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Humpback Highs and Lows Amid Shifting Seas and a Northeast Pacific Marine Heatwave: Whale Demographics in the Main Hawaiian Islands, 2002–2023

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ABSTRACT

North Pacific humpback whales are a celebrated conservation success, rebounding from extensive commercial whaling. Yet they remain vulnerable to the impacts of climate change, a multifaceted stressor that can exacerbate existing threats. During 2013–2016, a Northeast Pacific marine heatwave severely reduced forage availability in their feeding grounds, concurrent with diminished whale recruitment and increased mortality. We analyzed photo-identification data of whales that visited the Main Hawaiian Islands from 2002 to 2023 to estimate apparent survival, abundance, and distinct population segment (DPS) growth rates. Survival was high prior to (0.987; SE = 0.003), low during (0.684; SE = 0.022), and higher, but still reduced, after (0.956; SE = 0.006) the heatwave. Annual breeding season abundance estimates averaged 11,617 (SD = 1914) and included a striking 37% decrease from 2014/15 to 2021/22. While the average annual DPS growth rate was stable (1.00) over 20 breeding seasons, shorter periods included high growth (1.09) and steep decline (0.783). Depressed survival and abundance estimates may signal lingering heatwave effects or adjustment to current carrying capacity. Climate change predictions include more frequent, intense, and longer heatwaves; thus, this DPS serves as a crucial ecosystem-health indicator. Continued research and monitoring are essential to support resiliency against future climate perturbations.

HŌʻULUʻULU

He lanakila ka hoʻomaluō ʻana aku o nā koholā kuapuʻu o ka Pākīpika ʻĀkau, ko lākou ola ʻana hoʻi i ka nui o ke ʻō koholā ʻana. Mau nō naʻe ka pāhiki o ko lākou pā ʻana aku i ka loli aniau, he mea i nui ai kona mau ʻano i hiki ke pā i nā mea weliweli. Mai ka makahiki 2013 a i ka makahiki 2016, ua emi nui mai ka hiki ke loaʻa ka ʻai ma ko lākou mau wahi ʻai ma muli hoʻi o ka piʻi ʻana aku o ka wela ma ka māhele kai Pākīpika hikina ʻākau, a pēlā pū i ke emi ʻana mai o nā koholā hou a i ka piʻi ʻana mai ka heluna make. Ua kālailai aku nō mākou i ka ʻike pili kiʻi o nā koholā i kipa aku i ka paeʻāina Hawaiʻi mai ka makahiki 2002–2023 i mea e koho ai i ke ola, ka nui a me ka heluna piʻi o ka māhele pūʻuo kikoʻī (DPS). Ua nui ka heluna ola ma mua o (0.987; SE = 0.003), a ma loko o (0.684; SE = 0.022), a piʻi iki aʻe i loko nō o ke emi iki mai, ma hope o (0.956; SE = 0.006) ke au wela. ʻO ka ʻawelike o ke kau hoʻopiʻi ma kahi o ka 11,617 (SD = 1914) a helu pū ʻia ke emi pūʻiwa ʻana ma ke 37% mai ka makahiki 2014/15 a i ka makahiki 2021/22. I loko no naʻe o ka paʻa o ka ʻawelike kūmakahiki o ka piʻi DPS (1.00) ma o nā kau hoʻopiʻi he iwakālua, ʻo nā wā pōkole ka wā e loaʻa ai ka piʻina nui (1.09) a pēlā pū i ke emi nui (0.783). ʻO ka hua o kēia ʻano ola ʻana me ke koho nui, ʻo ia nō ka loaʻa paha o nā hopena au wela a i ʻole paha ka loli ʻana o ka nui o ke au. I loko o nā wānana loli aniau ka nui, ka ikaika a me ka lōʻihi o nā au wela; a no laila, koʻikoʻi loa kēia DPS i kuhikuhi o ke ola kaiaola. Koʻikoʻi maoli nō ka mau ʻana aku o ka noiʻi a me ka makaʻala i nā mea hoʻopilikia i ke aniau i kēia mua aku.

1 | Introduction

Effective conservation interventions and legal protections have enabled some formerly severely reduced wildlife populations to experience remarkable growth towards recovery, becoming celebrated examples of conservation success (e.g., the bald eagle, *Haliaeetus leucocephalus*, Zimmerman et al. 2022; North Pacific and Western and Eastern Australian humpback whales, *Megaptera novaeangliae*; Bejder et al. 2016; Brooks et al. 2025; Cheeseman et al. 2024; but see also Friedlaender 2026; Rocha et al. 2014; Surma and Pitcher 2015). Yet, numerical recovery does not necessarily equate to resiliency, as many populations remain vulnerable to direct and indirect effects of climate change (Hastings et al. 2020; Learmonth et al. 2006; MacLeod 2009; Tulloch et al. 2019; van Weelden et al. 2021). Climate change impacts can also exacerbate existing anthropogenic stressors (e.g., habitat destruction, pollution, etc.), further jeopardizing conservation gains (Learmonth et al. 2006; Gulland et al. 2022; Lettrich et al. 2023). Given the challenges in safeguarding populations that have benefited from past conservation investment, contemporary demographic estimates are critical to guide management decisions based on current conditions, rather than past successes (Higham and Bejder 2008; Tulloch et al. 2019; Tyne et al. 2014; Vivier et al. 2026).

Humpback whales in the North Pacific have achieved substantial numerical recovery after being severely depleted by commercial whaling (Cheeseman et al. 2024; Rocha et al. 2014; Surma and Pitcher 2015). Although coarse and possibly underestimated, the pre-whaling estimate was thought to number about 15,000 whales (Muto et al. 2021; Rice 1978), plummeting to as few as 1200–1600 whales following extensive exploitation (Gambell 1976; Johnson and Wolman 1984). After commercial whaling ceased in the North Pacific during the 1970s, a prolonged period of growth in whale abundance led to recent estimates exceeding 20,000 whales—surpassing the pre-whaling estimate (Barlow et al. 2011; Cheeseman et al. 2024).

Yet even as commercial whaling is no longer a species-wide danger to humpback whales, they remain susceptible to widespread anthropogenic impacts (Bettridge et al. 2015; Muto et al. 2021; Schakner et al. 2022). Whales face risks from entanglement with fishing gear (Tackaberry et al. 2022), vessel strikes (Bradford and Lyman 2018, 2019; Lammers et al. 2011; Neilson et al. 2012; Lomac-MacNair et al. 2018; Rockwood et al. 2017), marine pollution (Currie et al. 2017), unsustainable tourism (Currie et al. 2021; Stack et al. 2021), and acoustic disturbance and masking (Tyack 2008; Gabriele et al. 2018; Heenehan et al. 2019; Schakner et al. 2022). In addition to these impacts, climate change has emerged as a particularly concerning threat to whales that may compound and overshadow other stressors (Gulland et al. 2022; Lettrich et al. 2023) by reducing prey availability and quality and degrading the ecosystem (Hastings et al. 2020; Tulloch et al. 2019; von Hammerstein et al. 2022; Schakner et al. 2022).

From late 2013 through 2016, a natural experiment in climate impact to marine life transpired as an unprecedented marine heatwave occurred in the northeastern Pacific Ocean (Cornwall 2019; Di Lorenzo and Mantua 2016; Gentemann et al. 2017). Warm water anomalies associated with this Pacific marine heatwave (PMH) persisted through 2019 (Suryan et al. 2021), and in some locations, elevated temperatures remained in the water column even after sea surface temperatures normalized (Jackson et al. 2018). These thermal anomalies disrupted marine food webs (Cornwall 2019), reducing whale prey, including fish and krill (Arimitsu et al. 2021; Suryan et al. 2021). The affected area encompassed key feeding grounds of North Pacific humpback whales (Cheeseman et al. 2024; Gabriele et al. 2022), so it was not surprising that potential PMH impacts to whales were documented including lower crude birth rates, lower calf survival, longer calving intervals, lower encounter rates, emaciation, mass mortality, and, in some locations, abrupt declines in whale numbers (Arimitsu et al. 2021; Cartwright et al. 2019; Cheeseman et al. 2024; Frankel et al. 2022; Gabriele et al. 2022; Kügler et al. 2020; Moran et al. 2026; Neilson et al. 2025, 2026; NOAA 2019; Savage 2017).

