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A trans-Pacific movement reveals regular migrations of humpback whales *Megaptera novaeangliae* between Russia and Mexico

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ABSTRACT: Humpback whales *Megaptera novaeangliae* undertake extensive annual migrations, have complex migratory patterns, and have held several mammalian long-distance movement records. Here, we report on a whale known to feed in the Russian Far East that was sighted in breeding areas on either side of the North Pacific, the Mariana Islands and Mexico, in less than 1 yr (357 d apart). This is the longest published distance (11 261 km great-circle route) between 2 unique sightings of a photo-identified humpback whale to date. To understand the context of this movement, we investigated records of whales that had been sighted in Russian feeding areas and Mexican breeding areas using historic and newly available photo-identification data. We found 117 humpback whales documented in both countries between 1998 and 2021, revealing a substantial increase from the only 11 matches that were previously known. These whales exhibited high site fidelity to Mexico, with one-third seen in multiple years, and up to 10 yr. However, we also found that they changed breeding areas more frequently than Mexico whales matched to other feeding areas, illustrating how the Mariana Islands–Mexico movement may have occurred. We document the first complete round-trip migrations between Mexico and Russia, a journey of >16 400 km, the longest known migration of Northern Hemisphere humpback whales. Our data demonstrate regular trans-Pacific movements of humpback whales in the North Pacific, highlighting the importance of Mexico for the species ocean-basin-wide and the need for effective local management to aid in the conservation of multiple at-risk distinct population segments.

KEY WORDS: Migratory animals · Migration patterns · Long-distance movements · Movement ecology · Endangered populations · Recovering populations · Population management

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1. INTRODUCTION

Understanding population structure and mixing between population segments is essential for effective species management and conservation planning. Migration, the periodical large-scale movement of animals between distant locations (Baker 1978), varies greatly in length and duration across taxa (Dingle 1996). In long-lived animals, migration usually involves annual round trips, which typically cover thousands of kilometres (Dingle 1996). Such movements maximise individual survival by allowing the exploitation of different seasonal environments and resources, most commonly for food (Chapman et al. 2014), but also for breeding or refugia to avoid predators, parasites, or unfavourable environmental conditions (Cresswell et al. 2011). In widely distributed populations, movements of individuals or distinct groups of individuals may have profound implications for measuring population dynamics, estimating abundance, and implementing policies for protection and conservation. This is especially true for many of the mysticete whale species that often have multiple, overlapping populations or population segments, distributed over entire ocean basins and commonly migrate through the jurisdictional waters of several countries. Understanding detailed migration patterns of endangered and recovering populations of mysticete whales following their commercial exploitation has, therefore, become a focus of current research efforts worldwide.

The humpback whale *Megaptera novaeangliae* is a large mysticete whale with a worldwide distribution (NOAA 2016). The species undertakes extensive annual migrations between low-latitude (sub-)tropical winter breeding areas and high-latitude coldwater summer feeding areas (Dawbin 1966). Photo-identification (Katona & Whitehead 1981) has revealed that several Southern Hemisphere humpback whale populations have some of the longest migrations of any mammal, and regularly travel more than 8000 km between seasonal habitats (Stone et al. 1990, Palsbøll et al. 1997, Rasmussen et al. 2007, Robbins et al. 2011). Worldwide, photo-identification and genetic studies have found high site fidelity of humpback whales to seasonal breeding and feeding areas (Stevick et al. 2006, Calambokidis et al. 2008, Herman et al. 2011, Baker et al. 2013, Witteveen & Wynne 2017, Nakagun et al. 2020). However, with few physical barriers in open oceans to obstruct movements, humpback whales have occasionally been recorded to deviate from typical migration routes (e.g. Pomilla & Rosenbaum 2005, Stevick et al. 2013, Félix et al. 2020, Acevedo et al. 2022). These cases include a Southern Hemisphere humpback whale which moved between ocean basins and was photo-identified off both Brazil and Madagascar (Stevick et al. 2011). To date, this female whale holds the record for the longest documented distance between sightings for the species, with a minimum great-circle distance of 9800 km between the 2 wintering destinations (Stevick et al. 2011).

Humpback whale migration has been studied more intensively in the North Pacific than in any other region globally (Calambokidis et al. 2000, 2001, 2008, Urbán R et al. 2000, Mate et al. 2007, Gabriele et al. 2010). Annual migration lengths are known to vary from only 1900 km to a maximum of ~6000 km (Gabriele et al. 1996, Calambokidis et al. 2000, Zerbini et al. 2006, Lagerquist et al. 2008). One of the most in-depth collaborative studies of any large whale to date, the ocean-basin-wide study known as SPLASH — Structure of Populations, Level of Abundance and Status of Humpback Whales of the North Pacific — was conducted concurrently in 10 different countries between 2004 and 2006 and involved extensive photo-identification and biopsy sampling (Calambokidis et al. 2008). SPLASH revealed that seasonal migrations between feeding and breeding areas were generally separated into the western, central, and eastern portions of the North Pacific Ocean basin. In the east, whales of the breeding areas of coastal Mexico and Central America predominantly feed at lower latitudes along the US West Coast (Calambokidis et al. 2008). Centrally, the Hawaiian whales and Mexican Revillagigedo Archipelago whales feed mainly in Canada and Alaska. Lastly, the western North Pacific population (Japan and the Philippines) was found to feed almost exclusively in waters of Far East Russia and the Aleutian Islands.

Photo-identification studies during SPLASH found that humpback whales had a high degree of site fidelity to breeding areas, with only 2% of whales documented exchanging breeding areas in different years (Calambokidis et al. 2008). This aligned with genetic studies using SPLASH biopsy samples, which evidenced strong natal philopatry to breeding areas and site fidelity to feeding areas (Baker et al. 2013). Nevertheless, it was concluded that humpback whale migration patterns in the North Pacific are complex. Some unexpected migratory connections were found, including one whale sighted in Russia that was later documented in the Mexican Revillagigedo Archipelago. Additionally, one or more 'missing' breeding areas were suggested to exist in the western North Pacific, based on low re-sightings of whales between western feeding (Russia, eastern Aleutian Islands, and the Bering Sea) and breeding (Japan and the Philippines) areas sampled during the study.

