

Natural history, population dynamics, and habitat use of humpback whales over 30 years on an Alaska feeding ground

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Abstract. The rigorous program of monitoring humpback whales (*Megaptera novaeangliae*), implemented by Glacier Bay National Park and Preserve in 1985, augmented by additional data collected in southeastern Alaska since 1968, constitutes one of the longest studies of living whales in the world. This monitoring program, now a National Park Service (NPS) Inventory and Monitoring Program Vital Sign, employed consistent methods for summer surveys from 1985 to 2014 to document the number of whales and gather longitudinal records on individuals in Glacier Bay and Icy Strait. Survey effort averaged 355.4 h/yr (SD = 45.8), resulting in 9485 encounters with 662 individual whales, including 276 calves. The population increased at a rate of 5.1%/yr, from 41 individuals in 1985 to 239 individuals in 2013, primarily due to long-term site fidelity and local recruitment. We documented sighting histories of >30 yr in southeastern Alaska, for 54 whales, including one 45-yr sighting history. Almost half of the whales first identified as calves returned in subsequent years, at a mean age of 3.2 yr (SE = 0.28, range = 1–17 yr). Over 75% of females had their first calf by age 13. The maximum female reproductive span was 32 yr, and the maximum number of calves was 11. We estimated mean effective calving rate with a simple ratio and used logistic regression to estimate calving probability. Both methods resulted in similar maximal estimates that were somewhat lower than previously published values for this species: 0.324 (95% CL: 0.28–0.36) calves·female⁻¹·yr⁻¹ vs. calving probability of 0.319 (95% CL: 0.29–0.35). Minimal estimates, in which the first calf of each known-aged female was omitted, were 0.302 (95% CL: 0.27–0.34) calves·mature female⁻¹·yr⁻¹ vs. calving probability of 0.305 (95% CL: 0.27–0.34) calves·mature female⁻¹·yr⁻¹. This monitoring program has guided Park management actions and documented this once critically endangered population's trajectory toward recovery, often through collaboration with other agencies and organizations, fostering the continued protection and understanding of this distinctive species. Our findings highlight the value of marine protected areas for migratory species with strong seasonal site fidelity and the role of long-term monitoring in interpreting population-level responses to changing marine ecosystems.

Key words: abundance; calving rate; feeding ground; high latitude; humpback whale; long-term monitoring; mammal; marine protected area; *Megaptera novaeangliae*; neritic waters; photo-identification; site fidelity.

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INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a globally distributed, migratory baleen whale that was profoundly depleted by 20th-century commercial whaling (Rice 1978, Ivashchenko et al. 2015). During summer and fall, most humpback whale populations feed in high-latitude waters, building fat reserves that sustain oceanic migrations to and from low-latitude mating and calving grounds where the whales congregate and fast in winter (Dawbin 1966, Clapham and Mead 1999, Perry et al. 1999). The glacial fjord ecosystem of Glacier Bay National Park and Preserve (GBNP), in the southeastern Alaska archipelago, comprises an important summer feeding area for the humpback whales in the North Pacific (Baker et al. 1986, 2013, Straley et al. 2009). Systematic population monitoring of individually identified humpback whales has been conducted by GBNP biologists for over 30 years, offering a detailed account of baleen whale population ecology. Here, we examine the abundance of these whales over time and the habitat use patterns and reproductive performance that underlie the population's growth.

History of humpback whale population monitoring in Glacier Bay National Park and Preserve

In 1973, the humpback whale was listed as “endangered” under the Endangered Species Act (ESA) and considered “depleted” under the Marine Mammal Protection Act (Johnson and Wolman 1984). In the 1970s and 1980s, there was considerable interest in scientific study and effective conservation measures to help humpback whales recover (National Marine Fisheries Service [NMFS] 1991). Recognizing the value of maintaining a consistent source of data on the local population of humpback whales, GBNP initiated an ongoing annual humpback whale monitoring program in 1985. Humpback whales were later selected by the NPS as a Vital Sign in the Southeast Alaska Network Vital Signs Monitoring Plan. Population trends and biological parameters measured in the monitoring program (e.g., Neilson et al. 2015) are used in ESA consultations on the park's vessel management decisions. Whale-monitoring data also inform real-time decision-making on vessel course and

speed restrictions to reduce whale disturbance and collision risk (Code of Federal Regulations, Title 36, Part 13, Subpart N). Information on population demographics and spatial distribution of this key marine species is crucial to well-informed protected area management.

Population characteristics of humpback whales in southeastern Alaska

Humpback whales that feed in southeastern Alaska in the summer spend the winter breeding season in the Hawaiian Islands, although a small proportion winters in Mexico (Baker et al. 1986, 2013, Perry et al. 1990, Calambokidis et al. 1997, Wade et al. 2016). The Hawaii Distinct Population Segment (DPS) is one of nine DPSs worldwide recently removed from the U.S. Endangered Species List, while the Mexico DPS remains listed as “threatened” (National Oceanic and Atmospheric Administration [NOAA] 2016).

The most recent population estimate for the Hawaii DPS was 11,398 (CV = 0.04) whales in 2006 (Barlow et al. 2011, Wade et al. 2016). In 2008, the southeastern Alaska feeding herd was estimated at 1585 whales (95% central probability interval: 1455–1644; Hendrix et al. 2012), and in 2009, the Glacier Bay and Icy Strait study population was estimated at 181 whales (95% CI: 174–196; Saracco et al. 2013). Between 1985 and 2009, the estimated average annual rate of population growth in Glacier Bay–Icy Strait was 4.4% (95% CI: 1.7–7.0%); however, the rate accelerated to 7.7% between 2002 and 2009 (Saracco et al. 2013).

Humpback whales in Glacier Bay and Icy Strait feed primarily on small schooling fishes such as capelin (*Mallotus villosus*), juvenile walleye pollock (*Gadus chalcogrammus*), sand lance (*Ammodytes personatus*), and Pacific herring (*Clupea harengus pallasii*), although euphausiids (krill) are important prey in other parts of southeastern Alaska (Krieger and Wing 1986; NPS, unpublished data). Inter-annual site fidelity to Glacier Bay and Icy Strait is high, although whales move seasonally within southeastern Alaska (Straley et al. 2009, Hendrix et al. 2012). For example, individual whales that feed in the Glacier Bay area early in the summer often move to Frederick Sound in late summer to feed on krill (Baker et al. 1985, Straley 1994). Site fidelity and local recruitment have been identified as important drivers of population growth and the genetic composition of

humpback whale feeding aggregations on a generational time scale (Baker et al. 2013, Pierszalowski et al. 2016).