Under the U.S. Endangered Species Act (ESA), humpback whales that breed within the Main Hawaiian Islands (MHI) are considered a distinct population segment (DPS) of North Pacific humpback whales (Bettridge et al. 2015). In 2016, after decades of numerical growth of whales in the North Pacific, but while the PMH was still occurring in some areas, the Hawaiʻi DPS was delisted under the ESA (U.S. Federal Register 2016; Schakner et al. 2022). This DPS represents approximately half of the North Pacific humpback whales (Barlow et al. 2011; Calambokidis et al. 2008; Muto et al. 2021; Wade et al. 2021; Young et al. 2024). Whales in this DPS typically breed in Hawaiʻi

(Bettridge et al. 2015; Young et al. 2024) during late fall to early spring and return for the rest of the year to their higher latitude feeding grounds along the North Pacific rim, including primarily Southeast Alaska/Northern British Columbia and the Gulf of Alaska, and also Washington/Southern British Columbia, the Aleutian Islands/Bering Sea, and Russia (Calambokidis et al. 2008; Cheeseman et al. 2024; Young et al. 2024). Known as "koholā" in ʻŌlelo Hawaiʻi (Hawaiian language) (Pukui and Elbert 1992; cf. Herman 1979), these whales migrate to and throughout the Hawaiian Islands region with arrivals generally staggered by sex, age class, and reproductive status (Craig et al. 2003; Currie et al. 2018).

While site fidelity is generally high to the Hawaiian Islands breeding grounds (Herman et al. 2011; Baker et al. 2013), whales sighted there have also been observed infrequently in other breeding grounds such as Mexico and Japan (Cheeseman et al. 2024; Darling and Cerchio 1993; Darling et al. 2022; Salden et al. 1999). Also, females that are in poor condition due to the high energetic costs of reproduction (e.g., van Aswegen, Szabo, Currie, Stack, Evans, et al. 2025; van Aswegen, Szabo, Currie, Stack, West, et al. 2025) may forgo the energetically costly migration to lower latitude breeding grounds, while others may become pregnant enroute to the breeding grounds and return to the feeding grounds before arriving at the breeding grounds (Craig and Herman 1997). These detailed, DPS-specific insights have been made possible only through decades of dedicated whale research and monitoring—efforts that remain essential for effective adaptive management of this DPS (NOAA 2019; Schakner et al. 2022).

A primary method of long-term whale research in Hawaiʻi involves identifying individual humpback whales by the unique shape and color patterns on the ventral surface of their tail flukes (Katona et al. 1979), with the first of such humpback whale photo-identification studies in the Hawaiian Islands beginning in the late 1970s (Baker and Herman 1981, 1984, 1987; Cerchio 1998; Darling and Morowitz 1986). Photo-identification (hereafter, "photo-ID") data allow for tracking individual whales over time and space and can be used to estimate various population parameters including abundance (Hammond 1986, 1990; Hammond et al. 1990, 2021; Urian et al. 2015). Photo-ID based abundance estimates for the Hawaiʻi breeding grounds showed the DPS generally increased over time from 895 estimated off Maui during 1977–1979 (Darling et al. 1983), to 1407 during 1980–1983 (Baker and Herman 1987), to ~4000 during 1989–1993 (Cerchio 1998), to 4000 and 5200 during 1991–1993 (Calambokidis et al. 1997), to about 10,000 whales during 2004–2006 (Calambokidis et al. 2008). Although specific sampling areas and analytical methods varied across these studies, the combined results indicate the DPS grew during this period, spanning approximately one-quarter century.

More recent studies in the MHI have detected potential impacts of the PMH to this DPS (NOAA 2019), including declines in overall whale and calf numbers and calving rates off Maui and Hawaiʻi Island (Cartwright et al. 2019; Frankel et al. 2022) and reduced male song chorusing off Maui, a proxy for relative whale abundance (Kügler et al. 2020, 2021). Although the PMH officially ended by 2017, subsequent research in part of the Hawaiʻi DPS's feeding grounds found that crude birth rates had rebounded and even exceeded the pre-PMH mean (Gabriele et al. 2024). However, whale abundance in a well-studied feeding area in southeastern Alaska had not returned to pre-PMH levels (Neilson et al. 2025, 2026), similar to the observed trend of low whale numbers in Prince William Sound in southcentral Alaska (Moran and Straley 2024; Moran et al. 2026). Interestingly, evidence from a breeding ground study demonstrated that both crude birth rates and whale densities were at or above levels seen prior to the PMH (Mobley Jr. et al. 2023). The authors of that study suggested the DPS was resilient to this exceptional climatic event, but noted that because the study was not conducted throughout the MHI, it was unclear whether the return to pre-PMH densities was DPS-wide or a reflection of whales from elsewhere in the DPS moving to the preferred habitat of Maui Nui (Mobley Jr. et al. 2023). Further complicating the assessment, the period of comparison was 1993–2003, not the years immediately prior to the PMH when abundances were thought to be much higher (Cheeseman et al. 2024; Neilson et al. 2025). Another study that focused on waters off west Maui demonstrated that distance-sampling abundance estimates generally increased following the reported decline, but fluctuated during 2018–2021 (Zang and Lammers 2021). Similarly, declines in male humpback whale chorusing persisted after the PMH ended until increases were detected at some sites in the 2018/19 season (Kügler et al. 2020). The authors of the chorusing study noted their results could have been affected by a decrease in abundance, altered migration patterns, distributional changes, varying behavior, or a combination of these factors, and stressed that continued monitoring and further studies were warranted (Kügler et al. 2020).

While potential signals of PMH impacts were detected in the Hawaiʻi DPS (Cartwright et al. 2019; Cheeseman et al. 2024; Frankel et al. 2022; Kügler et al. 2020; see Mobley Jr. et al. 2023 for review; NOAA 2019), most studies were limited spatially, temporally, or methodologically. Given remaining uncertainty, a comprehensive survival, abundance, and DPS growth rate analysis prior to, during, and after the PMH was necessary (Cheeseman et al. 2024; NOAA 2019; Schakner et al. 2022). Such an analysis would also offer valuable insight into how humpback whale populations may respond to future climate-driven perturbations, informing longer-term trajectory forecasts and conservation strategies for populations exposed to extreme climate events, particularly as marine heatwaves are expected to increase in both frequency and intensity (NOAA 2019; Schakner et al. 2022; Cornwall 2019).

Recently consolidated MHI humpback whale photo-ID data from numerous research organizations and members of the public, curated through the web platform Happywhale (Cheeseman et al. 2023), have provided an unparalleled opportunity to assess Hawaiʻi humpback whale demographics at a resolution never before possible. In the study reported here, using over 20 years of photo-ID data, we applied capture-mark-recapture models (Hammond et al. 2021; Brooks et al. 2024) to estimate survival, abundance, and DPS growth rates—key metrics identified as ESA post-delisting monitoring priorities (NOAA 2019; Schakner et al. 2022). Our modeling approach directly incorporated heterogeneity (Pledger et al. 2010) to minimize bias from analyzing breeding-ground-only data (Smith et al. 1999) and from other sources, including differential migration, varying residency at the breeding ground, contrasting behavior based on reproductive state, and differential fluking rates (Carroll et al. 2013; Cerchio 1998; Craig et al. 2001; Hammond 1986, 1990; Herman et al. 2011; Smith et al. 1999). By spanning the period before, during, and after the PMH, our analyses provide a rare opportunity to examine potential longer-term impacts of the PMH event on survival, abundance, and population growth rates at the DPS level.