The detailed North Pacific migratory patterns revealed during SPLASH, and the data, biopsy samples, and photo-identification images from the project continue to be used for management and research allowing for an ever growing understanding of populations' divisions and movements (Fig. 1). In 2015, the US National Marine Fisheries Service (NMFS) produced a global status review of the species and used SPLASH information to identify 4 North Pacific distinct population segments (DPSs; Fig. 1), 3 of which were classified at risk under the US Endangered Species Act (Bettridge et al. 2015). The western North Pacific and the Central America DPSs were classified as endangered, and the Mexico DPS was classified as threatened (NOAA 2016). In a recapture study using all SPLASH photo-identification images but with a substantially larger sample from Russia (n = 1459, compared to only 102 from SPLASH), Titova et al. (2018) found 10 more matches of humpback whales between Mexico and Russia. However, in general, they reported very low match rates of Russia whales at low latitudes, further supporting the hypothesis of undiscovered humpback whale breeding areas. Additionally, for the first time, research efforts were initiated in the southern Mariana Islands. Using data collected from this new research, primarily between 2015 and 2018, and SPLASH data, Hill et al. (2020) established the archipelago as one of the previously unsampled western North Pacific breeding areas, with high-latitude matches found only to Russian feeding areas. Yet with so few whales photo-identified (n = 43), the authors concluded that further research is needed to identify where more of the 'missing' whales breed.

Additional evidence continues to accumulate that supports the conclusion that something more complex and as-of-yet undetermined is occurring in North Pacific humpback whale migration (Calambokidis et al. 2008). To date, 4 same breeding season photo-identification matches have been made between Mexico and the Hawaiian breeding areas (Forestell & Urbán R 2007, Darling et al. 2022, Happywhale unpubl. data). Mid-oceanic singing has been recorded at low latitudes across the tropics between western, central, and eastern North Pacific breeding areas (Darling et al. 2019a, 2021), and unexplained similarities in breeding ground song from the 3 regions (male song is typically unique to each population) remains the focus of ongoing studies (Cerchio et al. 2001, Darling et al. 2019b). Lastly, humpback whales sampled in the Mexican breeding areas have been found to have the highest haplotype diversity of mtDNA of any seasonal habitat of the ocean basin (Baker et al. 2013). Genetic

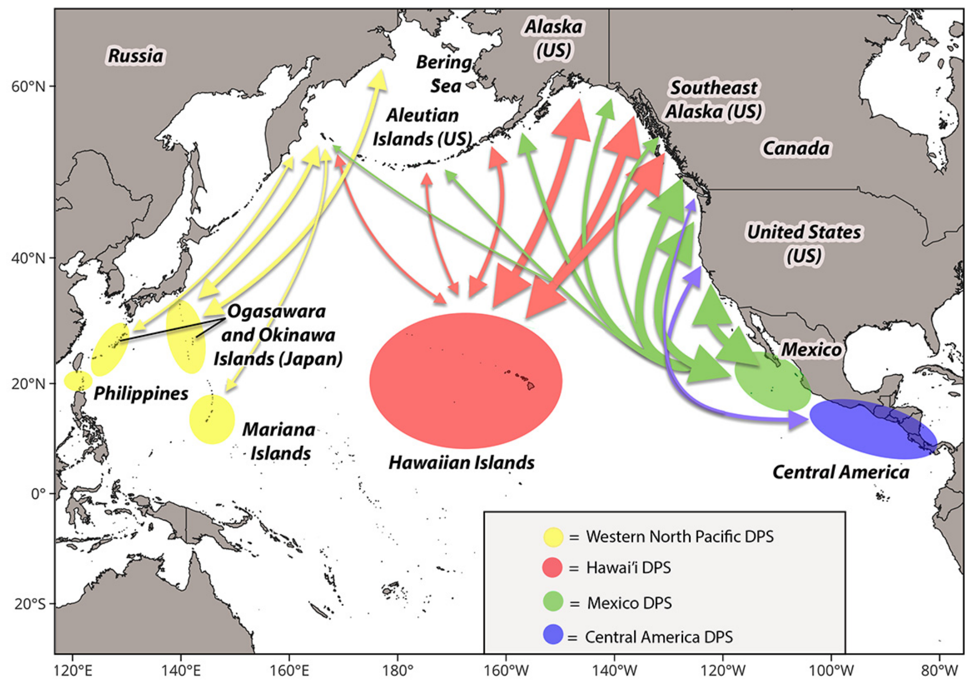

Fig. 1. Known migratory connections of humpback whale *Megaptera novaeangliae* distinct population segments (DPS) in the North Pacific Ocean basin (Calambokidis et al. 2008, Bettridge et al. 2015, Titova et al. 2018, Hill et al. 2020)

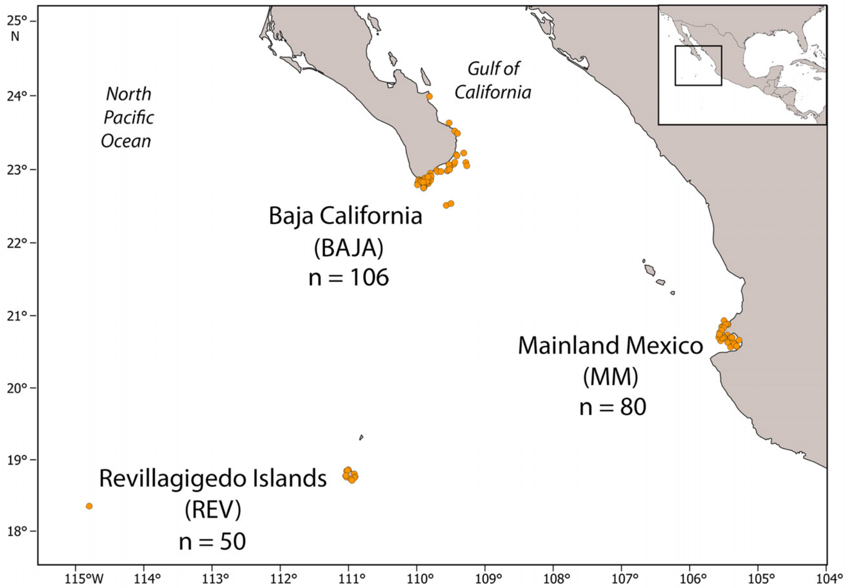

Fig. 2. Breeding areas of the Mexico distinct population segment (DPS) of humpback whales *M. novaeangliae* and regional sightings (orange dots; n = 236) of whales also identified in the Russian feeding areas (n = 117)

similarities have been found between distant breeding areas in the west and east of the ocean basin (Baker et al. 1998, 2013), including a recent study revealing shared mtDNA haplotypes of whales in the Mariana Islands and Mexico (Hill et al. 2020). Here, we report on an unprecedented movement: a humpback whale known to feed in Russia which was sighted in each of these 2 distant breeding areas, on opposite sides of the North Pacific, in less than 1 yr. This is a new long-distance between-sighting record for the species. To further understand the context of this long-distance movement and to explore the regularity of trans-Oceanic migrations of humpback whales in the North Pacific, we used newly available data to investigate how likely whales photo-identified in Russian feeding areas were to be present in the breeding areas of Mexico.

