

TRACKING NORTH PACIFIC HUMPBACK WHALES TO UNRAVEL THEIR BASIN-WIDE MOVEMENTS

Final Technical Report

Prepared for

Pacific Life Foundation
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30 June 2019

Suggested Citation:

Palacios, D.M., B.R. Mate, C.S. Baker, C.E. Hayslip, T.M. Follett, D. Steel, B.A. Lagerquist, L.M. Irvine, and M.H. Winsor. 2019. Tracking North Pacific Humpback Whales To Unravel Their Basin-Wide Movements. Final Technical Report. Prepared for Pacific Life Foundation. Marine Mammal Institute, Oregon State University. Newport, Oregon, USA. 30 June 2019. 58 pp.
doi:10.5399/osu/1117. https://ir.library.oregonstate.edu/concern/technical_reports/z890s0924

Funding & Support:



Executive Summary

In 2014, Oregon State University (OSU) initiated a multi-year project to study humpback whale (*Megaptera novaeangliae*) migrations in the North Pacific Ocean using satellite tracking technology in combination with genetic and photo-identification (photo-ID) analyses. The study is highly relevant to management, given the need for new information arising from the recent separation of humpback whales into Distinct Population Segments (DPS) for listing under the US Endangered Species Act, including four DPSs in the North Pacific (“Western North Pacific”, “Hawaii”, “Mexico”, and “Central America”) with different conservation statuses. The project’s objective was to conduct a comprehensive characterization of humpback whale movements during breeding, migration, and feeding periods by tagging animals in both a feeding area (southeastern Alaska) and a breeding area (Hawaii). In order to obtain representative results, the sampling plan called for two field efforts at each site, with Pacific Life Foundation funding the southeastern Alaska portion of the project (2014 and 2015 seasons), and the Hawaii portion being cost-shared through a combination of sources including the Makana Aloha Foundation (2015 season) and the US Department of the Navy (2018 season). This final report provides the combined results and accomplishments from these efforts.

Argos-based, fully implantable tags were deployed on 37 humpback whales in Seymour Canal and Frederick Sound, southeastern Alaska, in 2014 and 2015. Tracking periods ranged from 3.3 to 78.3 d (mean = 28.2 d, sd = 16.2 d), with distances traveled ranging from 73 to 6,503 km (mean = 2,010 km, sd = 1,649 km). The tracked locations for these animals ranged over 40 degrees of latitude, from Lynn Canal and Icy Strait (59°N) in southeastern Alaska to the southern tip of Hawaii Island (19°N) in the Hawaiian Archipelago.

Genetic and photo-ID analyses revealed that two of the whales tagged in 2014 were re-tagged in 2015, providing a unique opportunity to compare movements between years for the same individuals. For one of these animals the movements and their timing were similar between years, as it moved from Seymour Canal into Frederick Sound with a difference of 4 d between years. However, early failure of the tag in 2014 (after 6.2 d) prevented a longer comparison. In contrast, the movements of the second animal within southeastern Alaska were similar but the timing was very different between the two years, despite a similar tracking period (21.9 d in 2014 versus 19.1 d in 2015). In 2014 this animal spent a substantial amount of time in Seymour Canal (17 d) before moving into Stephens Passage for the remainder of its tracking period, while in 2015 the animal moved into Stephens Passage soon after tagging and only for a brief period before it moved into Frederick Sound, from where it initiated the migration toward Hawaii. Differences in timing notwithstanding, the similarities in the tracks between years for both animals provided some evidence of route fidelity, as has been recently shown for several species of migratory marine animals.

Twenty of the whales tagged in southeastern Alaska began their winter migration to a low-latitude breeding area, with start dates ranging from 19 November to 6 January. Three of these whales were tracked to breeding areas, two to Hawaii and one to the Mexican mainland. Another 16 whales were headed in the direction of Hawaii and one in the direction of Mexico when their tags quit. The duration

and distance spent on migration for the three animals that reached a breeding area ranged from 29 to 46 d and from 4,200 to 4,700 km, respectively. The two animals that arrived in Hawaii entered the archipelago at Hawaii Island.

Forty-five tags were deployed on humpback whales off Maui, Hawaii, in 2015 and 2018. Two of these tags provided no locations. Tracking periods for the remaining 43 whales ranged from 0.1 to 147.2 d (mean = 20.8 d, sd = 29.0 d), with distances ranging from 13 to 11,302 km (mean = 1,217 km, sd = 2,348 km). The tracked locations for these animals ranged over 43 degrees of latitude, from the south coast of Maui (21°N) to the Bering Sea (64°N).

While in Hawaiian waters, the majority of locations were in the Maui Nui region (the waters between the islands of Maui, Lanai, Molokai and Kahoolawe), during both in 2015 and 2018. Penguin Bank was another area heavily frequented by the tagged whales. Most tagged whales moved in a predominant northwesterly direction after tagging, with animals leaving Maui headed for Lanai, Molokai, and/or Penguin Bank. Several whales were also tracked to Oahu, and one whale was further tracked to both Kauai and Niihau. Only one whale was tracked southeast to Hawaii Island in 2015, but other tagging studies have documented eastward movements to Oahu, Penguin Bank, and Maui Nui, so it is apparent that whales may move extensively between islands, both in westerly and easterly directions.

Nine of the whales tagged in Hawaii began their migration to a high-latitude feeding area, with departure dates ranging from 29 January to 11 April. Four of these whales were tracked to feeding areas, three to northern British Columbia and one to the eastern Aleutian Islands. Another four whales were headed on a northeasterly trajectory toward northern British Columbia and three more on a northerly or northwesterly trajectory toward destinations in the Aleutian Island chain when their tags quit. The three whales that were tracked to northern British Columbia arrived in the Haida Gwaii Archipelago after having spent 30-44 d and 4,300-5,000 km on migration. The animal that migrated north to the eastern Aleutians arrived at an area approximately 200 km south of Unimak Pass, 28 d and 3,775 km after departing Hawaii. These results, together with those obtained from animals tagged in southeastern Alaska that migrated to a breeding area (Hawaii or Mexico), provide evidence that the travel time and distance covered by humpback whales while on migration across the North Pacific Basin can vary widely, with overall ranges of 28-46 d and 3,775-5,000 km, respectively.

A 50-km buffer zone around southeastern Alaska and Hawaii was used for purposes of characterizing whale movement speeds and residence times in the feeding and breeding areas (inside the buffer zones), as well as during migration (outside the buffer zones). Residence time was computed as the time period from tag deployment to when a whale crossed the buffer zone boundary as it departed on migration. Residence time in southeastern Alaska in late fall was estimated for 20 whales, ranging from 4.4 to 49.1 d (mean = 17.3 d), although additional information from earlier tagging studies indicated that individual humpback whales may use this feeding area for periods of up to four to five months. In contrast, residence time in Hawaii was estimated for nine whales, ranging from 3.3 to 23.2 d (mean = 14.8 d), consistent with earlier photo-ID and telemetry studies and lending support to the notion that that there is a rapid turnover of individuals in this breeding area during the winter season. In any case,

overall true residence time in these areas is likely longer than the minimum values we report based on satellite telemetry, as we cannot know the time a whale had spent in an area prior to tagging.

Movement speeds during the different phases of the migration (feeding, breeding, migrating) were calculated based on the portions of the tracks that occurred inside or outside the 50-km buffer zones. Whales tagged in southeastern Alaska moved at a mean speed of 1.01 km/h (median = 0.47 km/h, sd = 1.28 km/h) while in the southeastern Alaska feeding area; 5.51 km/h (median = 5.63 km/h, sd = 1.98 km/h) while migrating; and 1.49 km/h (median = 1.01 km/h, sd = 1.36 km/h) once they arrived in the Hawaii breeding area. Whales tagged in Hawaii moved at a mean speed of 1.36 km/h (median = 1.00 km/h, sd = 1.21 km/h) while in the Hawaii breeding area; 4.44 km/h (median = 4.32 km/h, sd = 2.18 km/h) while migrating; and 2.00 km/h (median = 1.53 km/h, sd = 1.53 km/h) once they arrived in the southeastern Alaska feeding area. These results showed that whales moved much slower while in the feeding and breeding areas than while migrating, and that travel speed from the feeding to the breeding areas was somewhat faster than from the breeding to the feeding areas.

Biopsy samples were collected from 27 of the whales tagged in southeastern Alaska in 2014 and 2015, and from 39 of the whales tagged in Hawaii in 2015 and 2018. These 66 samples were identified by a unique multi-locus genotype of at least 14 microsatellite loci, which indicated they represented 64 unique individuals (after accounting for the two animals that were re-tagged). The 25 individuals tagged in southeastern Alaska represented 14 females and 11 males. The 39 individuals tagged in Hawaii represented four females and 35 males. The DNA profiles of the 64 individuals were compared to a reference database of 1,805 individuals sampled from 2004 to 2006 in the North Pacific by the program SPLASH, which revealed nine matches (i.e., genotype recaptures). Of these, six matches were recaptures within an area (four within southeastern Alaska and two within Hawaii) and three were recaptures between whales tagged in Hawaii and sampled previously on feeding areas in either northern British Columbia ($n = 2$) or southeastern Alaska ($n = 1$).

Mitochondrial deoxyribonucleic acid (mtDNA) sequences of the 64 individuals resolved seven haplotypes for the consensus region of 500 base-pairs. All seven haplotypes had been previously described for North Pacific humpback whales by SPLASH, but only two occurred in the southeastern Alaska samples while all seven occurred in the Hawaii samples, supporting earlier results indicating a greater haplotypic diversity in the Hawaii breeding area than in the southeastern Alaska feeding area. Further, pairwise tests of differentiation between the tagging areas and the 18 SPLASH regional strata were consistent with those reported in that study, supporting our current understanding of humpback whale population structure, migratory destinations, and site fidelity in the North Pacific.

Photo-IDs (fluke photographs) were obtained from 30 whales tagged in southeastern Alaska and from 24 whales tagged in Hawaii. Comparisons with the online Happywhale photo-ID database as well as with OSU's own ID catalog revealed matches for 25 of the tagged whales (18 from southeastern Alaska and seven from Hawaii). Thirty-five percent of the tagged whales with an ID were found in Happywhale and 13 percent in OSU's catalog. Most matches (19 of 25) were made within the same area in which the whale was tagged, with time spans between sightings of up to 14 years. Two whales tagged in southeastern Alaska in 2014 each had only one photo-ID match in a different area than the one in which

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An additional 26 matches were found in Happywhale from among 149 fluke photographs of untagged whales collected by OSU in Hawaii. Of these, 13 matches were made within Hawaii (with a maximum time span between sightings of 21 years); nine matches were made between Hawaii and different parts of Alaska, including southeastern Alaska, Kodiak Island, Cook Inlet, and the Shumagin Islands; four matches were made between Hawaii and Washington State and Vancouver Island, British Columbia; and one match was made between Hawaii and the Chukchi Sea, near Kolyuchin Island, northeastern Russia.

Through the combined use of satellite tagging, genetics, and photo-ID, we characterized the patterns of humpback whale occupation in both a breeding and a feeding area in the North Pacific Ocean, as well as the long-distance migratory movements that these animals undertake seasonally between these areas. The results of this study revealed the complex migratory linkages between Hawaii and the high-latitude feeding areas with unprecedented detail. Genotype and photo-ID recaptures of multiple individuals between migratory destinations supported previously known strong connections between breeding and feeding areas (e.g., Hawaii and southeastern Alaska/northern British Columbia, and Hawaii and Washington/southern British Columbia). Satellite tracking also revealed the movements and migratory connections between Hawaii and feeding areas in the Aleutian Islands and the Bering Sea, while photo-ID recaptures demonstrated additional connections between Hawaii and feeding areas in the northern Gulf of Alaska (Shumagin Islands, Kodiak Island, Cook Inlet) and the Chukchi Sea.

Additional years of sampling during different parts of the reproductive season and in other parts of the main Hawaiian islands (e.g., Kauai and Hawaii), as well as in the northwestern Hawaiian Islands, would provide valuable information to address outstanding questions about the humpback whale DPS using this extensive breeding area, as well as its broader connections to remote feeding areas throughout the North Pacific Basin, most of which are poorly known. Also, while the majority of whales tracked from southeastern Alaska showed a strong connection to the Hawaii breeding area, a small proportion of these animals demonstrated a connection to the Mexican mainland breeding area, indicating some mixing of the Hawaii and Mexico DPSs in the southeastern Alaska feeding area. These animals are of particular interest, as in their transit along the western coast of North America they overlap with animals from the Central America DPS, which forages off California and Oregon. Further tagging work to better understand the patterns of habitat use and the extent of the overlap between the Mexico and Central America DPSs in this region would greatly help current needs to improve how animals are assigned to DPS for management purposes in the context of relative exposure to anthropogenic activities, given their different conservation statuses.

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1 Introduction

Recent studies using photo-identification (photo-ID) and genetic approaches have significantly advanced our understanding of the population structure, abundance, and migratory destinations of humpback whales (*Megaptera novaeangliae*) in the North Pacific Ocean (Calambokidis et al. 2008, Barlow et al. 2011, Baker et al. 2013). However, many questions still remain about humpback whale migration and movement behavior, as these techniques do not provide information about the actual routes followed by the animals or about their behavior while *en route*. Indeed, the precise migration routes and movement patterns for most whale populations remain poorly known (Corkeron and Connor 1999, Clapham 2001, Garrigue et al. 2015).

Satellite telemetry, on the other hand, provides accurate information on the departure and arrival timing at the migratory destinations, as well as spatially explicit details of the migration routes. Further, statistical tools allow us to estimate important movement parameters from the tracking data, as well as to derive measures of habitat use such as home range, spatial hotspots of aggregation, and migratory corridors. The development of suitable electronic tags and tag attachment methods for large whales has overcome significant logistical and technological challenges in the past 30 years, and satellite telemetry is now a viable technique for studying whale movements across ocean basins on a routine basis (Mate et al. 2007). In light of the increasing human pressures on the marine environment, the information generated by satellite telemetry and related bio-logging technology can also be highly relevant for management purposes, for example in terms identifying areas of high use by the whales, both in the breeding and feeding areas, and their overlap with shipping lanes, fishing grounds, and zones of military operation (Parks et al. 2012, Goldbogen et al. 2013, Irvine et al. 2014, Blair et al. 2016, Abrahms et al. 2019a).

Specifically with regard to the conservation status of humpback whales, in 2016 the National Marine Fisheries Service (NMFS) divided the global population into 14 Distinct Population Segments (DPSs) for purposes of listing under the US Endangered Species Act¹ (ESA). Four DPSs were designated for the North Pacific based on the location of distinct breeding areas (Federal Register 2016a, b): “Western North Pacific”, “Hawaii”, “Mexico”, and “Central America”. The corresponding ESA status is “Endangered” for both the Western North Pacific (estimated at 1,066 animals; Wade et al. 2016, Wade 2017) and the Central America DPSs (estimated at 783 animals; Wade et al. 2016, Wade 2017); “Threatened” for the Mexico DPS (estimated at 2,806 animals; Wade et al. 2016, Wade 2017); and “Not Listed” for the Hawaii DPS (estimated at 11,571 animals; Wade et al. 2016, Wade 2017).

The available information indicates that three of these DPSs, Hawaii, Mexico, and Central America, are primarily found along the western coast of North America during the summer-fall feeding season. During this season, these DPSs occur in somewhat distinct feeding aggregations, with Hawaii animals being found in southeastern Alaska and northern British Columbia; Mexico animals being found off northern Washington and southern British Columbia; and Central America animals being found off

¹ See: “Listing of Humpback Whale Under the ESA” <https://www.fisheries.noaa.gov/action/listing-humpback-whale-under-esa>

California and Oregon (Bettridge et al. 2015). However, some degree of mixing of DPSs occurs in the feeding areas, with Hawaii animals also being found throughout the Gulf of Alaska, the Aleutian Islands, and eastern Russia; and Mexico animals also being found off California and Oregon, as well as in the northern and western Gulf of Alaska and the Bering Sea (Bettridge et al. 2015). Finally, animals from the Western North Pacific DPS may also be present in small numbers in these areas (Bettridge et al. 2015). This mixing of DPSs in the feeding areas complicates unequivocal assignment of individuals to breeding stock for purposes of determining exposure to anthropogenic risks without further information. Consequently, there is a critical need for data on occurrence and habitat use by the different DPSs throughout their range.

Through the use of satellite tagging, genetic analyses, and photo-ID, this project sought to generate greater detail on the movements and migratory connectivity of North Pacific humpback whale DPSs, with emphasis on those using southeastern Alaskan waters during the feeding season and Hawaiian waters during the breeding season (i.e., the Hawaii DPS). With initial support from a Pacific Life Foundation grant, Oregon State University (OSU) conducted satellite tag deployments on humpback whales in southeastern Alaska in 2014 and 2015. Additional funding from the Makana Aloha Foundation in 2015, and from the US Department of the Navy (through Commander, Pacific Fleet, and Commander, Naval Sea Systems Command) in 2018, supported additional tag deployments in Hawaii. This Final Report covers the combined results from these four field efforts in southeastern Alaska and Hawaii. OSU has prepared separate reports for the Navy-funded efforts in Hawaii and off the US West Coast (Mate et al. 2018, 2019), and to the extent possible the material covered here is complementary rather than duplicative of the content presented in those reports.

1.1 Study Goals

The overall goal of the project was to conduct a comprehensive characterization of humpback whale movement behavior during breeding, migration, and feeding phases, based on tracking data from southeastern Alaska and Hawaii collected over the course of two field efforts at each site. The project's specific objectives were to:

- Identify habitat use during the late foraging season in southeastern Alaska, including spatial “hotspots” of aggregation;
- Determine the duration of whale residency in southeastern Alaskan waters prior to the start of the winter migration;
- Describe the migratory timing, departure points, and routes of whales leaving Alaska;
- Identify entry points to Hawaii and subsequent progression through the islands, including spatial “hotspots” of aggregation;
- Determine the duration of whale residency in Hawaiian waters to better quantify population turnover during the four-month-long breeding season; and
- Describe the migratory timing, departure areas, and routes of whales leaving Hawaii.

In order to obtain a sufficient number of complete migratory transits required to address these objectives, the study proposed to tag 20 animals at both ends of the migration (southeastern Alaska and Hawaii) during each of two field efforts at each site, for a total of 80 tagged animals. In addition, the

project incorporated photo-ID and genetic sex determination and haplotype sequencing from biopsy samples to further enhance the tracking results with population and life history information of known animals.

2 Methods

2.1 Field Efforts

Tagging operations were conducted from rigid-hulled inflatable boats in southeastern Alaska (6.4-m in 2014 and 6.1 m 2015) and from an 11-m aluminum-hulled, air/foam-collared vessel in Hawaii (2015 and 2018). The tagging crew consisted of a tagger, biopsy darter, photographer, data recorder, and boat driver. Candidate animals for tagging were selected based on visual observation of size and body condition. No whales were tagged that appeared too small, emaciated, or extensively covered by external parasites.

Satellite tags were deployed using the Air Rocket Transmitter System (Heide-Jørgesen et al. 2001), an air-powered applicator, following the methods described in Mate et al. (2007). Tags were deployed from distances of 1.5 to 4 m with 92- to 95-psi in the applicator's 70-cc pressure chamber. For the 2014 and 2015 field seasons, tags were placed 1-2 m forward of the dorsal fin, as the whales surfaced to breathe. An examination of tag attachment duration in relation to placement on the animal was conducted in 2016 using data from all fully implantable tags deployed by OSU on humpback whales at the time, which indicated that longest attachments were consistently achieved for tags placed close to the base of the dorsal fin (i.e., in the "dorsal hump") (OSU, unpublished data). Based on this information, beginning in 2016 we have only been placing tags in the dorsal hump area, including the tags deployed in 2018 in Hawaii.

Every effort was made to collect identification photographs of the flukes of the tagged whales, although this was not always possible, as some animals never exposed their flukes. Photographs of the dorsal fin were also collected to assist in photo-ID when fluke photographs were not available. Similarly, biopsy samples for genetic sex identification and genotype profiling were collected from tagged whales every time it was feasible.

2.2 Satellite Tags

The primary technology used for tracking the long-distance movements of large whales has been a fully implantable tag design in use since 1997 (Heide-Jørgensen et al. 2001, Zerbini et al. 2006, Mate et al. 2007). These tags can stay attached for long periods of time (typically several months), but the amount of data they can transmit through the Argos System has been limited by bandwidth, so their primary use has been for satellite-monitored radio tracking. For this reason, these devices are often referred to as "location-only" or LO tags (Mate et al. 2007).

For this study, several types of tags based on the original LO tag design were used, including Wildlife Computers SPOT5 (in 2014 and 2015) and SPOT6 (in 2015), and Telonics, Inc. ST-15 (in 2014), RDW-640 (in 2015), RDW-665 and RDW-665R (in 2018). The tags in the Telonics RDW series represent the next

generation of the technology, as they contain additional sensors (pressure and 3-D accelerometers) and are capable of transmitting dive summary information, although in this report we only focus on the location data, as the dive behavior results collected by these tags have been reported elsewhere (Mate et al. 2018, 2019). In all cases, the tag design consisted of a main body, a penetrating tip, and an anchoring system. The main body was made up of a stainless steel cylinder (1.9 cm in diameter × 20.7 cm in length for Telonics tags and 2.0 cm in diameter × 20.7 cm in length for Wildlife Computers tags) that housed a certified Argos transmitter and a 6-V lithium battery pack. A flexible whip antenna (15.8-cm long for Telonics tags and 15.0-cm long for Wildlife Computers tags) and a saltwater conductivity switch (SWS, 2.2-cm long for Telonics tags and 3.5-cm long for Wildlife Computers tags), both constructed of single-strand nitinol (1.27 mm in diameter), were mounted on the distal endcap of this cylinder, while a penetrating tip was screwed onto the other end. The endcap on the Telonics tags was made of polycarbonate and had two perpendicular stops (1.5 cm long × 0.9 cm wide × 0.6 cm thick) extending laterally to prevent tags from embedding too deeply on deployment or from migrating inward after deployment. The endcap on the Wildlife Computers tags was made of stainless steel and also had perpendicular stops (1.4 cm long × 0.6 cm wide × 0.83 cm thick). The penetrating tip was made of a Delrin[®] nose cone, into which a ferrule shaft was pressed with four double-edged blades. The anchoring system consisted of two rows of outwardly curved metal strips (each strip was 3.2 cm long × 0.6 cm wide) mounted on the main body at the nose cone (proximal) end. Maximum tag weight was 300 g for all tag types.