Female humpback whales mature and begin to reproduce at approximately 5–11 years of age, with variation within and between populations (Chittleborough 1955, Clapham 1992, Gabriele et al. 2007, Robbins 2007, Best 2011). Gestation lasts nearly 12 months (Chittleborough 1958). Estimated mean calving rates in the Northern Hemisphere are between 0.37 and 0.50 calves per mature female per year (Baker et al. 1987, Perry et al. 1990, Straley et al. 1994, Steiger and Calambokidis 2000, Clapham et al. 2003), and reproduction is annually variable (Robbins 2007). Female reproductive spans of up to 26 yr have been documented in Hawaii, including one female sighted with a calf in eight different years (Herman et al. 2011). Examination of humpback whale ovaries indicated as many as 38 ovulations occurred over the course of a whale's lifetime (Chittleborough 1955, 1959, Symons and Weston 1958, Nishiwaki 1959), although it is uncertain how many of these resulted in the birth of a calf (Chittleborough 1965).

Here, we characterize the reproductive performance, habitat use patterns, and population dynamics of humpback whales across 30 yr (1985–2014) on an Alaskan feeding ground as the species recovers from intensive commercial exploitation. This rigorous and extensive data set, augmented by additional data collected since 1968, spans up to four generations of whales and constitutes one of the longest running studies of large whale in the world. Our findings highlight the value of marine protected areas for migratory species with strong seasonal site fidelity and the role of long-term monitoring in interpreting population-level responses to changing marine ecosystems (Hoegh-Guldberg and Bruno 2010).

METHODS

Data collection

Vessel surveys.—We conducted vessel surveys for humpback whales in Glacier Bay and Icy Strait, Alaska, 4–5 d/week between 1 June and 31 August in each year, 1985–2014 (Fig. 1). We conducted opportunistic surveys outside of these dates, but those data are not included in analyses unless noted. The primary survey area (Fig. 1)

included the main body of Glacier Bay and central Icy Strait (770 km²). The remainder of the study area (898 km²) was surveyed sporadically as time allowed and when reported whale sightings warranted. Beginning in 1996, non-motorized waters (Fig. 1) were designated by the NPS in several areas in Glacier Bay and we stopped surveying these areas (Code of Federal Regulations, Title 36, Part 13, Subpart N). We surveyed Icy Strait approximately once per week, except when weather prevented it, or whale numbers in Icy Strait were high enough that two or more surveys were needed. Although much of Icy Strait is outside the park boundary, whales frequently move between Glacier Bay and Icy Strait; thus, we surveyed there to provide essential context for whale observations inside the park.

During surveys, one or two observers searched for, observed, and photographed humpback whales on day trips (average duration ~6 to 8 h) from 5- to 6-m outboard-equipped motorboats based in Bartlett Cove (Fig. 1). We defined survey effort hours as the total time we spent on the water each day (i.e., from the time we departed the dock until the time we returned). The intent of the survey protocol was to photographically identify as many humpback whales as possible in a manner that was comparable between years. We limited our observations to good and fair sea and visibility conditions (e.g., in most cases, Beaufort ≤ 3 , seas < 0.6 m, and visibility > 0.8 km), and we made periodic stops to scan with 10 \times 40 binoculars and to listen for blows to keep our detection rate of whales high. We used a mixed approach in which we went to “hotspots” where whale sightings had been reported or were very probable, while also surveying outlying areas where whales might be present. We generally did not survey the same area on consecutive days. However, where the whales were and how many there were dictated where surveys took place and how much area we covered in a given survey.

We defined a pod of whales as one or more whales within two to three body lengths of each other, surfacing and diving in unison (Baker 1985, Clapham 1993). We defined a shoal as a group of whales composed of subgroups that were within five body lengths of each other that were not necessarily surfacing and diving in unison and in which associations between individuals were ephemeral.