2. MATERIALS AND METHODS

2.1. Whale data and photo-identification images

Humpback whale sightings in Mexico were from the 3 principal breeding areas used by the Mexico DPS: the waters near mainland Mexico (MM), the Revillagigedo Archipelago (REV), and the coasts of Baja California Sur (BAJA) (Fig. 2). Overall, for all 3 regions, 7468 individuals (Table 1) were catalogued in the online automated photo-identification matching software Happywhale (www.happywhale.com). This included sighting and biopsy data collected during the SPLASH project (2004–2006), dedicated research trips, and opportunistic sightings collected on whale watch boats. Some individuals were documented in multiple Mexican breeding areas (Table 1).

Humpback whale surveys in the Mariana Islands were initiated in February–March 2015 and continued annually between January and March through 2018 (Table 1; Hill et al. 2020). Search effort was concentrated around the island of Saipan and at nearby offshore shallow reefs to the west and north of the island. Additional survey effort was also conducted around Tinian and Aguijan Islands to the south of Saipan. Photos and sighting data were collected during each humpback whale encounter, and biopsy samples were collected when possible and used to identify the sex and mtDNA haplotype of individuals. After accounting for 4 whales photo-identified proximate to Saipan during a 2007 ship survey (Fulling et al. 2011), a total of 43 non-calf humpback whales were identified in the southern Mariana Islands

Table 1. Survey types, timing, years, and number of sightings and individual humpback whales *Megaptera novaeangliae* identified in each survey region of this study

Region	Survey types	Individuals identified	No. of sightings	Years of surveys	No. of years of data	Months of survey data
MM	Research and tourism	3545	7700	1996–2021	26	Nov–Apr
BAJA	Research and tourism	4920	8059	2004–2021	18	Dec–May
REV	Research	693	2559	2004–2006	3	Jan–Apr
All Mexico	Research and tourism	7468	18318	1996–2021	26	Jan–Mar
Mariana Islands	Research	43	51	2007, 2015–2018	5	Jan–Mar
Russia	Research and tourism	2183	3692	2004–2021	18	Jun–Sep

through photos, and 24 of those individuals were biopsy-sampled.

Humpback whale surveys in the Russian Far East began during the SPLASH project in 2004 and have continued annually between June and September through 2021 (Table 1; Filatova et al. 2022). Sightings (n = 3692) were collected during dedicated survey efforts, and some photo-identified individuals were of known sex following biopsy sampling and genetic analysis. Surveys were predominantly conducted around the Commander Islands and off the eastern coast of Kamchatka and Chukotka (Titova et al. 2018). Additionally, in several years, some photo-identification images without sighting data were provided by tourism companies off Chukotka.

2.2. Photo-identification matches of individual whales and distances between sightings

Regional photo-identification data sets were first manually matched following methodology established by Katona & Whitehead (1981). All images were then matched against a North-Pacific-wide data set of 27 536 identified individuals using an artificial-intelligence-based image recognition algorithm within Happywhale (Cheeseman et al. 2022). The algorithm has been shown to find 97–99% of potential matches in good- to high-quality images (Cheeseman et al. 2022). Great-circle distances were calculated between sightings using the methodology of Bowditch (1995). Such formulas calculate the shortest distance between any 2 points on a sphere. We recognise that we have no information on the exact routes taken by individual whales, which prior tagging study information (Palacios et al. 2019) suggests were likely far greater than the great-circle distances that we calculated.

2.3. Data analyses

Sighting data of humpback whales photo-identified in Russia and Mexico (hereafter denoted as whales) were analysed, including sex, social groups, date of sighting, resight frequencies, and regional sighting locations in Mexico and Russia. We then analysed the sighting histories and sighting frequencies of Russia–Mexico whales across all North Pacific breeding areas to further investigate previously reported low sighting frequencies of humpback whales known to feed in Russia in North Pacific breeding areas (Calambokidis et al. 2008, Titova et al. 2018). To achieve this goal, we created 2 samples of whales for comparison. To reduce sampling bias, whales sighted only in REV were removed from the Russia–Mexico sample (n = 17, 14.5% Russia–Mexico whales), as only 3 yr of sighting data from the region were available. A sample of Mexico whales recaptured in feeding areas other than Russia was then created. Using Happywhale, all humpback whales were selected that had at least one sighting in the MM or BAJA breeding areas and at least one sighting in any feeding area of the North Pacific except Russia, provided permission was granted for use. The 'sample' function in R (R Core Team 2021) was then used to make a random sample of these whales with the same number of individuals as the Russia–Mexico sample. These 2 samples were termed the 'Russian sample' and 'non-Russian sample'.

For all whales, sighting frequency in North Pacific breeding areas was calculated as a ratio between the number of years the whales were seen in any breeding ground and sighting length (duration of time between first and last sighting in the North Pacific, including feeding and breeding regions). The program R (R Core Team 2021) was then used to test the suitability of data for statistical tests and compare the difference in sighting frequencies of the 2 samples, with the alpha level of significance set at 0.05 (5%). The normality of data was assessed using the Shapiro-Wilk test (W = 0.813, $p < 0.001$), and Levene's test (based on the median) was then chosen to check the variance of the 2 samples (F_{198} = 9.951, $p < 0.01$). The null hypothesis was rejected in both tests with the alpha value not met. The non-parametric Mann-Whitney U-test (MWU) was therefore selected as the preferred statistical test to compare the ratios of sighting frequencies of the 2 samples.

