The influence of local fidelity and recruitment on population dynamics and specialized foraging of humpback whales in Glacier Bay and Icy Strait, Alaska

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Acknowledgements

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BACKGROUND

In 1973, Charles Jurasz, a high school biology teacher from Juneau, Alaska, first began recording his observations of humpback whales in Glacier Bay. Jurasz pioneered a method called photo-identification, where scientists identify individual whales with photographs of black and white pigment patterns on the underside of a whale's tail, or flukes. Using photo-identification, researchers can track individual whales throughout their lives with subsequent re-sightings. Jurasz recorded the same whales in Glacier Bay year after year using this method. These whales were encountered so often that Jurasz and his family gave each of them a nickname, such as "Garfunkle" and "Chop Suey."

The legacy of Jurasz continues today; researchers at the Glacier Bay National Park Service, University of Alaska Southeast, University of Hawaii and Oregon State University have built on his early photo-identification collection, including genetic information about many of the whales Jurasz first described, to continue telling the stories of the whales that feed in Glacier Bay.

The number of humpback whales feeding in Glacier Bay has increased markedly since this species was protected from hunting in 1966. However, it is unclear whether this increase is caused by the same whales returning each year along with their offspring (i.e. fidelity and recruitment) or from immigration of whales from other feeding grounds. Of the whales that do return to Glacier Bay and Icy Strait, some exhibit a distinct form of sociality where whales form large, coordinated groups with repeated membership across several decades.

This project had two main goals. The first was to explore the degree of fidelity and recruitment to Glacier Bay over a 32-year period and to determine whether the increase in local abundance was mostly attributable to local fidelity and recruitment or immigration from outside of SEAK. The second goal was to investigate whether kinship, maternal lineage and/or sex had an effect on membership in large, stable groups of whales feeding in nearby Icy Strait. While addressing these two objectives, we unexpectedly discovered a new mtDNA haplotype in the North Pacific and a third goal emerged – to determine the number of individuals with heteroplasmy for the parental and newly derived genome and to search for evidence of germline segregation of the heteroplasmy leading to the fixation of the new haplotype.

METHODS

Photo identification (ID) records of SEAK humpback whales used in this thesis were collected by Charles Jurasz, J. Straley Investigation and the University of Alaska, Southeast (Jan Straley and Jen Cedarleaf), the University of Hawaii (C. Scott Baker) and the Glacier Bay National Park Humpback Whale Monitoring Program (Chris Gabriele, Janet Neilson and Phoebe Vanselow).

Genetic samples used in this thesis have been collected in SEAK by J. Straley Investigation and the University of Alaska Southeast (Jan Straley and Jen Cedarleaf), by C. Scott Baker, now at Oregon State University, and the Glacier Bay National Park Humpback Whale Monitoring Program (Chris Gabriele, Janet Neilson and Phoebe Vanselow).

Three research groups collected photo ID and genetic samples in SEAK during the Structure of Populations, Levels of Abundance, and Status of Humpbacks (SPLASH) project: The University of Alaska Southeast, the Glacier Bay National Park Humpback Whale Monitoring Program and the NOAA National Marine Mammal Laboratory. The majority of DNA profiles used in this thesis were generated by Debbie Steel at the OSU Cetacean Conservation Genomics Laboratory.

In order to address the three objectives of this project, I undertook an initial collation and reconciliation of the primary photo ID catalogues and DNA registry resulting from the sampling efforts described above. This resulted in the "SEAK DNA Register and Tissue Database," a comprehensive DNA registry in the form of an Excel spreadsheet wherein I have collated all existing records of tissue samples collected in SEAK, as well as DNA profiles generated form those samples. Using this Database, I was able to easily identify genetic information for individual whales that was needed to address the three objectives of this project. An electronic copy of the 'DNA register', representing the DNA profile (mtDNA haplotype, sex and 10 microsatellite genotypes) with associated information on the identity code of the individual whale (SEAK or SPLASH) has been submitted with this report as 'SEAK DNA Register and Tissue Database SPP 20March14.

