



Local recruitment of humpback whales in Glacier Bay and Icy Strait, Alaska, over 30 years

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ABSTRACT: We provide new information on the scale at which fidelity and recruitment underlie observed increases in humpback whale *Megaptera novaeangliae* populations. We used photo-identification records and DNA profiles from whales in Glacier Bay and Icy Strait (GBIS), southeastern Alaska (SEAK) to investigate 3 sources of population increase over 33 yr (1973–2005): local GBIS recruitment, recruitment from elsewhere in SEAK, and immigration from outside SEAK. We defined 2 temporal strata for these longitudinal records: 'founder' individuals identified from 1973 to 1985 (n = 74; n = 46 with DNA profiles) and 'contemporary' individuals identified from 2004 to 2005 (n = 171; n = 118 with DNA profiles). To distinguish between local recruitment and recruitment from elsewhere in SEAK, we estimated the proportion of the contemporary stratum that was either a returning founder or descended from a founder female. After excluding 42 contemporary whales without a known mother or genotype to infer maternity, 73.6% of the contemporary stratum was confirmed or inferred through parentage analysis to be either a returning founder or a descendant of a founder mother. Of the 25 females with genotypes in the founder stratum, 24 (96%) were either represented in the contemporary stratum, had at least 1 descendant in the contemporary stratum, or both. We found no significant differences in microsatellite allele or mtDNA frequencies between the strata, suggesting little or no immigration from other feeding grounds. Our results highlight the importance of local habitat protection for a recovering species with culturally inherited migratory destinations.

KEY WORDS: *Megaptera novaeangliae* · Recruitment · Fidelity · Population increase · North Pacific

INTRODUCTION

Humpback whales *Megaptera novaeangliae* in the North Pacific, first protected by the International Whaling Commission in 1965, were listed under the US Endangered Species Act in 1970 (Johnson & Wolman 1984). Pre-exploitation abundance of North Pacific humpback whales based on catch data has been approximated at about 15 000 prior to 1905 and

is thought to have decreased to less than 1000 by 1966 (Rice 1978). This oceanic population has now increased to an estimated abundance of over 21 000 individuals, as estimated using capture–recapture methods with fluke identification photographs collected from 2004 to 2006 (Barlow et al. 2011).

However, this oceanic recovery in the North Pacific humpback whale, and that of other species of exploited whales, is often variable on a local spatial and

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generational temporal scale (Baker et al. 1993, Best 1993). While some humpback whale populations have shown little sign of recovery since modern whaling (e.g. Moore et al. 1999), others have increased markedly, as demonstrated in southeastern Alaska (SEAK), a North Pacific feeding ground (Hendrix et al. 2012).

Reasons for spatial and temporal variability in recovery among humpback whale populations are, in most cases, unclear. For humpback whale populations that have overcome extreme depletion from exploitation, recovery can occur through immigration, repopulation from a remnant stock driven by local fidelity and recruitment, or some combination of both (Clapham et al. 2008).

Humpback whales in the North Pacific undertake annual migrations from high-latitude feeding regions along the Pacific Rim to tropical or sub-tropical breeding grounds around Central America, Mexico, Hawaii, and the Ryukyu and Ogasawara Islands (Johnson & Wolman 1984). Fidelity to feeding and breeding grounds has been well documented by photo-identification (photo-ID), using unique mark-

ings on the underside of a whale's flukes to identify an individual (Jurasz & Palmer 1981). Humpback whale fidelity to a feeding ground is maternally directed; a calf will migrate with its mother to a specific feeding ground and then independently return there in subsequent years as an adult (Martin et al. 1984, Baker et al. 1986, Clapham & Mayo 1987, Straley et al. 1993). Individual fidelity is also reflected in patterns of diversity in the maternally inherited mitochondrial (mt) DNA (Baker et al. 1990, 2013). Twenty-eight mtDNA haplotypes were resolved in humpback whales throughout the North Pacific in an ocean-wide survey of genetic diversity and analysis of population structure in the North Pacific humpback whales (Structure of Populations, Levels of Abundance, and Status of Humpbacks, SPLASH). These 28 mtDNA haplotypes showed marked frequency differences among feeding grounds and among breeding grounds (Baker et al. 2013). Within SEAK, the diversity of mtDNA was notably low, with the large majority of individuals having either haplotype A+ (27%) or A- (66%), suggesting strong fidelity of these 2 maternal lineages to SEAK (Baker et al. 2013).

Site fidelity also influences local habitat use on a fine-scale in SEAK (Hendrix et al. 2012). Using an open-population capture-recapture model based on photo-ID, Hendrix et al. (2012) found that the probability of whales returning to their original sighting location year to year (either Glacier Bay/Icy Strait, Sitka Sound, or Frederick Sound/Lynn Canal) was ≥ 0.75 throughout the study (1994–2008). Movement between feeding regions (both within and between seasons) is relatively infrequent and when it does occur, most transitions take place between adjacent feeding grounds (Witteveen et al. 2011).

In this study, we examined local fidelity, recruitment, and potential immigration on a decadal scale in Glacier Bay and Icy Strait (GBIS), a northern sub-region within the SEAK feeding ground (Fig. 1). Rapid environmental and anthropogenic changes have occurred in GBIS over the past 200 yr, thus providing an opportunity to evaluate recovery from exploitation within a changing environment. Glacier Bay was entirely glaciated in 1794 when the English explorer George Vancouver passed through Icy Strait (Bohn 1967).

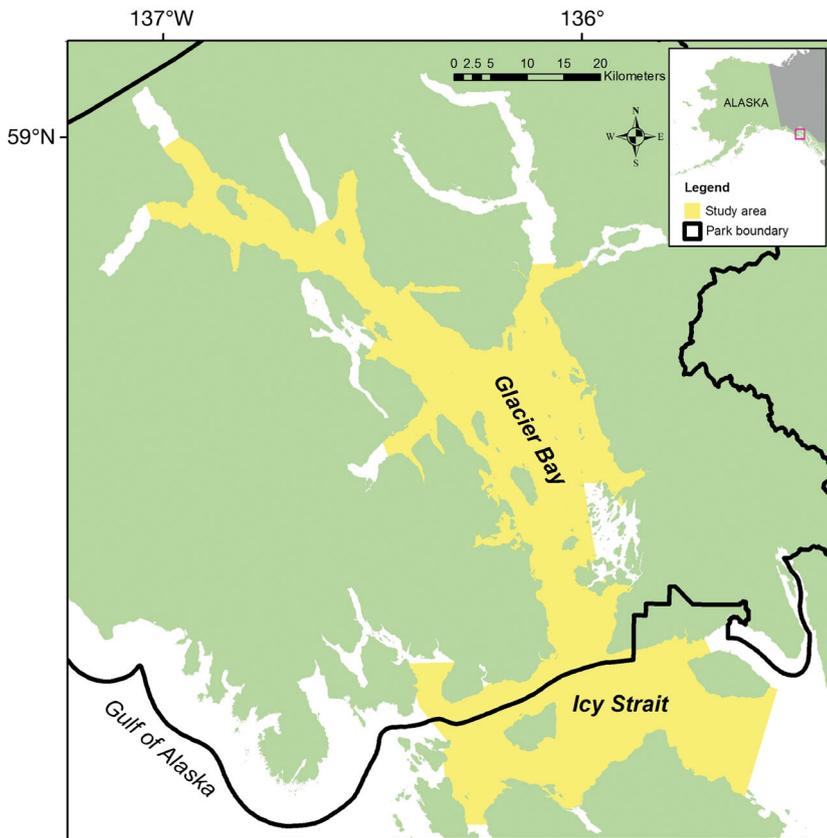


Fig. 1. US National Park Service (NPS) Humpback Whale Monitoring Program study area in Glacier Bay and Icy Strait, Alaska (USA), showing the boundary of Glacier Bay National Park and Preserve