3. RESULTS

3.1. Oceanic-basin-scale movement of a humpback whale between the Mariana Islands and Mexico

We documented the longest great-circle distance between unique sightings of a humpback whale to date (Fig. 3). On 11 February 2017, an adult humpback whale, individual MIMn-030, was photographed with another adult off the island of Saipan in the Mariana Islands (Fig. 3). On 2 February 2018, 357 d later and a distance of 11 261 km and 108.6° longitude away (the shortest great-circle route around the earth's sphere), MIMn-030 was photo-identified off the coast of Sayulita, Nayarit, Mexico,

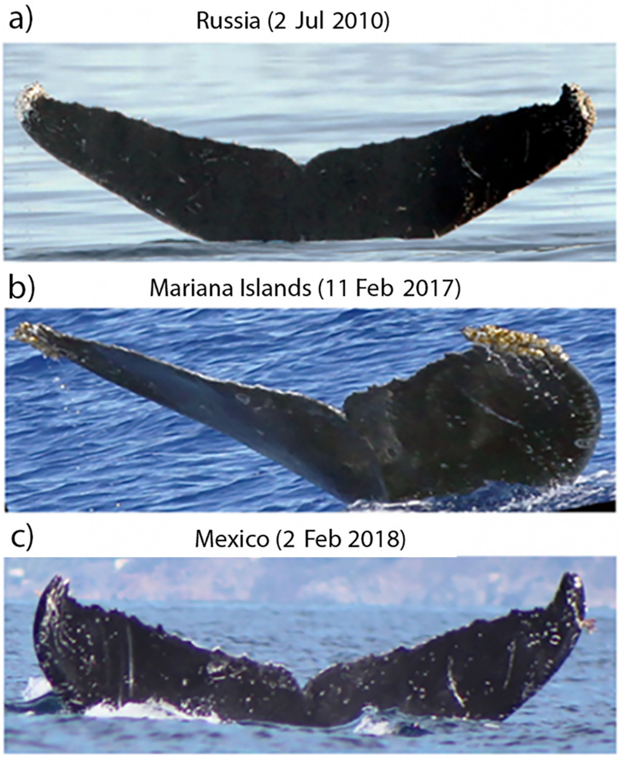

Fig. 3. (a–c) Ventral fluke image of humpback whale *M. novaeangliae* MIMn-030 (images taken by O.V.T., M.C.H., and N.R.)

in the MM breeding area in a competitive group of 5 whales. To date, these are the only existing 2 records of MIMn-030 in breeding areas. Previous to this, the whale has only been documented twice in the North Pacific, and both occasions were in the Commander Islands feeding area of Far East Russia (Fig. 4): 1 July 2010, and then 3 yr later on 19 July 2013 (Hill et al. 2020).

Although not verified through genetics, MIMn-030 is presumed to be a male, given that it was observed in groups containing a female during both breeding area sightings. Females rarely associate with one another in breeding areas (Glockner-Ferrari & Ferrari 1990, Clapham et al. 1992, Medrano et al. 1994, Craig et al. 2002, Herman et al. 2011), with very few cases in the North Pacific (Pack et al. 2012) despite over 40 yr of research. In the Mariana Islands, the whale accompanying MIMn-030 was genetically identified as a female (M. C. Hill unpubl. data), and in the MM breeding area, MIMn-030 was observed in a competitive group of 5 whales, which typically consists of just one adult female (with or without calf) and multiple males (Tyack & Whitehead 1983). One whale in the group was a known female, determined from previous years' sightings with associated calves (A. Frisch-Jordán unpubl. data). Interestingly, 4 of

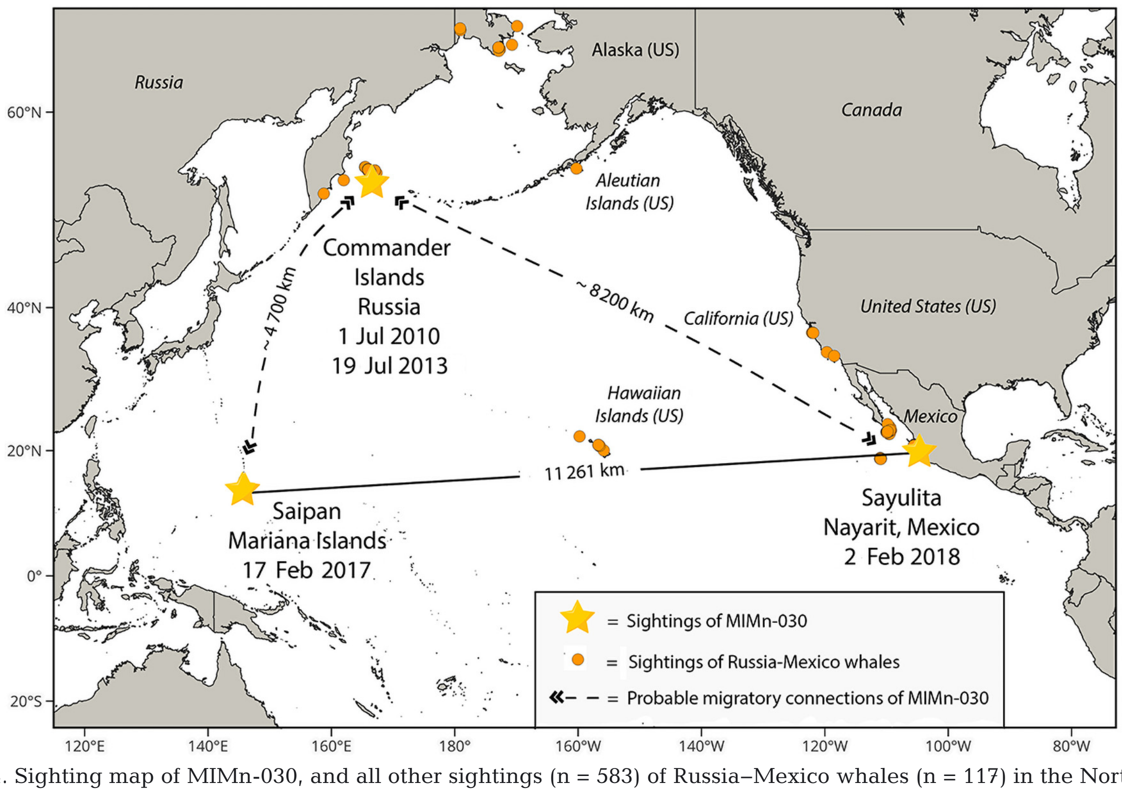

Fig. 4. Sighting map of MIMn-030, and all other sightings (n = 583) of Russia–Mexico whales (n = 117) in the North Pacific. Distances calculated are minimum great-circle distances (Bowditch 1995)

Table 2. Humpback whales *M. novaeangliae* seen in a competitive group with MIMn-030 in Sayulita, Nayarit, Mexico, on 11 February 2018. Source: Happywhale

Number	ID	First sighting (year)	Sex	Feeding area(s)
1	BREE-KOD06_0805_1_0024	2006	Female	Gulf of Alaska (2006)
2	CRC-15030	2009	Unknown	California (2009, 2013, 2017, 2018)
3	MIMn-030	2010	Unknown	Russia (2010, 2013)
4	CRC-15593	2012	Unknown	Washington (2012), Oregon (2018)
5	HW-MN0520082	2018	Unknown	Unknown

the 5 whales (including MIMn-030) have been sighted in different feeding regions of the North Pacific (Table 2).