2 | Methods

2.1 | Study Area and Data Collection

Our study occurred in the waters off the MHI, an area where many studies have occurred since the 1980s (Baker and Herman 1987; Cerchio 1998; Darling et al. 1983) and included the National Oceanic and Atmospheric Administration (NOAA) Hawaiian Islands Humpback Whale National Marine Sanctuary, a protected area considered vital for humpback whale breeding and calving (Aki et al. 1994). Encounters with humpback whales occurred from dedicated research vessels and from platforms of opportunity such as whale watching tours and private vessels. Photos of the ventral side of a whale's tail flukes during an encounter were collected to identify individuals based on the unique shape and pigmentation of the flukes (Katona et al. 1979). The location and date of each encounter were also recorded. All available humpback whale photo-ID data from the Hawaiian Islands region—sourced from both the research collaboration and community science contributors—were compiled, matched, and reconciled in Happywhale as per Cheeseman et al. (2022, 2023).

2.2 | Data Selection and Preparation

2.2.1 | Study Period

Whales are typically present in highest numbers during winter in Hawaiʻi, but many are also sighted in fall and spring. Available data included 37,384 sightings (i.e., photo-ID captures) of individual humpback whales submitted to Happywhale, comprised of fluke photos spanning 2002–2023. When pooled across years, whales were sighted in all months except June and September, with 99.97% of sightings occurring during November–May. Thus, we elected to use only data from November to May, in part, to help reduce potential heterogeneity in capture probability. Preliminary analysis indicated that, given the relatively low rates of capture at the DPS level, retaining flukes captured during November–May was more important than potentially further reducing the sampling period. Our final dataset comprised 21 years (i.e., "November–May breeding seasons") from November 2002 to May 2023.

2.2.2 | Screening of Calf Flukes

We removed animals that were identified as calves (i.e., born during the current breeding season) from the analysis (Ashe et al. 2013; Brooks et al. 2024; Calambokidis et al. 2008; Carroll et al. 2015) because they rarely show their flukes and their flukes do not typically display as many permanent and distinctive natural marks as adults (Brooks et al. 2024; Calambokidis et al. 1997; Cheeseman et al. 2022), which makes them difficult to individually identify reliably over time and violated our modeling framework assumptions (see assumption 1 below under Modeling Framework Assumptions; Williams et al. 2002). We reviewed comments associated with fluke images uploaded to Happywhale to discern calves. Since not all calves are specified during the submission process to Happywhale, we visually reviewed all fluke images of whales that were first sighted in Hawaiʻi to distinguish putative calves (these would be no older than 100 days per observed residency; Cerchio et al. 1998; Craig et al. 2001) based on fluke characteristics such as pale or gray coloration, small size, lack of barnacles (e.g., *Coronula diadema*), and general floppiness (Cartwright and Sullivan 2009; Kaufman and Forestell 1986, 2015; Ransome et al. 2022).

2.2.3 | Photo Quality

To reduce the probability of false negatives and minimize bias that can arise from the inclusion of poor-quality photos (Urian et al. 2015; Gabriele et al. 2022), we limited our analysis to images that scored 3 or higher on a quality scale from 0 to 5 (ranging from no visibly useful photo-ID details to excellent) that considered the proportion of the fluke visible, fluke angle, the photographer's lateral angle, focus, and exposure/contrast (Cheeseman et al. 2022). This quality threshold is similar to what others have used for humpback whale fluke data analyzed for capture-mark-recapture (Ashe et al. 2013; Barlow et al. 2011; Curtis et al. 2022, 2025; Gabriele et al. 2022; Wade et al. 2021).

2.2.4 | Encounter Histories

To reduce heterogeneity from whales captured multiple times during one breeding season, we pooled all sightings from individual whales at the breeding-season level. We generated encounter histories of 1 s (sighted) and 0 s (not sighted) for each unique whale per breeding season.

2.3 | Mark-Recapture Analysis

Demographic and geographic closure were unlikely throughout the duration of our 21-year study (Otis et al. 1978; Teerlink et al. 2015; White et al. 1982). Therefore, we applied open population models (Jolly 1965; Schwarz and Seber 1999; Seber 1965) to estimate the survival of and number of non-calf whales that used the MHI region during each breeding season. Because capture heterogeneity is a known issue when analyzing breeding-ground-only data (Smith et al. 1999), we employed open population models that incorporated heterogeneity (Pledger et al. 2010). Specifically, we used an open-capture recapture model that extended the Schwarz and Arnason (1996) JSSA model by including finite mixtures to model heterogeneity of capture and survival probabilities to reduce bias in abundance estimates for each session (i.e., JSSAN; Pledger et al. 2010). The modeling approach was full likelihood-based (rather than conditioned on the first capture) and thereby reduced bias in the survival estimates by modeling the uncaught animals as well as those captured (Pledger et al. 2010). Such survival estimates are also robust to random temporary emigration, though their variances may increase (Kendall et al. 1997). Pledger et al. (2010) note that the finite "...mixtures are merely a device to incorporate heterogeneity into the model in order to reduce bias in the population abundance estimates, and to make profile likelihood interval coverage more accurate" and one "need not assume the animal classes actually exist, and if they do exist our estimates may not accurately reflect the true proportions and the within-class capture and survival probabilities" (Pledger et al. 2010: 889). We implemented the JSSAN model using R version 4.4.2 (R Core Team 2024) via package openCR version 2.2.7 (Efford 2024).

2.3.1 | Modeling Framework Assumptions

Open population model assumptions included: (1) identifying marks were unique, not lost, and identified correctly; (2) all individuals had the same probability of capture, whether previously captured or not; (3) all individuals had the same probability of survival, whether previously captured or not; (4) capture and survival of individuals were independent between individuals; (5) the study area was consistent; and (6) sampling was instantaneous (Schwarz and Arnason 1996; Williams et al. 2002). Our photo-processing and matching protocols ensured that violations to assumption 1 were minimal (Cheeseman et al. 2022; Curtis et al. 2022). We reduced violations to assumptions 2, 3, and 4 by using non-invasive photo-ID data, condensing repeat sightings to the breeding-season level, excluding calves, and incorporating covariates to test directly for heterogeneity and effects from sampling effort. Our data were collected and submitted by researchers and members of the public that spanned the MHI, and individual whales are known to move among the MHI (e.g., Baker and Herman 1981; Cerchio et al. 1998; Calambokidis et al. 2008; Mate et al. 1998), indicating violations to assumption 5 were likely negligible. To address assumption 6, we reduced our sampling window to November–May and filtered repeat sightings therein to a single sighted/not sighted for each breeding season.

2.3.2 | Models Tested

The estimated parameters of the JSSAN model were capture probability, survival, and annual abundance of non-calves. Because mortality and permanent emigration are indistinguishable in open population models, survival estimates represent apparent survival (hereafter, "survival") and may underestimate true survival if the probability of study area fidelity is not one (Schaub and Royle 2014). We tested models that included (1) constant, (2) fully time-varying, and (3) time-varying based on periods related to potential PMH impacts (details below) for survival and capture probabilities, along with the heterogeneity covariate. We also evaluated research effort as a covariate on capture probability (details below). To address unidentifiability issues in time-varying models (Williams et al. 2002), we used a factor that constrained the first two time sessions as equal when applied to either capture or survival probabilities. The use of the heterogeneity covariate allowed the resulting capture probability and survival estimates to vary by finite mixture class. Abundance was modeled as fully time-varying without the constraint on the first two sessions. To help manage model complexity and because preliminary analyses revealed the data were too sparse to support interactions involving heterogeneity in estimating survival, heterogeneity was only evaluated as an additive effect.