By 1879, naturalist John Muir found that the glacial ice had retreated a distance of 77 km (Muir 1915). Sightings of humpback whales near the mouth of Glacier Bay were first reported in notes from the Harriman Expedition in 1899, and it is believed that humpback whales reached the middle of Glacier Bay as recently as 1938 (Vequist & Baker 1987). Today, the glaciers have retreated more than 90 km from the mouth of Glacier Bay, creating a productive marine ecosystem and suitable summer feeding habitat for humpback whales. Glacier Bay was set aside as a national monument in 1925 and became a national park and preserve in 1980. To manage the continuing demand for motorized vessel access to the spectacular wilderness, wildlife, and scenic beauty of Glacier Bay, the US National Park Service (NPS) has limited the number of vessel entries and maintained a system of whale approach regulations, vessel speeds, and course restrictions designed to reduce acoustic disturbance and the risk of whale–vessel collisions. These regulations fulfill the mandate of the US Endangered Species Act. In addition, entanglement in fishing gear affects this population in park waters and beyond. When the whales are elsewhere in SEAK or on their wintering grounds in Hawaii, the National Marine Fisheries Service manages human impacts with a 100 yard (91.44 m) minimum approach distance.

Research on humpback whales in SEAK began in the late 1960s, a few years after the cessation of commercial whaling. In one of the first uses of photo-ID, Jurasz & Palmer (1981) began identifying individual humpback whales based on stable black and white pigment patterns on the underside of the tail flukes. The first surveys of humpback whales in Glacier Bay date back to 1973 (Jurasz & Palmer 1981, Vequist & Baker 1987) and produced a catalog of individual whale flukes that allowed tracking of individuals up through the present day. The US NPS began making standardized annual counts of humpback whales in GBIS based on photo-ID surveys in 1985 (e.g. Neilson et al. 2015). This long-term research has been augmented with a substantial increase in photo-ID and genetic sampling efforts throughout SEAK during the collaborative SPLASH program (2004–2005).

Current work by the NPS brings together data from many sources to thoroughly document the GBIS population, making it a unique model for understanding the mechanisms of local population recovery. Longitudinal life history data on humpback whales in GBIS from 1973 to the present has resulted in a large, detailed database of information on the occurrence, distribution, known ages, and mother/offspring rela-

tionships of individual whales that have continued to visit GBIS for up to 4 decades (Southeast Alaska Regional Database; Neilson et al. 2013). Based on a robust design, capture–recapture model of the NPS’s longitudinal photo-ID database (Saracco et al. 2013), the GBIS population has increased annually by 4.4% in recent years (1985–2009). Genetic sampling has been conducted in GBIS since 1987 (e.g. Baker et al. 1990, Neilson et al. 2014), resulting in DNA profiles for hundreds of whales, many of which are also known from photo-ID (mtDNA control region, microsatellite genotypes, and sex; Baker et al. 2013).

Here, we integrated photo-ID records with DNA profiles to examine changes in the local GBIS population over 33 yr (1973–2005). First, we defined 2 temporal strata of humpback whales in GBIS separated by 20 yr, a period that represents approximately 1 generation for humpback whales (Taylor et al. 2007): (1) ‘founder’ individuals encountered early in the study of humpback whales in GBIS and (2) ‘contemporary’ individuals encountered during SPLASH. We considered 3 sources of increase: local recruitment, recruitment from elsewhere in SEAK, and immigration. We used photo-ID and DNA profiles to estimate the proportion of the contemporary stratum that was either a returning founder or descended from a founder female. To evaluate the extent of immigration from outside the SEAK feeding ground, we investigated temporal changes in mtDNA haplotype diversity and microsatellite differentiation between the 2 strata. Lastly, we used a paternity analysis to investigate whether founder males contributed through paternity with founder females, as evidence for breeding on the feeding grounds or during migration.

MATERIALS AND METHODS

Photo-ID

Photo-ID records of humpback whales have been collected in SEAK since the late 1960s by various research groups, including Sea Search, Ltd. (1968–1981), J. Straley Investigations and the University of Alaska Southeast (UAS, 1979–present), the University of Hawaii (1980–1984), the NPS Humpback Whale Monitoring Program (1985–present), and as part of the international, basin-wide, SPLASH study (2004–2005), which also included tissue sampling (Calambokidis et al. 2008). Rigorous stewardship of these data by the NPS and UAS has resulted in one of the longest-running photo-ID monitoring efforts of a whale species anywhere in the world (e.g. Neilson et

al. 2014). This effort has resulted in the SEAK Regional Database, which contains encounter histories for approximately 3500 individual humpback whales in SEAK from 1973 to present. Individual whales that are sighted more than once are assigned a sequential SEAK identification code (SEAK ID). Many maternal relationships and ages inferred for individual whales from photo-ID observations of females with dependent calves are available within this collection (e.g. Gabriele et al. 2007, Neilson et al. 2014). Hereafter, the SEAK Regional Database will be referred to simply as the 'database'.

Genetic samples and DNA profiles

Genetic samples used in this study were extracted from a comprehensive collection of 1026 SEAK tissue samples (692 with an associated SEAK ID), representing 25 yr of genetic sampling. Most samples associated with a SEAK ID were collected using a small biopsy dart (Lambertsen 1987). The majority of tissue samples used in this study were collected in SEAK during the SPLASH project by UAS (J. Straley) from 2004 to 2005. Additional samples were collected by the NPS and UAS pre-SPLASH since 1987, when tissue samples were first collected in association with photo-ID, and post-SPLASH to 2012. DNA profiling (500 bp of the mtDNA control region, 10 microsatellite loci, and sex) followed methods described previously for SPLASH (Baker et al. 2013).

Defining 'founder' and 'contemporary' users of GBIS

The spatial limits of the study area in GBIS are outlined in Fig. 1. For whales encountered within these limits, we defined 2 temporal strata to investigate changes in population structure over time. The 'founder' stratum consisted of all individuals photo-identified in GBIS from 1973 to 1985. This time period was chosen because it starts with the first year that photo-ID was conducted in GBIS and ends with the first year the NPS began systematic annual surveys in GBIS. Whales in the 'contemporary' stratum included all individuals that the NPS or UAS identified within the GBIS study area during the SPLASH program (2004 and 2005), except dependent calves (i.e. unless dependent calves in 2004 were re-sighted in 2005 without their mother). This period coincided with 2 yr of extensive sampling during the SPLASH program. A small number of individuals in the contemporary

stratum ($n = 8$) were identified during 2004 or 2005 by the distinctive shape or markings on their dorsal fins. These 'dorsal fin identifications' (Blackmer et al. 2000) were reconciled with encounters where matching dorsal fin photos and a fluke ID were obtained.