Objective 1 Methods – Fidelity and recruitment

We investigated changes in population structure in GBIS over 32 years (1973-2005) in order to determine whether the increase in local abundance was attributable to local fidelity and recruitment or immigration from outside of SEAK. Two temporal strata were defined: 'Founder' individuals identified between 1973-1985 (n = 74, n = 46with DNA profiles) and 'Contemporary' individuals identified between 2004-2005 (n =171, n = 114 with DNA profiles). We used photo-identification records and microsatellite DNA genotypes, or "genetic fingerprints," to investigate genetic and demographic change between the Founder and Contemporary group and determined the proportion of Contemporary whales that descended from the early Founder whales.

Objective 2 Methods – Coordinated group feeders

Using 21 years of group association records for humpback whales in Icy Strait (1985-2005, n = 2204 groups, n = 222 individuals, n = 114 with DNA profiles), we investigated whether kinship, maternal lineage and/or sex had an effect on membership in large, stable groups. We evaluated whether females that feed in large, stable groups recruit offspring into these groups, with the assumption that it might increase their own inclusive fitness.

Objective 3 Methods – A newly arising maternal lineage

To investigate the origins of a novel mtDNA haplotype (referred to as A8), we reviewed n = 1,089 electropherograms (including replicate samples) of n = 710 individuals with A- haplotypes from both the SEAK DNA Register and Tissue Database and the ocean-wide program, SPLASH to identify any heteroplasmy for A-/A8 mtDNA haplotypes. We then used genotype exclusion and likelihood to determine whether any of the heteroplasmic females was the likely mother of the A8 cow and grandmother of the A8 calf.

RESULTS

My research demonstrated that the majority of Contemporary whales are either a returning Founder or a descendant of a Founder mother, providing evidence that finescale fidelity and recruitment are primary drivers of population increase within Glacier Bay over the last three decades. In some cases, I have been able to track maternal relationships of whales within Glacier Bay over three generations using both photoidentification and genetic markers. These findings demonstrate the value in maintaining long-term, individual-based data for assessing recovery and documenting changes in populations of whales over time.

Further, results from this project indicate that kin selection is not the primary driver of membership in large, stable groups in Icy Strait. This finding poses an interesting dynamic in local habitat use: individuals are recruited to GBIS through local maternal fidelity but do not usually associate closely with direct maternal kin.

Finally, we identified two individuals with the newly arising mtDNA haplotype (a cow and calf, both sampled in GBIS) and n = 20 individuals with clear heteroplasmy for the new haplotype. The majority of the heteroplasmic individuals (n = 15) were sampled in SEAK. Genotype exclusion and likelihood were used to identify one of the heteroplasmic females, #196 (first sighted in SEAK in 1982), as the likely mother of the *A8* cow and grandmother of the *A8* calf, establishing the inheritance and germ-line fixation of the new haplotype from the parental heteroplasmy. Based on life history records and estimates of pairwise relatedness from microsatellite genotypes, it appears likely that the *A-/A8* and the *A8* individuals are descendants from a common maternal ancestor one or more generations prior to the three generations documented here.

CONCLUSIONS

The extensive collection of DNA profiles now archived with the individual-based data within the SEAK Regional Database allowed us to integrate genetics and photo ID to answer demographically relevant questions regarding the whales in GBIS. Together, these results demonstrate that GBIS provide habitat for a distinct collection of individuals that exhibit strong fidelity and local recruitment, some of which engage in a highly specialized feeding behavior. Further, GBIS is a local feeding habitat for two individuals with a newly arising North Pacific mtDNA haplotype. These findings reveal local genotypic variation, represented by the newly arising haplotype, and cultural variation, represented by the coordinated group feeding, highlighting the importance of local habitat protection for species with fine-scale habitat use and strong fidelity to migratory destinations.

PROFESSIONAL DEVELOPMENT

MSc in Fisheries and Wildlife at Oregon State University, titled "The Influence of Local Fidelity and Recruitment on Population Dynamics and Specialized Foraging of Humpback Whales in Glacier Bay and Icy Strait, Alaska," was completed on September 11th, 2014. Committee members included C. Scott Baker, Chris Gabriele, Jan Straley and Christine O'Malley. See thesis abstract in Appendix I.

