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The Decline of Humpback Whales in Prince William Sound, Alaska, Following the 2014–2016 Northeast Pacific Marine Heatwave

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Received: 9 September 2025 | **Revised:** 9 February 2026 | **Accepted:** 21 February 2026

Keywords: humpback whale | marine heatwave | *Megaptera novaeangliae* | population decline

In the early 1970s, all populations of humpback whales (*Megaptera novaeangliae*) were listed as endangered under the US Endangered Species Conservation Act of 1969 (Public Law 91-135, [n.d.](#)) and the Endangered Species Act in 1973 (Public Law 93-205, [n.d.](#)). Three decades later in 2006, the humpback whale population in the North Pacific Ocean had increased from approximately 1200–1400 (Johnson and Wolman 1984) to at least 21,000 individuals (Barlow et al. 2011) and continued increasing to over 30,000 individuals by 2013 (Cheeseman et al. 2024). In 2016, the National Marine Fisheries Service of the United States (NMFS) reassessed the listing of humpback whales under the Endangered Species Act. Worldwide, 14 distinct population segments (DPS) were identified, with four inhabiting the North Pacific. The Hawai'i DPS, that includes approximately 89% of the individuals that migrate to the Gulf of Alaska (Wade 2021), was delisted from the Endangered Species Act, the Mexico DPS was listed as threatened, while the Western North Pacific and Central American DPSs remained classified as endangered (Federal Register 2016). Coincident with this revised listing of humpback whales was the northeast Pacific marine heatwave (PMH), one of the strongest marine heatwaves recorded in recent decades (Di Lorenzo and Mantua 2016; Hobday et al. 2018).

The PMH of 2014–2016 affected many species across trophic levels with some marine mammals and marine bird populations in the Gulf of Alaska showing strong negative effects (Suryan et al. 2021). Common murre (*Uria aalge*) (Bien et al. 2024; Piatt et al. 2020; Renner et al. 2024), Steller sea lions (*Eumetopias jubatus*) (Hastings et al. 2023; McHuron et al. 2024), and humpback whales (Cartwright et al. 2019; Cheeseman et al. 2024; Frankel et al. 2022; Gabriele et al. 2022) all responded negatively to a

decline in forage fish abundance and nutritional value (Arimitsu et al. 2021; von Biela et al. 2019). The impact of the PMH on humpback whales and fin whales (*Balaenoptera physalus*) resulted in the declaration of an unusual mortality event by NMFS in Alaska and British Columbia (Savage 2017). A subsequent analysis in 2024 estimated a loss of ~7000 humpback whales from the North Pacific population following the PMH with the Hawai'i DPS suffering a decline of 34% from 2013 (Cheeseman et al. 2024). In the Gulf of Alaska, humpback whales prey on Pacific herring (*Clupea pallasii*), Pacific capelin (*Mallotus catervarius*), eulachon (*Thaleichthys pacificus*), juvenile walleye pollock (*Gadus chalcogrammus*), juvenile salmon (*Oncorhynchus* spp.), Pacific sand lance (*Ammodytes personatus*), and euphausiids (Boswell et al. 2016; Burrows et al. 2016; Chenoweth et al. 2017; Nemoto 1957; Szabo 2015; Witteveen et al. 2008). Within the waters of Prince William Sound, Alaska (PWS), Pacific herring dominate the diet of humpback whales particularly in the spring when herring aggregate to spawn and during the fall and winter when large overwintering shoals form (Moran et al. 2018; Straley et al. 2018). During the PMH, forage fish abundance declined dramatically in PWS (Arimitsu et al. 2021; Branch 2025; Dias et al. 2022; McGowan et al. 2021). PWS herring reached historical lows between 2016 and 2018, followed by a recovery, reaching pre-heatwave levels by 2022 (Branch 2025; Morella 2025).

We monitored humpback whale abundance within PWS (60°35'N, 147°10'W) from 2007 to 2024. PWS is 10,000 km² of relatively protected waters in the northern Gulf of Alaska, characterized by complex coastlines of glacial fjords and islands. Of the humpback whales feeding in the Gulf of Alaska, 89% breed in Hawaiian waters and 11% breed off the coast of Mexico

