HUMPBACK WHALE TAGGING IN SUPPORT OF MARINE MAMMAL MONITORING ACROSS MULTIPLE NAVY TRAINING AREAS IN THE PACIFIC OCEAN

Final Report for the Hawaiian Breeding Area in Spring 2018, Including Historical Data from Previous Tagging Efforts

Prepared for

Commander, U.S. Pacific Fleet and
Commander, Naval Sea Systems Command

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14. ABSTRACT
Three of the 14 Distinct Population Segments (DPSs) of humpback whales (Megaptera novaeangliae) recently designated by the National Marine Fisheries Service (NMFS) for listing under the Endangered Species Act (ESA) based on their winter breeding grounds ("Hawaii", "Mexico", and "Central America"), can be found along the western coast of North America during the feeding season. The mixing of whales from these DPSs in the feeding areas in different proportions complicates unequivocal assignment of individuals to breeding stock for management purposes without further information. As a result, there is an urgent need for data on occurrence and habitat use by these different DPSs throughout their range, as well as on their overlap with shipping traffic, fishing grounds, and areas of military operation, in order to prioritize management actions and to mitigate the impacts from these activities.

In 2018, Oregon State University (OSU) conducted a tagging and tracking study on Eastern North Pacific humpback whales to determine their movement patterns, occurrence, and residence times within United States (US) Navy training and testing areas in Hawaii and elsewhere in the North Pacific. This work was performed under a Cooperative Ecosystem Studies Unit (CESU) agreement in support of the

Navy's efforts to meet regulatory requirements for marine mammal monitoring under the ESA and the US Marine Mammal Protection Act. This report presents detailed results from the tagging, biopsy sampling, and photo-identification (photo-ID) efforts conducted in Hawaii in 2018, as well as results from previous OSU studies of humpback whales in Hawaii from 1995 to 2015. Whale use of Navy training and testing areas as well as their use of NMFS-identified Biologically Important Areas (BIAs) in Hawaii and Alaska is also examined.

Two types of fully implantable tags were used in 2018: Telonics Dive Monitoring (DM) tags, providing long-term tracking information via the Argos satellite system as well as dive behavior (duration, depth, and number of lunges per dive), and Telonics Dive Duration Monitoring Plus (DUR+) tags, providing longterm Argos tracking and dive behavior (duration and number of lunges per dive), without depth information. Both tag types followed the same general physical design as OSU's earlier Location-Only (LO) tag used during the historic tagging efforts from 1997 to 2000 and 2015). Externally-mounted tags, an early design no longer in use, were deployed during the 1995 and 1996 tagging efforts off Kauai and Hawaii. Twenty-five humpback whales (20 DM tags, 5 DUR+ tags) were tagged off Maui in March 2018. Argos locations were received from 22 of the 25 tags, with tracking periods ranging from 1.1 to 160.0 days (d) (mean = 25.8 d, standard deviation [SD] = 40.0 d, n = 17) for DM tags, and ranging from 2.2 to 104.5 d (mean = 33.5 d, SD = 43.4 d, n = 5) for DUR+ tags. A total of 77 humpback whales were tagged by OSU in Hawaii prior to 2018, covering the period 1995 to 2000, and 2015. Of these, 61 were deployed off Maui (in 1997, 1998, 1999, 2000, and 2015); 10 were deployed off Kauai (in 1995, 1996, and 1997); and 6 were deployed off Hawaii (in 1996). Tracking data was obtained for 59 whales (the remaining tags provided no locations), with tracking durations ranging from 0.04 to 152.8 d. For implantable tags, tracking periods for whales that migrated away from the Hawaiian archipelago (mean = 64.7 d, SD = 45.0, maximum = 160.0 d, n = 22) were longer than for whales that were only tracked within the archipelago (mean = 11.8 d, SD = 10.9 d, maximum = 44.4 d, n = 50). Hierarchical switching state-space models (hSSSM) were applied to the Argos locations from the DM and DUR+ tags deployed in 2018, and conventional switching state-space models (SSSM) to the Argos locations from the historical LO tags for the purpose of generating regularly spaced tracks with annotated movement behavior for use in analyses of dive behavior.

The aggregate tracking results within Hawaii support results of previous photo-ID studies and aerial surveys, showing high densities of whales in the Maui Nui region (the inner waters of the "four-island region" of Maui, Molokai, Lanai, and Kahoolawe, as well as Penguin Bank, and extensive interchange within the islands. Data from this study demonstrated that mean residence time in Hawaii from tagging to departure (for whales with known departure date from the archipelago) was 12.3 d (range = 1.1-42.8 d, SD = 9.9 d, n = 25), and was lower for females with a calf (mean = 10.4 d, range = 2.7-22.6 d, n = 3) than for males (mean = 15.8 d, range = 3.3-42.8 d, n = 8), lending support to earlier studies that found that there is a rapid turnover of individuals in this breeding area during the winter season, as well as differences between the sexes (although the sample size for females was quite small and did not include females without a calf). Migratory destinations were tracked for nine humpback whales tagged off Maui, supporting previous telemetry, genetic, and photo-ID studies, with five whales going to northern British Columbia and Southeast Alaska, and four going to the eastern Aleutian Islands. One of the latter four whales continued on to the Kamchatka Peninsula, while another traveled to the western end of the Aleutian Island chain off Kamchatka, then to the Bowers Basin in the southwestern Bering Sea, and ultimately north into the Gulf of Anadyr, Russia, just south of the Bering Strait.

A limited number of tagged whales spent time in the Navy training ranges off Hawaii, with Area W188A being the most heavily used (15 percent of tagged whales), followed by Area W188B (14 percent of tagged whales). Even fewer whales (7 percent of less) used the other ranges. A higher proportion of whales tagged off Kauai spent time in the Navy ranges compared to those tagged off Maui. No whales tagged off the island of Hawaii had locations in any of the Navy ranges. This is not surprising, with the ranges' close proximity to Kauai. The longest time spent within a Navy range (13.3 d), however, was from a whale tagged off Maui. More tagging off Kauai would improve our understanding of training range use by humpback whales in Hawaii and help determine whether the minimal use noted here is simply a function of tagging location bias. None of the tagged humpback whales from Hawaii were tracked within any Navy training areas along the US West Coast, but our small sample size of migrating whales reaching a feeding destination likely contributed to this finding, as our photo-ID data indicated matches to Washington and southern British Columbia.

Tagged humpback whales spent time in all Hawaiian BIAs, with the vast majority of locations occurring in the Maui BIA, where maximum residency was 30.2 d. This was not surprising, as most of the tag deployments took place within this BIA. More tagging off the islands of Hawaii and Kauai would further our understanding of BIA use in those areas. Of the five humpback whales migrating to the northwestern coast of the US and Canada, only two were tracked within the Southeast Alaska BIA. However, their residency there was extensive (maximum of 70 d), and could have been longer had the tags continued to transmit. Humpback whale use of feeding area BIAs outside the Southeast Alaska BIA was minimal, due in part to the small number of whales tracked to these areas, but also for the whales' preference for the southern and western side of the Aleutian Island chain. An area of high use approximately 160 km south of Akutan Island and Unimak Pass by two humpback whales tagged 19 years apart highlights this area as important feeding habitat for some humpbacks. The north and west coasts of Haida Gwaii, British Columbia, Canada, were also shown to be high use areas.

In 2018, DM and DUR+ tags summarized dives for a mean of 60.6 percent of the tracking duration. Dives on the breeding grounds were generally shallow (< 100 meters [m]), with occasional dives reaching 400 m. However, maximum dive depth was likely limited by bottom depth in many cases, and there were no discernable spatial patterns to dive behavior. Dive behavior during migration was generally similar to on the breeding grounds. However, for the first 7-14 d of migration whales consistently made deep (> 200 m), long-duration (> 15 minutes [min]) dives at night. The purpose of these dives is unclear, but may be related to acoustic orientation or magnetic navigation. Dives on the feeding grounds were very different between the two areas occupied (Haida Gwaii/Southeast Alaska versus eastern Aleutians/Kamchatka/Gulf of Anadyr). One whale (#5736, a male) showed a consistent diel trend in both dive duration and dive depth near the Aleutian Islands and in the western Bearing Sea, while the whales near Haida Gwaii showed no temporal trends and made generally shallower dives.

Biopsy samples were collected from 23 of the 25 tagged whales in Hawaii in 2018. Mitochondrial deoxyribonucleic acid (DNA) sequences of the samples resolved six haplotypes for the consensus region of 500 base-pairs. All haplotypes have been previously described for North Pacific humpback whales. All samples were identified by a unique multi-locus genotype of at least 14 loci, indicating that each sample represented an individual whale. The 23 Hawaii individuals represented three females and 20 males. The DNA profiles of the 23 individuals were compared to a reference database of 1,805 individuals sampled previously in the North Pacific by the program SPLASH, and two matches (i.e., genotype recaptures) were detected, one to an individual sampled in Hawaii in 2004 and one to an individual sampled in northern British Columbia in 2005.

Of the 25 whales tagged in Hawaii in 2018, 14 had fluke photos that could be used for identification purposes. Out of these 14 whales, one had been previously identified in the Happywhale photo-ID database. This whale had been sighted off Washington State and Vancouver Island, Canada, going back to 2013. It was resighted after tagging in the Straights of Georgia east of Vancouver Island in May, August, and September 2018. Out of the other 74 photo-IDs collected by OSU of non-tagged whales in Hawaii during 2018, five had also been previously identified in the Happywhale photo-ID database. Four of these were new records for Hawaii, although they had been previously sighted off Washington State (3) and west of Vancouver Island (1). One whale had been sighted by OSU during tagging efforts off Oregon in 2017. Photographs of two Hawaii-tagged whales that were resighted by other researchers after migrating to waters near Vancouver Island allowed us to make an assessment of the tag site and conclude that they were healing normally.

With the first year of this CESU agreement to study humpback whales in Hawaii through the use of satellite telemetry, dive behavior, genetics, and photo-ID, we have characterized this DPS' breedingseason occupation, connectivity, and residence time, and use of Navy training and testing areas as well as NMFS-designated BIAs. The results of this study have also revealed the complex migratory linkages of this DPS to high-latitude feeding areas. The Hawaii field efforts so far have concentrated around the Maui Nui region. Additional years of sampling with increased effort during different parts of the reproductive season, 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 Papahanaumokuakea 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 Ocean, some of which may be related to reproductive timing.

15. SUBJECT TERMS

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Executive Summary

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Acronyms, Abbreviations, and Units

°C	Degrees Celsius
ANOVA	Analysis of variance
Area W188(A)	Warning Area-188(A) within the Hawaii Range Complex that includes the Pacific Missile Range Facility
Area W188(B)	Warning Area-188(B) within the Hawaii Range Complex
Area W186	Warning Area-186 within the Hawaii Range Complex
Area W237	Warning Area-237 within the Northwest Training and Testing Study Area
ARS	Area-restricted searching
BARSTUR	Barking Sands Tactical Underwater Range
BIA	Biologically Important Area
bp	Base pair
BSURE	Barking Sands Underwater Range Expansion
CESU	Cooperative Ecosystem Studies Unit
cm	Centimeter
d	Day
deg	Degrees
DM	Dive-Monitoring tag (model Telonics RDW-665)
DNA	Deoxyribonucleic acid
DON	Department of the Navy
DPS	Distinct Population Segment
DUR	Duration-only tag (model Telonics RDW-640)
EEZ	Exclusive Economic Zone
ESA	Endangered Species Act
g	Gram
GOA	Gulf of Alaska Temporary Maritime Activities Area

h	Hour
HR	Home range
HRC	Hawaii Range Complex
hSSSM	Hierarchical switching state-space model
IACUC	Institutional Animal Care and Use Committee
ID	Identification
km	Kilometer
LC	Argos location class
LO	Location-Only tag (either model Telonics ST-15, or models Wildlife Computers SPOT6 or SPOT6)
m	Meter
min	Minute
mm	Millimeter
MMPA	Marine Mammal Protection Act
mo	Month
mtDNA	Mitochondrial deoxyribonucleic acid
NAVFAC	Naval Facilities Engineering Command
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NWTRC	Northwest Training Range Complex
NWTT	Northwest Training and Testing Study Area
OSU	Oregon State University
PCR	Polymerase chain reaction
PDI	Post-dive interval
PMRF	Pacific Missile Range Facility
PT MUGU	Point Mugu Range Complex

R/V	Research Vessel
s	Second
SD	Standard deviation
SEAK	Summer and fall Southeast Alaska Biologically Important Area
SEAFAC	Southeast Alaska Acoustic Measurement Facility
SOAR	Southern California Anti-submarine warfare Offshore Range subarea
SOCAL	Southern California Range Complex
SPLASH	Structure of Populations, Levels of Abundance and Status of Humpbacks program
SSSM	Conventional switching state-space model
SWS	Saltwater conductivity switch
US	United States
V	Volt

1 Introduction

The purpose of this Cooperative Ecosystem Studies Unit (CESU) agreement between the Department of the Navy (Navy) and Oregon State University (OSU) is to support marine mammal studies in compliance with the Letters of Authorization and Biological Opinions issued by the United States (US) National Marine Fisheries Service (NMFS) to the Navy for activities in all Pacific Ocean testing and training range complexes. With regard to humpback whales (*Megaptera novaeangliae*), in 2016 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 2017) and the Central America DPSs (estimated at 783 animals; Wade 2017); "Threatened" for the Mexico DPS (estimated at 2,806 animals; Wade 2017); and "Not Listed" for the Hawaii DPS (estimated at 11,571 animals; Wade 2017) (Federal Register 2016a, b).

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 Southeast Alaska and northern British Columbia; Mexico animals being found off northern Washington-southern British Columbia; and Central America animals being found off 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 etal. 2015). The mixing of whales from these DPSs in the feeding areas in different proportions complicates unequivocal assignment of individuals to breeding stock for management purposes without further information. As a result, there is an urgent need for data on occurrence and habitat use by these different DPSs throughout their range, as well as on their overlap with shipping traffic, fishing grounds, and areas of military operation, in order to prioritize management actions and to mitigate the impacts from these activities.

OSU conducted early tagging efforts on humpback whales in the Hawaiian breeding area between 1995 and 2000. These studies showed that some whales migrated north from Hawaii into the Gulf of Alaska, with some turning west towards Russia, while others migrated more directly from Hawaii to Southeast Alaska and northern British Columbia (Mate et al. 1998, Mate et al. 2007), with the implication that humpback whales from the Hawaii DPS may spend time in Navy activity areas throughout the Gulf of Alaska and the Pacific Northwest. However, it is unknown what portion of the Hawaii DPS is present in

[1] See: "Listing of Humpback Whale Under the ESA" https://www.fisheries.noaa.gov/action/listing-humpback-whale-under-esa

these feeding areas relative to the other North Pacific DPSs, or the proportion of time they spend in them.

Within Hawaii, the tracking studies revealed substantial inter-island movements from Kauai to Oahu to Maui Nui (i.e., the group of islands comprised by Maui, Molokai, Lanai, and Kahoolawe; also known as the "four-islands region"). The whales also made extensive use of the windward side of the islands and of the offshore Penguin Bank, areas where traditional fieldwork is often precluded due to prevalence of high winds (Mate et al. 1998, 2007). Additionally, the tracking data indicated that the whales' remaining residence time in the islands after tagging was, on average, only 13.4 days (d) regardless of the month of tagging (December, February, March or April) (Mate et al. 1998), lending support to earlier studies that found that there is a rapid turnover of individuals in the breeding area during the winter season (Craig et al. 1997, 2003, Darling 2009). Thus, tracking studies of humpback whales in the Hawaiian breeding area also provide valuable information that could be relevant to understanding how whales from the Hawaii DPS spend time in local Navy activity areas within Hawaiian waters.

Through the use of satellite telemetry, genetic analyses, and photo-identification (photo-ID), this CESU agreement option seeks to provide greater detail on the Hawaii DPS of humpback whales in terms of use of Navy activity areas in the North Pacific Ocean as well as in NMFS-identified Biologically Important Areas (BIAs) in US waters. As part of this CESU agreement, in spring 2018 OSU conducted new satellite tag deployments in Hawaii to track the migrations of humpback whales throughout the Pacific basin for multiple weeks to multiple months after deployment. This Final Report covers the results of those tagging efforts, and also includes comparison with the historical data from previous tagging efforts by OSU in Hawaii (1995-2000, 2015).

1.1 Study Goals

With this project, OSU sought to tag humpback whales and to collect photo-IDs and genetic samples (taken during tag placement) in Hawaii to describe their breeding-season occupation, connectivity, and residence time, as well as their migration to feeding areas, including habitat use. Data from tagged whales also provided detail on dive duration, feeding activity, and behavioral characteristics over periods spanning multiple weeks to multiple months. Specifically, the type and number of tags deployed in Hawaii in 2018 included:

- 20 Telonics RDW-665 Dive Monitoring (DM) satellite tags (equipped with depth sensors, accelerometers, and lunge-detection software) to monitor detailed diving (depth and duration) and movement behavior.
- 5 Telonics RDW-665 Dive Duration Monitoring Plus (DUR+) satellite tags (equipped with accelerometers and lunge-detection software, but not depth sensors) to monitor dive duration and movement behavior.

Additionally, through the collection of biopsy samples and genetic analyses of tagged whales, this study sought to provide:

- Sex determination

- Individual identification using mitochondrial haplotype sequencing and nuclear microsatellite loci, including matching with individually identifying photographs and tissue samples from whales previously sampled.
- Genetic profiling through mitochondrial haplotype sequencing and nuclear microsatellite loci, with population structure analysis including comparison to existing published databases for humpback whales in the Pacific Ocean.

2 Methods

2.1 Field Efforts

2.1.1 Tag Deployment

All tagging efforts were conducted from the 10-m R/V *Kohola*, chartered from the Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS). The tagging crew consisted of a tagger, biopsy darter, photographer, data recorder, and boat driver. Candidate whales for tagging were selected based on visual observation of body condition. No whales were tagged that appeared emaciated or that were 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-pound force per square inch in the applicator's 70-cubic centimeter pressure chamber.

2.1.2 Previous Tagging Efforts

Humpback whales were tagged by OSU during previous field seasons in Hawaii, from 1995 through 2000, and in 2015. During these field efforts, 10 whales were tagged off Kauai, 6 off Hawaii, and 61 off Maui, with deployments taking place from December to April (Mate et al. 1998, 2007).

2.2 Satellite Tags

Two types of fully implantable, non-recoverable, Argos-based tags were used in 2018 to track humpback whales: Telonics RDW-665 Dive Monitoring (DM) tags and Telonics RDW-665 Dive Duration Monitoring Plus (DUR+) tags. Both tag types follow the same design of our earlier Location-Only (LO) tag used in previous tagging efforts (Mate et al. 2007, 2018a, 2018b), which is composed of a main body, a penetrating tip, and an anchoring system (**Figure 1**). The main body consisted of a stainless steel cylinder (1.9 centimeter [cm] in diameter × 20.7 cm in length) that houses a certified Argos transmitter and a 6 volt (V) lithium battery pack. A flexible whip antenna (15.8 cm long) and a saltwater conductivity switch (SWS, 2.2 cm long), both constructed of single-strand nitinol (1.27 millimeter [mm] in diameter), were mounted on the distal endcap of this cylinder, while a penetrating tip was screwed onto the other end. The polycarbonate endcap 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 penetrating tip consisted 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 is 3.2 cm long × 0.6 cm wide) mounted on the main body at the nose cone (proximal) end. Maximum tag weight was 300 grams (g) for both 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 whale probably due to hydrodynamic drag and/or the natural migration of foreign objects out of the tissue (Mate et al. 2007). 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 35 d (standard deviation [SD] = 36 d, median = 25.7 d, n = 180), with a maximum duration of 220 d (OSU, unpublished data).

2.2.1 DM Tag Programing

DM tags contain a pressure sensor and tri-axial accelerometers and are able to record dive depth, dive duration (based on the wet/dry status of the SWS), changes in body orientation, and motion while attached to a whale. During a deployment, dive depth was recorded every 5 seconds (s) with 2-m vertical resolution up to a maximum of 511 m. Dive duration was recorded at 1-s resolution up to a maximum of 4,095 s using the tag's SWS. Accelerometer readings were recorded every 0.25 s.

DM tags were designed with onboard processing software for detecting behavioral events described by marked changes in the motion data indicative of increased activity, such as when animals lunge. When on the foraging grounds, lunge-feeding behavior produces stereotypical signatures in the acceleration data (Calambokidis et al. 2007, Goldbogen et al. 2008), which can be used as a measure of feeding effort (Mate et al. 2018a, b). When on the breeding grounds, the whales typically do not feed, so we use lunge events as a more general metric of activity level, perhaps associated with reproductive behavior.

Lunge events were derived from the motion data for selected dives (i.e., dives > 2 min in duration and 10 m in depth), as follows. For every selected dive, the magnitude of the acceleration vector (*A*) was calculated as in Simon et al. (2012):

$$A = \sqrt{ax^2 + ay^2\ az^2}$$

Where *ax*, *ay*, and *az* are the *x*, *y*, and *z* components of the acceleration vector relative to the Earth's gravitational field.

The rate of change in this acceleration vector, or Jerk (Simon et al. 2012), was then calculated as:

$$\text{Jerk} = A_{(t+1)} - A_{(t)}$$

Lunge events are associated with a peak followed by a minimum in Jerk (Allen et al. 2016), so we identified lunge events as instances when the Jerk value exceeded 3.0 SD above the mean, followed by a value less than the mean within 30 s after the Jerk peak. The mean Jerk value was continually updated following each selected dive and therefore represented a "grand mean" across all dives. Acceleration data recorded in the first 5 s or final 5 s of a selected dive were not used in these calculations to eliminate spurious peaks from strong fluking at the start or end of a dive. Lunges for each selected dive were then counted if they occurred more than 30 s from the previous lunge.

Argos messages for DM tags consisted of the start date and time of each selected dive, dive duration, maximum depth, and number of lunges for four to six consecutive selected dives, depending on data compression. The tag maintained an Argos message buffer that holds up to 10 messages in the tag's memory. When enough selected dives were recorded to create a new message, it was added to the buffer. If there were already 10 messages in the buffer, the oldest message was discarded to make space for the new message. Every time the tag transmitted, it randomly selected one of the messages for transmission from the buffer and every third transmission was a diagnostic message, containing the tag's current temperature and voltage. The current Jerk mean and SD values were included in the diagnostic message to monitor for any potential drift in the lunge detection criteria over time. DM tags were programmed to transmit only when out of the water during six 1-hour (h) periods every day. The transmission periods were chosen to coincide with times when satellites were most likely to be overhead. With such a transmission schedule, the life expectancy of the DM tag's battery was approximately 90 to 120 d.

2.2.2 DUR+ Tag Programing

DUR+ tags lacked a depth sensor, but were otherwise configured the same way as the DM tag, with a SWS for submergence detection and tri-axial accelerometers, and onboard processing software to detect behavioral events in the motion data. Argos messages for DUR+ tags consisted of the start date and time of each selected dive (dives > 2 min duration), dive duration, and number of lunges for a variable number of consecutive selected dives, typically four to six depending on data compression. The tag maintained an Argos message buffer like that of the DM tag, with similar transmission protocols (described above in **Section 2.2.1**). DUR+ tags were also programmed to transmit during six 1-h periods per day coinciding with times when satellites were most likely to be overhead, and had an electronic life expectancy of approximately 90 to 120 d.

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 kilometers (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).

Before generating a complete Argos track, OSU implemented a sequential data editing protocol on the received ("raw") Argos locations from each tag to retain the best locations. First, locations occurring on land were excluded. Then, LC-Z locations were removed from analyses 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 kilometers per h (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 distance from shore, occurrence in Navy areas and BIAs, residence time, kernel density estimation, and connectivity within the Hawaiian breeding area (see **Sections 2.4**-**2.8** below).

2.3.2 Track Regularization and Behavioral Annotation with State-Space Models

The dive behavior analyses (see **Section 2.10** below) 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 hierarchical state-space model (hSSSM) (Jonsen 2016) in the software package R v. 3.4.4 using the bsam and rjags libraries (which interfaced with the software package JAGS v. 4.3 to run Markov chain Monte Carlo simulations using the Gibbs sampler). This model is structurally similar to the conventional switching state-space model (SSSM; Jonsen et al. 2005) that has been applied to marine mammal tracking data for many years (e.g., Bailey et al. 2009, Irvine et al. 2014). However, the estimates for parameters driving different behavioral modes are generated from all tracks simultaneously rather than separately for each track, as with the conventional SSSM. This process assumes that all tracks share an underlying set of movement parameters, which can be used to derive behavioral modes for each individual. Using multiple tracks simultaneously allows for greater precision when estimating behavior modes and for scaling individual movements up to the population level to better examine individual variation in foraging behavior (Jonsen 2016).

The model output provided a regularized track with three estimated locations per day, after accounting for Argos satellite location errors (based on Vincent et al. 2002) and movement dynamics of the animals. The hSSSM ran two Markov chain Monte Carlo simulations 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 20^{th} to reduce autocorrelation, yielding a final 2,000 samples to be used (Jonsen 2016). 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 Markov chain Monte Carlo samples provided a continuous value from 1 to 2 for each location (Jonsen 2016). As in Bailey et al. (2009) and 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".

For the analysis of historical data from previous tagging efforts in Hawaii (1995-2000, 2015), fewer transmission periods were scheduled per day to prolong battery life (see Mate et al. 2007), and thus fewer locations were received per day than for the 2018 tags. For this reason, conventional SSSMs (Jonsen et al. 2005) were applied to the historical tracks to produce regularized tracks with only one estimated location per day (Bailey et al. 2009, Irvine et al. 2014, Mate et al. 2018a, 2018b).

2.4 Calculation of Distance from Shore

The closest point on land was determined for each filtered Argos location using the NEAR toolbox function in ESRI® ArcMap v.10.3. The geodesic distance was then computed between each point and its corresponding whale location using the WGS 1984 ellipsoid parameters in ESRI® ArcMap v. 10.3.

2.5 Occurrence in Navy Areas and BIAs

The number of locations occurring inside versus outside Navy areas was computed for each edited Argos track, with the percentage of locations inside reported as a proportion of the total number of locations obtained for each whale. The Navy areas considered within the Hawaii Range Complex (HRC) were: (1) W188(A), (2) Area W188(B), (3) Area W186, (4) Barking Sands Tactical Underwater Range (BARSTUR), and (5) Barking Sands Underwater Range Expansion (BSURE). Additional Navy areas in the North Pacific Ocean included: (6) the Southeast Alaska Acoustic Measurement Facility (SEAFAC), (7) the Northwest Training Range Complex (NWTRC), (8) Area W237 of the NWTRC, (9) the Gulf of Alaska Temporary Maritime Activities Area (GOA), (10) the Southern California Range Complex (SOCAL), (11) the Southern California Anti-submarine warfare Offshore Range subarea (SOAR), and (12) the Point Mugu Range Complex (PT MUGU).

The number of locations and corresponding percentages were also computed for areas of interest to NMFS, such as the BIAs that were identified for humpback whales in US waters of the Pacific Ocean (Baird et al. 2015, Calambokidis et al. 2015, Ferguson et al. 2015a, b). The breeding (typically December through April) BIAs considered within Hawaiian waters were: (1) Kauai and Niihau ("Kauai"), (2) Oahu, Molokai, Lanai, and Maui ("Maui"), and (3) Hawaii. Feeding BIAs considered were: (4) spring, summer, and fall Southeast Alaska ("SEAK"), (5) Bristol Bay (highest densities June through September), (6) Aleutian Islands ("Aleutian"; highest densities June through September), and (7) Shumagin Islands ("Shumagin"; greatest densities in July and August). We note that the spring (March through May), summer (June through August), and fall (September through November) SEAK BIAs identified in Ferguson et al. (2015a) were combined for this report due to their substantial overlap and the fact that some humpback whales were tracked in the area in both spring and summer.

To compute estimates of residence time inside Navy areas and BIAs, interpolated locations were derived from the edited Argos tracks at 10-min intervals between locations, assuming a linear track and a constant speed. These interpolated locations provided evenly spaced time segments from which reasonable estimates of residence time could be generated, especially within the smaller Navy areas and BIAs. Residence time was calculated as the sum of all 10-min segments from the interpolated tracks that were completely within each area of interest. The amount of time spent inside these areas was expressed as the number of days as well as the proportion (percentage) of the total track duration.

2.6 Residence Time in Hawaii

We objectively defined the Hawaii breeding area as the zone extending 50 km seaward from the coastline around the main Hawaiian Islands. The determination of 50 km for this buffer zone was based on examination of the behavioral mode predicted for each location by the SSSM/hSSSM for all tracks (1995-2000, 2015, 2018), which indicated that at this distance all locations had switched from ARS mode (indicative of residence in Hawaii) to transiting mode (indicative of migration). To avoid discontinuities of the buffer zone where expanses of water within the main Hawaiian Islands were separated by more than 50 km, we joined the discontinuous polygons so that they formed a continuous buffer zone. This joining was implemented via ESRI® ArcMap v. 10.3 editing, wherein selected portions of the buffer polygons were converted to Bézier curves, then manually stretched to achieve a smoother boundary.

To compute residence time in the Hawaii breeding area, we first determined the date a tracked whale crossed the 50-km buffer boundary as it departed on migration, following the same interpolation approach described in **Section 2.5** to derive residence time inside Navy areas and BIAs. For each track that crossed the buffer zone, residence time was calculated as the time interval from tagging to departure, expressed as number of days.

2.7 Kernel Density Utilization Distributions

Home range analysis (as performed in previous OSU technical reports to the Navy; e.g., Mate et al. 2018a, b) was not conducted for this report because none of the tracking periods in Hawaii (within the 50-km buffer zone around the main Hawaiian Islands) exceeded the 30-d minimum requirement for such analysis (Seaman et al. 1999). Instead, the spatial pattern of whale occupation was characterized using kernel density estimation (Worton 1989) from edited Argos tracks that lasted at least 10 d before either transmissions stopped or whales migrated away from the islands (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.

Kernel density utilization distributions of Argos locations in the feeding grounds were also computed, with separate analyses conducted for whales that migrated to the Aleutian Islands and Bering Sea and for whales that migrated to British Columbia and Southeast Alaska, because these two areas were widely separated with no locations in between. Kernel density estimation for the Aleutian Islands and Bering Sea locations were computed with a cell size of 0.5 × 0.5 degrees given this area's large geographic extent, whereas the cell size used for British Columbia and Southeast Alaska was 0.1 × 0.1 degrees.

2.8 Connectivity Between Islands/Areas Within Hawaii

To assess connectivity or interchange among Hawaiian Islands and Penguin Bank, we counted the number of islands visited by tagged whales during their tracking period using the edited Argos tracks. Whales were considered to have visited an island if any of their locations were located within 5 km of the island. All islands in the main Hawaiian archipelago (Niihau, Kauai, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii) and Penguin Bank were considered in this analysis.

2.9 Historical Comparisons

Comparisons between the historical tagging years (1995-2000, 2015) and the 2018 season were conducted for tracking duration and total distance traveled for each whale using the STATGRAPHICS® Centurion XVI v. 16.1.03 software package. Analysis of variance (ANOVA) was used to test whether the 2018 means were equal to the pre-2018 means, using a significance level of 0.05. Kernel density utilization distributions for whales tagged prior to 2018 were qualitatively (graphically) compared to those for whales tagged in 2018.

2.10 Dive Behavior Analyses

The goals of the analyses in this section were to characterize the diving and feeding behavior of tagged whales over their tracked duration (weeks to months) and to examine how it changed temporally and spatially, using the dive data from the DM and DUR+ tags. As described in **Section 2.2**, both tag types had a similar design but the DUR+ tag lacked the pressure sensor of the DM tag, so it was only capable of reporting dive durations (via submergence of the SWS) and number of lunge events from the accelerometer.

2.10.1 DM and DUR+ Tag Analysis

The percent of the tracking duration summarized by reported dives[2] from the tags was calculated as the sum of all received dive durations plus the sum of all received post-dive intervals (PDI; i.e., the time between the end of one selected dive and the start of the next one). We only calculated PDI for dives reported within the same transmission because we could not be sure dives were sequential from one transmission to the next (e.g., if there was a 15-min time difference between the end of the last dive in one received transmission and the start of the first dive of the next received transmission, it is possible the whale made no selected dives during that time, or made a series of short-duration selected dives that were packaged into a transmission that was not received).

Summary plots showing dive duration versus date and versus time of day were generated for each individual tag and for all tags combined to visualize temporal and diel trends in the dive data. Due to the large number of plots generated, only the plots aggregating all tag data are presented here to illustrate the trends that are described in the results, unless an individual tag is presented as an example result. Additional plots showing dive depth and number of feeding lunges were generated for DM-tagged whales.

Each reported dive was assigned a location along the track by linear interpolation, using the proportional time difference between the start of each dive and the two temporally closest hSSSM locations (i.e., before and after the start of the dive) to determine where on the line the dive should fall. The dives for each whale were then mapped onto a 0.1-degree hexagonal grid. Median dive durations were calculated for all dives occurring in each cell. This process was repeated for each tagged whale, and then the value of each grid cell was averaged across all tagged whales to produce a map showing the spatial distribution of dive durations after accounting for day-to-day differences in the number of dives, both within and between whales. Cells that averaged data from a greater number of whales were more likely to be representative of the overall behavior occurring in that cell, so the gridded map of dive durations is presented with a corresponding map showing the number of tagged whales that occupied each grid cell and a map showing the total number of dives that occurred in each cell. These maps indicate where tagged whales spent more time diving. A similar process was followed to show the spatial distribution of maximum dive depths for all DM-tagged whales.

The number of lunges for each whale was also mapped onto a 0.1-degree hexagonal grid so that each grid cell contained the total number of lunges that occurred within that cell for one whale. The number of lunges in each cell was then divided by the sum of the dive durations for all dives occurring in the cell (i.e., the total time spent diving in that cell) to get the number of lunges per h reported for each grid cell.

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[2] In the past (e.g., Mate et al. 2018a, b), DM and DUR+ tags have occasionally reported abnormally long-duration ("anomalous") dives lasting from 44 min up to the maximum possible value recorded by the tag (4,095 s or 68.3 min). These anomalous dives could be related to times when the whales surfaced in such a way that the tag was not lifted out of the water (e.g., when the whales surface to breathe or rest at the surface), but diagnostic information is limited to conclude this definitively. The longest dive duration reported during this tagging effort was 35 min and whales were documented in the field regularly diving for 20–25 min, so no dives were removed as "anomalous" in this report.