Genetic diversity and temporal differentiation

The DNA profiles provided information on sex, mtDNA haplotypes (as defined by Baker et al. 2013), and 10 microsatellite loci. The program GenAlex v6.5 (Peakall & Smouse 2006) was used to calculate the number of alleles (K), the observed and expected heterozygosity (H_o and H_e), the deviation from Hardy-Weinberg equilibrium (HWE), and the probability of identity ($P_{(ID)}$ – the probability that 2 individuals drawn at random will have the same genotype; and $P_{(ID)SIBS}$ – the probability that 2 siblings drawn at random will have the same genotype) for each microsatellite locus. All pairs of loci were tested for gametic disequilibrium in Genepop v4.2 (Raymond & Rousset 1995). Differences in allele frequencies between strata were performed using Fisher's exact test with Markov chain parameters set to 5000 dememorization steps followed by 500 batches of 2000 iterations per batch in Genepop v4.2. Weir & Cockerham's (1984) F_{ST} was used to assess the difference between founder and contemporary strata using Genepop v4.2 for microsatellite genotypes and Arlequin 3.1 (Excoffier & Lischer 2010) for mtDNA. Sex ratios among strata were compared using an exact binomial test based on the null hypothesis of a 1:1 sex ratio.

Observed and inferred maternity

We searched the database for mother/offspring pairs identified by photo-ID in the summer of the calf's birth. These were referred to as 'observed maternities.' When DNA profiles were available for both the mother and offspring, the relationship was confirmed by strict exclusion; i.e. an observed mother/offspring pair was 'confirmed' by a shared allele at all microsatellite loci, allowing for 1 mismatch due to mutation or allelic dropout (e.g. Carroll et al. 2012) and by a matching mtDNA haplotype, when available.

Many dependent calves do not show their flukes and, in these cases, we are not able to link a calf with its mother in future years by observation alone. Thus, in most cases, contemporary whales did not have

observed mothers documented by photo-ID. When DNA profiles were available for individuals without a photo-ID confirmed mother, we conducted a likelihood-based parentage analysis in CERVUS v3.0 (Kalinowski et al. 2007) to infer maternity. The set of possible mothers included all confirmed founder females with genotypes ($n = 25$) and an outgroup of randomly selected non-founder females sampled throughout SEAK ($n = 25$). We considered an individual to be a likely founder descendant if: (1) a founder female was assigned with the highest, positive logarithm of the odds (LOD) score of all putative parents (i.e. the natural log, \ln , of the multilocus likelihood ratio), (2) the mother/offspring pair was not excluded by having different haplotypes (except in cases of heteroplasmy), and (3) the mother/offspring pair had mismatching alleles at no more than 1 microsatellite locus with 8 or more loci compared. Again, 1 mismatch was allowed to account for mutation or allelic dropout (Carroll et al. 2012).

Inferring paternity

We also attempted to infer paternity for 'confirmed' contemporary offspring of founder mothers using CERVUS v3.0 (Kalinowski et al. 2007). For this, we used the 1-parent known option to increase the power of the paternity inference. The set of possible fathers included all founder males with DNA profiles ($n = 21$) and an outgroup of randomly selected non-founder males sampled throughout SEAK ($n = 21$). Photo-ID records for putative fathers were reviewed to determine whether life history information (e.g. age) was consistent or inconsistent with inferred paternity.

RESULTS

Founder and contemporary strata

The founder stratum included 74 whales. Of these 74 individuals, 46 had DNA profiles. The contemporary stratum included 171 whales, of which 118 had DNA profiles. Five individuals were first identified as dependent calves in 2004 by photo-ID but returned in 2005 as yearlings and, thus, were included in the contemporary stratum.

Photo-ID and genotype matching confirmed that 38 of 74 founder whales were represented in the contemporary stratum. Thus, 2 variants of the contemporary stratum were established for all analyses,

C_1 : contemporary whales including extant founder whales ($n = 171$, 118 with DNA profiles), and C_2 : contemporary whales excluding extant founder whales ($n = 133$, 84 with DNA profiles). In total, 207 individuals were represented in the 2 strata, of which 130 had at least a partial DNA profile, i.e. a haplotype and/or genotype combined with sex information when available (Table 1).

The sex ratio did not differ significantly from 1:1 within the founder stratum ($p = 0.659$) or within the C_1 stratum ($p = 0.108$). However, there was a significant male bias within the C_2 stratum ($p = 0.031$).

mtDNA diversity and temporal differentiation

Mitochondrial DNA haplotypes were available for 46 founder whales, 111 C_1 whales, and 77 C_2 whales (Table 1). There were no significant differences in mtDNA haplotype frequencies between the founder and contemporary strata when sexes were pooled (founder vs. C_1 : $p = 0.898$; founder vs. C_2 : $p = 0.821$). However, sex-specific tests revealed a significant difference in haplotype frequencies between founder males and C_2 males ($p = 0.012$), attributable to an increase in the A+ haplotype (Fig. 2).

There was an increase in the number of haplotypes observed in the C_1 and C_2 strata. The founder stratum included only A- and A+ haplotypes while the C_1 and C_2 strata included 2 additional rare haplotypes (E2 and A8), only 1 of which (E2) has been reported previously in the North Pacific (Baker et al. 2013).

Following the discovery of the novel A8 haplotype, electropherograms were reviewed for potential heteroplasmy (the presence of more than 1 mtDNA variant within an organism; e.g. Hoeh et al. 1991).

Table 1. Sample sizes of individual humpback whales *Megaptera novaeangliae* used in the stratification of photo-ID and DNA profiles from Glacier Bay and Icy Strait, Alaska (USA) as founders, C_1 (contemporary whales including extant founder whales), and C_2 (contemporary whales excluding extant founder whales) with at least a partial DNA profile ('DNA profile'). 'Total' reflects the total number of individuals represented in each column

Stratum	Total	DNA profile	Genotypes	Haplotype	Female	Male
Founders	74	46	46	46	25	21
C_1	171	118	114	111	47	65
C_2	133	84	80	77	29	49
Total	207	130	126	123	54	70

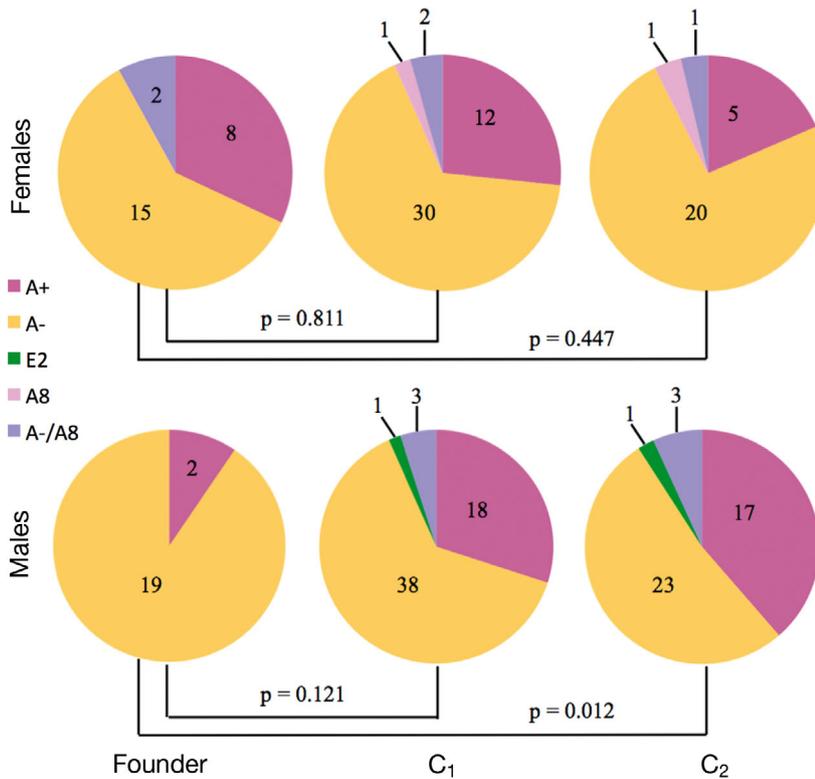


Fig. 2. mtDNA haplotype frequencies for individual humpback whales *Megaptera novaengliae* in the founder (n = 46), C₁ (contemporary whales including extant founders, n = 105), and C₂ (contemporary whales excluding extant founders, n = 71) strata with genetically confirmed sex. Note that totals do not match Table 1 because only whales with both mtDNA haplotype and genetic sex are represented here

