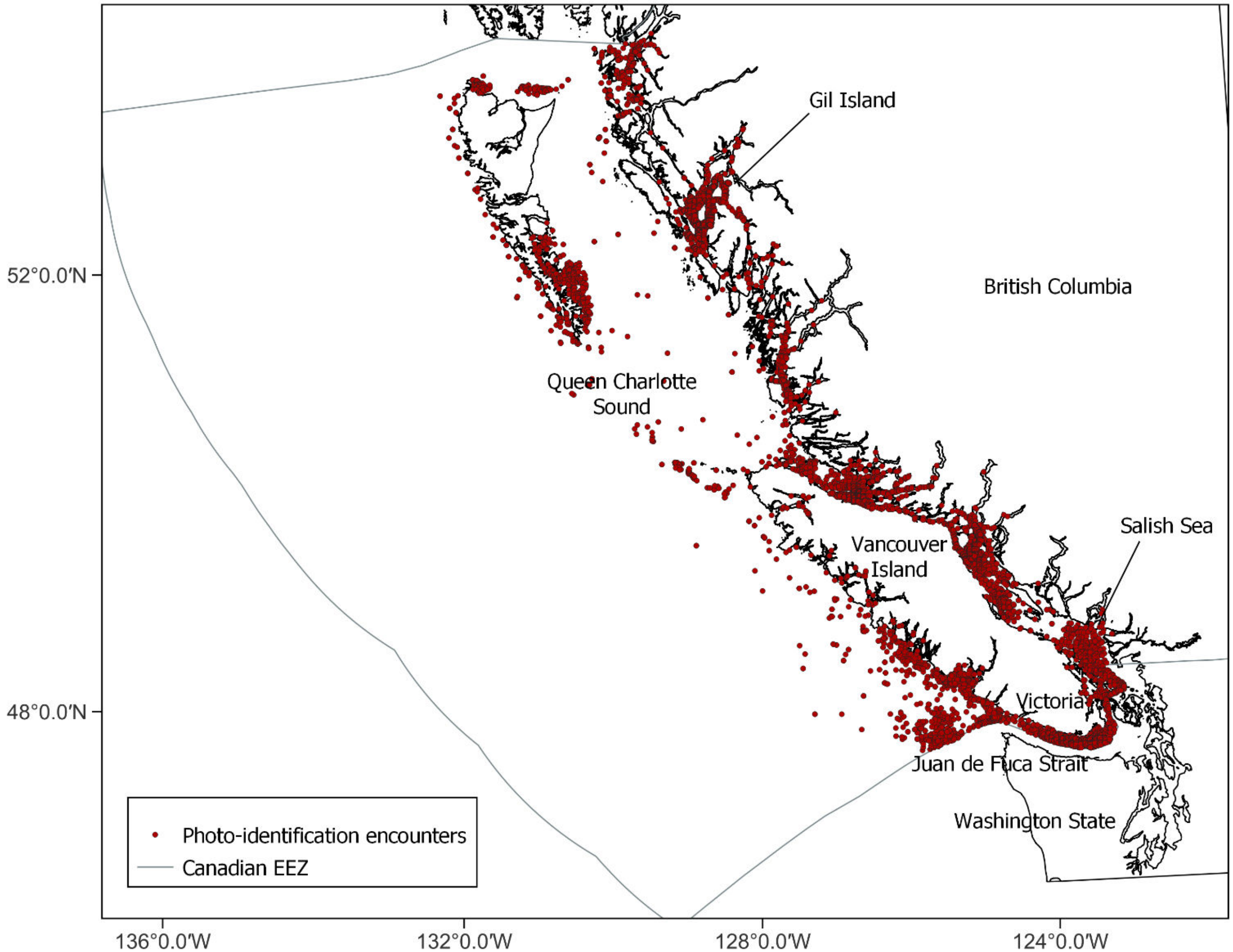


Figure 1. Locations of all humpback whale photographic identification encounters (35,872 encounters of 3,376 individuals) from Canadian Pacific waters contributed to the “Happywhale” data set between 1985 and May 2022 and included in the current analyses.