Tag cylinders were partially coated with a long-dispersant polymer matrix (Resomer[®] or Eudragit[®]) in which a broad-spectrum antibiotic (gentamicin sulfate) was mixed, to allow for a continual release of antibiotic into the tag site for an extended period of time to reduce the chances of infection (Mate et al. 2007). The tags were designed to be almost completely implantable (except for the perpendicular stops, antenna, and SWS), and were ultimately shed from the whales, probably due to hydrodynamic drag and/or the natural migration of foreign objects out of the tissue (Mate et al. 2007).

To prolong battery life, the Wildlife Computers SPOT5/SPOT6 tags and the Telonics ST-15 and RDW-640 tags were programmed to transmit only when out of the water during four 1-h periods per day, coinciding with times when satellites were most likely to be overhead. With such a duty cycle, the life expectancy of these tags' battery was over one year. To accommodate the higher number of transmissions required to send dive summary data to the satellites, the Telonics RDW-665/RDW-665R tags were programmed to transmit during six 1-h periods every day. The life expectancy of these tags was shorter (approximately 90 to 120 d) due to the higher battery consumption by the extra sensors and the more frequent transmission schedule. However, the operational duration of these tags was almost always limited by issues related to retention on the whale rather than by battery life. To date, the mean duration of the fully implantable tags deployed by OSU on humpback whales has been 33 d (median = 23.9 d, sd = 35.4 d, n = 245), with a maximum duration of 220 d (OSU, unpublished data).

2.3 Tracking Analyses

2.3.1 Argos Track Editing

Tag transmissions were processed by Service Argos using the Kalman filter to calculate locations (Collecte Localisation Satellites 2015). Service Argos assigned a quality to each location, depending, among other things, on the number and temporal distribution of transmissions received per satellite pass (Collecte Localisation Satellites 2015). The quality assigned to each Argos location was reported as one of seven possible location classes (LCs; from low to high: Z, B, A, 0, 1, 2, and 3), with accuracies ranging from less than 200 m (LC 3) to greater than 5 km (LC B). Locations of quality LC Z are generally considered invalid because of the unbounded errors associated with them (Collecte Localisation Satellites 2015, Vincent et al. 2002).

In order to generate a complete track from the Argos location data, OSU implemented a sequential data editing protocol on the received (“raw”) locations from each tag to retain the best locations for analysis. First, locations occurring on land were excluded. Then, LC-Z locations were removed and the remaining locations were further filtered by LC, as follows. Lower-quality LCs (0, A, or B) were not used if they were received within 20 min of higher-quality locations (LC 1, 2, or 3). Finally, speeds between remaining locations were computed, and if a speed between two locations exceeded 14 km/h, one of the two locations was removed, with the location resulting in a shorter overall track length being retained. These edited Argos tracks were used for analyses involving calculation of residence time and kernel density estimation (see **sections 2.4 and 2.5** below).

2.3.2 Track Regularization and Behavioral Annotation with State-Space Models

Several of the analyses covered by this report, including kernel home range and calculation of travel speeds during the different phases (feeding, breeding, migrating), further required that track locations be spaced at regular intervals and have a behavioral mode annotation. For these purposes, the raw Argos locations (i.e., prior to applying the sequential data editing protocol described in **section 2.3.1**) were used largely unedited (except for the removal of LC-Z locations) as input into a Bayesian switching state-space model (SSSM; Jonsen et al. 2005) in the software packages R v. 2.12.1 and WinBUGS v. 1.4.3. For each raw Argos track, the model provided a regularized track with one estimated location per day, after accounting for Argos satellite location errors (based on Vincent et al. 2002) and the movement dynamics of the animals (Jonsen et al. 2005). The SSSM model ran two Markov chain Monte Carlo (MCMC) simulations each for 30,000 iterations, with the first 10,000 iterations being discarded as a burn-in, and the remaining iterations being thinned, removing every fifth observation to reduce autocorrelation (Jonsen et al. 2005).

Included in the model was the classification of locations into two behavioral modes based on mean turning angles and autocorrelation in speed and direction: “transiting” (mode 1) and “area-restricted searching” (ARS; mode 2). Although only two behavioral modes were modeled, the means of the MCMC samples provided a continuous value from 1 to 2 for each location (Jonsen et al. 2005). As has been the practice in other studies (Jonsen et al. 2005, Bailey et al. 2009, Irvine et al. 2014), we chose values greater than 1.75 to represent ARS mode and values lower than 1.25 to represent transiting mode, while values in between were considered “uncertain”.

Taking advantage of the higher number of locations received per day for the Telonics RDW-665/RDW-665R tags, we generated regularized tracks with three estimated locations per day (rather than one) for the tracking data collected in 2018. Also, for these data we applied the recent hierarchical implementation of the SSSM (hSSSM; Jonsen 2016), which is structurally similar to the SSSM but the estimates for parameters driving the different behavioral modes are generated from all tracks simultaneously rather than separately for each track, allowing for greater precision when estimating behavioral modes and for scaling individual movements up to the population level (Jonsen 2016). The hSSSM was implemented in the software package R v. 3.4.4 using the *bsam* library (Jonsen 2016). The *rjags* library was used to interface with the software package JAGS v. 4.3, which ran two MCMC chains with the Gibbs sampler, each for 60,000 iterations, with the first 40,000 iterations being discarded as a burn-in and the remaining iterations being thinned by removing every 20th observation (Jonsen 2016).

2.4 Residence Time in the Feeding and Breeding Areas

We objectively defined the feeding and breeding areas as the zone extending 50 km seaward from the coastline around each of the two tagging areas, southeastern Alaska during the feeding season and Hawaii during the breeding season. The determination of 50 km for this buffer zone was based on the distance at which the SSSM/hSSSM applied to the tracks (see **section 2.3.2**) estimated that all locations had switched from ARS mode, indicative of residence, to transiting mode, indicative of migration (**Figure 1**).

To compute residence time in southeastern Alaska and Hawaii, we first determined the date a tracked whale crossed the 50-km buffer boundary as it departed on migration. For this purpose, we interpolated the edited Argos tracks at 10-min intervals to obtain evenly and finely spaced track segments from which more precise estimates of departure time could be generated. Finally, for each track that crossed the buffer boundary, residence time was calculated as the time interval from tagging to departure, expressed as number of days.

For animals that migrated between the southeastern Alaska and Hawaii tagging areas, residence time at the migratory destination was calculated as the time interval from arrival (i.e., when a track crossed the buffer boundary at the migratory destination) to the date the last transmission from the tag was received, expressed as number of days. For these animals, the difference between departure and arrival dates represented the time they spent on migration. For animals that migrated to other destinations, migration duration and distance were estimated based the date on which a persistent (i.e., several days) switch in behavioral mode from transiting to ARS in the SSSM/hSSSM tracks occurred as the animals approached the destination, or on the last location received in close proximity to a known destination if no behavioral switch was detected in the SSSM/hSSSM tracks.

2.5 Kernel Home Range Analysis within the Feeding and Breeding Areas

To identify spatial hotspots of whale aggregation in southeastern Alaska, we created feeding-area kernel home ranges for the portions of SSSM tracks (see **section 2.3.2**) that contained at least 30 d of regularly estimated locations (Seaman et al. 1999) within the 50-km buffer zone, using the least-squares cross-validation bandwidth selection method (Worton 1995, Powell 2000), as implemented in the R package v. 3.5.3 by the *adehabitatHR* library v. 0.4.16 (Calenge 2006, 2017). The 90 percent isopleth (i.e., the home

range) was produced for each state-space modeled track and isopleth portions that overlapped land were removed using ESRI® ArcMap v. 10.3. Spatial hotspots were identified based on the amount of overlap between the individual home ranges.

A full home range analysis (i.e., estimation of isopleths) was not conducted for the Hawaii breeding area because none of the tracking periods within the 50-km buffer zone around the main Hawaiian Islands exceeded the 30-d minimum requirement for this method (Seaman et al. 1999). Instead, spatial hotspots of whale aggregation were characterized more simply by kernel density estimation (Worton 1989) from the edited Argos tracks (see **section 2.3.1**) that lasted at least 10 d before either transmissions stopped or whales migrated away from the islands (i.e., out of the 50-km buffer zone). Kernel densities of the pooled Argos locations within the buffer zone were computed using the Kernel Density toolbox function in ESRI® ArcMap v. 10.3, with a user-specified cell size of 0.1×0.1 degrees.

2.6 Genetics

2.6.1 DNA Extraction and mtDNA Sequencing

Total genomic deoxyribonucleic acid (DNA) was extracted from skin tissue following standard proteinase K digestion and phenol/chloroform methods (Sambrook et al. 1989) as modified for small samples by Baker et al. (1994). An approximate 800 base-pair (bp) fragment of the mitochondrial deoxyribonucleic acid (mtDNA) control region was amplified with the forward primer M13Dlp1.5 and reverse primer Dlp8G (Dalebout et al. 2004) under standard conditions (Baker et al. 2013). Control region sequences were edited and trimmed to a 500-bp consensus region in Sequencher v. 4.6. Unique haplotypes were then aligned with previously published haplotypes downloaded from GenBank® (Baker et al. 2013).

2.6.2 Microsatellite Genotypes

Up to 15 microsatellite loci were also amplified for each sample using previously published conditions (Baker et al. 2013). These included the following loci: EV1, EV14, EV21, EV37, EV94, EV96, EV104 (Valsecchi and Amos 1996); GATA28, GATA417 (Palsbøll et al. 1997); rw31, rw4-10, rw48 (Waldick et al. 1999); and GT211, GT23, GT575 (Bérubé et al. 2000). Microsatellite loci were amplified individually in 10-microliter reactions and co-loaded in four sets for automated sizing on an ABI 3730xl (Applied Biosystems™) DNA analyzer. Microsatellite alleles were sized and binned using Genemapper v. 4.0 (Applied Biosystems™) and all peaks were visually inspected.

2.6.3 Sex Determination

Sex was identified by multiplex polymerase chain reaction (PCR) using primers P1-5EZ and P2-3EZ to amplify a 443–445-bp region on the X chromosome (Aasen and Medrano 1990) and primers Y53-3C and Y53-3D to amplify a 224-bp region on the Y chromosome (Gilson et al. 1998).

2.6.4 Individual Identification

Individual whales were identified from the multi-locus genotypes using CERVUS v. 3.0.3 (Marshall et al. 1998). An initial mismatch of up to three loci were allowed as a precaution against false exclusion due to allelic dropout and other genotyping errors (Waits and Leberg 2000, Waits et al. 2001).

Electropherograms from mismatching loci were reviewed and corrected or repeated. A final “DNA profile” for each sample included up to 15 microsatellite genotypes, sex, and mtDNA control region

sequence or haplotype. The expected probability of identity (P_{ID}) for a given number of loci was calculated with GenAlex (Peakall and Smouse 2006). The P_{ID} reflects the probability of a pair of individuals sharing a multi-locus genotype by chance, given the frequency of alleles at each microsatellite locus. This probability is typically very low for the loci chosen in this study, providing confidence in the identification of individuals (Baker et al. 2013).

2.6.5 Species and Stock Identification

Species identity from field observations was confirmed by submitting mtDNA sequences to the web-based program DNA-surveillance (Ross et al. 2003) and by Basic Local Alignment Search Tool (BLAST) search of GenBank®.

For analysis of population differentiation and for matching of individual genotypes, there is a large “DNA register” (i.e., a searchable electronic database of DNA profiles; DeSalle and Amato 2004) available from the ocean-wide survey referred to as the Structure of Populations, Levels of Abundance and Status of Humpbacks program, or SPLASH. This register includes mtDNA haplotypes, sex, and microsatellite genotypes at 10 loci, sufficient for individual identification of 1,805 individuals sampled in all known breeding and feeding areas in the North Pacific Ocean (Baker et al. 2013). Consequently, the mtDNA of tagged humpback whales can be used for comparisons to haplotype frequencies from any selected regions of the North Pacific and microsatellite genotypes can be used to search for recaptures of individuals represented in the DNA register. Tests of differentiation in mtDNA haplotype frequencies among the tagging data sets and between the tagging data sets and the 18 regional strata defined during SPLASH for the North Pacific (Baker et al. 2013) were conducted with the program Arlequin (Excoffier and Lischer 2010).

2.7 Photo-Identification

Photographs of the whales’ tail flukes and dorsal fins were taken during field efforts for ID purposes (Katona et al. 1979), as well as to identify previously tagged whales to document wound healing in subsequent encounters. Besides tagged whales, photographs were taken of all other whales seen while tagging for ID purposes and to examine for tag wounds or scars. Once back at the lab, each individual whale that had a recognizable fluke was compared to our existing OSU photo catalog to determine if it had previously been identified. If not in the catalog, it was given a unique ID number and the best fluke photo was added.

Once this process was completed, we uploaded our photo-IDs of tagged and untagged animals to the online resource “Happywhale” (<http://happywhale.com>), a global database of photo-IDs contributed by the public and other researchers that provides automated matching using state-of-the-art algorithms and machine learning, to determine if our tagged whales have been seen previously or after tagging. In this report, photo-ID matches to Happywhale are presented as of 31 March 2019. We also note that photo-IDs of untagged whales from the southeastern Alaska tagging efforts (2014 and 2015) have not yet been submitted to Happywhale, so we expect to increase the number of individuals matched to our catalog in the future. Finally, we also shared our photo-IDs with other researchers (J. Straley, University of Alaska Southeast Sitka, and C. Gabriele, Glacier Bay National Park) for comparison with their catalogs, which will result in additional matches and resighting histories in the future.

3 Results

Throughout this report we refer to individual whales by their tag number for convenience. For example, a whale instrumented with tag No. 1386 will be hereafter referred to as “tag 1386”. Additionally, since the tag numbers assigned by the Argos system can be recycled in subsequent deployments, we mention the year associated with each tag deployment explicitly to avoid confusion.

3.1 Satellite Tracking

3.1.1 Southeastern Alaska

Thirty-seven tags (1 ST-15, 20 SPOT5, 9 SPOT6, and 7 RDW-640) were deployed on humpback whales in Seymour Canal and Frederick Sound, southeastern Alaska in 2014 and 2015 (**Table 1**, **Figure 2**). In addition, tag 23035 from 2015 bounced off the whale during deployment and was lost, although both a biopsy sample and a fluke ID were collected from this animal (**Table 1**). Argos satellite locations were received from all deployed tags. Tracking periods ranged from 3.3 to 78.3 d (mean = 28.2 d, sd = 16.2 d, n = 37), with distances traveled ranging from 73 to 6,503 km (mean = 2,010 km, sd = 1,649 km, n = 37; **Table 1**). The number of filtered Argos satellite locations received per tag ranged from 18 to 437 (mean = 124, sd = 76, n = 37; **Table 1**). Locations for humpback whales tagged in southeastern Alaska ranged over 40 degrees of latitude, from Lynn Canal and Icy Strait (59°N) in southeastern Alaska to the southern tip of Hawaii Island (19°N) in the Hawaiian Archipelago, as shown in **Figure 2**.

3.1.1.1 Feeding Area Movements, Home Range, and Residency

While in southeastern Alaska’s inland waters, the majority of tracked locations were in Seymour Canal and Frederick Sound, with most whales then moving southward through Chatham Strait as they exited into the Pacific Ocean (**Figure 2**). Once in the Pacific Ocean, several animals continued moving southeastward along the coast toward Haida Gwaii (including one animal that made brief use of the Dixon Entrance), but most animals moved on a southwestward heading toward Hawaii (**Figure 2**). Two whales from 2015 made more extensive use of southeastern Alaska’s inland waters, with one animal (tag 23030, a female) moving from Seymour Canal northward through Stephens Passage toward Lynn Canal before its tag quit near Juneau after 21 d and 771 km (**Table 1**). The other animal (tag 827, a female) initially moved into the eastern portion of Frederick Sound near Petersburg and then undertook a clockwise circuit from Frederick Sound westward into Chatham Strait, then northward into Icy Strait and Lynn Canal, and then southward through Stephens Passage back to the eastern portion of Frederick Sound, where the tag quit after 37 d and 1,537 km (**Table 1**).

Two of the 20 whales tagged in southeastern Alaska in 2014 were re-tagged in 2015. This was discovered through genotype matching while analyzing the biopsy samples from both animals (see **section 3.2**), and confirmed by photo-ID matching for one of the animals (see **section 3.3.3**). The animal tagged in 2014 with tag 5883 (biopsy sample Mno14AK010, a female) was re-tagged in 2015 (tag 23041, biopsy sample Mno15AK003), and the animal tagged in 2014 with tag 23039 (biopsy sample Mno14AK006, a male) was re-tagged in 2015 (tag 5655, biopsy sample Mno15AK001; **Table 1**). Both animals were tagged in Seymour Canal in both years, with a difference of 9 d in tag deployment date between the two years. Tags 5883/23041 followed a similar route and timing within southeastern Alaska inland waters between the two years, as the animal moved into Frederick Sound with a difference of

about 4 d between years (**Figure 3**). However, in 2014 the tag stopped working after 6.2 d while the animal was still in Frederick Sound, while in 2015 the animal was tracked for 29 d as it moved southward past Haida Gwaii and into the North Pacific Basin on an apparent route toward Hawaii (**Figure 3**). In contrast, the movements of tags 23039/5655 within southeastern Alaska were similar but the timing was very different between the two years (**Figure 4**). In 2014 this animal spent a substantial period of time in Seymour Canal before moving into Stephens Passage, while in 2015 the animal moved briefly into Stephens Passage soon after tagging and then initiated the migration toward Hawaii (**Figure 4**). Thus, despite a similar tracking period in the two years (21.9 d in 2014 versus 19.1 d in 2015), this animal only covered 487 km in 2014 while it covered 2,034 km in 2015 (**Table 1**).

Five whales tagged in the fall of 2014 and 2015 were tracked for at least 30 d within the 50-km southeastern Alaska buffer zone. Kernel density home ranges for these animals showed highest use of Seymour Canal, on the east side of Admiralty Island, and in the southern part of Stephens Passage. Areas of high use also occurred in Frederick Sound (**Figure 5**).

Residence time in southeastern Alaska, computed as the time period from tag deployment to when a whale crossed the 50-km buffer boundary as it departed on migration, was available for 20 whales and ranged from 4.4 to 49.1 d (mean = 17.3 d, sd = 11.5 d; **Table 2**). Seven of these whales were female, six were male, and seven were of unknown sex (**Table 2**).

While inside the southeastern Alaska buffer zone, tagged whales moved at a mean speed of 1.01 km/h (median = 0.47 km/h, sd = 1.28 km/h, n = 668 SSSM locations; **Table 3, Figure 6a**). ARS behavior was largely restricted to southeastern Alaska waters for most tagged whales (**Figure 1**), with a mean speed of 0.90 km/h (median = 0.57 km/h, sd = 0.96 km/h, n = 141 SSSM locations; **Table 3, Figure 6b**).

3.1.1.2 Migration

Twenty of the tagged whales began their winter migration (i.e., crossed the 50-km buffer zone around southeastern Alaska), with start dates ranging from 19 November to 6 January (**Table 2**). Two of these whales were tracked to Hawaii and one to Mexico (**Figure 2**). Of the two whales that arrived in Hawaii, tag 845 from 2014 (sex unknown) was tracked for a total of 6,503 km and 78 d. This animal departed southeastern Alaska on 2 December 2014 and crossed the Hawaiian 50-km buffer zone on 8 January 2015, having spent 37 d and 4,744 km on migration (**Tables 1 and 2**). Tag 10833 from 2015 (a male) was tracked for a total of 5,431 km and 71 d. It departed southeastern Alaska on 28 November 2015 and arrived in Hawaii on 13 January 2016, after spending 46 d and 4,303 km on migration (**Tables 1 and 2**). Sixteen more whales were headed in the direction of Hawaii when their tags quit. Several of these animals were projected to arrive along the northern coasts of the main Hawaiian Islands (**Figure 2, Table 2**).

Tag 10834 from 2015 (a female) migrated south along the western coast of North America to the tip of the Baja California Peninsula, Mexico, and then it moved eastward while crossing the entrance to the Gulf of California when its tag ceased working (**Figure 2**). This animal was tracked for a total distance of 5,084 km. It departed southeastern Alaska on 30 November 2015 and its last location was received on 29 December 2015. We projected an imminent arrival of this animal on the coast of Nayarit State,

mainland Mexico, a well-known breeding area, and estimated a migration duration and distance of about 28 d and 4,213 km, respectively (**Tables 1 and 2**). In 2014 another whale (tag 4173 from 2014, a female; **Table 2**) traveled along a similar route (presumably to Mexico as well) before its tag stopped transmitting off Point Arena, California. A third animal (tag 23041 from 2015, a female) that was tracked for a shorter distance also moved initially along this route, but then it appeared to veer toward Hawaii before its tag stopped transmitting offshore of Oregon (**Figure 2, Tables 1 and 2**).

While on migration (i.e., outside the southeastern Alaska and Hawaii buffer zones), whales tagged in southeastern Alaska moved at a mean speed of 5.51 km/h (median = 5.63 km/h, sd = 1.98 km/h, n = 361 SSSM locations; **Table 3, Figure 6a**). Although transiting behavior was recorded both inside and outside the buffer zones, it was the predominant behavioral mode while on migration, and had a mean speed value of 4.57 km/h (median = 4.76 km/h, sd = 2.42 km/h, n = 470 SSSM locations; **Table 3, Figure 6b**). Travel speeds during the migration phase for the three SSSM tracks that lasted until arrival at the migratory destination were not sustained but showed oscillations over time, with periods of increased and decreased speed lasting several days (**Figure 7**).