Table 2. Microsatellite loci used for individual identification, parentage, and analysis of temporal population structure of humpback whales *Megaptera novaengliae* in Glacier Bay and Icy Strait. Results were generated from the combined 46 founder and 80 C₂ (contemporary whales excluding extant founders) genotypes (n = 126). Reported are the number of whales genotyped (n), allelic range (Range), number of alleles (K), probability of identity ($P_{(ID)}$) and $P_{(ID) SIBS}$; see 'Materials and methods', observed (H_o) and expected (H_e) heterozygosities, and significant deviations from Hardy-Weinberg equilibrium (HWE, ns: not significant, *: significant at $p < 0.05$). $P_{(ID)}$ and $P_{(ID) SIBS}$ are reported as the overall value for the 10 loci combined

Locus	n	Range	K	$P_{(ID)}$	$P_{(ID) SIBS}$	H_o	H_e	HWE
Ev14 ^a	125	131–141	6	0.22	0.51	0.600	0.579	ns
Ev37 ^a	120	192–216	12	0.031	0.32	0.892	0.867	ns
Ev96 ^a	122	149–167	8	0.076	0.38	0.787	0.786	ns
GATA417 ^b	124	191–230	12	0.027	0.32	0.863	0.878	ns
GATA28 ^b	123	147–187	6	0.49	0.72	0.317	0.311	ns
GT211 ^c	123	100–118	9	0.097	0.40	0.805	0.755	ns
GT23 ^c	125	109–121	7	0.17	0.47	0.720	0.649	ns
GT575 ^c	123	143–165	12	0.053	0.35	0.821	0.823	ns
rw4-10 ^d	126	196–208	6	0.14	0.44	0.683	0.688	*
rw48 ^d	121	112–122	6	0.13	0.43	0.711	0.701	ns
Overall	126	–	$\bar{x} = 8.4$	1.1×10^{-10}	1.8×10^{-4}	$\bar{x} = 0.720$	$\bar{x} = 0.704$	–

^aValsecchi & Amos (1996); ^bPalsbøll et al. (1997); ^cBérubé et al. (2000); ^dWaldick et al. (1999)

mtDNA heteroplasmy was defined as the presence of a second peak at a height greater than 20% of the primary peak. This revealed a single-base heteroplasmy for nucleotides C and T at position 283, representing a combination of haplotypes A- and A8. This was found in 2 individuals in the founder stratum (IDs 193 and 215), 1 of which was represented in the C₁ stratum (ID 193), and 5 individuals in the C₂ stratum (IDs 196, 875, 1795, 1809, and 1817).

Microsatellite diversity and temporal differentiation

A total of 46 founders, 114 C₁, and 80 C₂ individuals were genotyped at 8 or more loci (Table 1). The number of alleles per locus ranged from 6 to 12, the $P_{(ID)}$ for each locus ranged from 0.027 to 0.485, and the combined $P_{(ID)}$ for all 10 loci was 1.1×10^{-10} . The $P_{(ID) SIBS}$ was 1.8×10^{-4} . All but 1 locus were in HWE (rw4-10, Table 2). There was no significant gametic disequilibrium among the loci after Bonferroni correction. There was no significant differentiation in microsatellite allele frequencies between the founder and contemporary strata (founder vs. C₁: $p = 0.996$; founder vs. C₂, $p = 0.707$).

Recruitment and fidelity within the founder stratum

To determine the proportion of founders that were locally recruited (i.e. offspring of founder females), we first searched the database for 'observed' mother/offspring relationships within the founder stratum. Eight founder whales were born to founder mothers based on photo-ID records first documenting the offspring as calves (Table 3). In other words, local recruitment was responsible for at least 10.8% of the founder stratum itself between 1973 and 1985. In 3 of

Table 3. Founder humpback whales *Megaptera novaeangliae* born to mothers in the founder stratum (listed by Southeast Alaska ID code) as documented by photo-ID and, when possible, genotypic confirmation; na: not available

Off-spring	Mother	Year of birth	Genotypically confirmed?
186	530	1982	Y
352	530	1984	Y
353	581	1984	Y
198	539	1982	na
349	535	1984	na
382	573	1984	na
383	236	1984	na
800	155	1985	na

the 8 observed pairs, there were DNA profiles for both the mother and offspring, which, in all cases, confirmed the observed relationship.

A total of 38 founders were re-encountered in GBIS from 2004 to 2005 (Fig. 3), thus representing 22.2% of the contemporary (C_1) stratum. Of all genetically confirmed females with genotypes in the founder stratum, 24 of 25 (96%) were either represented in the contemporary stratum, had at least 1 descendant in the contemporary stratum, or both (Table 4).

Maternity with photo-ID and DNA profiles

To determine the proportion of the C_2 stratum (contemporary whales excluding extant founder whales) that descended from a founder female, we first searched for mother/offspring relationships using photo-ID and DNA profiles. Thirty-two individuals in the C_2 stratum (18.7% of $n = 171$) had a founder mother based on photo-ID sighting records (Table 5). Of these 32 pairs, 22 were confirmed by genotypes. The remaining 10 pairs lacked a DNA profile for either the offspring, the mother, or both.

Of the 32 C_2 individuals identified as offspring of founder females, 5 were females observed with a calf in the C_2 stratum (i.e. 5 C_2 whales had a founder grandmother). These mother/offspring relationships were confirmed with a DNA profile when available (Table 6). The 5 C_2 whales with founder grandmothers make up another 2.9% of the total C_1 stratum descended from a founder female (Fig. 3).

Only 5 other C_2 whales had observed mothers based on photo-ID sighting records, none of which were founder females. Two C_2 whales had a mother in the C_2 stratum but did not have a known link to a founder female, i.e. these were internally recruited from the C_2 stratum, but recruitment from the founder stratum was unconfirmed (Fig. 3). Another 3