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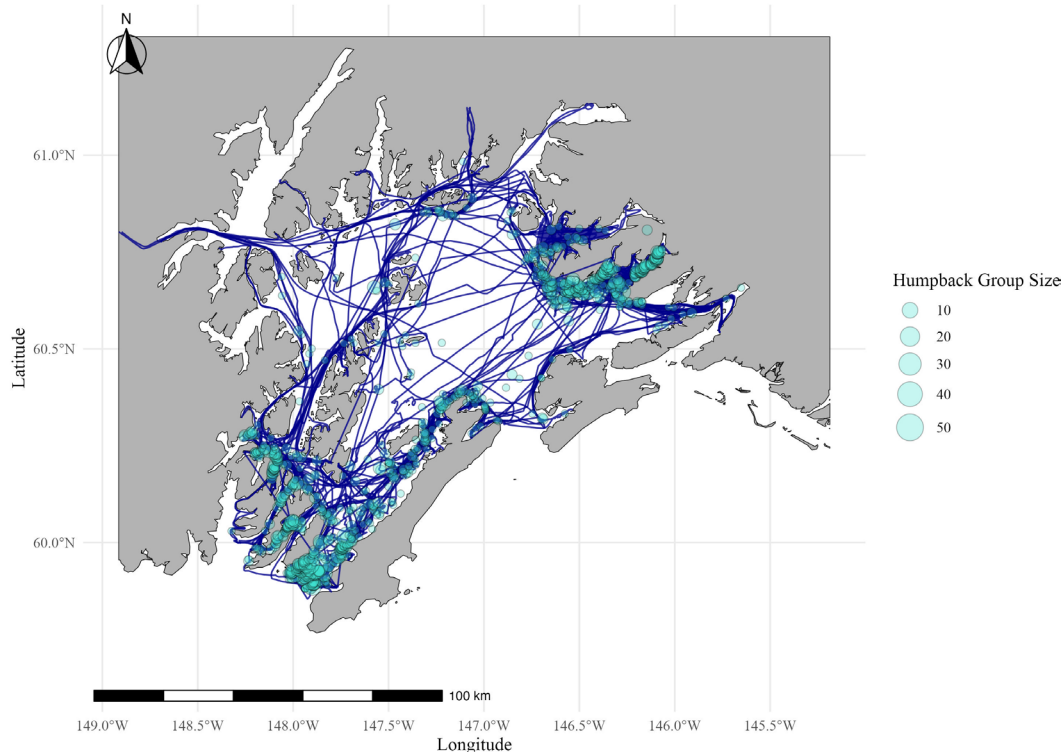


FIGURE 1 | The distribution of humpback whale sightings and survey coverage in Prince William Sound, AK. Group size ranged from 1 to 50 with a mean of 2.5.

(Wade 2021). Within PWS, humpback whales are present throughout the year with numbers peaking in October through November, then dropping during late December through early January (Moran et al. 2018; Straley et al. 2018); however, some individuals have skipped the migration south and remained in Alaska waters over winter (Moran et al. 2018; Straley 1990; Straley et al. 2018). Although there is some exchange between feeding areas, adults tend to show a strong fidelity to a specific feeding ground (Baker et al. 2013; Cheeseman et al. 2023; Martien et al. 2023). Migration between the Gulf of Alaska and the breeding grounds take approximately 30 days (Mate et al. 1998; Gabriele et al. 1996) with limited opportunity to feed along the way, especially for individuals migrating to Hawai'i (Frisch-Jordán et al. 2019; Gendron 1993; Lammers et al. 2024; Ransome et al. 2024); thus, a healthy forage base in high latitude waters is critical to support the year-round energy budget for North Pacific humpback whales. In PWS, large shoals of Pacific herring made up the majority of prey for humpback whales (Straley et al. 2018).

During the study period, we conducted 42 vessel-based surveys, ranging from 5 to 10 days of the areas most frequented by humpback whales in PWS during spring (March–April) and fall/winter (September–December). The timing of these surveys corresponded to the herring spawn in the spring and the migration of adult herring into PWS prior to overwintering (Bishop and Eiler 2018). We used systematic photographic surveys to identify individual whales over an 18-year period (September 2007–September 2024) (Figure 1) (Straley et al. 2018) to estimate inter-annual variation in abundance before, during, and after the PMH.

By using the unique markings on the flukes (Katona et al. 1979) from our surveys and opportunistically collected photographs, 381 whales were individually identified from November of 2007 through September of 2024 (allowing mark recapture abundance estimates through 2023). We used the Rcapture (Rivest and Baillargeon 2022) package (R version 4.1.3; R Core Team 2022) and Jolly-Seber-Cormack Estimator to estimate humpback whale abundance within PWS. The model uses encounter histories for the humpback whales as a function of year (resighting probability in a given year) and accounts for individual heterogeneity in resighting effect due to either poor fluke photo quality, individual behavior, or survey effort. We defined the year for a marking period beginning on 15 March to coincide with the migration cycle of humpback whales to the breeding grounds (i.e., a whale seen prior to 15 March would be included in year x , on or after that date they would be included in year $x + 1$).