This process was repeated for each DM-tagged whale, and then the value of each grid cell was averaged across all whales and relativized so that all values fell from 0 to 1. The result shows the spatial distribution of "relative activity" after accounting for day-to-day differences in the number of dives, both within and between whales. A corresponding map showing the number of DM-tagged whales that occupied each grid cell and a map showing the number of dives made per cell was also generated as described above.

2.11 Genetics

2.11.1 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).

2.11.2 Microsatellite Genotypes

Up to 16 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); GT211, GT23, GT575 (Bérubé et al. 2000); and 464/465 (Schlötterer et al. 1991). 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. One of the 16 microsatellite loci failed to give readable results across all samples and was removed from the data set resulting in a maximum of 15 microsatellite loci for each sample.

2.11.3 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). To supplement sex information for tagged animals for which no biopsy sample was obtained, sex was conservatively assigned from field observations to mothers with calves (as females) and to singers (as males).

2.11.4 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).

2.11.5 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 individual identification of humpback whales, there is a large "DNA register" 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 grounds 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 between the 2018 Hawaii tagging data set 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), using a significance level of 0.05.

2.12 Photo-Identification

Photographs of the whales' tail flukes and dorsal fins were taken during field efforts for identification (ID) purposes, as well as to document tag placement, wound condition, and to identify previously tagged whales during resightings to examine wound healing. Besides tagged whales, photographs were taken of all other whales seen while tagging for ID purposes and to examine for tag wounds or scars. 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 is completed, our photo-IDs are submitted to other researchers to compare with their photo-ID catalogs to determine if there are matches that can show us the sighting histories of tagged whales. OSU has also submitted our photo-IDs to the online resource "Happywhale" (http://happywhale.com), a global database of photo-IDs contributed by the public that provides automated matching using state-of-the-art algorithms and machine learning, which will allow us to know where many of our tagged whales have been seen historically as well as where and when they are resighted in the future.

3 Results

3.1 Tagging Rates

A total of 228 humpback whales were approached during 9 d of tagging efforts off Maui in 2018. Twenty-five tags were deployed, for a tagging rate of 2.7 tags per d. Throughout this report individual whales will be referred to by their tag number. Also, for purposes of presentation, the results of the analyses will be divided into three broad-scale functional behavior categories: breeding grounds, migration, and feeding grounds.

3.2 Behavioral Responses to Tagging

Seven of the 25 humpback whales tagged off Maui in 2018 exhibited short-term startle responses to the tagging/biopsy process. These responses consisted of mild (3 whales) to moderate (4 whales) tail flicks. A tail flick is defined here as a swift or abrupt movement of the tail flukes dorso-ventrally (up and down). The level of response follows definitions described in Weinrich et al. (1992), Hooker et al. (2001), and Baumgartner et al. (2015), with "moderate" referring to relatively forceful modifications to behavior (such as hard tail flicks) with no prolonged evidence of behavioral disturbance.

3.3 Wound Healing

Only two of 25 humpback whales tagged in 2018 were resighted during the field efforts in Hawaii. One was seen 2 d after tagging (#5655, a male) and the second 7 d after tagging (#836, a male). Whale #5655 had an area of moderate swelling surrounding the tag site, approximately 40 cm in diameter and 5 cm in height. No swelling was seen around the tag site for whale #836.

One tagged whale (#5843, a male) was resighted by local researchers off southern Vancouver Island, on 27 and 30 August 2018 (161 and 164 d after tagging). The tag was no longer attached to the whale, and there was a divot (approximately 25 cm in diameter and 10 cm in depth) but no swelling at the tag site.

Another tagged whale (#5685, a male), identified in the Happywhale photo-ID database, was resighted three times after tagging in the Strait of Georgia, between Vancouver Island and mainland British Columbia (in May, August, and September 2018). We have only been able to review one photograph taken on 4 September 2018 (171 d after tagging and 166 d after the last transmission) that showed the tag site. A divot (approximately 20 cm in diameter and 5 cm in depth) was seen, but no swelling.

3.4 2018 Maui Tagging

3.4.1 Tracked Movements

Twenty-five tags (20 DM and 5 DUR+) were deployed on humpback whales off Maui, Hawaii, from 12 to 21 March 2018, between the islands of Maui, Lanai, and Kahoolawe (**Figure 2**). Argos satellite locations were received from all but one of the 25 tags (**Table 1**). Two other tags provided two locations each, but none passed our location filtering criteria, so these tags were also not included in summary statistics. Tracking periods for DM tags ranged from 1.1 to 160.0 d (mean = 25.8 d, SD = 40.0 d, n = 17). Tracking periods for DUR+ tags ranged from 2.2 to 104.5 d (mean = 33.5 d, SD = 43.4 d, n = 5). Minimum distance traveled averaged 1,984 km (SD = 3,391 km, maximum = 12,442 km, n = 17) for DM tags, and 2,429 km

(SD = 3,430 km, maximum = 8,170 km, n = 5) for DUR+ tags (**Table 1**). Neither tracking periods nor minimum distance traveled differed significantly between the two tag types (ANOVA *p*-values > 0.72).

Locations for humpback whales tagged off Maui ranged over 43 degrees of latitude, from the south coast of Maui (21°N) to the Bering Sea (64°N; **Figure 3**). While in Hawaiian waters, the majority of locations were in the Maui Nui region (i.e., the inner waters of the "four-island region" of Maui, Molokai, Lanai, and Kahoolawe; **Figure 3**). Penguin Bank was another area heavily frequented by the tagged whales, with nine humpbacks spending time there. Eight whales also spent time off the north coast of Maui, but with an obvious avoidance of the nearshore waters off Kahului Harbor.

3.4.1.1 Breeding Grounds

3.4.1.1.1 Residency

The tracks of seven humpback whales tagged in 2018 crossed the 50-km buffer boundary (**Figure 3**) as they departed on migration. Four of these were male (whales #4172, 5641, 5736, and 5800), one was a female with a calf (whale #5784), and two whales were of unknown sex (whale #843 and 10833) (**Table 2**). Departure dates for these whales spanned the period 17 March to 11 April 2018, with the time from tag deployment to departure ranging from 3.3 to 23.2 d (mean = 13.5 d, n = 7) (**Table 2**). The sample size for this set of tracks was too small for meaningful comparison between the sexes.

3.4.1.1.2 Kernel Density Utilization Distributions

Ten humpback whales tagged in 2018 were tracked for at least 10 d within the 50-km Hawaiian Island buffer zone. Kernel density utilization distributions computed from the pooled Argos locations of these whales showed highest use at the southwest corner of Penguin Bank (**Figure 4**). The next highest density of locations was found within the Maui Nui region.

3.4.1.1.3 Connectivity

All but one of the 22 whales (95 percent) tracked in 2018 moved to another island (or to Penguin Bank) during their tracking periods within Hawaii (within the 50-km buffer; **Figure 5**). For 18 of these whales there was one predominant direction of travel, and 82 percent of these was to the northwest, with animals leaving Maui and heading to Lanai, Molokai, and/or Penguin Bank. Eighty-six percent (19 of 22) of the whales tagged off Maui were tracked within 5 km of Molokai (minimum distance between Maui and Molokai of ~13 km) and Lanai (minimum distance between Maui and Lanai of ~13 km), 54 percent (12 of 22) were tracked to Penguin Bank (minimum distance between Maui and Penguin Bank of ~60 km), and 27 percent (6 of 22) were tracked to Oahu (minimum distance between Maui and Oahu of ~105 km). Twenty-seven percent (6 of 22) of whales were also tracked to Kahoolawe (minimum distance between Maui and Kahoolawe of ~10 km). One whale was tracked to both Kauai and Niihau (minimum distances between Maui and Kauai and Niihau of ~294 and ~364 km, respectively). No whales were tracked southeast to the island of Hawaii (minimum distance between Maui and the island of Hawaii of ~46 km). The average number of areas visited by tagged whales while in the Hawaiian breeding area (including the tagging area) was 3.9 (SD = 1.4, range = 1 to 7). After accounting for a positive relationship between number of days in Hawaii and number of areas visited (general linear model *p* = 0.001), there was a significant difference between the number of areas visited by females (mean = 2.4, standard error

[SE] = 0.51, n = 4) and the number visited by males (mean = 4.1, SE = 0.25, n = 17; general linear model p = 0.009).

3.4.1.2 Migration

Seven humpback whales began their northbound migration, and four of these whales reached a high-latitude feeding area during their tracking periods (**Table 2, Figure 3**). While still in Hawaiian waters, there was a tendency for whales to travel north and northwest through the Hawaiian Island chain after leaving Maui, with migratory departures beginning off the north coast of Oahu (four whales), the north coast of Niihau (one whale), the north coast of Molokai (one whale), and the north coast of Maui (one whale).

Two humpback whales departing from Oahu (whales #10833 and #843, both of unknown sex) traveled northwest on a trajectory toward the Aleutian Islands (**Figure 3**). These tags stopped transmitting approximately 2,200 and 2,400 km northwest of Oahu, 25 and 40 d after departure, respectively. Whale #5736 (a male), also departing from Oahu, maintained a more northerly trajectory initially, before heading slightly northwest, arriving to an area approximately 200 km south of Unimak Pass on 28 April (28 d after departure; **Figure 3**).

The tracks of four other migrating whales followed a northeasterly trajectory toward northern British Columbia (**Figure 3**). Three whales traveled to the Haida Gwaii Archipelago, reaching the islands on 16 April (whale #4172, a male; 30 d after leaving Molokai), 8 May (whale #5800, a male; 36 d after leaving Niihau), and 9 May (whale #5784, a female with a calf; 46 d after leaving Maui). Both whales #4172 and #5800 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. The fourth whale with a northeast migratory trajectory (whale #5641, a male) was tracked approximately 630 km northeast of its departure point on Oahu before its tag stopped transmitting, on 2 April (4 d after departure).

3.4.1.3 Feeding Grounds

Upon arriving at the area south of Unimak Pass, whale #5736 stayed in the area for 23 d, after which it headed west along the southern edge of the Aleutian Island chain for 21 d. Whale #5736 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 (160 d after tagging; **Figure 6**). During its time in the Bering Sea, whale #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.

Whale #4172 spent two weeks traveling along the west and north 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 6**). Whale #5800 spent 8 d traveling up the west coast of Haida Gwaii to Prince of Wales Island in Southeast Alaska before its tag stopped transmitting on 17 May (**Figure 6**). Whale #5784 migrated to the northwest coast of Moresby Island, and spent the remainder of its tracking period (ending on 1 July) off the west and north coast of Graham Island (the northernmost of the two main islands in the Haida Gwaii Archipelago; **Figure 6**).

3.4.1.3.1 Kernel Density Utilization Distributions

Kernel density utilization distributions computed from the pooled Argos locations of the three humpback whales that migrated to the northern British Columbia feeding ground showed highest use at the northwest corner of Haida Gwaii, and another concentration of locations at the southeastern edge of Hecate Strait, between mainland British Columbia and Haida Gwaii (**Figure 7**). Utilization distributions for the filtered Argos locations of whale #5736, that migrated to the Aleutian Islands and beyond, showed the area of highest density to be an area approximately 160 km south of Akutan Island and Unimak Pass in the eastern Aleutians (**Figure 6**). The next area of high density locations was in the southern Bering Sea, approximately 175 km northeast of Attu Island at the western end of the Aleutian Island chain (**Figure 8**).

3.4.2 Use of Navy Training Areas

Only two of the humpback whales tagged off Maui in 2018 had locations in Navy training areas. One whale (#843, of unknown sex) passed through both Area W188A and Area W188B while migrating north, spending 2.8 d (3 percent of locations, 4 percent of the total tracking period) within Area W188A, and 0.9 d (1 percent of both locations and total tracking period) within Area W188B (**Table 3, Figures 9 and 10**). Another whale (#5800, a male) spent time in all five training areas in Hawaii, with number of days in the areas ranging from 0.2 d (in BARSTUR) to 3.2 d (in Area W188A; **Table 3, Figures 9 through 13**). This represented from 0 to 5 percent of locations and < 1 to 6 percent of the total tracking period for this whale. Distance to shore in Areas W188A and W188B for whale #843 averaged 266 km (maximum = 365 km) and 107 km (maximum = 123), respectively (**Table 4**). Average distance to shore for whale #5800 ranged from 9 km in Area W186 (maximum = 9 km) to 275 km in Area W188B (maximum = 305 km; **Table 4**). All humpback whale locations in the Hawaii training areas occurred during the month of April. None of the tagged humpback whales from 2018 were tracked within any Navy training areas along the US West Coast.

3.4.3 Use of Hawaii BIAs

As tagging took place within the Maui BIA, all tagged whales had locations within this area (**Figure 14**). The amount of time spent in the Maui BIA for the 22 tracked whales ranged from 1 to 100 percent of the total tracking periods (0.3 to 15.7 d; **Table 5**). This represented 1 to 100 percent of the total number of locations for these whales. One whale (#5800, a male) had 1 percent of its locations and 1 percent of its total tracking period within the Kauai BIA, representing 0.8 d (**Figure 15**). This same whale was also tracked in the SEAK BIA, with 2 percent of locations and 2 percent of its tracking period there, for 1.5 d (**Figure 16**). Humpback whale locations occurred in both the Maui and Kauai BIAs during March and April, and in the SEAK BIA in May. None of the humpback whales tagged off Maui in 2018 had locations in the Hawaii, Aleutians, Shumagin, or Bristol Bay BIAs.

3.4.4 Dive Behavior

Of the 25 tagged whales, 20 were males, 4 were females, and 1 was of unknown sex (**Table 6**). One DM tag (whale #5701, a male) failed to transmit any dive data. DUR+ and DM tags provided a mean of 1,967 dive summaries (range = 15-13,983; **Table 6**). The number of dives reported summarized a mean of 60.6 percent of the tracking duration (range = 28.4 to 99.5 percent). The number of lunges detected was low relative to the number of dives reported, both on the breeding grounds and for tags that reached the feeding grounds.

3.4.4.1 Breeding Grounds

Dive depths of DM-tagged whales on the breeding grounds were generally less than 100 m. However, half of the DM-tagged whales made occasional dives exceeding 200 m and three dove to depths almost reaching 400 m (**Figure 17)**. Dive durations for all tagged whales were highly variable across individuals, generally ranging from 3-15 min in duration with occasional dives lasting over 30 min (**Figure 18**). Dive depths and durations were generally similar across all hours of the day, although the deepest dives generally occurred during daylight hours **(Figures 19 and 20).** Lunges occurred across all hours of the day, with slightly more recorded during daylight hours (**Figure 20)**. Spatial distribution of dive durations, depths and lunges were relatively uniform across the areas used **(Figures 21 and 22)** and there were no discernable temporal patterns in dive depth or duration either within or across individuals**.**

Inferences about sex-related differences in behavior are precluded due to the much larger number of male whales tagged and the relatively limited number of dives received by the four females tagged while in the breeding grounds. Dive depths were generally similar to other whales for the three females tagged with DM tags (**Figure 17).** Dive durations for two females spanned almost the entire range of dive durations made by other tagged whales, while dives for the other two females were short in duration (**Figure 18**).

3.4.4.2 Migration

Overall dive behavior of the six whales tracked during migration was similar to behavior on the breeding grounds. Mean dive depths were less than 50 m with occasional dives exceeding 200 m, with the exception of whale #843 (a female), which made deeper dives overall and had some that approached 400 m (**Figure 23**). Dive durations were more variable but generally less than 15 min with occasional dives lasting over 20 min, and whale #843 reported the shortest mean dive duration of migrating tagged whales (mean = 5.6 min; **Figure 24**). When dive behavior during migration was examined as a time series, a distinct pattern emerged with whales making deep (> 200 m), long duration (> 15 min) dives at night during the first 7–14 d of the migration (**Figure 25**). Dives during the remainder of the migratory track returned to more typical ranges of depths < 100 m and durations < 10 min with no strong diel pattern.

Lunges were recorded by five of six whales tracked into migration (no lunges for whale # 5736), with many lunges occurring near the breeding grounds or as the whale approached the feeding grounds. Two tagged whales were responsible for the vast majority of recorded lunges. Whale #843 recorded 61 percent of lunges during migration (197 of 319 total lunges) and whale #5784 recorded an additional 24 percent of migration lunges (77 of 319). Both tags recorded lunges during extended periods (5-7 d) of the migration while the whales made limited, or no deviation in heading. Both whales were female while the other four whales making few lunges were male. Lunges occurred across a wide range of dive depths and durations, although they were generally concentrated in deeper dives of medium duration (**Figure 26**).

3.4.4.3 Feeding Grounds

Four tags functioned long enough to track whales to their migratory destination. Three of those tagged whales traveled to the area near Haida Gwaii, while the other (whale #5736, a male) traveled to the Aleutian Islands, west to near the Kamchatka Peninsula and then north into the Bering Sea. Dive depths of tagged whales were very different between the two feeding areas, as whale #5736 dove deeper than the two DM-tagged whales near Haida Gwaii (**Figure 27**). However, there was not a corresponding difference in dive durations across these whales (**Figure 28**). Examination of hourly dive and duration plots indicated that whale #5736 followed a diel cycle, making deeper, longer-duration dives during the day, with more lunge events (**Figure 29**), while the whales near Haida Gwaii showed no temporal trends in their dive depths or duration (example from whale #4172: **Figure 30**), and lunge events were more common during afternoon and nighttime periods (example from whale #4172: **Figure 31**). The diel trend of dives made by whale #5736 persisted throughout its movements from its initial arrival point in the feeding grounds south of the eastern Aleutian Islands (28 April 2018), through its movement near the Kamchatka Peninsula (6 June 2018 arrival date), and into the Bering Sea (14 June 2018 arrival date; **Figures 32 and 33**). Seafloor depths differed dramatically between the areas used near Haida Gwaii and the western Aleutians/Bering Sea (median water depth = 170 m versus 3,900 m, respectively), although they were deep enough to not be a limiting factor for most dive depths recorded. No spatial trend in behavior was apparent for tagged whales using the area near Haida Gwaii (**Figures 34 and 35**).

3.4.5 Genetics

Biopsy samples were collected from 23 of the 25 tagged whales and all samples provided DNA profiles sufficient for subsequent analyses. The mtDNA sequences of the 23 samples resolved six haplotypes for the consensus region of 500 bp (**Table 7**). 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 (**see Table 7**).

The 23 samples were represented by a unique multi-locus genotype of at least 14 loci with an average of 14.91 loci across the dataset. The probability of identity for any given set of 14 loci ranged from $P_{ID} = 3.7 \times 10^{-13}$ to 2.7×10^{-14}, providing confidence that the 23 unique multi-locus genotypes represent 23 individual whales. These 23 individuals included three females and 20 males. The DNA profiles of the 23 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), and two recaptures were detected. The first (biopsy sample Mno18HI007, whale #5641, a male), was matched by genotyping to an individual sampled in Hawaii on 22 April 2004 (SPLASH ID 430296). The sample was linked through photo-ID from the SPLASH project to a resighting in Hawaii near the island of Hawaii on 14 February 2005 and then again near Maui on 18 March 2005. The second (biopsy sample Mno18HI016, whale #5784, a female), was matched by genotyping to an individual sampled in northern British Columbia on 15 June 2005 (SPLASH ID 560234) and linked through photo-ID to resightings on 13 and 15 September 2005.

The mtDNA haplotype frequencies of the Hawaiian tagging samples differed significantly in pairwise comparisons with each of the SPLASH breeding areas described in Baker et al. (2013), with the exception of Hawaii (**Figure 36** and **Table 8**). The Hawaiian tagging samples also differed significantly from six of the 10 SPLASH feeding grounds described in Baker et al. (2013). The haplotype frequencies of the tagging samples were not significantly different from the western Aleutians (likely due to a small sample size), eastern Aleutians, northern Gulf of Alaska, and north British Columbia (**Table8**).

The distribution of mtDNA haplotypes on the feeding grounds in SPLASH was also reflected in the migratory destinations of the tagged whales (**Figure 37**). The three haplotypes of the five individuals migrating towards southeastern Alaska or northern British Columbia (whales #4172, 5784, and 5800) were consistent with the haplotypes common to those regions ("A-", "A+" and "E2"). The haplotype of the one individual migrating to the Aleutian Islands and continuing on to Russia (whale #5736) was consistent with a haplotype common to that region ("E1").

3.4.6 Photo-Identification

A total of 11,401 photographs were taken of humpback whales in Hawaii during the 2018 field season. From these photographs a total of 75 individuals were identified and added to our Hawaii humpback whale photo-ID catalog. There were no matches to whales identified during the 2015 field season. Of the 25 whales tagged in 2018, 14 had fluke photos that could be used for ID purposes. Out of these 14 whales, one (whale #5685, a male tracked for 4.7 d and 280 km) had been previously identified in the Happywhale photo-ID database. To date, this whale has been sighted off Washington State and Vancouver Island every year beginning in 2013. After tagging, whale #5685 was resighted (without its tag) in the Strait of Georgia, east of Vancouver Island, in May, August, and September 2018, indicating a migratory connection between Hawaii and the southern British Columbia/northern Washington feeding area. Out of the other 61 identified untagged whales, five had also been previously identified in the Happywhale photo-ID database. Four of these identifications were new records for Hawaii and had previously been sighted off Washington State (3 animals) and west of Vancouver Island (1 animal). The fifth whale had been sighted by OSU off Oregon during tagging work in 2017 funded by this CESU agreement (Mate et al. 2018b).

3.5 Historical Comparisons

3.5.1 Tracked Movements

A total of 77 humpback whales were tagged by OSU in Hawaii prior to 2018 (covering the period 1995 to 2000, and 2015), providing tracking data for 59 whales (the remaining tags provided no locations; **Figures 38 and 39**). Tracking periods for these whales ranged from 0.04 to 152.8 d (mean = 24.8 d, SD = 32.6 d). Tags deployed in 1995 and 1996 were externally-mounted (with two bladed attachment posts; Mate et al. 1998) rather than implanted like the ones used after 1996, and as a result were subjected to more hydrodynamic drag on a whale. Tracking period was significantly different (ANOVA of log-transformed tracking period, p-value = 0.02) between the two types of attachments, with external tags lasting an average of 6.2 d (SD = 5.4 d, n = 9) and implanted tags lasting an average of 28.2 d (SD = 34.3 d, n = 50). When only implanted tags were considered, tracking periods were not significantly different between the pre-2018 seasons and 2018 (ANOVA, p-value = 0.95; **Table 9**), nor were they different between males and females when all years were combined (ANOVA, *p*-value = 0.54). The average tracking period for all implanted tags deployed by OSU on humpback whales in Hawaii from 1997 through 2018 was 28.0 d (SD = 35.8 d, median = 15.6 d, maximum = 160.0 d, n = 72). Tracking periods were significantly different between whales that were only tracked within the 50-km buffer around Hawaii (mean = 11.8 d, SD = 10.9 d, maximum = 44.4 d, n = 50) and those that traveled beyond the buffer (mean = 64.7 d, SD = 45.0, maximum = 160.0 d, n = 22; ANOVA of log-transformed tracking period, *p*-value < 0.0001).

There was a positive relationship between tracking period and total distance traveled by individual humpback whales with implantable tags (linear regression using log-transformed variables, *p*-value < 0.0001). After accounting for this relationship, distance traveled was not significantly different between humpback whales tagged in 2018 and those tagged prior to 2018 (general linear model of log-transformed variables, *p*-value = 0.85; **Table 9**).

The latitudinal range, or the difference between the latitudes of the northernmost and southernmost locations was slightly larger for humpback whales tagged off Maui in 2018 (43 degrees) than for whales tagged prior to 2018 (40 degrees; **Figure 39**). The longitudinal range, or the difference between the longitudes of the easternmost and westernmost locations was virtually the same between whales tagged in 2018 (70 degrees) and those tagged prior to 2018 (71 degrees). Within 50 km of the main Hawaiian Islands (i.e., the buffer zone we used to objectively designate the breeding grounds for tracking purposes; see **Section 2.6**), latitudinal and longitudinal ranges were slightly larger for whales tagged prior to 2018 (latitudinal range of 4 degrees, longitudinal range of 6 degrees) than those tagged in 2018 (latitudinal range of 2 degrees, longitudinal range of 4 degrees; **Figure 38**).

3.5.1.1 Breeding Grounds

3.5.1.1.1 Residency

The tracks of 18 humpback whales tagged prior to 2018 crossed the 50-km buffer boundary as they departed on migration. Four of these whales were male, two were females with calves, and twelve were of unknown sex (**Table 2**). Departure dates for these whales were as early as 20 December (for whale #4177, of unknown sex tagged off Maui in 1999) and as late as 3 May (for whale #828, a female tagged off Maui in 1997). The residence time inside the 50-km buffer for these 18 whales ranged from 1.1 to 42.8 d (mean = 11.9 d, SD = 10.9 d) (**Table 2**). There was no difference in residence time between whales tagged in 2018 (mean = 13.5 d, SD = 7.1 d) and those tagged prior to 2018 (ANOVA, *p*-value = 0.73).

Overall mean residence time in Hawaii from tagging to departure for all 25 whales with known departure date over the period 1995-2018 was 12.3 d (range = 1.1-42.8 d, SD = 9.9 d), and was lower for females with calves (mean = 10.4 d, range = 2.7-22.6 d, n = 3) than for males (mean = 15.8 d, range = 3.3-42.8 d, n = 8), although the sample size was too small for a statistical comparison.

3.5.1.1.2 Kernel Density Utilization Distributions

Twenty-nine humpback whales tagged in Hawaii prior to 2018 spent at least 10 d in the 50-km Hawaii buffer zone. The results of kernel density estimation of the pooled locations for these whales were very similar to the results from the 2018 locations, with the area of highest use being the southwest tip of Penguin Bank (**Figure 40**). The area of next highest density of locations was, as in 2018, within Maui Nui.

3.5.1.1.3 Connectivity

Fifty-one (86 percent) of the 59 humpback whales tracked from 1995 to 2015 moved to another island (or to Penguin Bank) during their tracking periods within Hawaii (within the 50-km buffer; **Table 10**, **Figures 38 and 39**). As with whales tagged in 2018, the predominant direction of this travel was to the northwest (82 percent of whales), with animals leaving Maui and heading to Lanai, Molokai, and/or Penguin Bank. Ninety-two percent (46 of 50) of the whales tagged off Maui prior to 2018 were tracked to other areas, with 66 percent going to Lanai (33 of 50), 62 percent (31 of 50) going to Molokai, and 56 percent (28 of 50) going to Penguin Bank (**Figure 41**). Fewer than 20 percent of the whales tagged off Maui prior to 2018 visited Oahu, Kauai, Niihau, Kahoolawe, or Hawaii (**Table 10, Figure 41**). Seventy-five percent of the whales tracked from the island of Hawaii (3 of 4) traveled to other areas, with the majority of this movement being to Maui and Lanai (**Figure 42**). Only one (whale #10826 tagged in 1995; **Table 10**) of the five whales tracked from Kauai (20 percent) visited other areas within Hawaii, traveling southeast to Oahu, Penguin Bank, Molokai, and Lanai during its tracking period, as previously documented in Mate et al. (1998). The average number of areas visited in Hawaii by whales tracked from 1995 to 2015 (including the tagging area) was 3.1 (SD = 1.4, range = 1 to 6). In contrast to whales tagged off Maui in 2018, no significant difference was found between males and females (tagged off Maui prior to 2018) in the number of areas visited (general linear model p-value = 0.14), after accounting for the positive relationship between number of days in Hawaii and number of areas visited (general linear model p-value < 0.001). Whales tagged off Kauai and Hawaii were not included in the latter analysis due to lack of sex information for these whales.

3.5.1.2 Migration

Three of the 88 humpback whales tagged by OSU in Hawaii prior to 2018 were tracked for their full migration to a summer feeding area (**Figure 39**). Two more whales had locations in a summer feeding area but large gaps existed in their tracks, so migratory route and timing could not be determined. Of these five whales, three were tracked to the Aleutian Islands and two were tracked to northern British Columbia (Haida Gwaii) and Southeast Alaska. These migratory destinations were similar to the destinations of humpback whales tagged in Hawaii in 2018 (three to British Columbia, with one of these also going to Southeast Alaska, and one to the Aleutian Islands and Bering Sea). Partial migration was tracked for 13 more humpback whales tagged in Hawaii prior to 2018, with four on a trajectory toward the Aleutians, three on a trajectory toward southern British Columbia/northern Washington, two on a trajectory toward the western Gulf of Alaska, one on a trajectory toward northern British Columbia/Southeast Alaska, and one on a trajectory toward Southeast Alaska. Too few locations were received during the partial migration of the remaining two whales to determine a trajectory. Mate et al. (2007) documented that initial migratory heading is not necessarily an indication of final destination, showing one whale tagged off Maui in 1999 (#10828, of sex unknown) heading initially toward British Columbia but ending up in the Aleutians (**Figure 39**). Migratory departure sites from Hawaii were unknown for six of these 18 whales, due to gaps in tracking information. Four migrating whales departed from Kauai (three of which were tagged there), four departed from Oahu, two departed from Molokai, one departed from Maui, and one departed from Middle Bank, northwest of Kauai.

3.5.1.3 Feeding Grounds

One of the whales migrating to the Aleutian Islands (tagged off Maui in 1999) was tracked for 59 d after migration and spent an extended period of time (36 d) south of Akutan Island and Unimak Pass (**Figure 39**). This whale was last located near Sanak Island, southeast of Unimak Island. Another whale migrating to the Aleutians (tagged off Maui in 1997) headed toward Unimak Pass and turned west upon reaching the Aleutian Trench, south of the Aleutian Islands (**Figure 39**). This whale traveled along the southern edge of the entire Aleutian Island chain and was last located within 75 km of the southeast coast of the Kamchatka Peninsula. The third whale tracked to the eastern Aleutians (tagged off Maui in 2000) had only two locations south of Unalaska Island (after a 74-d gap in tracking information) before its tag stopped transmitting.

One whale migrating to northern British Columbia/Southeast Alaska (tagged off Maui in 1998) was tracked for 75 d in the feeding grounds, with extended stays in several areas during that time, ranging from the north coast of Haida Gwaii in northern British Columbia to the southern tip of Baranoff Island in Southeast Alaska (**Figure 39**). The other whale tracked to Southeast Alaska (tagged off Maui in 1999) had only four locations there, spanning a 93-d period, ranging from the west coast of Prince of Wales Island to the southwest coast of Baranoff Island.

3.5.1.3.1 Kernel Density Utilization Distributions

Kernel density utilization distributions for the two whales that migrated to the northern British Columbia/Southeast Alaska feeding areas showed the area of highest density to be at the southeastern end of Chatham Strait, followed by the central west coast of Prince of Wales Island (**Figure 43**). Kernel density utilization distributions for the three whales tracked to the Aleutian Islands prior to 2018 showed the area of highest density to be in the same area as that for whale #5736, tagged in 2018, approximately 160 km south of Akutan Island and Unimak Pass in the eastern Aleutians (**Figure 44**).

3.5.2 Use of Navy Training Areas

Area W188A was the most heavily used Navy training range for all tagged humpback whales in Hawaii, with 15 percent of tracked whales having locations there (**Table 11, Figure 9**), followed by adjacent Area W188B (14 percent of tracked whales; **Figure 10)**. The mean number of days spent in Area W188A ranged from 3.0 d (in 2018) to 4.3 d (prior to 2018), with a maximum residency in this area of 13.3 d (for a whale tagged off Maui in February 2000). The mean number of days spent in Area W188B ranged from 1.0 d (in 2018) to 1.8 d (prior to 2018), with a maximum residency in this area of 5.3 d (for a whale tagged off Maui in February 2000). Seven percent of whales had locations within the BSURE range, with number of days ranging from a mean of 0.5 d (prior to 2018) to 0.6 d (in 2018), and a maximum of 1.2 d (for a whale tagged off Kauai in March 1995; **Table 11, Figure 12**). Six percent of the tracked whales had locations in areas W186 and BARSTUR, with number of days spent in Area W186 ranging from 0.4 d (in 2018) to a mean of 2.2 d (prior to 2018) (maximum of 4.2 d for a whale tagged off Maui in December 1999; **Table 11, Figure 11**) and number of days spent in BARSTUR ranging from 0.2 d (in 2018) to a mean of 0.5 d (prior to 2018) (maximum of 0.7 d for a whale tagged off Kauai in March 1995; **Table 11, Figure**

13). Sample sizes were not large enough to permit meaningful statistical comparisons of residency between 2018 and pre-2018 in any of the Navy training areas. None of the humpback whales tagged in Hawaii prior to 2018 were tracked within any Navy training areas along the US West Coast.

Humpback whale locations in the Hawaii Navy training areas occurred in the winter and spring for whales tagged in all years. Humpback locations occurred in Area W188B during five months (December, February through May), in Area W188A during four months (February through May), and in BSURE during three months (February through April). Locations occurred in Area W186 during two months (March and April) and in BARSTUR only during March.

In most cases (except for Area W186), mean distances to shore in Hawaii Navy areas were greater for whales tagged in 2018 than those tagged prior to 2018 (**Table 12**). However, sample sizes in Navy areas were not large enough to permit meaningful statistical comparisons between the two tagging periods. Overall, mean distance to shore ranged from 9 km in Area W186 (for a whale tagged off Maui in 2018) to 188 km in Area W188B (for a whale tagged off Maui in 2018; **Table 12**). The whales with the greatest distances to shore in Navy areas were those individuals that were migrating north to feeding areas.

3.5.3 Use of BIAs

Fifty of the 59 humpback whales tracked prior to 2018 were tagged within the Maui BIA, contributing to the high proportion of tagged whales having locations there. Four other humpbacks spent time in the Maui BIA (one tagged off Kauai and three tagged off Hawaii), resulting in 92 percent of tracked whales having locations there (**Table 13, Figure 45**). Average time spent in the Maui BIA was 7.6 d prior to 2018 and 7.1 d in 2018, with a maximum of 30.2 d. Fourteen percent (8 of 59) of the humpbacks tagged prior to 2018 spent time in the Kauai BIA, averaging 1.0 d (maximum 3.5 d; **Table 13, Figure 46**), compared to 4 percent of the whales tagged in 2018 (1 of 22, for 0.8 d). Ten percent of whales tagged prior to 2018 had locations in the Hawaii BIA (6 of 59, 4 of which were tagged there), with an average residency of 1.7 d (maximum 6.2 d; **Table 13, Figure 47**), compared to none in 2018.