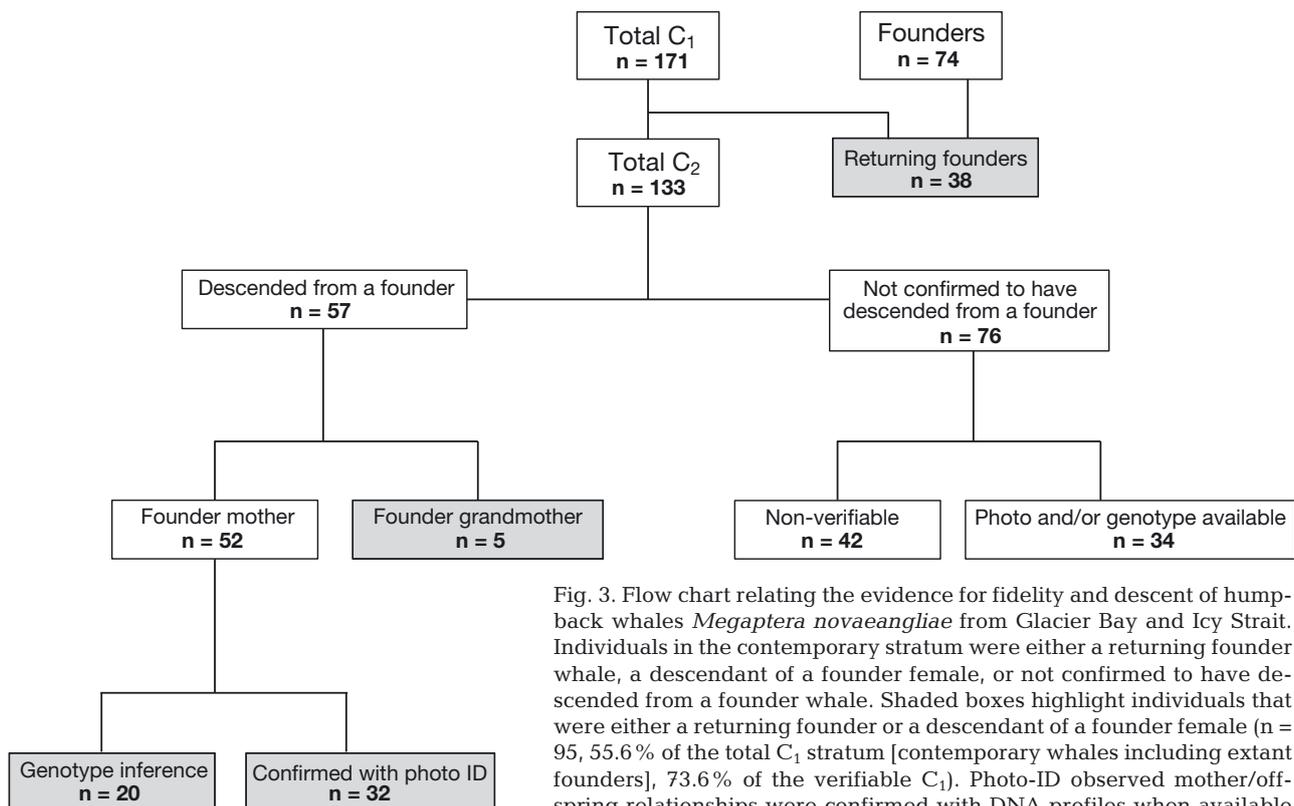


Fig. 3. Flow chart relating the evidence for fidelity and descent of humpback whales *Megaptera novaeangliae* from Glacier Bay and Icy Strait. Individuals in the contemporary stratum were either a returning founder whale, a descendant of a founder female, or not confirmed to have descended from a founder whale. Shaded boxes highlight individuals that were either a returning founder or a descendant of a founder female ($n = 95$, 55.6% of the total C_1 stratum [contemporary whales including extant founders], 73.6% of the verifiable C_1). Photo-ID observed mother/offspring relationships were confirmed with DNA profiles when available

Table 4. Representation and recruitment to the contemporary stratum of 25 founder female humpback whales *Megaptera novaeangliae* with DNA profiles to confirm or infer offspring. Offspring that were inferred are in *italics*, offspring that were observed with photo-ID are marked with an asterisk, offspring that were observed with photo-ID and confirmed with a DNA profile are underlined. Only 1 founder female (in **bold**) was not documented in the contemporary stratum and did not have an offspring in the contemporary stratum. SEAK: southeast Alaska

Founder mother SEAK ID	Return to contemporary?	Contemporary offspring	Contemporary descendant – 3 rd generation
68		<i>1441</i>	
155	Y	<i>397, 541, 1438</i>	
161	Y	<i>1299, 283, 1233, 1293</i>	
193	Y	<i>1306, 196, 1432</i>	
215		<i>1815</i>	
219	Y	<i>1031, 1485, 1803</i>	<i>1475</i>
225	Y	<i>1807</i>	
232	Y		
235	Y	<i>1079, 1461</i>	1836*
236		<i>1014, 1046, 1302, 1313*</i>	<i>1838</i>
353	Y	<i>1474</i>	
455		<i>1297*</i>	
530		<i>1019, 1304, 1083</i>	
535	Y		
539	Y	<i>1057</i>	
573	Y	<i>1088*, 1423</i>	
581	Y	<i>1042, 1090*, 1802, 1659</i>	1480*
587	Y	<i>1298, 1421*, 1063, 2168</i>	<i>1900</i>
801	Y	<i>1049, 1065*, 1486, 1654, 1018, 1473, 1658, 1895</i>	
817	Y		
944	Y	<i>1846*</i>	
965	Y	<i>1428</i>	
1011	Y	<i>1882</i>	
1460		<i>1470</i>	
569	–	–	–

individuals within the C₂ stratum had observed mothers based on photo-ID, documented within the database, but the mothers were not classified as either a founder or contemporary whale.

Maternity inference

To investigate the potential for maternity not documented by photo-ID and field observations, we undertook a likelihood analysis of parentage using microsatellite genotypes in CERVUS v3.0. After subtracting the C₂ whales that had observed mothers based on photo-ID, 91 individuals remained without a recorded mother or link to founders. Of these, 49

had a genotype available for maternity inference. Based on a comparison of these 49 individuals to founder females (n = 25) and an outgroup of 25 females selected randomly from SEAK, 12 founders were considered likely mothers of 20 of the 49 C₂ whales. These inferred maternity relationships represented 11.7% of the total C₁ stratum (Table 7).

Paternity inference

To investigate the potential for paternal contribution to local recruitment in GBIS, we used the n = 22 photo-ID and genotypically confirmed C₂ offspring/founder mother pairs to conduct a '1 parent known' paternity analysis. This analysis provided 1 case of a founder male that matched at all loci with a contemporary offspring and showed a relatively high LOD score when compared to the mother/offspring pair. The individual SEAK ID 117 was assigned as the likely father to ID 1470, a calf born in 1998 whose mother was confirmed to be ID 1460 by photo-ID and DNA profile (trio LOD = 4.19). The probability of non-exclusion was 0.024 and 0.010 for the first and second parent, respectively. A total of 8 loci were compared among the trio with alleles inconsistent with parentage at only 1 locus between the mother and offspring. Because the relationship between the mother and offspring was confirmed with photo-ID, we presume this mismatch is due to mutation or allelic dropout. All 3 whales had the A- haplotype. The individual SEAK ID 117, nicknamed 'White Eyes,' was first documented in 1977 by Sea Search, Ltd (National Marine Mammal Lab, unpublished data). Thus, life history information for this putative father was considered consistent with the assigned paternity.