Because it is unlikely that we photographed all of the whales within PWS, 381 individuals photographed should be considered a minimum number of observed non-calf humpback whales found within PWS during the study period. The total estimated number of whales that inhabited PWS during our study period estimated from the Jolly-Seber-Cormack mark-recapture model (Rivest and Baillargeon 2022) was 473 (SE = 15.3) individuals, excluding calves of the year, and ranged from an annual high of 298 whales pre-PMH in 2012 to a low of 57 whales 7 years after the PMH (Table 1). This represents a 50% decline in the median population size before (2007–2014) versus after (2015–2023) the PMH. Counts of calves and the number of whales seen during fall surveys followed a similar pattern, with a decline after the PMH (Table 1).

In Summary, humpback whale numbers have failed to recover in PWS following a decline that was coincident with the 2014–2016 PMH in the Gulf of Alaska. The initial decline of humpback whales was also coincident with a decline in the aerial mile-days-of-milt (the linear distance and the duration of beaches receiving herring spawn) (Hulson et al. 2008), an index of the herring biomass, in PWS (Figure 2) (Morella 2025; Muradian et al. 2017), a key foraging opportunity for this local population of whales (Moran et al. 2018; Straley et al. 2018). The dramatic

decline in herring spawn reflected an overall decline of herring biomass in PWS (Branch 2025; Dias et al. 2022; McGowan et al. 2021). The herring population increased to pre-PMH levels by 2022; however, the humpback whale population did not reflect the same increase (Figure 2).

Upper trophic level predators in the northeastern Gulf of Alaska, including PWS, appear to have been more affected by the PMH than adjacent areas. The largest counts of dead or moribund common murrens occurred in the northeastern Gulf of Alaska during a PMH-associated mass murre mortality event (Piatt et al. 2020) that contributed to an estimated total mortality of four million murrens, 50% of the population, in Alaska (Renner et al. 2024). Following the PMH, Steller sea lion pup production in the northeastern Gulf of Alaska was reduced by 33.5% (McHuron et al. 2024) and prime-age female survival rates in PWS dropped by -0.233 and took longer to recover than adjacent areas (Hastings et al. 2023; McHuron et al. 2024). The distinct population segment of North Pacific humpback whales with the greatest loss of individuals after the PMH (6561 individuals, 35% of the population) included those that migrate to the Gulf of Alaska (Cheeseman et al. 2024), with the PWS whale population exhibiting an even greater proportional decline post-PMH (50%). These subsequent analyses of predator populations are consistent with previous analyses indicating that mid and upper trophic-level species in the northeastern Gulf of Alaska were more negatively affected during the PMH (Suryan et al. 2021).

Humpback whale populations have the potential to increase up to 11.8% annually (Zerbini et al. 2010). Within the Gulf of Alaska, the Glacier Bay population increased at 5.1% annually between 1985 and 2013 (Gabriele et al. 2017). Given the recovery of their primary prey to pre-heatwave levels and observations of other populations showing signs of recovery, such as humpback whales in Glacier Bay, Alaska (Neilson et al. 2024; Neilson et al. 2025), we expected that humpback whale abundance in PWS would follow similar patterns.

Why humpback whale populations in PWS remain depressed 7 years after the PMH is unclear but is possibly related to mortality and low calf production. With strong foraging site fidelity in adult whales (Baker et al. 2013; Cheeseman et al. 2023;

TABLE 1 | Annual abundance estimates ($\pm$ SE) derived from Jolly-Seber-Cormack (open) estimators for Prince William Sound.

Year	Estimated abundance	SE	Whales seen	Calf counts
2007	135	11.0	95	4
2008	196	11.5	71	7
2009	No survey	—	No survey	No survey
2010	No survey	—	No survey	No survey
2011	175	12.3	62	2
2012	298	15.4	81	5
2013	196	16.3	113	6
2014	270	22.4	181	1
2015	190	49.2	No survey	0
2016	No survey	—	No survey	No survey
2017	128	25.9	12	0
2018	106	24.1	17	1
2019	94	18.0	35	0
2020	85	27.3	14	2
2021	85	17.1	23	0
2022	98	21.2	19	1
2023	57	12.4	34	4

Note: Calves were excluded from mark-recapture abundance estimates but are provided to show relative changes over time. No surveys were done in 2009, 2010, or 2016.