Guest Lectures/Presentations:

- Poster Presentation. "mtDNA heteroplasmy and the origins of a new maternal lineage in humpback whales of southeastern Alaska." 14th International Conference of the American Cetacean Society. Newport Beach, California. 7-8 November 2014.
- Oral Presentation. "Local recruitment and maternal fidelity of humpback whales to Glacier Bay and Icy Strait, Alaska." 11th Annual Research Advances in Fisheries, Wildlife and Ecology Symposium (RAFWE). Corvallis, Oregon. 20 February 2014.
- Guest Lecture. "A tail of a whale has a tale to tell." Science-Palooza, Newport High School. Organizer: Mary Koike. Newport, Oregon. 5 February 2014.
- Oral Presentation. "Adventures with whales." Marine Biology. Instructor: K McCready. Rainier Christian High School. Auburn, Washington. 3 September 2013.
- Oral Presentation. "Kinship and local structure of humpback whales in Glacier Bay and Icy Strait." Glacier Bay National Park Service, lunchtime seminar. Gustavus, Alaska. 24 July 2013.
- Guest Lecture. "Marine mammal science and conservation genetics." BIO 305: Biology and Conservation of Marine Mammals. Instructor: Renee Albertson. OSU, Dept. FW. 1 July 2013.
- Poster Presentation. "Influence of fidelity and kinship on local structure in a recovering population of humpback whales in southeastern Alaska." 19th Annual Markham Symposium. Newport, Oregon. 19 June 2013.

Workshop and Conference Attendance:

• Introduction to R. Shawn O'Neil and Andi Stephens. Newport, Oregon, July 2013. Workshop.

• 10th Annual Research Advances in Fisheries, Wildlife and Ecology Symposium (RAFWE), Corvallis, Oregon, February 2013.

Selected Professional Outreach and Service

- 2012-14 Oregon State University Hatfield Student Organization Vice President, Director of the Research Experience for Undergraduate Mentoring Program, Student panel for hiring a new Hatfield Marine Science Center Director, Student delegate on annual fundraiser committee
- 2012-14 Oregon State University Fish and Wildlife Graduate Student Assoc. Official graduate student liaison to the Hatfield Marine Science Center, New Student Orientation coordinator, Planning committee for our annual graduate student symposium

Supplementary grants and scholarships:

- 2014 ACS Oregon Chapter Student Research & Travel Grant Award
- 2014 Mastin Travel Award (\$1,000)
- 2014 Thomas G. Scott Grant Scholarship
- 2014 Reynolds Scholarship
- 2014 Joan Crebbin Fellowship
- 2013 Mamie Markham Research Award (\$7,000)
- 2013 Hatfield Student Organization Travel Grant

APPENDIX I.

MSc thesis abstract:

Humpback whales (Megaptera novaeangliae, Borowski 1781) in the North Pacific migrate from mid- to high- latitude summer feeding grounds along the Pacific Rim, including areas off the coasts of the U.S., Canada, Russia and eastern Asia, to tropical breeding grounds each winter along Pacific coasts of Mexico and Central America as well as the offshore islands of Mexico, Hawaii, and Japan. Humpback whales in the North Pacific and elsewhere were reduced to very low numbers during a period of intense commercial exploitation that ended in 1965. As the population recovers in abundance, the range of cultural and genetic diversity that survived the exploitationdriven bottleneck is able to adapt, endure and evolve. My work uses genetic tools and photo identification data to investigate the population dynamics, mitochondrial (mt) DNA control region evolution and potential drivers of a specialized feeding behavior in a recovering subpopulation of humpback whales in the Glacier Bay and Icy Strait (GBIS) sub-region of the southeastern Alaska (SEAK) feeding ground. I first collated and reconciled available DNA profiles (mtDNA control region, 10 microsatellite loci and sex) from 556 individuals using tissue samples collected from 1987 to 2012. Photo identification records associated with 692 of 1,026 total genetic samples collected in SEAK (now archived within the SEAK DNA Register and Tissue Database) corresponded to extensive life-history information, extending back to the early 1970s, as archived within the SEAK Regional Database, curated by the National Park Service (NPS) and University of Alaska, Southeast (UAS).