DISCUSSION

Haplotype stability suggests lack of immigration

The GBIS area has maintained relatively low haplotype diversity over time (Baker et al. 1998, Fig. 2). Despite the fact that there were 13 different haplotypes on the northern Gulf of Alaska (NGOA) feeding ground when sampled during the SPLASH effort

Table 5. Individual humpback whales *Megaptera novaeangliae* in the C₂ stratum (contemporary whales excluding extant founders) with a reported founder mother based on photo-ID (n = 32, listed by southeast Alaska ID code of offspring). When available, genotypes were compared to confirm the relationship (n = 22). Hap: haplotype, na: not available, LOD: logarithm of the odds

Off-spring	Sex	Hap	Mother Hap	Hap	No. loci mismatch	No. loci compared	Genotypically confirmed?	LOD score	Non-exclusion probability
933	M	A+	566	na	na	na	na	na	na
1014	F	A-	236	A-	0	10	Y	3.552	0.009
1019	F	A-	530	A-	1	10	Y	-0.140 ^a	0.001
1031	F	A-	219	A-	0	10	Y	4.085	0.003
1042	F	A+	581	A+	0	9	Y	6.301	0.008
1046	F	A-	236	A-	0	10	Y	2.659	0.005
1049	M	A-	801	A-	0	10	Y	5.894	0.007
1057	F	A-	539	A-	0	10	Y	6.616	0.013
1065	-	na	801	A-	na	na	na	na	na
1079	F	A-	235	A-	0	10	Y	3.913	0.003
1088	-	na	573	A-	na	na	na	na	na
1090	-	na	581	A+	na	na	na	na	na
1297	-	na	455	A-	na	na	na	na	na
1298	F	na	587	A+	0	9	Y	3.877	0.062
1299	M	A-	161	A-	0	10	Y	4.032	0.004
1302	F	A-	236	A-	0	10	Y	2.497	0.028
1304	F	A-	530	A-	0	10	Y	5.307	0.008
1306	M	A-	193	A-/A8	0	8	Y	7.188	0.014
1313	-	na	236	A-	na	na	na	na	na
1421	-	na	587	A+	na	na	na	na	na
1423	-	na	573	A-	na	na	na	na	na
1428	F	A+	965	A+	1	10	Y	1.237	0.004
1438	M	A-	155	A-	0	8	Y	4.723	0.005
1470	F	A-	1460	A-	1	8	Y	-0.186 ^a	0.024
1474	M	A+	353	A+	0	10	Y	8.987	0.004
1485	M	A-	219	A-	0	10	Y	1.825	0.028
1486	F	A-	801	A-	0	10	Y	7.786	0.022
1531	-	na	250	na	na	na	na	na	na
1654	M	na	801	A-	0	10	Y	8.018	0.006
1802	M	A+	581	A+	0	10	Y	6.144	0.005
1803	M	A-	219	A-	0	10	Y	6.975	0.001
1846	-	na	944	A+	na	na	na	na	na

^aNegative LOD scores can theoretically occur when mother and offspring share very common alleles at each locus

Table 6. Five C₂ (contemporary individuals excluding extant founders) humpback whales *Megaptera novaeangliae* with mothers in the C₂ stratum and grandmothers in the founder stratum (listed by southeast Alaska ID code). Haplotypes and the first year each founder grandmother was seen in Alaska are reported in parentheses; na: not available

C ₂ off-spring	C ₂ mother	Offspring/mother genotypically confirmed?	Founder grandmother	Mother/grandmother genotypically confirmed?
1475 (A-)	1031 (A-)	Y	219 (A-, 1982)	Y
1480	1042 (A+)	na	581 (A+, 1982)	Y
1836	1079 (A-)	na	235 (A-, 1977)	Y
1838 (A-)	1302 (A-)	Y	236 (A-, 1975)	Y
1900 (A+)	1298	Y	587 (A+, 1973)	Y

(Baker et al. 2013), only 2 NGOA haplotypes were shared in GBIS (the common A+ and A-). Due to the consistent frequencies of these 2 common haplotypes in GBIS over time, it is unlikely that the population increase within GBIS is due to immigration of whales from other feeding regions (Baker et al. 1998, 2013). Instead, the relative stability in haplotype frequencies over time suggests strong regional fidelity of the maternal lineages represented in GBIS between 1973 and 1985 and persisting to the present day.

If immigration had occurred at any appreciable demographic rate in GBIS, we would expect to see additional haplotypes from other feeding grounds appear since 1985. Based on the known distribution of humpback whale haplotype frequencies across the North Pacific (Baker et al. 2013), it seems unlikely that the 2 haplotypes found only in the C₂ stratum (A8 and E2) were introduced into GBIS from outside of the SEAK feeding ground. In fact, A8 seems to have arisen from the fixation of the A-/A8 heteroplasmy detected almost exclusively in SEAK and Hawaii, the primary migratory destination for whales in SEAK (Pierszalowski 2014). Based on SPLASH surveys, the only published record of the E2 haplotype on a feeding ground outside of SEAK and NBC is 1 individual sampled in the west-

ern Gulf of Alaska (Baker et al. 2013). Therefore, the E2 individual in the contemporary stratum (ID 1489, first documented in GBIS in 1999) is likely to have shifted habitat use to GBIS from another area in SEAK or northern British Columbia.

We detected an increase in the frequency of the A+ haplotype between founder males and C₂ males. However, of the 17 males with the A+ haplotype in the C₂ stratum, at least 8 descended from a founder or C₂ female, indicating that internal recruitment largely drove this increase in males with the A+ haplotype (Rosenbaum et al. 2002).

Table 7. Twenty C_2 (contemporary individuals excluding extant founders) humpback whales *Megaptera novaeangliae* with founder mothers assigned using maternity inference (listed by southeast Alaska ID code). Hap: haplotype, LOD: logarithm of the odds, na: not available

C_2 off-spring	Hap	Loci typed	Non-exclusion probability	Putative founder mother	Hap	Loci typed	Pair loci compared	Pair loci mis-matching	Pair LOD score
196	A-/A8	9	0.003	193	A-/A8	9	8	0	7.20
283	A-	10	0.015	161	A-	10	10	0	2.18
397	A-	9	0.002	155	A-	10	9	0	4.64
541	A-	9	0.009	155	A-	10	9	0	5.32
1018	A-	10	0.003	801	A-	10	10	0	7.05
1063	A+	10	0.003	587	A+	10	10	0	4.39
1083	A-	9	0.027	530	A-	10	9	0	4.05
1233	A-	10	0.013	161	A-	10	10	0	4.37
1293	A-	10	0.004	161	A-	10	10	0	6.34
1432	A-	10	0.001	193	A-/A8	9	9	1	0.51
1441	A-	10	0.001	68	A-	10	10	1	3.04
1461	na	10	0.010	235	A-	10	10	0	4.16
1473	A-	10	0.033	801	A-	10	10	0	5.45
1658	A-	10	0.002	801	A-	10	10	0	8.82
1659	A+	9	0.013	581	A+	10	9	0	6.25
1807	A-	10	0.010	225	A-	10	10	0	4.84
1815	na	10	0.001	215	A-/A8	10	10	1	0.24
1882	A-	10	0.025	1011	A-	10	10	0	4.03
1895	A-	10	0.002	801	A-	10	10	0	4.84
2168	A+	10	0.006	587	A+	10	10	0	2.20

Local fidelity and recruitment

Twenty-four of 25 genetically confirmed females with genotypes in the founder stratum were either represented in the C_1 stratum, had at least 1 descendant in the contemporary stratum, or both. The 1 female without representation in the C_1 stratum (SEAK ID 569) was sighted elsewhere in SEAK during SPLASH and up through 2009.

More than half of the 74 founders were still alive and returning to GBIS 20 yr later, such that 22.2% of the C_1 stratum consisted of individual founder whales returning to GBIS in 2004/2005 ($n = 38$). This finding provides evidence that the increase in population size within GBIS is largely maintained through survival and sustained local fidelity. One-third of the total C_1 stratum (33.3%) was shown to have descended from a founder mother or founder grandmother using a combination of photo-ID, DNA profiles, and maternity inference analysis. This indicates that recruitment is another key driver of population increase in GBIS.