2.3.3 | PMH Periods

In addition to evaluating constant and time-varying capture and survival probabilities, we assessed whether temporal variation in these probabilities could be described by three distinct periods related to potential PMH impacts: pre-event, impact, and subsequent. This approach allowed the subsequent period to be modeled as distinct from the pre-event period, permitting potential lingering effects to be documented. Because the oceanographic anomalies observed during the PMH were not uniform across the North Pacific (Jackson et al. 2018), we evaluated a suite of biologically plausible onsets and durations for the middle impact period based on documented impacts (Cartwright et al. 2019; Cheeseman et al. 2024; Gabriele et al. 2022). Specifically, we tested 5 competing hypotheses regarding the timing of the middle impact period:

1. pmh13.18: Impact period from 2013/14 through 2018/19;
2. pmh14.18: Impact period from 2014/15 through 2018/19;
3. pmh13.14: Impact period from 2013/14 through 2014/15;
4. pmh13: Impact period restricted to 2013/14; and
5. pmh14: Impact period restricted to 2014/15.

We note that because capture probability is estimated at sampling occasions (i.e., breeding seasons), whereas survival is estimated between occasions, the years denoted in the PMH suite apply to the breeding season for capture probability and to the subsequent interval for survival probability, respectively. We hypothesized that PMH-impacts to survival might be realized via forage limitation (Arimitsu et al. 2021; Cornwall 2019; Gentemann et al. 2017; Savage 2017; Suryan et al. 2021) and were likely of shorter duration (given that we only included non-calves and adult survival is typically high and constant in long-lived mammals; Eberhardt 2002). We hypothesized that PMH-impacts to capture probability could include temporary emigration (e.g., skipped or altered migration due to nutritional stress; Straley et al. 2018) and other impacts such as behavioral that could affect fluking rates (e.g., we considered the possibility that nutritionally-stressed whales may exhibit fewer fluke-up dives if such dives are energetically costly). Given our aim was not to elucidate specific causal mechanisms of PMH-impacts, but to document corresponding changes in survival and capture probabilities—we assessed the potential 5 impact periods above. Because PMH-related stressors may affect survival differently than capture probability, we did not constrain the two parameters to the same PMH period within a single model. Survival and capture probability were modeled independently; each able to be configured with any single PMH period, a time-varying structure, or a constant (null) structure.

2.3.4 | Research Effort Covariate

We calculated research effort as a covariate ("effort") by summing the number of photographic days per breeding season across all research collaborators (Mizroch et al. 2004). We did not include opportunistic observations from the public in our effort calculations. Photographic days were tallied for each date when at least one fluke was contributed to our dataset by a collaborating research organization (Mizroch et al. 2004). In cases where multiple research organizations collaborated on the same vessel and contributed fluke photos of the same whales on the same day, only one day total was counted (not one day per organization). In cases where multiple independent research organizations contributed fluke photos on the same day but were working independent of one another, one photographic day for each organization was tallied for that day. Thus, total research effort (photographic days) could exceed the total number of calendar days in a November–May breeding season. To improve numerical stability in modeling, the research effort covariate was scaled to a mean of 0 and standard deviation of 1.

2.3.5 | Model Selection and Goodness-Of-Fit

We evaluated models using Akaike Information Criterion corrected for small samples (AIC_c; Anderson et al. 1994; Burnham and Anderson 2002). Given the large initial candidate model set ($n = 364$ combinations), we employed a sequential screening process. Because a primary research objective was estimating survival, we first performed univariate screenings of survival structures within the PMH suite, while holding capture probability at time-varying with additive heterogeneity; pmh14 emerged as the most informative, outperforming other variants by > 29 ΔAIC_c units. Consequently, to minimize spurious correlations (Burnham and Anderson 2002), we excluded other PMH variations from the final survival model set. However, we retained one instance of each excluded PMH variant in our final model suite to provide a direct comparison of their relative performance (Tables S1 and S2).

From our final model suite of 30 models (Tables S1 and S2), we selected the model with the lowest AIC_c score as the top-performing model. Models within < 4 ΔAIC_c were considered competitive, provided they did not differ from the top model solely by the addition of a single uninformative parameter (Arnold 2010). Following Arnold (2010), we identified uninformative parameters as those whose beta estimate 85% confidence interval included zero. In the case of more than one competitive model, we generated parameter estimates via model averaging (Burnham and Anderson 2002).

Because goodness of fit tests are not available for JSSAN models in openCR (Efford 2024), we conducted a sensitivity analysis of variance inflation factors ($\hat{c}$), replacing the default value of 1 with values ranging from 1.5 to 4 at 0.5 intervals, representing varying degrees of overdispersion in the data (Lebreton et al. 1992; White and Burnham 1999), to assess the robustness of model selection via quasi-Akiake Information Criterion corrected for small samples ($QAIC_c$) (Anderson et al. 1994). We followed the same selection procedures and model averaging as above for AIC_c.

2.3.6 | DPS Growth Rates

We derived average annual DPS growth rates (λ) based on the geometric mean with breeding season abundance point estimates following the approach of Olson et al. (2025):

$$\text{Average annual DPS growth rate} = \lambda = \left(\frac{N_{t+x}}{N_t}\right)^{\frac{1}{x}} \tag{1}$$

where N_t was the estimated abundance in the initial breeding season of interest, N_{t+x} was estimated abundance in the final breeding season for the period of interest, and x was the number of years spanning the period of interest. We assessed DPS growth rates for the full study period and also internal periods of growth, stability, and decline. Values of $\lambda = 1.00$ indicated no change, values above 1.00 indicated growth (e.g., $1.05 = 5\%$ growth), and values below 1.00 indicated decline (e.g., $0.95 = 5\%$ decline).

3 | Results

3.1 | Whale Sightings and Associated Effort

A total of 27,698 individual whale photo-ID sightings with a fluke image quality scoring 3 or above were recorded across 21 breeding seasons from November–May 2002/03 to 2022/23. We identified 369 whale sightings as probable calves representing 367 unique calves. Excluding calves, 10,371 unique whales were identified at least once via photo-ID. The number of unique non-calves sighted in each breeding season averaged 943 and ranged from a low of 217 sightings during 2008/09 to a high of 2517 during 2022/23 (Figure 1). Capture rates for individual whales pooled at the breeding season level across all breeding seasons averaged 1.91 (SD = 1.36) and ranged from 1 to 13 captures. Nearly half of the unique non-calves identified (4731; 45.6%) were sighted in at least two breeding seasons. The discovery curve (Figure 2) of cumulative non-calves captured during the study indicated new individuals were captured each breeding season. Research effort averaged 153.14 photographic days per breeding season (SD = 63.20), ranging from a low of 71 during 2008/09 to a peak of 276 in 2005/06.

3.2 | Model Selection

The top AIC_c model included time-varying capture probability (with the first two sessions set as equal) with additive heterogeneity and survival composed of three periods related to the PMH: pre-event from 2002/03 to 2014/15, impact during the single interval from 2014/15 to 2015/16, and subsequent from 2015/16 to 2022/23 (Table 1). While the second model was within 4 AIC_c of the top model (0.957 ΔAIC_c units), it differed only by the addition of a single parameter (heterogeneity in survival) whose beta estimate 85% confidence interval included zero (beta estimate = 0.12; SE = 0.12; 85% CI = −0.05–0.29), and so was not considered a competitive model (Table S1). The top model remained the top model under $QAIC_c$ model selection across the sensitivity analysis of variance inflation factors from 1.5 through 4, at 0.5 increments, and there were similarly no competing models that differed by more than only a single uninformative parameter (Table S2).