3.2. Migratory connections between Russia and Mexico of humpback whales

In total, 117 individuals (569 sightings) were identified on Happywhale in the waters of both Mexico (MM, BAJA, and REV) and Russia between 1998 and 2021. Of these whales, 27 (23.0%) were of known sex, consisting of 19 females (14 with dependent calves) and 8 males. The calves were not included in the total number of 117 identified whales.

Nearly all the whales (n = 115) were documented only in Russian feeding areas (n = 333 sightings). A total of 105 of these whales (89.7%) were seen in waters around the Commander Islands and Kamchatka peninsula (where survey effort has been highest) and the remaining 12 whales (10.3%) were seen further north off Chukotka (Fig. 4), with no movements of any of the Russia–Mexico whales documented between the 2 areas. Only 2 of the 117 Russia–Mexico whales have been photographed in other feeding areas in addition to Russia; one whale was seen once in the Aleutian Islands in 2002 and the other was seen 3 times off Northern California within 1 mo in 2019 (Fig. 4). Approximately one-quarter of the whales were sighted in Russian waters during multiple years (n = 31, 26.5%), ranging from 2–8 yr (x = 3.0) and 2–28 unique sightings (x = 6.7).

Russia–Mexico whales were sighted in all 3 of the main breeding areas in Mexico (Figs. 2 & 5a), and although most (n = 96) were sighted in only one Mexican breeding area, 21 (17.9%) were seen in more than one region. None were documented on Happywhale as being in southern Mexico or Central America at the time of analysis. Whilst surveys were only made in the Revillagigedo Islands during the 3 years of SPLASH, during that period over half of the individuals were sighted in REV (56.8%, 25 of 44 whales), whereas 22.7% (10 of 44 whales) were sighted in MM and 20.5% (9 of 44 whales) in BAJA (Fig. 5a). Information of social groups was available for 41.5% of sightings (n = 98). Whales were seen in all known types of breeding ground social groups (Fig. 5b) in the Mexican breeding grounds, with the largest proportion of sightings (41.8%, n = 41) in courtship groups (competitive groups or mother, calf and escort(s) groups). Reports of competitive groups varied in size from 4 to an estimated 15 adult whales. Additionally, 7 whales (n = 10 sightings) were seen feeding in the Banderas Bay region of MM (N. Ransome et al. unpubl. data).

Approximately one-third of all Russia–Mexico whales (n = 41, 35.0%) were seen in multiple years in Mexico and in up to 10 different years (Fig. 5c). We documented 19 whales that were seen in consecutive years in Mexico. Three of these whales were seen in Mexico for 3 consecutive years, and 2 of these whales were sighted in the Commander Islands of Russia in the intervening feeding season of consecutive year sightings in Mexico. By computing a minimum great-circle route between the 2 locations, a round-trip Mexico–Russia–Mexico migration of >16 400 km was established (Fig. 4), representing the longest documented return migration of a Northern Hemisphere humpback whale to date. Both whales made the round-trip journey in less than 1 yr (337 and 348 d, respectively; Table 3). Additionally, 18 whales were documented making one leg of the migration to Russia from Mexico or vice versa, >8200 km and crossing ~89° of longitude (Fig. 4), with times between breeding and feeding ground sightings varying between 115 and 207 d ($x \pm$ SD: 158.1 ± 24.3 d).

Sightings of Russia whales in Mexico with exact dates (n = 228) occurred in February (n = 90, 39.5%), followed by March (n = 75, 32.9%), then January (n = 42, 18.4%). Only 14 sightings occurred in April (6.1%) and just 7 sightings (3.1%) in December (Fig. 5d). We evaluated the timing of whale sighting