Taken together, a minimum of 55.5% of the total C_1 stratum was found to be either a returning founder whale or a descendant of a founder female. We consider this to be a minimum estimate because the ability to detect all mother/offspring pairs would require

photo-ID records of every individual, as well as field notes indicating their relationships to each other or DNA profiles with which to confirm or infer maternity—this was not always the case with the available data. In total, 42 of 171 C_1 whales (24.6%) did not have a photo-ID link to a mother or a genotype with which to infer maternity, i.e. we had no methods of determining whether they were a descendant of a founder female. We can adjust for these unverifiable whales by subtracting them from the C_1 stratum and arrive at a total of 129 C_1 whales for which we were able to investigate maternity. After this adjustment, 73.6% of the C_1 stratum was either a returning founder or a descendant of a founder female. A final bias is the absence of genetic samples for 28 founders, half of which are presumably female. This limitation is more difficult to account for. If any of these founders are sampled in the future, it seems likely they will explain more of the contemporary stratum.

Testing explicitly for recruitment within the greater SEAK feeding ground reaches beyond the scope of this study. However, due to the small impact of immigration, demonstrated by stability in mtDNA haplotypes over time, it is presumable that some proportion of the population increase in GBIS is attributable to recruitment from whales sighted elsewhere in SEAK.

Detecting paternity among GBIS founders

It is generally assumed that most humpback whales from SEAK migrate to Hawaii where males and females mate with individuals from SEAK and other North Pacific feeding grounds (Baker et al. 1986). However, behaviors associated with mating on breeding grounds have also been documented in GBIS, including singing (Gabriele & Frankel 2002) and interactions resembling competitive group behavior (Neilson & Gabriele 2009, Neilson et al. 2012, 2013). Numerous humpback whales are present in SEAK during fall and winter (Straley 1990, 1994, Straley et al. 1993), where some continue to exhibit breeding ground behavior throughout the fall with full song heard in winter (Straley 1990). Researchers have long wondered whether these feeding ground behaviors result in pregnancy or promote preferential mating when whales do return to their breeding ground (Weinrich 1991, Clapham 1993, Ramp et al. 2010). Our finding of only 1 likely paternity among the 22 confirmed C_2 offspring/founder mother pairs suggests that feeding ground interactions do not often result in breeding. However, the founder males included in the paternity search were selected based primarily on shared feeding habitat with females during summer months. A more comprehensive survey of males from Hawaii and those documented in SEAK during late fall and winter is needed to judge the relative contribution of within-feeding ground paternity (e.g. Garrigue et al. 2004).

Conservation implications

Our results confirm strong maternally directed fidelity on a fine geographical scale. These findings highlight the importance of maternal migratory traditions, which have been key to the recovery of humpback whale populations. Baker et al. (2013) suggested that maternal traditions of migration should be considered as units to conserve. Our study highlights the importance of local habitat protection for species with culturally inherited migratory destinations, given that population growth for this single, well-studied population is largely attributable to local site fidelity and recruitment. However, we do not intend to suggest that these phenomena are unique to this sub-region of SEAK. Local fidelity and recruitment may have led to population growth in other regions within SEAK and on other humpback whale feeding grounds.

Given the estimated longevity of humpback whales (70+ yr, Gabriele et al. 2010), it is likely that many of the founder whales in this study are survivors of modern whaling and continued to inhabit GBIS despite the overall reductions in humpback whale numbers throughout the North Pacific. Thus, it seems plausible that a remnant stock (i.e. the founder stratum) was sufficient for population recovery in GBIS, driven primarily by local fidelity and recruitment, versus immigration from other feeding grounds. This population recovery has occurred over the course of 40 yr (1965–2005), demonstrating the slow rate of recovery when it is driven primarily by fidelity and recruitment. Today the whales that return to GBIS represent a growing local population. However, the strong fidelity of whales to GBIS makes this population vulnerable to local impacts, and careful management will be needed to ensure the health of this population. Limiting vessel traffic in important habitats, maintaining regulatory vessel approach distances to whales, reducing the risk of fishing gear entanglement, and maintaining stranding networks with the capacity to disentangle whales are all important factors for protecting humpback whales in the North Pacific. However, it is ultimately the health of the marine ecosystem that underlies the success of a population. As the global climate warms and ocean acidification affects the marine food web, marine protected areas like Glacier Bay that control vessel traffic and other anthropogenic impacts will become increasingly important to the continued success of humpback whales around the world.

Acknowledgements. All research was conducted under appropriate permits issued by the US National Marine Fisheries Service, in accordance with the US Marine Mammal Protection Act and the US Endangered Species Act, including nos. 325, 571, 767, 933, 0473-1433, 0473-1700, and 14122 issued to J.M.S., nos. 945-1499-02 and 473-1700-00 issued to the Glacier Bay National Park, and no. 675 issued to C.S.B. Support for this work was provided by a cooperative agreement between Oregon State University and the National Park Service (Pacific West Region Cooperative Ecosystems Study Unit Task Agreement P12AC15004). Additional funding was provided through various Oregon State University awards, including the Mamie Markham Research Award, Joan Crebbin Memorial Fellowship, Lylian Brucefield Reynolds Scholarship, Thomas G. Scott Grant Scholarship, and the Hatfield Marine Science Center Student Organization Travel Grant. Thanks to P. Clapham and S. Mizroch from NOAA's National Marine Mammal Laboratory for instigating this collaboration and for facilitating access to the FlukeFinder Database, respectively. Fluke photography and tissue sampling were conducted under scientific research permits issued by the National Marine Fisheries Service. A special thanks to Charles Jurasz for his insight and foresight in documenting individual whales.