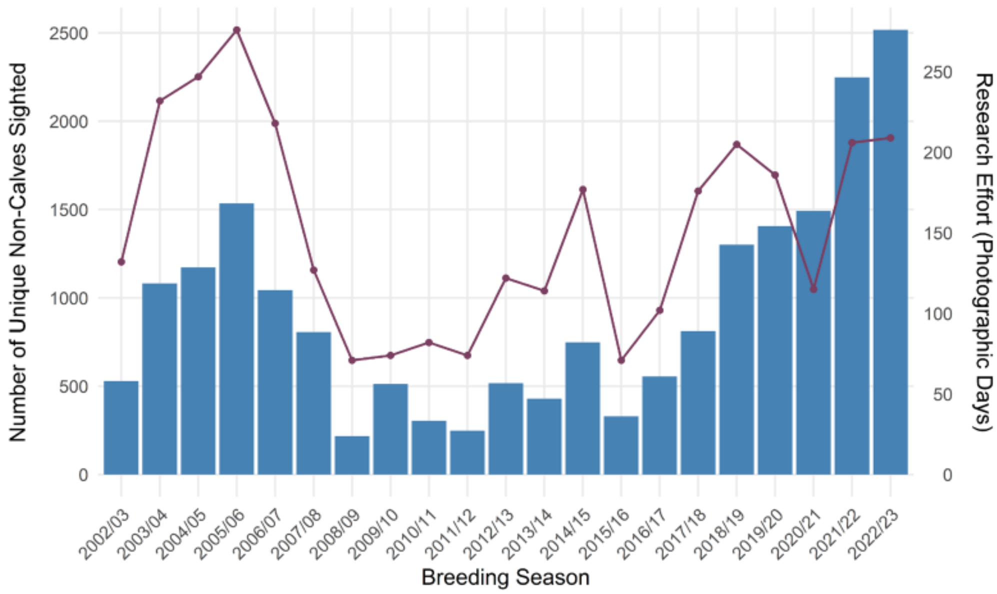

FIGURE 1 | Bar plot of the number of unique non-calf humpback whales (*Megaptera novaeangliae*) photo-identified with a quality score of 3+ during each breeding season from November–May 2002/03 to 2022/23 in the Main Hawaiian Islands region. Research effort (photographic days) for each breeding season is plotted as a line.

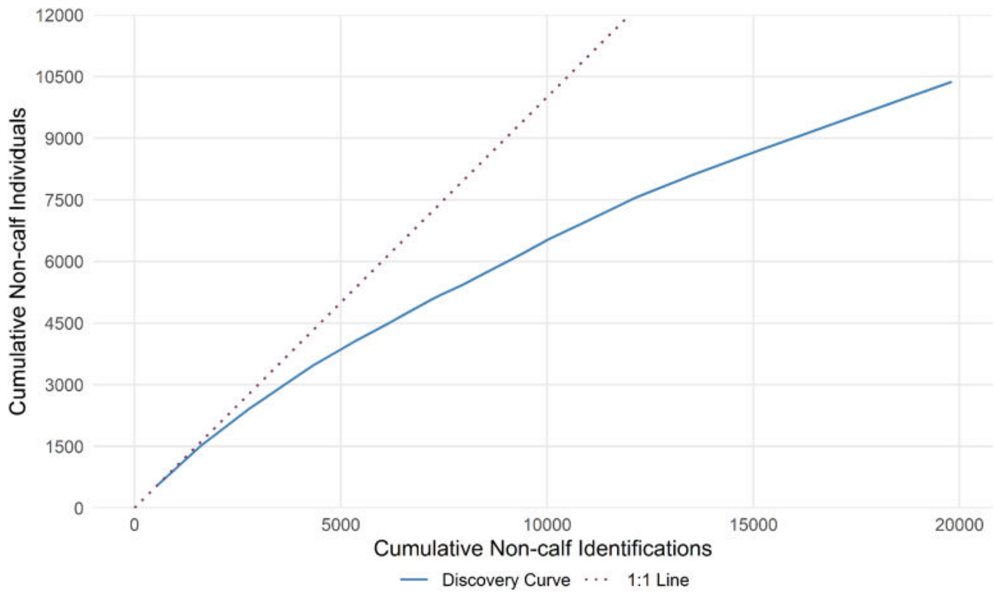

FIGURE 2 | Discovery curve comparing cumulative total non-calf humpback whales (*Megaptera novaeangliae*) photo-identified with a quality score of 3+ to the cumulative annual breeding season identifications during November–May 2002/03 to 2022/23 in the Main Hawaiian Islands region. The 1:1 linear trend represents the plot that would result if a new individual was added with each identification.

3.3 | Heterogeneity and Breeding Season Recapture Rates

The selected model included two finite mixture classes with estimated membership probability of 0.183 (class 1) associated with higher capture probability and a second finite mixture class with membership probability of 0.817 (class 2) associated with lower capture probability. Recall that the finite mixture classes are merely a modeling device to incorporate heterogeneity to reduce bias in abundance estimates and need not reflect any actual animal groups (Pledger et al. 2010). The class 1 mixture averaged 0.232 (SD = 0.148) capture probability with a minimum of 0.042 (SE = 0.004) during 2008/09 and a maximum of 0.549 (SE = 0.015) during 2022/23. The class 2 mixture averaged 0.062 (SD = 0.050) capture probability with a minimum of 0.008 (SE = 0.001) during 2008/09 and a maximum of 0.188 (SE = 0.010) during 2022/23.

3.4 | Survival

Apart from a single interval coinciding with the PMH, we estimated relatively high survival, a result generally expected given calves were excluded from our analysis (Gabriele

TABLE 1 | Estimates (SE) of capture probability, survival, and abundance from the top performing model per AIC_c (Akiake Information Criterion corrected for small samples) selection using breeding season sighting data of non-calf humpback whales (*Megaptera novaeangliae*) photo-identified during November–May 2002/03 to 2022/23 in the Main Hawaiian Islands.

Breeding	Class 1		Class 2						
	Capture probability		Capture probability		Survival		Abundance		
Season	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	95% CI
2002/03	0.292	0.026	0.073	0.009	0.987	0.003	4700	511	3798-5817
2003/04	0.292	0.026	0.073	0.009	0.987	0.003	9578	924	7928-11,573
2004/05	0.310	0.016	0.079	0.006	0.987	0.003	9711	533	8721-10,813
2005/06	0.357	0.014	0.095	0.006	0.987	0.003	10,728	446	9890-11,638
2006/07	0.244	0.011	0.058	0.004	0.987	0.003	11,398	471	10,511-12,360
2007/08	0.186	0.010	0.042	0.003	0.987	0.003	11,840	500	10,900-12,861
2008/09	0.042	0.004	0.008	0.001	0.987	0.003	15,067	1239	12,824-17,702
2009/10	0.108	0.007	0.023	0.002	0.987	0.003	13,443	715	12,112-14,920
2010/11	0.062	0.005	0.012	0.001	0.987	0.003	14,109	935	12,390-16,066
2011/12	0.056	0.005	0.011	0.001	0.987	0.003	12,904	847	11,346-14,676
2012/13	0.115	0.007	0.024	0.002	0.987	0.003	12,678	626	11,508-13,966
2013/14	0.083	0.006	0.017	0.002	0.987	0.003	14,714	878	13,091-16,539
2014/15	0.142	0.008	0.030	0.002	0.683	0.022	14,736	736	13,361-16,252
2015/16	0.082	0.007	0.017	0.002	0.956	0.006	11,537	761	10,138-13,129
2016/17	0.140	0.009	0.030	0.003	0.956	0.006	11,088	596	9979-12,321
2017/18	0.217	0.011	0.050	0.004	0.956	0.006	10,116	421	9324-10,976
2018/19	0.318	0.012	0.081	0.005	0.956	0.006	10,441	374	9734-11,200
2019/20	0.365	0.013	0.099	0.006	0.956	0.006	9554	318	8951-10,198
2020/21	0.386	0.013	0.107	0.006	0.956	0.006	9457	318	8855-10,101
2021/22	0.531	0.015	0.177	0.009	0.956	0.006	9311	306	8730-9931
2022/23	0.549	0.015	0.188	0.010	NA	NA	9921	325	9304-10,578

Note: The top model, p (t + h2) Φ (pmh14) N (t), included capture probability (p) that was time-varying with the first two sessions set as equal and an additive effect of 2 heterogeneous mixture classes (h2), apparent survival (Φ) described by three periods (pmh14; survival before 2014/15, survival between breeding seasons 2014/15 and 2015/16, and survival after 2015/16), and abundance (N) that was fully-time varying. The heterogeneous finite mixture classes were estimated with membership probabilities of 0.183 (class 1) and 0.817 (class 2).

et al. 2001). Coincident with the PMH, survival declined from a high of 0.987 (SE = 0.003) observed during breeding seasons prior to 2014/15, to a low of 0.684 (SE = 0.022) during the interval between breeding seasons 2014/15 and 2015/16, and did not fully recover to prior levels thereafter (survival = 0.956, SE = 0.006) (Table 1).