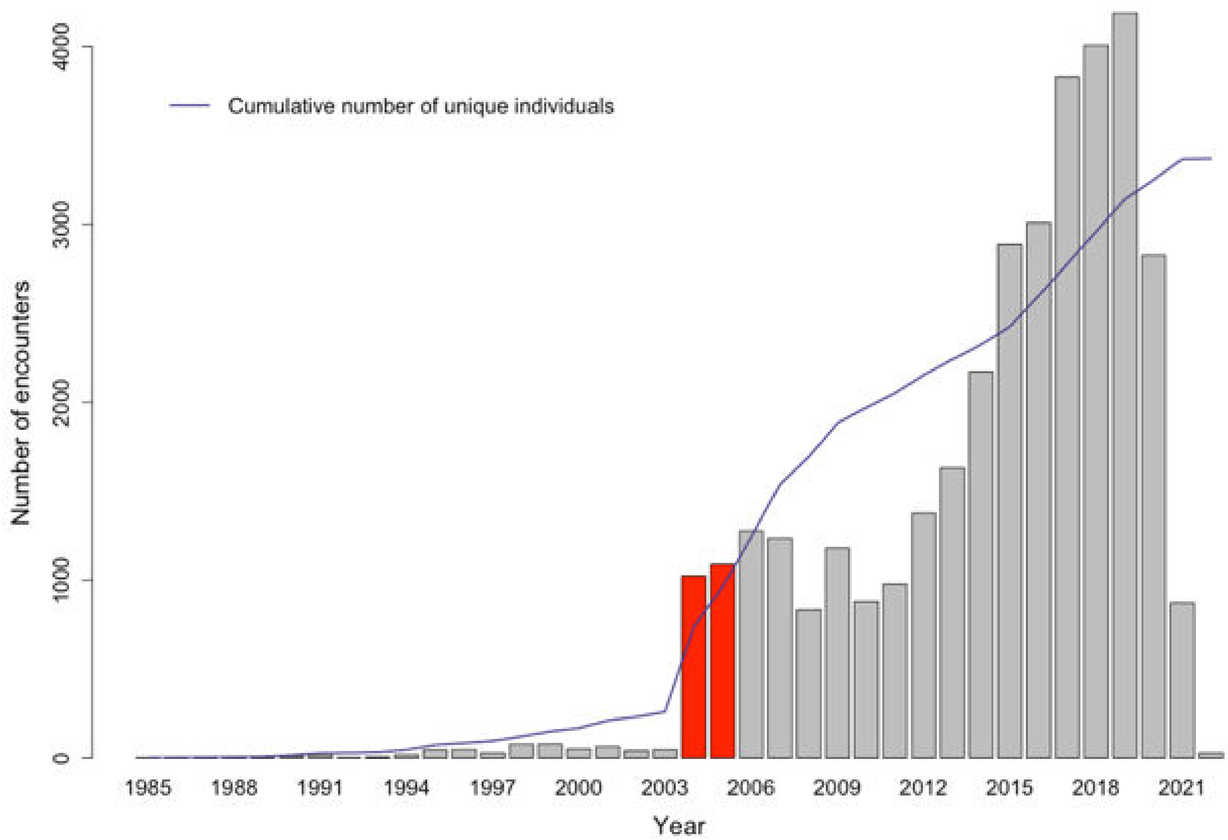


Figure 2. Annual number of humpback whale photographic identification encounters (each encounter was defined as a single sighting of an individual humpback whale, recorded on a specific day at a specific location) from Canadian Pacific waters included in the current analyses, and cumulative number of unique individuals identified by year. Red bars indicate the years of the “SPLASH” (Structure of Populations, Levels of Abundance, and Status of Humpbacks) project, upon which previous North Pacific humpback whale abundance estimates and population structure information were based. Note that there are data from 2020 – 2022 that have not yet been processed and included in the “Happywhale” data set, making effort appear low in these years.

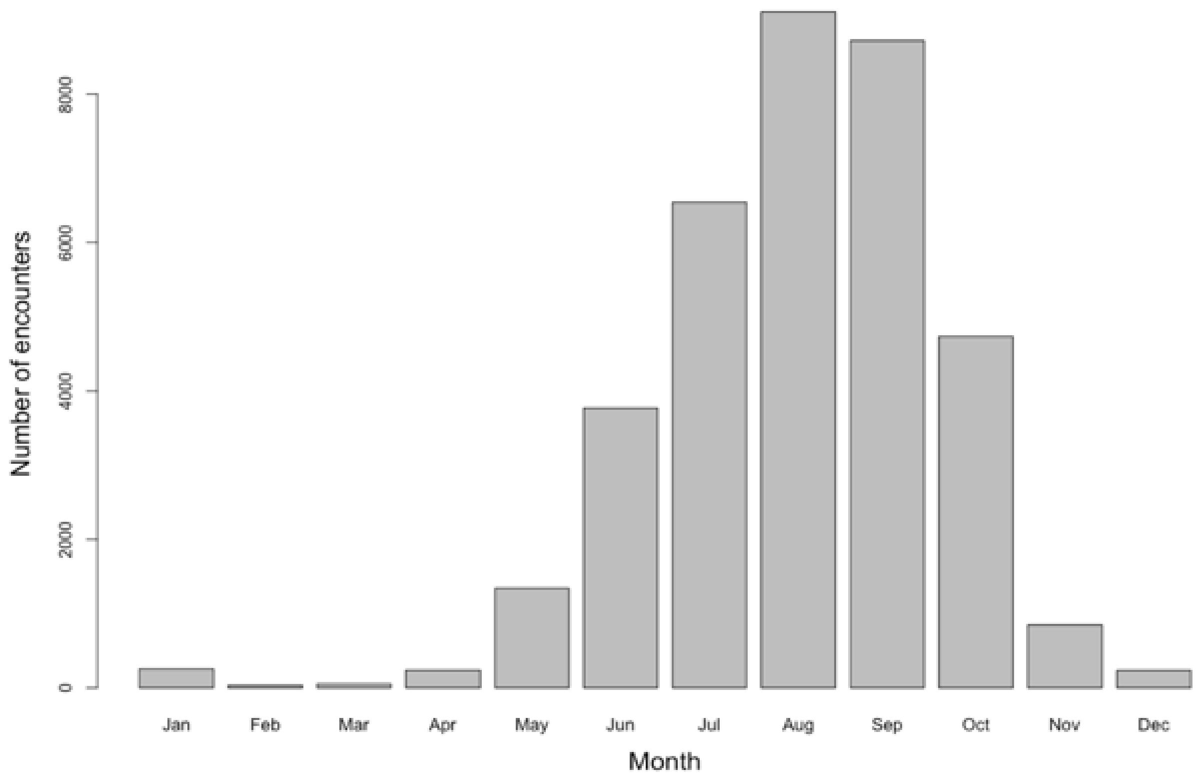


Figure 3. Number of humpback whale photographic identification encounters in Canadian Pacific waters included in the current analyses, grouped by month (all years combined).