3.1.1.3 *Breeding Area Arrival, Movements, and Residency*

As described in the previous section, two of the whales tagged in southeastern Alaska arrived in the Hawaii breeding area (i.e., crossed the 50-km buffer zone around Hawaii) during this study. Tag 845 from 2014 entered the Hawaiian Archipelago from the southeast on 8 January 2015, rounding the southern tip of Hawaii Island and then transiting northward along its western coast before moving to Maui Nui (the waters between the islands of Maui, Lanai, Molokai and Kahoolawe) and Penguin Bank west of Molokai, where it remained until the tag stopped transmitting 27 d later (**Figure 2, Table 2**). Tag 10833 from 2015 entered Hawaii waters on 13 January 2016 on the northeastern coast of Hawaii Island, and over the following 9 d it rounded the northern tip of the island and then started to move southward along the western coast before the tag quit (**Figure 2, Table 2**).

Once inside the Hawaii buffer zone, these two tagged whales moved at a mean speed of 1.49 km/h (median = 1.01 km/h, sd = 1.36 km/h, n = 37 SSSM locations; **Table 3, Figure 6a**). No movements or residency information were available for the third tagged whale with a projected arrival in the mainland Mexico breeding area (tag 10834 from 2015), as the tag ceased working just before arrival.

3.1.2 **Hawaii**

Forty-five tags (20 SPOT5, 20 RDW-665, 5 RDW-665R) were deployed on humpback whales off Maui, Hawaii, in 2015 and 2018 (**Table 1, Figure 8**). Argos satellite locations were received from all but one of the tags (tag 5701 from 2018). One other tag (tag 832 from 2018) provided two locations, but none passed the location filtering criteria, so this tag was also not included in the summary statistics in **Table 1**. Tracking periods ranged from 0.1 to 147.2 d (mean = 20.8 d, sd = 29.0 d, n = 43; **Table 1**), with distances ranging from 13 to 11,302 km (mean = 1,217 km, sd = 2,348 km, n = 43; **Table 1**). The number of filtered Argos satellite locations received per tag ranged from 1 to 913 (mean = 87, sd = 173, n = 43; **Table 1**). Locations for humpback whales tagged off Hawaii ranged over 43 degrees of latitude, from the south coast of Maui (21°N) to the Bering Sea (64°N), as shown in **Figure 8**.

3.1.2.1 *Breeding Area Movements, Distribution, and Residency*

While in Hawaiian waters, the majority of locations were in the Maui Nui region in both 2015 and 2018. Penguin Bank was another area heavily frequented by the tagged whales, with nine of the humpbacks spending time there in each year (**Figures 1 and 8**). Most tagged whales moved in a predominant northwesterly direction after tagging, with animals leaving Maui heading to Lanai, Molokai, and/or Penguin Bank (inset map in **Figure 8**). Eight whales were also tracked to Oahu, and one whale was further tracked to both Kauai and Niihau (tag 5800 from 2018, a male; **Figure 8**). Only one of the whales tagged off Maui during this study was tracked southeast to Hawaii Island (tag 23034 from 2015, a male; **Figure 8**).

Twenty-one humpback whales were tracked for at least 10 d within the 50-km Hawaiian Island buffer zone during this study. Kernel density utilization distributions computed from the pooled Argos locations of these whales showed highest use at the southwest corner of Penguin Bank (**Figure 9**). The next highest density of locations was found within the Maui Nui region (**Figure 9**). The northern coasts of Maui, Molokai, Oahu, Kauai, and Niihau were also used at much lower densities (**Figure 9**).

Residence time in Hawaii, computed as the time period from tag deployment to when a whale crossed the 50-km buffer boundary as it departed on migration, was available for nine whales, ranging from 3.3 to 23.2 d (mean = 14.8 d, sd = 8.4 d; **Table 2**). Five of these were male (tag 830 from 2015 and tags 4172, 5641, 5736, and 5800 from 2018), one was a female (tag 5784 from 2018), and three whales were of unknown sex (tag 5746 from 2015, and tags 843 and 10833 from 2018; **Table 2**).

While inside the Hawaii buffer zone, tagged whales moved at a mean speed of 1.36 km/h (median = 1.00 km/h, sd = 1.21 km/h, n = 870 SSSM/hSSSM locations; **Table 3, Figure 6c**). While engaged in ARS behavior, travel speed for these whales had a mean of 1.31 km/h (median = 1.00 km/h, sd = 1.22 km/h, n = 713 SSSM/hSSSM locations; **Table 3, Figure 6d**).

3.1.2.2 *Migration*

Nine humpback whales began their northbound migration during this study (i.e., crossed the 50-km buffer zone around Hawaii), with departure dates spanning the period 29 January to 11 April. Four of these whales (all tagged in 2018) reached a high-latitude feeding area during their tracking periods (**Figure 8**). As described in **section 3.1.2.1**, there was a tendency for most tagged whales to travel north and northwest through the Hawaiian Island chain after being tagged off Maui, with migratory departures beginning off the northern coast of Oahu (five animals), the northern coast of Molokai (two animals), the northern coast of Maui (one animal), and the northern coast of Niihau (one animal), as shown in the inset map in **Figure 8**.

Of the five humpback whales departing from Oahu, two animals (tags 10833 and 843 from 2018, both of unknown sex) traveled northwest on a trajectory toward the central Aleutian Islands (**Table 2, Figure 8**). These tags stopped transmitting approximately 2,200 and 2,400 km northwest of Oahu, 25 and 40 d after departure, respectively. Tag 5736 from 2018 (a male) maintained a more northerly trajectory initially, before heading slightly northwest, arriving to the feeding area approximately 200 km south of Unimak Pass, eastern Aleutian Islands, on 28 April (28 d and 3,775 km after departure; **Figure 8**). Tag

5746 from 2015 (sex unknown) departed on a very similar northerly route to tag 5736 from 2018, but this tag stopped transmitting after only 9 d from departure (**Table 2, Figure 8**). Finally, tag 5641 from 2018 (a male) was tracked on a northeasterly trajectory toward northern British Columbia for approximately 630 km before the tag stopped transmitting 4 d after departure (**Table 2, Figure 8**).

The tracks of four other migrating whales followed a northeasterly trajectory toward northern British Columbia (**Table 2, Figure 8**). Tag 830 from 2015 (a male) departed from Molokai and was tracked for 7 d before the tag stopped transmitting (**Table 2, Figure 8**). Three tagged whales reached a feeding area off the Haida Gwaii Archipelago: tag 4172 from 2018, a male departing from Molokai, arrived on 16 April (after migrating for 30 d and 4,339 km); tag 5800 from 2018, a male departing from Niihau, arrived on 8 May (after migrating for 35 d and 5,030 km); and tag 5784 from 2018, a male departing from Maui, arrived on 9 May (after migrating for 45 d and 4,662 km). Both tags 4172 and 5800 from 2018 traveled to the southwest side of Moresby Island (the southernmost of the two main islands in the Haida Gwaii Archipelago), reaching points within 5 km of one another at the end of their migration, albeit more than three weeks apart (**Table 2, Figure 8**).

While on migration (i.e., outside the Hawaii and southeastern Alaska buffer zones), whales tagged in Hawaii moved at a mean speed of 4.44 km/h (median = 4.32 km/h, sd = 2.18 km/h, n = 573 SSSM/hSSSM locations; **Table 3, Figure 6c**). Although transiting behavior was recorded both inside and outside the buffer zones, it was the predominant behavioral mode while on migration, and had a mean speed value of 4.44 km/h (median = 4.32 km/h, sd = 2.18 km/h, n = 573 SSSM/hSSSM locations; **Table 3, Figure 6d**). Travel speeds during the migration phase for the four hSSSM tracks that lasted until arrival at the migratory destination in 2018 were not sustained but showed oscillations over time, with periods of increased and decreased speed lasting several days (**Figure 7**).

3.1.2.3 Feeding Area Arrival, Movements, and Residency

The 50-km buffer zones around southeastern Alaska and Hawaii (**Figure 1**) were created for estimating residence time around the two tagging areas. The two feeding areas reached by the four whales tagged in Hawaii in 2018, south of the eastern Aleutian Islands and off northern British Columbia, were partially or entirely outside the southeastern Alaska buffer zone. For the three whales that reached northern British Columbia we report residence times since the southeastern Alaska buffer zone extended to this area, although we note that residence time for tag 4172 is underestimated, as a portion of this track occurred outside the buffer (inset map in **Figure 8**). For the whale that arrived in the eastern Aleutian Islands we describe its feeding-area movements and residency more generally, since this track occurred outside a buffer zone (**Figure 5**).

The three whales that arrived in northern British Columbia in 2018 spent 8.7 to 53.6 d in the 50-km buffer zone around southeastern Alaska (mean = 25.5 d; **Table 2**). Tag 4172 (a male) spent two weeks traveling along the western and northern coast of Haida Gwaii before heading south (along the west coast) to Queen Charlotte Sound, where it remained for 5 d until its tag stopped transmitting on 6 May (**Figure 8**). Tag 5800, also a male, spent 8 d traveling up the west coast of Haida Gwaii to Prince of Wales Island in southeastern Alaska before its tag stopped transmitting on 17 May (**Figure 8**). Tag 5784 (a female) migrated to the northwest coast of Moresby Island, and spent the remainder of its tracking

period (ending on 1 July) off the west and northern coast of Graham Island (the northernmost of the two main islands in the Haida Gwaii Archipelago; **Figure 8**). While inside the southeastern Alaska buffer zone, these three tagged whales moved at a mean speed of 2.00 km/h (median = 1.53 km/h, sd = 1.53 km/h, n = 232 hSSSM locations; **Table 3, Figure 6c**).

The whale that arrived in the eastern Aleutian Islands south of Unimak Pass (tag 5736 from 2018, a male) stayed in this area for 23 d, after which it headed west along the southern edge of the Aleutian Island chain, following the Aleutian Trench, for 21 d (**Figure 8**). This whale traveled as far west as 161.6°E, coming within 171 km of the southeast coast of Kamchatka Peninsula, and then headed northeast, ultimately into the Gulf of Anadyr in the northwestern Bering Sea, where it remained until its tag stopped transmitting on 25 August (**Figure 8**). During its time in the Bering Sea, tag 5736 spent an extended period (31 d) in Bowers Basin at the western edge of Bowers Ridge, approximately 175 km northeast of Attu Island. This was followed by a 10-d period spent in the middle of the Aleutian Basin and a 12-d period just slightly further north, still in the Aleutian Basin (**Figure 8**). At a total of 147 d and 11,302 km after tagging, these were the longest tracked movements of a humpback whale to date.

3.2 Genetics

Biopsy samples were collected from 12 whales tagged in southeastern Alaska in 2014, 15 in southeastern Alaska in 2015, 16 in Hawaii in 2015, and 23 in Hawaii in 2018 (**Table 1**). The 66 samples were represented by a unique multi-locus genotype of at least 13 loci with an average of 14.62 loci across the data set. Based on a minimum of 13 microsatellite loci, the probability of identity for the southeastern Alaska samples ranged from $P_{ID} = 1.7 \times 10^{-10}$ to $P_{ID} = 8.1 \times 10^{-13}$ and from $P_{ID} = 3.5 \times 10^{-11}$ to $P_{ID} = 1.3 \times 10^{-13}$ for the Hawaiian samples, confirming that the probability of a match by chance was very low. Genotype matching of the 66 samples revealed two recaptures between the 2014 and 2015 southeastern Alaska tagging data sets. One individual was initially sampled in southeastern Alaska on 19 November 2014 and then again almost a year later on 11 November 2015 (tags 23039/5655). The other individual was sampled in southeastern Alaska on 20 November 2014 and then again on 11 November 2015 (tags 5883/23041). No genotype recaptures were found among the whales tagged in Hawaii or between the whales tagged in Hawaii and southeastern Alaska. Accounting for the two matches resulted in a total of 64 unique individuals tagged in either southeastern Alaska or Hawaii. The 25 individuals tagged in southeastern Alaska represented 14 females and 11 males (**Table 1**). The 39 individuals tagged in Hawaii represented four females and 35 males (**Table 1**).

The DNA profiles of the 64 tagged individuals were compared to a reference database of 1,805 individuals sampled previously in the North Pacific by the program SPLASH as reported in Baker et al. (2013). This comparison revealed nine matches (i.e., genotype recaptures), including two reported previously elsewhere (Mate et al. 2019). Of these nine matches, five were within-region and four were between breeding and feeding areas (**Table 4**).

Comparisons to other regional DNA registers provided one additional match between a whale tagged in southeastern Alaska in 2015 (biopsy sample Mno15AK006, tag 848, a female; **Table 1**) and a sample collected in southeastern Alaska in 2009 [biopsy sample Mno09SEAK036 (SEAK ID 2271); courtesy of J.

Straley, University of Alaska Southeast Sitka]. Tag 848 spent its entire tracking period (28.3 d and 654 km; **Table 1**) inside Seymour Canal, where it was tagged.

3.2.1 mtDNA and Population Differentiation

The mtDNA sequences of the 64 tagged individuals resolved seven haplotypes for the consensus region of 500 bp (**Table 5**). Based on submission to DNA-surveillance and a BLAST search of GenBank®, all of the mtDNA haplotypes were consistent with field identification of humpback whales. All haplotypes have been previously described for North Pacific humpback whales (Baker et al. 2013) and so are in the public domain and archived in GenBank. Only two haplotypes were resolved from the 25 animals that were biopsy sampled in southeastern Alaska (A+ = 36 percent and A- = 64 percent; **Table 5, Figure 10**), while seven haplotypes were resolved from the 39 animals that were biopsy sampled in Hawaii (A+ = 20.5 percent, A- = 41 percent, A3 = 2.6 percent, E1 = 5.1 percent, E2 = 10.3 percent, E5 = 5.1 percent, and F2 = 15.4 percent; **Table 5, Figure 10**).

The mtDNA haplotype frequencies of the southeastern Alaska samples from 2014 and 2015 ($n = 25$) did not differ significantly ($F_{ST} = 0.0000$, p -value = 0.9999) and these two data sets were pooled for further comparisons (**Table 6, Figure 10**). The mtDNA haplotype frequencies of the Hawaii samples from 2015 and 2018 ($n = 39$) did not differ significantly ($F_{ST} = 0.0000$, p -value = 0.8525) and these two datasets were also pooled for further comparisons (**Table 6, Figure 10**). Comparison of mtDNA haplotype frequencies between the southeastern Alaska and Hawaii samples revealed a weak but significant difference ($F_{ST} = 0.0531$, p -value = 0.0471).

The mtDNA haplotype frequencies of the pooled southeastern Alaska tagging samples differed significantly in pairwise comparisons with each of the 18 SPLASH strata described in Baker et al (2013) except southeastern Alaska and northern British Columbia (**Table 6**). The haplotype frequencies of the Hawaii tagging samples differed significantly from each of the eight SPLASH breeding areas, with the exception of Hawaii, and from six of the 10 feeding areas described in Baker et al. (2013) (**Table 6**). The haplotype frequencies of the Hawaii tagging samples were not significantly different from the western Aleutians (likely due to a small sample size for the latter), eastern Aleutians, northern Gulf of Alaska, and northern British Columbia (**Table 6**).

Visualization of the individual tracks followed by the tagged whales for which a biopsy sample was also collected provided further detail to the connections between feeding and breeding areas in the context of genetic composition and differentiation of North Pacific populations. Fifteen out of 25 biopsied animals in southeastern Alaska departed on migration (i.e., crossed the 50-km buffer zone), with 13 of these animals following a trajectory toward Hawaii and two toward Mexico, and with both the A+ ($n = 6$) and A- ($n = 9$) haplotypes being represented in these animals regardless of migratory destination (**Figure 11**). In contrast, six out of 39 biopsied animals in Hawaii departed on migration, with the five animals moving on a northeasterly trajectory toward northern British Columbia having the A+ ($n = 2$), A- ($n = 2$), and E2 ($n = 1$) haplotypes, while the single animal that migrated on a northerly route toward the eastern Aleutians had the E1 haplotype (**Figure 12**).

3.3 Photo-Identification

3.3.1 Southeastern Alaska

A total of 19,026 photographs were taken of humpback whales encountered during tagging field efforts in southeastern Alaska; 9,604 in Fredrick Sound, Seymour Canal, and near Petersburg in 2014, and 9,422 in Seymour Canal and near Petersburg in 2015. From these photographs a total of 233 individuals were identified by their flukes and added to OSU's southeastern Alaska humpback whale photo-ID catalog. This included 16 tagged whales and 203 untagged whales from 2014, and 14 tagged² whales from 2015 (presently only flukes from tagged whales have been processed by OSU for 2015). As noted in **section 2.7**, at the time of report preparation only the flukes of tagged whales from the 2014 and 2015 field seasons in southeastern Alaska have been submitted to the Happywhale online database.

Photo-ID matches were found for 18 of the whales tagged in southeastern Alaska, with 11 of these coming from Happywhale, six from OSU's catalog, and one from both Happywhale and OSU (**Table 7**), for a total of 40 percent of the tagged whales with an ID from southeastern Alaska matched to Happywhale and 23 percent matched to OSU's catalog. Fluke matches for the majority of these whales (15 of 18) were within southeastern Alaska, with time spans between first and last sighting ranging from 1 to 13 years (**Table 7, Figure 13**). Two of these latter whales also had photo-ID matches to Hawaii, spanning periods of 5 and 29 years, respectively. Two other whales tagged in southeastern Alaska had matches only to Hawaii, over periods of 10 and 17 years, respectively (**Table 7, Figure 13**). One whale was resighted off central California in the spring of two years (2017 and 2018), after being tagged in southeastern Alaska in late fall of 2014 (**Table 7, Figure 13**).

The number of years in which the tagged whales were identified ranged from two to six. Eight of the resighted tagged whales (not including the two that were re-tagged) were seen in subsequent years, spanning periods of one to four years after tagging (**Table 7**). Four of these latter whales were also seen in years prior to tagging. For eight other whales, matches were made to photos prior to tagging only, spanning periods from one to 17 years (**Table 7**). In the case of the two whales that were re-tagged in subsequent years, both whales were resighted one year after the first tagging, and one of these whales was also seen four years after re-tagging.

3.3.2 Hawaii

A total of 17,205 photographs were taken of humpback whales encountered during tagging field efforts off Maui; 5,804 in 2015, and 11,401 in 2018. From these photographs a total of 173 individuals were identified by their flukes and added to OSU's Hawaii humpback whale photo-ID catalog. This included 10 fluke photographs of tagged whales in 2015 and 14 fluke photographs of tagged whales in 2018. Eighty-eight and 61 fluke photographs of untagged whales were obtained in 2015 and 2018, respectively. As noted in **section 2.7**, fluke photographs of both tagged and untagged whales have been submitted to Happywhale for matching at the time of report preparation.

² In 2015 we obtained a fluke photograph and biopsy sample from a whale whose tag bounced off during deployment and was lost. This whale is included here despite the fact that other untagged whale photo-IDs from 2015 have not yet been processed.

Photo-ID matches were found in Happywhale (but not in OSU's catalog) for seven of the humpback whales tagged in Hawaii (**Table 7, Figure 14**), for a total of 29 percent of the tagged whales with an ID from Hawaii matched to Happywhale. Six of these whales have only been identified in Hawaii, in two or three separate years. The seventh whale (tag 5685) was seen in southern British Columbia/northern Washington every year from 2013 to 2018 (**Table 7, Figure 14**). In addition to being identified up to five years before tagging, tag 5685 was also resighted after tagging (without its tag) by whale-watch operators in the Strait of Georgia, east of Vancouver Island, in May, August, and September 2018 (**Figure 14**). One other whale tagged in Hawaii was identified three years after tagging, also in Hawaii. The remaining resights of tagged whales were from before tagging, with time spans between sightings from three to 14 years (**Table 7**).

Of the 149 untagged whales that were identified in Hawaii during the 2015 and 2018 field seasons, 26 were matched to whales in the Happywhale database (**Figure 14**), for a total of 17.5 percent of the untagged whales with an ID from Hawaii matched to Happywhale. Thirteen of these were matches within Hawaii, going back as early as 1997. One of these 13 whales had also been identified near the Shumagin Islands, Alaska, in July 2005. Another whale had also been sighted during summer around the Shumagins in five different years (2004, 2005, 2007, 2009, 2010), and once off the southern tip of the Baja California Peninsula, Mexico, in winter 2014 (indicating a switch in breeding area for this animal). Four whales had been previously sighted around Kodiak Island, Alaska (from 2003 to 2013), and one of these was also resighted in Cook Inlet, Alaska, in 2018. Three whales were identified in southeastern Alaska; one in 2010 and 2016, one in 2012, and one in 2016. Four whales were matched to sightings off Washington (from 2004 to 2018), with one of these also being identified west of Vancouver Island, British Columbia (in 2017). The final match was to a sighting, after tagging, in the Chukchi Sea, near Kolyuchin Island, northeastern Russia, in August 2018 (**Figure 14**).

4 Discussion

4.1 Satellite Tracking

The overall distribution of humpback whales tagged in the southeastern Alaska feeding area during our study (see **Figures 1 and 2**) aligned well with sighting data published by Dahlheim et al. (2009) as well as unpublished information from opportunistic and line-transect boat-based surveys (Ferguson et al. 2015). The majority of whale locations in Seymour Canal and Frederick Sound reflected where tagging was conducted as well as the timing (November; see **Table 1**). This seasonal concentration of locations likely also reflects a documented shift in distributions and types of prey at the approach of winter, which confines whales to smaller areas where they can feed (Straley et al. 2018).

The re-tagging of two whales in two consecutive years in southeastern Alaska afforded us a unique opportunity to compare movements between years for the same individuals. The movements and the timing of the movements for one animal were very similar between years, while for the other animal the movements were similar but the timing was different. However, the results were limited due to the early failure of one tag and the relatively short tracking periods for the other three tags (up to 29 d), such that only movements within southeastern Alaska's inland waters could be compared. Nevertheless,

the similarities in the tracks between years for both animals provide some evidence of route fidelity, as has been recently shown for several species of migratory marine animals (Horton et al. 2017, McHuron et al. 2018, Abrahms et al. 2019b). Future studies involving re-tagged individual animals to increase this sample size and tracking duration will likely further advance our understanding of route fidelity in humpback whale migration and navigation.