Occupancy in the SEAK BIA was noted for two whales (3 percent) tagged prior to 2018, for an average of 54.8 d (maximum 70.0 d, **Table 13, Figure 48**), and one whale in 2018 (1.5 d). Two whales tagged prior to 2018 also had locations in the Aleutians BIA, averaging 0.6 d (maximum 1.0 d, **Table 13, Figure 49**), while none had locations there in 2018. No humpback whales tagged in Hawaii by OSU had locations in the Bristol Bay or Shumagin BIAs.

Seasonality in humpback whale locations within the Hawaiian breeding BIAs was similar between whales tagged in 2018 and those tagged previously. Locations of humpback whales tagged in Hawaii prior to 2018 were found within the Maui BIA during five months (December through April), within the Kauai BIA during three months (February through April), and in the Hawaii BIA in January and March. Locations within the SEAK BIA occurred during five months (February, May through August), and within the Aleutians BIA during three months (April, May, June).

3.5.4 Genetics

Biopsy samples from several of the historical tagging seasons were collected and are currently archived at OSU, but their analysis and interpretation will require additional funding.

3.5.5 Photo-Identification

OSU is in the process of submitting photo-IDs to Happywhale from the historical tagging seasons. We also plan to share our catalog with other researchers working in the Eastern North Pacific. However, the matching as well as the integration with the tracking and genetics data streams will require additional funding.

4 Discussion

4.1 Tracked Movements

This report details the results of a satellite telemetry study on humpback whales tagged by OSU off Maui, Hawaii, in 2018, with comparison to humpback whales tagged by OSU in Hawaii in prior years (1995-2000, 2015). The resulting tracking data expands our understanding of humpback whale movements, distribution, and residence within the Hawaiian Islands during winter and spring, and provides documentation of migration routes, timing, and destinations for several whales, as well as feeding area movements in the spring and summer for some whales. The results also provide information on humpback whale occurrence and use of Navy training and testing ranges in the North Pacific, as well as NMFS-identified BIAs for humpback whales. The DM and DUR+ tags deployed in 2018 allow for a characterization of diving behavior with a behavioral comparison between breeding and feeding areas and during migration. The biopsy samples collected provided sex determination for tagged whales and individual identifications, as well as stock structure information. Similarly, the photographs collected provided valuable information about tag wound healing, individual identification, resighting histories, and migratory connections.

The average tracking period for implantable tags on humpback whales in this study (mean = 28.0, n = 72) was quite a bit shorter than tracking periods for similar tags deployed by OSU on blue (mean = 73.4 d, n = 82) and fin (mean = 55.4 d, n = 25) (Mate et al. 2018a). The reason for these differences is unclear, but may be related to species differences in tissue composition that leads to better retention of tags on some species than others. It could also be related to seasonal differences in tissue composition. Blue and fin whale tagging took place during summer months, when the whales were feeding, compared to winter/spring tagging of humpback whales on their breeding grounds. Blubber and muscle characteristics may differ significantly between times when whales are feeding versus fasting, the latter of which is considered the case for humpback whales on their breeding grounds. Behavioral differences between feeding and breeding whales may also play a role in different tracking periods, as tag retention may be compromised by the physical competitive behavior between male humpback whales during the breeding season, or close tactile contact between mothers and young calves.

Tracking periods for humpback whales in this study were significantly longer for whales that departed on migration than for those that stayed within the 50-km buffer of the Hawaiian Islands, lending support to the physical contact hypothesis. Tracking periods for implantable tags deployed by OSU on humpback whales in their feeding grounds, however, off California and Oregon in 2017 (mean = 40.8 d, n = 18) and off California, Oregon, and Alaska between 1997 and 2016 (mean = 32.9 d, n = 67), were only slightly longer than for the whales in this study, and still shorter than for blue and fin whales. This points to a difference between species rather than the proposed behavioral or tissue composition differences between breeding and feeding seasons.

The tracking results within Hawaii support results of previous photo-ID studies and aerial surveys, showing high densities of whales in the Maui Nui region between Maui, Molokai, Kahoolawe, and Lanai, as well as Penguin Bank (Mobley et al. 2001), and extensive interchange within the islands (Cerchio et al. 1998, Calambokidis et al. 2008, Baird et al. 2015). The preponderance of tag deployments off Maui likely had an impact on these results; however, aerial surveys throughout all main Hawaiian Islands also point to high densities of humpback whales in the Maui Nui region and Penguin Bank (Mobley et al. 2001), highlighting the areas' importance.

Our 2018 results showed a significant difference between males and females in the number of areas (eight main Hawaiian Islands and Penguin Bank) they visited while in Hawaii, with females visiting fewer areas than males. While only four females were tagged in 2018, three of these were mothers with calves. In Hawaii, humpback mothers with calves have been shown to be more common in the Maui Nui and Penguin Bank regions than elsewhere (Craig and Herman 2000, Craig et al. 2014), and to have a preference for shallow, nearshore waters (Craig et al. 2014, Currie et al. 2018, Pack et al. 2018). Perhaps the difference in movement shown here between males and females tagged off Maui is simply a reflection of mothers remaining in preferred habitat. There was no difference in number of areas visited between males and females tagged off Maui prior to 2018, although the proportion of females prior to 2018 that were mothers with calves (4 of 6) was lower than in 2018. Perhaps the inter-area movements of unaccompanied females contributed to the lack of difference between males and females prior to 2018. Sample sizes of females were very small in all years, so such differences, or lack thereof, should be treated with caution, and comparisons between sexes would benefit from tagging of more females.

While the predominant direction of travel within the islands was to the northwest for whales tagged off Maui and Hawaii, our sample sizes for other islands were far too small to adequately address directionality more comprehensively (although we note that one whale tagged off Kauai followed the opposite pattern, as documented in Mate et al. 1998). Migration departure occurred from all islands (except Hawaii) and Middle Bank, a seamount northwest of Kauai. Only three of the departing whales were tagged off Kauai, and all three of these animals began their migrations off the north coast of Kauai. The rest of the migrating whales were tagged off Maui, but the majority of their departures took place from the north coast of Oahu (8 of 19 known departure points). Henderson et al. (2018) reported migration departure for two of seven whales tagged off Kauai, with departure points off Niihau and seamounts northwest of the northwestern island of Nihoa.

The migratory destinations of humpbacks tagged in Hawaii support previous telemetry, genetic, and photo-ID studies, which show the majority of humpbacks wintering in Hawaii traveling to feeding grounds in northern British Columbia and Southeast 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). Of the nine tagged whales that were tracked to a feeding ground (1995 to 2018 combined; two of which had large gaps in coverage *en route*), almost equal numbers of animals migrated to northern British Columbia/Southeast Alaska (5 whales) and to the Aleutian Islands and Bering Sea (4 whales). In northern British Columbia/Southeast Alaska, the high-use areas identified through the kernel density utilization distributions were located in Southeast Alaska for whales tagged prior to 2018 and in northern British Columbia for whales tagged in 2018. Small sample sizes and large differences in the number of locations per whale prevent any meaningful comparison between the two periods, however. Humpback locations occurred in both areas during both periods, including those from the same individuals (one whale tagged in 1998 and one in 2018). These connections are reinforced by the lack of significant genetic differentiation between humpback whales in northern British Columbia and Southeast Alaska (Baker et al. 2013) and support the treatment of northern British Columbia and Southeast Alaska as one grouping for abundance estimation (Wade et al. 2016).

Wade et al. (2016) grouped humpback whales from the Aleutians and the Bering Sea together for abundance estimation based on photo-ID matches, a lack of genetic differentiation, and the close proximity of the areas, based on studies by Calambokidis et al. (2008) and Baker et al. (2013). The track of whale #5736 from 2018 supports this connection and also details extensive long-range movements throughout the entire Aleutian Island chain (also demonstrated by whale #830 from 1997) and much of the Bering Sea. All of the Aleutian locations of humpbacks tracked from Hawaii in this study were on the southern side of the Aleutian Island chain, in contrast to other telemetry results from tagging out of Dutch Harbor, in the eastern Aleutians, that showed most humpback occurrence on the north side of the islands (Kennedy et al. 2014, Mate et al. 2018b). The fact that two tagged whales spent 36 d and 23 d, respectively, in an area south of Akutan Island and Unimak Pass suggests the south side of the eastern Aleutians also provides foraging habitat for humpback whales.

Results from photo-ID of humpback whales in Russia indicate some 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, based on a lack of resightings between these areas (Calambokidis et al. 2008, Titova et al. 2017). Differences in winter destinations also existed among humpback whales from the three Russian areas, with whales from the east side of Kamchatka having higher photo matches to Asian wintering areas, and those from the Commander Islands and the Gulf of Anadyr having more matches to Hawaii and Mexico (Calambokidis et al. 2008, Titova et al. 2017). Whale #5736 traveled within 170 km of the southeast coast of Kamchatka Peninsula and within 63 km of the Commander Islands before ultimately heading to the Gulf of Anadyr. Another whale tagged off Maui in 1997 (#830, of unknown sex), also traveled to the southeast corner of Kamchatka Peninsula, coming as close as 75 km, and remaining there for the final 19 days of its tracking period. These results suggest that there may be more movement among Russian feeding areas than once thought.

4.2 Use of Navy Training Areas

The tracking data obtained from humpback whales through this CESU agreement also contribute to our understanding of whale use of Navy training and testing areas in Hawaii. A limited number of tagged whales spent time in the Hawaii training ranges, with Area W188A being the most heavily used (15 percent of tagged whales) followed by Area W188B (14 percent of tagged whales). Even fewer whales (7 percent of less) used the other ranges. The training ranges are all located near the island of Kauai, and as the vast majority of whales were tagged off Maui and the areas of highest use were Penguin Bank and

Maui Nui, the low use of Navy ranges is not surprising. Four of the five whales tagged off Kauai had locations in the Navy ranges, compared to only 11 of 72 whales tagged off Maui. It is interesting to note, however, that the whale that had the longest residency in a training range (13.3 d in Area W188A) was a whale tagged off Maui in February 2000. No whales tagged off the island of Hawaii had locations in any of the Hawaii Navy training ranges. More tagging off Kauai would improve our understanding of training range use by humpback whales in Hawaii and help determine whether the minimal use noted here is simply a function of tagging location bias, since other studies have demonstrated humpback whale density has increased around Kauai and Niihau (Mobley et al. 1999).

None of the humpback whales tagged in Hawaii were tracked within any Navy training areas along the US West Coast. Humpback whales are the most common baleen whale found in the Gulf of Alaska, with high densities in numerous coastal areas, from northern British Columbia to the Aleutian Islands (Ferguson et al. 2015a). Presumably some of these animals migrate through the Navy's GOA training range, particularly those that migrate to Prince William Sound and perhaps areas around Kodiak Island. The lack of humpback whale use within this training range may be a function of sample size, with only a small percentage of whales tagged in Hawaii being tracked to a feeding destination. It may also reflect a preference of Hawaiian whales for feeding areas other than those in the northern Gulf of Alaska. Tagging humpback whales in northern Gulf of Alaska feeding areas would help document their use of the GOA training range.

There was also no use of the Navy's NWTT range by humpback whales tagged in Hawaii. However, as outlined below in the photo-ID section, humpback whales from Hawaii have been resighted off the coasts of Oregon, Washington, and southern British Columbia, which would result in time within the NWTT. Our small sample of migrating whales may again be the reason for this lack of use of NWTT.

4.3 Use of BIAs

Tagged humpback whales spent time in all Hawaiian BIAs, during the time of year for which these BIAs are designated (December through April). The vast majority of locations occurred in the Maui BIA, which is not at all surprising, as most of the tag deployments took place within this BIA. Fewer whales used the other Hawaiian BIAs, but this is partially due to the small number of tag deployments in those areas. More tagging off the islands of Hawaii and Kauai would further our understanding of BIA use in those areas. Acoustic detections (Lammers et al. 2011) and habitat modeling (Johnston et al. 2007) suggest that Papahanaumokuakea Marine National Monument, in the northwestern Hawaiian Islands, may represent an extension of humpback whale wintering habitat, but Baird et al. (2015) note that there is not enough data to delineate a BIA in that area. Interestingly, only one location from all 81 of our tracked humpback whales (1995 to 2018) occurred within the Papahanaumokuakea Marine National Monument, as an animal tagged off Maui in 2000 traveled to the eastern edge of Middle Bank, a seamount on the eastern boundary of the monument, spending 7 d in the area before migrating north. This suggests limited use of this area, although more tag deployments off Kauai may tell a different story. Indeed, Henderson et al. (2018) reported four of seven humpback whales tagged off Kauai in March 2017 traveling west/northwest after tagging to Middle Bank, with one also continuing northwest to the island of Nihoa, within the Papahanaumokuakea Marine National Monument.

While only two tagged whales were tracked within the SEAK BIA, residency was extensive, with a maximum of 70 d there, beginning as early as the second week of February for one whale. The designation of a spring SEAK BIA, covering the period of March through May (Ferguson et al. 2015a) does not preclude the occurrence of humpback whales in that BIA earlier than March. Humpbacks are known to have a staggered departure from and arrival to Southeast Alaska feeding grounds, with some departing early and arriving early and vice versa (Ferguson et al. 2015a). The high density of humpback locations around Haida Gwaii, reveals this area to be of importance to feeding humpback whales, and were it not for international boundaries, inclusion of this area as a BIA seems reasonable.

Humpback whale use of feeding area BIAs outside of Southeast Alaska was minimal, due in part to the small number of whales tracked to these areas, but also for the whales' preference for the southern and western side of the Aleutian Island chain. The high density of humpback whale locations south of Akutan Island and Unimak Pass suggests this area for inclusion in the Aleutian BIA, although more data would be desirable from this area before such a determination could be made. In terms of seasonality, some tagged whale locations occurred in the Aleutian BIA earlier (April and May) than the timing associated with BIA designation (June through September). Seasonality associated with BIAs, however, is derived both from timing of densest sightings and from the timing of survey effort, which took place from June through September (Ferguson et al. 2015b), and does not preclude humpback whale occurrence in the area outside those months.

4.4 Residence Time in Hawaii

Since we cannot know a whale's initial arrival time in Hawaii prior to tagging, we expect our satellite-telemetry-derived residence times from tagging to departure (mean = 12.3 d, SD = 9.9 d, n = 25) to represent the minimum. Photo-ID studies have concluded that there is a rapid turnover of individuals in this breeding area throughout the winter season, with an overall residency estimated at two weeks or less (Craig et al. 2001). Therefore, it is reasonable to assume that at the time of tagging some whales had just arrived in Hawaii and some had been there for a long enough time that they were ready to leave regardless of the month. This is supported by our highly variable minimum residence times recorded across the breeding season (range = 1.1-42.8 d), with tagging in all months from December to April. Based on this information, we emphasize that the overall true residence time is likely longer than the satellite-telemetry-based mean minimum value we report.

More importantly, Craig et al. (2001) found significant differences in residency between age and sex classes, with residence time being shorter for juveniles and females (with or without a calf) than for males. While limited by sample size (we lacked sex information for 14 of the 25 whales for which we recorded departure date), our sex-specific results also support this notion (mean minimum residence: 10.4 d for females with a calf and 15.8 d for males). Our longest minimum residence time was 42.8 d (whale #10836, a male tagged off Maui in 1999), while the longest residence reported by Craig et al. (2001) for a male was 76 d.

Migratory timing in and out of Hawaii has also been found to be dependent on sex, age, and reproductive status, with juveniles and females without a calf arriving earlier and females with a calf and males arriving later, and with departure dates following the same progression (Craig et al. 2003). Our results were limited by sample size, but were generally consistent with the Craig et al. (2003) study: the departure dates for the three females with a calf (all tagged late in the season, between mid-March and early April), ranged between late March and early May, while the departure dates for the eight males (tagged between mid-January and mid-April) ranged between late January and late April.

4.5 Dive Behavior

Tags summarized dive behavior for about 60 percent of the tracking duration despite transmitting for only 6 h each day. A larger percentage of the tracking period may be summarized by increasing the number of transmit periods per day, although increases in the number of transmit periods come with a corresponding reduction in the maximum functional life of the tag's battery, so research priorities should be carefully considered when deciding on the desired level of data recovery. The number of lunge events recorded by the tags was more limited than expected, suggesting some behavior was not recorded. The detection algorithm will be assessed for areas to improve prior to subsequent deployments.

The extended attachment durations of some DUR+ and DM tags allowed for an examination of humpback whale diving behavior across as many as three broad-scale regimes based on functional behavior: breeding, migrating, and feeding.

4.5.1.1 Breeding Grounds

To date, information about humpback whale diving behavior off Hawaii was generated from either short-duration archival tags or surface-based observations (Chu 1988, Baird et al. 2000, Herman et al. 2007) and one recent study with Argos-transmitting tags (Henderson et al. 2018). Humpback whales are not feeding while on the Hawaiian breeding grounds, so reported dive behavior is likely related either to reproduction (via competition for mates or selection of partners) or resting. While there was some individual variability, the tagged whales spent the majority of their time near the surface, with infrequent dives deeper than 100 m. With no prey available, the reasons for whales to make deep dives are unclear, as it is an energetically costly activity (Carbone & Houston 1996). Additionally, male humpback whales pursue reproductively available females in groups near the surface where they compete for position with violent contact and other expressions of aggression like bubble blasts (Tyack and Whitehead 1983, Baker and Herman 1984, Herman 2016). The purpose of the occasional deeper dives (> 300 m in some cases) made by some whales is unclear. As previously observed near Kauaii (Henderson et al. 2018), maximum dive depths were likely limited by seafloor depth in many cases, as the most used areas generally ranged in depth from 50 to 150 m. So the deeper dives could also be related to previously undocumented aspects of competitive behavior that occur at a lower rate due to the generally shallow seafloor.

Dive durations were more variable across individuals than dive depths, and long-duration dives (> 20 min) were relatively common in the data. Male humpback whales are known to make long-duration dives while they are vocalizing (singing; Herman 2016) but they will also make "drift dives" where they lay motionless below the surface for extended periods of time (Baird et al. 2000, Darling 2009). Multiple whales were engaged in this behavior when they were tagged and continued subsequent to tag deployment, making dives lasting > 20 min. The purpose behind this behavior is unclear, but it is likely a strategy to conserve energy or rest. However, whales observed making these dives in the field were typically part of a dyad with both whales making these drift dives and laying in close proximity, so there may be a social component to the behavior as well.

Dive behavior was distributed approximately equally across the breeding grounds with no apparent spatial differences in dive depths, duration or activity (lunges). Additionally, the lack of temporal trends within the tracks suggests that whales were behaving similarly across the study area. Spatial segregation between male and female humpbacks using the Hawaiian waters has been documented (Smultea 1994, Craig et al. 2014), which would suggest a spatial component to dive behavior could be possible. However, our tracks were heavily biased toward males, so that additional level of detail may not be visible in our data.

4.5.1.2 Migration

Migrating whales would be expected to make shallow dives of consistent duration to limit unnecessary energy expenditure (Braithwaite et al. 2015). While this was generally the case, the records of deep, long-duration dives occurring at night suggests that there is an aspect of the whale's migratory behavior that is important enough to outweigh the additional energetic costs associated with the dives. While humpback whales are known to suspend their migration to feed when encountering prey along the migratory route (Mate et al. 2007, Stamation et al. 2007), a lunge was only detected during one dive > 200 m, suggesting the purpose was not related to feeding. A more likely explanation is that these dives are in some way related to the whales finding navigation cues to keep themselves on a constant heading. Humpback whales can maintain a constant heading with deviations of less than one degree across hundreds of kilometers, while crossing varying currents and ocean conditions (Horton et al. 2011, 2017). How the whales maintain such an accurate heading is a matter of debate, with some work suggesting lunar phase and the Earth's core magnetic field having an effect (Horton et al. 2017). It is unclear how the observed behavior would fit with these ideas, or other possibilities like the whales using auditory cues to navigate. Deep dives could be explained as the whale descending to avoid surface noise or to improve its sensing of the geomagnetic signal by moving closer to the source, although the reasons why this would only happen at night are not apparent.

While the deep dives do not appear to have been related to feeding, a surprisingly high number of lunges were made by migrating tagged whales. While lunges at the start or end of migration might be related to departure from the breeding area or arrival into more productive waters of the feeding grounds, two of the tagged whales, both females with calves, recorded lunges across a relatively long time period in the middle of their migration. While these whales did not suspend their migrations to feed as has been previously observed (Mate et al. 2007, Stamation et al. 2007), it suggests they may have been attempting to supplement energy reserves diminished by lactation.

4.5.1.3 Feeding grounds

Three of the four tagged whales that reached the feeding grounds in 2018 went to the area near Haida Gwaii, while the last one went to the western Aleutian Islands and Bering Sea. The difference in dive behavior between whales using the two areas suggests different foraging strategies and likely that the whales were feeding on different prey. Humpback whales are flexible foragers, capable of feeding on both fish and krill off the US West Coast (Clapham et al. 1997, Fleming et al. 2016). The diel behavior of whale #5736 along the Aleutians and the Bering Sea was characteristic of rorqual krill-feeding behavior, with lunges and deeper dives occurring during the day (Calambokidis et al. 2007, Goldbogen et al. 2008, Mate et al. 2017, 2018a). It was surprising to see this diel dive behavior continue, as this whale moved during its time on the feeding grounds and suggests that it was able to find consistent, low levels of forage as it moved, or that the deeper daytime dives also represented food-searching behavior.

The dive behavior of the whales that traveled to Haida Gwaii was very consistent both temporally and spatially. There were no apparent diel trends in dive behavior or lunge events, suggesting these whales may have been feeding on fish. Dives were generally closely associated with the western and northern coastline of Haida Gwaii, further suggesting the whales may have been feeding on prey attracted to topographically driven productivity (Whitney et al. 2005). While the bulk of the dives occurred at the northwest end of the island, that is likely biased by the much longer tracking duration of whale #5784 compared to the other two whales using the area.

4.6 Genetics

4.6.1 Population Structure of Feeding Areas

The DNA profiles, combined with the tagging and photo-ID data collected during this project, add to existing information and ongoing efforts seeking to help assign individual whales to their DPS and, ultimately, to estimate the proportion of the DPS using various areas of Naval activity. Here, the genetic identity of the 23 whales tagged in Hawaii in 2018 was consistent with the existing description of the Hawaii DPS, as characterized by the previous 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 34**) and quantitatively by the pairwise F_{ST} value in the test of differentiation (**Table 8**). In comparisons to breeding grounds characterized by SPLASH, the 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 to feeding grounds, the Hawaiian tagging samples showed the greatest similarity to the SPLASH samples from the northern Gulf of Alaska and the greatest differences with California/Oregon and with Russia.

It is well established from previous studies using telemetry, photo-ID, and genetic markers, that the migratory connections of the Hawaiian breeding grounds to feeding grounds is complex (Baker et al. 2013). Although migratory fidelity is strong in both seasonal habitats, there is no simple relationship between breeding and feeding grounds. Instead, the Hawaii DPS includes individuals with fidelity to feeding grounds extending from British Columbia to Russia, with the strongest connections to southeastern Alaska and the northern Gulf of Alaska (Calambokidis et al. 2008, Baker et al. 2013). This individual variation in migratory fidelity was again evident in the relationship of the mtDNA of the Hawaiian whales tagged in this study and their feeding ground destinations. Although the sample size was small, the tagged individuals with the "A-", "A+" and "E2" haplotypes migrated to southeastern Alaska and northern British Columbia. These are the most common haplotypes for these feeding areas, as characterized in SPLASH, indicating a good agreement in the describing population from both lines of evidence. In contrast, the tagged individual with an "E1" haplotype migrated to the Aleutians and on to

Russia (**Figure 35**). This haplotype is relatively widespread among feeding areas, except southeastern Alaska, where it is absent in the SPLASH samples (Baker et al. 2013).

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. Here, comparing the genotype of one of the tagged whales (biopsy sample Mno18HI016, whale #5784, a female) with the SPLASH database provided a 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 grounds, even within a few kilometers of her previous sighting location, 13 years later. This specific example of regional return and local fidelity is further evidence of the potential for improved modeling of cumulative exposure to local stressors, including Naval activity, on both feeding and breeding habitat.

4.7 Photo-Identification

Photo-ID results using tagged as well as untagged whales can greatly increase the number of migratory connections not only for tagged whales that are not tracked to a migratory destination, but also for whales seen in the vicinity of tagged whales. The number of photo-IDs from Hawaii submitted to Happywhale by other researchers, while limited in the past, is now increasing rapidly, which will allow us to expand the overall interpretation and significance of our tagging and genetic results. 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 telemetry, 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). For example, through Happywhale we discovered that a whale tagged in 2018 in Hawaii (#5685, a male) has been seen every year in waters of Washington State and Vancouver Island since 2013, and that an additional five untagged whales photographed by us in Hawaii in 2018 had also been previously identified off Vancouver Island, Washington, and Oregon.

Similarly, as outlined above, through genotype and photo-ID matching with the SPLASH database (collection years 2004, 2005, 2006) we discovered that another whale tagged in 2018 in Hawaii (biopsy sample Mno18HI016, whale #5784, a female) had been previously biopsy-sampled and photographed in northern British Columbia in 2005, while the satellite track showed this individual returning to the same feeding ground 13 years later. 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 the Mexico (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker et al. 1986, Forestell and Urbán-R 2007) breeding areas.

Photo-ID is a powerful tool for identifying whales over time and distance, but is limited by the amount of cooperation between researchers in sharing their catalogs and the amount of time needed to review IDs for matches, compile, and exchange the results. 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. However, since not all researchers submit their photo-IDs to

Happywhale, more detailed work will also have to involve direct collaboration with those researchers 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.

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6 Literature Cited

Aasen, E. and J.F. Medrano. 1990. Amplification of the ZFY and ZFX genes for sex identification in humans, cattle, sheep and goats. Nature Biotechnology 12:1279-1281.

Allen, A.N., J.A. Goldbogen, A.S. Friedlaender, and J. Calambokidis. 2016. Development of an automated method of detecting stereotyped feeding events in multisensor data from tagged rorqual whales. Ecology and Evolution 6:7522-7535

Bailey, H., B.R. Mate, D.M. Palacios, L. Irvine, S.J. Bograd, and D.P. Costa. 2009. Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. Endangered Species Research 10, 93-106. doi:10.3354/esr00239

Baird, R.W, A.D. Ligon, and S. Hooker. 2000. Sub-surface and night-time behavior of humpback whales off Maui, Hawaii: A Preliminary Report. Report prepared under Contract #40ABNC050729 from the Hawaiian Islands Humpback Whale National Marine Sanctuary, Kihei, HI, to the Hawaii Wildlife Fund, Paia, HI.

Baird, R.W., D. Cholewiak, D.L. Webster, G.S. Schorr, S.D. Mahaffy, C. Curtice, J. Harrison, and S.M. Van Parijs. Biologically important areas for cetaceans within U.S. waters – Hawai'i Region. Aquatic Mammals 41:54-64. doi:10.1578/AM.41.1.2015.54

Baird, R. W., S.D. Mahaffy, A.M. Gorgone, T. Cullins, D.J. McSweeney, E.M. Oleson, A.L. Bradford, J. Barlow and D.L. Webster. 2015. False killer whales and fisheries interactions in Hawaiian waters: Evidence for sex bias and variation among populations and social groups. Marine Mammal Science 31: 579-590. doi:10.1111/mms.12177

Baker, C.S. and L.M. Herman. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Canadian Journal of Zoology 62:1922-1937.

Baker, C.S., L.M. Herman, A. Perry, W.S. Lawton, J.M. Straley, A.A. Wolman, G.D. Kaufman, H.E. Winn, J.D. Hall, J.M. Reinke, and J. Ostman. 1986. Migratory movement and population structure of humpback whales (Megaptera novaeangliae) in central and eastern North Pacific. Marine Ecology Progress Series 31:105-119.

Baker, C.S., R. Slade, J.L. Bannister, and R. Abernethy. 1994. Hierarchical structure of mitochondrial DNA gene flow among humpback whales *Megaptera novaeangliae*, world-wide. Molecular Ecology 3:313-327.

Baker, C.S., D. Steel, J. Calambokidis, E. Falcone, U. González-Peral, J. Barlow, A.M. Burdin, P.J. Clapham, J. Ford, C.M. Gabriele, D. Mattila, L. Rojas-Bracho, J.M. Straley, B.L. Taylor, J. Urban, P.R. Wade, D. Weller, B.H. Witteveen, and M. Yamaguchi. 2013. Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. Marine Ecology Progress Series 494:291-306. doi:10.3354/meps10508.

Baumgartner, M.F., T. Hammar, and J. Robbins. 2015. Development and assessment of a new dermal attachment for short-term tagging studies of baleen whales. Methods in Ecology and Evolution 6:289-297.

Bérubé, M., H. Jørgensen, R. McEwing, and P.J. Palsbøll. 2000. Polymorphic di-nucleotide microsatellite loci isolated from the humpback whale, *Megaptera novaeangliae*. Molecular Ecology 9(12):2181-2183.

Bettridge, S., C.S. Baker, J. Barlow, P.J. Clapham, M. Ford, D. Gouveia, D.K. Mattila, R.M. Pace III, P.E. Rosel, G.K. Silber, and P.R. Wade. 2015. Status Review of the Humpback Whale (*Megaptera novaeangliae*) Under the Endangered Species Act. NOAA Technical Memorandum NMFS-SWFSC-540. National Marine Fisheries Service, La Jolla, California. 240 pp.

Braithwaite, J.E., J.J. Meeuwig and M.R. Hipsey. 2015. Optimal migration energetics of humpback whales and the implications of disturbance. Conservation Physiology 3. Braithwaite, J. E., J. J. Meeuwig, and M. R. Hipsey. 2015. Optimal migration energetics of humpback whales and the implications of disturbance. Conservation Physiology 3. doi:10.1093/conphys/cov001.

Calambokidis, J., G.S. Schorr, G.H. Steiger, J. Francis, M. Bakhtiari, G. Marshall, E.M. Oleson, D. Gendron, and K. Robertson. 2007. Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imagine tag (Crittercam). Marine Technology Society Journal 41:19-29.

Calambokidis, J., E.A. Falcone, T.J. Quinn, A.M. Burdin, P.J. Clapham, J.K.B. Ford, C.M. Gabriele, R. LeDuc, D. Mattila, L. Rojas-Bracho, J.M. Straley, B.L. Taylor, J. Urbán-R., D. Weller, B.H. Witteveen, M. Yamaguchi, A. Bendlin, D. Camacho, K. Flynn, A. Havron, J. Huggins, and N. Maloney. 2008. SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific. Final report for Contract AB133F-03-RP-00078, U.S. Dept of Commerce, Western Administrative Center, Seattle, Washington.

Calambokidis, J., G.H. Steiger, C. Curtice, J. Harrison, M.C. Ferguson, E. Becker, M. DeAngelis, and S.M. Van Parijs. 2015. Biologically Important Areas for selected cetaceans within U.S. waters - West Coast Region. Aquatic Mammals 41:39-53.

Carbone, C. and A.I. Houston. 1996. The optimal allocation of time over the dive cycle: An approach based on aerobic and anaerobic respiration. Animal Behaviour 51:1247-1255.

Cerchio, S. 1998. Estimates of humpback whale abundance off Kauai, 1989 to 1993: Evaluating biases associated with sampling the Hawaiian Islands breeding assemblage. Marine Ecology Progress Series 175:23–34.

Chu, K. C. 1988. Dive Times and Ventilation Patterns of Singing Humpback Whales (*Megaptera novaeangliae*). Canadian Journal of Zoology-Revue Canadienne De Zoologie 66:1322–1327.

Clapham P.J., S. Leatherwood, I. Szczepaniak, and R.L. Brownell, Jr. 1997. Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919-1926. Marine Mammal Science 13:368–394.

Collecte Localisation Satellites. 2015. Argos User's Manual. Available at: http://www.argos-system.org/files/pmedia/public/r363_9_argos_users_manual-v1.6.4.pdf.

Craig, A.S. and Herman, L.M. 1997. Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. Canadian Journal of Zoology 75:1923–1933.

Craig, A.S. and L.M. Herman. 2000. Habitat Preferences of Female Humpback Whales *Megaptera novaeangliae* in the Hawaiian Islands Are Associated with Reproductive Status. Marine Ecology Progress Series 193:209–216.

Craig, A.S., L.M. Herman, C.M. Gabriele and A.A. Pack. 2003. Migratory timing of humpback whales (*Megaptera novaeangliae*) in the central North Pacific varies with age, sex and reproductive status. Behaviour 140:981–1001.

Craig, A.S., L.M. Herman, and A.A. Pack. 2001. Estimating residence time of humpback whales in Hawaii. Report prepared for the Hawaiian Islands Humpback Whale National Marine Sanctuary Office of National Marine Sanctuaries, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and the Department of Land and Natural Resources State of Hawaii. 22p.

Craig, A.S., L.M. Herman, A.A. Pack and J.O. Waterman. 2014. Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? Behaviour. 151:613-631.

Currie, J.J., S.H. Stack, J.A. McCordic and J. Roberts. 2018. Utilizing occupancy models and platforms-of-opportunity to assess area use of mother-calf humpback whales. Open Journal of Marine Science. 8:276-292. https://doi.org/10.4236/ojms.2018.82014.

Dalebout, M.L., C.S. Baker, J.G. Mead, V.G. Cockcroft, and T.K. Yamada. 2004. A comprehensive and validated molecular taxonomy of beaked whales, Family Ziphiidae. Journal of Heredity 95:459-473.

Darling, J.D., and C.M. Jurasz. 1983. Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). Pages 359-368 in R. Payne, ed. Communication and behavior of whales. AAAS Selected Symposia Series, Westview Press, Boulder, CO.

Darling, J.D., and D.J. McSweeney. 1985. Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). Canadian Journal of Zoology 63:308-314.

Darling, J.D., and S. Cerchio. 1993. Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. Marine Mammal Science 9(1):84–89.

Darling, J. 2009. Humpbacks: unveiling the mysteries. Granville Island Publishing Ltd., Vancouver, BC, Canada, 239 p.

Excoffier, L., and H.E.L Lischer. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10:564-567.

Federal Register. 2016a. Department of Commerce, NOAA, 50 CFR Parts 223 and 224, Endangered and Threatened Species; Identification of 14 Distinct Population Segments of the Humpback Whale (*Megaptera novaeangliae*) and Revision of Species-Wide Listing. Vol. 81, No. 174, 62260-62320, Thursday, September 8, 2016.

Federal Register. 2016b. Department of the Interior, Fish and Wildlife Service, 50 CFR Part 17, Endangered and Threatened Wildlife and Plants; Identification of 14 Distinct Population Segments of the Humpback Whale and Revision of Species-Wide Listing. Vol. 81, No. 245, 93639-93641, Wednesday, December 21, 2016.