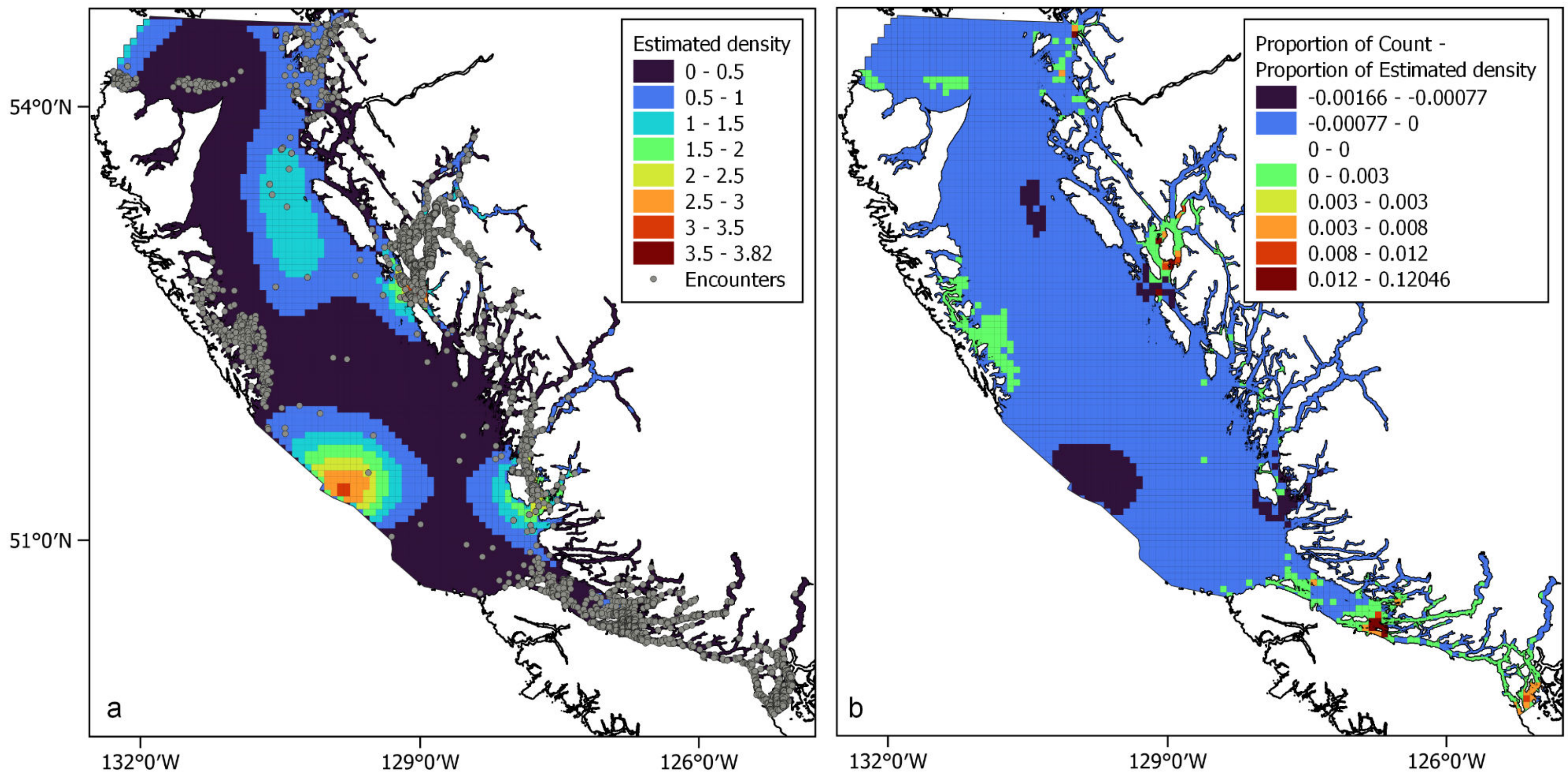


Figure 4. a. Estimated density of humpback whales per 25 km² grid cell in the North Coast portion of Canadian Pacific waters based on visual line-transect surveys and density surface modelling (from Wright et al. 2021; displayed as a coloured grid), and location of photo-identification encounters included in the current data set (grey points); b. Estimated difference between the proportion of photo-identification encounters and the proportion of estimated density in each 25 km² grid cell in the North Coast portion of Canadian Pacific waters.

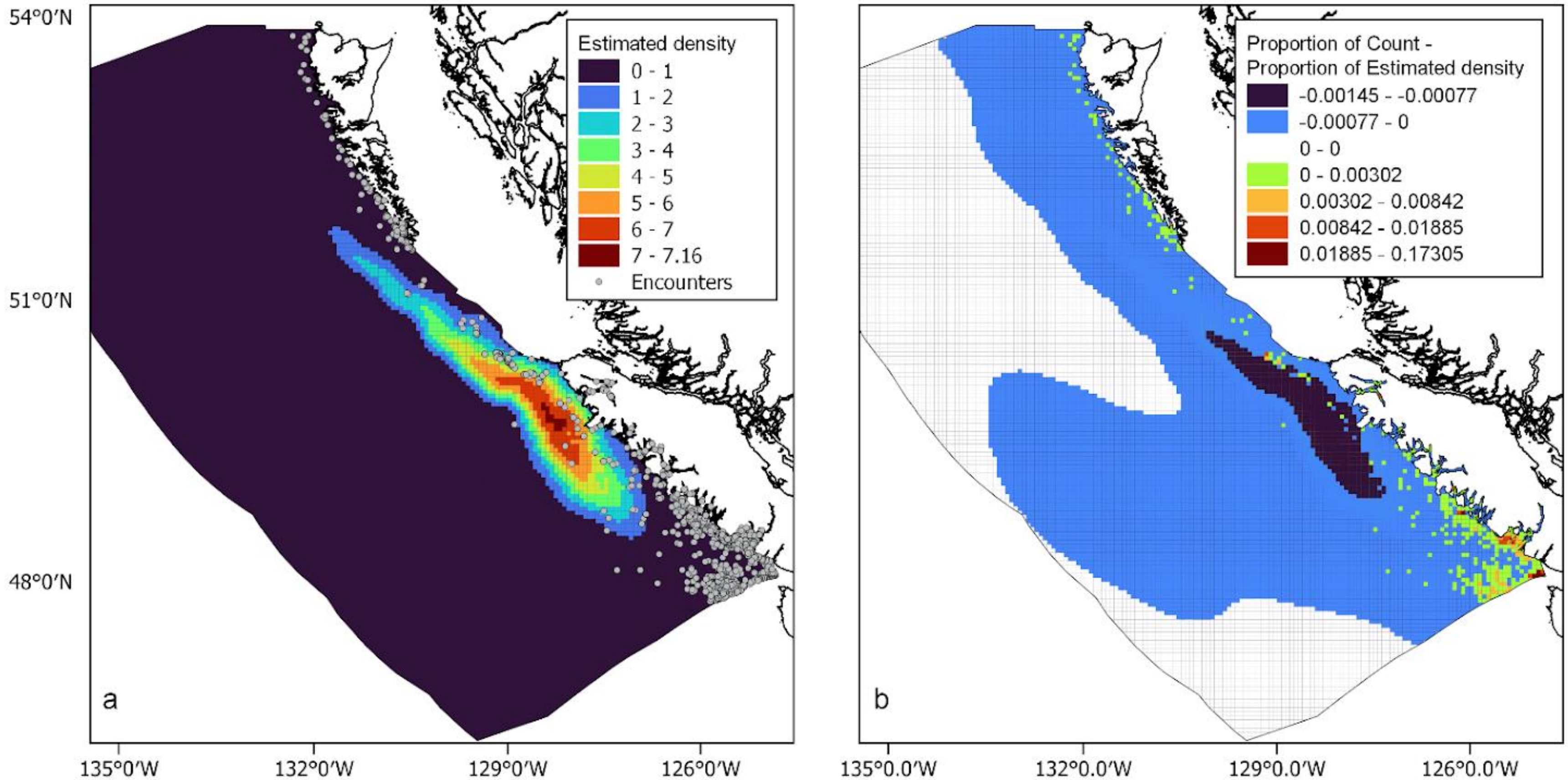


Figure 5. a. Estimated density of humpback whales per 25 km² grid cell in the Offshore portion of Canadian Pacific waters based on visual line-transect surveys and density surface modelling (from Wright et al. 2021; displayed as a coloured grid), and location of photo-identification encounters included in the current data set (grey points); b. Estimated difference between the proportion of photo-identification encounters and the proportion of estimated density in each 25 km² grid cell in the Offshore portion of Canadian Pacific waters.