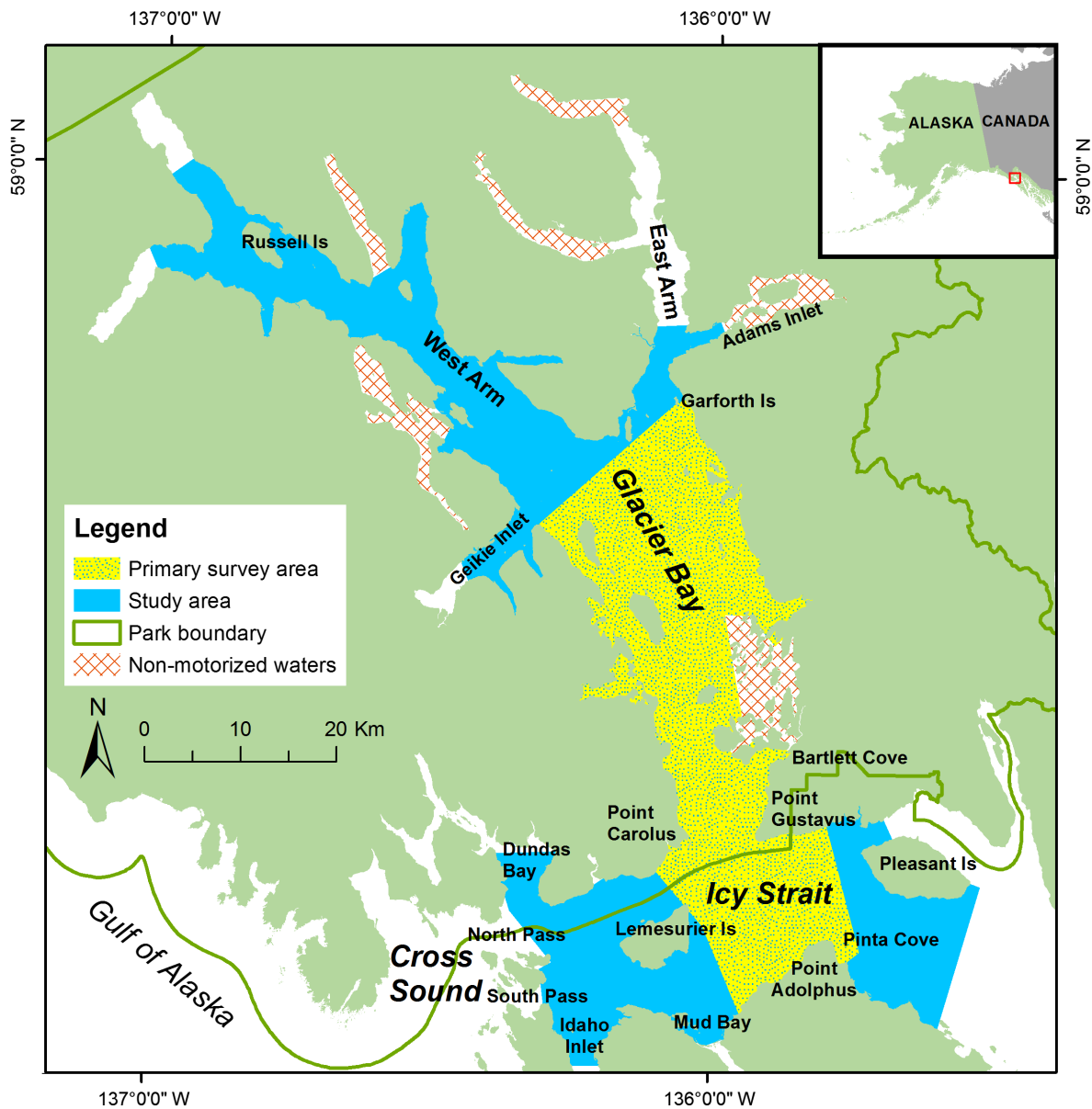


Fig. 1. Study area in Glacier Bay and Icy Strait, Alaska, showing primary survey area (in yellow) surveyed each week, weather permitting. The remainder of the study area (in blue) was surveyed sporadically.

We recorded field data pertaining to the pod or shoal in field notes or data forms. In 2014, we also used a GPS-enabled iPad with Tap Forms software version 3.8.3 (Tap Zapp Software, Calgary, Alberta, Canada) to record sighting data. Beginning in 1993, upon locating a pod or shoal, we used a GPS to determine the whales' initial location. Prior to 1993, we noted the whale(s) initial location using common place names.

Individual identification.—We used photographs of each whale's flukes and dorsal fin, taken with single-lens reflex cameras equipped with 300-mm telephoto or 70- to 210-mm zoom lenses, to identify individual humpback whales. The ventral surface of each whale's flukes has a distinct, stable black and white pigment pattern that allows for individual identification (Katona et al. 1979, Jurasz and Palmer 1981). The shape and

Table 1. Quality criteria for fluke photographs used for individual identification of humpback whales in Glacier Bay and Icy Strait.

Criteria	Quality			
	Good	Fair	Poor	Insufficient quality
% of flukes visible	80–100	50–80	<50	<25
Angle of flukes	Perpendicular to water	Not perpendicular but trailing edge visible	Trailing edge partially visible	Trailing edge not visible
Lateral angle of photographer	Photographer directly behind whale	Angled about 45°, markings still visible	Angled <45°, markings still visible	Angle so great, markings are distorted
Focus	Sharp, in focus clear grain	Good focus with minimal loss of detail	Moderate focus with some loss in detail	Very poor focus, extreme loss in detail
Lighting/exposure	Excellent, no loss in visibility of markings	Fair to good, minimal loss in visibility of markings	Poor to fair, moderate loss in visibility of markings	Very poor focus, high loss in visibility of markings

scarification of the dorsal fin also serve as unique identifiers (Blackmer et al. 2000). We compared the best fluke and dorsal fin photographs of each whale to previous NPS photographs and to photographs of other humpback whales from southeastern Alaska (University of Alaska Southeast [UAS], *unpublished data*) to determine the identity and past sighting history of each whale. Each fluke photograph was classified as “good,” “fair,” “poor,” or “insufficient” quality based on the proportion of the flukes that was visible and the angle, focus, and exposure of the photograph (Table 1). Fluke photographs classified as “insufficient” quality were omitted from further analysis. Any whale identified based solely on its dorsal fin must have been identified as a unique individual in a previous encounter based on fluke photographs.

Photographic and sighting data for whales with “good,” “fair,” “poor,” and “dorsal fin only” identifications were added to a relational database collaboratively maintained by GBNP and UAS. A unique identification number was issued to each whale (see Neilson et al. 2015).

Whale counts

We defined annual whale counts as the number of unique whales identified per year and relative annual abundance as the number of unique whales identified per year per survey hour. We estimated the average population growth rate as the geometric mean of the annual year-to-year population changes in (1) annual whale counts and (2) relative annual abundance. In the latter calculation, survey effort hours were

not available in 1986 and 1987, although the number of surveys was comparable to other years (see *Results*) so we assumed the mean effort hours for all years. We estimated average population changes and 95% confidence intervals based on geometric means and standard errors of annual changes in the counts (or effort-corrected counts).

Age–sex classification.—We identified a whale as a mother by her close, consistent affiliation with a much smaller whale that we presumed to be her calf, characterized by small size, mottled gray coloration behind and below the dorsal fin, and grayish coloration of the flukes (after Gabriele et al. 2007). Calves were presumably born during the previous winter breeding season and, consequently, were <1 yr old when sighted. We defined “known-aged” whales as non-calves whose birth year is known from photo-identification in southeastern Alaska (GBNP and UAS, *unpublished data*).

Habitat use

We used sighting histories of individual whales across years to assess within- and between-year site fidelity in the study area, augmented with additional sightings that we and other researchers (Perry et al. 1988; Sea Search Ltd, *unpublished data* [1968–1980]; Kewalo Basin Marine Mammal Laboratory, *unpublished data* [1981–1984]; D. Matkin, *unpublished data* [1989–2005]) documented in southeastern Alaska from 1968 through 2015. Using all available data from 1985 through 2014, the first and last sighting dates (Julian dates; i.e., the number of days since January 1 of that year)

of individuals were used to infer the minimum residence times of individual whales. We classified a whale as “resident” in the study area if it was photographically identified in Glacier Bay and/or Icy Strait over a span of ≥ 20 d within a survey year (after Baker 1986). A whale was classified as “transitory” in the study area if it was photographically identified in Glacier Bay and/or Icy Strait on 1 d only within a survey year. The analysis of year-to-year site fidelity included whales that were documented just one year during our study but also documented prior to 1985 or outside the 1 June–31 August survey period in at least one additional year. The analysis of continuous sighting histories included all whales of unknown age and sighting data for known-aged whales at ages four and higher. We assessed the patterns of calf return to the study area using the Fisher exact test for 2×2 contingency tables.

Reproduction and recruitment

We calculated the 1985–2014 effective calving rate of each mother who had at least one calf during an annual sighting history spanning at least five consecutive years. We excluded females whose first calf was the only calf in their sighting history ($n = 5$), to avoid including preceding years in which the whale was immature. If a female’s sighting history was broken by one or more missing years, but still contained at least five consecutive years, then both segments were used to calculate her calving rate. Most sighting data were from the study area in the 1 June–31 August timeframe, but sightings from elsewhere and in all months of the year were used if needed to fill in missing years (UAS, *unpublished data*; D. Matkin, *unpublished data*). It was assumed that the sighting probability of a female was independent of the presence or absence of a calf.