Ferguson, M.C., C. Curtice, and J. Harrison. 2015a. Biologically Important Areas for Cetaceans Within U.S. Waters – Gulf of Alaska Region. Aquatic Mammals 41:65-78. doi:10.1578/AM.41.1.2015.65.

Ferguson, M.C., J.M. Waite, C. Curtice, J.T. Clarke, and J. Harrison. 2015b. Biologically Important Areas for Cetaceans Within U.S. Waters – Aleutian Islands and Bering Sea Region. Aquatic Mammals 41:79-93. doi:10.1578/AM.41.1.2015.79.

Fleming, A.H., C.T. Clark, J. Calambokidis, and J. Barlow. 2016. Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. Global Change Biology 22:1214-1224.

Forestell P.H., and Urbán-R, J. 2007. Movement of a humpback whale (*Megaptera novaeangliae*) between the Revillagigedo and Hawaiian Archipelagos within a winter breeding season. Latin American Journal of Aquatic Mammals 6:97-102.

Gilson, A., M. Syvanen, K. Levine, and J. Banks. 1998. Deer gender determination by polymerase chain reaction: validation study and application to tissues, bloodstains, and hair forensic samples in California. California Fish and Game 84:159-169.

Goldbogen, J.A., J. Calambokidis, D.A. Croll, J.T. Harvey, K.M. Newton, E.M. Oleson, G. Schorr, and R.E. Shadwick. 2008. Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. Journal of Experimental Biology 211:3712-3719. doi:10.1242/jeb.023366.

Heide-Jørgensen, M.P., L. Kleivane, N. Oien, K.L. Laidre, and M.V. Jensen. 2001. A new technique for deploying satellite transmitters on baleen whales: Tracking a blue whale (*Balaenoptera musculus*) in the North Atlantic. Marine Mammal Science 17:949-954. doi:10.1111/j.1748-7692.2001.tb01309.x.

Henderson, E.E., J. Aschettino, M. Deakos, G. Alongi, and T. Leota. 2018. Satellite tracking of migrating humpback whales in Hawai'i. SPAWAR Systems Center Pacific Technical Report 3106, San Diego, CA, 26 pp.

Herman, L., P. Forestell and R.C. Antinoja. 1980. The 1976/77 Migration of humpback whales into Hawaiian waters: Composite description. Doi:10.13140/RG.2.1.4741.1604.

Herman, E.Y.K., L. M. Herman, A.A. Pack, G. Marshall, C.M. Shepard, and M. Bakhtiari. 2007. When whales collide: CRITTERCAM offers insight into the competitive behavior of humpback whales on their Hawaiian wintering grounds. Marine Technology Society Journal 41:35-43.

Herman, L. M. 2016. The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. Biological Reviews 92:1795-1818.

Hooker, S.K., R.W. Baird, S. Al-Omari, S. Gowans, and H. Whitehead. 2001. Behavioral reactions of northern bottlenose whales (Hyperoodon ampullatus) to biopsy darting and tag attachment procedures. Fishery Bulletin 99:303-308.

Horton, T.W., R.N. Holdaway, A.N. Zerbini, N. Hauser, C. Garrigue, A. Andriolo, and P.J. Clapham. 2011. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. Biology Letters 7:674-679.

Horton, T.W., N. Hauser, A.N. Zerbini, M.P. Francis, M.L. Domeier, A. Andriolo, D.P. Costa, P.W. Robinson, C.a.J. Duffy, N. Nasby-Lucas, R.N. Holdaway, and P.J. Clapham. 2017. Route Fidelity during Marine Megafauna Migration. Frontiers in Marine Science 4:422.

Irvine, L.M., B.R. Mate, M.H. Winsor, D.M. Palacios, S.J. Bograd, D.P. Costa, and H. Bailey. 2014. Spatial and temporal occurrence of blue whales off the U.S. West Coast, with implications for management. PLoS ONE 9:e102959. doi:10.1371/journal.pone.0102959.s011.

Johnston, D.W., M.E. Chapla, L.E. Williams and D.K. Matilla. 2007. Identification of humpback whale *Megaptera novaeangliae* wintering habitat in the Northwestern Hawaiian Islands using spatial habitat modeling. Endangered Species Research. 3:249-257. Doi:10.3354/esr00049.

Jonsen, I., J. Flemming, and R. Myers. 2005. Robust state-space modeling of animal movement data. Ecology 86:2874-2880.

Jonsen, I. 2016. Joint estimation over multiple individuals improves behavioural state inference from animal movement data. Scientific Reports 6:19052. doi:10.1038/srep20625.

Kennedy, A.S., A.N. Zerbini, B.K. Rone and P.J. Clapham. 2014. Individual variation in movements of satellite-tracked humpback whales *Megaptera novaeangliae* in the eastern Aleutian Islands and Bering Sea. Endangered Species Research. 23:187−195.

Lagerquist, B.A., B.R. Mate, J.G. Ortega-Ortiz, M. Winsor, and J. Urbán-Ramirez. 2008. Migratory movements and surfacing rates of humpback whales (*Megaptera novaeangliae*) satellite tagged at Socorro Island, Mexico. Marine Mammal Science 24:815-830.

Lammers, M.O., P.I. Fisher-Pool, W.W.L. Au, C.G. Meyer, K.B. Wong and R.E. Brainard. 2011. Humpback whale *Megaptera novaeangliae* song reveals wintering activity in the Northwestern Hawaiian Islands. Marine Ecology Progress Series 423:261-268. https://doi.org/10.3354/meps08959 .

Marshall, T.C., J. Slate, L.E. Kruuk, and J.M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639-655.

Mate, B.R., R. Gisiner, and J. Mobley. 1998. Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. Canadian Journal of Zoology 76:863-868.

Mate, B.R., R. Mesecar, and B. Lagerquist. 2007. The evolution of satellite-monitored radio tags for large whales: One laboratory's experience. Deep-Sea Research II 54:224-247. doi:10.1016/j.dsr2.2006.11.021.

Mate, B.R., L.M. Irvine, and D.M. Palacios. 2017. The development of an intermediate-duration tag to characterize the diving behavior of large whales. Ecology and Evolution 7:585-595.

Mate, B.R., D.M. Palacios, C.S. Baker, B.A. Lagerquist, L.M. Irvine, T. Follett, D. Steel, C.E. Hayslip, and M.H. Winsor. 2018a. Baleen Whale Tagging in Support of Marine Mammal Monitoring Across Multiple Navy Training Areas Covering the Years 2014, 2015, 2016, and 2017. Final Report Prepared for Commander, U.S. Pacific Fleet. Submitted to Naval Facilities Engineering Command Pacific, Pearl Harbor, Hawaii under Contract No. N62470-15-8006-17F4016 issued to HDR, Inc., San Diego, California. August 2018.

Mate, B.R., D.M. Palacios, C.S. Baker, B.A. Lagerquist, L.M. Irvine, T. Follett, D. Steel, C.E. Hayslip, and M.H. Winsor. 2018b. Humpback Whale Tagging in Support of Marine Mammal Monitoring Across Multiple Navy Training Areas in the Pacific Ocean: Final Report for Feeding Areas off the US West Coast in Summer-Fall 2017, Including Historical Data from Previous Tagging Efforts. Prepared for Commander, US Pacific Fleet. Submitted to Naval Facilities Engineering Command Southwest, San Diego, California, under Cooperative Ecosystem Studies Unit, Department of the Navy Cooperative Agreement No. N62473-17-2-0001. 19 October 2018.

Mobley, J.R. Jr., G.B. Bauer, and L.M. Herman. 1999. Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaii. Aquatic Mammals 25:63-72.

Pack, A.A., L.M. Herman, A.S. Craig, S.S. Spitz, J.O. Waterman, E.Y.K. Herman, M.H. Deakos, S. Hakala, and C. Lowe. 2018. Comparing depth and seabed terrain preferences of individually identified female humpback whales (*Megaptera novaeangliae*), with and without calf, off Maui, Hawaii. Marine Mammal Science 34:1097-1110. https://doi.org/10.1111/mms.12495

Palsbøll, P.J., M. Bérubé, A.H. Larsen, and H. Jørgensen. 1997. Primers for the amplification of tri- and tetramer microsatellite loci in baleen whales. Molecular Ecology 6:893-895.

Peakall, R., and P.E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288-295.

Ross, H.A., G.M. Lento, M.L. Dalebout, M. Goode, G. Ewing, P. McLaren, A.G. Rodrigo, S. Lavery, and C.S. Baker. 2003. *DNA surveillance*: web-based molecular identification of whales, dolphins and porpoises. Journal of Heredity 94:111-114.

Salden, D.R., L.M. Herman, M. Yamaguchi, and F. Sato. 1999. Multiple visits of individual humpback whales (*Megaptera novaeangliae*) between the Hawaiian and Japanese winter grounds. Canadian Journal of Zoology 77: 504–508.

Sambrook, J., E.F. Fritsch, and T. Maniatis. 1989. Molecular cloning: a laboratory manual 2nd ed. Cold Spring Harbor Laboratory Press, Cold Sprink Harbor, New York.

Schlötterer, C., W. Amos, and D. Tautz. 1991. Conservation of polymorphic simple sequence loci in cetacean species. Nature 354:63-65.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. The Journal of Wildlife Management 63(2): 739-747. https://www.jstor.org/stable/3802664.

Simon, M., M. Johnson, and P.T. Madsen. 2012. Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. Journal of Experimental Biology 215:3786-3798.

Smultea, M.A. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. Canadian Journal of Zoology 72:805-811.

Stamation, K.A., D.B. Croft, P.D. Shaughnessy, and K. Waples. 2007. Observations of humpback whales (*Megaptera novaeangliae*) feeding during their southward migration along the coast of southeastern New South Wales, Australia: Identification of a possible supplemental feeding ground. Aquatic Mammals 33:165-174.

Titova, O.V., O.A. Filatova, I.D. Fedutin, E.N. Ovsyanikova, H. Okabe, N. Kobayashi, J.M.V. Acebes, A.M. Burdin, and E. Hoyt. 2017. Photo-identification matches of humpback whales (*Megaptera novaeangliae*) from feeding areas in Russian Far East seas and breeding grounds in the North Pacific. Marine Mammal Science 34(1):100–112.

Tyack, P. and H. Whitehead. 1983. Male competition in large groups of wintering humpback whales. Behaviour 83:132-154.

Valsecchi, E., and W. Amos. 1996. Microsatellite markers for the study of cetacean populations. Molecular Ecology 5:151-156.

Vincent, C., B.J. McConnell, V. Ridoux, and M.A. Fedak. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. Marine Mammal Science 18:156-166.

Wade, P.R., T.J. Quinn II, J. Barlow, C.S. Baker, A.M. Burdin, J. Calambokidis, P.J. Clapham, E. Falcone, J.K.B. Ford, C.M. Gabriele, R. Leduc, D.K. Mattila, L. Rojas-Bracho, J. Straley, B.L. Taylor, J. Urbán R., D. Weller, B.H. Witteveen, and M. Yamaguchi. 2016. Estimates of abundance and migratory destination for North Pacific humpback whales in both summer feeding areas and winter mating and calving areas. Paper SC/66b/IA21 submitted to the Scientific Committee of the International Whaling Commission, June 2016, Bled, Slovenia. 41pp. Available at https://archive.iwc.int/.

Wade, P.R. 2017. Estimates of abundance and migratory destination for North Pacific humpback whales in both summer feeding areas and winter mating and calving areas – revision of estimates in SC/66b/IA21. Paper SC/A17/NP11 presented to the IWC Workshop on the Comprehensive Assessment of North Pacific Humpback Whales, 18-21 April 2017, Seattle, USA. 9pp. Available at https://archive.iwc.int/.

Waits, J.L., and P.L. Leberg. 2000. Biases associated with population estimation using molecular tagging. Animal Conservation 3:191-199.

Waits, L.P., G. Luikart, and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Molecular Ecology 10(1):249-256.

Waldick, R.C., M.W. Brown, and B.N. White. 1999. Characterization and isolation of microsatellite loci from the endangered North Atlantic right whale. Molecular Ecology 8:1763-1765.

Weinrich, M.T., R.H. Lambertson, C.R. Belt, M.R. Schilling, H.J. Iken, and S.E. Syrjala. 1992. Behavioral reactions of humpback whales *Megaptera novaeangliae* to biopsy procedures. Fishery Bulletin 90:588-598.

Whitney, F.A., W.R. Crawford, and P. Harrison. 2005. Physical processes that enhance nutrient transport and primary productivity in the coastal and open ocean of the subarctic NE Pacific. Deep-Sea Research Part II-Topical Studies in Oceanography 52:681-706.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Table 1. Deployment and performance data for 25 satellite-monitored radio tags deployed on humpback whales off Maui, Hawaii, during March 2018. In the Sex column, U = unknown sex, in cases when no biopsy sample was collected. See Section 2.3.1 for location filtering method.

Tag #	Sex	Tag Type	Deployment Date	Most Recent Location	# Days Tracked	# Filtered Locations	# Argos Locations	Total Distance (km)
832*	M	DM	14-Mar-18	15-Mar-18	0.9	0	2	0
836	M	DM	12-Mar-18	25-Mar-18	13.0	80	104	833
839	M	DM	13-Mar-18	29-Mar-18	15.3	96	108	645
843	F/C	DM	15-Mar-18	17-May-18	63.0	145	197	3,313
849	F/C	DM	13-Mar-18	25-Mar-18	11.4	18	26	276
4172	M	DM	14-Mar-18	6-May-18	53.7	412	599	6,373
5641	M	DM	16-Mar-18	2-Apr-18	17.2	93	118	1,357
5655	M	DM	17-Mar-18	22-Mar-18	4.3	20	30	144
5685	M	DM	17-Mar-18	22-Mar-18	4.7	24	36	280
5701*	M	DM	18-Mar-18	-	-	-	-	-
5736	M	DM	18-Mar-18	25-Aug-18	159.9	977	1384	12,442
5742	M	DM	18-Mar-18	22-Mar-18	4.5	20	34	198
5743	M	DM	18-Mar-18	21-Mar-18	2.4	7	14	61
5746	M	DM	18-Mar-18	26-Mar-18	8.0	51	58	429
5800	M	DM	19-Mar-18	17-May-18	58.2	232	387	6,394
5843*	M	DM	20-Mar-18	20-Mar-18	0.1	0	2	0
5878	F	DM	20-Mar-18	21-Mar-18	1.1	8	12	103
5938	M	DM	20-Mar-18	31-Mar-18	11.1	59	70	437
10827	M	DM	20-Mar-18	28-Mar-18	7.3	38	48	268
10829	M	DM	21-Mar-18	25-Mar-18	4.0	26	31	171
Mean		**DM**			**25.8**	**121**	**172**	**1,984**
Median		**DM**			**11.1**	**38**	**48**	**429**
4177	M	DUR+	15-Mar-18	18-Mar-18	2.2	12	18	126
5644	M	DUR+	17-Mar-18	28-Mar-18	11.1	54	78	576
5784	F/C	DUR+	19-Mar-18	1-Jul-18	104.5	717	1013	8,170
5826	M	DUR+	19-Mar-18	24-Mar-18	4.2	24	30	204

10833	U	DUR+	21-Mar-18	6-May-18	45.4	74	84	3,070
Mean		**DUR+**			**33.5**	**176**	**245**	**2,429**
Median		**DUR+**			**11.1**	**54**	**78**	**576**

KEY: DM = Telonics RDW-665 Dive-Monitoring tag; DUR+ = Telonics RDW-665 Dive Duration Monitoring Plus tag (no depth); km = kilometer(s); F = Female; F/C = Female with a calf; M = Male; U = unknown; # = number; * = not included in the computation of Mean or Median.

Table 2. Residence time in Hawaii for 25 tagged whales with known departure based on the date their track crossed the 50-km buffer zone around the archipelago. For each whale, also reported is the sex, the tag deployment area and date, the date the track crossed the buffer zone, the date the last location was received, the total duration and total distance covered by the track, and the feeding-area destination (inferred for incomplete tracks based on the direction of the trajectory when possible; in parenthesis and italics). KRS = Kermit-Roosevelt Seamount. Nine of the tags lasted at least until arrival to a feeding area (last two columns). Note that separate mean values are reported for the historical (1995-2015) and the 2018 tagging periods, as well as the overall mean values.

Tag #	Sex	Deploy Area	Deploy Date	Migration Depart	Residence in HI (d)	Last Location	Duration (d)	Distance (km)	Destination	Complete Migration
10822	U	Kauai	27-Mar-1995	29-Mar-1995	1.2	7-Apr-1995	11.0	1,223	(*Western Gulf of Alaska*)	No
10824	F/C	Kauai	26-Mar-1995	29-Mar-1995	2.7	31-Mar-1995	4.5	451	-	No
23038	U	Kauai	2-Apr-1995	3-Apr-1995	1.1	19-Apr-1995	17.0	1,631	(*Western Gulf of Alaska*)	No
828	F/C	Maui	9-Apr-1997	3-May-1997	22.6	21-May-1997	42.7	3,339	*(Aleutians)*	No
830	U	Maui	5-Apr-1997	9-Apr-1997	3.7	23-Jun-1997	79.0	7,255	Kamchatka	Yes
831	U	Maui	5-Apr-1997	13-Apr-1997	1.2	24-Apr-1997	18.2	2,418	-	No
847	U	Maui	14-Apr-1998	20-Apr-1998	6.0	23-May-1998	38.3	3,390	(*Southern British Columbia/Northern Washington*)	No
848	U	Maui	8-Apr-1998	13-Apr-1998	4.9	4-May-1998	25.9	2,215	*(Aleutians)*	No
10826	M	Maui	15-Apr-1998	26-Apr-1998	10.8	10-Aug-1998	117.0	7,884	Northern British Columbia/Southeast Alaska	Yes
10828	U	Maui	11-Feb-1999	23-Feb-1999	12.5	3-Jul-1999	142.6	10,279	Aleutians (via KRS)	Yes
10830	M	Maui	10-Feb-1999	1-Mar-1999	18.8	6-Mar-1999	23.9	1,626	*(Southeast Alaska)*	No
10836	M	Maui	10-Feb-1999	25-Mar-1999	42.8	17-Apr-1999	65.4	4,621	*(Northern British Columbia/Southeast Alaska)*	No

10842	U	Maui	14-Feb-1999	2-Mar-1999	15.4	8-Mar-1999	21.7	1,588	*(Aleutians)*	No
4177	U	Maui	11-Dec-1999	20-Dec-1999	8.4	12-May-2000	152.8	4,675	Southeast Alaska	Yes
835	U	Maui	5-Feb-2000	19-Feb-2000	14.1	25-Mar-2000	49.7	3,651	*(Southern British Columbia/Northern Washington)*	No
843	U	Maui	4-Feb-2000	13-Feb-2000	9.5	5-May-2000	91.1	3,991	Aleutians	Yes
830	M	Maui	20-Jan-2015	29-Jan-2015	9.5	5-Feb-2015	16.25	1,541	(*Southern British Columbia/Northern Washington*)	No
5746	U	Maui	15-Jan-2015	13-Feb-2015	29.0	22-Feb-2015	37.98	2,487	*(Aleutians)*	No
Mean 1995-2015					**11.9**		**53.1**	**3,570**		
Tag #	**Sex**	**Deploy Area**	**Deploy Date**	**Migration Depart**	**Residence in HI (d)**	**Last Location**	**Duration (d)**	**Distance (km)**	**Destination**	**Complete Migration**
843	U	Maui	15-Mar-2018	8-Apr-2018	23.2	17-May-2018	63.0	3,294	*(Aleutians)*	No
4172	M	Maui	14-Mar-2018	17-Mar-2018	3.3	6-May-2018	53.7	6,296	Northern British Columbia	Yes
5641	M	Maui	16-Mar-2018	29-Mar-2018	13.5	2-Apr-2018	17.2	1,019	Northern British Columbia	No
5736	M	Maui	18-Mar-2018	31-Mar-2018	13.7	12-Aug-2018	147.2	11,302	Aleutians/Kamchatka/ Bering Sea	Yes
5800	M	Maui	19-Mar-2018	3-Apr-2018	14.4	17-May-2018	58.2	6,259	Northern British Columbia	Yes
5784	F/C	Maui	19-Mar-2018	25-Mar-2018	5.9	1-Jul-2018	104.5	8,065	Northern British Columbia	Yes

10833	U	Maui	21-Mar-2018	11-Apr-2018	20.5	6-May-2018	59.5	860	(Aleutians)	No
Mean 2018					13.5		71.9	5,299		
Overall Mean					**12.3**		**58.3**	**4,054**		

KEY: d = days; km = kilometer(s); F = Female; F/C = Female with a calf; M = Male; U = unknown; # = number.

Table 3. Percentage of filtered Argos locations and time spent inside Navy activity areas W186, W188A, W188B, BSURE and BARSTUR for 22 humpback whales tagged off Maui, Hawaii, 2018. See Section 2.2.2 for location filtering method.

Tag #	Tag Type	Total		W186			W188A			W188B			BSURE			BARSTUR		
		# Locs	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days
836	DM	81	13.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
839	DM	97	15.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
843	DM	146	63.0	0	0	0	3	4	2.8	1	1	0.9	0	0	0	0	0	0
849	DM	19	11.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4172	DM	413	53.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5641	DM	94	17.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5655	DM	21	4.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5685	DM	25	4.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5736	DM	977	159.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5742	DM	21	4.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5743	DM	8	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5746	DM	52	8.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5800	DM	233	58.2	<1	1	0.4	5	6	3.2	1	2	1.1	<1	1	0.6	0	<1	0.2
5878	DM	9	1.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5938	DM	60	11.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10827	DM	39	7.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10829	DM	27	4.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4177	DUR+	13	2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5644	DUR+	55	11.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5784	DUR+	718	104.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5826	DUR+	25	4.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10833	DUR+	75	45.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mean+		**146**	**27.6**	**<1**	**1**	**0.4**	**4**	**5**	**3.0**	**1**	**2**	**1.0**	**<1**	**<1**	**0.6**	**0**	**<1**	**0.2**
Median+		**54**	**11.1**	**<1**	**1**	**0.4**	**4**	**5**	**3.0**	**1**	**2**	**1.0**	**<1**	**<1**	**0.6**	**0**	**<1**	**0.2**

KEY: DM = Telonics RDW-665 Dive-Monitoring tag; DUR+ = Telonics RDW-665 Dive Duration Monitoring Plus tag (no depth); Locs = Locations; # = number; + Summary statistics do not include zero values in their calculation.

Table 4. Geodesic distances (km) to nearest point on shore in Navy activity areas for 22 humpback whales tagged off Maui, Hawaii, in 2018 (including mean, median, and maximum distance to shore). The number of locations includes filtered Argos locations (see Section 2.3.1 for filtering method) plus deployment location (when the deployment location occurred in a Navy range).

Tag #	Tag Type	W186				W188A				W188B				BSURE				BARSTUR			
		n	Mean	Median	Max	n	Mean	Median	Max	n	Mean	Median	Max	n	Mean	Median	Max	n	Mean	Median	Max
836	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
839	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
843	DM	0	-	-	-	4	266	253	365	2	107	107	123	0	-	-	-	0	-	-	-
849	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
4172	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5641	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5655	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5685	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5736	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5742	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5743	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5746	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5800	DM	2	9	9	9	12	102	95	226	3	275	261	305	1	72	72	72	0	-	-	-
5878	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5938	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
10827	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
10829	DM	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
4177	DUR+	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5644	DUR+	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5784	DUR+	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
5826	DUR+	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
10833	DUR+	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
Mean*		**2**	**9**	**9**	**9**	**8**	**184**	**174**	**296**	**2.5**	**191**	**184**	**214**	**1**	**72**	**72**	**72**	**0**	-	-	-
Median*		**2**	**9**	**9**	**9**	**8**	**184**	**174**	**296**	**2.5**	**191**	**184**	**214**	**1**	**72**	**72**	**72**	**0**	-	-	-

KEY: DM = Telonics RDW-665 Dive-Monitoring tag; DUR+ = Telonics RDW-665 Dive Duration Monitoring Plus tag (no depth); # = number; * Summary statistics do not include zero values in their calculation.

Table 5. Percentage of filtered Argos locations and time spent inside BIAs for 22 humpback whales tagged off Maui, Hawaii, during March 2018. See Section 2.3.1 for location filtering method.

		Filtered Locations																			
		Total		Maui			Kauai			Hawaii			SEAK			Aleutians					
Tag #	Tag Type	# Locs	# Days	% Locs	% of Days	# Days	% Locs	% of Days	# Days	% Locs	% of Days	# Days	% Locs	% of Days	# Days	% Locs	% of Days	# Days			
836	DM	81	13.0	85	87	11.3	0	0	0	0	0	0	0	0	0	0	0	0			
839	DM	97	15.3	81	86	13.1	0	0	0	0	0	0	0	0	0	0	0	0			
843	DM	146	63.0	18	19	12.1	0	0	0	0	0	0	0	0	0	0	0	0			
849	DM	19	11.4	100	99	11.2	0	0	0	0	0	0	0	0	0	0	0	0			
4172	DM	413	53.7	3	3	1.8	0	0	0	0	0	0	0	0	0	0	0	0			
5641	DM	94	17.2	48	50	8.5	0	0	0	0	0	0	0	0	0	0	0	0			
5655	DM	21	4.3	100	100	4.3	0	0	0	0	0	0	0	0	0	0	0	0			
5685	DM	25	4.7	92	95	4.5	0	0	0	0	0	0	0	0	0	0	0	0			
5736	DM	977	159.9	7	8	12.1	0	0	0	0	0	0	0	0	0	0	0	0			
5742	DM	21	4.5	100	100	4.5	0	0	0	0	0	0	0	0	0	0	0	0			
5743	DM	8	2.4	100	100	2.4	0	0	0	0	0	0	0	0	0	0	0	0			
5746	DM	52	8.0	94	92	7.4	0	0	0	0	0	0	0	0	0	0	0	0			
5800	DM	233	58.2	13	17	10.1	1	1	<1	0	0	0	2	3	1.5	0	0	0			
5878	DM	9	1.1	33	30	0.3	0	0	0	0	0	0	0	0	0	0	0	0			
5938	DM	60	11.1	90	90	10.0	0	0	0	0	0	0	0	0	0	0	0	0			
10827	DM	39	7.3	100	100	7.3	0	0	0	0	0	0	0	0	0	0	0	0			
10829	DM	27	4.0	93	93	3.7	0	0	0	0	0	0	0	0	0	0	0	0			
4177	DUR+	13	2.2	100	100	2.2	0	0	0	0	0	0	0	0	0	0	0	0			
5644	DUR+	55	11.1	80	82	9.1	0	0	0	0	0	0	0	0	0	0	0	0			
5784	DUR+	718	104.5	1	1	0.8	0	0	0	0	0	0	0	0	0	0	0	0			
5826	DUR+	25	4.2	100	100	4.2	0	0	0	0	0	0	0	0	0	0	0	0			
10833	DUR+	75	45.4	84	35	15.7	0	0	0	0	0	0	0	0	0	0	0	0			
Mean*		**146**	**27.6**	**69**	**68**	**7.1**	**1**	**1**	**<1**	**-**	**-**	**-**	**2**	**3**	**1.5**	**-**	**-**	**-**			
Median*		**54**	**11.1**	**88**	**89**	**7.4**	**1**	**1**	**<1**	**-**	**-**	**-**	**2**	**3**	**1.5**	**-**	**-**	**-**			

KEY: DM = Telonics RDW-665 Dive-Monitoring tag; DUR+ = Telonics RDW-665 Dive Duration Monitoring Plus tag (no depth); Locs = Locations; SEAK = Southeast Alaska BIAs; # = number; * Summary statistics do not include zero values in their calculation.

Table 6. Summary of dive data summarized by 25 DM and DUR+ tags deployed on humpback whales off Maui, Hawaii, during March 2018.

Tag #	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	Median Dives Per Day	Min Dives Per Day	Max Dives Per Day
832	DM	M	0.4	22	79.7%	22	22	22
836	DM	M	12.0	1270	61.1%	113	7	127
839	DM	M	15.1	1213	62.4%	73	13	123
843	DM	F/C	62.8	3538	33.2%	55	6	103
849	DM	F/C	11.3	599	28.4%	53	8	72
4172	DM	M	53.5	3729	79.0%	67	2	159
4177	DUR+	M	2.1	329	94.9%	82.5	2	162
5641	DM	M	22.8	718	38.9%	38	4	65
5644	DUR+	M	10.9	957	47.1%	78.5	29	122
5655	DM	M	4.2	174	31.9%	27	7	52
5685	DM	M	4.6	454	53.5%	81.5	4	125
5701	DM	M	-	-	-	-	-	-
5736	DM	M	159.8	13190	66.6%	80.5	4	152
5742	DM	M	4.4	355	51.7%	72	27	105
5743	DM	M	2.4	152	49.4%	24	6	98
5746	DM	M	7.9	565	44.5%	60	7	103
5784	DUR+	F/C	104.4	13983	73.1%	133	56	258
5800	DM	M	57.8	1651	63.8%	23	1	88
5826	DUR+	M	4.0	297	45.7%	57	1	95
5843	DM	M	0.1	15	99.5%	15	15	15
5878	DM	F	1.0	121	89.4%	60.5	15	106
5938	DM	M	11.0	878	71.4%	72.5	24	130
10827	DM	M	7.2	534	65.2%	68	1	108
10829	DM	M	3.9	381	58.7%	85	34	102
10833	DUR+	U	20.0	2089	65.2%	98	27	174
	Mean		**24.3**	**1967**	**60.6%**	**64**	**13**	**111**

KEY: DM = Telonics RDW-665 Dive-Monitoring tag; DUR+ = Telonics RDW-665 Dive Duration Monitoring Plus tag (no depth); F = Female; F/C = Female with a calf; M = Male; U = unknown; Min = minimum; Max = maximum; # = number; % = percent.

Table 7. The identity, frequency, and percentage of the six mtDNA haplotypes, including GenBank codes, resolved for the 23 whales sampled off Maui, Hawaii, during 2018. This haplotype composition is also shown in Figure 36b.

Haplotype code	GenBank code	Number of tagged Hawaii whales with haplotype	Percentage of tagged Hawaii whales with haplotype
A+	KF477244	10	43
A-	KF477245	4	17
E1	KF477249	2	9
E2	KF477256	2	9
E5	KF477258	2	9
F2	KF477266	3	13
Total		23	100

Table 8. Results of pairwise tests of differentiation of mtDNA haplotype frequencies between the Hawaii (n = 23) tagging sample and the 18 regional strata (feeding areas and breeding grounds) defined in SPLASH (Baker et al. 2013). The regional abbreviations and associated sample sizes are consistent with Figure 34. The sample sizes refer to the number of individuals sampled in each region. Rows in italics indicate low sample numbers for comparisons with western Aleutians and the Philippines.

		Hawaii tagging n=23	
Region	**n**	**F_{ST}**	***p*-value**
Feeding Areas			
Russia (RUS)	70	0.1070	<0.0001*
Western Aleutians (WAL)	*8*	*0.0263*	*0.2222*
Bering (BER)	114	0.0801	0.0011*
Eastern Aleutians (EAL)	36	0.0354	0.0701
Western Gulf of Alaska (WGOA)	96	0.0359	0.0325*
Northern Gulf of Alaska (NGOA)	233	0.0075	0.2385
Southeast Alaska (SEA)	183	0.0664	0.0251*
Northern British Columbia (NBC)	104	0.0366	0.0804
Southern British Columbia/Washington (SBC/WA)	51	0.0476	0.0260*
California/Oregon (CA/OR)	123	0.1242	<0.0001*
Breeding Grounds			
Philippines (PHI)	*13*	*0.2326*	*0.0002**
Okinawa (OK)	72	0.2365	<0.0001*
Ogasawara (OG)	159	0.0857	<0.0001*
Hawaii (HI)	227	0.0056	0.2784
Mexico-Archipelago Revillagigedo (MX-AR)	106	0.0601	0.0023*
Mexico-Baja California (MX-BC)	110	0.0451	0.0062*
Mexico-Mainland (MX-ML)	62	0.0626	0.0027*
Central America (CENTAM)	36	0.1702	0.0002*

KEY: * = significant difference.

Table 9. Mean (and SE) values for individual tracking durations and total distance traveled for 81 humpback whales tagged in Hawaii from 1997 to 2018. Information from nine externally-mounted tags deployed in 1995 and 1996 is not included here.

	Tracking Duration (d)			Total Distance (km)		
	n	**Mean**	**SE**	**n**	**Mean**	**SE**
1997-2015	50	28.2	4.9	50	1601.4	306.1
2018	22	27.6	8.5	22	2085.0	708.4

KEY: d = days; km = kilometers; n = sample size; SE = standard error.

Table 10. Connectivity between islands/areas for 59 humpback whales satellite-tagged in Hawaii from 1995 to 2015. The first column refers to deployment location, and subsequent columns along a given row reflect the number of whales tagged in that location that visited other islands/areas after tagging. Note that the numbers in the "Areas visited after tagging" columns do not necessarily reflect different whales. For instance, even though only one whale tagged in Kauai in 1995 (#10826, of unknown sex) visited other areas, this whale visited four other areas during its tracking period. Cells contain dashes in cases where no whales were tagged at a particular island.

Deployment Location (# tags tracked)	Areas visited after tagging								
	Niihau	Kauai	Oahu	Penguin Bank	Molokai	Lanai	Maui	Kahoolawe	Hawaii
Niihau (0)	-	-	-	-	-	-	-	-	-
Kauai (5)	0	5	1	1	1	1	0	0	0
Oahu (0)	-	-	-	-	-	-	-	-	-
Penguin Bank (0)	-	-	-	-	-	-	-	-	-
Molokai (0)	-	-	-	-	-	-	-	-	-
Lanai (0)	-	-	-	-	-	-	-	-	-
Maui (50)	1	3	9	28	31	33	50	4	2
Kahoolawe (0)	-	-	-	-	-	-	-	-	-
Hawaii (4)	0	0	0	0	1	2	3	1	4

KEY: # = number.

Table 11. Mean and maximum number of days spent inside Hawaii Navy activity areas for 81 humpback whales tagged in Hawaii from 1995 to 2018. For areas in which only one whale spent time, the numbers in the mean and max columns represent that whale's residency in the range, rather than a mean and max.