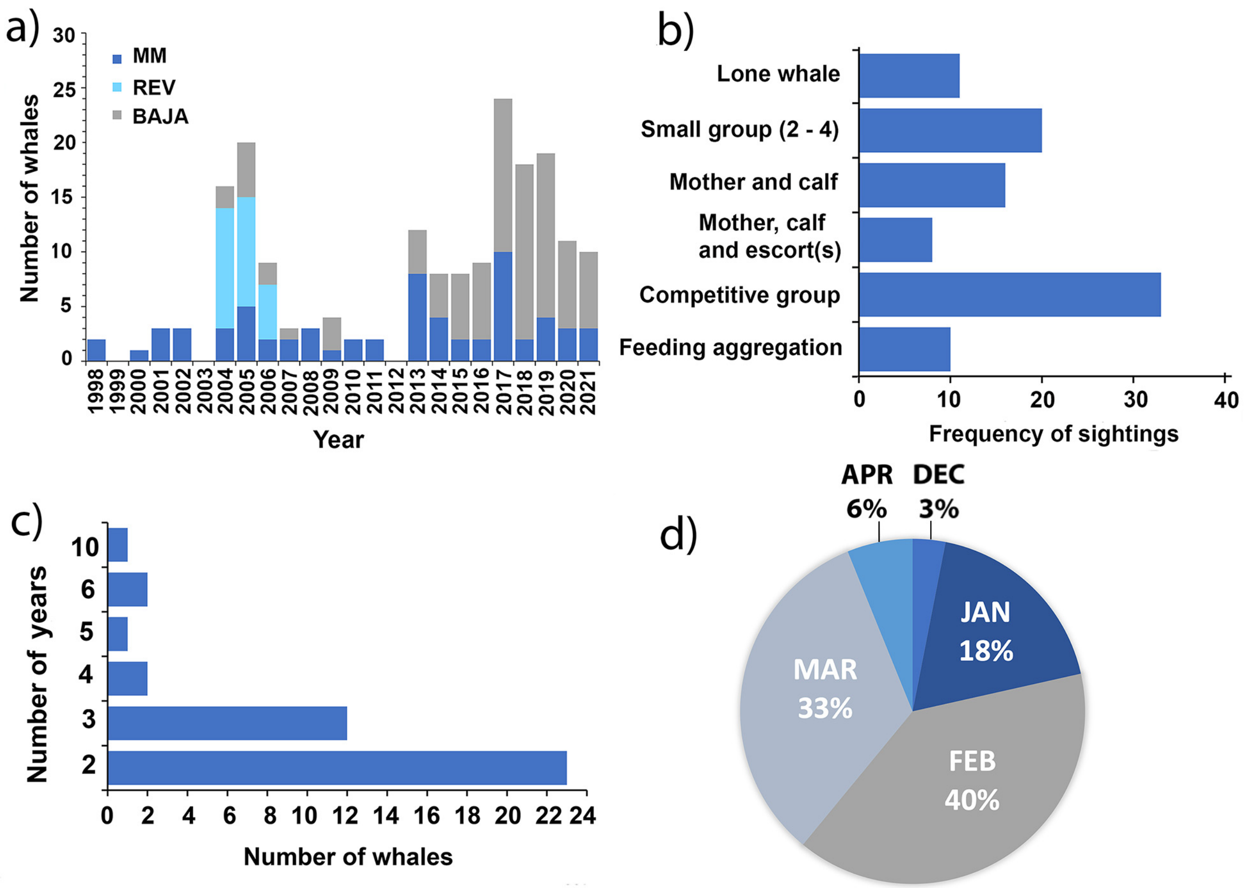

Fig. 5. (a) Number of Russia humpback whales *M. novaeangliae* seen per year in different breeding areas of Mexico (n = 237; one whale seen in different regions in the same year). MM: mainland Mexico; REV: Revillagigedo Archipelago; BAJA: Baja California. (b) Different social groups in which Russia whales were documented in the Mexican breeding grounds. (c) Russia–Mexico humpback whales seen in Mexico in multiple years (n = 41), and (d) proportion of sightings by month in Mexico (n = 231; some historic sighting images were without known date)

dates in each of the 3 regions of Mexico across years to investigate potential patterns, and while there were 2 cases when a whale was sighted on the same day in different years, in general there was little synchrony. In total, there were 58 cases in which Russia whales were spotted in the same region of Mexico in multiple years, and the average (±SD) number of days between yearly sighting dates was 21.5 ± 16.5 d (range: 0–67 d).

3.3. Intra- and inter-year resightings of Russia–Mexico whales

In total, 68.6% of Russia–Mexico whale sightings (162 of 236) were unique sightings of that year in a Mexican breeding ground, and only 22 whales were seen more than once within a year. The time between same-year sightings in Mexico varied from 1–37 d (x = 13.6 d), and all whales were resighted in

Table 3. Resightings of 2 adult humpback whales *M. novaeangliae* of unknown sex that were documented completing full Mexico–Russia–Mexico return migrations in less than 1 yr. MM: Mainland Mexico; Baja: Baja California

ID	1st sighting	1st location	2nd sighting	2nd location	3rd sighting	3rd location	Days between sightings
RCHP-12RUC0983	27 Jan 2015	MM	26 Jun 2015	Kamchatka, Russia	30 Dec 2015	BAJA	337
RCHP-13RUC01373	1 Mar 2013	MM	15 Aug 2013	Kamchatka, Russia	12 Feb 2014	MM	348

the same Mexican breeding region, except one whale that was seen in BAJA and MM in the same year. In REV, 8 whales were sighted within the same year (n = 36 sightings), including one male sighted 7 times in a year and twice in another year, and 2 females (without calves) seen 4 times in a year each. In BAJA and MM, there were only 14 whales that were seen more than once in a year (n = 33 sightings). Five of these same-year sightings involved females with dependent calves, and one whale was seen feeding on 3 occasions over 6 d in MM (N. Ransome et al. unpubl. data).

3.4. Sighting frequency of whales migrating between Russia and Mexico in North Pacific breeding areas

The Russian sample of whales seen in Mexico (whales: n = 100; average sighting frequency of 0.16 and seen on average every 8.9 yr) had significantly lower sighting frequencies (MWU = 6972, $p < 0.001$) in North Pacific breeding areas than the non-Russian sample (whales: n = 100; average sighting frequency of 0.27 and seen on average every 5.9 yr). In total, over half of the Russian sample (n = 58, 58.0%) were only documented during one year in a North Pacific breeding area (sighting histories: 5–24 yr, x ± SD: 12.0 ± 4.3 yr), even though 41 of those whales had sighting histories of over 10 yr. By contrast, only approximately one-quarter of whales in the non-Russian sample (n = 28, 28.0%) were documented in only one year in a breeding area (sighting history length: 3–18 yr, x ± SD: 10.1± 5.3 yr), and only 14 of these whales had sighting histories longer than 10 yr. Whales in the Russian sample were also far more likely to have been encountered in a different breeding area other than Mexico, with 9 individual whales (9.0% of the sample) encountered in 14 different years in Hawaiʻi (n = 13) or the Mariana Islands (n = 1; Fig. 4, Table A1 in the Appendix). Conversely, there was higher fidelity to the Mexican breeding ground by non-Russian sampled whales, with only one sighting in a different breeding area (Hawaiʻi). All whales (from both samples) of known sex (confirmed by genetic analysis) that changed breeding grounds (n = 3) were male.

4. DISCUSSION

With 11 246 km and ~109° longitude between breeding area sighting locations, the atypical movement of a humpback whale (MIMn-030) presented here, between the 2 distant breeding areas of the Mariana Islands and Mexico and in less than 1 yr, is the longest recorded great-circle distance between 2 photo-identification images of a humpback whale to date (Fig. 3). In a recent study, Hill et al. (2020) found unexpected genetic similarities (i.e. no significant differentiation in mtDNA haplotype frequencies) between humpback whales of Mexico and the Mariana Islands. Although this finding was possibly biased by the small sample size from the Mariana Islands, such similarities had previously been found between biopsy samples collected in Japan and Mexico (Baker et al. 1998), and this long-distance movement of MIMn-030 demonstrates the potential for trans-Pacific gene flow between these distant breeding regions. It also builds on earlier photo-identification studies that show some individuals, particularly males, do occasionally change breeding ground destinations (Darling & Cerchio 1993, Salden et al. 1999, Calambokidis et al. 2001, 2008, Darling et al. 2022). High mtDNA haplotype diversity in North Pacific humpback whale breeding areas (despite evidence of strong natal philopatry) led Baker et al. (2013) to suggest that some male humpback whales occasionally change breeding areas, but likely do not abandon their natal fidelity and return to migrate to the breeding areas of their birth. To help elucidate this hypothesis, continued investment into photo-identification studies and ongoing collaboration between data set holders through research tools such as Happywhale is essential.