3.5 | Abundance

As is sometimes the case with population models that consider time-varying capture probability, estimates from the first period can be unreliable (e.g., Barber-Meyer et al. 2024; Courtin et al. 2023; Teerlink et al. 2015). Our first non-calf abundance estimate of 4700 whales (SE = 511.2) during breeding season 2002/03 is one such example (Table 1). This non-calf abundance estimate is likely underestimated by about half and is an artifact of constraining the first two occasions in the time-varying probability of capture to be equal. Presuming the general trend of more effort results in more whale sightings, rather than being equal, the probability of capturing whales during the first occasion was probably about half the probability of capture during the second occasion (Figure 1). Excluding the first season's estimate, breeding season non-calf abundance estimates averaged 11,617 (SD = 1914), with the apex of 15,067 in 2008/09 and the nadir of 9311 during 2021/22 (Table 1; Figure 3). We note a striking 37% decline in the point estimates of abundance from 2014/15 to 2021/22 (Table 1; Figure 3).

3.6 | DPS Growth Rates

Excluding the first breeding season abundance estimate, the average annual DPS growth rate from breeding season 2003/04 to

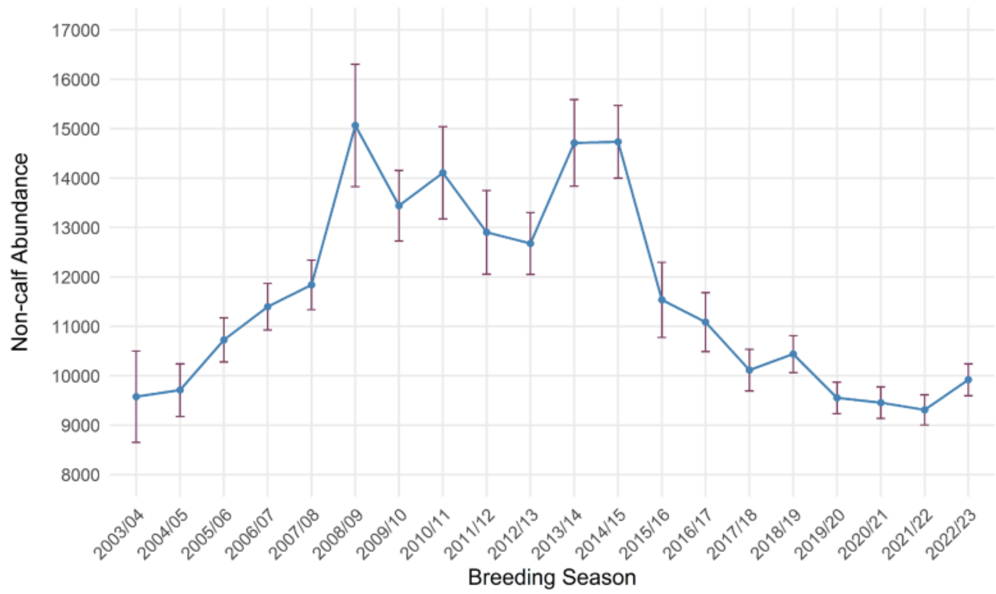

FIGURE 3 | Humpback whale (*Megaptera novaeangliae*) breeding season non-calf abundance estimates (filled circles) from November–May 2003/04 to 2022/23 in the Main Hawaiian Islands region. Error bars are +/−1 standard error. The line segments connect breeding season non-calf abundance point estimates. Given the unreliability of the first abundance estimate sometimes observed in this family of population models when considering time-varying capture probability, data from the second estimate onward are plotted.

2022/23 was $\lambda = 1.00$, indicating a stable DPS over 20 breeding seasons. However, that result only accounted for the early and final estimates—not changes within. Therefore, shorter periods within the study may reveal variation otherwise missed. From 2003/04 to 2008/09, the DPS growth rate ($\lambda = 1.09$) indicated an average of 9% growth each season. During 2008/09 through 2014/15, abundance estimates were variable, but the overall trajectory was generally stable with $\lambda = 0.996$ or ~1.00. The steepest decline was observed in a single breeding season change from 2014/15 to 2015/16 with $\lambda = 0.783$ (i.e., 21.7% decline). During a multi-year decline, the average annual DPS growth rate from 2014/15 through 2021/22, was $\lambda = 0.937$ (6.3% annual decline). From 2019/20 through the end of our study in 2022/23, abundance appeared to stabilize with possible slight growth at $\lambda = 1.01$.

4 | Discussion

Our findings across two decades fill the identified knowledge gap of abundance, survival, and DPS growth rate dynamics before, during and after the PMH (NOAA 2019). Although humpback whales in the MHI rebounded following protections from industrial whaling, our results confirm a severe recent decline, with abundance not yet recovered to levels observed immediately prior to 2015/16. While we did not explicitly consider alternative hypotheses for the decline that would have required additional or longer data streams (e.g., toxicants, natural variation, changes in habitat use from anthropogenic disturbances, etc.), our results demonstrate that humpback whales in the MHI experienced this pronounced decline coincident with the PMH (Frankel et al. 2022; NOAA 2019). Our estimates of abundance from later years indicate a period of stabilization and possibly slight growth following the precipitous decline, but whether that recent trend will continue remains uncertain. After its removal from the U.S. Endangered Species list, there is an ongoing need for accurate monitoring of the Hawaiʻi DPS (Schakner et al. 2022).

4.1 | Mitigating Heterogeneity and Other Potential Sources of Bias

Given the importance of accurate DPS information, careful consideration of potential biases and efforts to minimize them were essential. Heterogeneity in capture rates can lead to biased abundance estimates (Barlow et al. 2011; Cerchio 1998). While heterogeneity is anticipated in capture-recapture data when using breeding-ground-only data (Smith et al. 1999), our approach included multiple mitigations to help minimize the impact of that and other sources of potential heterogeneity (Carroll et al. 2013; Cerchio 1998; Craig et al. 2001; Hammond 1986, 1990; Herman et al. 2011; Smith et al. 1999). We reduced potential capture heterogeneity in our data by removing calves, excluding very poor- and poor-quality photos, subsetting our sampling period to November–May, and condensing sightings to one per unique whale per breeding season. Further, our modeling approach directly incorporated heterogeneity via finite mixture classes (Pledger et al. 2010), and we evaluated varying research effort as a predictor of capture probability (Abadi et al. 2013).

Mismatching of individuals (misidentification) is another issue that can lead to unreliable photo-ID estimates (Link et al. 2010; Yoshizaki et al. 2009). Both false positives (i.e., a fluke image is incorrectly matched to an existing whale in the photo-ID catalog) and false negatives (i.e., failure to match a fluke image to an existing whale in the photo-ID catalog) can occur. False positives are likely to be rare in our dataset because all matches in Happywhale require manual confirmation. False negatives were limited via the process for assigning a new whale ID in Happywhale, whereby the assignment of new IDs (i.e., no match is found, a new whale is declared) are restricted to only fluke photos scoring 3 or higher on the Happywhale scale of 0 to 5 (Cheeseman et al. 2022). Prior Happywhale testing indicated this process resulted in false negative rates of 1%–3% (Cheeseman et al. 2022). Overall bias from misidentification is expected to be minimal in our dataset given our photo quality threshold, our exclusion of calves (with fewer and more mutable fluke features), our use of Happywhale's matching algorithm, and because all matches were manually verified (Cheeseman et al. 2022; Curtis et al. 2022).