The start of migration to breeding areas in Hawaii and Mexico was documented for 54 percent of all whales tagged in southeastern Alaska (20 out of 37 animals), after a mean residence time of 17.3 d in southeastern Alaska waters (see **Table 2**). This relatively high percentage of documented departures for the breeding areas (ranging from mid-November to early January) was likely due to the fact that tagging was conducted in late fall (November), toward the end of the feeding season. In contrast, the start of migration was documented for only 21 percent of all whales tagged in Hawaii (nine out of 43 functional tags) in mid-January 2015 and mid-March 2018, with a range of departure dates from late January to mid-April, after a mean residence time of 14.8 d. The reason for these differences is unclear, but may be related to seasonal changes in blubber/muscle tissue characteristics that may result in differences in tag retention for animals that are feeding versus animals that are fasting while on the breeding grounds. Behavioral differences between feeding and breeding whales may also play a role in the different tracking periods, as tag retention in the breeding areas may be compromised by energetic displays by individuals, by the physical competitive behavior between males, or by close tactile contact between mothers and young calves. Additionally, compared to other species including blue, fin, gray, and sperm whales that have been studied by OSU, tag retention times in humpback whales have been consistently shorter for reasons that are not entirely understood (Mate et al. 2007, 2018, 2019).

The tracked locations within Hawaii (see **Figures 1 and 8**) support results of previous photo-ID studies and aerial surveys showing high densities of whales in the Maui Nui region and Penguin Bank (Mobley et al. 2001), as well as extensive interchange within the islands (Cerchio et al. 1998, Calambokidis et al. 2008, Baird et al. 2015). While the predominant direction of travel within the islands was to the northwest for whales tagged off Maui, one tagged whale moved southeast to Hawaii Island in 2015. A previous OSU study also showed eastward movement for two whales tagged off Kauai in 1995, one reaching Oahu and the other one reaching Maui Nui (Mate et al. 1998), while a recent study similarly documented eastward movement to Oahu for a whale tagged off Kauai in 2018 (Henderson et al., in review). Therefore, additional tagging in other parts of the main Hawaiian islands (e.g., Kauai and Hawaii) would improve our understanding of connectivity and exchange between islands (see also Mate et al. 2019).

The migratory destinations of humpback whales tagged in Hawaii support previous genetic and photo-ID studies, which show the majority of whales wintering in Hawaii traveling to feeding areas in northern British Columbia and southeastern Alaska, with fewer numbers going to the Gulf of Alaska, the Aleutian Islands and Bering Sea, and fewer numbers still going to northern Washington/southern British Columbia (Mate et al. 2007, Baird et al. 2015, Calambokidis et al. 2008, Wade et al. 2016, Wade 2017). An earlier tagging study also tracked a humpback whale from Hawaii to northern British Columbia and southeastern Alaska in 1998 (Mate et al. 2007, 2019). This connection is reinforced by the lack of significant genetic differentiation between humpback whales in northern British Columbia and

southeastern Alaska (Baker et al. 2013), and supports the treatment of northern British Columbia and southeastern Alaska as one grouping for abundance estimation (Wade et al. 2016, Wade 2017).

Tag 5736 from 2018 lasted for 147 d and 11,302 km as it traveled from Hawaii to the eastern Aleutians and then to the western Aleutians and into the Bering Sea (see **Figure 8**), representing the longest continuously tracked movements of a humpback whale to date. [The previous longest-tracked movements were for a mother/calf pair tagged in Socorro Island, in the Revillagigedo Archipelago, Mexico, in 2003, that were tracked to Kodiak Island, Alaska, over a total of 149 d and 10,481 km (Lagerquist et al. 2008)]. Previously, two other whales tagged in Hawaii had been tracked to the eastern Aleutians in 1997 and 1999, both arriving and spending time in the same general area of the Aleutian Trench south of Unimak Pass (Mate et al. 2007, 2019). Similar to tag 5736 from 2018, the animal from 1997 then moved rapidly westward past the western Aleutians and was last located 75 km off the southeastern tip of Kamchatka Peninsula when the tag quit (Mate et al. 2007, 2019). Thus, satellite tracking has thus demonstrated the connection between Hawaii, the Aleutian Islands, and the Bering Sea with unprecedented detail (see also Kennedy et al. 2014), supporting the treatment of the Aleutians and the Bering Sea together for abundance estimation (Wade et al. 2016, Wade 2017). Interestingly, results from photo-ID and genetic studies of humpback whales in eastern Russia indicate a high degree of separation between the Commander Islands (at the western end of the Aleutians), the east side of Kamchatka Peninsula, and the Gulf of Anadyr, despite their geographic proximity (Calambokidis et al. 2008, Titova et al. 2017, Richard et al. 2018). However, the satellite tracking data from 1997 and 2018 indicated that whales from Hawaii may visit several of these areas, even within the same feeding season.

Residence time in southeastern Alaska for whales tagged in late fall of 2014 and 2015 ranged from 4.4 to 49.1 d (mean = 17.3 d, n = 20; see **Table 2**). Previous tagging in southeastern Alaska in early summer 1997 resulted in tracking periods between 4 and 145 d (n = 9), with migration departure being documented for one animal that spent 141 d in within the southeastern Alaska buffer zone (Mate et al. 2007, 2018; OSU, unpublished data). Residence time for whales tagged in Hawaii in 2018 that arrived in northern British Columbia and spent time inside the southeastern Alaska buffer zone ranged from 8.7 to 53.6 d (mean = 25.5 d, n = 3; **Table 2**). Previously, a whale tagged in Hawaii in 1998 was tracked for 75 d within the southeastern Alaska buffer zone from arrival to when the tag quit (Mate et al. 2007, 2019; OSU, unpublished data), while another whale tagged in Hawaii in 1999 was tracked for 120 d within the southeastern Alaska buffer zone (although with only a few locations received from this tag, this estimate may be highly inaccurate; OSU, unpublished data). Together, this information indicates that individual humpback whales using the southeastern Alaska feeding area between spring and late fall may occur there for periods of up to four to five months.

In contrast, the overall mean residence time in Hawaii from tagging to departure in 2015 and 2018 (mean = 14.8 d, n = 9; see **Table 2**) was consistent with values reported by Mate et al. (2019) for a larger data set from Hawaii that also included additional animals tagged from 1995 to 2000 (mean = 12.3 d). Lagerquist et al. (2008) also reported similar values (mean = 13.6 d) for the time spent from tagging to departure at the Socorro Island breeding area off Mexico. Additionally, photo-ID studies have determined an overall residency in Hawaii of two weeks or less (Craig et al. 2001), all of which lends

support to the existing notion that there is a rapid turnover of individuals in this breeding area during the winter season (Craig and Herman 1997, Craig et al. 2001, Darling 2009). However, Craig et al. (2003) also found important differences between age and sex classes, with residence time being shorter for juveniles and females with no calf than for males. In this regard, although based on a small sample size, Mate et al. (2019) also found evidence that residence time was shorter for females with calves (mean = 10.4 d) than for males (mean = 15.8 d). As an additional caveat, it is important to keep in mind that overall true residence times in the breeding and feeding areas are likely longer than the minimum values we report based on satellite telemetry, as we cannot know the time a whale had spent in an area prior to tagging.

The duration of migration from southeastern Alaska to breeding areas in Hawaii and Mexico (29-46 d) was similar to the duration of migration from Hawaii to feeding areas in northern British Columbia and the eastern Aleutians (28-46 d). For a mother/calf pair tracked from Socorro Island, Mexico, to Kodiak Island, Alaska, Lagerquist et al. (2008) reported 49 d and 6,236 km while on migration. Together, this information indicates a wide variability in the time individual humpback whales spend on migration. To date, the fastest documented migrations between southeastern Alaska and Hawaii had been 36 and 39 d based on photo-ID data (Gabriele et al. 1996, Calambokidis et al. 2001), although we note that satellite tracking provides the most accurate estimates of migration duration and travel speeds.

Examination of movement speeds by migration phase showed that humpback whales moved much slower while in the southeastern Alaska feeding area (mean = 1.01 km/h, median = 0.47 km/h) and the Hawaii breeding area (mean = 1.36 km/h, median = 1.00 km/h) than while migrating, and that migration speed from the feeding to the breeding areas (mean = 5.51 km/h, median = 5.63 km/h) was somewhat faster than from the breeding to the feeding areas (mean = 4.44 km/h, median = 4.32 km/h; **Table 3, Figures 6 and 7**). Within Hawaiian waters and during early departure, Henderson et al. (in review) estimated travel speeds of 0.9-1.1 km/h during milling behavior and 6.6-6.8 km/h during directed travel for animals tagged off Kauai. Mate et al. (1998) reported average travel speeds of 4.5 km/h and 6.2 km/h for two whales migrating between Hawaii and the Aleutian Islands. Lagerquist et al. (2008) reported average speeds of 1.2 km/h in the breeding areas and 2.2 km/h in feeding areas for animals tagged in the Revillagigedo Islands, Mexico, and tracked to feeding destinations in the North Pacific, while the average speed during migration was 4.0 km/h. While in feeding areas in the eastern Aleutians and the Bering Sea, Kennedy et al. (2014) reported travel speeds of 0.94-2.15 km/h for seven whales that spent most of their time foraging, and 4.57 km/h for a whale that spent most of its time transiting. For humpback whales migrating from breeding to feeding grounds in the southern hemisphere, Horton et al. (2011) reported travel speeds of 2.8 to 6.5 km/h during long-distance, constant-course track segments in the western South Atlantic and the western South Pacific, while Félix and Guzmán (2014) reported travel speeds of 2.72 to 7.04 km/h in the eastern South Pacific. Finally, Kennedy et al. (2013) reported a mean travel speed of 1.7 km/h while in the breeding grounds for humpback whales tagged in the Caribbean, and mean travel speed of 4.3 km/h while migrating to feeding areas in the eastern and western North Atlantic. Together, the above information indicates that humpback whales can have variable travel speeds, but generally they are above 4.0 km/h while migrating, and about half that speed (or lower) when in feeding or breeding areas.

Finally, the delineation of buffer zones around the tagging areas (see **Figure 1**) facilitated the objective estimation of residence time and movement speeds during the different phases of the migration (feeding, breeding, migrating), based on the portion of the tracks that occurred inside or outside of them. However, there are limitations to this approach that are worthy of highlighting. First, a robust delineation of the buffer zones requires a representative number of tracks collected at both ends of the migration to fully encompass the breadth the area, including the departure and arrival sites. We anticipate future refinements will be necessary to both our southeastern Alaska and Hawaii buffer zones, to better capture the full range of movements in these areas. Also, several humpback whale populations have migratory routes that are largely contained within the coastal domain, and for these the delineation of the buffer zone boundary becomes more complicated than simply determining when animals reach a given distance from shore. This was the case for the two animals in this study that migrated toward Mexico along the coast. Conversely, migratory destinations may occur entirely away from the land margin, as exemplified by tag 5736 from 2018 from Hawaii that arrived at the Aleutian Trench more than 200 km away from land, and then continued moving along the Trench at distances from the coast often greater than 50 km. In these cases, subjective decisions or more complex criteria are required.

4.2 Genetics

The genetic identity of the tagged whales was consistent with the previous descriptions of the Hawaiian breeding area and the southeastern Alaska feeding area, as characterized by the SPLASH program from samples collected in 2004, 2005, and 2006 (Baker et al. 2013). This is best represented visually in the pie charts of haplotype frequencies (**Figure 10**) and corresponding tracking maps (**Figures 11 and 12**), and quantitatively by the pairwise F_{ST} value in the test of differentiation (**Table 6**). In comparison with other breeding areas, the Hawaiian tagging samples showed the greatest similarity (i.e., the lowest F_{ST}) with the SPLASH samples from Hawaii and the greatest differences with those from Okinawa and Central America. In comparisons with other feeding areas, the southeastern Alaska tagging samples showed the greatest similarity to the SPLASH samples from southeastern Alaska and northern British Columbia.

However, it is well established from previous studies using tagging, photo-ID, and genetic markers, that the migratory connections of the Hawaiian breeding area to feeding areas is complex (Mate et al. 2007, Calambokidis et al. 2008, Baker et al. 2013). Although migratory fidelity is strong in both seasonal habitats, there is no simple relationship between breeding and feeding areas. Instead, the Hawaii DPS includes individuals with fidelity to feeding areas extending from British Columbia to Russia (as exemplified by our sample of tracked and/or photo-identified animals; see **Figures 12 and 14**), with the strongest connections to southeastern Alaska and the northern Gulf of Alaska (Calambokidis et al. 2008, Baker et al. 2013).

As shown here, genotype matching and photo-ID have the potential to further enhance information on the migratory fidelity of tagged whales by integrating long-term sighting histories. The three genotype recaptures reflecting migratory destinations are consistent with the previously known strong connection between southeastern Alaska/northern British Columbia and Hawaii. One of these tagged whales (biopsy sample Mno18HI016, tag 5784, a female) provided a genotype match with an individual previously sampled and photographed in northern British Columbia in 2005 (SPLASH ID 560234). The

satellite tagging showed this individual returning to the same feeding area, even within a few kilometers of her previous sighting location, 13 years later (**Figures 8 and 12**). Other, within-region genotype matches confirm the long-term fidelity of individuals to both the Hawaiian breeding area and the southeastern Alaska feeding area.

4.3 Photo-Identification

Photo-ID results using tagged as well as untagged whales greatly augmented the number and diversity of migratory connections obtained through tagging in this study. The number of photo-IDs from southeastern Alaska and Hawaii available in the Happywhale database at the time we conducted the matching was limited. Not surprisingly, the number of matches between southeastern Alaska and Hawaii from this study was low. Also, there were no matches between southeastern Alaska and Hawaii in the OSU catalog, and only four matches between southeastern Alaska and Hawaii in Happywhale. Some of this low incidence of matches can be attributed to the fact that, for our southeastern Alaska field seasons, we have currently only contributed photos of tagged whales to Happywhale, rather than both tagged and untagged whales as we have done for our Hawaii seasons. Additionally, the number of photo-IDs from these two areas being uploaded to Happywhale by other researchers is increasing rapidly, which will allow us to expand the overall interpretation and significance of our tagging and genetic results in the future.

In contrast, the number of photo-IDs in Happywhale from the southern British Columbia/northern Washington feeding area is much larger, which can result in differences in the proportion of identifications between Hawaii and the various feeding areas in the North Pacific compared to previous tagging, genetic, and photo-ID studies (Mate et al. 2007, Calambokidis et al. 2008, Baker et al. 2013, Baird et al. 2015, Wade et al. 2016, Wade 2017). For example, through Happywhale we discovered that a whale tagged in 2018 in Hawaii (tag 5685, a male) had been seen every year in waters of Washington State and Vancouver Island since 2013, and that an additional four untagged whales photographed by OSU in Hawaii in 2018 had also been previously identified off Vancouver Island and Washington (**Figure 14**). Similarly, as discussed in **section 4.2**, through genotype and photo-ID matching with the SPLASH database we discovered that another whale tagged in 2018 in Hawaii (biopsy sample Mno18HI016, tag 5784, a female) had been previously biopsy-sampled and photographed in northern British Columbia in 2005 (**Table 4**). The satellite track showed this individual returning to this area 13 years later (**Figures 8 and 12**), demonstrating a remarkable migratory fidelity to this feeding ground.

These examples of strong migratory fidelity in North Pacific humpback whales notwithstanding, changes in both breeding and feeding destinations for individual whales have also been documented, with animals from Hawaii also being seen in the Japan (Darling and Cerchio 1993, Salden et al. 1999) and Mexico (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker et al. 1986, Forestell and Urbán-R 2007) breeding areas. Photo-ID matches from this study provided further evidence of changes in breeding and feeding destinations, as one whale identified by OSU in Hawaii in 2015 had previously been seen off southern Baja California, Mexico, in 2014 (**Figure 14**). A second whale identified by OSU in Seymour Canal, southeastern Alaska, in November 2014 was seen in a different feeding area off Half Moon Bay and Monterey Bay, central California, in spring 2017 and 2018 (**Figure 13**). It is unclear from these sightings whether they represent a change in breeding/feeding areas between years or if these

whales are visiting more than one breeding/feeding area in a season. Further tagging, which provides continuous locations over time, gives us the best chance of answering this question.

The photo-ID matches from our two field seasons in Hawaii showed a marked difference in feeding-area destinations, with whales from 2015 being matched to feeding areas in the Gulf of Alaska (Shumagin Islands, Kodiak Island, Prince William Sound, and southeastern Alaska) and those from 2018 being matched to Oregon, Washington, and southern British Columbia waters (**Figure 14**). Since the 2015 field season was conducted in January and the 2018 season was conducted in March, it is tempting to infer that these were whales from different feeding areas, using Hawaii waters at different times during the breeding season, which extends from December to April (Darling 2009). This is also supported by the fact that there were no photographic matches between the 98 individual whales identified in 2015 and the 75 whales identified in 2018 (see **section 3.3.4**). However, a preliminary examination using all the photographs in the Happywhale database from these areas did not support this conclusion at this time (T. Cheeseman, personal communication). Also, as described in **section 3.2.1**, the mtDNA haplotype frequencies of the Hawaii samples from 2015 and 2018 did not reveal a significant difference, although this comparison was based on a small sample size ($n = 16$ versus 23).

Photo-ID is a powerful tool for identifying whales over time and space, but is limited by the amount of cooperation between researchers in sharing their catalogs and the amount of time needed to review photographs for matches, compile, and exchange the results within and between regions. By using Happywhale, which automates much of the work and brings together many sources, we have been able to overcome some of these limitations to make more connections between areas. Further, a major improvement to the automated matching algorithm used by Happywhale was very recently implemented, which will result in a higher number of matches. However, since not all researchers submit their photo-IDs to Happywhale, additional detailed work involving direct collaboration with those researchers is required to get a more complete picture of where the tagged whales go after the tags have stopped transmitting and where they have been seen historically.

5 Concluding Remarks

Through the combined use of satellite tagging, genetics, and photo-ID over the course of four field seasons, we characterized the patterns of humpback whale occupation in both a breeding and a feeding area in the North Pacific Ocean, as well as the long-distance migratory movements these animals undertake seasonally between these areas. The results of this study revealed the complex migratory linkages between Hawaii and the high-latitude feeding areas with unprecedented detail. Additional years of sampling during different parts of the reproductive season and in other parts of the main Hawaiian islands (e.g., Kauai and Hawaii), as well as in the northwestern Hawaiian Islands (in waters of the Papahānaumokuākea Marine National Monument), would provide valuable information to address outstanding questions about the humpback whale population using this extensive breeding area, as well as its broader connections to remote feeding areas throughout the North Pacific Basin, most of which are poorly known.

Also, while the majority of whales tracked from southeastern Alaska showed a strong connection to the Hawaii breeding area, a small proportion of these animals also demonstrated a connection to the Mexican mainland breeding area, indicating some mixing of the Hawaii and Mexico DPSs in the southeastern Alaska feeding area. These animals are of particular interest, as in their transit along the western coast of North America they overlap with animals from the Endangered Central America DPS, which forages off California and Oregon. Further tagging work to better understand the patterns of habitat use and the extent of the overlap between the Mexico and Central America DPSs in this region would help improve how animals are assigned to DPS for management purposes in the context of relative exposure to anthropogenic activities, given their different conservation statuses.

The funding support from Pacific Life Foundation had significant reach beyond the results of this project. The 2016 changes to the ESA have led to a need for further information on humpback whale DPS use of US West Coast waters, particularly in relation to human activities. In this regard, in 2018 NMFS invited us to provide scientific expertise at a workshop to inform the preparation of a Draft Biological Opinion toward a federally mandated Critical Habitat designation that is in the process of being finalized. Additionally, the work conducted under this grant left OSU well-positioned to undertake further satellite tagging efforts, not only in Hawaii, but also in waters off California, Oregon, and Washington on behalf of the US Navy's marine mammal monitoring efforts from 2016 to 2019, which is resulting in a revised and expanded understanding of North Pacific humpback whale movements, population structure, and habitat use, as reported elsewhere (Mate et al. 2019, 2019).

6 Acknowledgements

Funding for this project came from Pacific Life Foundation, the Makana Aloha Foundation, and the US Department of the Navy (via Commander, Pacific Fleet, and Commander, Naval Sea Systems Command) through Cooperative Ecosystem Studies Unit (CESU) Cooperative Agreement No. N62473-17-2-0001, administered by Naval Facilities Engineering Command (NAVFAC) Southwest. We thank the representatives for Commander, Pacific Fleet, and Commander, Naval Sea Systems Command, as well as the representatives for NAVFAC for technical and administrative support of this Cooperative Agreement.

Humpback whale tagging activities in southeastern Alaska and Hawaii were conducted under the authorization of NMFS Marine Mammal Protection Act (MMPA)/Endangered Species Act (ESA) Research/Enhancement Permit No. 14856, and OSU Institutional Animal Care and Use Committee (IACUC) Permit Nos. 4495 and 4884.

In southeastern Alaska we thank Captain Dennis Rogers and the crew of the M/V *Northern Song* for providing a safe operation and for their invaluable local knowledge. In Hawaii we thank Ed Lyman and Marc Lammers of the NOAA Hawaiian Islands Humpback Whale National Marine Sanctuary for logistical help, and for the use of the Sanctuary boat *Koholā*. Competent vessel operation in Hawaii was provided by Carmen De Fazio, Casey Cohan, Lee James, Grant Thompson, Sara Thompson, and Ted Grupenhoff. We also thank Whale Trust Maui (Flip Nicklin, Jim Darling, and Meagan Jones) for additional support. Finally, we thank OSU volunteers Dave Gosselin, Brian Thorsness, and Ken Sexton for help in the field.

We are also grateful to Kathy Minta, Mark Wilke, and Minda Stiles at the OSU Marine Mammal Institute office for the invaluable logistical and administrative support they provided to this project.