We found that Russia–Mexico whales had been documented changing breeding areas 14 times more frequently than a sample of Mexico whales with migratory connections to other feeding areas. While the reason for this is currently unclear, we speculate that intermixing of whales from different breeding areas in feeding areas could potentially lead to whales changing low-latitude winter destinations. We note that the Commander Islands of Russia (where MIMn-030 was sighted in 2 different years) is one of the few North Pacific feeding areas where whales mix from all known regional breeding areas except Central America (Calambokidis et al. 2008, Titova et al. 2018). Another possible explanation is related to mid-oceanic mixing of whales. Due to the geographic locations of seasonal habitats, whales that undertake a trans-Pacific migration between Russia and Mexico must cross migratory paths with whales that migrate between Hawaiʻi and Alaska. This provides an additional source for intermixing of whales which may lead to individuals travelling to new breeding areas, as well as providing another mechanism for gene flow and transmission of song (Cerchio et al. 2001, Acebes et al. 2007, Darling et al. 2019b).

In our study, an unprecedented number of humpback whales from Russian feeding grounds were documented in the breeding grounds of Mexico. A total of 117 whales known to feed in Russia were sighted in Mexico over 23 yr. This unexpectedly high number of whales demonstrates trans-Pacific movements across the North Pacific Ocean basin, consisting of whales of both sexes and females with dependent calves. While this may still be a relatively small number compared with the total number of whales identified in Mexico (~7500 animals on Happywhale), approximately one-third of these whales were documented in multiple years in Mexican Pacific waters and one whale in 10 different years. Additionally, 19 whales were documented in 2 consecutive years in Mexico and 3 whales were documented in 3 consecutive years. This demonstrates high site fidelity to the breeding areas of Mexico and establishes, for the first time, that a subset of whales that feed in Russia regularly migrate east across the entire ocean basin to breed. It may also explain the high haplotype diversity of mtDNA of the Mexico DPS (Baker et al. 2013). While the peak of the breeding season in MM is in December and January (Espinoza Rodríguez et al. 2021), we note that very few Russia–Mexico whales were documented in December. It appears that much of the intermixing of distant feeding areas is likely to be occurring later in the breeding season in Mexico, in the months of February and March. This is exemplified by the competitive group that MIMn-030 was sighted in (in February) containing whales from 4 different feeding areas.

Norris et al. (1999) were the first to suggest that some whales that breed in Mexico may be migrating to Russia, at a time when no photo-identification matches existed between the 2 countries. This speculation was based on opportunistic data collection during a sperm whale *Physeter macrocephalus* acoustic research survey, which included the detection of mid-oceanic humpback whale song and observations of a mother and calf humpback whale ~1000 km from the northern California coast. Prior to our study, only 11 individuals had been matched between Mexico and Russia (Calambokidis et al. 2008, Titova et al. 2018), and it was unknown if these were outliers or regular movements. Our findings suggest that such movements are regular and highlight that the Mexican breeding areas are used by humpback whales from all over the North Pacific. It also confirms the conclusion of Calambokidis et al. (2008) that humpback whale migratory patterns in the North Pacific Ocean basin are more complex than previously thought.

Over one-quarter of the Russia–Mexico whales were seen in Russia in multiple years, providing further supporting evidence that these movements represent regular migrations between Russia and Mexico. Of the only 2 Russia–Mexico whales (1.7 %) seen in other feeding areas, we note that the region of the Aleutian Islands where one whale was sighted is the exact location where multiple tagged whales travelled when migrating between Hawaiʻi and the Commander Islands of Russia (Mate et al. 2007, Palacios et al. 2019). While to date we know nothing about the route taken by whales migrating between Mexico and Russia, it seems highly plausible that the Aleutian Island chain (which due to remoteness is substantially underrepresented on Happywhale) may be used by whales travelling between the Commander Islands and central (Hawaiʻi) and eastern (Mexico) North Pacific breeding areas.

The identification of a subset of humpback whales with Mexico–Russia migratory connections has relevance to the management of the species regionally. The US Marine Mammal Protection Act outlines the need for the identification of demographically independent populations (DIPs) (Martien et al. 2019). In 2021, NMFS outlined the existence of more than one DIP within the Mexico DPS, including the Mexico–Northern Pacific unit (Mex–NPac), a subset of the Mexico DPS that migrates to Alaska and potentially Russia, and it discussed the possibility of Mex–NPac being broken down further into multiple DIPs (Taylor et al. 2021).While they concluded that there was not enough data at the time to support the theory, our findings support the delineation of the Mex–NPac DIP for improved regional management. Aligning with this information, Martinez-Loustalot et al. (2023) proposed the presence of 3 different population units in the Mexican Pacific: the Central America population unit, the Mexico coastal population unit, and the Mexican offshore population unit, which includes humpback whales with feeding areas in the Gulf of Alaska and Aleutian Islands. Results from our study suggest that the feeding areas for this unit should be extended to include waters of the Russian Far East. Lastly, a recent publication outlined the concept of a novel unit for population management of large whales, coined ‘migratory whale herds’, defined as conspecific whales that migrate between the same feeding and breeding areas (Martien et al. 2023). Our findings suggest high site fidelity of a 'herd' of humpback whales that migrate between Russia and Mexico, which aligns with this new management policy.

We documented 2 cases of humpback whales that made the round-trip journey of Mexico–Russia–Mexico (~16 400 km) in consecutive years (~340 d), which is the longest documented humpback whale migration in the Northern Hemisphere. In the Southern Hemisphere, Riekkola et al. (2020) showed that by travelling faster, longer migrations are not necessarily more energetically demanding for humpback whales than shorter migrations. Globally, humpback whale migrations usually cross extensive latitudinal ranges but remain at similar longitudes (Stevick et al. 2011). Here, we document regular migrations crossing ~89° of longitude. These findings are similar to known migratory movements of a subset (or herd) of the North Atlantic population. Humpback whales that feed in Norway are known to breed in both the West Indies and the Cape Verde Islands (Stevick et al. 2016, Wenzel et al. 2020), on opposite sides of the ocean basin. The minimum great-circle distance between the furthest sightings of humpback whales in Norway and the western Caribbean is an estimated 8080 km, with the migration crossing ~80° of longitude (Stevick et al. 2003). As with the Russia–Mexico whales, both males and females make this trans-Atlantic migration (Stevick et al. 1999, 2003, 2016).