4.2 | Discovery Curve and Resighting Rates

As misidentification bias was likely minimal, our extensive dataset provided a robust basis for examining DPS-level patterns. Our analysis benefited from the largest ever assembly of photo-ID data for the MHI across a 21-yr period (Cheeseman et al. 2023, 2024). The slope of our discovery curve based on our photo-ID sightings was less than the 1:1 line that represented each captured animal as a new animal, reflecting the ongoing process of new individuals that were either recruited into the DPS through birth or immigration or were existing animals from the beginning of our study and sighted for the first time (Figure 2). The continued decline in the slope of the discovery curve as the study progressed in combination with the ongoing process of new animals being added was not unexpected for a DPS of this size with data spanning more than 20 years.

Past studies have reported resighting rates of 25% during 1978–1984 from 72 whales identified in Hawai'i (Baker et al. 1987) and 19% during 1977–1985 from 634 whales (Perry et al. 1988). The earlier rates are not directly comparable with ours (45.6%) given our study benefited from greater temporal (21 breeding seasons) and spatial (many researchers and members of the public across the MHI) effort, improved technology (high-resolution digital cameras), and the central data repository of Happywhale that greatly facilitated compilation and matching of images (Cheeseman et al. 2023).

4.3 | Model Selection

Because resighting rates may vary with heterogeneous detectability and fluctuating effort, we incorporated both into our model selection process. Our AIC_c-selected model—which incorporated time-varying capture probability with additive heterogeneity and survival modeled as three periods related to the PMH—had no competing models and was robust to variance inflation as per the $QAIC_c$ results. Based on our AIC_c model rankings, incorporating heterogeneity into the capture probability improved the top model by over 918 ΔAIC_c, indicating a significantly superior fit that likely corrected for much of the potential overdispersion (e.g., Péron et al. 2010). The capture probabilities for each heterogeneous finite mixture class were similar to those observed throughout a long-term study of Eastern Australia humpback whales at a migratory stopover site (Brooks et al. 2024, 2025). Although we evaluated effort as another potential means to minimize capture heterogeneity, effort was not included in the top model. This likely stems from the apparent early positive correlation between research effort and unique whale sightings dissipating in later years (Figure 1) and may also reflect that our research effort estimate was not an exact representation of realized effort.

4.4 | Survival in the Context of the PMH

Our annual survival estimates generally reflected high and consistent survival, an expected result for long-lived mammals given calves were excluded from our analysis (Eberhardt 2002; Zerbini et al. 2010). A significant one-year decline in survival occurred between breeding seasons 2014/15 and 2015/16. Because mortality is confounded with permanent emigration in open population models, this decline may represent either animals that died or emigrated outside of the MHI region. This marked decline coincided with the PMH and aligns with previously observed signals of demographic and behavioral changes in humpback whales (Arimitsu et al. 2021; Cartwright et al. 2019; Cheeseman et al. 2024; Frankel et al. 2022; Gabriele et al. 2022; Kügler et al. 2020; Moran et al. 2026; Neilson et al. 2025, 2026; Savage 2017). The abrupt decline was likely related to the widespread marine ecosystem disruption, including forage collapse (Arimitsu et al. 2021; Cornwall 2019; Gentemann et al. 2017; Suryan et al. 2021) in habitat critical to the whales we studied (Cheeseman et al. 2024; Gabriele et al. 2022). Our results are reinforced by the 2015 large whale Unusual Mortality Event that involved high mortality rates (including humpback whales) within the Hawai'i DPS known feeding ranges (Savage 2017). Overall, our results generally support the trend of non-calf survival rates reported in southeastern Alaska as higher prior to (0.982; 95% CI = 0.976–0.987) and lower after (0.899; 95% CI = 0.876–0.918) the PMH (Gabriele et al. 2022). Excluding our lower survival rate during the PMH, our results approximated survival rates reported for humpback whales based on annual sightings in Hawai'i during 1979–1996 (0.963; 95% CI = 0.944–0.978; Mizroch et al. 2004).

4.5 | Abundance Dynamics

In their report on humpback whales in Hawai'i, Young et al. (2024) state that 11,278 individuals (95% CI = 4049–31,412; Becker et al. 2022) estimated for 2020 is considered the best current estimate for Hawai'i. Our corresponding 2019/20 abundance estimate (9554, 95% CI = 8951–10,198) was lower than that estimate, but within the confidence interval. Differences in the results between the studies may be expected, in part, because Becker et al. (2022) modeled the U.S. Exclusive Economic Zone around the Hawaiian Islands, whereas our study focused on whales using the MHI. Furthermore, the exclusion of calves in our analysis introduced a known negative bias (Barlow et al. 2011; Curtis et al. 2022). One study of North Pacific humpback whales estimated a −10.5% bias due to exclusion of calves (Barlow et al. 2011), meaning our results reflect a conservative subset of the true abundance of all humpback whales that used the MHI each winter.

Our breeding season abundance estimates peaked between breeding seasons 2008/09 through 2014/15 before precipitously declining—a trend consistent with other studies (Cartwright et al. 2019; Cheeseman et al. 2024; Frankel et al. 2022; Kügler et al. 2020). This decline appeared to continue until at least the 2019/20 breeding season, after which the rate of loss slowed, with the point estimate slightly higher in the final survey period.

Despite significant methodological differences, it is striking that our results corroborate the general trajectory for Hawai'i's relative abundance from the most recent North Pacific basin-wide assessment reported by Cheeseman et al. (2024). While Cheeseman et al. (2024) utilized a broader dataset including genetic matches, calves, and feeding ground data to report a 34% decline in relative abundance by 2021, our breeding ground analysis detected a nearly identical 37% decline from 2014/15 to 2021/22. The alignment of the trajectory and percent decline across different modeling approaches reinforces the reality of a systemic DPS contraction following the PMH.

Variation prior to the PMH (Figure 3) may suggest, as others have, that perhaps the DPS was near its then-carrying capacity (Frankel et al. 2022; Gabriele et al. 2022; Kügler et al. 2020; Mobley Jr. et al. 2023). Density-dependent reductions in large whale populations often occur via change in one demographic parameter at a time (Fowler 1984; Williams et al. 2013), whereas the evidence during and after the PMH was from simultaneous changes in multiple demographic parameters (Gabriele et al. 2022), indicating a more systemic decline than might be expected merely from a density-dependent adjustment to a reasonably stable carrying capacity. Although the PMH caused forage collapse and marine ecosystem disruption (Arimitsu et al. 2021; Cornwall 2019; Gentemann et al. 2017; Suryan et al. 2021) and demographic signals hypothesized as PMH-related had been observed (Cartwright et al. 2019; Cheeseman et al. 2024; Frankel et al. 2022; Kügler et al. 2020; NOAA 2019), quantification of DPS-level impacts to survival and abundance of the whales using the MHI breeding grounds was limited prior to this study. Our results demonstrate a clear PMH-associated decline in both abundance and survival, underscoring the vulnerability of even recovered large whale populations to extreme climate events.

4.6 | DPS Growth Rates and Association With the PMH

Our DPS growth rates were derived from breeding season abundance estimates and elapsed time. We attempted to model growth rates directly in a *Lambda* growth rate model (e.g., JSSANl or JSSANlCL in openCR; Efford 2024), but we encountered problems of parameter identifiability, likely due to data sparseness relative to model complexity. However, Olson et al. (2025) showed close agreement between derived-growth rates based on abundance estimates (the same approach we used) and Pradel model-estimated *Lambda* growth rates (i.e., 1.10 and 1.11, respectively). The period of maximum increase during our study occurred from breeding season 2003/04 through 2008/09. Our growth rate during this period (9%) was lower than that estimated from a Pradel mark-recapture model using data from Hawai'i for 1980 to 1996 (10%; Mizroch et al. 2004) but higher than that estimated from distance sampling data of MHI humpback whales during 1993 to 2000 (7%; Mobley Jr. 2004). We consider our growth rate estimate during the period of maximum increase reasonable given it is within previously observed values for this DPS (Young et al. 2024) and was within the 95% confidence intervals of plausible rates of increase for humpback whales estimated via multiple approaches (Zerbini et al. 2010). Our steepest decline was observed between breeding seasons 2014/15 and 2015/16. While there are competing, non-mutually exclusive hypotheses for this decline such as nutritional stress, changing distributions of whales, human impacts, natural cyclical variability, and unknown factors (Hastings et al. 2020; NOAA 2019), this decline coincided with the lowest survival during the study and was likely related to PMH impacts. Evidence from a distance sampling study during 2019–2020 indicated that whale densities were at or above those observed using identical methods during 1993–2003 (Mobley Jr. et al. 2023). Comparable whale densities across these two periods revealed that the rates of population increase recorded in the earlier study did not persist throughout the 17-year intervening period (Mobley Jr. et al. 2023). Likewise, our overall growth rate demonstrates that the earlier, higher rate of increase we documented was not sustained. Whether the DPS will continue to grow as potentially indicated by the last breeding season assessed and ultimately rebound to levels prior to the PMH, will depend, in part, on future environmental conditions and carrying capacity. Current and future carrying capacities will depend on the rapidly changing climate, a dynamic ocean, and shifting prey distributions.