LITERATURE CITED

- Baker CS, Herman LM, Perry A, Lawton WS and others (1986) Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Mar Ecol Prog Ser* 31:105–119
- Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidis J, O'Brien SJ (1990) Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344: 238–240
- Baker CS, Perry A, Bannister JL, Weinrich MT and others (1993) Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proc Natl Acad Sci USA* 90:8239–8243
- Baker CS, Medrano-Gonzalez L, Calambokidis J, Perry A and others (1998) Population structure of nuclear and mitochondrial DNA variation among humpback whales in the North Pacific. *Mol Ecol* 7:695–707
- Baker CS, Steel D, Calambokidis J, Falcone E and others (2013) Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Mar Ecol Prog Ser* 494:291–306
- Barlow J, Calambokidis J, Falcone EA, Baker CS and others (2011) Humpback whale abundance in the North Pacific estimated by photographic capture-recapture with bias correction from simulation studies. *Mar Mamm Sci* 27: 793–818
- Bérubé M, Jørgensen H, McEwing R, Palsbøll PJ (2000) Polymorphic di-nucleotide microsatellite loci isolated from the humpback whale, *Megaptera novaeangliae*. *Mol Ecol* 9:2181–2183
- Best P (1993) Increase rates in severely depleted stocks of baleen whales. *ICES J Mar Sci* 50:169–186
- Blackmer AL, Anderson SK, Weinrich MT (2000) Temporal variability in features used to photo-identify humpback whales (*Megaptera novaeangliae*). *Mar Mamm Sci* 16: 338–354
- Bohn D (1967) *Glacier Bay, the land and the silence*. Sierra Club Press, San Francisco, CA
- Calambokidis J, Falcone EA, Quinn TJ, Burdin AM and others (2008) SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific. Final Report for Contract AB133F-03-RP-00078. https://swfsc.noaa.gov/uploadedFiles/Divisions/PRD/Projects/Research_Cruises/Hawaii_and_Alaska/SPLASH/SPLASH-contract-Report-May08.pdf
- Carroll EL, Childerhouse SJ, Christie M, Lavery S and others (2012) Paternity assignment and demographic closure in the New Zealand southern right whale. *Mol Ecol* 21: 3960–3973
- Clapham PJ (1993) Social organization of humpback whales on a North Atlantic feeding ground. *Symp Zool Soc Lond* 66:131–145
- Clapham PJ, Mayo CA (1987) Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay, 1979–1985. *Can J Zool* 65:2853–2863
- Clapham PJ, Aguilar A, Hatch LT (2008) Determining spatial and temporal scales for management: lessons from whaling. *Mar Mamm Sci* 24:183–201
- Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol Ecol Resour* 10: 564–567
- Gabriele C, Frankel A (2002) The occurrence and significance of humpback whale songs in Glacier Bay, Southeastern Alaska. *Arct Res US* 16:42–47
- Gabriele CM, Straley JM, Neilson JL (2007) Age at first calving of female humpback whales in southeastern Alaska. *Mar Mamm Sci* 23:226–239
- Gabriele CM, Lockyer C, Straley JM, Jurasz CM, Kato H (2010) Sighting history of a naturally marked humpback whale (*Megaptera novaeangliae*) suggests ear plug growth layer groups are deposited annually. *Mar Mamm Sci* 26:443–450
- Garrigue C, Dodemont R, Steel D, Baker CS (2004) Organismal and 'gametic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Mar Ecol Prog Ser* 274:251–262
- Hendrix AN, Straley J, Gabriele CM, Gende SM (2012) Bayesian estimation of humpback whale (*Megaptera novaeangliae*) population abundance and movement patterns in southeastern Alaska. *Can J Fish Aquat Sci* 69: 1783–1797
- Hoeh WR, Blakley KH, Brown WM (1991) Heteroplasmy suggests limited biparental inheritance of *Mytilus* mitochondrial DNA. *Science* 251:1488–1490
- Johnson JH, Wolman AA (1984) The humpback whale, *Megaptera novaeangliae*. *Mar Fish Rev* 46:30–37
- Jurasz C, Palmer V (1981) Censusing and establishing age composition of humpback whales (*Megaptera novaeangliae*) employing photodocumentation in Glacier Bay National Monument, Alaska 1973–79. Sea Search, Ltd., Auke Bay, AK
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106
- Lambertsen RH (1987) A biopsy system for large whales and its use for cytogenetics. *J Mammal* 68:443–445
- Martin AR, Katona SK, Mattila D, Hembree D, Waters TD (1984) Migration of humpback whales between the Caribbean and Iceland. *J Mammal* 65:330–333
- Moore MJ, Berrow SD, Jensen BA, Carr P and others (1999) Relative abundance of large whales around South Georgia (1979–1998). *Mar Mamm Sci* 15:1287–1302
- Muir J (1915) *Travels in Alaska*. Houghton Mifflin Harcourt, Boston, MA
- Neilson JL, Gabriele CM (2009) Results of humpback whale monitoring in Glacier Bay and adjacent waters: 2009. Annual Report. U.S. National Park Service, Glacier Bay National Park and Preserve, Glacier Bay, AK
- Neilson JL, Gabriele CM, Vanselow PBS (2012) Results of humpback whale monitoring in Glacier Bay and adjacent waters: 2011. Annual Report. U.S. National Park Service, Glacier Bay National Park and Preserve, Glacier Bay, AK
- Neilson JL, Gabriele CM, Vanselow PBS (2013) Results of humpback whale monitoring in Glacier Bay and adjacent waters 2012: annual progress report. Natural Resource Tech Rep NPS/GLBA/NRTR—2013/796. National Park Service, Fort Collins, CO
- Neilson JL, Gabriele CM, Vanselow PBS (2014) Humpback whale monitoring in Glacier Bay and adjacent waters 2013: annual progress report. Natural Resource Tech Rep NPS/GLBA/NRTR—2014/886. National Park Service, Fort Collins, CO
- Neilson JL, Gabriele CM, Vanselow PBS (2015) Humpback whale monitoring in Glacier Bay and adjacent waters

- 2014: annual progress report. Natural Resource Tech Rep NPS/GLBA/NRR—2015/949. National Park Service, Fort Collins, CO
- Palsbøll PJ, Bérubé M, Larsen AH, Jørgensen H (1997) Primers for the amplification of tri- and tetramer microsatellite loci in baleen whales. *Mol Ecol* 6:893–895
 - Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol Ecol Notes* 6:288–295
- Pierszalowski SP (2014) The influence of local fidelity and recruitment on population dynamics and specialized foraging of humpback whales in Glacier Bay and Icy Strait, Alaska. MSc thesis, Oregon State University, Corvallis, OR
- Ramp C, Hagen W, Palsbøll P, Bérubé M, Sears R (2010) Age-related multi-year associations in female humpback whales (*Megaptera novaeangliae*). *Behav Ecol Sociobiol* 64:1563–1576
- Raymond M, Rousset F (1995) GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *J Hered* 86:248–249
- Rice DW (1978) The humpback whale in the North Pacific: distribution, exploitation, and numbers. In: Norris KS, Reeves RR (eds) Report on a workshop on problems related to humpback whales (*Megaptera novaeangliae*) in Hawaii. Marine Mammal Commission 77-03. Nat Tech Info Serv PB-280 794. U.S. Dept. of Commerce, Springfield, VA, p 29–44
 - Rosenbaum HC, Weinrich MT, Stoleson SA, Gibbs JP, Baker CS, DeSalle R (2002) The effect of differential reproductive success on population genetic structure: correlations of life history with matriline in humpback whales of the Gulf of Maine. *J Hered* 93:389–399
 - Saracco JF, Gabriele CM, Neilson JL (2013) Population dynamics and demography of humpback whales in Glacier Bay and Icy Strait, Alaska. *Northwest Nat* 94:187–197

Straley J (1990) Fall and winter occurrence of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Rep Int Whaling Comm (Special Issue 12)*:319–323

Straley J (1994) Seasonal characteristics of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. MSc thesis, University of Alaska, Fairbanks, AK

Straley J, Gabriele CM, Baker CS (1993) Seasonal characteristics of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Proc Third Glacier Bay Sci Symp*

Taylor BL, Chivers SJ, Larese J, Perrin WF (2007) Generation length and percent mature estimates for IUCN assessments of cetaceans. Administrative Report LJ-07-01. National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA
 - Valsecchi E, Amos W (1996) Microsatellite markers for the study of cetacean populations. *Mol Ecol* 5:151–156

Vequist GW, Baker CS (1987) Humpback whales in Glacier Bay, Alaska: a long-term history of habitat use. Glacier Bay National Park and Preserve, Glacier Bay, AK
 - Waldick RC, Brown MW, White BN (1999) Characterization and isolation of microsatellite loci from the endangered North Atlantic right whale. *Mol Ecol* 8:1763–1765
 - Weinrich MT (1991) Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Can J Zool* 69:3012–3019
 - Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution* 38:1358–1370
 - Witteveen BH, Straley JM, Chenoweth E, Baker CS and others (2011) Using movements, genetics and trophic ecology to differentiate inshore from offshore aggregations of humpback whales in the Gulf of Alaska. *Endang Species Res* 14:217–225

Editorial responsibility: Clive McMahon,
Darwin, NT, Australia

Submitted: March 15, 2016; Accepted: August 15, 2016
Proofs received from author(s): October 10, 2016