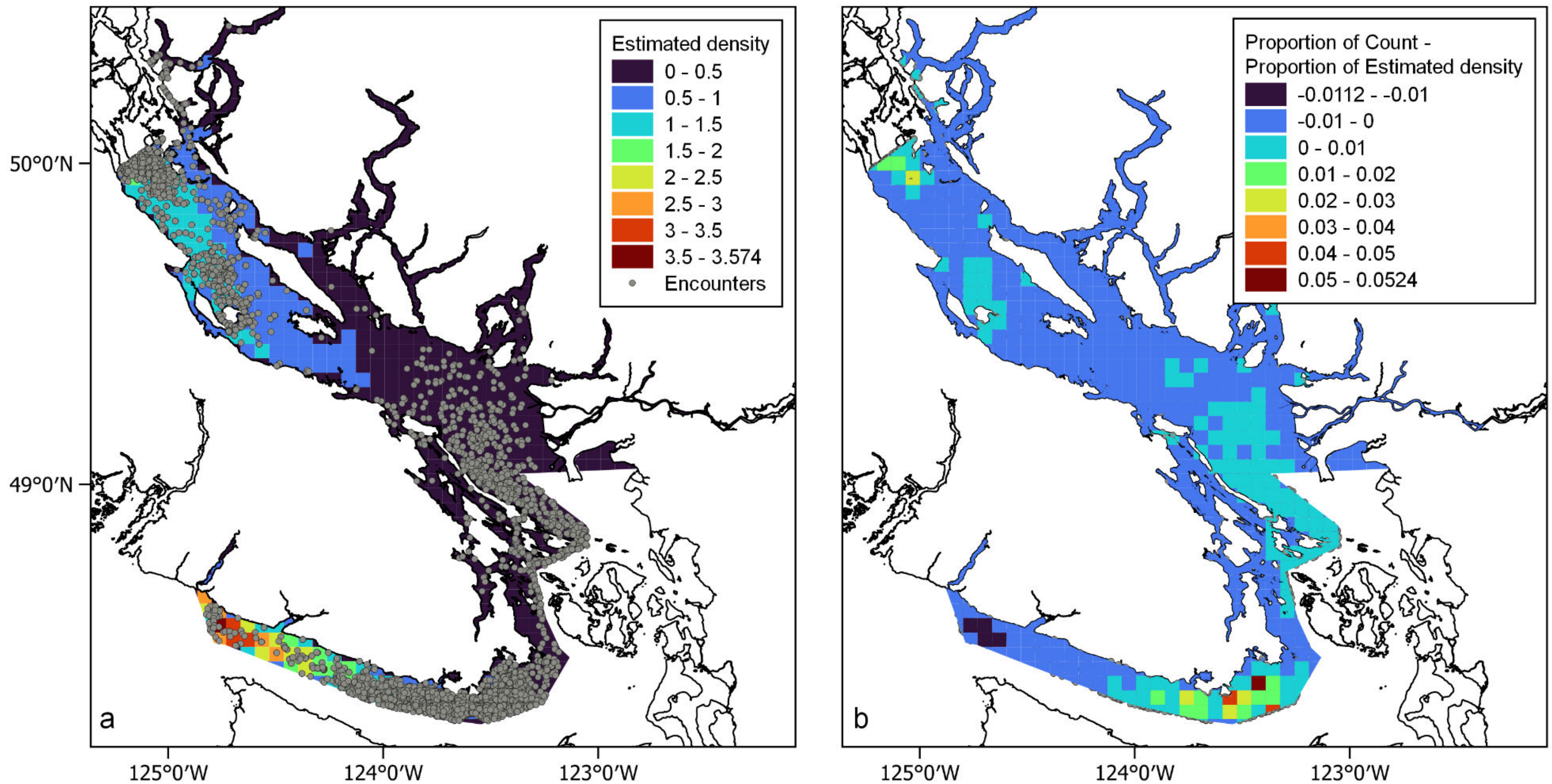
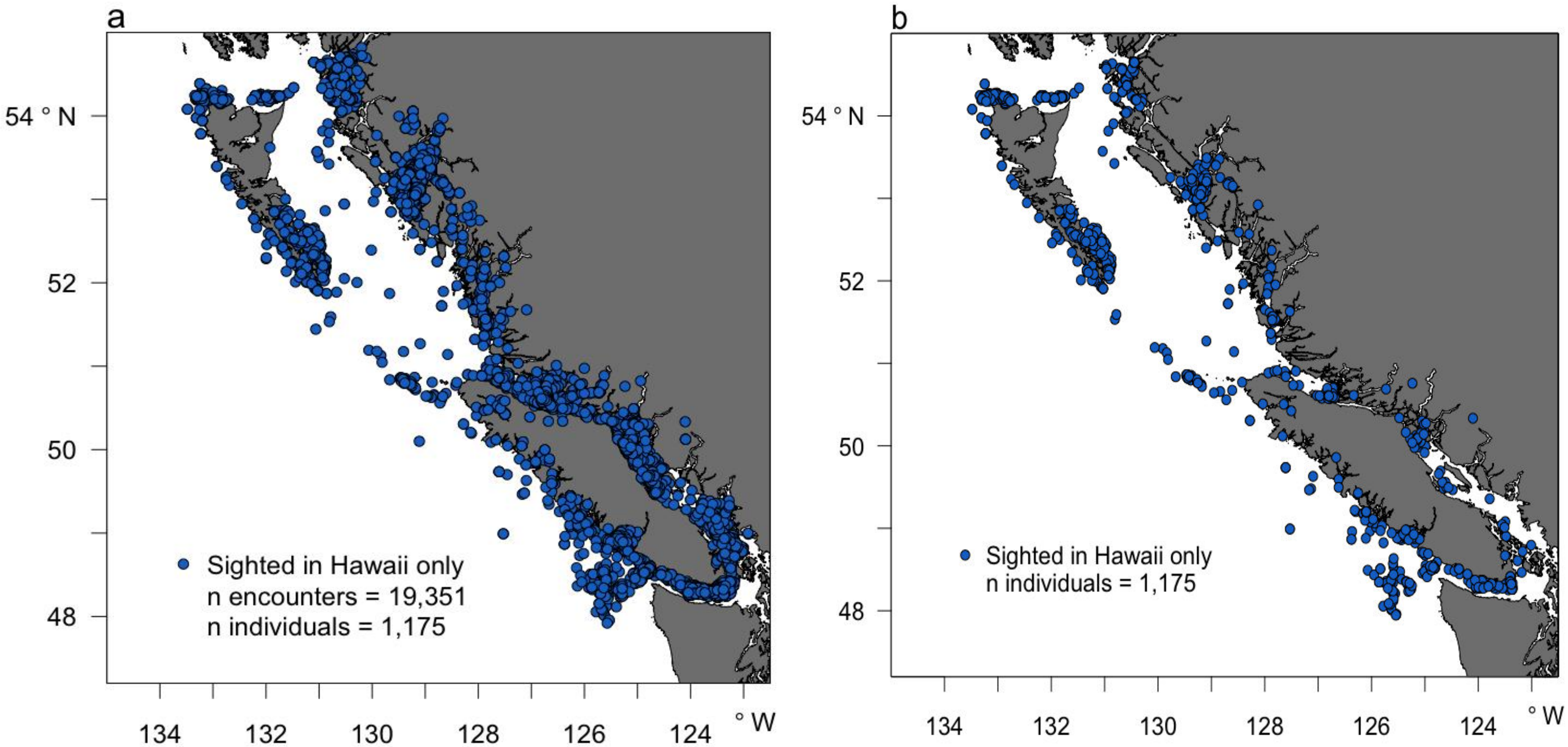