Permission to access the southeastern Alaska regional DNA register for genotype matching was kindly granted by Janice Straley (University of Alaska Southeast Sitka) and Christine Gabriele (Glacier Bay National Park). We thank Ted Cheeseman and Ken Southerland at Happywhale for their assistance with uploading our ID photographs, as well as the many researchers and citizens who have submitted ID photographs to this online resource. We also thank Erin Johns Gless and Alethea Leddy, naturalists at Island Adventures Whale Watching (Anacortes, Washington), for providing us with ID and tag wound site photographs of tag 5685, which was tagged in Hawaii in March 2018 and resighted off Vancouver Island in August 2018.

The Argos Data Collection and Location System used for this project (<http://www.argos-system.org/>) is operated by Collecte Localisation Satellites. Argos is an international program that relies on instruments provided by the French Space Agency flown on polar-orbiting satellites operated by the US National Oceanic and Atmospheric Administration, the European Organisation for the Exploitation of Meteorological Satellites, and the Indian Space Research Organization.

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Table 1. Deployment and performance information for 83 satellite-monitored radio tags deployed on humpback whales in southeastern Alaska in 2014 (n = 20) and 2015 (n = 18), and in Hawaii in 2015 (n = 20) and 2018 (n = 25). Also reported is the information associated with the biopsy samples (n = 66) and photo-IDs collected (n = 54 flukes and n = 81 dorsal fins).

Tag No.	Tag type	Biopsy No.	Sex	Haplo	Photo-ID	Fluke ID	Dorsal ID	Deployment date	Last transmission	Days tracked	Filtered locations	Distance (km)
SE Alaska												
5743	ST-15	Mno14AK013	F	A-	MnSEAK-213	Yes	Yes	23-Nov-2014	4-Jan-2015	42.0	110	1,826
826	SPOT5	NA	U	NA	MnSEAK-035	Yes	Yes	14-Nov-2014	22-Nov-2014	8.0	40	315
835	SPOT5	NA	U	NA	MnSEAK-133	No	Yes	14-Nov-2014	13-Dec-2014	28.5	165	2,277
836	SPOT5	NA	U	NA	MnSEAK-074	No	Yes	14-Nov-2014	21-Nov-2014	6.7	35	395
841	SPOT5	Mno14AK004	F	A+	MnSEAK-012	Yes	Yes	19-Nov-2014	13-Dec-2014	23.0	76	217
843	SPOT5	Mno14AK002	M	A-	MnSEAK-049	Yes	Yes	16-Nov-2014	18-Dec-2014	31.3	126	4,372
845	SPOT5	NA	U	NA	MnSEAK-078	Yes	Yes	20-Nov-2014	5-Feb-2015	78.3	437	6,503
2082	SPOT5	NA	U	NA	MnSEAK-157	Yes	Yes	20-Nov-2014	20-Dec-2014	29.2	153	965
4172	SPOT5	Mno14AK008	M	A-	MnSEAK-143	Yes	Yes	20-Nov-2014	22-Dec-2014	31.1	123	3,234
4173	SPOT5	Mno14AK012	F	A-	MnSEAK-180	Yes	Yes	21-Nov-2014	3-Jan-2015	44.0	188	2,755
4176	SPOT5	Mno14AK011	F	A-	MnSEAK-145	Yes	Yes	21-Nov-2014	24-Dec-2014	34.6	194	666
5670	SPOT5	Mno14AK005	F	A+	MnSEAK-146	No	Yes	19-Nov-2014	17-Dec-2014	27.9	138	1,478
5679	SPOT5	NA	U	NA	MnSEAK-051	Yes	Yes	14-Nov-2014	10-Dec-2014	25.3	101	2,278
5719	SPOT5	Mno14AK001	M	A+	MnSEAK-018	Yes	Yes	13-Nov-2014	11-Dec-2014	27.4	129	2,756
5843	SPOT5	Mno14AK003	M	A-	MnSEAK-077	Yes	Yes	17-Nov-2014	26-Nov-2014	8.2	42	199
5878	SPOT5	Mno14AK009	M	A-	MnSEAK-175	Poor	Yes	20-Nov-2014	24-Nov-2014	3.3	18	73
5882	SPOT5	NA	U	NA	MnSEAK-117	Yes	Yes	17-Nov-2014	27-Dec-2014	39.9	208	2,711
5883 ^a	SPOT5	Mno14AK010	F	A+	MnSEAK-216	No	Yes	20-Nov-2014	27-Nov-2014	6.2	50	137
5910	SPOT5	NA	U	NA	MnSEAK-025	Yes	Yes	13-Nov-2014	13-Dec-2014	30.0	137	4,389
23039 ^b	SPOT5	Mno14AK006	M	A-	MnSEAK-150	Yes	Yes	19-Nov-2014	11-Dec-2014	21.9	127	487
23041 ^a	SPOT5	Mno15AK003	F	A+	MnSEAK-216	Yes	Yes	10-Nov-2015	9-Dec-2015	29.0	142	1,876
5641	SPOT6	NA	U	NA	MnSEAK-229	No	Yes	16-Nov-2015	14-Dec-2015	28.0	141	1,833
5655 ^b	SPOT6	Mno15AK001	M	A-	MnSEAK-012	Yes	Yes	10-Nov-2015	29-Nov-2015	19.1	99	2,034

5685	SPOT6	Mno15AK008	M	A-	MnSEAK-225	No	Yes	15-Nov-2015	7-Dec-2015	21.7	109	3,062
10829	SPOT6	Mno15AK015	F	A-	MnSEAK-232	Yes	Yes	17-Nov-2015	1-Dec-2015	13.4	59	603
10830	SPOT6	Mno15AK014	M	A+	MnSEAK-209	Yes	Yes	17-Nov-2015	27-Nov-2015	9.2	50	660
10833	SPOT6	Mno15AK005	M	A-	MnSEAK-222	No	No	11-Nov-2015	22-Jan-2016	71.4	72	5,431
10834	SPOT6	Mno15AK009	F	A+	MnSEAK-226	Yes	Yes	15-Nov-2015	29-Dec-2015	43.1	165	5,084
10840	SPOT6	Mno15AK002	M	A-	MnSEAK-062	Yes	Yes	10-Nov-2015	30-Nov-2015	20.0	92	545
23029	SPOT6	NA	U	NA	MnSEAK-192	Yes	Yes	16-Nov-2015	15-Dec-2015	29.1	142	3,094
827	RDW-640	Mno15AK004	F	A+	MnSEAK-221	No	Yes	10-Nov-2015	18-Dec-2015	37.4	124	1,537
848 ^c	RDW-640	Mno15AK006	F	A-	MnSEAK-223	Yes	Yes	11-Nov-2015	10-Dec-2015	28.3	83	654
1386	RDW-640	Mno15AK016	F	A-	MnSEAK-233	Yes	Yes	17-Nov-2015	16-Dec-2015	28.3	144	3,948
2083	RDW-640	Mno15AK018	F	A+	MnSEAK-235	Yes	Yes	17-Nov-2015	13-Dec-2015	25.0	71	932
4175	RDW-640	Mno15AK017	F	A-	MnSEAK-212	Yes	Yes	17-Nov-2015	12-Jan-2016	55.7	287	2,640
5746	RDW-640	NA	U	NA	MnSEAK-224	Yes	Yes	12-Nov-2015	30-Nov-2015	18.6	72	1,636
23030	RDW-640	Mno15AK010	F	A-	MnSEAK-006	Yes	No	16-Nov-2015	7-Dec-2015	21.0	129	771
23035 ^d	RDW-640	Mno15AK013	M	A+	MnSEAK-230	Yes	Yes	17-Nov-2015	NA	NA	NA	NA
Mean										28.2	123.7	2,010

Hawaii

827	SPOT5	Mno15HI0028	M	A-	MnHI-017	Yes	Yes	20-Jan-2015	20-Jan-2015	0.1	1	15
830	SPOT5	Mno15HI0026	M	A+	MnHI-015	No	Yes	20-Jan-2015	5-Feb-2015	16.2	55	1,592
834	SPOT5	Mno15HI0025	M	A+	MnHI-014	Yes	Yes	19-Jan-2015	5-Feb-2015	16.9	52	631
848	SPOT5	Mno15HI0017	M	A-	MnHI-004	Yes	Yes	15-Jan-2015	20-Jan-2015	5.0	20	187
1386	SPOT5	Mno15HI0020	M	A-	MnHI-008	No	Yes	17-Jan-2015	24-Jan-2015	6.2	19	134
1387	SPOT5	Mno15HI0024	M	A+	MnHI-013	No	Yes	19-Jan-2015	24-Jan-2015	5.0	18	279
1389	SPOT5	Mno15HI0022	M	A+	MnHI-010	Yes	Yes	18-Jan-2015	1-Feb-2015	13.4	43	542
1390	SPOT5	NA	U	NA	MnHI-006	Yes	Yes	16-Jan-2015	8-Feb-2015	22.8	64	705
2083	SPOT5	NA	U	NA	MnHI-020	No	Yes	21-Jan-2015	29-Jan-2015	7.4	24	259
4174	SPOT5	Mno15HI0021	M	F2	MnHI-009	Yes	Yes	18-Jan-2015	30-Jan-2015	12.0	42	500
4175	SPOT5	Mno15HI0030	M	A3	MnHI-019	Yes	Yes	21-Jan-2015	23-Jan-2015	1.9	8	144
5709	SPOT5	Mno15HI0015	M	A-	MnHI-001	Yes	Yes	15-Jan-2015	11-Feb-2015	26.3	92	1,030

5746	SPOT5	NA	U	NA	MnHI-002	No	Yes	15-Jan-2015	22-Feb-2015	38.0	86	2,103
5938	SPOT5	Mno15HI0016	F	F2	MnHI-003	Yes	Yes	15-Jan-2015	1-Feb-2015	16.9	64	705
10822	SPOT5	NA	U	NA	MnHI-012	No	Yes	19-Jan-2015	6-Feb-2015	18.6	68	816
10842	SPOT5	Mno15HI0019	M	E2	MnHI-007	Yes	Yes	16-Jan-2015	5-Feb-2015	20.0	32	524
23034	SPOT5	Mno15HI0018	M	E2	MnHI-005	No	Yes	15-Jan-2015	20-Jan-2015	4.7	13	238
23035	SPOT5	Mno15HI0029	M	A-	MnHI-018	No	Yes	20-Jan-2015	22-Jan-2015	2.0	8	79
23038	SPOT5	Mno15HI0027	M	A-	MnHI-016	No	Yes	20-Jan-2015	8-Feb-2015	19.8	56	681
23043	SPOT5	Mno15HI0023	M	F2	MnHI-011	No	Yes	18-Jan-2015	3-Feb-2015	15.3	47	630
832	RDW-665	Mno18HI005	M	E2	MnHI-115	No	Yes	14-Mar-2018	15-Mar-2018	0.9	0	0
836	RDW-665	Mno18HI001	M	F2	MnHI-111	Yes	Yes	12-Mar-2018	25-Mar-2018	13.0	78	751
839	RDW-665	Mno18HI002	M	A-	MnHI-112	Yes	Yes	13-Mar-2018	29-Mar-2018	15.3	97	647
843	RDW-665	NA	U	NA	MnHI-116	No	Yes	15-Mar-2018	17-May-2018	63.0	143	3,294
849	RDW-665	Mno18HI003	F	A+	MnHI-113	No	Yes	13-Mar-2018	25-Mar-2018	11.3	18	276
4172	RDW-665	Mno18HI004	M	A-	MnHI-114	No	Yes	14-Mar-2018	6-May-2018	53.7	385	6,296
5641	RDW-665	Mno18HI007	M	A-	MnHI-118	No	Yes	16-Mar-2018	2-Apr-2018	17.2	82	1,019
5655	RDW-665	Mno18HI009	M	A-	MnHI-120	Yes	Yes	17-Mar-2018	22-Mar-2018	4.3	20	144
5685	RDW-665	Mno18HI010	M	A-	MnHI-121	Yes	Yes	17-Mar-2018	22-Mar-2018	4.8	22	264
5701	RDW-665	Mno18HI011	M	A-	MnHI-122	No	Yes	18-Mar-2018	NA	NA	NA	NA
5736	RDW-665	Mno18HI012	M	E1	MnHI-123	Yes	Yes	18-Mar-2018	12-Aug-2018	147.2	913	11,302
5742	RDW-665	Mno18HI013	M	F2	MnHI-124	Yes	Yes	18-Mar-2018	22-Mar-2018	4.5	20	204
5743	RDW-665	Mno18HI014	M	E1	MnHI-125	Yes	Yes	18-Mar-2018	21-Mar-2018	2.5	7	61
5746	RDW-665	Mno18HI015	M	F2	MnHI-126	Yes	Yes	18-Mar-2018	26-Mar-2018	8.0	49	429
5800	RDW-665	Mno18HI017	M	E2	MnHI-128	Yes	Yes	19-Mar-2018	17-May-2018	58.2	214	6,259
5843	RDW-665	Mno18HI019	M	A-	MnHI-130	No	Yes	20-Mar-2018	20-Mar-2018	0.1	2	13
5878	RDW-665	Mno18HI020	F	A+	MnHI-131	Yes	Yes	20-Mar-2018	21-Mar-2018	1.1	8	117
5938	RDW-665	Mno18HI021	M	E5	MnHI-132	Yes	Yes	20-Mar-2018	31-Mar-2018	11.1	58	438
10827	RDW-665	Mno18HI022	M	A-	MnHI-133	Yes	Yes	20-Mar-2018	28-Mar-2018	7.4	38	266
10829	RDW-665	Mno18HI023	M	A+	MnHI-134	Yes	Yes	21-Mar-2018	25-Mar-2018	4.0	25	169
4177	RDW-665R	Mno18HI006	M	A-	MnHI-117	No	Yes	15-Mar-2018	18-Mar-2018	2.2	11	126
5644	RDW-665R	Mno18HI008	M	A-	MnHI-119	No	Yes	17-Mar-2018	28-Mar-2018	11.1	53	576

5784	RDW-665R	Mno18HI016	F	A+	MnHI-127	No	Yes	19-Mar-2018	1-Jul-2018	104.5	679	8,065
5826	RDW-665R	Mno18HI018	M	E5	MnHI-129	Yes	Yes	19-Mar-2018	2-May-2018	43.3	23	200
10833	RDW-665R	NA	U	NA	MnHI-135	Yes	Yes	21-Mar-2018	20-May-2018	59.5	51	860
Mean										20.8	86.5	1,217

^a Animal tagged in 2014 with tag 5883 and biopsy sample Mno14AK010 that was re-tagged in 2015 with tag 23041 and biopsy sample Mno15AK003

^b Animal tagged in 2014 with tag 23039 and biopsy sample Mno14AK006 that was re-tagged in 2015 with tag 5655 and biopsy sample Mno15AK001

^c Animal tagged in 2015 with tag 848 and biopsy sample Mno15AK006 that was matched to biopsy sample Mno09SEAK036 (SEAK ID 2271) collected in southeastern Alaska in 2009 by J. Straley, University of Alaska Southeast Sitka

^d Tag 23035 bounced off the whale and was lost, but a biopsy sample and a photo-ID were collected

Table 2. Residence time in the southeastern Alaska (SEAK) and Hawaii (HI) 50-km buffer zones for 29 tagged whales with known departure date (n = 20 in SEAK and n = 9 in HI). For each whale, also reported is sex (F = female, M = male, U = unknown), haplotype, tag deployment, departure date, arrival date, and the migratory destination (in parenthesis and italics if inferred for incomplete tracks based on the direction of the trajectory). Note that for the seven tags that lasted until arrival at the migratory destination (last column), additional details are provided in the footnotes including migration duration and distance, and movements after initial arrival at the destination.

Tag No.	Biopsy No.	Sex	Haplo	Deployment date	Departure date	Arrival date	Destination	Residence SEAK (d)	Residence HI (d)	Complete migration
SE Alaska										
5743	Mno14AK013	F	A-	23-Nov-2014	27-Dec-2014	NA	<i>(Hawaii)</i>	33.4	NA	No
835	NA	U	NA	14-Nov-2014	4-Dec-2014	NA	<i>(Hawaii)</i>	19.7	NA	No
843 ^a	Mno14AK002	M	A-	16-Nov-2014	25-Nov-2014	NA	Hawaii	8.3	NA	Almost
845 ^b	NA	U	NA	20-Nov-2014	2-Dec-2014	8-Jan-2015	Hawaii	12.4	27.3	Yes
4172	Mno14AK008	M	A-	20-Nov-2014	26-Nov-2014	NA	<i>(Hawaii)</i>	5.8	NA	No
4173	Mno14AK012	F	A-	21-Nov-2014	17-Dec-2014	NA	<i>(Mexico)</i>	27.1	NA	No
5670	Mno14AK005	F	A+	19-Nov-2014	15-Dec-2014	NA	<i>(Hawaii)</i>	25.4	NA	No
5679	NA	U	NA	14-Nov-2014	19-Nov-2014	NA	<i>(Hawaii)</i>	4.4	NA	No
5719	Mno14AK001	M	A+	13-Nov-2014	1-Dec-2014	NA	<i>(Hawaii)</i>	17.6	NA	No
5882	NA	U	NA	17-Nov-2014	17-Dec-2014	NA	<i>(Hawaii)</i>	30.2	NA	No
5910 ^c	NA	U	NA	13-Nov-2014	19-Nov-2014	NA	Hawaii	5.7	NA	Almost
23041 ^d	Mno15AK003	F	A+	10-Nov-2015	28-Nov-2015	NA	<i>(Hawaii or Mexico?)</i>	17.6	NA	No
5641	NA	U	NA	16-Nov-2015	11-Dec-2015	NA	<i>(Hawaii)</i>	23.7	NA	No
5655	Mno15AK001	M	A-	10-Nov-2015	22-Nov-2015	NA	<i>(Hawaii)</i>	11.3	NA	No
5685	Mno15AK008	M	A-	15-Nov-2015	22-Nov-2015	NA	<i>(Hawaii)</i>	6.3	NA	No
10833 ^e	Mno15AK005	M	A-	11-Nov-2015	28-Nov-2015	13-Jan-2016	Hawaii	16.6	8.8	Yes
10834 ^f	Mno15AK009	F	A+	15-Nov-2015	30-Nov-2015	29-Dec-2015	Mexico mainland	14.4	NA	Yes
23029	NA	U	NA	16-Nov-2015	27-Nov-2015	NA	<i>(Hawaii)</i>	10.7	NA	No
1386	Mno15AK016	F	A-	17-Nov-2015	24-Nov-2015	NA	<i>(Hawaii)</i>	6.6	NA	No
4175	Mno15AK017	F	A-	17-Nov-2015	6-Jan-2016	NA	<i>(Hawaii)</i>	49.1	NA	No
Mean								17.3	18.1	

Hawaii										
830	Mno15HI0026	M	A+	20-Jan-2015	29-Jan-2015	NA	(Southeastern Alaska/ northern British Columbia)	NA	9.5	No
5746	NA	U	NA	15-Jan-2015	13-Feb-2015	NA	(Eastern Aleutians)	NA	29.3	No
843	NA	U	NA	15-Mar-2018	8-Apr-2018	NA	(Western Aleutians)	NA	23.2	No
4172 ^g	Mno18HI004	M	A-	14-Mar-2018	17-Mar-2018	16-Apr-2018	Northern British Columbia	14.2	3.3	Yes
5641	Mno18HI007	M	A-	16-Mar-2018	29-Mar-2018	NA	(Northern British Columbia)	NA	13.5	No
5736 ^h	Mno18HI012	M	E1	18-Mar-2018	31-Mar-2018	28-Apr-2018	Eastern Aleutians	NA	13.7	Yes
5800 ⁱ	Mno18HI017	M	E2	19-Mar-2018	3-Apr-2018	8-May-2018	Northern British Columbia	8.7	14.4	Yes
5784 ^j	Mno18HI016	F	A+	19-Mar-2018	25-Mar-2018	8-May-2018	Northern British Columbia	53.6	5.9	Yes
10833	NA	U	NA	21-Mar-2018	11-Apr-2018	NA	(Central/Western Aleutians)	NA	20.5	No
Mean								25.5	14.8	

^a Tag 843 from 2014. 300 km shy of buffer.

^b Tag 845 from 2014. Migration duration: 37.2 d. Migration distance: 4,744 km. Destination movements: arrival at southern coast of Hawaii Island, and continued around south side up to Maui and over to Penguin Bank.

^c Tag 5910 from 2014. 180 km shy of buffer.

^d Tag 23041 from 2015. Initial migration along coast down to Washington/Oregon waters, then veered toward Hawaii.

^e Tag 10833 from 2015. Migration duration: 46.2 d. Migration distance: 4,303 km. 31-d gap at start, only 11 locations for majority of track. Destination movements: arrival at northern coast of Hawaii Island.

^f Tag 10834 from 2015. Migration duration: 28.1 d. Migration distance: 4,213 km. Destination movements: tag stopped when animal was at the Gulf of California entrance, moving toward the Mexican mainland.

^g Tag 4172 from 2018. Migration duration: 29.8 d. Migration distance: 4,339 km. Destination movements: arrival at and extensive movements around Haida Gwaii.

^h Tag 5736. Migration duration: 28 d. Migration distance: 3,775 km. Destination movements: arrival at Aleutian Trench approximately 200 km south of Unimak Pass, then west toward Kamchatka (within 171 km), and north into the Bering Sea. At a total tracking distance of 11,302 km, these were the longest movements of a humpback whale tracked to date.

ⁱ Tag 5800 from 2018. Migration duration: 34.5 d. Migration distance: 5,030 km. Destination movements: arrival at and extensive movements around Haida Gwaii.

^j Tag 5784. Migration duration: 44.8 d. Migration distance: 4,662 km. Destination movements: arrival at and extensive movements around Haida Gwaii.

Table 3. Summary statistics for travel speed (in km/h) between location pairs for 76 humpback whale tracks on which SSSM/hSSSM were run. Values are reported by migration phase, as determined by occurrence inside or outside the southeastern Alaska (SEAK) and Hawaii (HI) 50-km buffer zones (upper part of the table), and by estimated behavioral mode (lower part of the table). Also reported are the 95th sample quantile (qtl) and the lower and upper 95 percent confidence intervals (CI) around the mean.