	# Days														
Season (# Whales Tracked)	**W186**			**W188A**			**W188B**			**BSURE**			**BARSTUR**		
	n	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**
1995-2015 (59)	4	2.2	4.2	10	4.3	13.3	9	1.8	5.3	5	0.5	1.2	4	0.5	0.7
2018 (22)	1	0.4	0.4	2	3.0	3.2	2	1.0	1.1	1	0.6	0.6	1	0.2	0.2
All Seasons (81)	**5**	**1.3**	**4.2**	**12**	**3.6**	**13.3**	**11**	**1.4**	**5.3**	**6**	**0.6**	**1.2**	**5**	**0.4**	**0.7**

KEY: n = sample size; # = number.

Table 12. Summary statistics (mean, median and maximum [Max]) for distance to shore (km) inside the W186, W188A, W188B, BSURE, and BARSTUR Navy activity areas from 81 humpback whales tagged in Hawaii from 1995 to 2018. Distance to shore was calculated as the mean geodesic distance from filtered Argos locations to nearest point on shore for each whale. See Section 2.3.1 for location filtering method.

Season	W186				W188A				W188B				BSURE				BARSTUR			
(# whales)	n	Mean	Median	Max	n	Mean	Median	Max	n	Mean	Median	Max	n	Mean	Median	Max	n	Mean	Median	Max
1995-2015 (59)	3	13	12	19	10	137	112	414	6	129	125	202	4	37	31	65	2	16	16	18
2018 (22)	1	9	9	9	2	143	155	365	2	188	181	305	1	72	72	72	0	-	-	-
Overall Mean+	**-**	**11**	**11**	**14**	**-**	**140**	**134**	**390**	**-**	**158**	**153**	**254**	**-**	**54**	**52**	**68**	**-**	**16**	**16**	**18**
Overall Median+	**-**	**11**	**11**	**14**	**-**	**140**	**134**	**390**	**-**	**158**	**153**	**254**	**-**	**54**	**52**	**68**	**-**	**16**	**16**	**18**

KEY: n = sample size; # = number; + Summary statistics do not include zero values in their calculation.

Table 13. Mean and maximum number of days spent inside BIAs in Hawaii, Southeast Alaska (SEAK), and Aleutian Island areas for 81 humpback whales tagged in Hawaii from 1995 to 2018.

	# Days														
Season (# Whales Tracked)	**Maui**			**Kauai**			**Hawaii**			**SEAK**			**Aleutians**		
	n	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**
1995-2015 (59)	54	7.6	30.2	8	1.0	3.5	6	1.7	6.2	2	54.8	70.0	2	0.6	1.0
2018 (22)	22	7.1	15.7	1	0.8	0.8	-	-	-	1	1.5	1.5	-	-	-
All Seasons (81)	**76**	**7.4**	**30.2**	**9**	**0.9**	**3.5**	**6**	**1.7**	**6.2**	**3**	**28.2**	**70.0**	**2**	**0.6**	**1.0**

KEY: n = sample size; # = number.

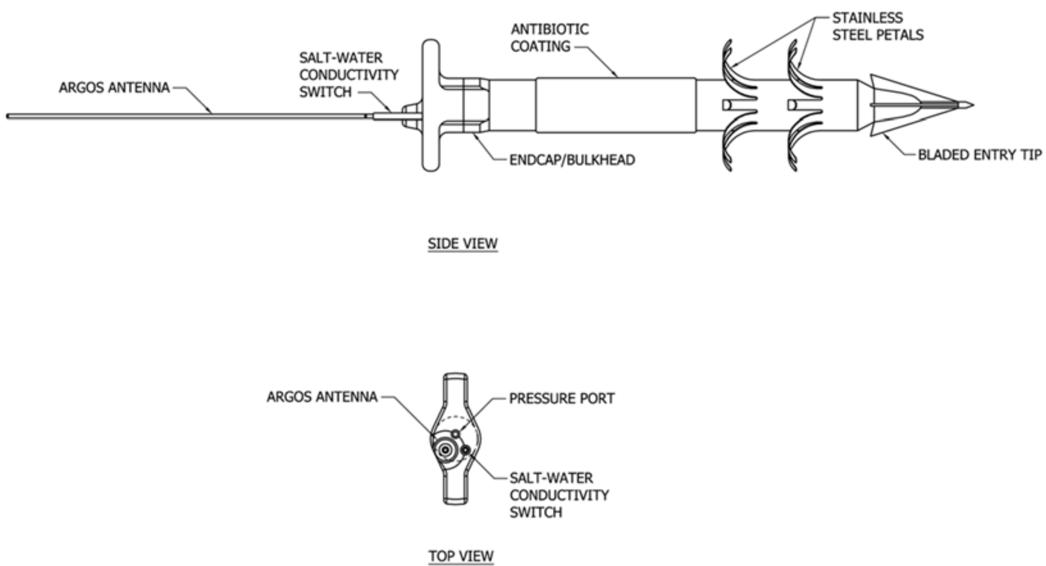


Figure 1. Schematic diagram of the Telonics RDW-665 DM tag showing the main body, the distal endcap with the antenna and saltwater conductivity switch endcap, as well as the penetrating tip and anchoring system.

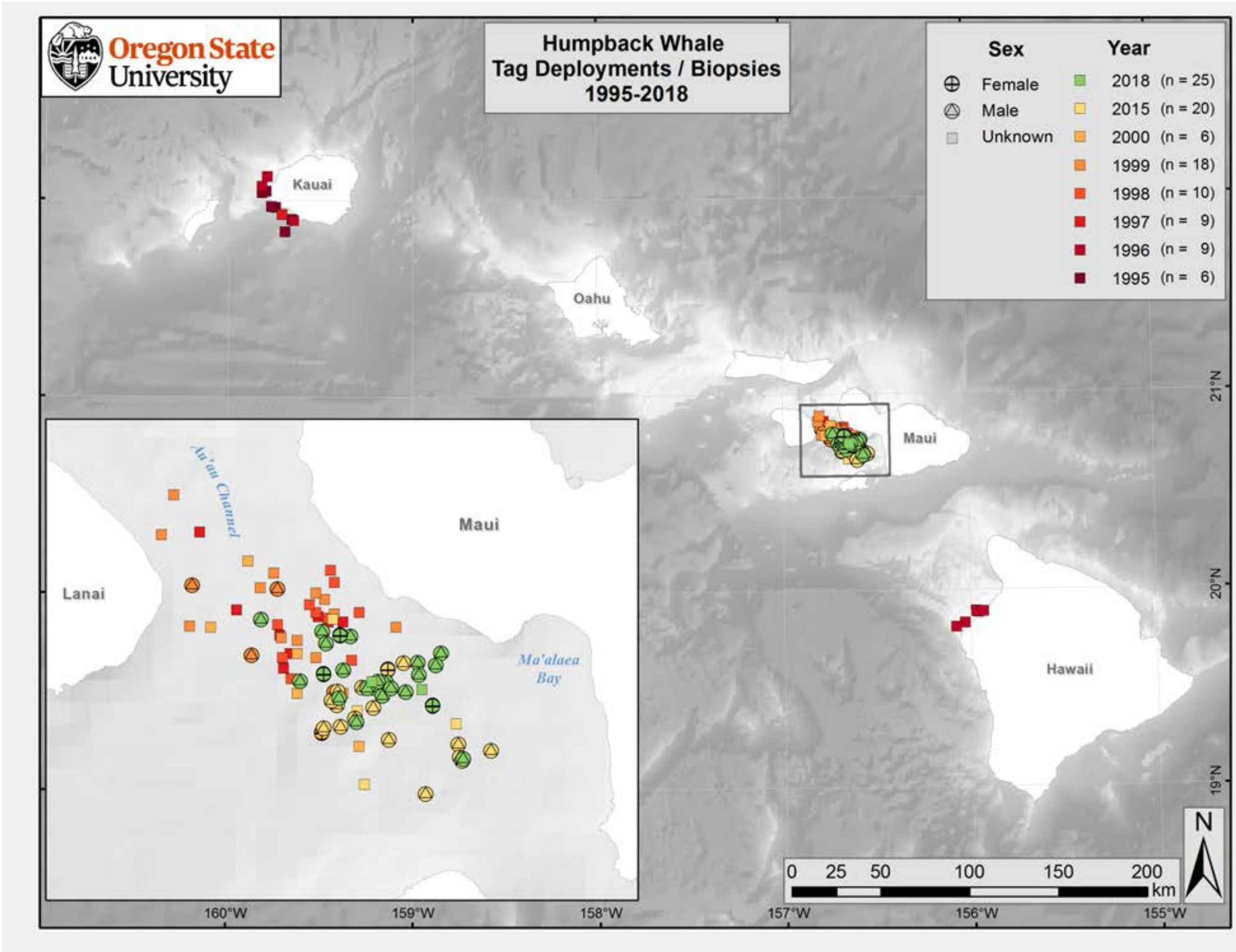


Figure 2. The locations of tag deployment (n = 81) and biopsy sample collection from humpback whales tagged in Hawaii from 1995 to 2018.

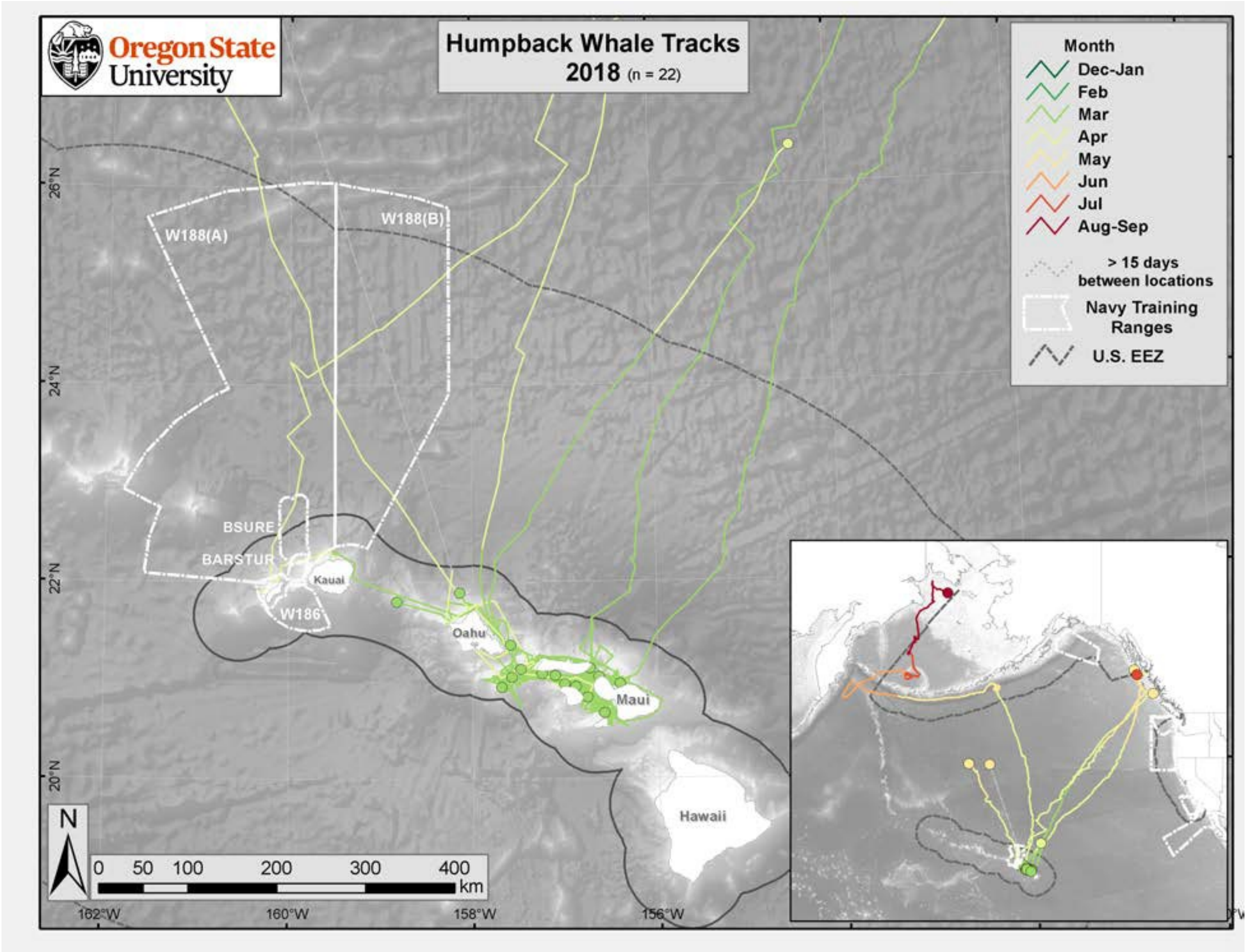


Figure 3. Satellite-monitored tracks for humpback whales tagged off Maui, Hawaii, in March 2018 (17 DM tags, 5 DUR+ tags). The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding ground (see Section 2.6 for details).

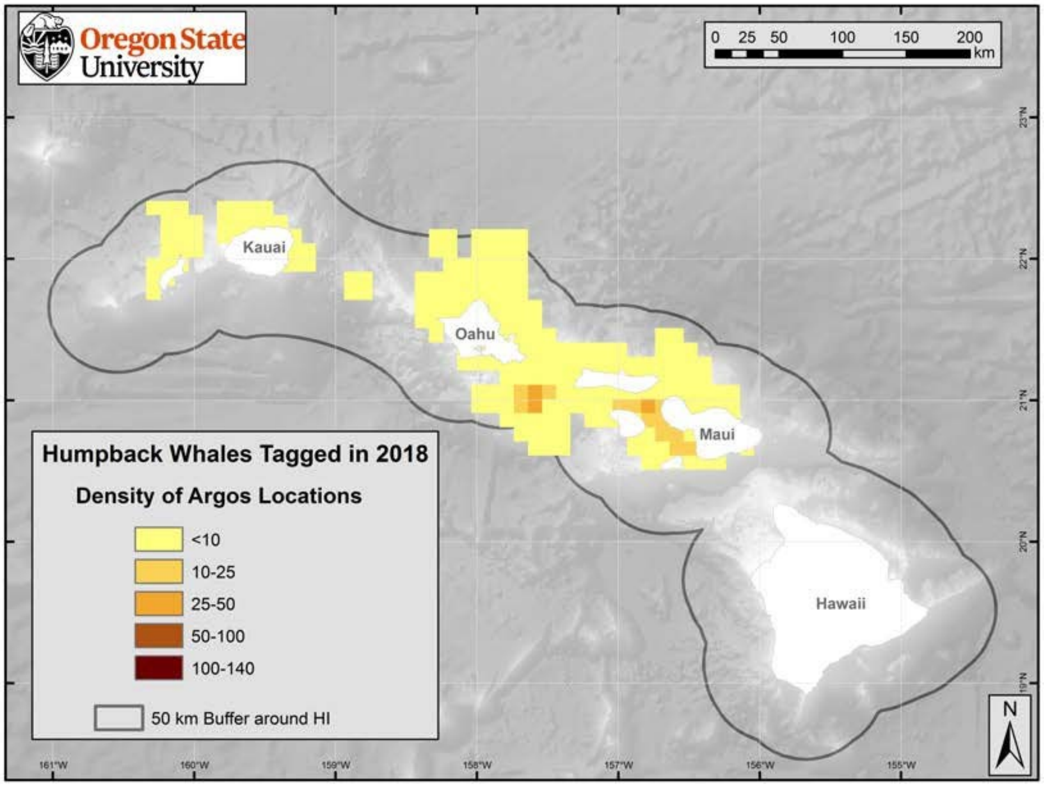


Figure 4. Kernel density utilization distribution for Argos locations in Hawaii of humpback whales tagged off Maui, Hawaii, in March 2018 (17 DM tags, 5 DUR+ tags). Grid cell size is 0.1 × 0.1 degrees. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding ground (see Section 2.6 for details).

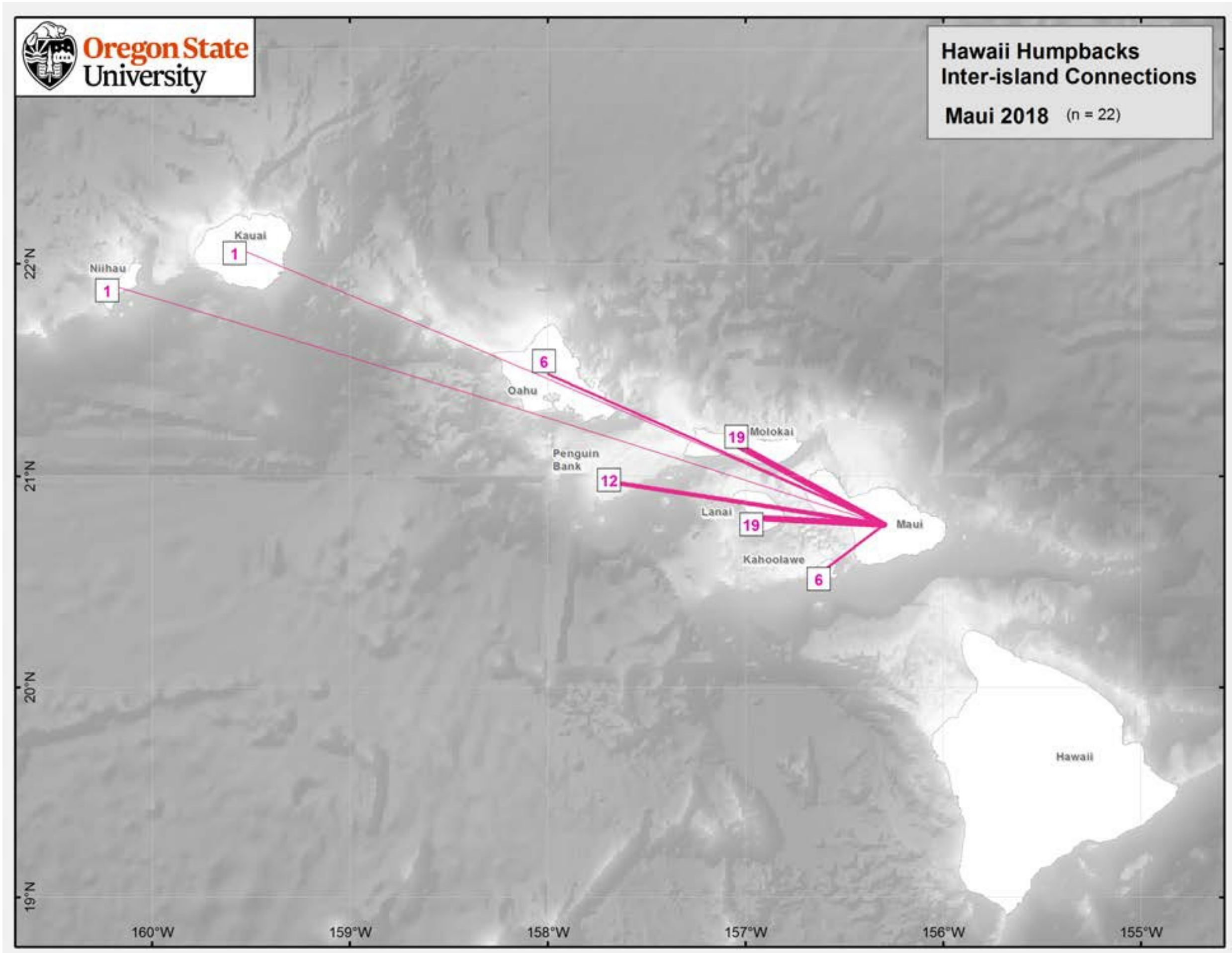


Figure 5. The number of whales (shown in boxes) tagged off Maui, Hawaii, in 2018 that had locations within 5 km of the other main Hawaiian Islands and Penguin Bank.

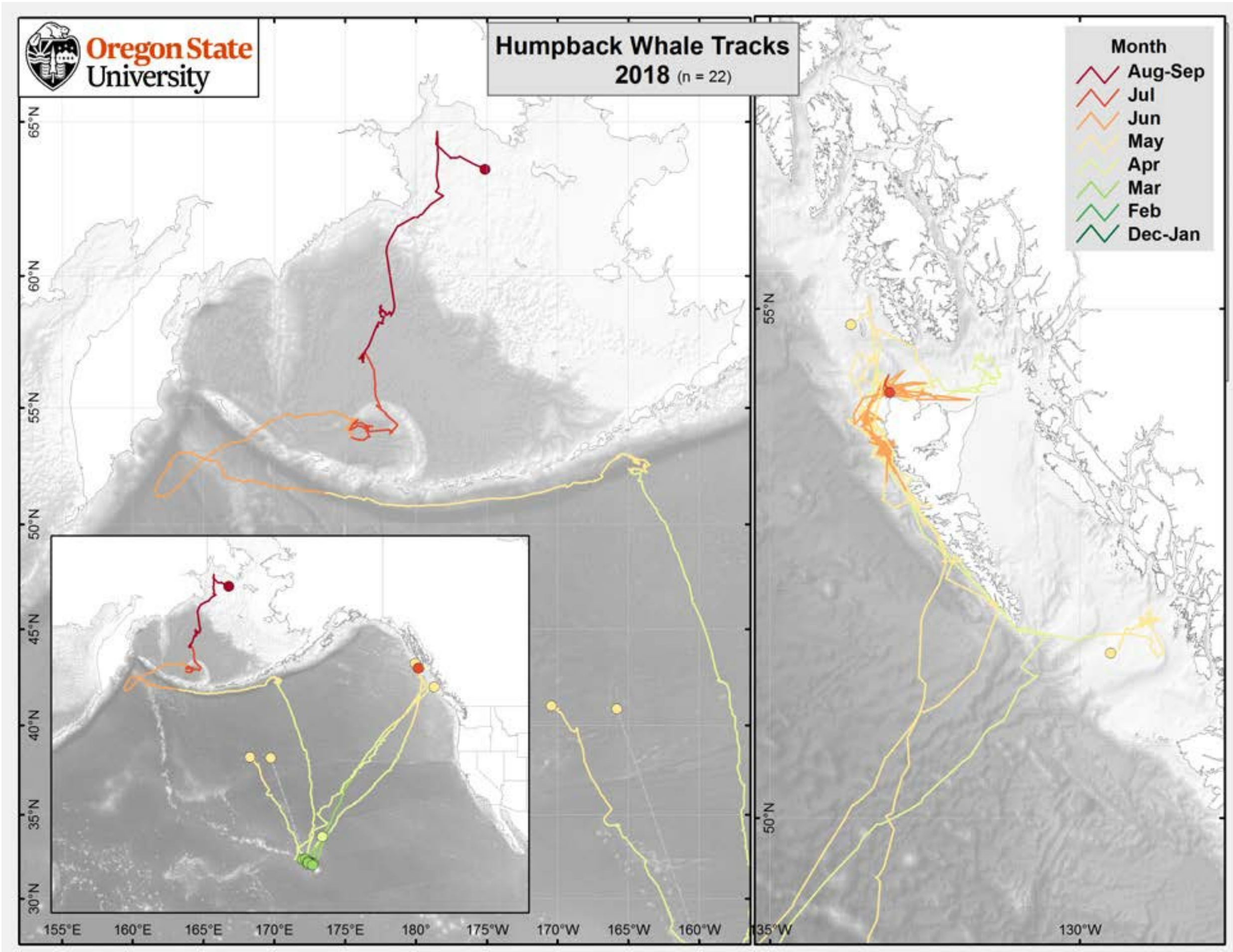


Figure 6. Satellite-monitored tracks for humpback whales tagged off Maui, Hawaii, in March 2018 (17 DM tags, 5 DUR+ tags), highlighting migration and movement in feeding grounds.

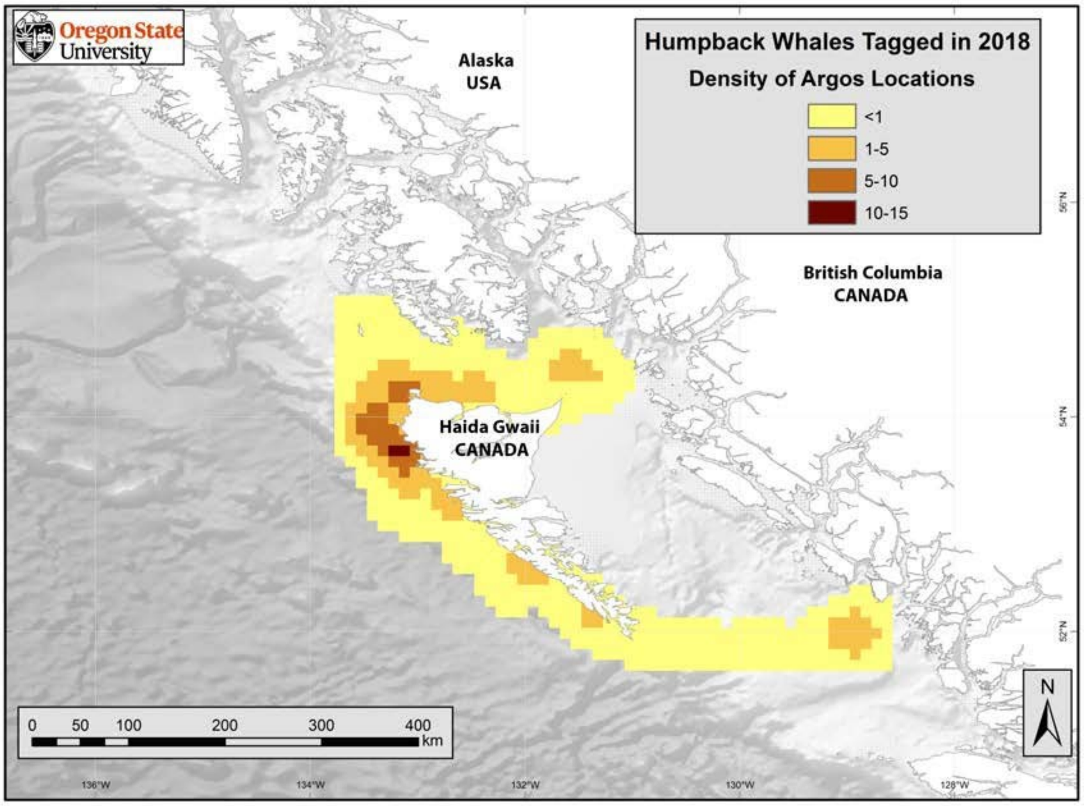


Figure 7. Kernel density utilization distribution for Argos locations in northern British Columbia and Southeast Alaska of humpback whales tagged off Maui, Hawaii, in March 2018 (2 DM tags, 1 DUR+ tag). Grid cell size is 0.1 × 0.1 degrees.

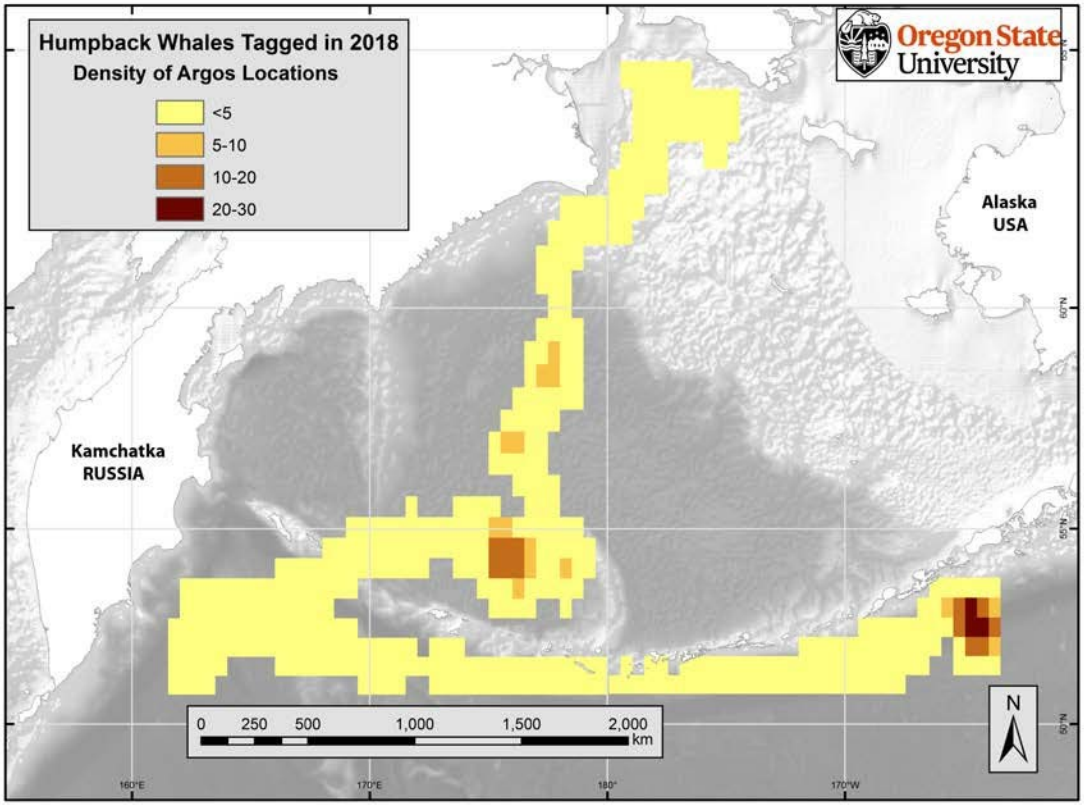


Figure 8. Kernel density utilization distribution for Argos locations in the Aleutian Islands and the Bering Sea of a humpback whale tagged off Maui, Hawaii, in March 2018 (1 DM tag, #5736, a male). Note that the grid cell size is 0.5 × 0.5 degrees in this representation.

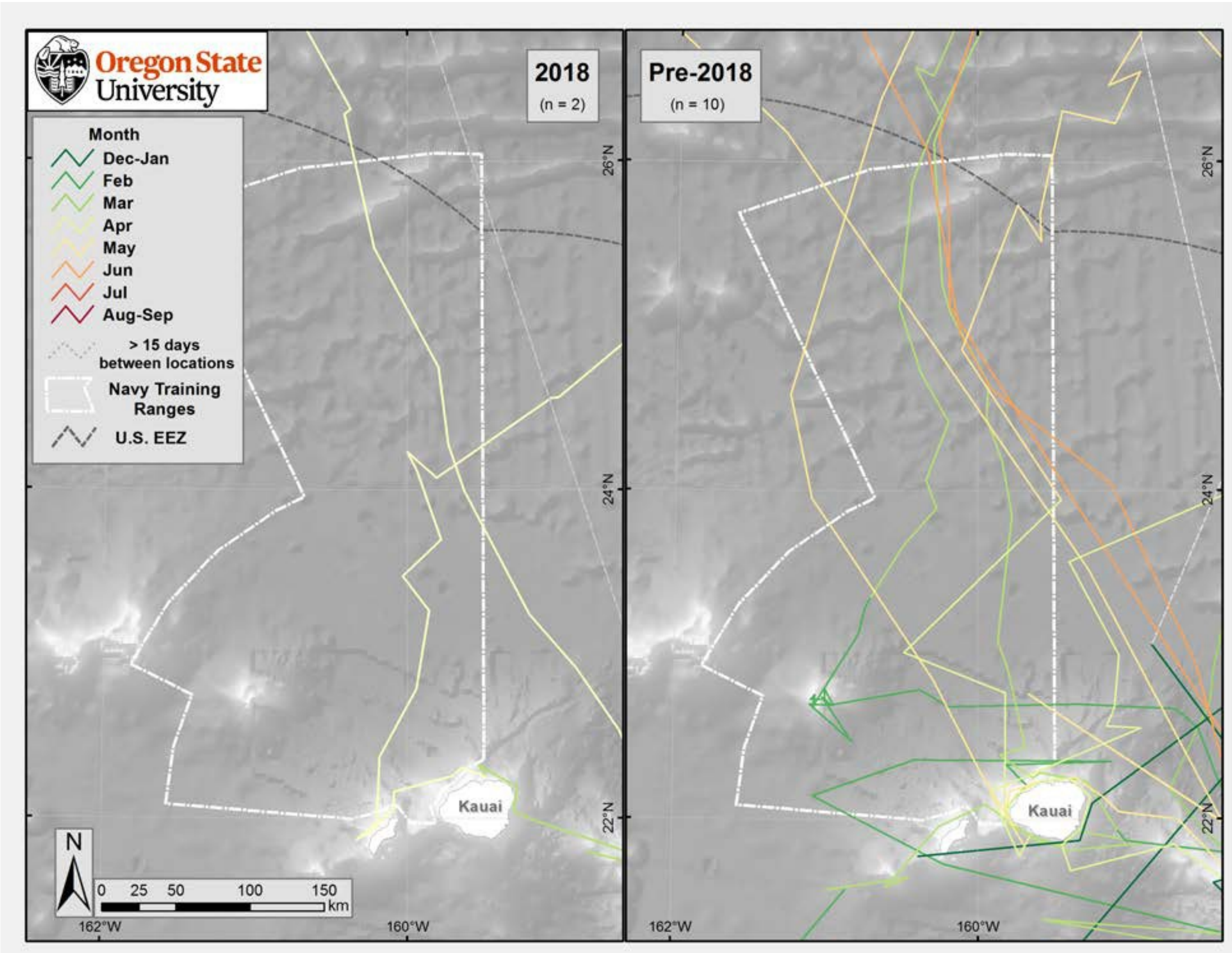


Figure 9. Satellite-monitored tracks in Area W188A for humpback whales tagged off Maui, Hawaii, in March 2018 (left panel), and off Maui and Kauai from 1995 to 2015 (right panel).