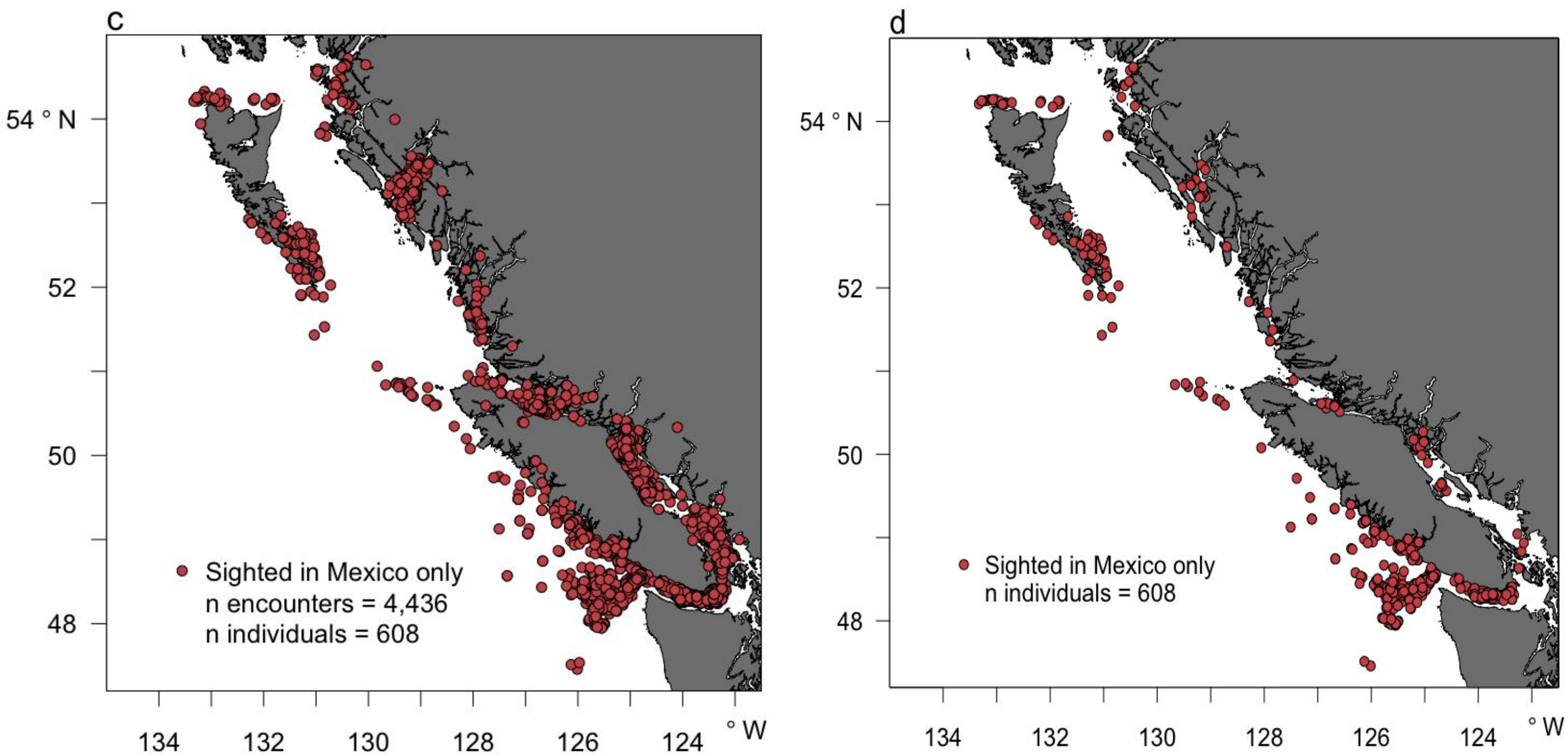