Tagging Area	Phase	N	Mean	Median	sd	95 th qtl	Lower CI	Upper CI
SEAK	SEAK	668	1.01	0.47	1.28	4.22	0.91	1.10
	Migration	361	5.51	5.63	1.98	8.59	5.31	5.72
	HI	37	1.49	1.01	1.36	4.74	1.05	1.92
HI	HI	870	1.36	1.00	1.21	3.74	1.28	1.44
	Migration	573	4.44	4.32	2.18	7.80	4.26	4.62
	SEAK	232	2.00	1.53	1.53	5.26	1.80	2.19
Tagging Area	Behavioral Mode	N	Mean	Median	sd	95 th ptl	Lower CI	Upper CI
SEAK	ARS	141	0.90	0.57	0.96	3.01	0.74	1.06
	Uncertain	418	0.69	0.35	0.95	2.48	0.60	0.78
	Transiting	470	4.57	4.76	2.42	8.27	4.36	4.79
HI	ARS	713	1.31	1.00	1.22	3.49	1.22	1.40
	Uncertain	345	1.47	1.11	1.26	3.63	1.33	1.60
	Transiting	598	4.55	4.42	1.98	7.75	4.39	4.70

Table 4. Biopsy number, sex (F = female, M = male), tag number, location, and date information for the nine genotype recaptures identified between the tagging data set and the reference SPLASH database (Baker et al. 2013). SEAK = southeastern Alaska, HI = Hawaii, NBC = northern British Columbia.

Tagging data set information					SPLASH database information			
Biopsy No.	Sex	Tag No.	Location	Date	Genetic ID	SPLASH ID	Location	Date
Within region								
Mno14AK003	M	5843	SEAK	17-Nov-2014	gSEA04-45778	474387	SEAK	3-Dec-2004
Mno15AK008	M	4172	SEAK	15-Nov-2015	gSEA04-41512	474279	SEAK	28-Jun-2004
Mno15AK013	M	23035	SEAK	17-Nov-2015	gSEA05-52886	574059	SEAK	17-Oct-2005
Mno15AK016	F	1386	SEAK	17-Nov-2015	gSEA05-52882	574463	SEAK	15-Oct-2005
Mno15HI025	M	834	HI	19-Jan-2015	gHi04-41122	430326	HI	4-Mar-2004
Mno18HI007	M	5641	HI	15-Mar-2018	gHi04-41285	430296	HI	22-Apr-2004
Between region								
Mno15HI020	M	1386	HI	17-Jan-2015	gNBC04-43431	470012	NBC	2-Jul-2004
Mno18HI016	F	5784	HI	18-Mar-2018	gNBC05-53102	560234	NBC	15-Jun-2005
Mno15HI024	M	1387	HI	19-Jan-2015	gSEA04-43481	470736	SEAK	7-Jul-2004

Table 5. The identity and frequency of the seven mtDNA haplotypes, including GenBank codes, resolved for the 25 whales sampled in southeastern Alaska (SEAK) in 2014 and 2015, and the 39 whales sampled in Hawaii (HI) in 2015 and 2018. Numbers in parenthesis refer to totals after recaptures were removed.

Haplotype code	GenBank code	SEAK 2014 tagging	SEAK 2015 tagging	HI 2015 tagging	HI 2018 tagging
A+	KF477244	4	6 (5)	4	4
A-	KF477245	8	9 (8)	6	10
A3	KF477246			1	
E1	KF477249				2
E2	KF477256			2	2
E5	KF477258				2
F2	KF477266			3	3
Total		12	15 (13)	16	23

Table 6. Results of pairwise tests of differentiation of mtDNA haplotype frequencies between the southeastern Alaska (SEAK; n = 25) and Hawaii (HI; n = 39) tagging samples and the 18 regional strata (feeding areas and breeding areas) defined in SPLASH (Baker et al. 2013). The regional abbreviations and associated sample sizes are consistent with Figure 7. The sample sizes refer to the number of individuals with associated haplotypes. Rows in italics indicate low sample numbers for comparisons with the western Aleutians and the Philippines.

SPLASH Region	n	2014 and 2015 SEAK tagging n = 25		2015 and 2018 HI tagging n = 39	
		F _{ST}	p-value	F _{ST}	p-value
Feeding Areas					
Russia (RUS)	70	0.2497	<0.0001	0.1219	<0.0001
<i>Western Aleutians (WAL)</i>	<i>8</i>	<i>0.2307</i>	<i>0.0066</i>	<i>0.0423</i>	<i>0.1351</i>
Bering (BER)	114	0.1767	<0.0001	0.0729	0.0002
Eastern Aleutians (EAL)	36	0.1542	0.0005	0.0317	0.0526
Western Gulf of Alaska (WGOA)	96	0.1442	<0.0001	0.0441	0.0043
Northern Gulf of Alaska (NGOA)	233	0.0592	0.0079	0.0068	0.1900
Southeastern Alaska (SEA)	183	0.0000	0.6183	0.0755	0.0041
Northern British Columbia (NBC)	104	0.0000	0.7141	0.0408	0.0301
Southern British Columbia/Washington (SBC/WA)	51	0.1269	0.0012	0.0531	0.0052
California/Oregon (CA/OR)	123	0.2854	<0.0001	0.1248	<0.0001
Breeding Grounds					
<i>Philippines (PHI)</i>	<i>13</i>	<i>0.4430</i>	<0.0001	<i>0.2448</i>	<0.0001
Okinawa (OK)	72	0.3901	<0.0001	0.2516	<0.0001
Ogasawara (OG)	159	0.2144	<0.0001	0.1009	<0.0001
Hawaii (HI)	227	0.0367	0.0486	0.0023	0.2954
Mexico-Archipelago de Revillagigedo (MX-AR)	106	0.1687	<0.0001	0.0629	<0.0001
Mexico-Baja California (MX-BC)	110	0.1573	<0.0001	0.0515	0.0001
Mexico-Mainland (MX-ML)	62	0.1897	<0.0001	0.0654	0.0001
Central America (CENTAM)	36	0.3710	<0.0001	0.1773	<0.0001

Table 7. Resighting years and areas for humpback whales tagged in southeastern Alaska (2014 and 2015) and Hawaii (2015 and 2018), number of years between first and last sighting (time span), and source of the resight photograph. Years in red signify the year and area in which a whale was tagged.

Tag No.	Southeastern Alaska	Hawaii	Central California	SBC/NWA	Maximum time span (years)	Resight source
Humpback whales tagged in Southeastern Alaska – 2014 and 2015						
826	2014, 2016				2	Happywhale
841	2009, 2011, 2014, 2015				6	Happywhale
843	2003, 2009, 2011, 2014, 2015, 2016	1987			29 between areas, 13 within areas	Happywhale
845	2014	2004			10	Happywhale
2082	2014, 2018				4	Happywhale
4173	2014		2017, 2018		4	Happywhale
4176	2014, 2016				2	Happywhale
5719	2014	1997			17	Happywhale
5883/23041	2014, 2015				1	OSU
5910	2010, 2014, 2017				7	Happywhale
23039/5655	2014, 2015, 2019	2019			5 between areas, 5 within areas	OSU, Happywhale
4175	2014, 2015				1	OSU
10830	2014, 2015				1	OSU
10834	2009, 2010, 2015, 2016, 2018				9	Happywhale
10840	2014, 2015				1	OSU
23029	2014, 2015				1	OSU
23030	2014, 2015				1	OSU
23035	2011, 2015				4	Happywhale
Humpback whales tagged in Hawaii – 2015 and 2018						
827		2005, 2015			10	Happywhale
1390		2015, 2018			3	Happywhale
836		2005, 2018			13	Happywhale

5655		2008, 2014, 2018			10	Happywhale
5685		2018		2013, 2014, 2015, 2016, 2017, 2018	5	Happywhale, Island Adventures Whale Watching
5736		2014, 2018			4	Happywhale
5826		2004, 2018			14	Happywhale

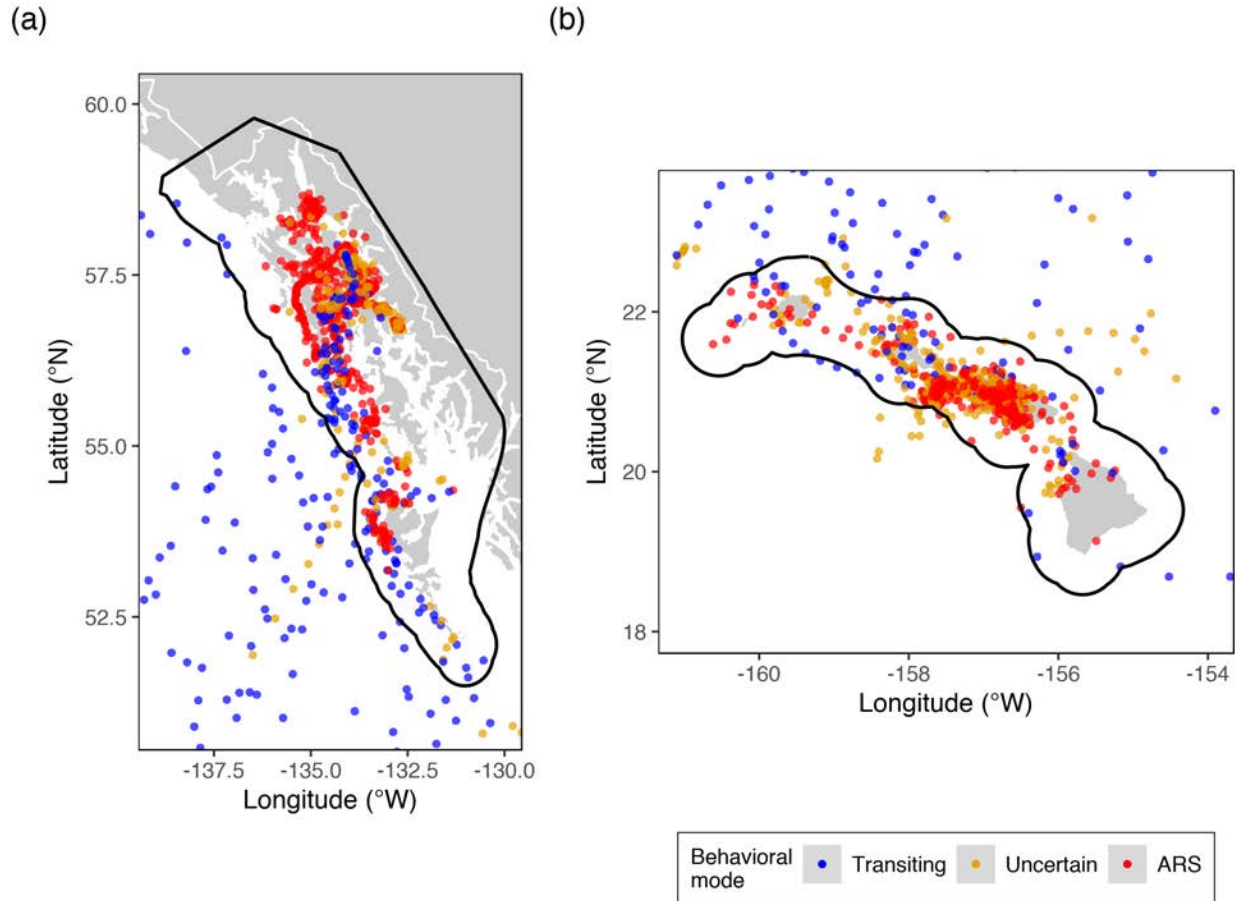


Figure 1. The boundary of the 50-km buffer zone (black polygon) around (a) the southeastern Alaska feeding area and (b) the Hawaii breeding area, the two areas where humpback whales were tagged in this study. Points are locations estimated by SSSM/hSSSMs applied to the raw Argos tracking data, with colors indicating estimated behavioral mode, as shown in the key. Both maps show that at 50 km from the coastline all locations switched from ARS (resident) to transiting (migration) behavior, so this distance was used for purposes of characterizing whale movements and residence time in the feeding and breeding areas (inside the buffer zones) as well as during migration (outside the buffer zones).

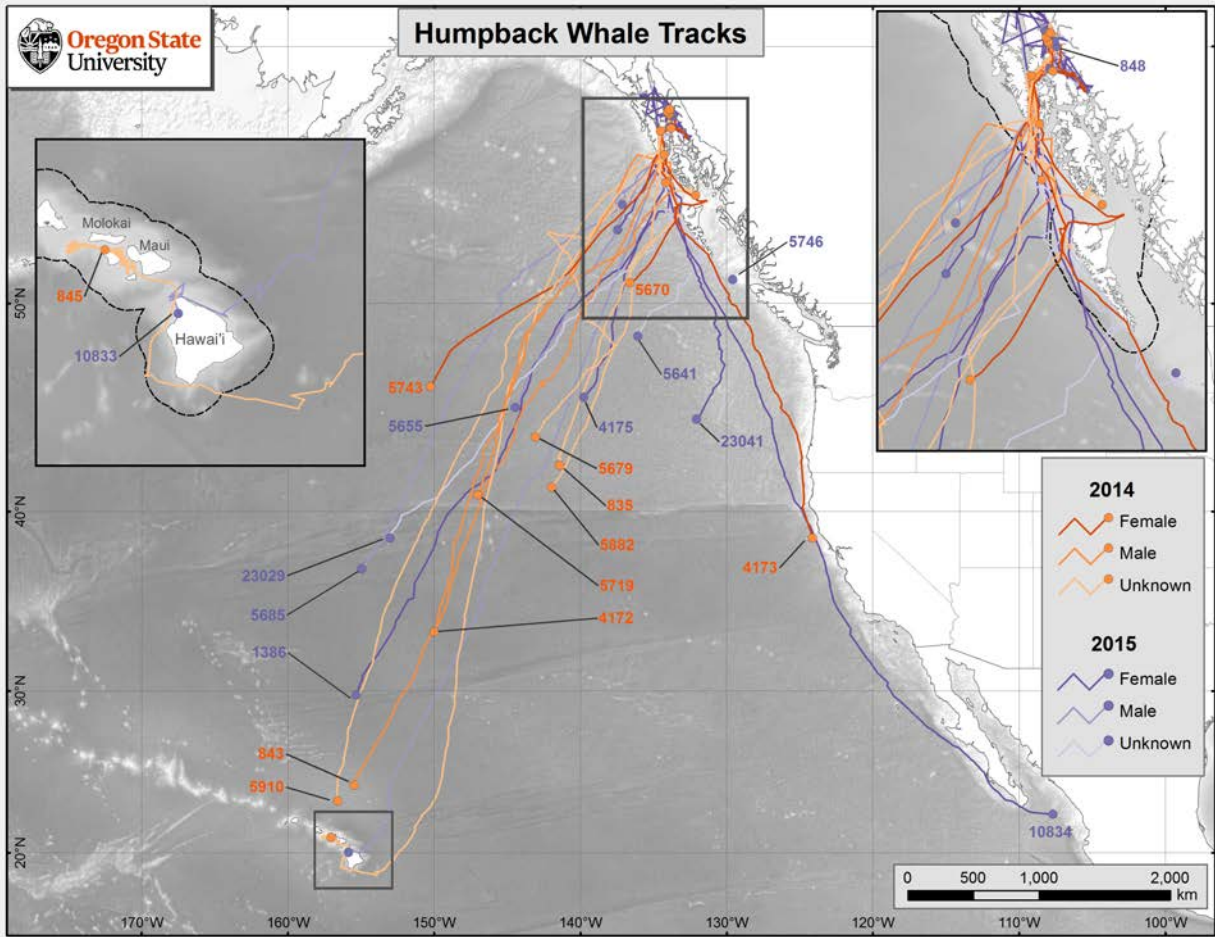


Figure 2. The satellite-monitored tracks of humpback whales tagged in southeastern Alaska in 2014 (n = 20; in orange) and 2015 (n = 17; in purple). Sex, when known, is indicated by line tone, as shown in the key. Right inset map shows departure points from southeastern Alaska for 20 animals for which the start of migration was recorded. Left inset map shows the final approach, arrival, and movements in Hawaiian waters for two animals for which the complete migration to Hawaii was recorded. The black dashed polygons in the inset maps correspond to the boundary of the 50-km buffer zones around southeastern Alaska and Hawaii.

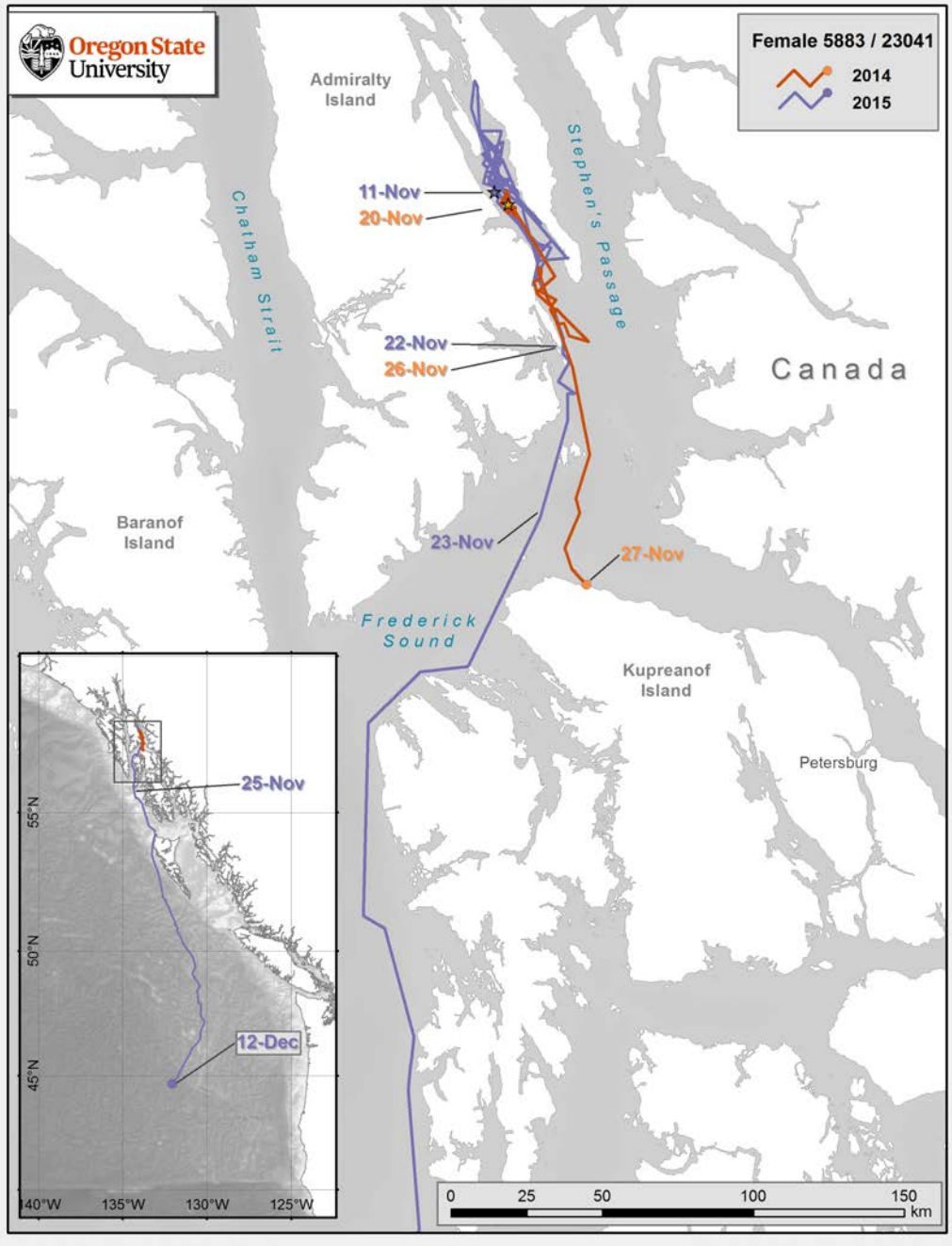


Figure 3. The satellite-monitored tracks of a female humpback whale tagged in 2014 (tag 5883, biopsy sample Mno14AK010; in orange) and re-tagged in 2015 (tag 23041, biopsy sample Mno15AK003; in purple) in southeastern Alaska. The tagging dates and locations are indicated by a star, and the last location received by a circle. The movements and timing within southeastern Alaska were similar between the two years.