Estimating the calving rate in cetaceans is subject to many sources of bias, especially because calf presence is the primary means of determining female sexual maturity. Including sighting data from years prior to the first observed birth raises concern that one is including years in which the female was sexually immature. Therefore, for known-aged mothers, sighting data prior to 8 years of age were excluded from analysis for calving rate and age at first calving, as eight is the youngest age at first calving documented in

southeastern Alaska (Gabriele et al. 2007). Conversely, when the age at first calving is known, calculating the calving rate starting with the first observed calf will overestimate the calving rate, while excluding the first birth event causes an underestimate (Barlow and Clapham 1997). Therefore, for known-aged mothers, we estimated their calving rates twice: including and excluding their first calf to provide minimal and maximal calving rate estimates. Calving rates were calculated only for whales that had been observed every year during the interval. Some whales were not observed every year, so this method is biased toward documenting shorter calving intervals. Moreover, a calving rate based on observations on the feeding grounds is negatively biased in that it incorporates neonatal mortality, that is, some proportion of calves may have died between birth on the breeding grounds and migration to the feeding grounds (Gabriele et al. 2001); thus, we use the term “effective calving rate.” Similarly, the term “first successful calving” highlights that documenting calving on the summer feeding grounds includes the calf’s survival for the first several months of life. We calculated the reproductive span for each female, by determining the number of years elapsed between a female’s earliest calf and her most recent one.

We used two statistical methods to investigate the effective calving rate. First, to ensure comparability with previous studies (after Baker et al. 1987), we calculated the reproductive performance as the number of calves per female per year (a proportion ranging from 0 to 1). We also calculated the effective calving probability with a logistic regression model in the statistical program R (R Development Core Team 2015), where calving events were also scored as a binomial trait (0 = did not produce a calf in that year, 1 = produced a calf in that year). To estimate annual calving probabilities and 95% profile confidence intervals, we used a model with fixed-year effects and no intercept. We tested whether calving probabilities differed between the first and second halves of the study with a model including an indicator variable denoting early (<2000) or late (≥ 2000). We also used a logistic regression model to examine whether effective calving probability changed with the age of the female.

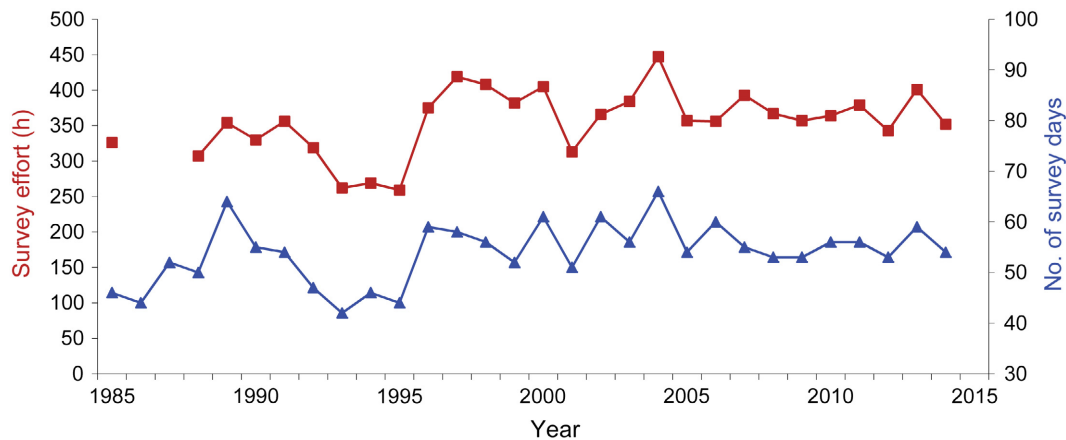


Fig. 2. Annual number of survey effort hours and survey days, 1985–2014. Survey effort hours were not available for 1986–1987.

RESULTS

Whale counts

Four of the authors were responsible for data collection and data management across the 30-yr study period resulting in a high level of consistency and quality in the data. We averaged 53.9 survey d/yr (SD = 5.9; Fig. 2). Survey effort averaged 355.4 h/yr (SD = 45.8). Survey effort hours were not available for 1986–1987. Minor annual fluctuations occurred due to factors including weather variability and mechanical difficulties.

We collected 14,983 identification photographs representing 9372 pods and 113 shoals. Pods ranged in size from 1 to 20 whales. Most pods did not contain a calf (86.7%). Most non-calf pods contained one or two whales (78.8% and 13.0%, respectively). Most calf pods ($n = 1250$) were composed of just the mother and the calf (66.6%). Large groups containing six or more whales were rare (2.3%). Shoals ranged in size from 3 to 37 whales (median = 7), and most shoals (71.7%) did not contain a calf. Each sighting (of a pod or shoal) averaged 14.4 min per sighting (SD = 12.1 min, range = 1–114 min).

The photographic data represented 662 individual humpback whales (276 calves and 386 non-calves). “Dorsal fin only” identifications constituted 28% (SD = 6.5%) of all identifications each year on average, with identifications based on flukes accounting for the remainder (72%, SD = 6.5%).

We documented an increasing trend in the number of individual whales counted each year, from a low of 41 whales in 1985 to a high of 239 whales in 2013 (Fig. 3). We found an average rate of increase of 5.1%/yr from 1985 to 2014 (95% CI: –1.3% to 11.9%) with an accelerated rate of growth from 2002 to 2011 (11.1%/yr, 95% CI: 4.1–18.6%). In 2014, we documented a 28% decline in whale counts compared to 2013, which represented the largest inter-annual decline in whale counts in 30 years of monitoring (median = +10%, range = –28% to +38%).

Controlling for variability in survey effort (Fig. 2), relative annual abundance yielded an average rate of increase from 1985 to 2014 of 4.8%/yr (95% CI: –1.9% to 12.3%) with an accelerated rate of growth from 2002 to 2011 at 10.7%/yr (95% CI: 2.9% to 19.1%; Fig. 3). In 2014, the relative abundance of whales was 18% lower than in 2013.

Habitat use

The majority of whales arrived in the study area between late May and late June (Fig. 4). Within-year site fidelity was variable. The number of whales considered “resident” each year varied, ranging from 44% to 76%, with an overall mean of 62% (SD = 8.2%). The number considered “transitory” varied annually as well with 17–44% sighted on just 1 d. The mean residency duration for whales that were sighted on more than 1 d was 67 d ($n = 2015$, SD = 38.3, range = 2–219 d).