Figure 6. a. Estimated density of humpback whales per 25 km^2 grid cell in the Salish Sea portion of Canadian Pacific waters based on visual line-transect surveys and density surface modelling (from Wright et al. 2021; displayed as a coloured grid), and location of photo-identification encounters included in the current data set (grey points); b. Estimated difference between the proportion of photo-identification encounters and the proportion of estimated density in each 25 km^2 grid cell in the Salish Sea portion of Canadian Pacific waters.


a
54 ° N
52
50
48
134
132
130
128
126
124
° W
Sighted in Hawaii only
n encounters = 19,351
n individuals = 1,175
b
54 ° N
52
50
48
134
132
130
128
126
124
° W
Sighted in Hawaii only
n individuals = 1,175


c
54 ° N
52
50
48
134
132
130
128
126
124
° W
Sighted in Mexico only
n encounters = 4,436
n individuals = 608
d
Sighted in Mexico only
n individuals = 608

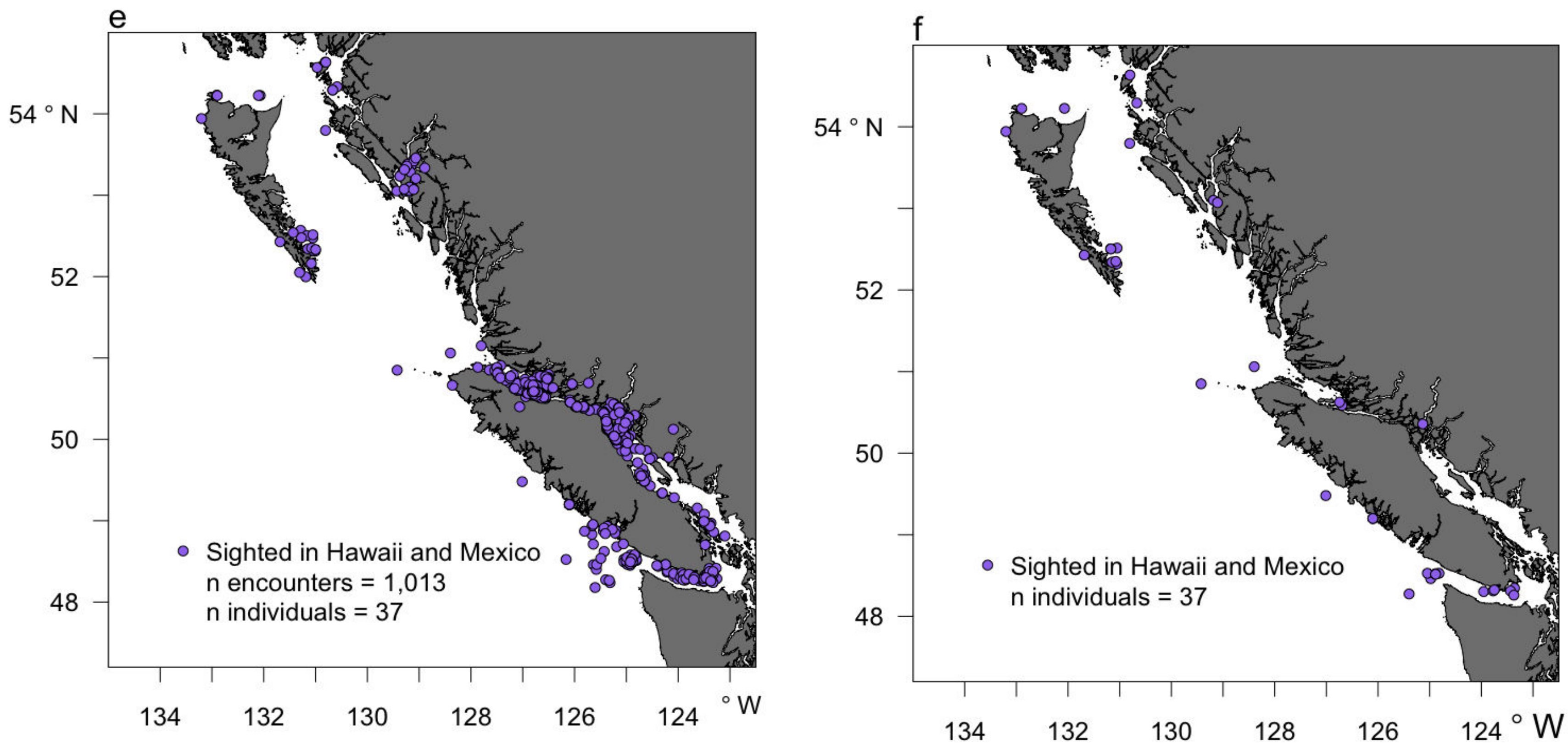


Figure 7. a. Locations of all humpback whale photo-identification encounters in Canadian Pacific waters for individuals that were matched to Hawaiian wintering areas only; b. Location of the encounter in Canadian Pacific waters with the median latitude for each individual humpback whale that was matched to Hawaiian wintering areas only; c. Locations of all humpback whale photo-identification encounters in Canadian Pacific waters for individuals that were matched to Mexican wintering areas only; d. Location of the encounter in Canadian Pacific waters with the median latitude for each individual humpback whale that was matched to Mexican wintering areas only; e. Locations of all humpback whale photo-identification encounters in Canadian Pacific waters for individuals that were matched to Hawaiian and Mexican wintering areas; f. Location of the encounter in Canadian Pacific waters with the median latitude for each individual humpback whale that was matched to both Hawaiian and Mexican wintering areas.