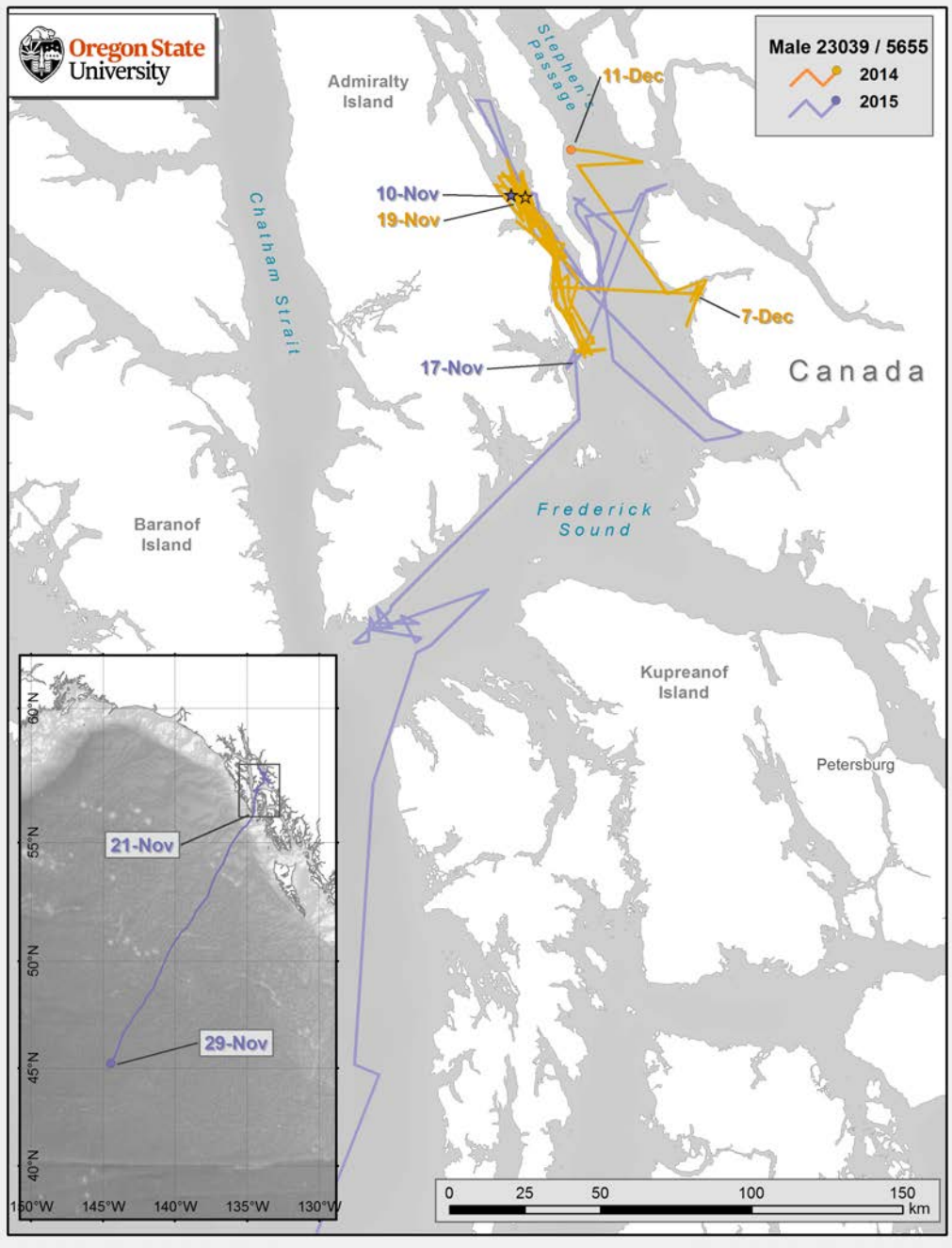


Figure 4. The satellite-monitored tracks of a male humpback whale tagged in 2014 (tag 23039, biopsy sample Mno14AK006; in orange) and re-tagged in 2015 (tag 5655, biopsy sample Mno15AK001; in purple) in southeastern Alaska. The tagging dates and locations are indicated by a star, and the last location received by a circle. The movements within southeastern Alaska were similar between the two years but the timing was different despite only a nine-day calendar date difference in tag deployment.

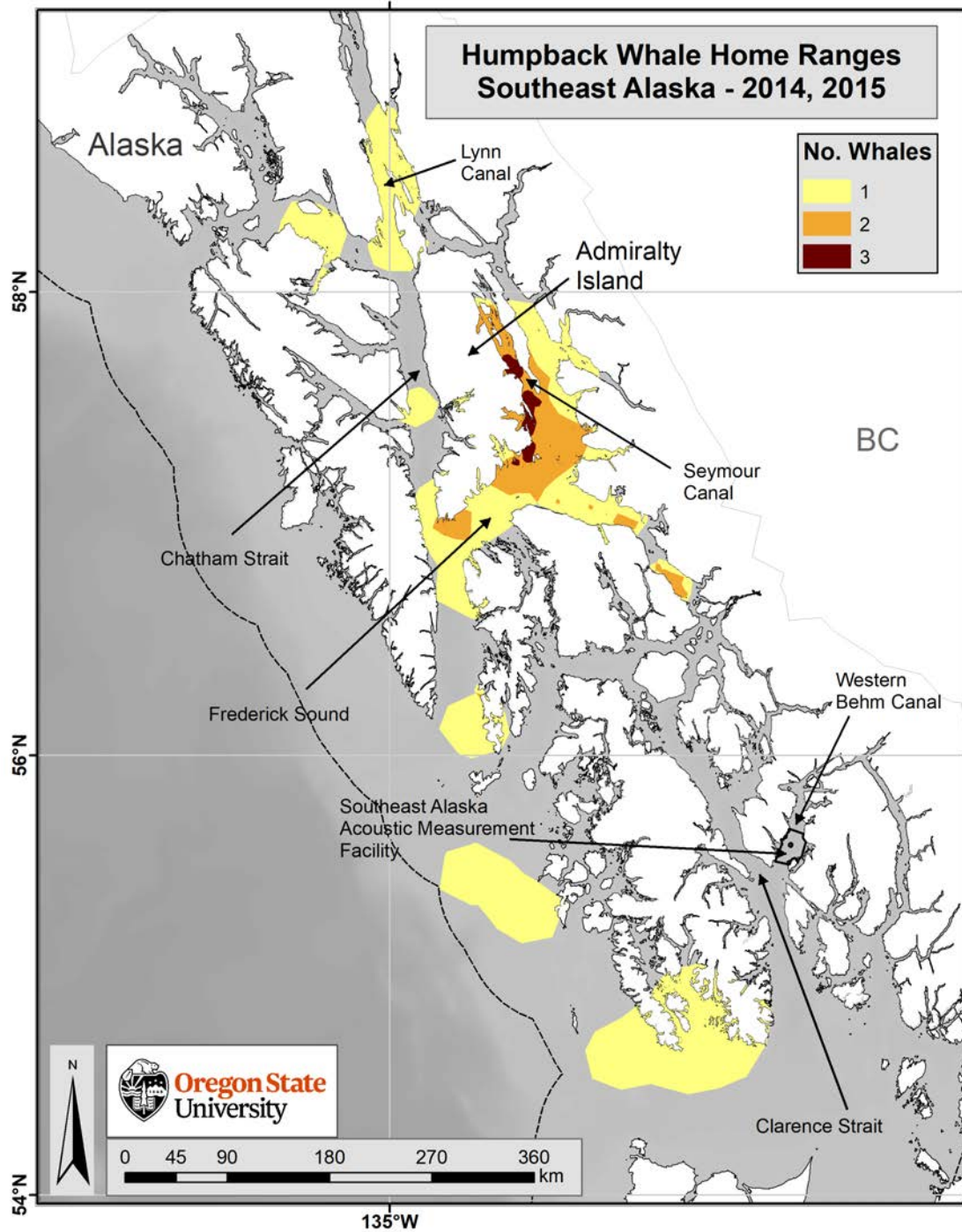


Figure 5. Feeding-area kernel home ranges for the SSSM tracks of humpback whales tagged in southeastern Alaska in 2014 and 2015 ($n = 5$ track portions lasting more than 30 d). Shading represents the number of individual whales with overlapping home ranges, as indicated in the key. The black dashed polygon corresponds to the boundary of the 50-km buffer zone delineating the southeastern Alaska feeding area.

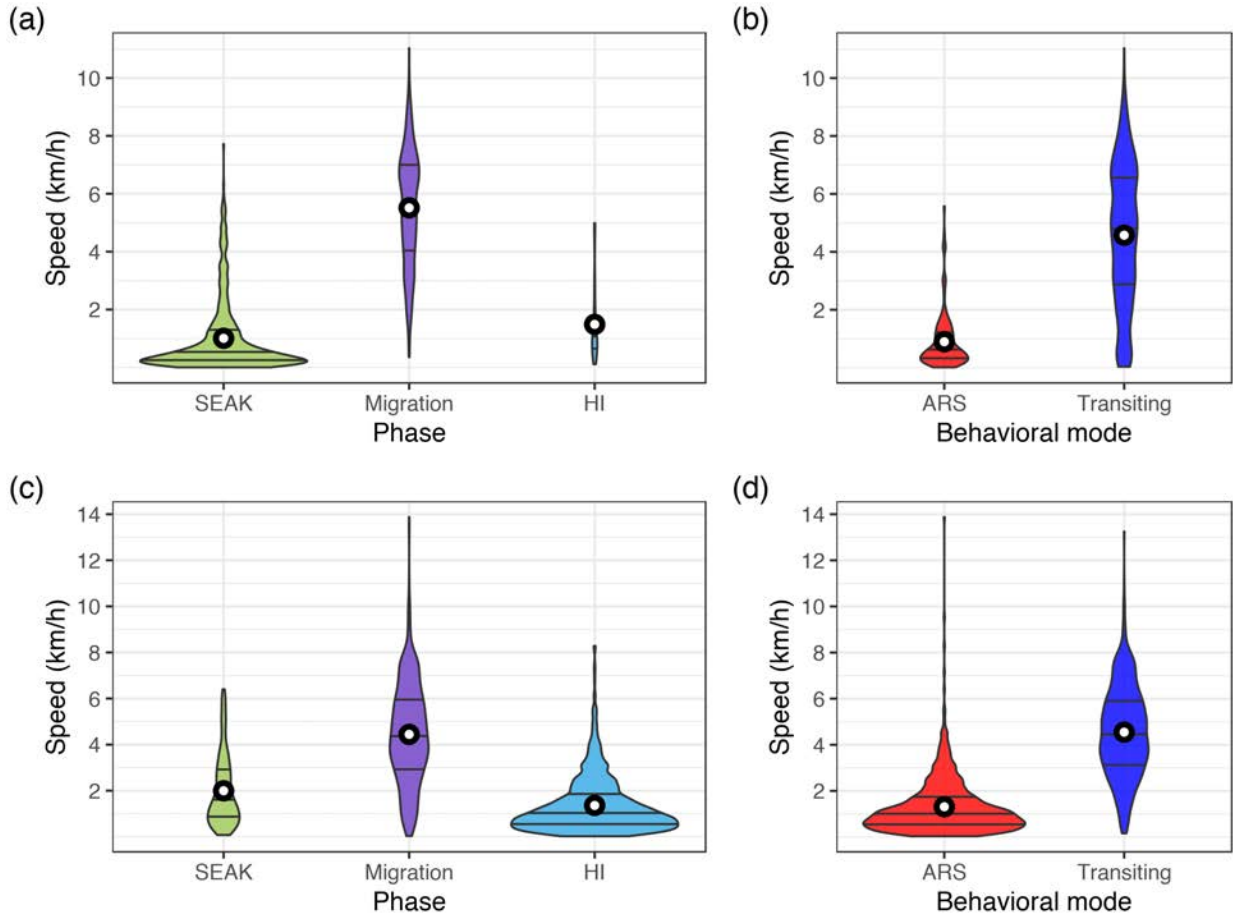


Figure 6. Violin plots of travel speed (in km/h) between location pairs for 76 humpback whale tracks on which SSSM/hSSSM were run. Top panels (a and b) show the data for animals tagged in southeastern Alaska (SEAK) in 2014 and 2015, and bottom panels for animals tagged in Hawaii (HI) in 2015 and 2018 (c and d). Left panels (a and c) show the data by migration phase, as determined by occurrence inside or outside the 50-km buffer zones, and right panels (d and d) by behavioral mode. Horizontal lines inside the violins correspond to the sample quartiles and the circle corresponds to the mean. Violin areas are scaled proportionally to the number of observations in each grouping, as reported in Table 3.

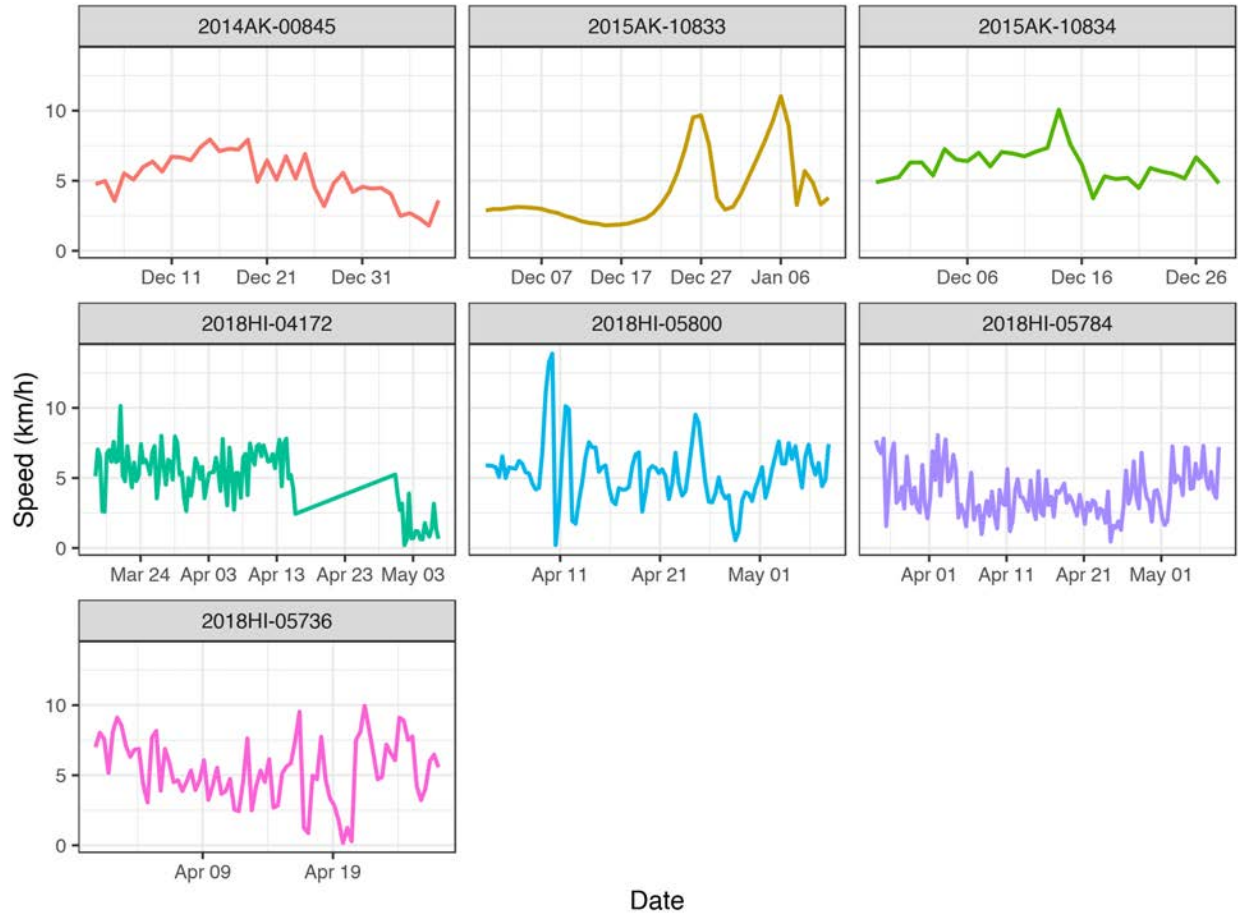


Figure 7. Travel speed (in km/h) along time during the migration phase for the seven SSSM/hSSSM tracks that lasted until arrival at the migratory destination, as reported in Table 2. Tag numbers are shown above each panel along with year and deployment area (HI = Hawaii, AK = southeastern Alaska).

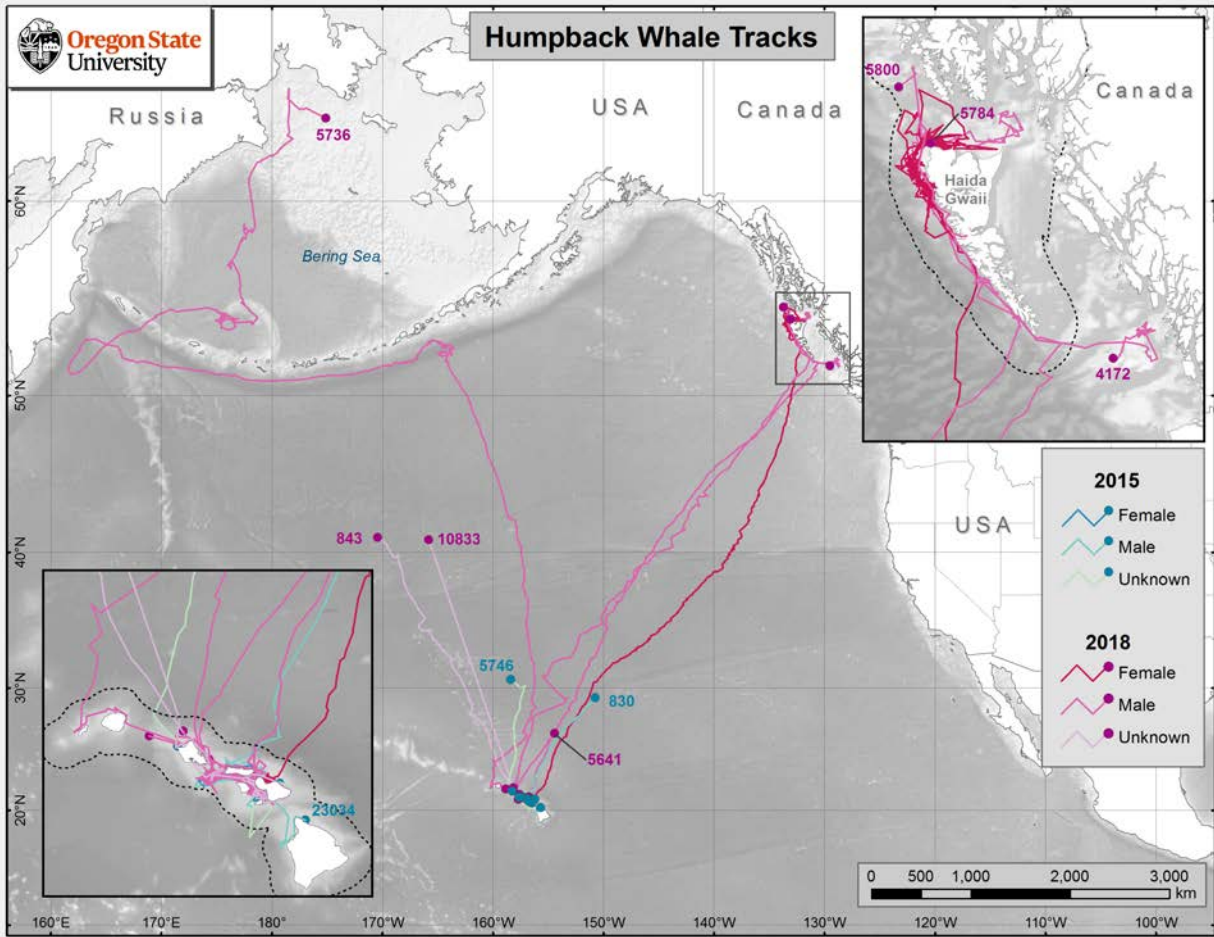


Figure 8. The satellite-monitored tracks of humpback whales tagged in Hawaii in 2015 ($n = 20$; in blue) and 2018 ($n = 25$; in pink). Sex, when known, is indicated by line tone, as shown in the key. Lower left inset map shows departure points from the main Hawaiian Islands for nine animals for which the start of migration was recorded. Upper right inset map shows the final approach, arrival, and movements in Haida Gwaii waters for three animals for which the complete migration to the southeastern Alaska/northern British Columbia feeding area was recorded. A fourth complete migration was recorded for an animal that arrived in the eastern Aleutian Islands feeding area, and subsequently moved to Kamchatka and the Bering Sea. The black dashed polygons in the inset maps correspond to the boundary of the 50-km buffer zones around southeastern Alaska and Hawaii.