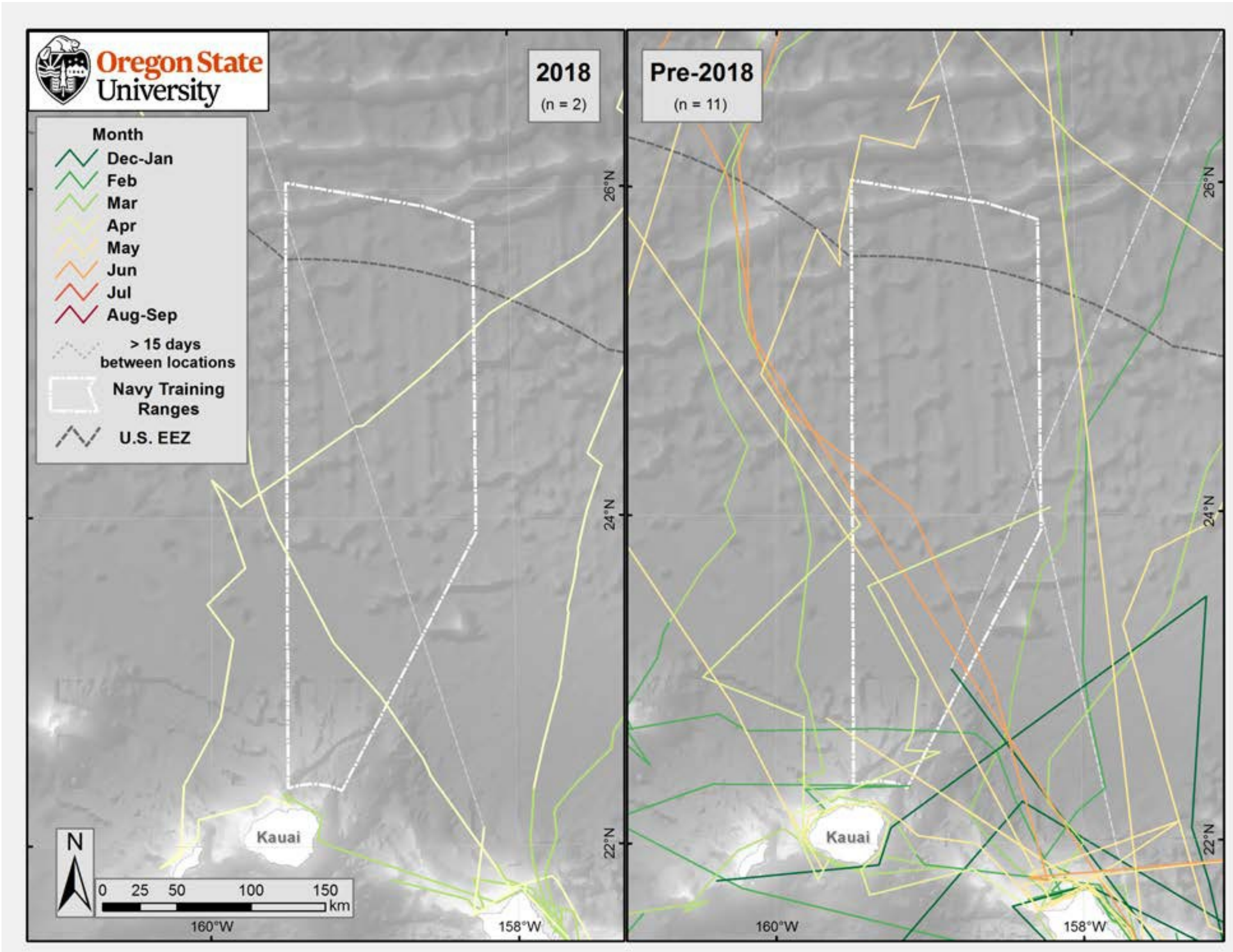


Figure 10. Satellite-monitored tracks in Area W188B for humpback whales tagged off Maui, Hawaii, in March 2018 (left panel), and off Maui and Kauai from 1995 to 2015 (right panel).

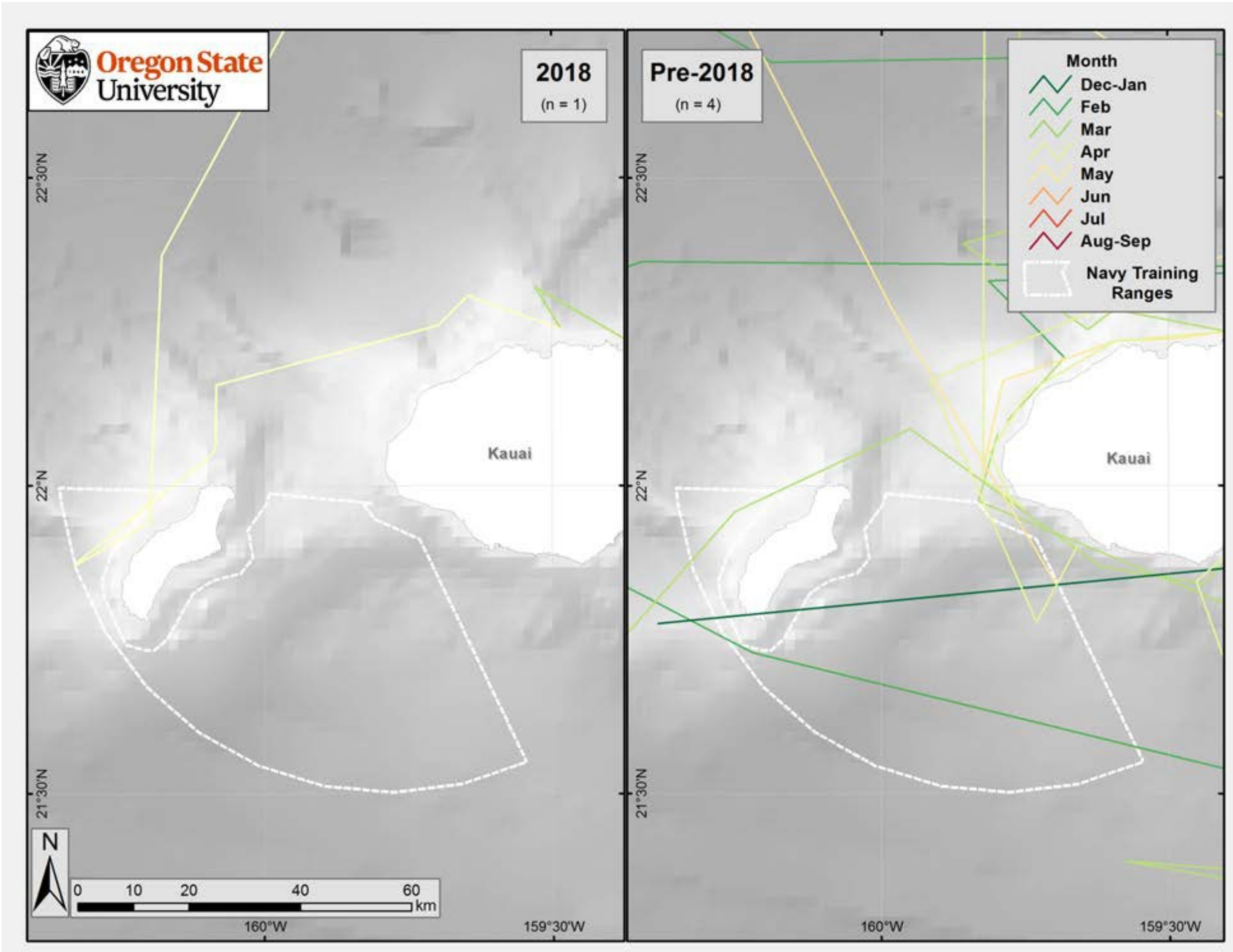


Figure 11. Satellite-monitored tracks in Area W186 for humpback whales tagged off Maui, Hawaii, in March 2018 (left panel), and off Maui and Kauai from 1995 to 2015 (right panel).

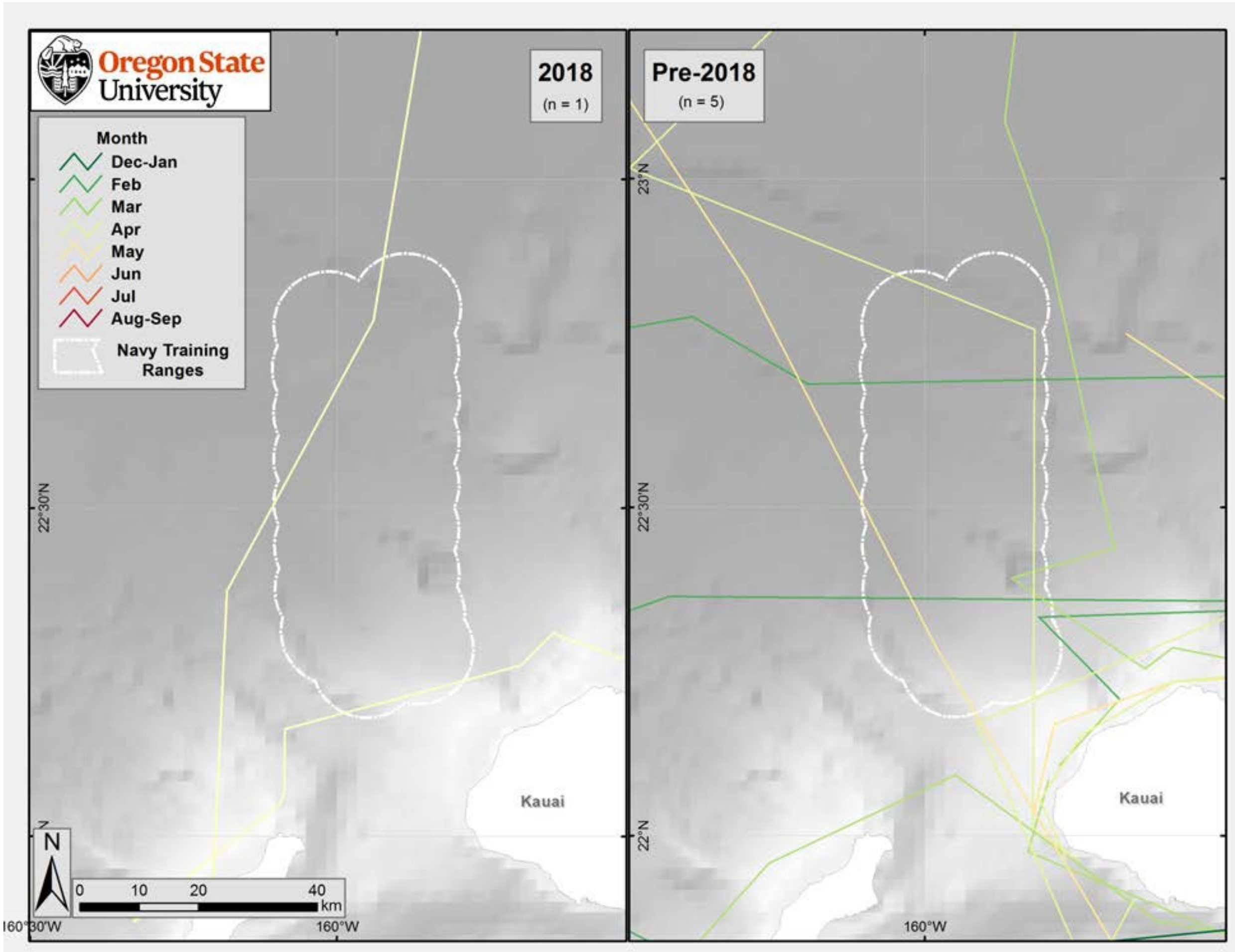


Figure 12. Satellite-monitored tracks in BSURE for humpback whales tagged off Maui, Hawaii, in March 2018 (left panel), and off Maui and Kauai from 1995 to 2015 (right panel).

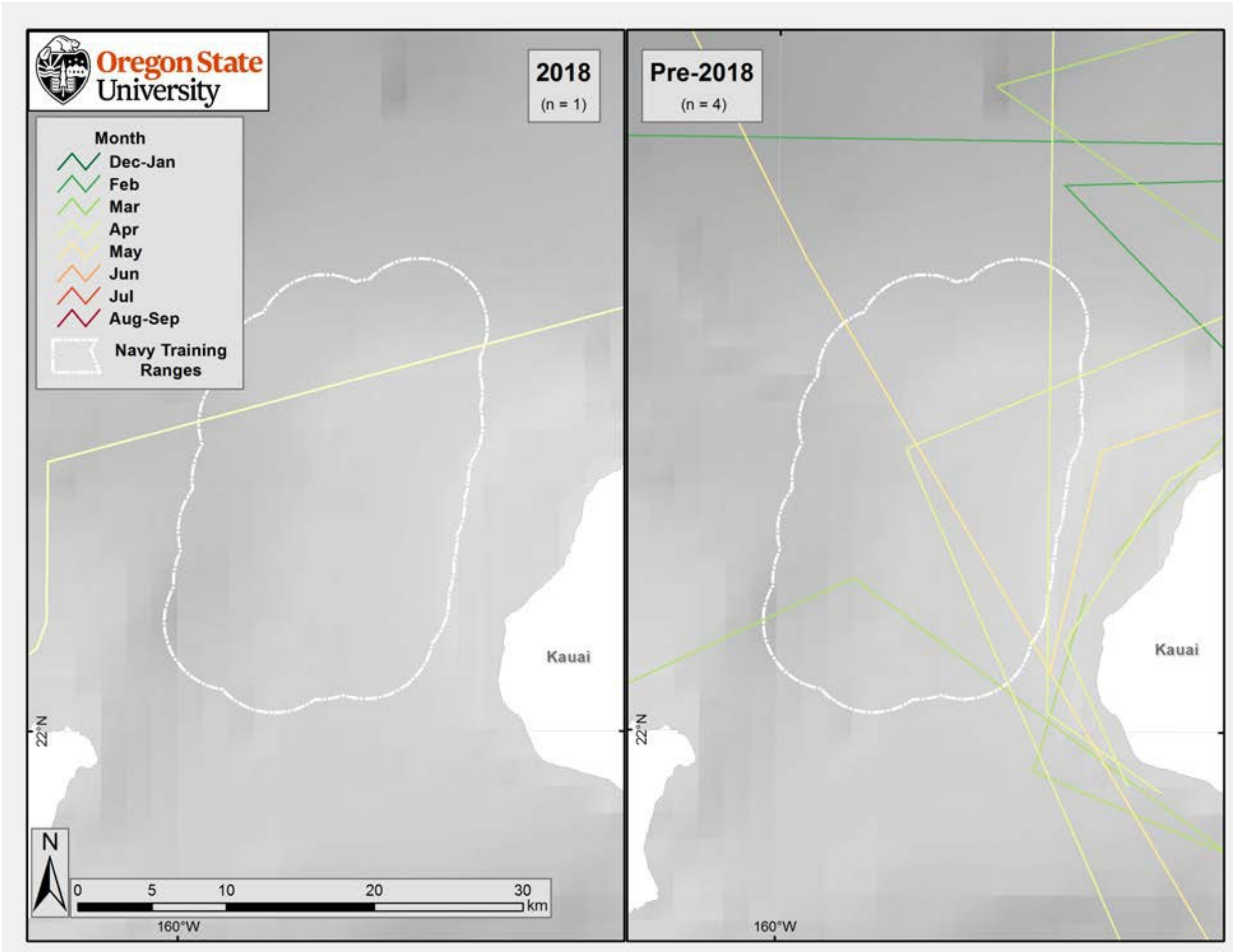


Figure 13. Satellite-monitored tracks in BARSTUR for humpback whales tagged off Maui, Hawaii, in March 2018 (left panel), and off Maui and Kauai from 1995 to 2015 (right panel).

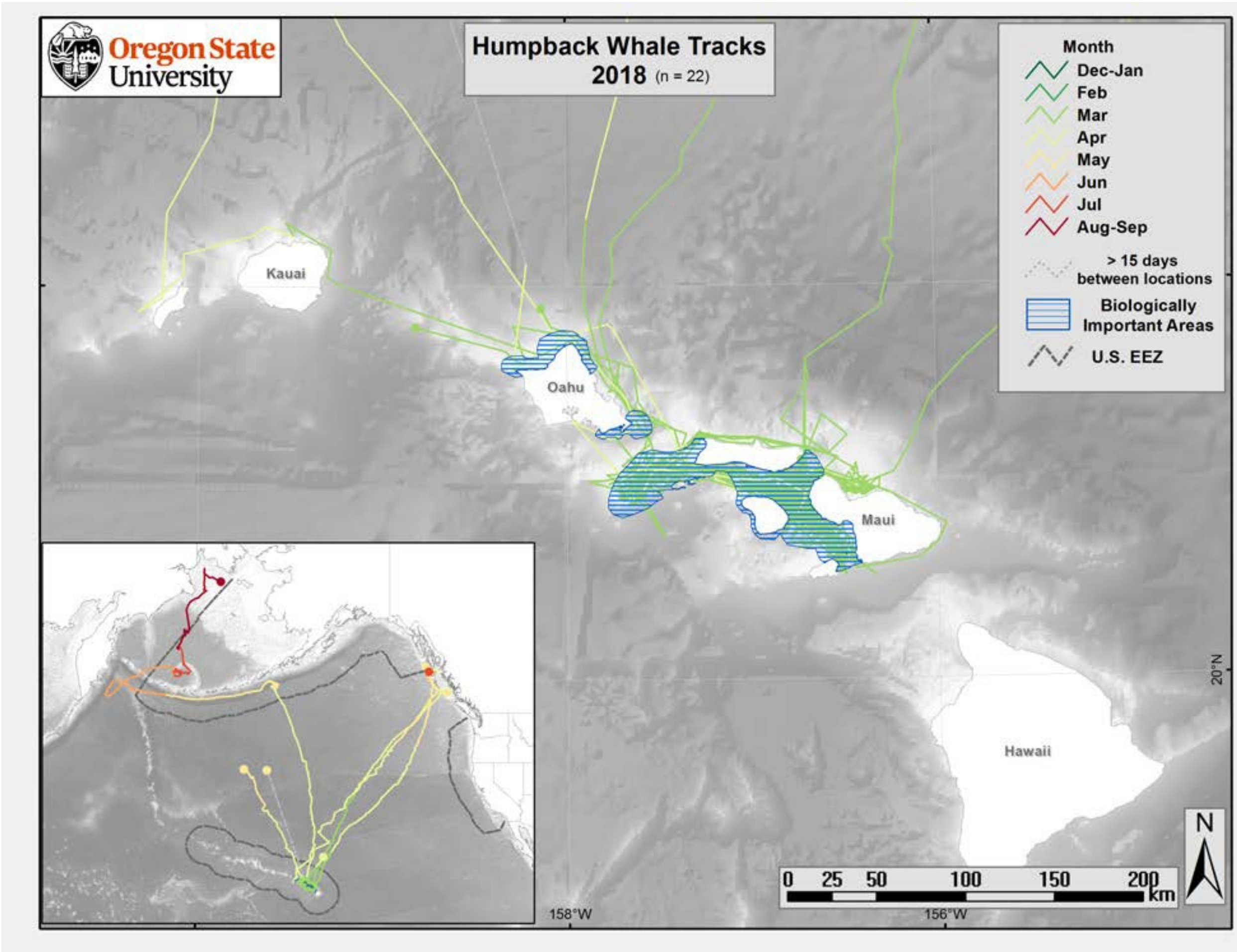


Figure 14. Satellite-monitored tracks in the Maui BIA for humpback whales tagged off Maui, Hawaii, in March 2018 (17 DM tags, 5 DUR+ tags).

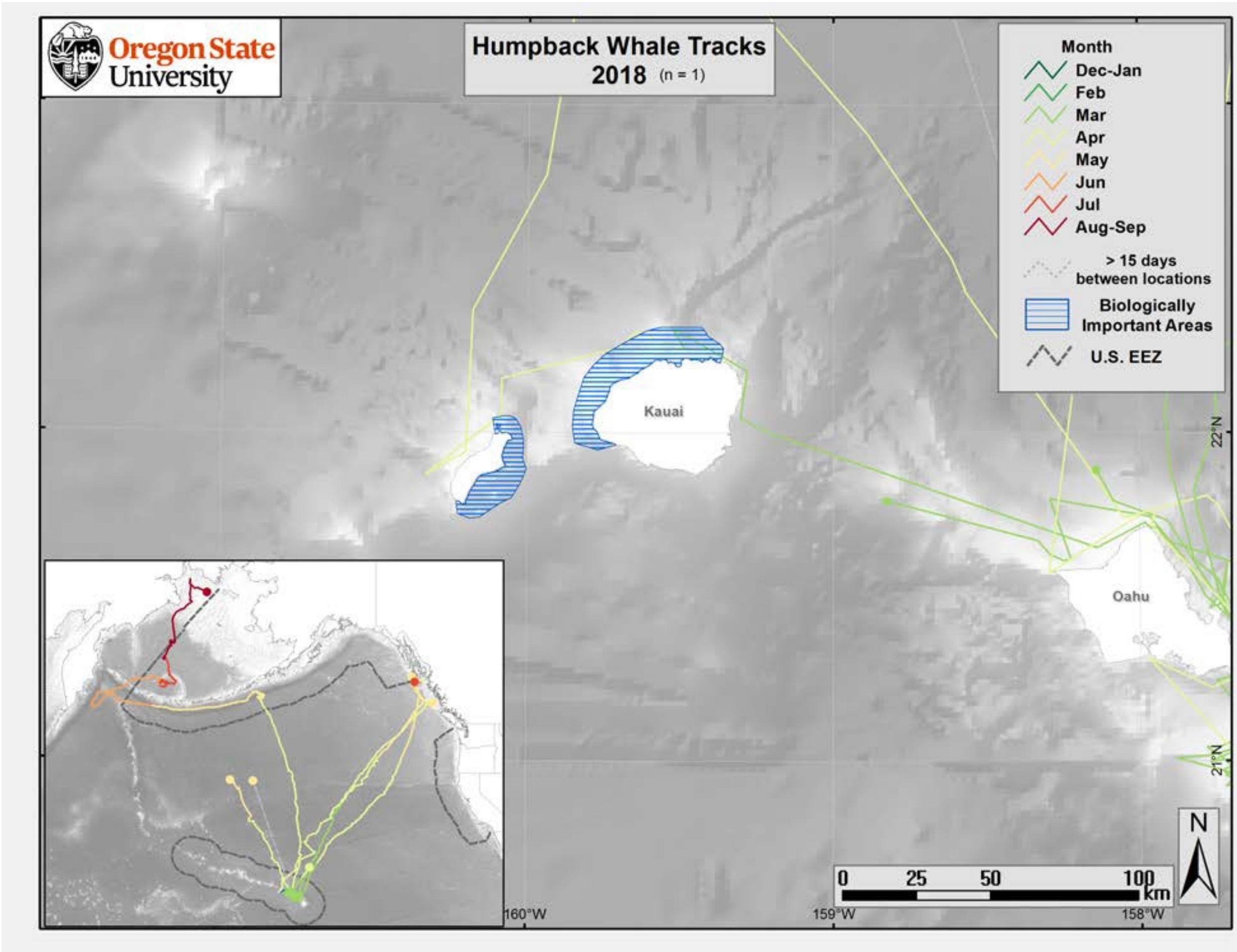


Figure 15. Satellite-monitored tracks in the Kauai BIA for a humpback whale tagged off Maui, Hawaii, in March 2018 (1 DM tag).

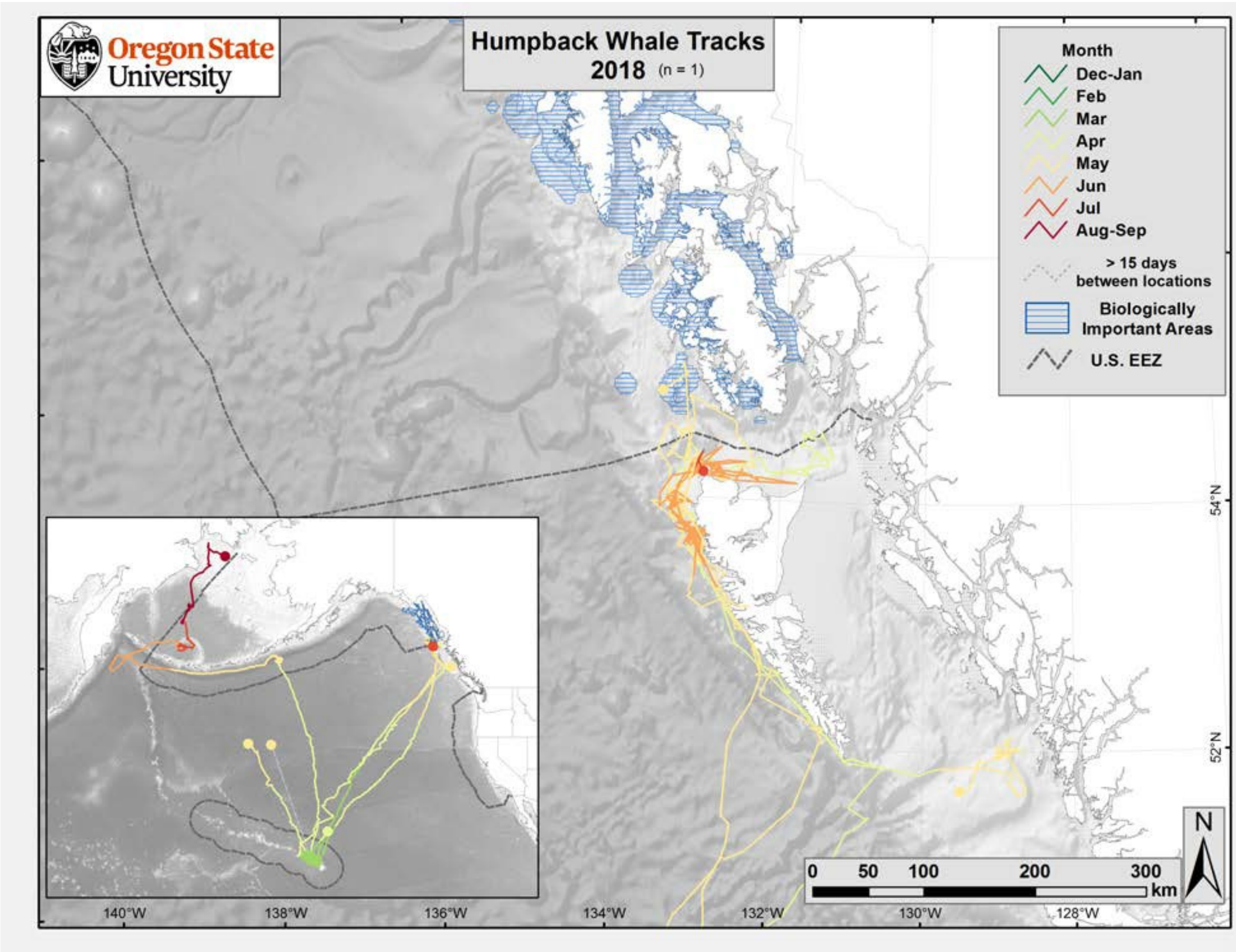


Figure 16. Satellite-monitored tracks in the Southeast Alaska BIA for a humpback whale tagged off Maui, Hawaii, in March 2018 (1 DM tag, #5800, a male).

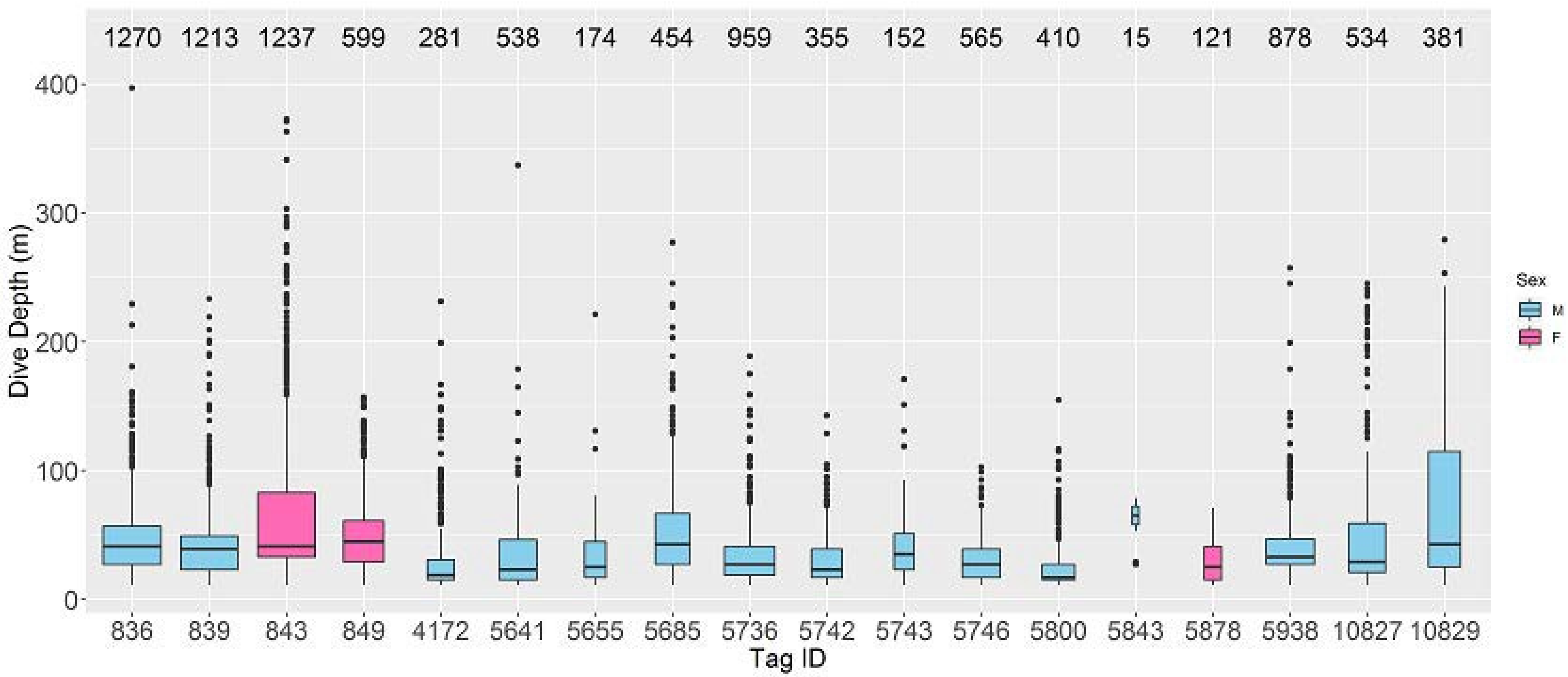


Figure 17. Dive depth while on the breeding grounds of DM-tagged humpback whales (n = 18) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box. Sex of the animals are indicated by color.

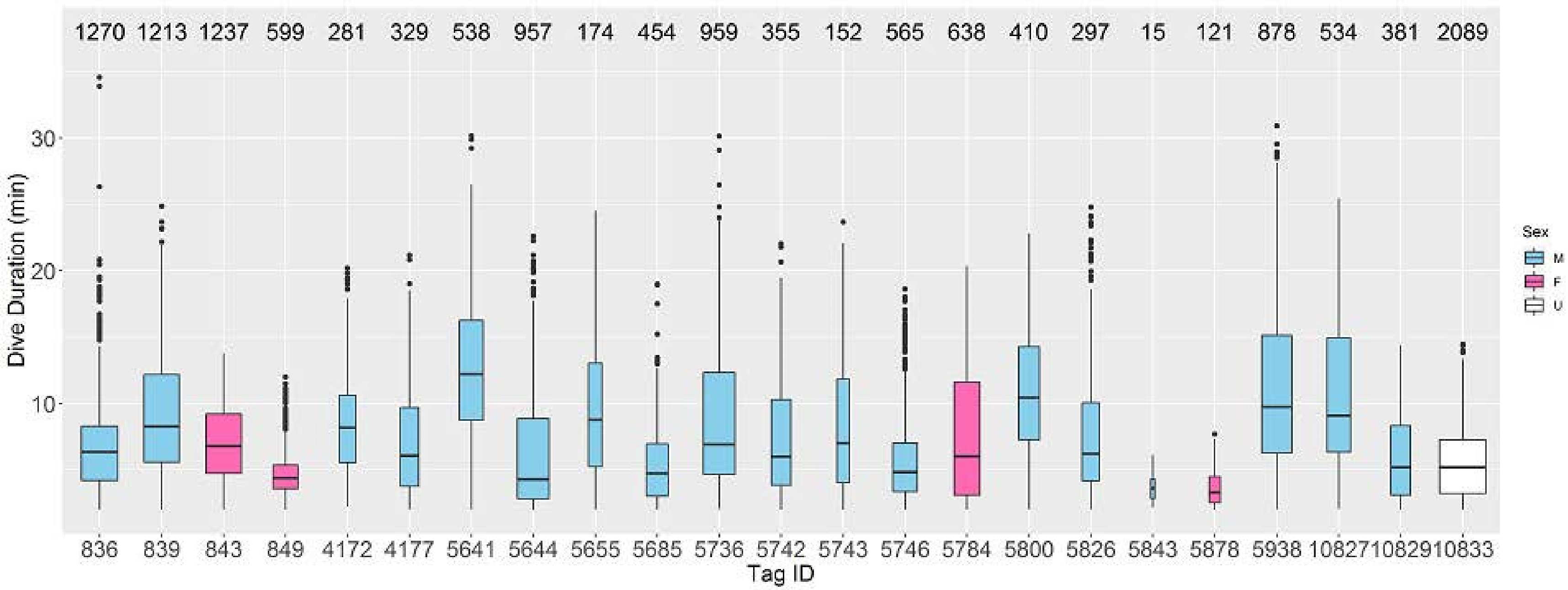


Figure 18. Dive duration while on the breeding grounds of DM- and DUR+-tagged humpback whales (n = 23) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box. Sex of the animals are indicated by color.