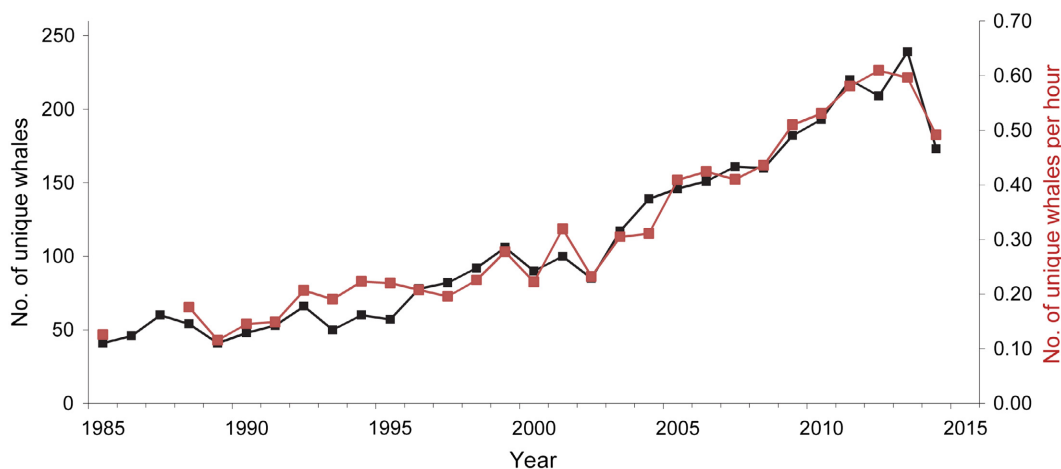


Fig. 3. Annual whale counts (black) and relative annual abundance (red) of unique whales individually identified each year in Glacier Bay and Icy Strait from 1 June through 31 August 1985–2014. Annual counts are the number of unique whales identified/yr, and relative annual abundance is the number of unique whales identified·yr⁻¹·survey h⁻¹. Relative abundance is not available for 1986–1987.

Sixty-three percent ($n = 244$) of the non-calves that we documented in the study area from 1985 to 2013 ($n = 386$) returned to Glacier Bay and/or Icy Strait in more than 1 yr. Many whales were sighted annually ($n = 66$, including 21 females, 31 males, and 14 whales of unknown sex) or missed just 1 yr ($n = 39$, including 12 females, 15 males, and 12 whales of unknown sex). In total, these individuals represent 58% of the whales that were

sighted in more than 1 yr. Eleven whales (seven males and four females) were identified in the study area every year from 1985 to 2014. One individual (male #516) photographed as a calf in 1974 (Jurasz and Palmer 1981) has been documented in the study area every year since 1981 (Kewalo Basin Marine Mammal Laboratory, *unpublished data*).

Incorporating all available sighting data prior to 1985, we found 54 whales (21 males, 29

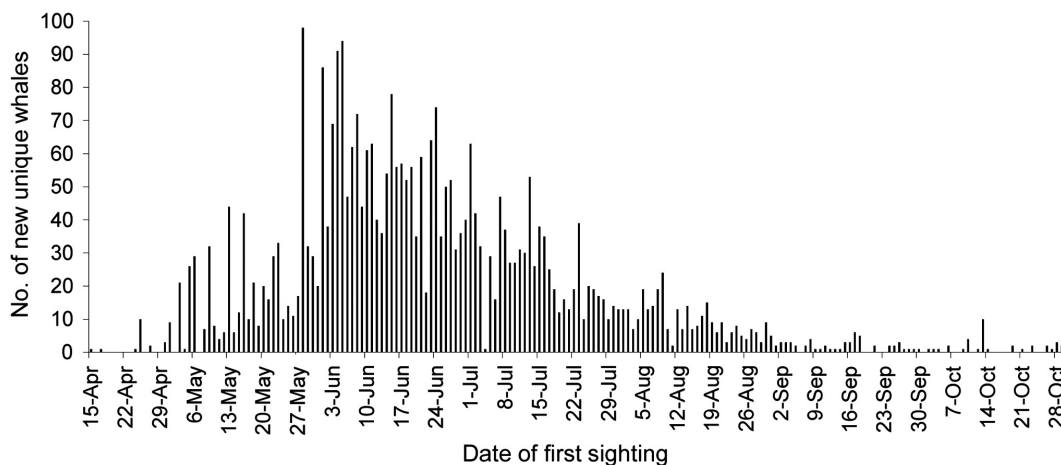


Fig. 4. Number of new unique whales identified per survey date, summed across all years, 1985–2014. Dates before and after the standardized survey period (1 June–31 August) are included to show the seasonal influx of whales into the study area.

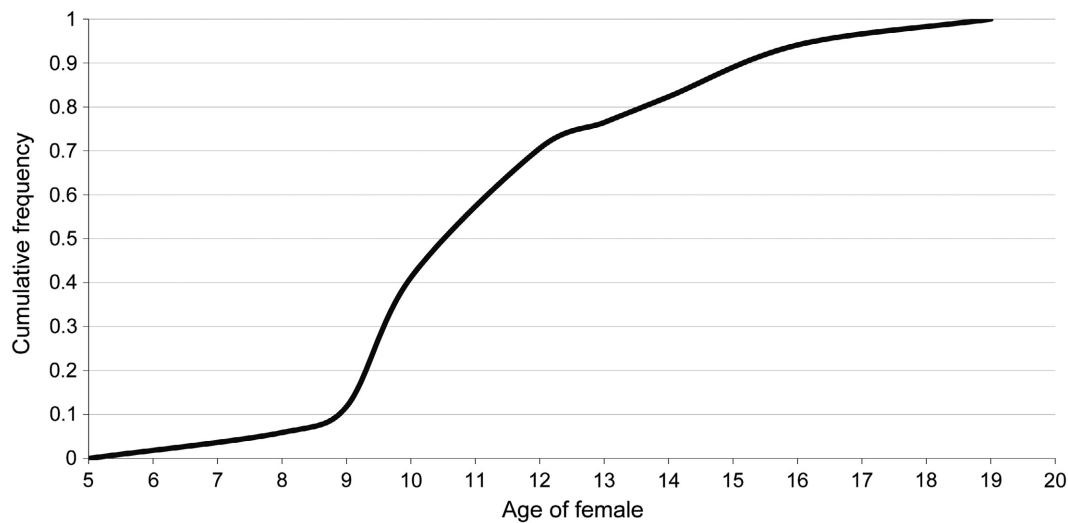


Fig. 5. Cumulative frequency distribution of observed age at first effective calving for female humpback whales in Glacier Bay and Icy Strait. Over 75% of females have given birth to their first observed calf by age 13.

females, and four whales of unknown sex) with sighting histories of ≥ 30 yr in southeastern Alaska. Of these, 13 whales (six males and seven females) had sighting histories ≥ 40 yr. One whale (female #193) had a sighting history spanning 44 yr (1972–2015). Male #441, first sighted in 1972, was found dead in Icy Strait in 2016, ending his 45-yr sighting history (SeaSearch and GBNP, unpublished data).