Changes in population structure in GBIS over 32 years (1973-2005) were investigated in order to determine whether the increase in local abundance was attributable to local fidelity and recruitment or immigration from outside of SEAK. Two temporal strata were defined: 'Founder' individuals identified between 1973-1985 (n = 74, n = 46 with DNA profiles) and 'Contemporary' individuals identified between 2004-2005 (n = 171, n = 114 with DNA profiles). There was no significant genetic differentiation between the strata, indicating that it is unlikely that the population increase within GBIS was due largely to immigration of whales from elsewhere in the North Pacific. However, two additional haplotypes were documented in the Contemporary stratum at low frequency, one of which was previously unreported in the North Pacific (haplotype A8, see below). This relative stability in haplotype frequencies over time argues for strong regional fidelity of the maternal lineages represented in GBIS between 1973 and 1985. After excluding the 42 Contemporary whales with no photo ID record of a mother or genotype available for maternity inference, at least 73.6% (n = 95) of the Contemporary stratum was either a returning Founder or a recruited descendant of a Founder female. Of all genetically confirmed females with genotypes in the Founder stratum, 96% (n = 24) were either represented in the Contemporary stratum, had at least one confirmed descendant in the Contemporary stratum, or both. This high proportion, in addition to the large proportion of the

verifiable Contemporary stratum that were either returning Founders or a descendant of a Founder female, provides clear evidence for local fidelity and recruitment to GBIS.

The discovery of the A8 haplotype, which differs by one base pair from a common haplotype referred to as A-, represents an increase in mtDNA diversity for the North Pacific humpback whale from 28 to 29 haplotypes. To investigate the origin of this new haplotype, we re-evaluated n = 1089 electropherograms of n = 710 individuals with A- haplotypes from both the SEAK DNA Register and Tissue Database and the oceanwide program, SPLASH (Baker et al. 2013). From this review, we identified two individuals with the A8 haplotype (a cow and calf, both sampled in GBIS) and n = 20individuals with clear heteroplasmy for haplotypes A-/A8. The majority of A-/A8 individuals (n = 15) were sampled in SEAK. Genotype exclusion and likelihood were used to identify one of the heteroplasmic females, #196 (first sighted in SEAK in 1982), as the likely mother of the A8 cow and grandmother of the A8 calf, establishing the inheritance and germ-line fixation of the new haplotype from the parental heteroplasmy. Based on life history records and estimates of pairwise relatedness from microsatellite genotypes, it appears likely that the A-/A8 and the A8 individuals are descendants from a common maternal ancestor one or more generations prior to the three generations documented here.

Humpback whale sociality takes a distinct form in Icy Strait, where whales form large, coordinated groups with repeated membership across several decades. Twentyone years of group association records (1985-2005, n = 2,204 groups) were used to investigate the hypothesis that kin selection influences membership in large, stable groups. Of the 2204 groups recorded, 113 consisted of 6 or more individuals; a size considered unexpectedly large assuming a Poisson distribution of group size with a mean of 1.7. A total of n = 71 individuals (n = 48 with DNA profiles) were encountered in a large group in at least one year, n = 38 individuals (n = 34 with DNA profiles) were encountered in a large group in at least two years, n = 29 individuals (n = 27 with DNA profiles) were encountered in a large group in at least three years, decreasing to n = 2individuals (n = 2 with DNA profiles) that were encountered in a large group in at least 20 years. There were no significant differences in mtDNA frequencies between large group feeders and the Founder and Contemporary strata or when compared to whales never encountered in large groups in Icy Strait, indicating that group membership is not predominately passed through one maternal lineage. Sex ratios did not deviate significantly from 1:1 for those feeding in large groups over an increasing number of years, as would be expected if females were actively recruiting offspring into large groups. The average pairwise relatedness for large group feeders was not significantly greater than expected by chance and did not increase for those feeding in large groups over an increasing number of years. Of the 179 known offspring of females encountered in a large group, only 6% were also encountered in a large group in Icy Strait as an adult and only 2.2% in the same large group as their mother. These results indicate that kin selection is not the primary driver of membership in large, stable groups and pose an interesting dynamic in local habitat use: individuals are recruited to GBIS through local maternal fidelity but do not usually associate closely with direct maternal kin.

The extensive collection of DNA profiles now archived with the individual-based

data within the SEAK Regional Database allowed us to integrate genetics and photo ID to answer ecologically relevant questions regarding the whales in GBIS. Together, these results demonstrate that GBIS provide habitat for a distinct collection of individuals that exhibit strong fidelity and local recruitment, some of which engage in a highly specialized feeding behavior. Further, GBIS is a local feeding habitat for two individuals with a newly arising North Pacific mtDNA haplotype. These findings reveal local genotypic and cultural variation and highlight the importance of habitat protection for species with fine-scale habitat use and strong fidelity to local migratory destinations.