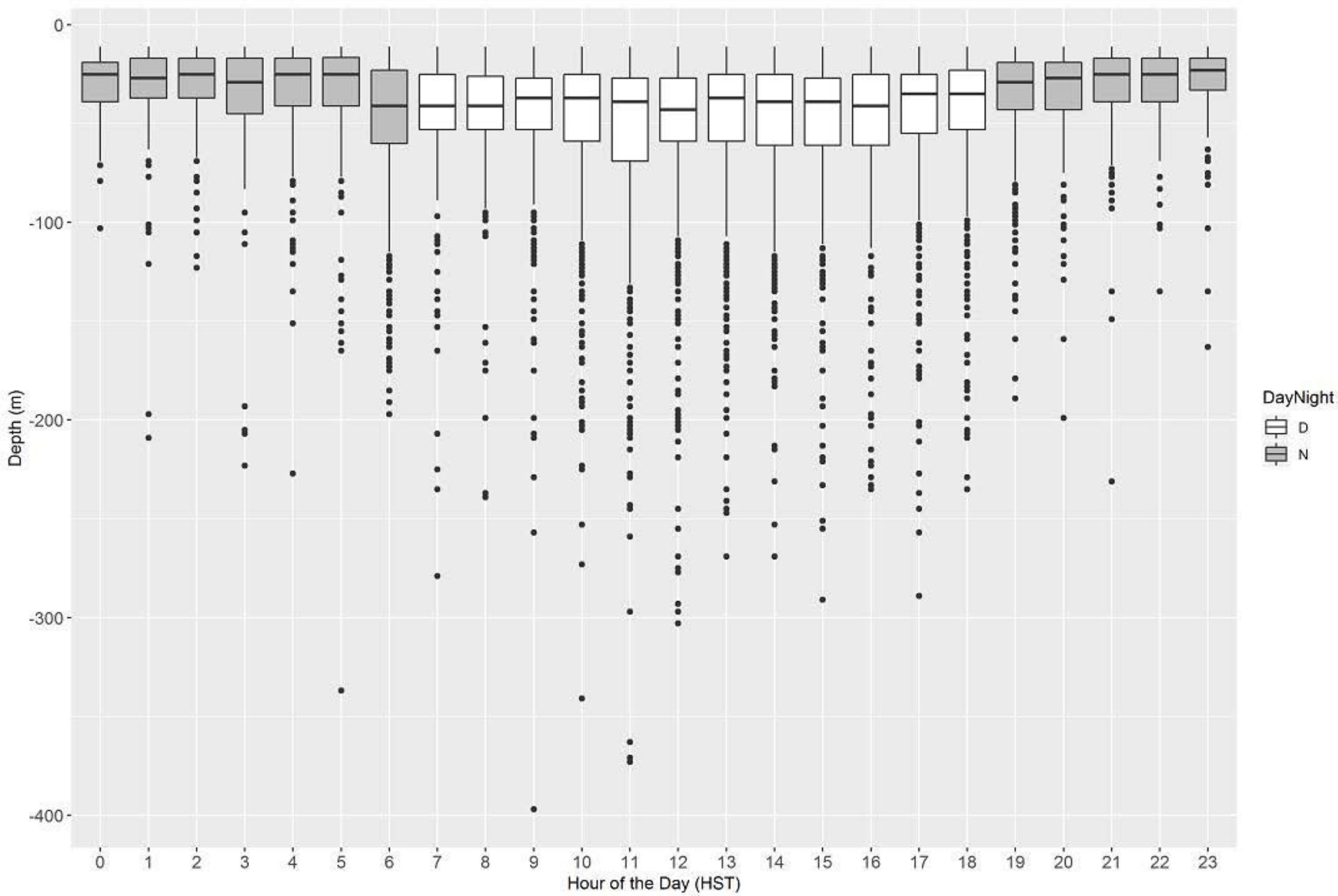


Figure 19. Hourly distribution of dive depth while on the breeding grounds of DM-tagged humpback whales (n = 18) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

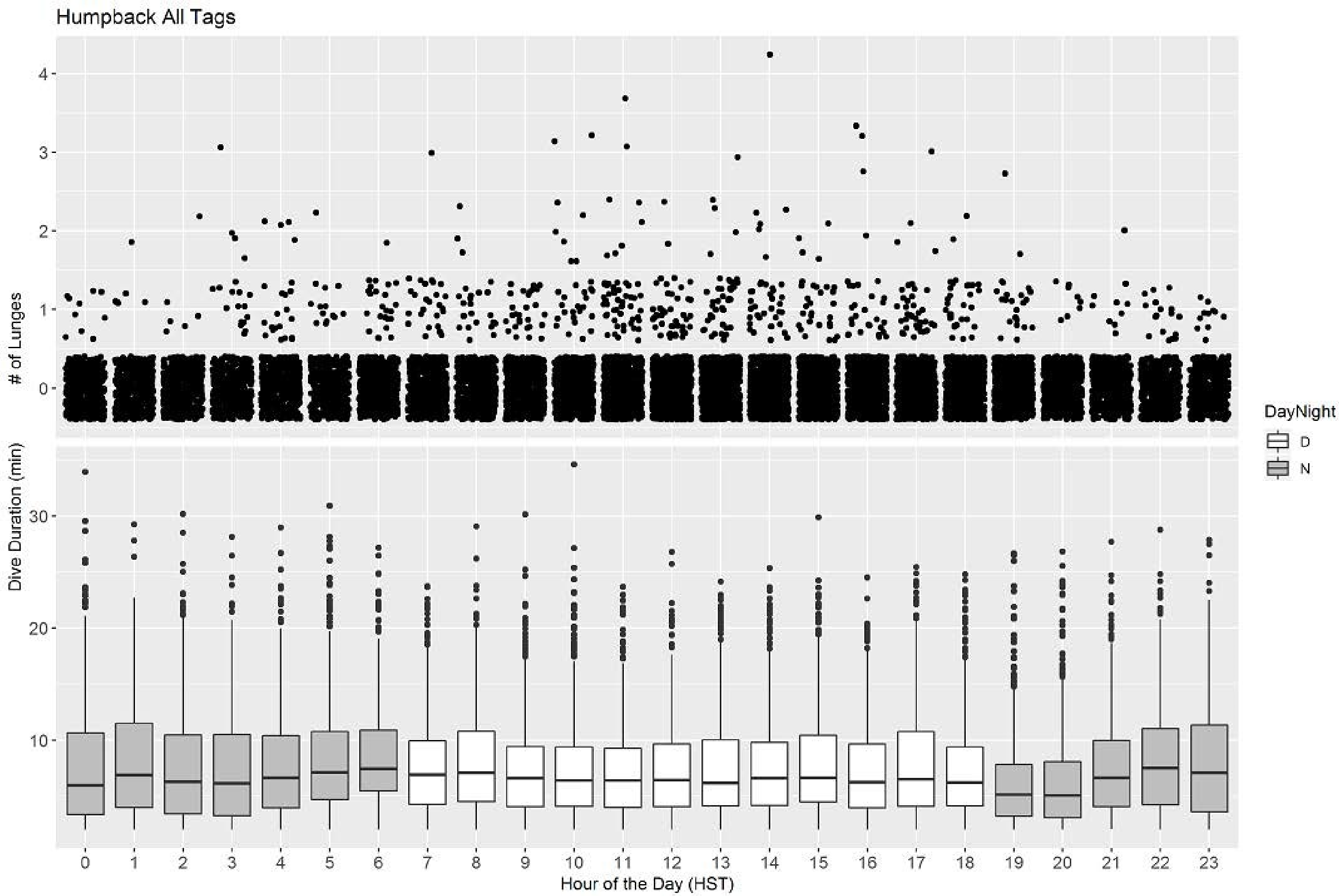


Figure 20. Hourly distributions of number of lunges (top) and dive durations (bottom) while on the breeding grounds for DM- and DUR+-tagged humpback whales (n = 23) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

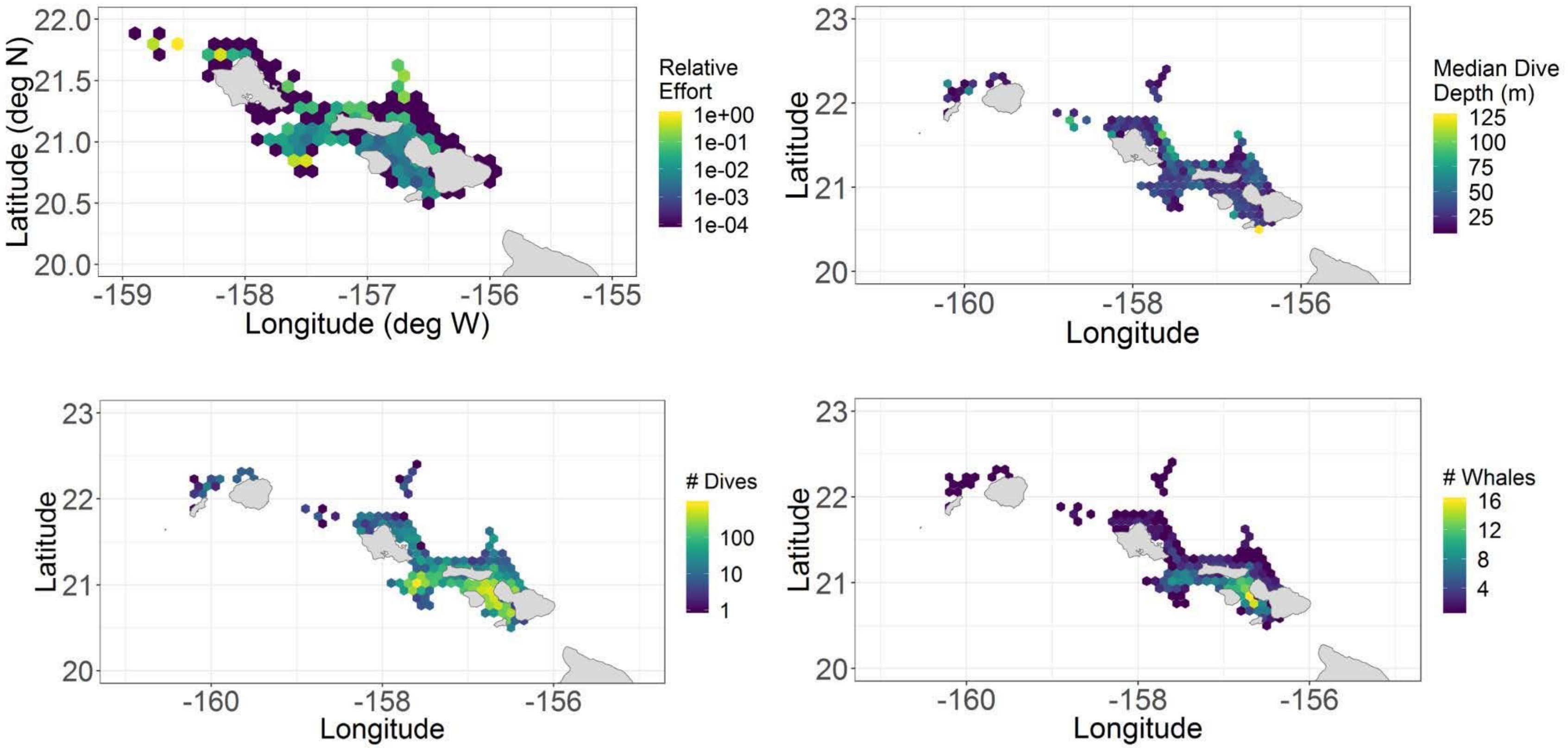


Figure 21. Data from DM-tagged humpback whales tagged off Hawaii in March 2018 summarized in 0.1-degree hexagonal grids showing a relative measure of where lunges occurred (top left), the median maximum dive depth (top right), number of dives (bottom left), and number of tagged whales (bottom right) recorded in each grid cell while on the breeding grounds.

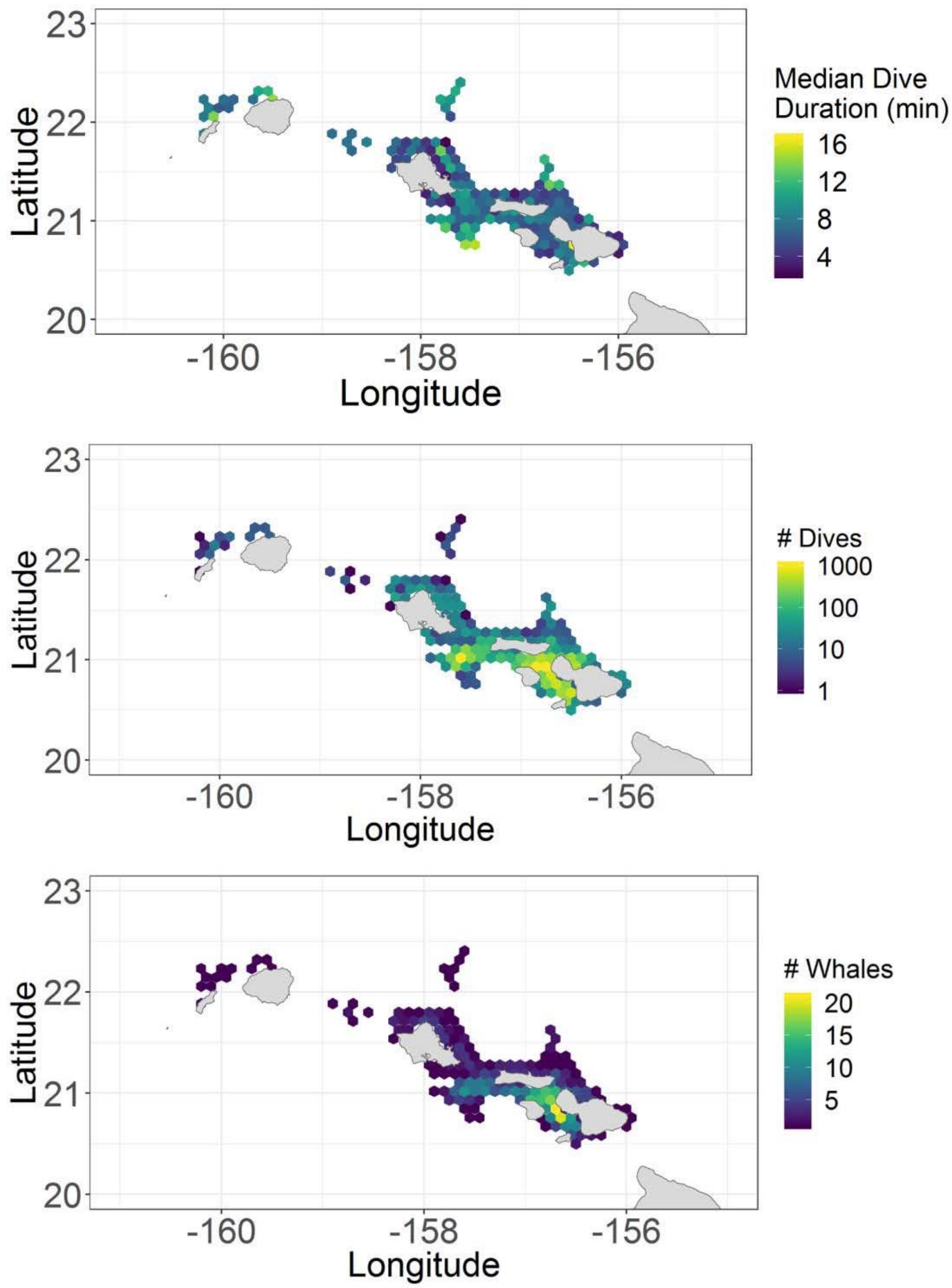


Figure 22. Data from DM- and DUR+-tagged humpback whales tagged off Hawaii in March 2018 summarized in 0.1-degree hexagonal grids showing the median dive duration (top), number of dives (middle), and number of tagged whales (bottom) recorded in each grid cell while on the breeding grounds.

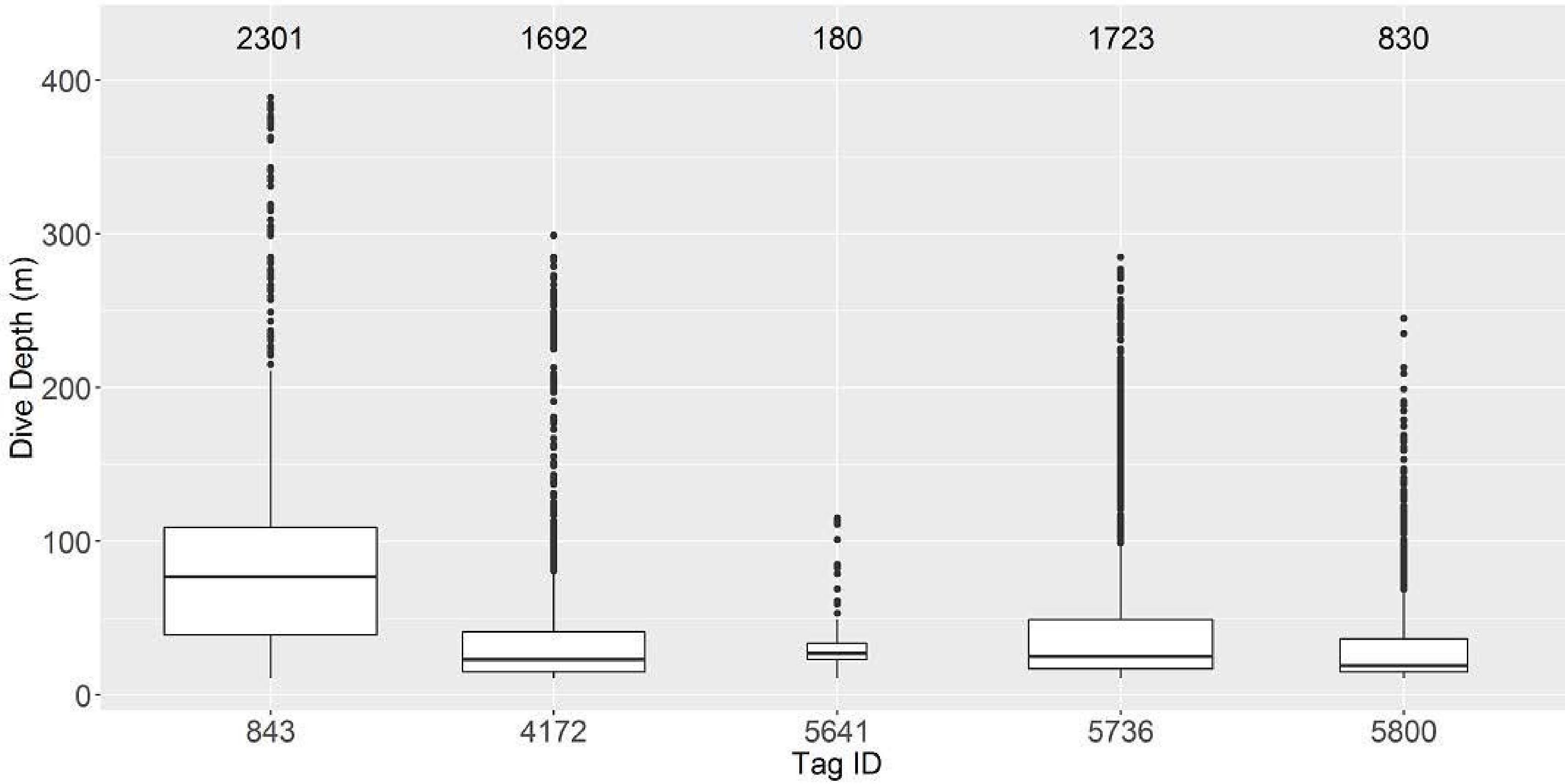


Figure 23. Dive depth during migration of five DM-tagged humpback whales tagged off Hawaii in March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box.

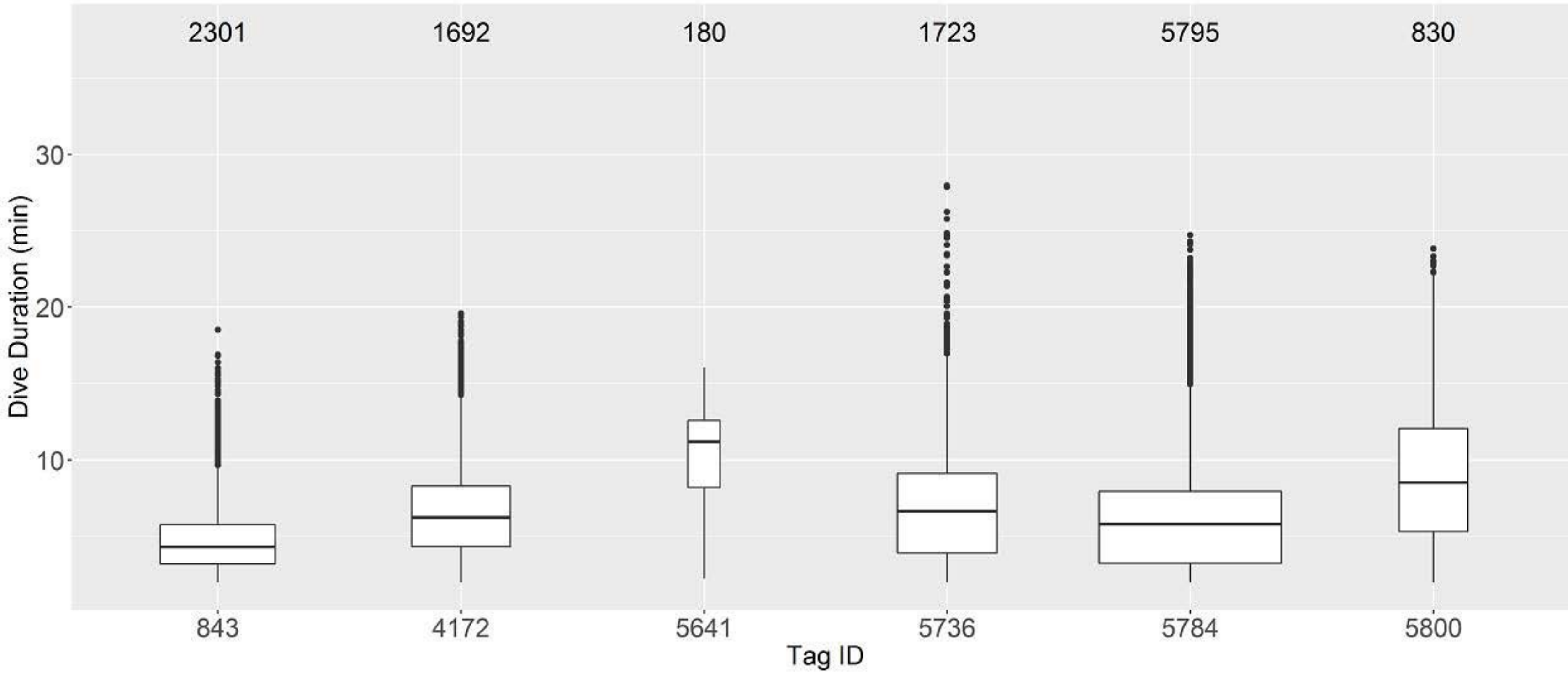


Figure 24. Dive duration during migration of six DM- and DUR+-tagged humpback whales tagged off Hawaii in March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box.

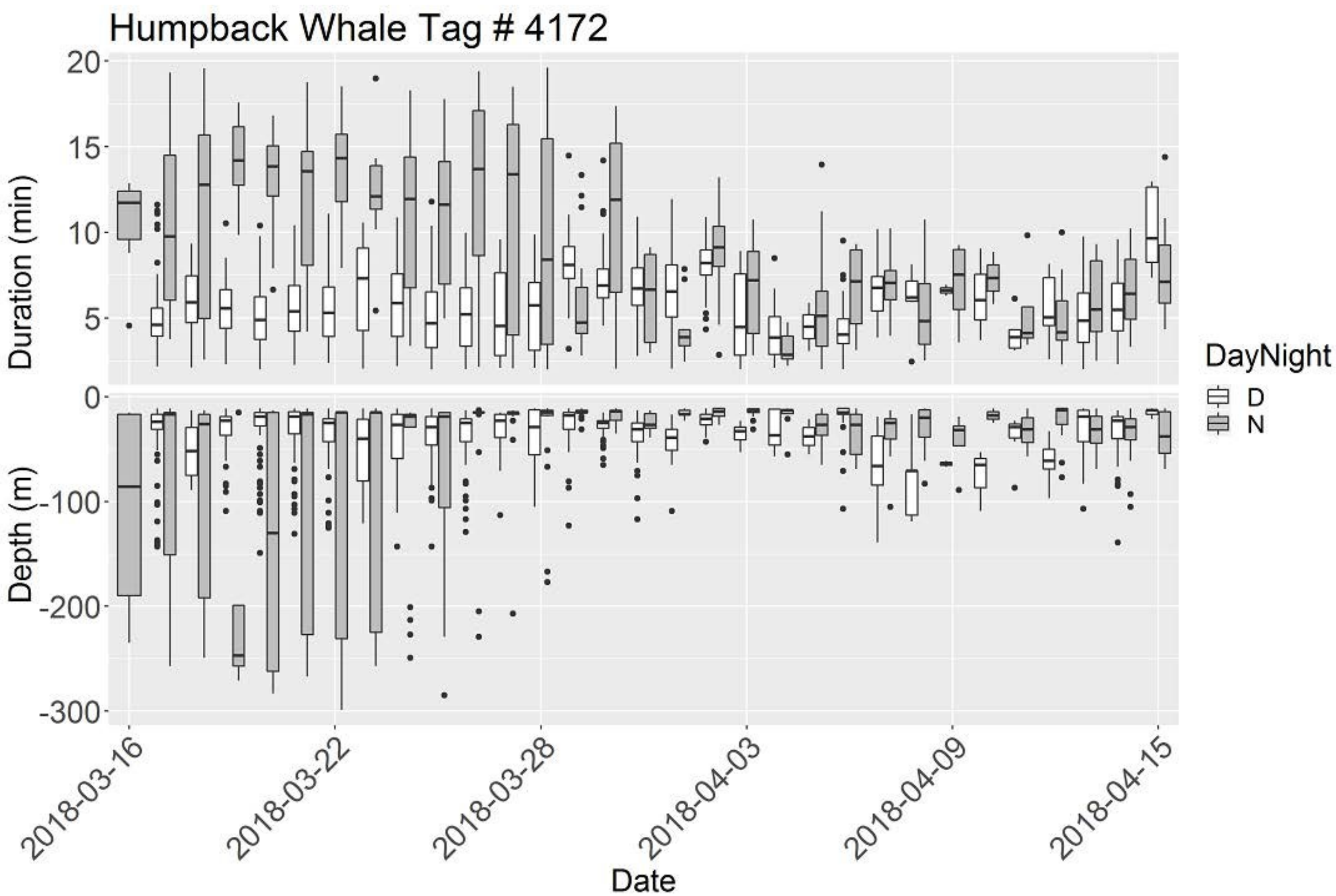


Figure 25. Data from an example track showing the distribution of dive duration (top panel) and dive depth (bottom panel) during migration of a DM-tagged humpback whale (#4172, a male) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

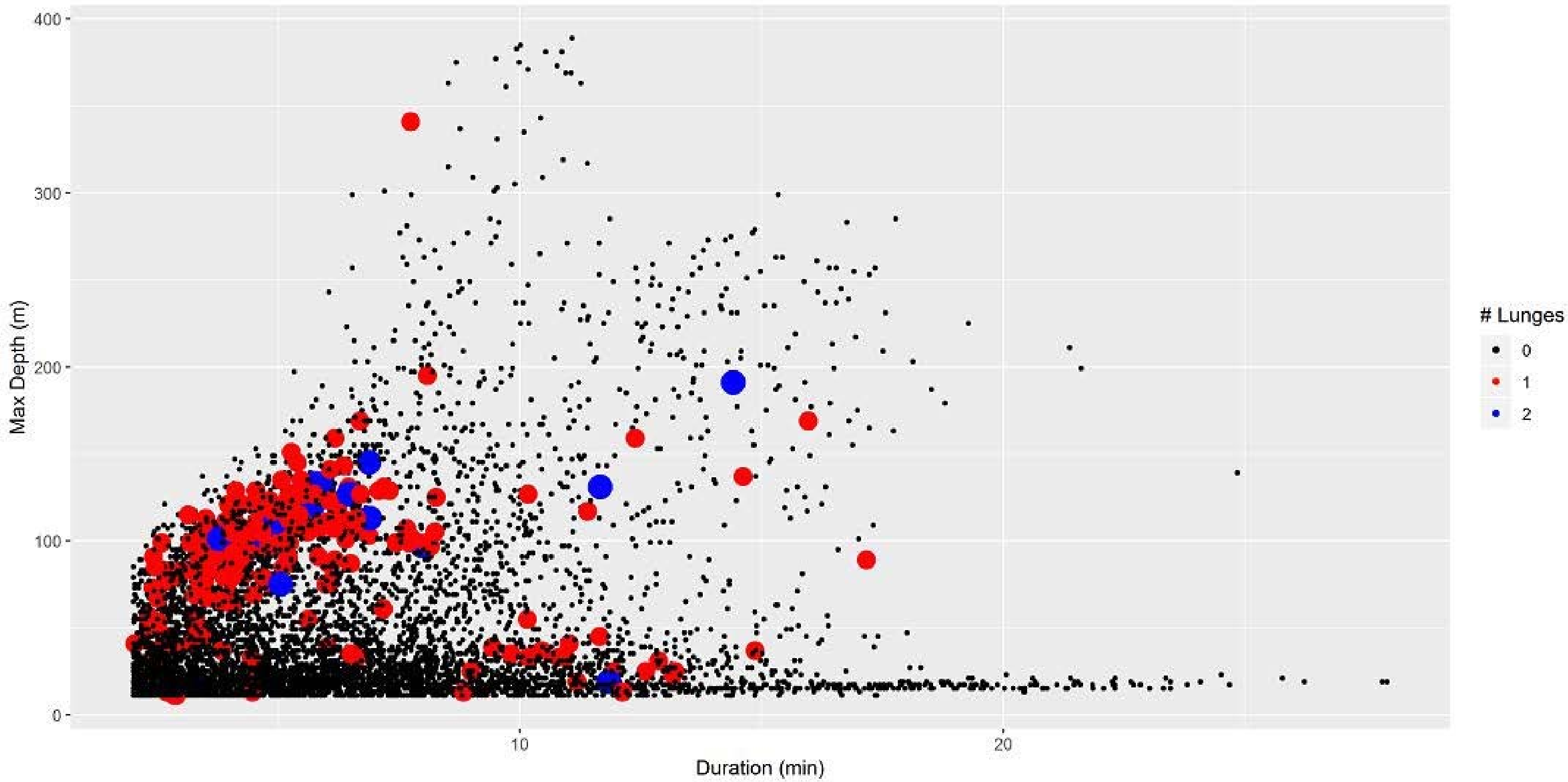


Figure 26: Depth and duration of dives made by DM-tagged humpback whales tracked during their migration from Hawaii toward their feeding grounds. Color of the circles represent the number of lunges recorded during each dive. Whales were tagged off Hawaii during March 2018 and migrated during April and May.

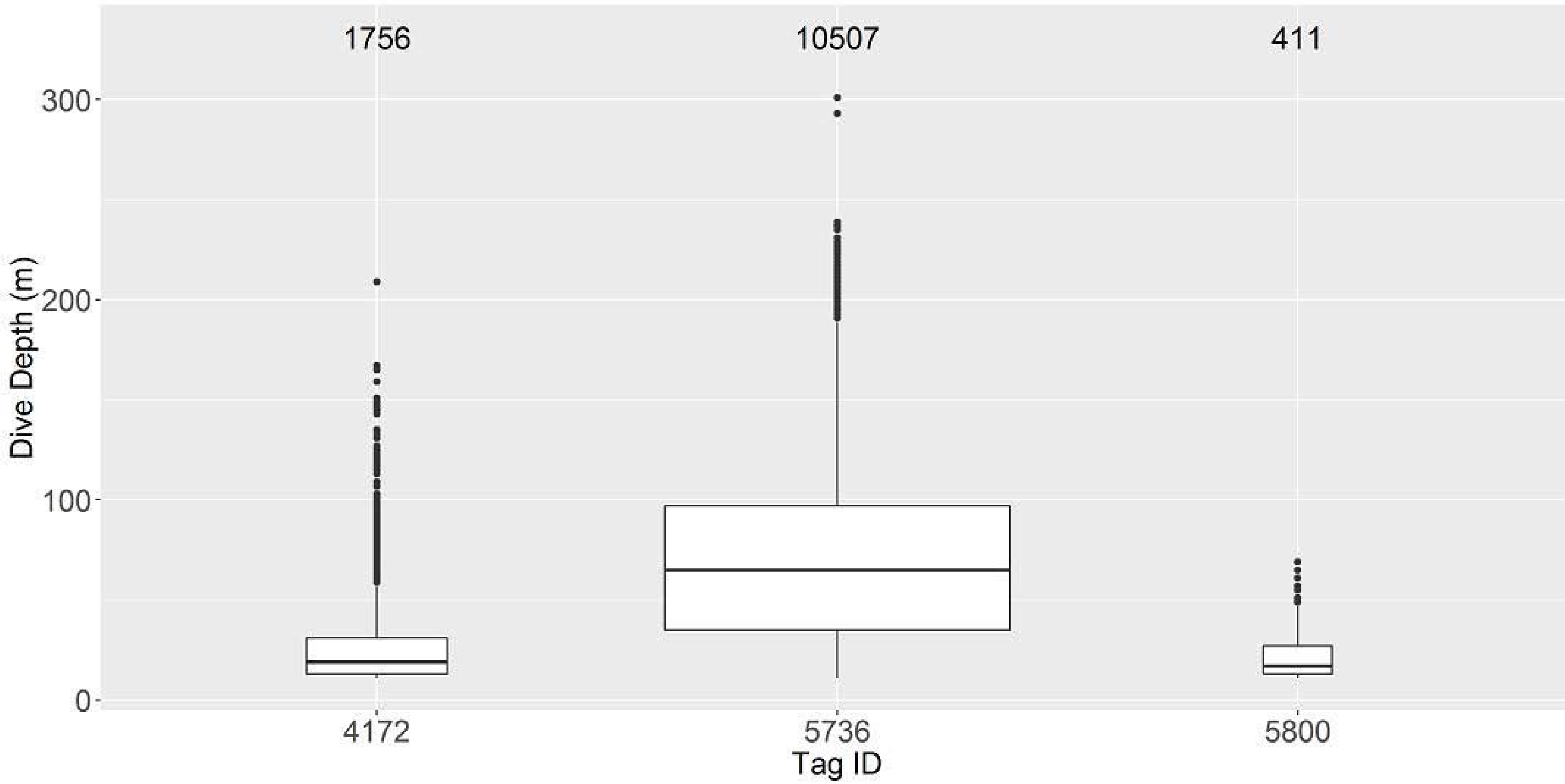


Figure 27. Dive depth while on the feeding grounds (Haida Gwaii: whale #s 4172 and 5800, western Aleutians: whale # 5736) of three DM-tagged humpback whales tagged off Hawaii in March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box.