Sixty-seven percent ($n = 185$) of all calves accompanied mothers who were “resident” in their birth year, whereas 21% were with “transitory” mothers who were sighted on a single day. Of the 276 calves we documented, fluke photographs of sufficient quality were obtained for 196 (71%) individuals. For fluke-identified calves born from 1985 through 2013 ($n = 191$), approximately half (48%, $n = 92$) returned to the study area in subsequent years (including all encounter dates; not just 1 June–31 August). The age at which we documented calves first returning to the study area ranged from 1 to 17 yr (median = 3 yr, mean = 3.2 yr, SD = 2.7). Some of these calves ($n = 19$) later became mothers that we have documented with a total of 60 calves. Fluke-identified calves that were resident in their birth year were equally likely to return in subsequent years as non-residents (47% vs. 54%, respectively, Fisher exact test, $df = 189$, $P = 0.482$). Fluke-identified calves of known sex

were equally likely to return regardless of whether they were male or female (0.71 vs. 0.75, respectively, Fisher exact test, $df = 80$, $P = 0.803$).

Reproduction and recruitment

The mean age at first successful calving in the study area, documented for females with continuous sighting histories since age eight, was 12.1 yr ($n = 17$, SD = 2.9, range = 8–19 yr; Fig. 5). Fifty mothers had unbroken annual sighting histories of ≥ 5 yr (range = 5–30 yr; Appendix S1). The longest documented reproductive span was 32 yr, and 14 females had a reproductive span of ≥ 24 yr (Table 2). Four different females had 11 calves each. Based on all available sighting data (1972–2016), the oldest known mother was #193, who was at least 44 yr old when she had a calf in 2013 (SeaSearch, unpublished data). In addition, based on ear plug growth layer group counts (Gabriele et al. 2010) whale #539, who was killed by ship strike in summer 2014, is estimated to have been at least 70 yr old at the time of her death (C. Lockyer, H. Kato and GBNP, unpublished data) and was therefore at least 54 yr old in 2005 when she was last sighted with a calf.

Computing the effective calving rate as a simple ratio (Table 3) yielded an estimate of 0.324 (95% CL: 0.28–0.36) calves per mature female per year if the first calf of each known-aged animal ($n = 17$) was counted (maximal rate) and 0.302

Table 2. Reproductive spans for Glacier Bay and Icy Strait females with a sighting span greater than 20 yr: 1972–2014.

SEAK ID	First sighted	First calf	Last sighting	Last calf	Number of calves	Sighting span	Calving span
155	1978	1982	2014	2013	8	37	32
573	1981	1984	2015	2014	11	35	31
535	1974	1981	2014	2010	7	41	30
541	1975	1983	2012	2012	4	38	30
235	1977	1984	2014	2012	11	38	29
193	1972	1986	2015	2013	7	44	28
944	1985	1985	2015	2012	5	31	28
941	1986	1986	2013	2013	7	28	28
161	1977	1986	2016	2012	8	40	27
581	1982	1984	2013	2010	11	32	27
219	1982	1988	2014	2013	11	33	26
801	1985	1986	2016	2010	8	32	25
587	1973	1984	2016	2007	7	43	24
539	1975	1982	2014	2005	4	40	24
250	1980	1996	2016	2014	5	37	19
397	1978	1998	2015	2013	5	38	16
236	1975	1984	1999	1999	5	25	16
1460	1973	1998	2015	2007	2	43	10
232	1974	2005	2016	2013	4	43	9

Note: Calving data for these females with strong site fidelity to Glacier Bay and Icy Strait include all years and all locations within southeastern Alaska.

(95% CL: 0.27–0.34) calves per mature female per year if the first calf of a known-aged animal was not counted (minimal rate; Table 3). Computing the effective calving probability using an intercept-only logistic regression model resulted in a maximal calving probability of 0.319 (95% CL: 0.29–0.35) and a minimal calving probability of 0.305 (95% CL: 0.27–0.34). This rate was relatively variable during the early years of the study, with calving rates during the late 1980s and early 1990s exceeding >0.5 in several years (Fig. 6). All of these estimates are somewhat lower than previously documented for this population (Perry et al. 1990; UAS, unpublished data); therefore, we investigated whether the effective

calving rate changed between the first and second half of the study. Overall, the average calving rate does not appear to have changed much before and after 2000 ($z = -0.584$, $P = 0.559$, mean = 0.31, 95% CL: 0.25–0.37 in years <2000 vs. mean = 0.29, 95% CL: 0.25–0.33 in years >2000). Only including females with five or more years of annual sightings in both time periods ($n = 15$), the effective calving probability was not significantly different between time periods (Table 3). An analysis of 18 known-aged females with complete calving histories suggests that calving probability increases with age, at least up to age 28 (regression coefficient = 0.05; 95% CL: 0.00–0.11; Fig. 7).

Table 3. Estimated calving rates of mature female humpback whales in Glacier Bay and Icy Strait: 1985–2014.

Calving rate type	Number of females	Number of calving events	Simple ratio	Calving probability
Minimal	50	206	0.302 (0.27–0.34)	0.305 (0.27–0.34)
Maximal	50	221	0.324 (0.28–0.36)	0.319 (0.29–0.35)

Notes: Cells contain mean with 95% binomial confidence limits (in parentheses). The maximal calving rate is a simple ratio of number of calves/number of years and includes first calf of known-aged mothers. Minimal calving rate excludes first calf of known-aged mothers. Calving probability was calculated using a logistic regression model in R (R Development Core Team 2015).

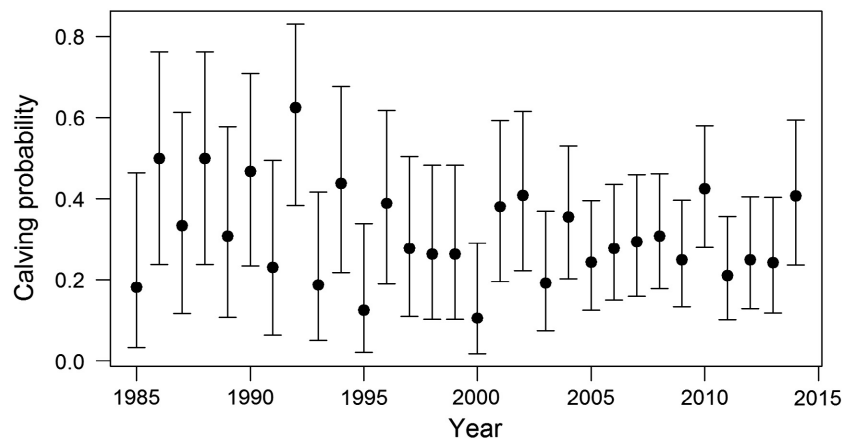


Fig. 6. Annual calf production (calves-female⁻¹·yr⁻¹) estimated with logistic regression. Error bars denote upper and lower 95% confidence limits.