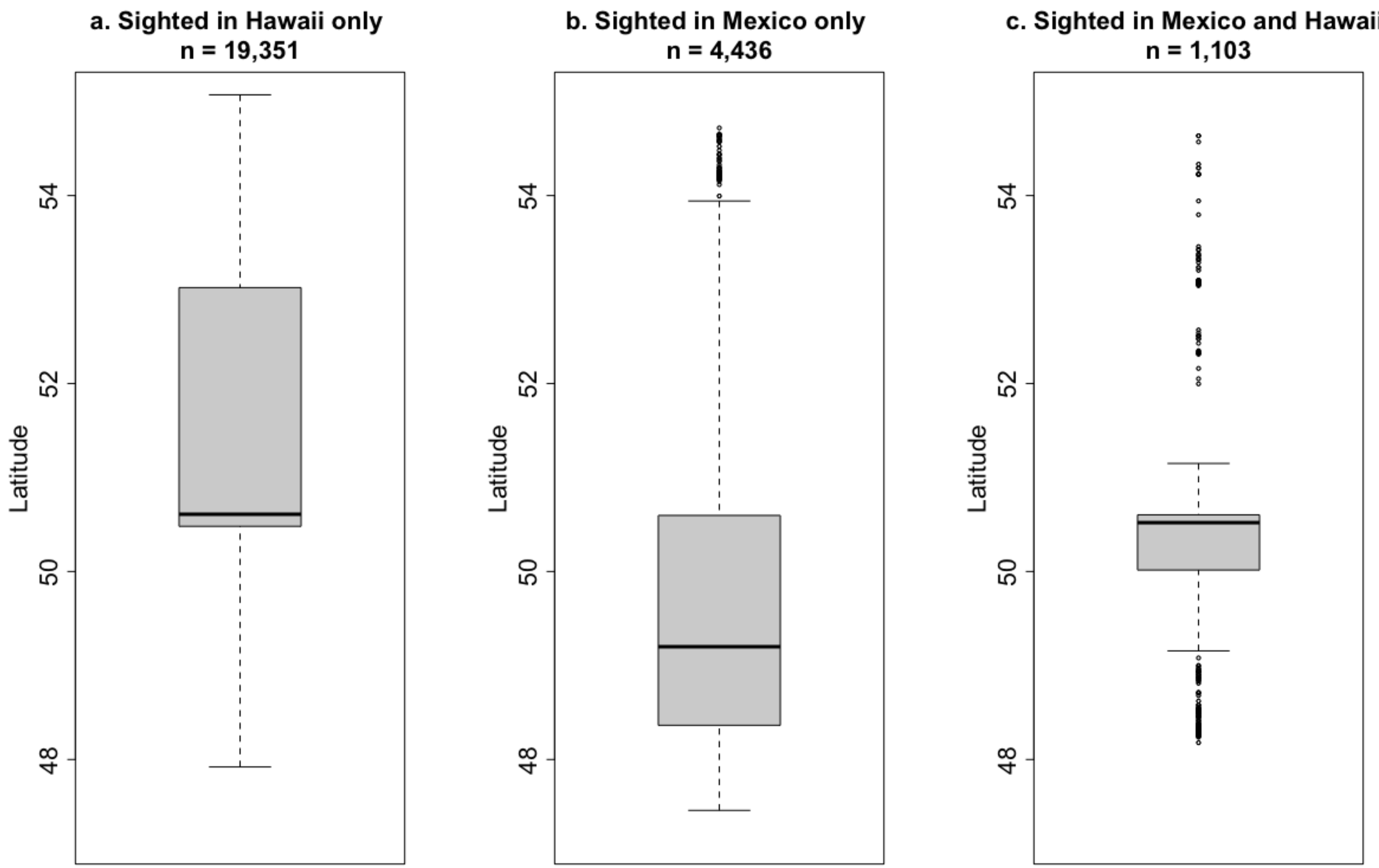


Figure 8. Boxplots indicating the latitude of photo-identification encounters in Canadian Pacific waters of humpback whales matched to: a. Hawaiian wintering areas only; b. Mexican wintering areas only; and c. both Hawaiian and Mexican wintering areas. The black line within each plot represents the median latitude, and the extents of each of the boxes represent the first quartile (25%) and third quartile (75%) of encounters. The whiskers represent the minimum and maximum extents of the encounter latitudes, with the exception of outliers, which are represented as circles

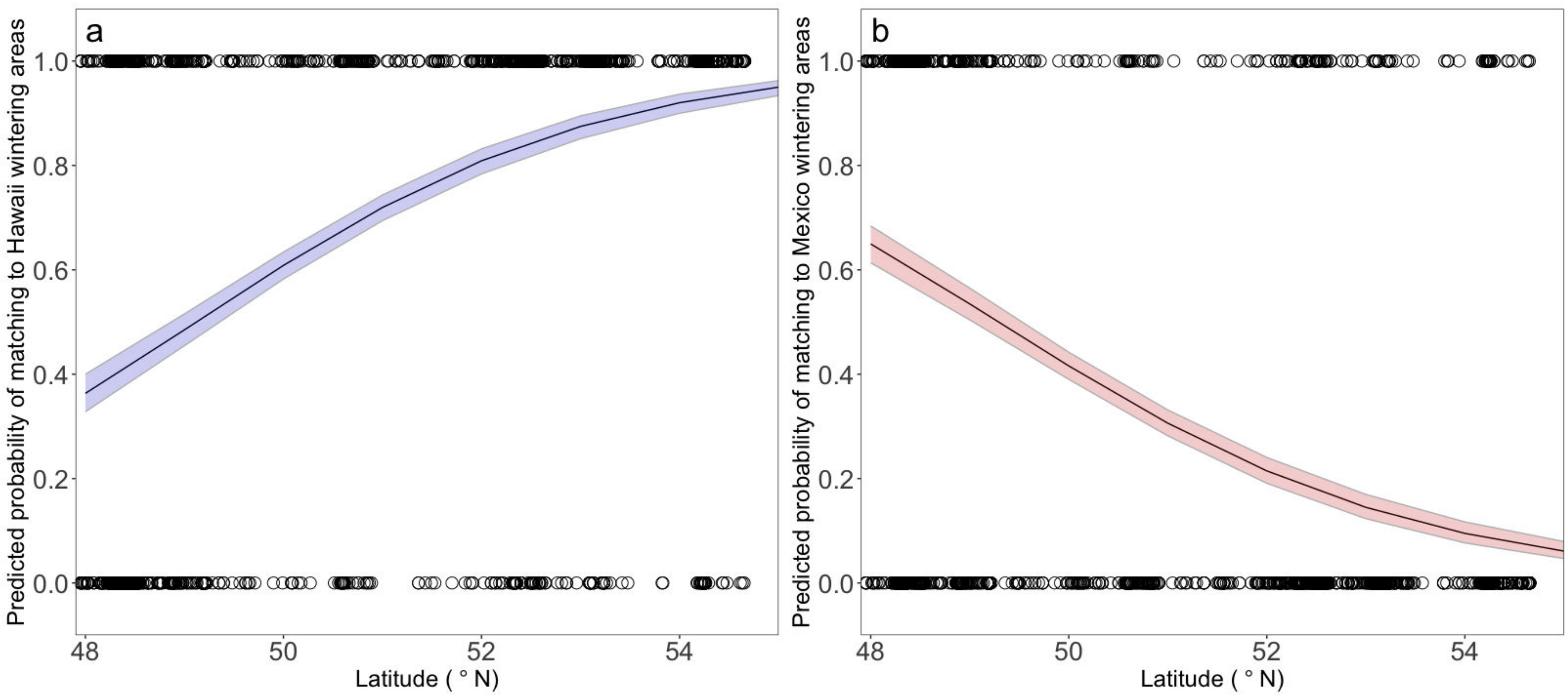


Figure 9. Predicted probability of a humpback whale being matched to: a. Hawaiian; and b. Mexican wintering areas, based on generalized linear models and the median latitude of its sightings in Canadian Pacific waters. The extent of the shaded areas represent the upper and lower bounds of a 95% confidence interval. Circles represent data points, where a 0 indicates that the individual at the plotted latitude was matched to a wintering area other than the one represented in the panel, and a 1 indicates that the individual at the plotted latitude was matched to a. Hawaii; or b. Mexico.