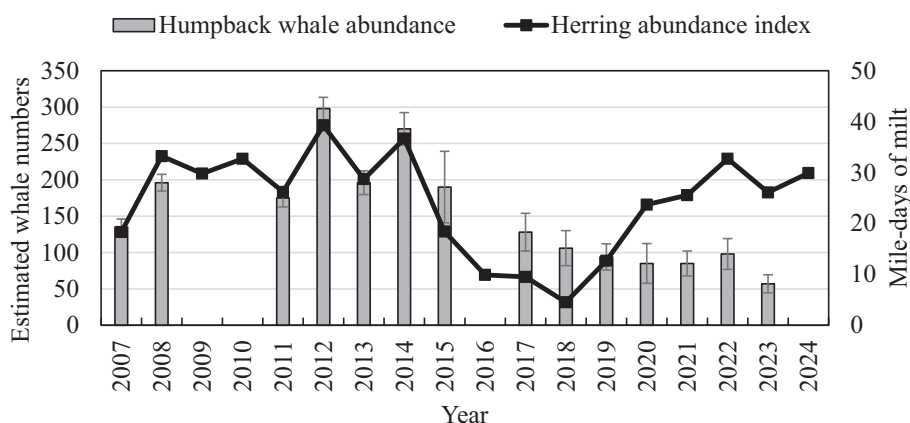


FIGURE 2 | Estimated annual humpback whale abundance in Prince William Sound, AK, and an index of herring abundance from aerial surveys during spawning (mile-days of milt). No whale surveys occurred in 2009, 2010, or 2016.

Witteveen and Wynne 2017), immigration to and emigration from PWS is likely low. Furthermore, with consistently low calf production in PWS since the heatwave (Table 1), the population has been slow to replace itself. Given the high energetic cost of gestation and migration (van Aswegen et al. 2025), the lack of late-season, energy-rich herring is likely a factor in the decline, whereas waters in Southeast Alaska supporting whales inhabiting Glacier Bay seemed to have provided a larger buffer with faster recovery for prey resources (Brooks et al. 2025). Given that oil from the TV Exxon Valdez oil spill has been sequestered in sediments and no longer bioavailable since at least 2015 (Lindeberg et al. 2018), it seems reasonable to rule out lingering oil spill effects in limiting post-heatwave recovery. The first sign of potential recovery for PWS humpback whales, however, occurred in 2023 when calf counts finally approached pre-PMH levels (Table 1). The response to heatwaves by whales is not unique to PWS. The effects on whales from heatwaves are diverse and have been widely reported (Barlow et al. 2023, Cartwright et al. 2019, Cheeseman et al. 2024, Frankel et al. 2022, Gabriele et al. 2022); however, PWS appears to be an extreme example of impacts to a local population, suggesting that the current Hawai'i breeding DPS designation may not fully capture finer scale trends in abundance that are affected by local conditions on disparate summer feeding groups. Our study demonstrates that it will be more than a decade post-heatwave before the local population of humpback whales in PWS recovers and highlights the importance of maintaining research and monitoring efforts to understand the long-term effects of major ecosystem perturbations.

Author Contributions

John R. Moran: conceptualization, data collection, funding acquisition, original draft, project administration. **Janice M. Straley:** conceptualization, data collection, data curation, funding acquisition, review, editing and permitting (NOAA and IACUC). **Jacek M. Maselko:** statistical analysis, review and editing. **Lauren A. Wild:** data collection, data curation, review, permit reporting and editing. **Robert M. Suryan:** data collection, funding acquisition, review and editing.

Acknowledgments

We thank the Exxon Valdez Oil Spill Trustee Council for funding this project and additional support and resources provided by the National Marine Fisheries Service. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of the reviewers, supporting institutions, the Exxon Valdez Oil Spill Trustee Council, NOAA, or the U.S. Department of Commerce. All humpback whale photographic data collected was authorized under scientific research permit number 473-1700-00 issued to Janice M. Straley from National Marine Fisheries Service, Office of Protected Resources, Washington, D.C., and with the approval of the Institutional Animal Care and Use Committee, University of Alaska Fairbanks. The Alaska Department of Fish and Game provided herring data and is not responsible for errors or deficiencies in reproduction, subsequent analysis, or interpretation. Special thanks to the captains of the M/V Auklet, M/V Babkin and M/V Island C, for their knowledge of PWS and all the crew that joined us on our surveys. Thanks to those who braved the waters of PWS to help us in the field: Yumi Arimitsu, Tayler Bare, Mariela Brooks, Kelly Cates, Jennifer Cedarleaf, Ellen Chenoweth, Ben Gray, Kristen Gorman, Madison Kosma, Caitlin Marsteller, Annie Masterman, Andy McLaughlin, Kate McLaughlin, Heather Riley, Anne Schaefer, Andy Szabo, Johanna

Vollenweider, and Bree Witteveen. Thanks to Jennifer Morella and Scott Pegau for his insight into herring and reviewing this paper.

Funding

Funding was provided by Exxon Valdez Oil Spill Trustee Council with additional support and resources from NOAA Fisheries, Alaska Fisheries Science Center.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from Gulf Watch Alaska data portal, https://gulf-of-alaska.portal.aos.org/#search?type_group=all&tagtag=evos-gulf-watch-projects&page=1.

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