DISCUSSION

This intensive study of a humpback whale feeding ground with consistent methods over 30 years has characterized inter-annual variability in numbers and documented an overall upward population trajectory. Although humpback whales are migratory and highly mobile, their remarkable within- and between-year site fidelity to Glacier Bay and Icy Strait has enabled us to document individual reproductive performance over time periods that will one day encompass entire life spans.

Whale counts

The whale population has increased over the study period (Fig. 3), a trend that is consistent

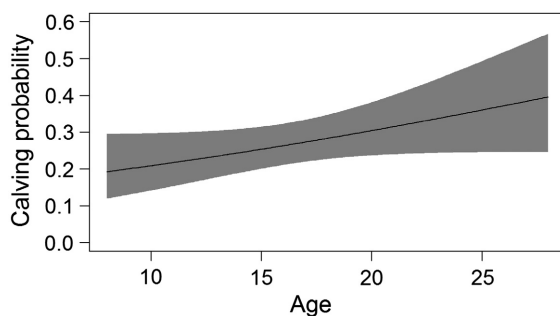


Fig. 7. Calving probability with respect to age of female estimated with logistic regression. Shaded area denotes upper and lower 95% confidence limits.

with population growth in southeastern Alaska and the North Pacific (Hendrix et al. 2012, Wade et al. 2016). Individual identification demonstrates that this population grows primarily as a function of annual return of individual whales and their offspring, corroborating earlier genetic mark-recapture work (Pierszalowski et al. 2016). Capture-recapture statistical techniques applied to 1985–2009 data revealed that our annual whale counts accurately capture about 90% of the non-calf whales in the study area (Saracco et al. 2013). Earlier investigation of whale monitoring survey effort using a bootstrap technique recommended that 45–60 survey days between 1 June and 31 August were sufficient to yield an adequate whale count (Gabriele et al. 1995). Every year within the study period has met that criterion (Fig. 2). Therefore, we believe the counts from surveys reflect the numbers of whales in our study area each year.

The average annual rates of population increase documented in Glacier Bay/Icy Strait in 1985–2014 were similar regardless of whether they were based on annual counts (5.1%/yr) or relative abundance (4.8%/yr). Both estimates are slightly higher than the mark-recapture estimates of population growth reported in Glacier Bay/Icy Strait in 1985–2009 (4.4%/yr, Saracco et al. 2013) but match the rate calculated for southeastern Alaska from 1986 to 2008 (5.1%/yr, Hendrix et al. 2012) and are within the range of variability reported elsewhere in the North

Pacific (Zerbini et al. 2006, Barlow et al. 2011). Differences in population growth rates between studies likely reflect disparities in the spatial and temporal scales of analyses, as well as how the rates were calculated. Saracco et al. (2013) noted an accelerated rate of population growth in 2002–2009 (7.7%/yr). We surmise that this elevated rate continued past the end of that study (we estimated 11.1%/yr in 2002–2011) and positively influenced the average rate of growth we calculated for 1985–2014. Covering the longest time series to date for this area, our estimate may be more robust to fluctuations in population growth over time.

Although the number of whales had been increasing for several years (Fig. 3), the 28% decline observed in 2014 represents the largest inter-annual decline in whale counts in the study period. Annual counts and relative abundance (i.e., counts corrected for survey effort) both corroborated the sharp decline in the number of whales in 2014. We believe that the 2014 decline was genuine for the following reasons. First, this study has benefited from a high level of consistency in observers, equipment, and data management; and weather conditions in 2014 were similar to past years. Second, there is no evidence (from plentiful anecdotal whale sightings each year from kayakers, tour operators, and staff) that unusually high numbers of whales were distributed in un-surveyed areas in 2014. Third, there is no evidence indicating that whale detection probability was lower in 2014. We use dorsal fin photographs as well as flukes for individual identification, so even a change in whale behavior would not lead to a change in detectability. We speculate that the proximate cause of the decline was that whales fed elsewhere in southeastern Alaska in 2014.

Habitat use

Humpback whale habitat use in Glacier Bay and Icy Strait is characterized by strong site fidelity within and between years. Although there was some annual variability, over 60% of adult whales remained in the study area to feed for more than 20 d, with a mean residence time of 9 weeks or more. Fluke-identified calves were equally likely to return after independence from their mother regardless of whether the mother was “resident” in the study area in their calf year.

Calves were also equally likely to return regardless of their sex.

Inter-annual site fidelity was high, consistent with prior work indicating that the probability of a whale returning in subsequent years to its original sighting location (e.g., Sitka Sound, Frederick Sound/Lynn Canal, or Glacier Bay/Icy Strait) was ≥ 0.75 (Hendrix et al. 2012). Almost half of the fluke-identified calves born to females who frequent the study area were documented to return in subsequent years, reinforcing the importance of maternally directed fidelity to summer feeding grounds to humpback whales (Baker et al. 2013). The remaining calves, especially those who were not fluke-identified as a calf, may be present but undetected in the study area, or they may frequent other parts of their mother’s home range in southeastern Alaska. This is consistent with genetic mark–recapture work showing that a high proportion of whales documented in the Glacier Bay and Icy Strait region in 2004–2006 are descendants of whales first sighted prior to 1985 (Pierszalowski et al. 2016). Our findings reinforce the importance of local habitat protection for species with culturally inherited migratory destinations, as they are vulnerable to local impacts that could affect population stability. As noted by Chenoweth et al. (2011), focusing protective measures on small but important habitats can yield a disproportionately large biological advantage to vulnerable species.

Reproduction and recruitment

Long-term studies of the reproductive performance of individual whales are as important as they are rare, particularly in a recovering endangered species. New data presented in this study corroborate the mean age at first successful calving in Glacier Bay and Icy Strait to be around 12 yr (Gabriele et al. 2007) and document that 75% of females are observed with their first calf by age 13 (Fig. 5). This is considerably older than the 5–7 yr documented in the Gulf of Maine (Clapham 1992, Robbins 2007) although several lines of evidence indicate that the apparent age at first birth there has increased to at least 7.8 yr (Robbins 2007). The 19-yr age at first calving (whale #1233; Appendix S1) seems extreme and may have included one or more unsuccessful and undetected calving events. Although a

relatively low proportion of whales reared in the study area have yet been documented to return with a calf, over time their reproductive contribution will be substantial.