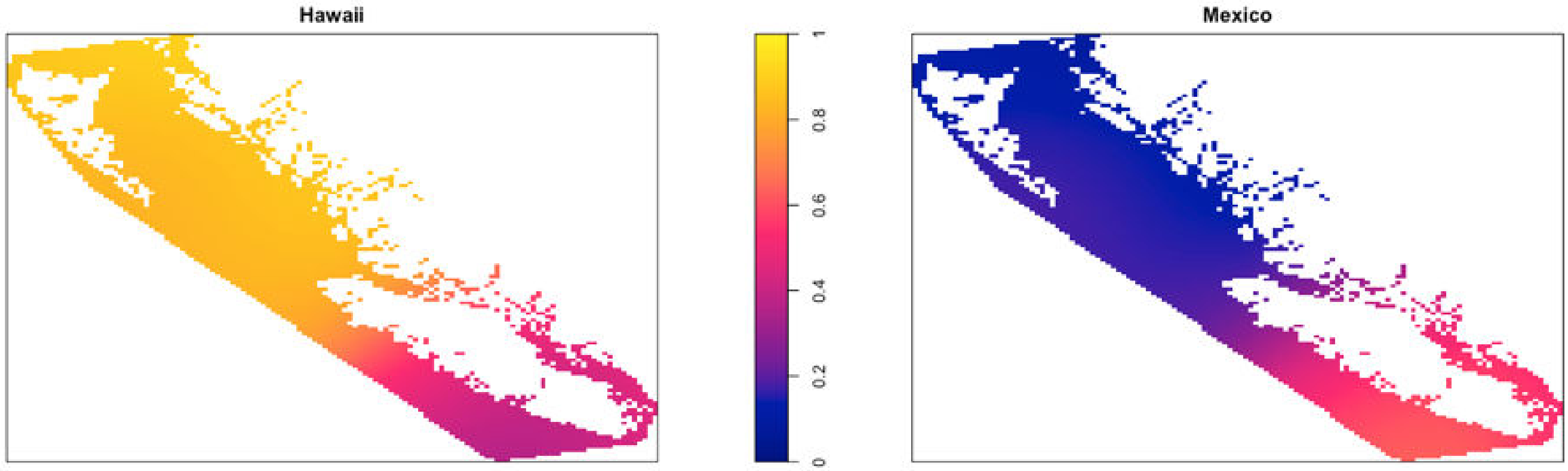


Figure 10. Spatially-varying probability of a humpback in Canadian Pacific waters being documented in Hawaiian wintering grounds only (left panel) and Mexican wintering grounds only (right panel), based on Nadaraya-Watson type kernel regression, using a Gaussian kernel with a bandwidth of 1.02

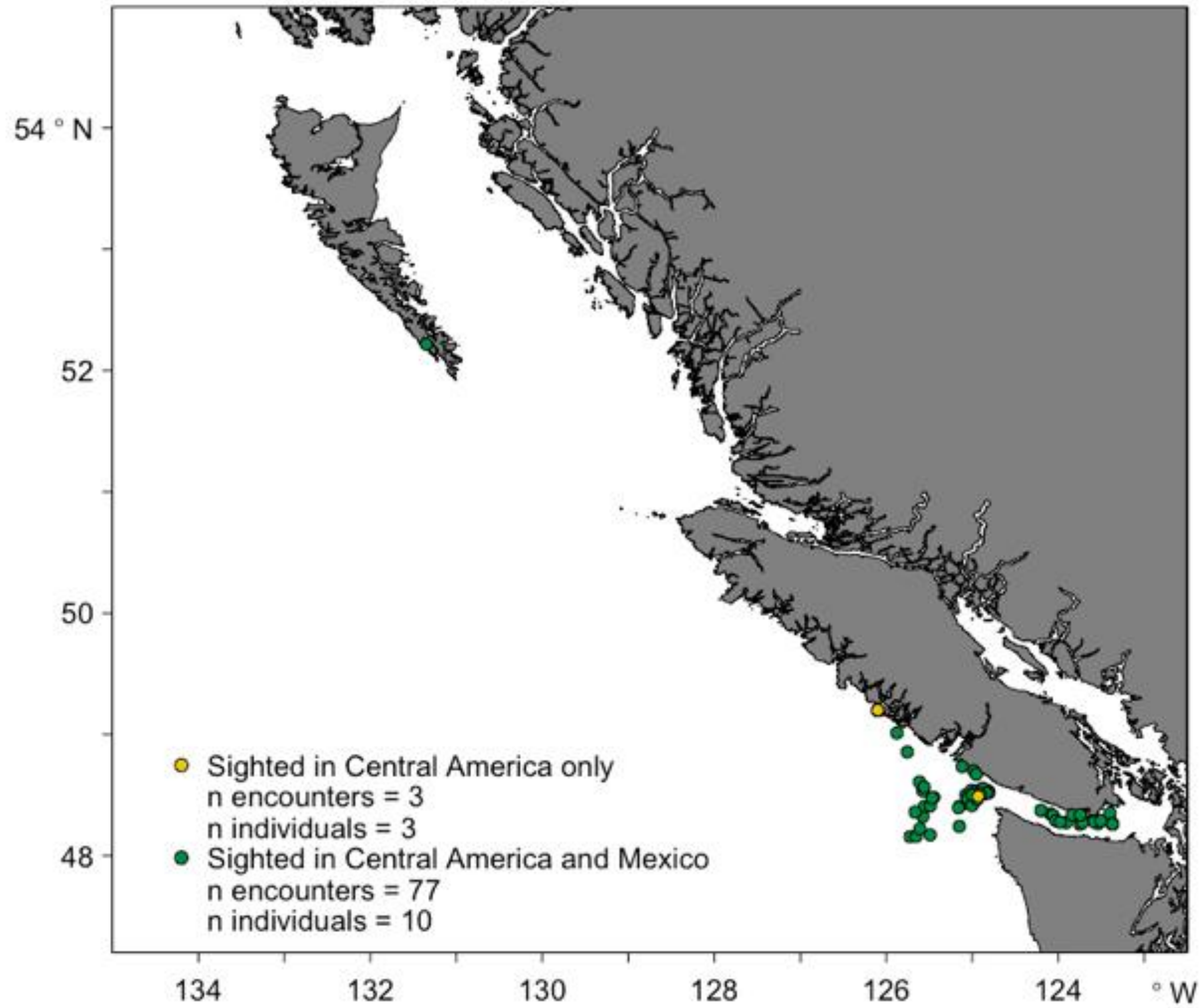


Figure 11. Locations of humpback whale encounters in Canadian Pacific waters for individuals that were matched to Central American wintering areas only and individuals matched to both Central American and Mexican wintering areas.