4.7 | Resiliency

Our comprehensive survival, abundance, and DPS growth rate analysis of the whales that visited the MHI before, during and after the PMH substantiates the signals of harmful impacts that were detected by other shorter or less spatially expansive studies (e.g., Cartwright et al. 2019; Frankel et al. 2022; Kügler et al. 2020). Our results also support studies that demonstrated post-PMH abundance levels comparable to some pre-PMH estimates observed in the early 2000s (e.g., Frankel et al. 2022; Mobley Jr. et al. 2023). However, this does not necessarily constitute resiliency to the PMH climatic event, as our findings also confirm that the most recent abundance estimates have not rebounded to the highs observed in the years immediately prior to the PMH (e.g., Frankel et al. 2022). Thus, defining what is specifically meant by resiliency (e.g., a return to equilibrium, the capacity to recover, reaching abundance levels documented during a particular time; Wade et al. 2012; Wilbrink 2023), and identifying the period of comparison is important. This is especially true for a historically decimated, k-selected species with relatively low reproductive rates adapted for long-term, relative population stability near carrying capacity (Estes 1979; Tulloch 2025). Our study found stable abundance when comparing early and late periods, suggesting a degree of persistence. However, ecological resilience includes future adaptive capacity as well. The ability to recover from future stochastic events may be compromised if demographics (e.g., survival, abundance) have not fully recovered to pre-disturbance levels, as is also the case in our study. If we define resilience as a return to peak abundance observed in the early 2010's, our results indicate the DPS remains in a state of vulnerability. The apparent stabilization and possible slight increase in abundance in later years may be cautiously interpreted as nascent resilience-in-progress, rather than full restoration, or alternatively, as a shift to a lower post-PMH baseline, raising concerns about the DPS's long-term resilience to subsequent climatic stressors.

4.8 | Future Research

While our study was the most comprehensive to date for Hawai'i humpback whales, our analysis focused on the MHI where photo-ID effort is concentrated. If there are whales in the Hawai'i DPS that, hypothetically, only visit the Northwestern Hawaiian Islands (NWHI), they would not have been available for capture in our MHI-focused study. Whales have been documented in the NWHI, such as the 19 humpback whales documented during March 2007 on 15 d research cruise across the NWHI (Johnston et al. 2007). Similarly, a passive acoustic survey documented humpback whale song at seven sites in the NWHI during 2008–2009 (Lammers et al. 2011). Subsequent acoustic survey research revealed nearly the entire Hawaiian archipelago is used by humpback whales during winter and early spring, with the possibility of two subpopulations existing (Lammers et al. 2023). The interchange of whales among the MHI is well-documented (e.g., Baker and Herman 1981; Calambokidis et al. 2008; Cerchio et al. 1998; Mate et al. 1998), but the frequency and patterns of interchange between whales in the NWHI and the MHI remain unclear (Johnston et al. 2007; Kügler et al. 2020; Lammers et al. 2011, 2023). As climate change progresses, it remains to be seen whether the NWHI will serve as additional habitat for whales that have primarily used the MHI to expand into and whether this process may already be underway (Allen et al. 2021; Hastings et al. 2020; Lammers et al. 2023; Mobley et al. 1999).

The uncertainty around the movements of whales between the MHI and the NWHI further highlights the need for continued refinement of approaches to better account for this, and other sources, of capture heterogeneity. While many improvements in minimizing the impacts of capture heterogeneity have been related to study design (e.g., Carroll et al. 2015) or analytical methods (e.g., Abadi et al. 2013; Brooks et al. 2025; Pledger et al. 2010; Straley et al. 2009) – field techniques are also evolving to address this issue, such as the use of aerial imagery to increase resight rates of whales (Evans et al. 2025). Such research could uniquely benefit breeding-ground-only studies by informing both the availability for capture and the traditional fluke-image capture probability given presence. Additional analytical improvements allowing increased flexibility in how individual heterogeneity is modeled and the incorporation of heterogeneity into more complex models such as the Multi-state Open Robust Design (e.g., Brooks et al. 2024; Brooks et al. 2025) would similarly likely improve population estimates in breeding-ground-only studies.

5 | Conclusion

During our two-decade study, the Hawai'i DPS of humpback whales achieved no net growth, and most North Pacific humpback whales lost protection under the ESA (U.S. Federal Register 2016). The high abundance, survival, and population growth rates that we document in the Hawai'i DPS prior to the status review (Bettridge et al. 2015) did not persist. Although we observed robust growth during a period characterized by high survival, this was followed by a major marine heatwave that coincided with dramatic DPS-level effects, including a severe decline in abundance. The final breeding season abundance estimate suggests a potential slight increase. Our results, based on fluke images collected across the MHI over two decades, provide a timely update at a robust resolution never before achieved for this DPS.

Our findings illustrate that even a DPS considered numerically recovered from historic lows may still require vigilant monitoring to ensure conservation successes are maintained (Schakner et al. 2022). In the case of the Hawai'i DPS of humpback whales, as climate change ramifications are realized, direct and indirect effects of climate change will likely negatively impact reproductive success, survival, distribution, and other DPS-level characteristics (Learmonth et al. 2006). Our results demonstrate that, although a DPS may appear numerically secure, resiliency to future environmental anomalies cannot be assumed. The speed and extent of the DPS's recovery following the PMH will help inform the management of other recovered baleen whale populations that migrate great distances between high latitude feeding grounds and low latitude breeding grounds (Brooks et al. 2024; Smith et al. 1999; Tulloch 2025). Considered a conservation success, humpback whales in the Hawai'i DPS remain an important sentinel, highlighting how climate-linked ecosystem disturbances can levy significant impacts to even previously thriving populations. Ongoing monitoring, fostered by methodological and analytical advancements, will best inform the adaptive management of this ecosystem-indicator DPS (Cheeseman et al. 2024; for example, Linsky et al. 2024), helping to distinguish temporary, minor perturbations from more prolonged declines and supporting humpback whale conservation far into the future (Schakner et al. 2022).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The photo-identification catalogs contributing to this study are archived on Happywhale and are accessible in accordance with the data sharing policies of the contributing organizations. Due to ethical agreements and data-sharing restrictions, these catalogs cannot be downloaded in bulk; however, data requests can be made through the Happywhale platform.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Model results from AIC_c (Akiake Information Criterion corrected for small samples) selection using breeding season sighting data of non-calf humpback whales (*Megaptera novaeangliae*) photo-identified during November–May 2002/03 to 2022/23 in the Main Hawaiian Islands. **Table S2:** Model results from $QAIC_c$ (Quasi Akiake Information Criterion corrected for small samples) selection using breeding season sighting data of non-calf humpback whales (*Megaptera novaeangliae*) photo-identified during November–May 2002/03 to 2022/23 in the Main Hawaiian Islands. **Appendix S1:** Barber-Meyer_etal_2026_Acknowledgements.doc.