The length of reproductive spans of these whales (maximum 32 yr) and calf production (maximum 11 calves) are longer than documented by studies on the Hawaiian breeding grounds (Herman et al. 2011) likely due to the higher likelihood of annual sightings in feeding areas (Baker 1985). In both cases, the maximal reproductive spans and calf production seem more likely limited by the length of the studies than by the reproductive capacity of the females, as suggested by anatomical studies of humpback whale ovulation (Chittleborough 1955, 1959, Symons and Weston 1958, Nishiwaki 1959). Annual calving has rarely been detected since the 1990s (Straley et al. 1994; Appendix S1). We detected a trend for calving probability increasing with age (Fig. 7), but the oldest female available for this analysis was just 28 years old, less than half the projected lifespan for this species (Gabriele et al. 2010). While there was no clear indication of reproductive senescence in the 32 whales of unknown age, it will be worthwhile to reassess this age-related effect as the known-aged whales grow older.

The numerous unbroken female sighting histories in our long-term data set allowed the most rigorous assessment of the reproductive rate of humpback whales in southeastern Alaska to date. Potential sources of bias in estimating age at first calving are covered in detail elsewhere (Barlow and Clapham 1997, Gabriele et al. 2007). The present study has eliminated some sources of bias by only including females with complete sighting histories, producing a minimal and a maximal calving rate and by estimating calving probability using a logistic regression model. The resulting estimates of effective calving rates were similar using all methods, ranging from 0.302 vs. 0.324 calves·female⁻¹·yr⁻¹ (equivalent to a birth interval of 3.1–3.3 yr) with strongly overlapping 95% confidence limits (Table 3). This calving rate is lower than the 2.56 yr estimated with a birth interval model on the Gulf of Maine feeding ground in 1992–2000 (Clapham et al. 2003). Previous Gulf of Maine work had estimated a mean birth interval of 2.38 (SE = 0.1) yr for 1979–1991 (Barlow and Clapham 1997). Similarly, our

estimates were also lower than the 0.37 rate (equivalent to one calf every 2.7 years) consistently reported in previous studies of southeastern Alaska humpback whales using data through 1988 (Perry et al. 1990, Straley et al. 2001). While the difference could be explained by a change in calving rate, we found no statistically detectable change in the average calving rate before vs. after 2000. The calving rate was relatively variable during the early years of the study (Fig. 6), so the difference in estimates may be explained by the smaller sample sizes available in earlier studies (Baker et al. 1987, Perry et al. 1990, Straley et al. 2001). It is also possible that the proportion of young reproductive females in the population is greater now than it was earlier in the study, in which case it could negatively bias the calving rate estimates in two ways. First, the age-related increase in calving probability (Fig. 7) would result in a lower overall calving rate. Second, because we did not know the age of every female, we may have inadvertently included data from females that were reproductively immature during some of the years used in the analysis (e.g., #1018 and #1088 in Appendix S1). Further work with greater sample sizes may further illuminate potential changes in calving rate as the age structure of the population changes over time.

Conservation implications

The humpback whale is one of many baleen whale populations that have declined greatly as the result of commercial hunting (Clapham et al. 2008). This exploitation of primary consumers, and their eventual protection and recovery has had far-reaching impacts on the marine food web, due mainly to the size of these whales, the quantity of prey that they consume, and the fact that their lives span several decades. Although the ecological impacts of humpback whales on the Glacier Bay area ecosystem are not well understood, it is likely that they are profound (e.g., Roman et al. 2014). Humpback whales clearly use Glacier Bay and adjacent waters intensively and consistently over the course of their long lives, depending on the area during critical life stages such as pregnancy and calf rearing. These data have been used effectively in GBNP management, but their broader significance lies in demonstrating the importance of

reproduction and recruitment by a localized portion of a high-latitude feeding herd to the population numbers in the much larger DPS managed under the Endangered Species Act. The biological knowledge gained from long-term humpback whale monitoring in Glacier Bay has contributed to whale biology across the globe (e.g., Branch et al. 2004, Taylor et al. 2007, Zerbini et al. 2010, Best 2011) as well as being valuable to federal managers seeking to mitigate impacts and engage stakeholders in resource protection efforts in Glacier Bay and beyond (e.g., Abramson et al. 2011, NOAA 2013).

Multiple simultaneous sources of environmental variability, acting on different temporal scales (Torres et al. 2008, Torres 2009), may influence life history parameters of whales and other marine vertebrates. Long-term monitoring effectively detected a significant change in whale abundance in 2014 but would be ill-equipped to assign causation, because the drivers of humpback whale distribution in southeastern Alaska remain poorly understood, aside from broad seasonal trends (Straley 1994) and the presumption that movement is prey-related. Interpreting changes in whale prey distribution is challenging and will likely become more so as forage fish populations respond to changing ocean temperature and ocean chemistry (Rose 2005, Hoegh-Guldberg and Bruno 2010, Zador 2015). Standardized assessments of the temporal and spatial patterns of key forage fish species are needed to begin to understand how they are reflected in the distribution and abundance of whales and myriad marine predators (e.g., Robards et al. 2003, Arimitsu et al. 2008, Hebert and Dressel 2015). For example, capelin is one of the most often identified prey species in Glacier Bay and Icy Strait, due to its distinctive cucumber-like smell in air and habit of schooling near the sea surface (Johnson et al. 2015, Neilson et al. 2015). Years with high whale counts appear to be associated with years where capelin were observed or collected frequently (GBNP, *unpublished data*), although quantitative data on forage fish distribution and abundance are sparse (Arimitsu et al. 2008, Hebert and Dressel 2015). Herring populations are also in need of sustained study throughout southeastern Alaska, as they are ecologically important and their population structure is not well understood (Wildes et al. 2011, McKechnie et al. 2014), although they

are commercially exploited and there have been concerns about the long-term viability of some herring stocks in southeastern Alaska (NMFS 2014). Vital Sign monitoring of oceanographic parameters in Glacier Bay offers valuable empirical data in which to detect oceanographic changes (Etherington et al. 2007) that may affect forage fish distribution (Renner et al. 2012, Womble et al. 2014) in the Glacier Bay area. Integrating whale-monitoring data in the context of oceanography, hydrology, weather, and climate data will offer the best chance to inform future park management and protect this charismatic species and its role in the ecosystem.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1641/full>