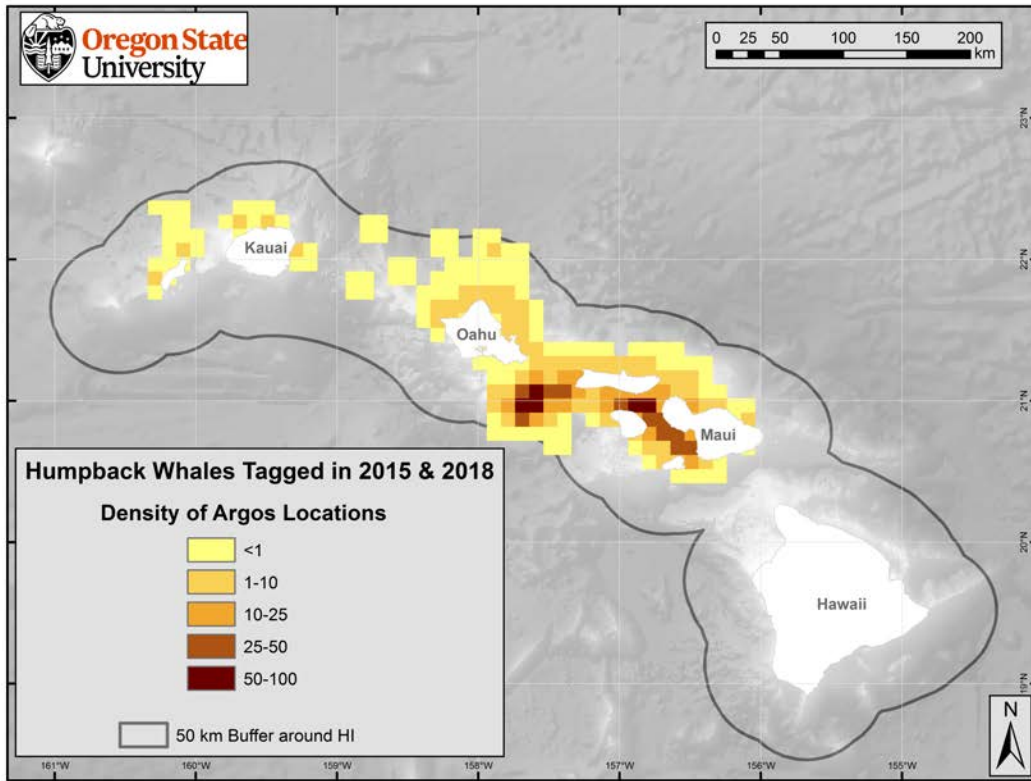
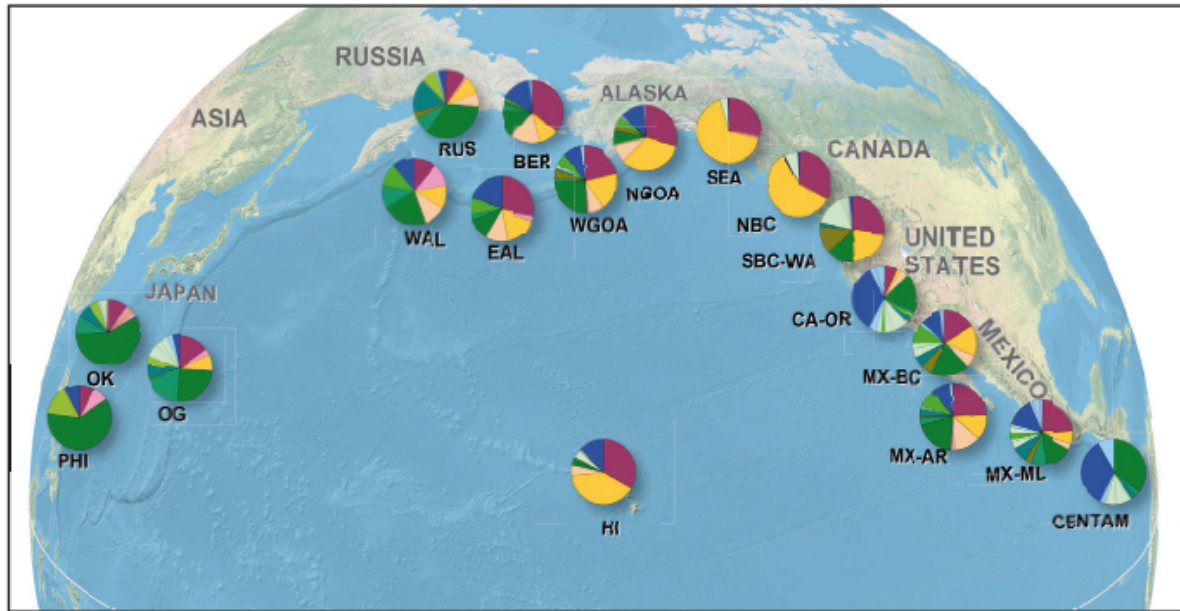


Figure 9. Breeding-area kernel density estimates for Argos locations from 21 humpback whales tagged off Maui, Hawaii, in 2015 and 2018, and tracked for at least 10 d within the breeding area. Grid cell size is 0.1×0.1 degrees. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaii breeding area.

a)



b)

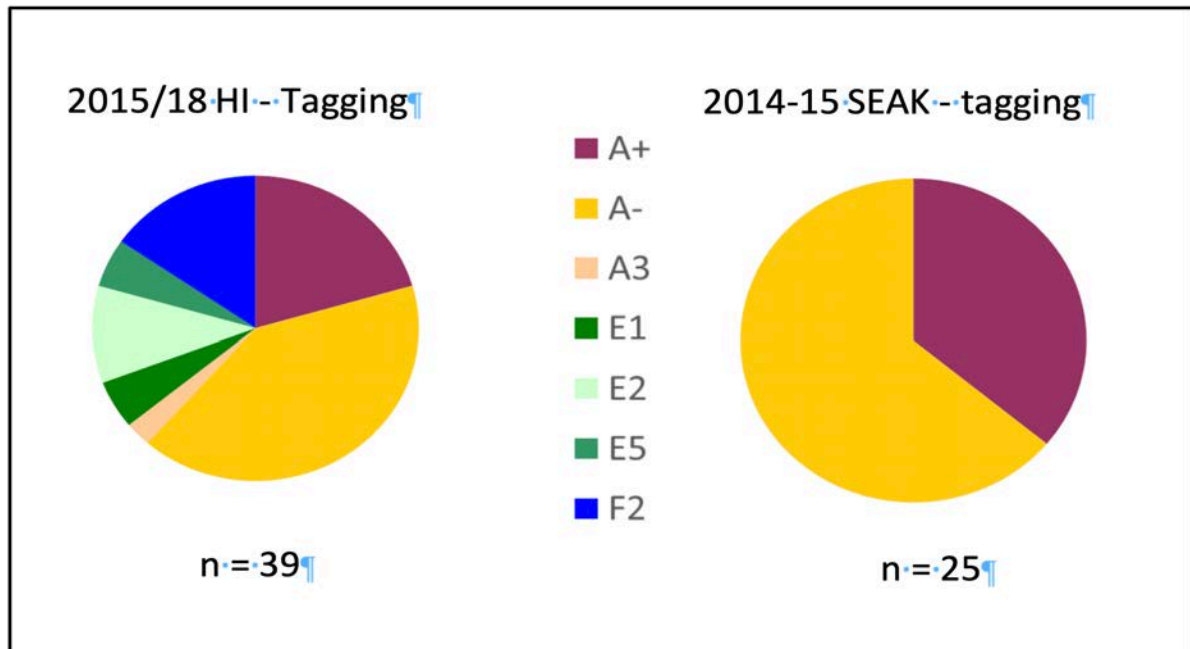


Figure 10. (a) The proportion of mtDNA haplotypes for individual humpback whales sampled in the 10 feeding areas and on the eight breeding grounds in the North Pacific during the SPLASH program, as modified from Figure 2 in Baker et al. (2013). (b) Proportion of mtDNA haplotypes for individual humpback whales biopsy-sampled during tagging efforts in Hawaii (HI) in 2015 and 2018 (left) and in southeastern Alaska (SEAK) in 2014 and 2015 (right).

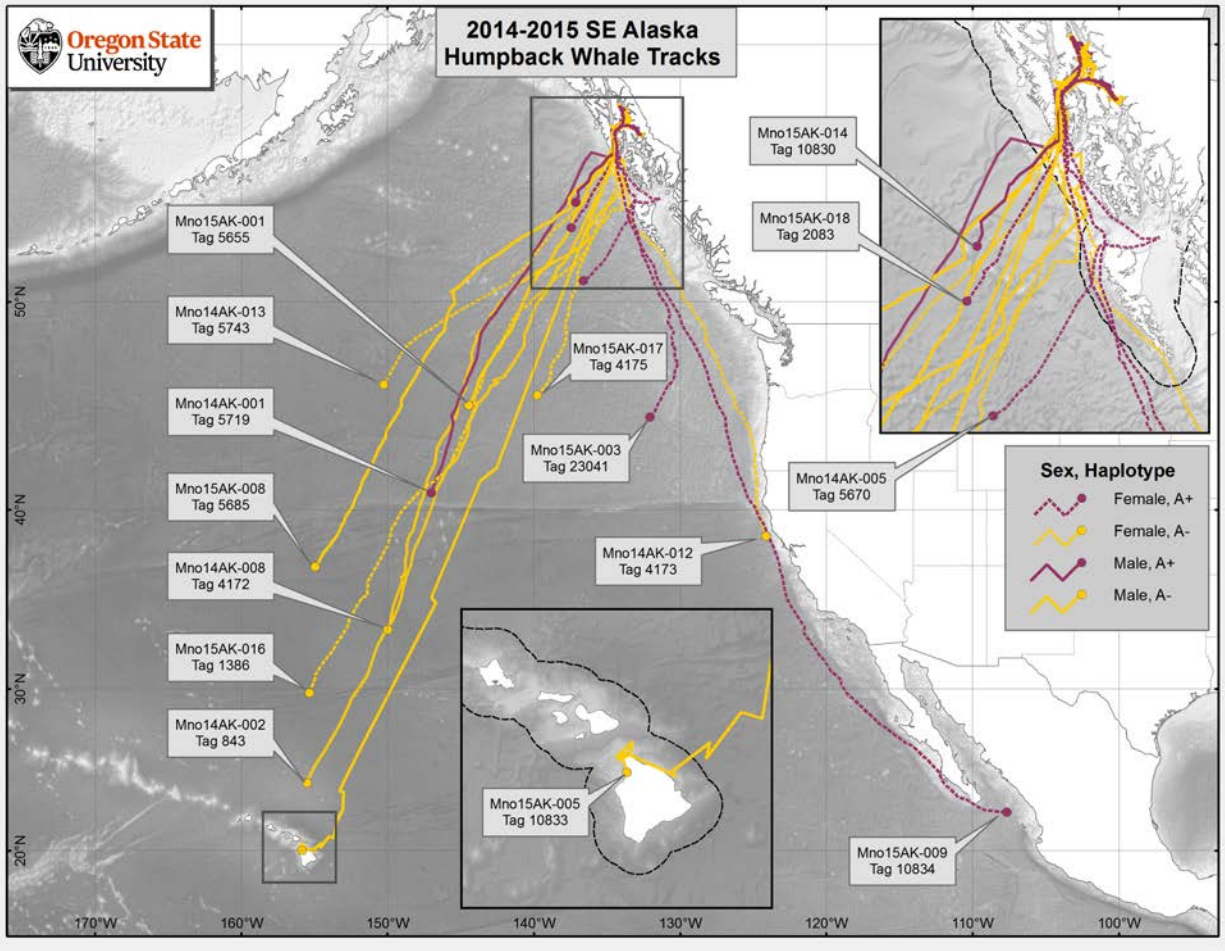


Figure 11. The migratory destinations or partial trajectories of 25 tracked animals for which a biopsy sample was collected in southeastern Alaska during the 2014 and 2015 field efforts. Individual haplotypes are colored according to Figure 10, and sex is indicated by line decoration (dashed for females, solid for males), as shown in the key. Upper right inset map shows the departure points from southeastern Alaska for 13 animals for which the start of migration was recorded. Lower left inset map shows the final approach, arrival, and movements in Hawaiian waters for one biopsied animal for which the complete migration was recorded. The black dashed polygons in the inset maps correspond to the boundary of the 50-km buffer zones around southeastern Alaska and Hawaii.

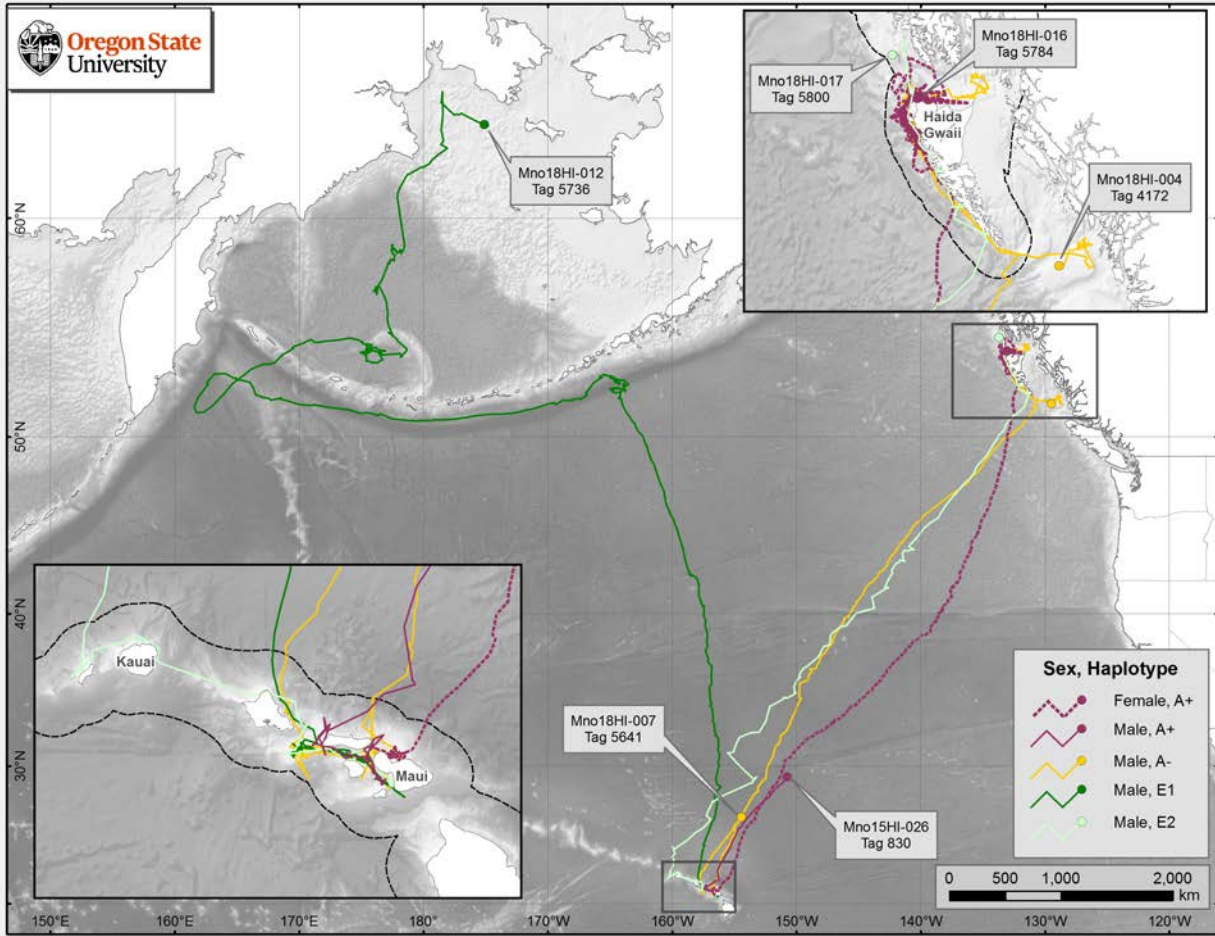


Figure 12. The migratory destinations or partial trajectories of six tracked animals for which a biopsy sample was collected in Hawaii during the 2015 and 2018 field efforts. Individual haplotypes are colored according to Figure 10, and sex is indicated by line decoration (dashed for females, solid for males), as shown in the key. Lower left inset map shows departure points from the main Hawaiian Islands for six animals for which the start of migration was recorded. Upper right inset map shows the final approach, arrival, and movements in Haida Gwaii waters for three biopsied animals for which the complete migration to the southeastern Alaska/northern British Columbia feeding area was recorded. A fourth complete migration was recorded for a biopsied animal that arrived in the Aleutian Islands feeding area, and subsequently moved to Kamchatka and the Bering Sea. The black dashed polygons in the inset maps correspond to the boundary of the 50-km buffer zones around southeastern Alaska and Hawaii. Note that tag 5784 (biopsy sample Mno18HI016, a female) was also matched by genotypes to a whale identified in Haida Gwaii in 2005 during SPLASH (SPLASH ID 560234).

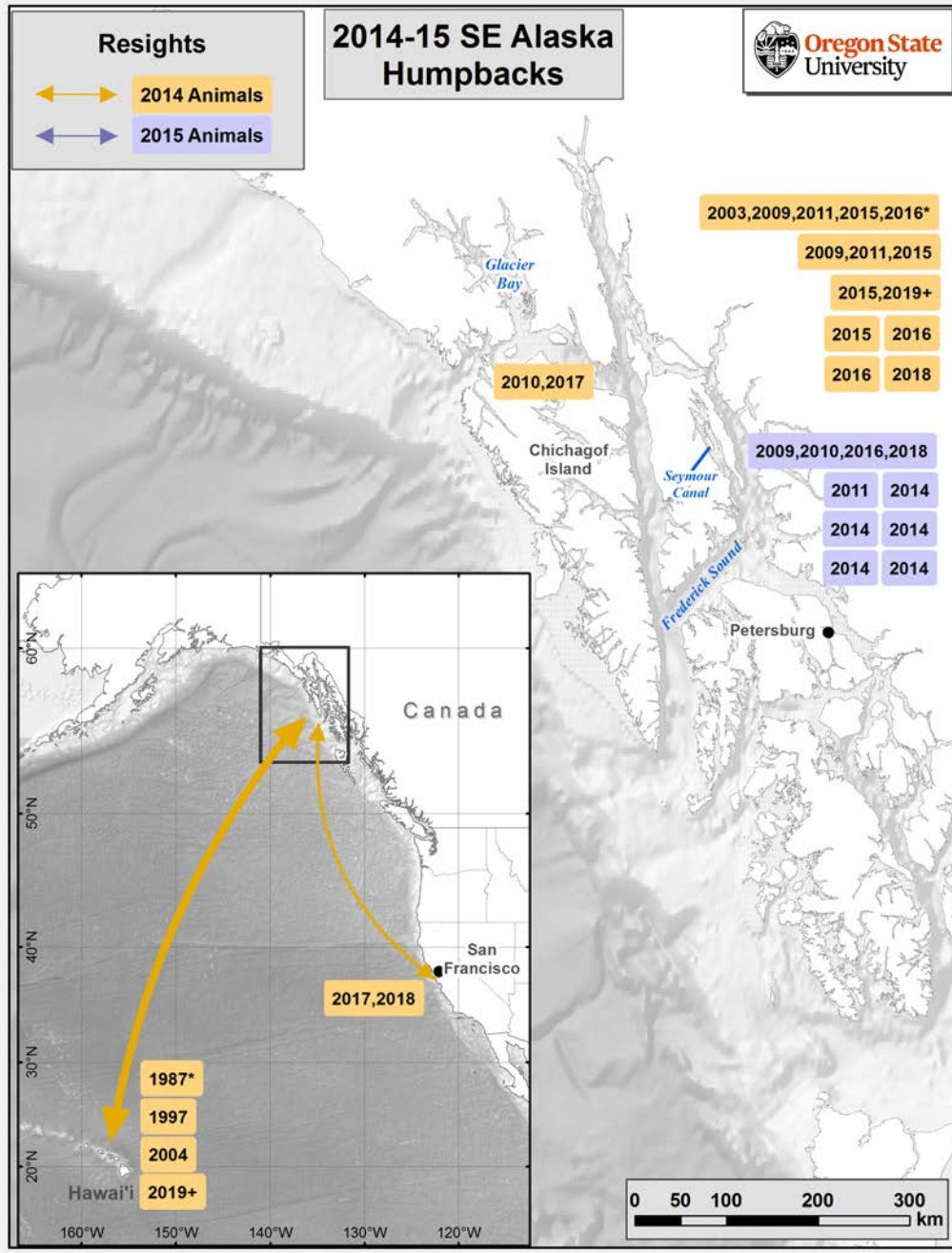


Figure 13. Photo-ID matches in Happywhale for whales photographed by OSU in southeastern Alaska in 2014 (orange cells and arrows) and 2015 (purple cells). Matches within southeastern Alaska are shown in the main map and matches to other areas of the North Pacific are shown in the inset map. Each cell represents an individual animal. The years an individual whale was photographed are listed inside each cell. Symbols next to the years (*, +) are paired to indicate individuals that were matched across regions in addition to being matched within a region. Note that only tagged whales are shown, as photographs of untagged whales for these years have not yet been submitted to Happywhale.

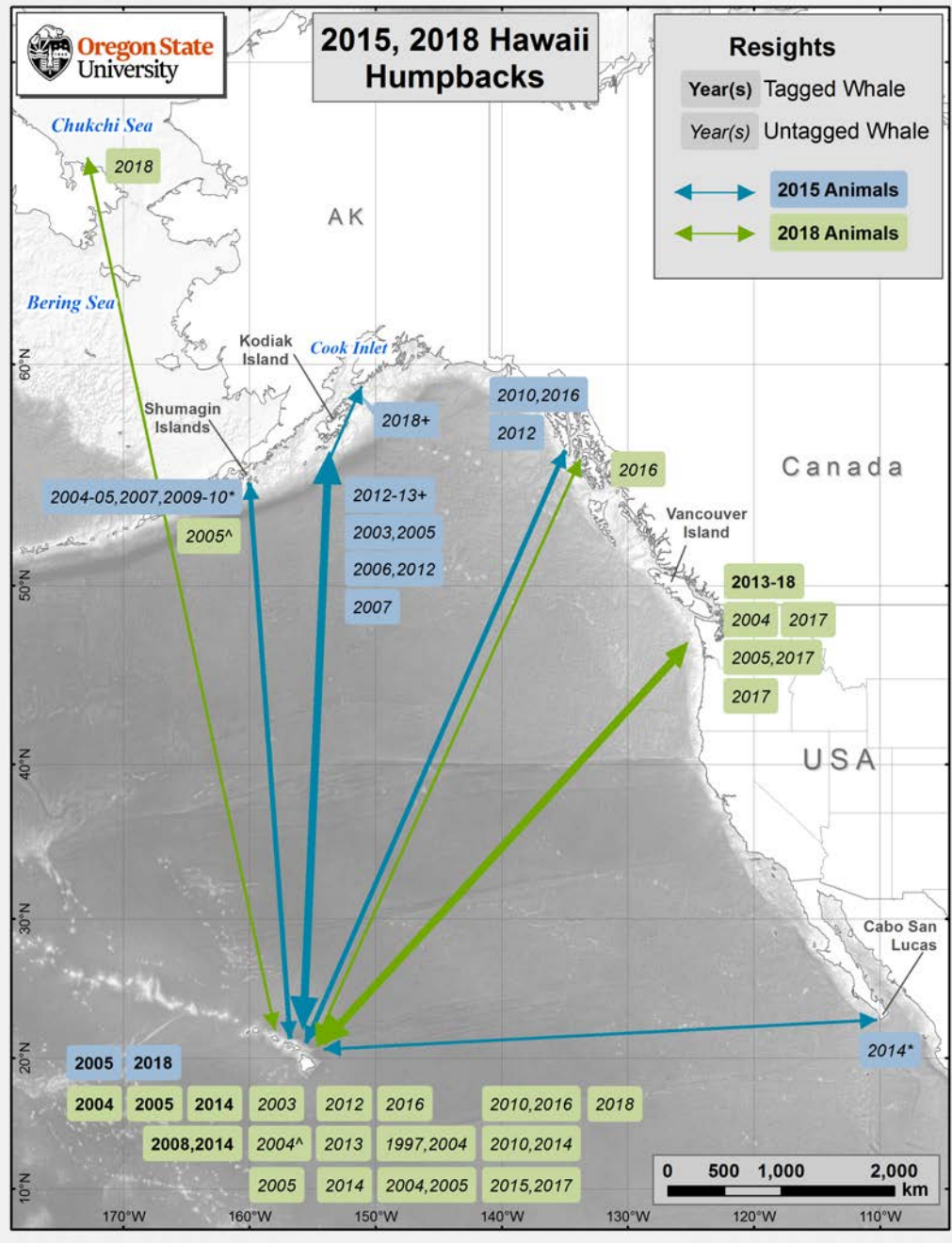


Figure 14. Photo-ID matches in Happywhale for whales photographed by OSU in Hawaii in 2015 (blue cells and arrows) and 2018 (green cells and arrows). Each cell represents an individual animal, with tagged whales represented in bold font and untagged whales in italics. The years an individual whale was photographed are listed inside each cell. Symbols next to the years (*, +, ^) are paired to indicate individuals that were matched across regions in addition to being matched within a region.