Comparable to the history of intensive whaling and slow population recovery in the western North Pacific (Calambokidis et al. 2008, NOAA 2016), the closest breeding ground to Norway, the Cape Verde Islands, is a small, endangered breeding population (~300 individuals) that has not recovered well from heavy exploitation during the commercial whaling era (Wenzel et al. 2020). While it is impossible to know how these atypical migrations evolved, in both the eastern North Atlantic and western North Pacific, intensive whaling resulted in very few whales migrating seasonally to these island breeding areas by the mid-twentieth century (Wenzel et al. 2009, Bettridge et al. 2015, Hill et al. 2020). We hypothesise that today, such trans-Oceanic migrations may be a relic of the impacts of whaling on these once heavily exploited humpback whale populations. Reliability of resources such as breeding partners is essential for migration to evolve and be maintained, whereas uncertainty in resources leads to changes in migration or even the development of more nomadic, unpredictable seasonal movements (Jonzén et al. 2011).

Compared to those whales in the Mexican breeding grounds with migratory connections to other feeding areas, Mexico humpback whales matched to Russian feeding grounds had significantly lower breeding ground sighting frequencies. Over one-third of Russia–Mexico whales (n = 41, 35%) had only been seen in one year in any breeding area, despite sighting histories in the North Pacific ranging 10–24 yr. While we recognize that some breeding areas (e.g. Japan) are less represented on Happywhale, this aligns with previous findings from SPLASH, and more recent research from Russia, which found low sighting frequencies of Russia humpback whales in breeding areas (Calambokidis et al. 2008, Titova et al. 2018). It is also consistent with the underrepresentation of Russia and Aleutian Island whale mtDNA haplotypes in known North Pacific breeding areas found during genetic analysis of SPLASH biopsy samples (Baker et al. 2013). Whilst it is also possible that the absence of data from the REV region influenced the low recapture rate of Russia–Mexico whales, the archipelago was extensively surveyed during the SPLASH study (Calambokidis et al. 2008), and it was the biopsies used from that project that revealed an under-representation of Russia and Aleutian Island whale haplotypes at low latitudes (Baker et al. 2013).

While we still cannot rule out the existence of an additional unknown breeding area, it is plausible that the migratory behaviour and movement patterns of Russia whales is the cause of the low breeding ground encounter rates. In 2003, a tagging study in REV found that of 3 tagged whales that had a migratory trajectory towards Russia or the Aleutian Islands, 2 whales spent extensive time offshore whilst in Mexico, constantly travelling rather than having a terminal end of their migration, and visited all 3 of the main breeding regions of the Mexico DPS (Lagerquist et al. 2008; Fig. 2). This is in contrast to 4 whales tagged in Southeast Alaska (n = 1), Oregon (n = 1) and California (n = 2) between 2004 and 2017 that were documented migrating down to Mexico: all these whales had very coastal movements when in the Mexican breeding areas (Mate et al. 2018). Constant travel and visiting multiple regional breeding areas was similarly documented in a tagging study in the Southwest Indian Ocean, which the authors suggested was a strategy to maximise mating opportunities (Dulau et al. 2017). Such behaviour of extensive offshore movements and constant travel may lead to low detection rates of Russia whales in Mexico as a result of under sampling, especially in consideration of the large area used by the Mexico DPS and the 3 isolated coastal/island regions from where most data are collected (Fig. 2). This may mean that far more Russia whales are regularly visiting Mexico than our findings suggest. Continued and increased survey efforts (especially in REV) will, therefore, likely lead to greater numbers of these whales eventually being recorded.

Migratory behaviour of constant travel and offshore movements of Russia–Mexico whales may also involve the use of seamounts. Tagging and acoustic studies have shown that seamounts are used for breeding activities in the Southern Hemisphere (Dulau et al. 2017, Derville et al. 2019, Ross-Marsh et al. 2022). The western North Pacific Ocean basin has more seamounts per square kilometre than any other oceanic region globally (Kitchingman et al. 2008). The use of seamounts as breeding habitat may explain the genetic underrepresentation and low sighting frequencies of Russia whales in North Pacific breeding areas (Calambokidis et al. 2008, Baker et al. 2013, Titova et al. 2018). Lastly, while there is no available information on the route that whales take while migrating across the Pacific between Russia and Mexico, our findings of 13 distinct seasonal sightings in Hawaiʻi of Russia–Mexico whales, in combination with the findings of other studies documenting (1) mid-oceanic singing at low latitudes directly between the Mexican and Hawaiian breeding areas (Darling et al. 2019a) and (2) 4 whales being documented in the 2 breeding areas during the same year (Forestell & Urbán R 2007, Darling et al. 2022, Happywhale unpubl. data) also lend to the possibility that some whales may be visiting Hawaiʻi whilst transiting the Pacific between Russia and Mexico.

We predict that with continued collaboration and focused localised research ocean-basin-wide, greater evidence of migratory connections (e.g. through photo-identification, genetics, acoustics, and potentially, telemetry) will continue to be found between the 3 North Pacific breeding regions and the 4 DPSs that use them. Annually higher numbers of Russia–Mexico whales will be encountered, and with time, a greater proportion of the herd will be photo-identified on Happywhale. We believe that more in-depth and collaborative studies into Russia and Aleutian Island humpback whales at low latitudes, and the life histories of whales documented in different breeding areas and/or with very low sighting rates, will aid in resolving many of the questions that remain about North Pacific humpback whale migration and population structure. Lastly, our findings support the need for improved protection and effective regional management of humpback whales in Mexico to aid in the conservation of multiple at-risk DPSs of the species.

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Appendix.

Table A1. Sightings of humpback whales *Megaptera novaeangliae* from the Russia sample and non-Russian sample (*) in Hawai‘i. Public data from Happywhale and permission of use for other sightings granted by Pacific Whale Foundation and Whale Trust

Number	Happywhale ID	Sighting date 1	Sighting date 2
1	RCHP-10RUCO489	24 Feb 2018	NA
2	HW-MN0300047	03 Mar 2010	22 Feb 2019
3	RCHP-13RUCO1408	03 Mar 2020	NA
4	RCHP-13RUCH1457	22 Feb 2019	11 Jan 2021
5	RCHP-17RUAN1842	17 Dec 2018	08 Jan 2018
6	RCHP-16RUCO1640	13 Feb 2013	NA
7	RCHP-17RUAN1860	25 Mar 2004	11 Mar 2020
8	RCHP-17RUEC1711	24 Jan 2018	12 Jan 2020
9*	HW-MN0400685	24 Jan 2020	NA

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