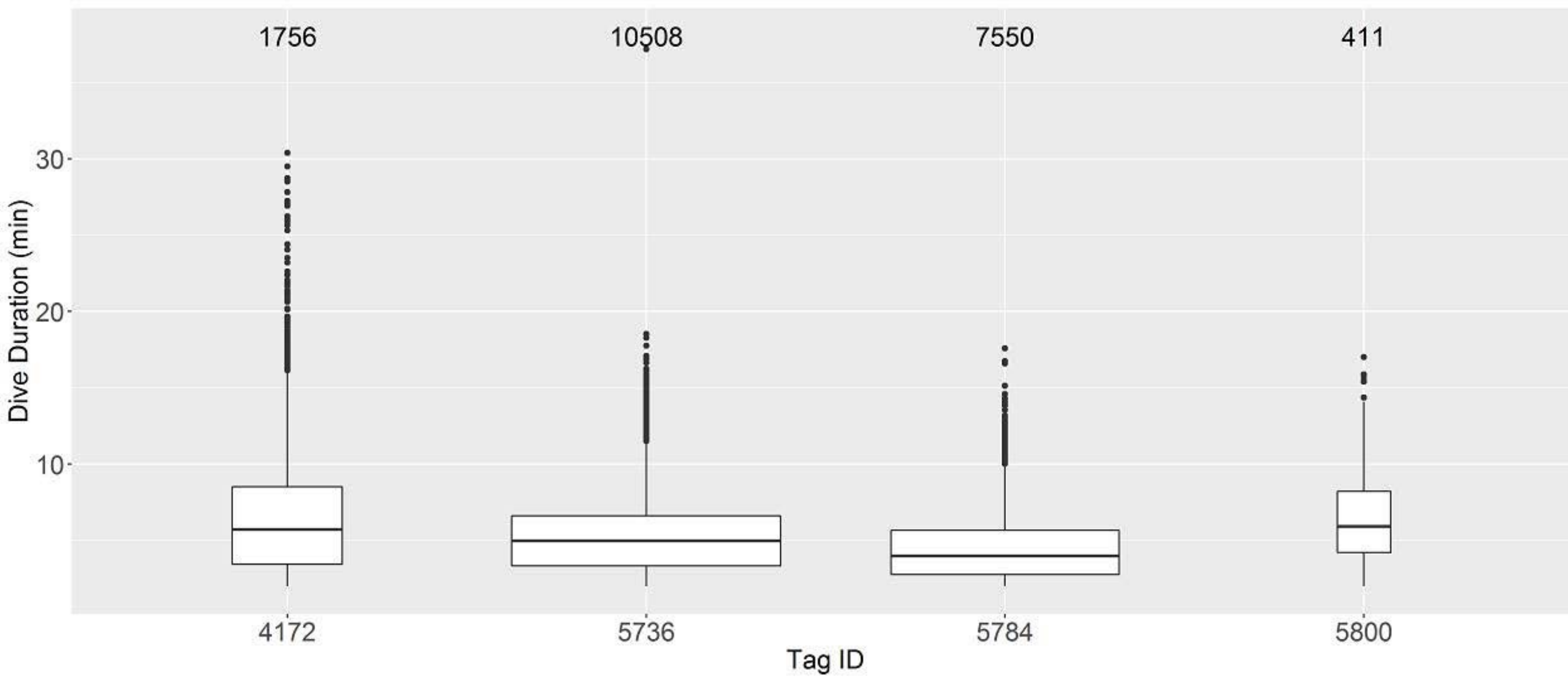


Figure 28. Dive duration while on the feeding grounds (Haida Gwaii: whale #s 4172, 5784 and 5800, western Aleutians: whale # 5736) of four DM- and DUR+-tagged humpback whales tagged off Hawaii in March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box.

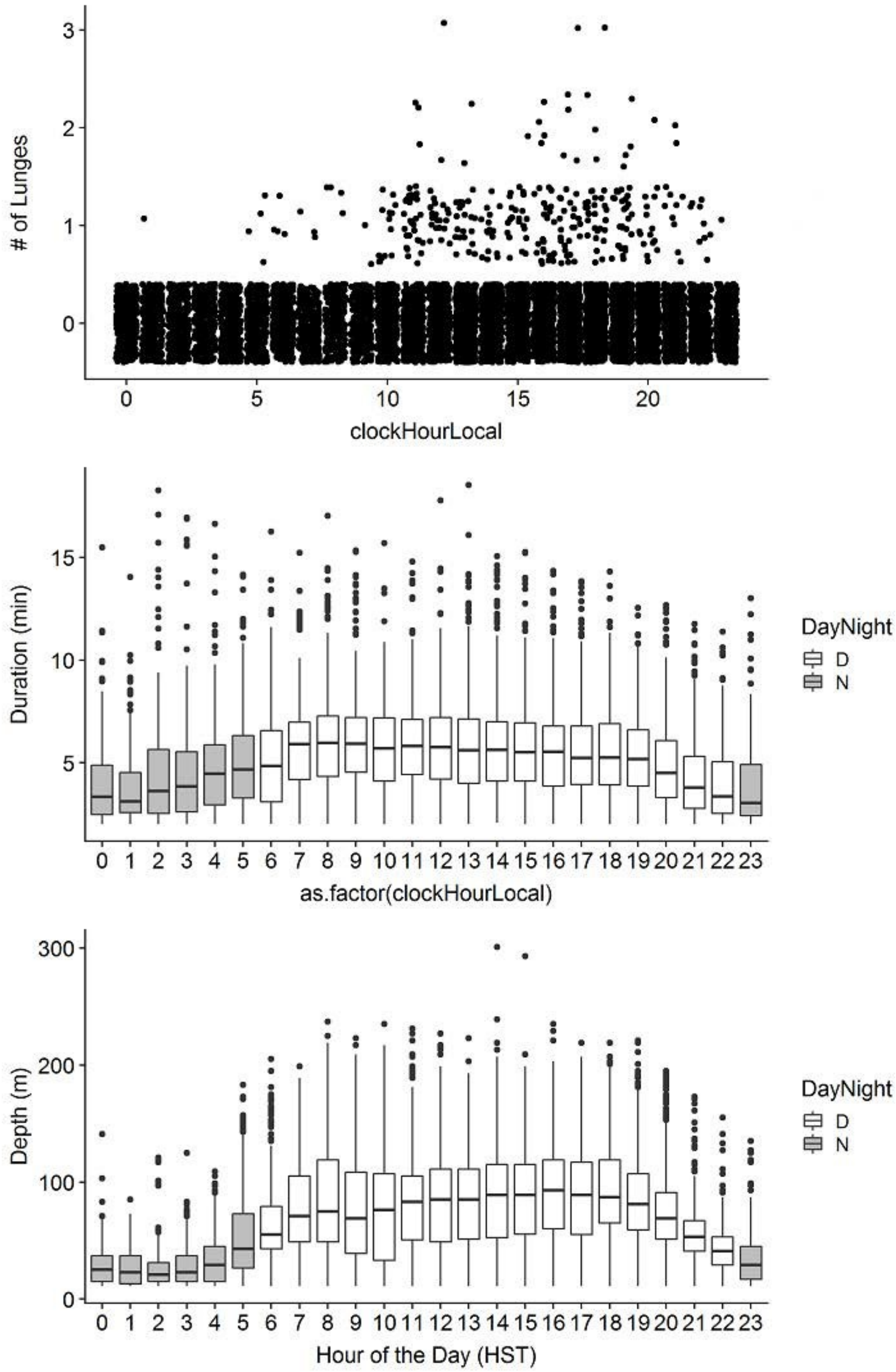


Figure 29. Hourly distribution of the number of lunges (top panel), dive duration (middle panel), and dive depth (bottom panel) while on feeding grounds near the western Aleutian Islands and Bearing Sea for a DM-tagged humpback whale (#5736, a male) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

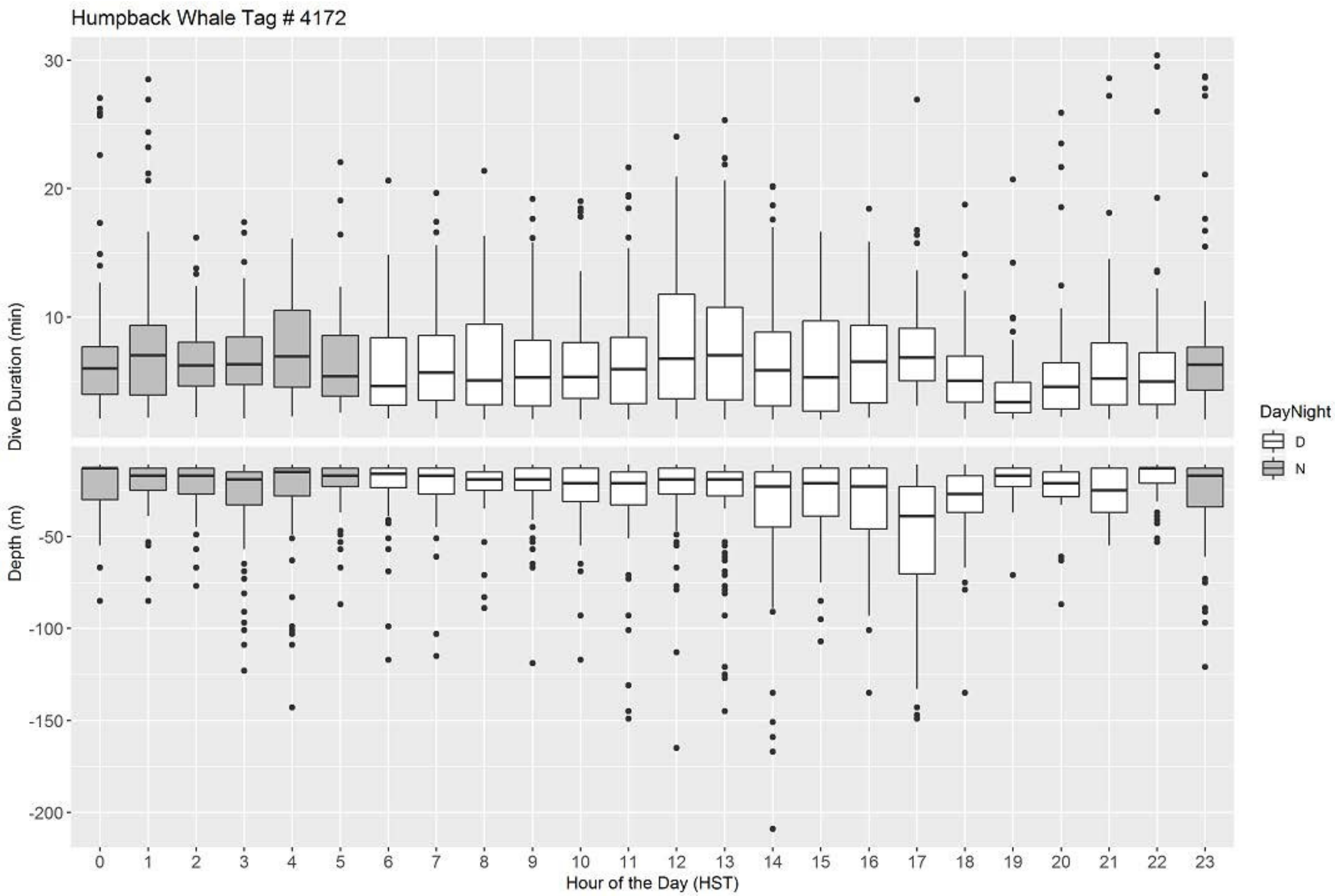


Figure 30. Data from an example track showing the hourly distribution of dive duration (top panel) and dive depth (bottom panel) while on feeding grounds near Haida Gwaii, Canada, for a DM-tagged humpback whale (#4172, a male) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

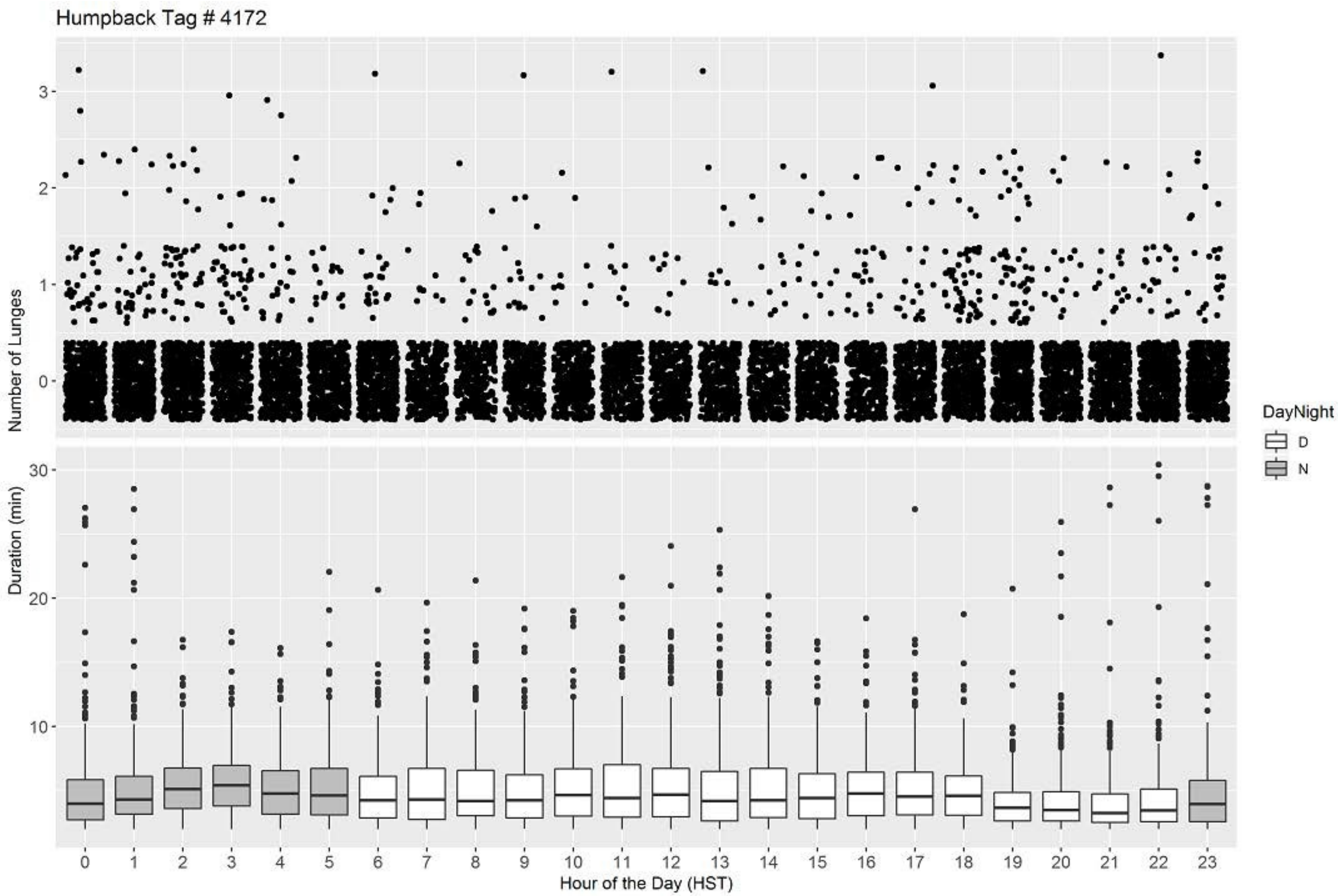


Figure 31. Data from an example track showing the number of lunges per dive (upper panel) and dive duration (lower panel) while on the feeding grounds near Haida Gwaii, Canada, for a DM-tagged humpback whale (#4172, a male) tagged off Hawaii during March 2018. Boxes in the lower plot represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Points in the upper plot are jittered for better visualization.

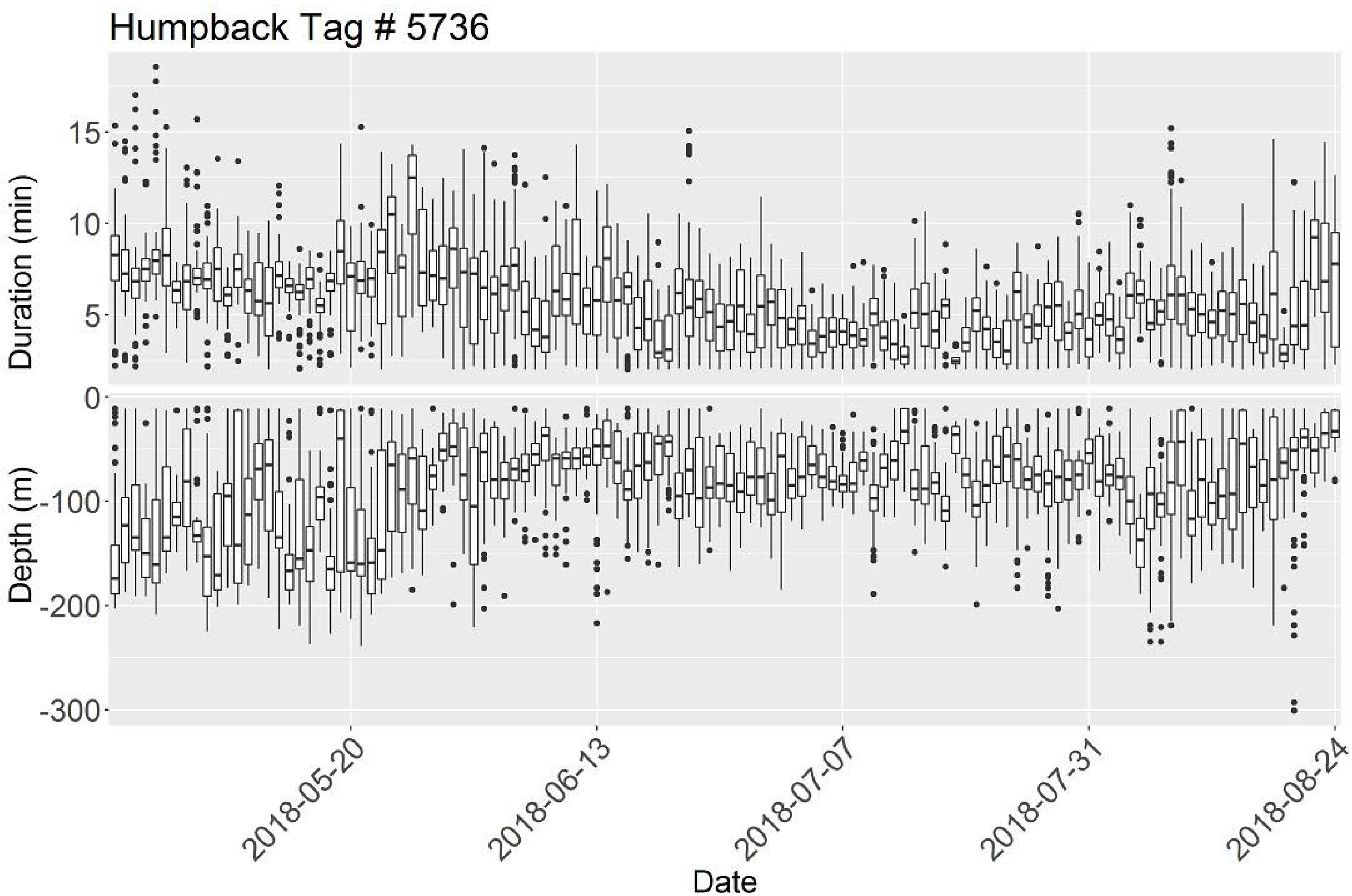


Figure 32:Distribution of daytime dive duration (top panel) and dive depth (bottom panel) during movements on the feeding grounds near the western Aleutian Islands and Bering Sea of a DM-tagged humpback whale (#5736, a male) tagged off Hawaii during March 2018

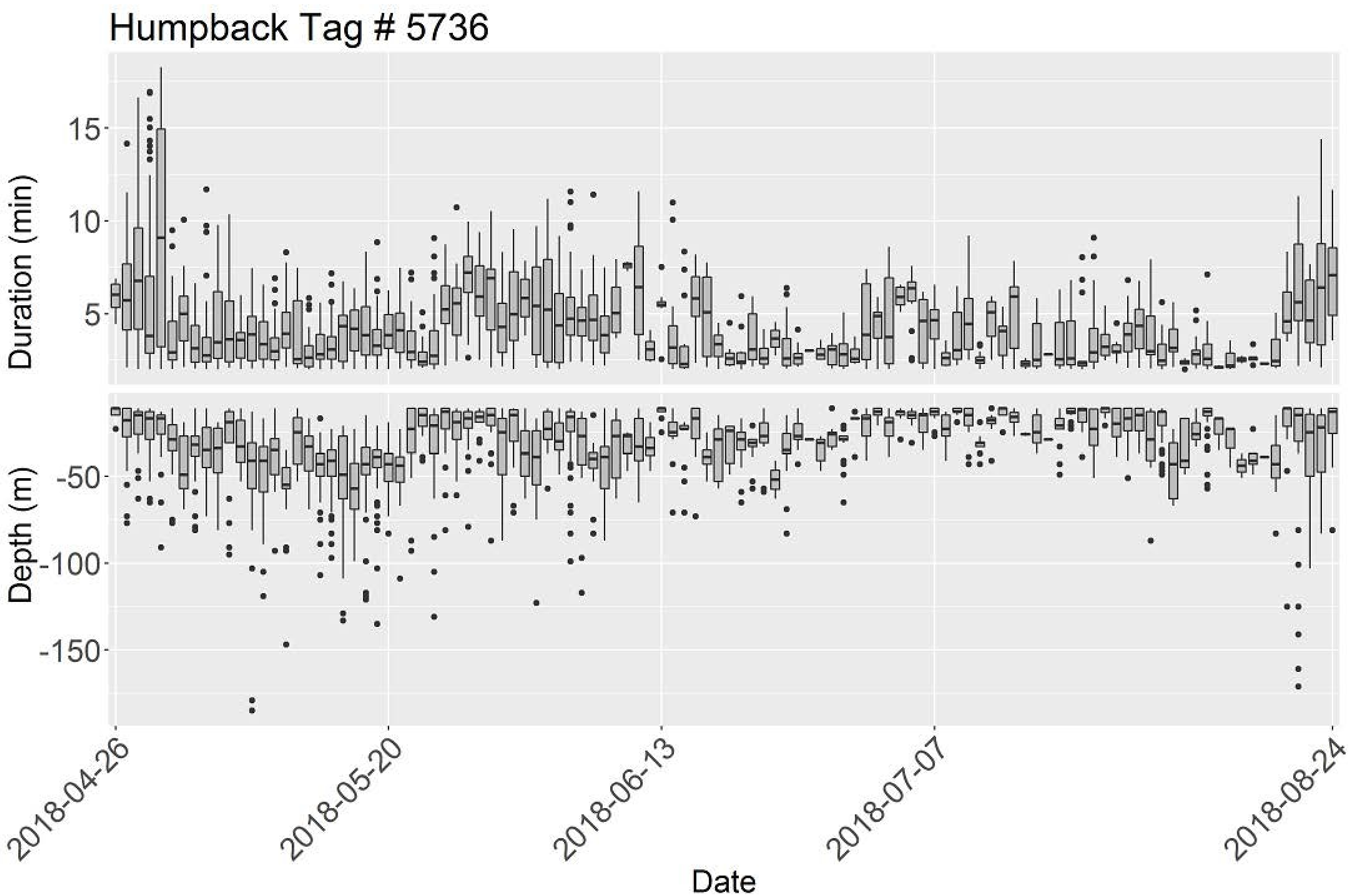


Figure 33. Distribution of nighttime dive duration (top panel) and dive depth (bottom panel) during movements on the feeding grounds near the western Aleutian Islands and Bering Sea of a DM-tagged humpback whale (#5736, a male) tagged off Hawaii during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

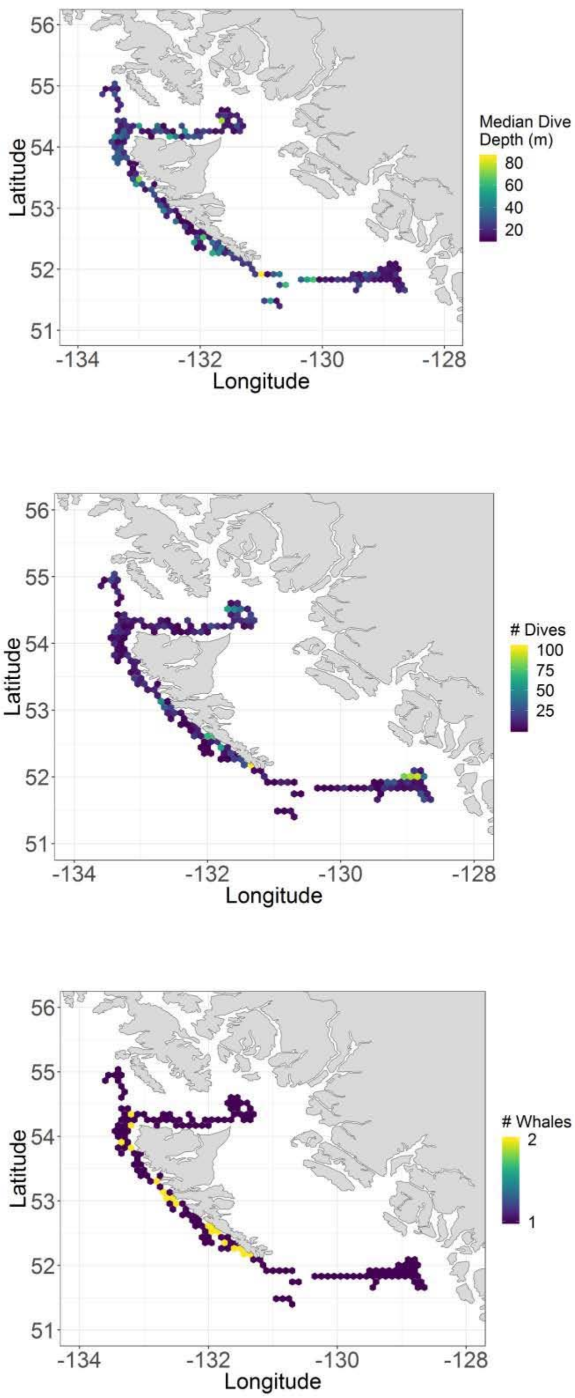


Figure 34. Feeding ground behavior for two DM-tagged humpback whales (#4172 and #5800, both males) tagged off Hawaii in March 2018 that migrated to the area near Haida Gwaii, Canada. Data are summarized in 0.1-degree hexagonal grids showing the median maximum dive depth (top), number of dives (middle), and number of tagged whales (bottom) recorded in each grid cell.

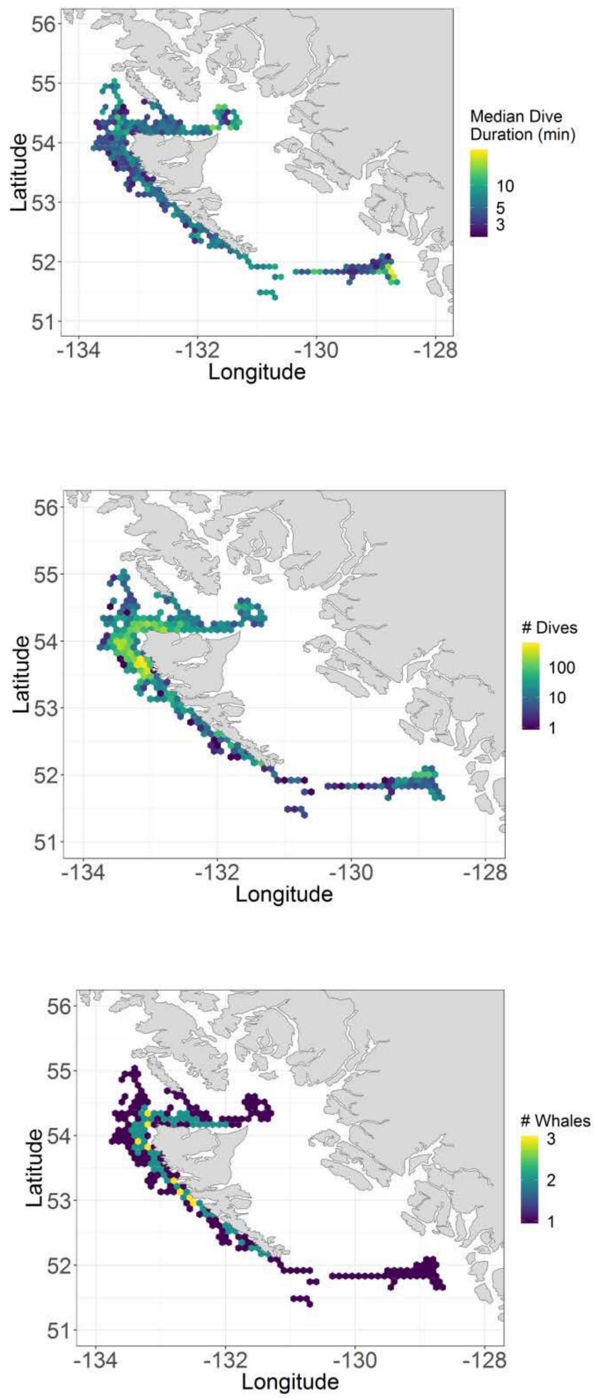
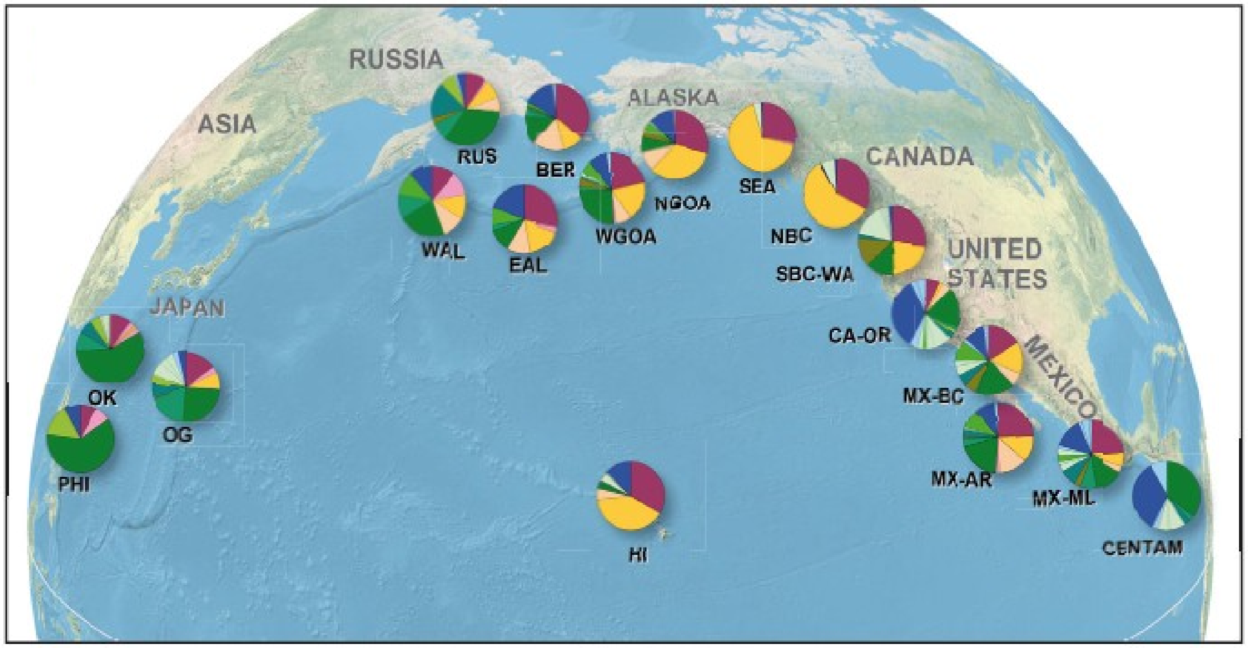


Figure 35. Feeding ground behavior for three DM- and DUR+-tagged humpback whales (#4172 and #5800, both males, and #5784, a female) tagged off Hawaii in March 2018 that migrated to the area near Haida Gwaii, Canada. Data are summarized in 0.1-degree hexagonal grids showing the median dive duration (top), number of dives (middle), and number of tagged whales (bottom) recorded in each grid cell.

a)



b)

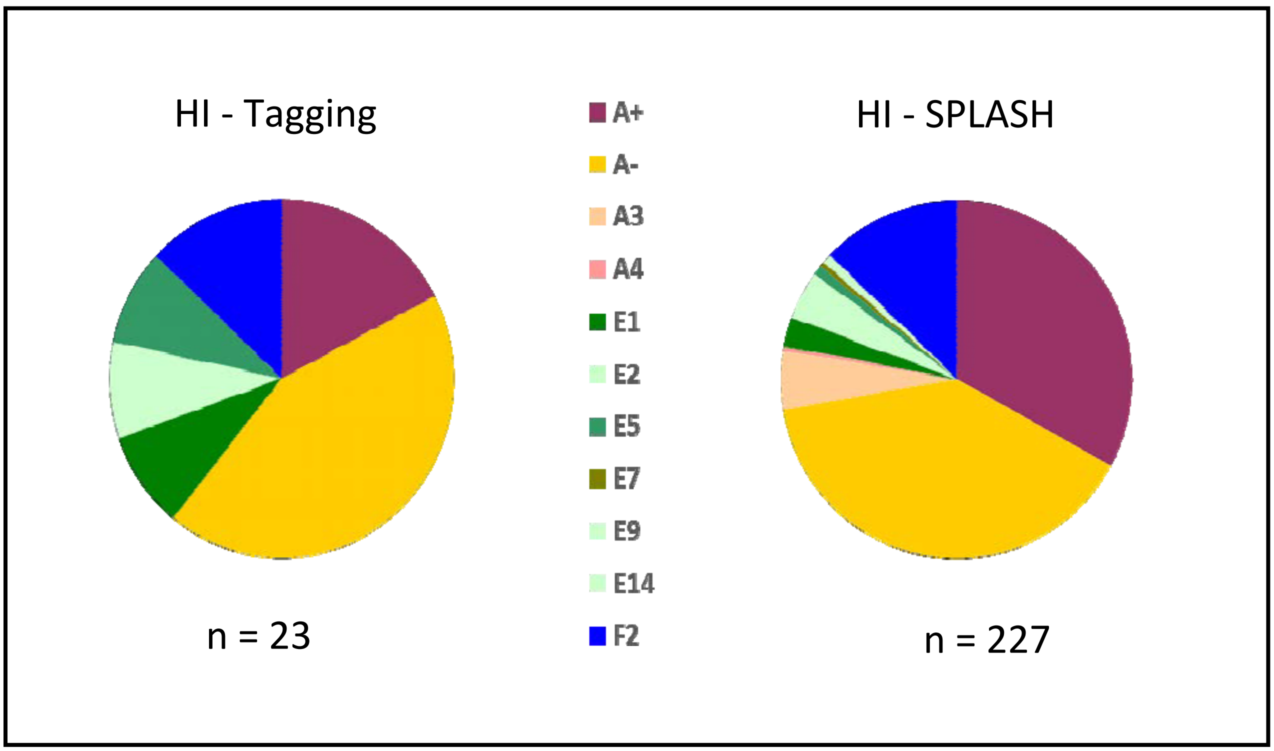


Figure 36. a) The proportion of mtDNA haplotypes for individual humpback whales sampled in the 10 feeding areas and on the eight breeding grounds in the North Pacific during the SPLASH program, as modified from Figure 2 in Baker et al. (2013). b) Proportion of mtDNA haplotypes for individual humpback whales sampled in Hawaii during the 2018 tagging effort (left) and during SPLASH (right). The percentage values are listed in Table 7.

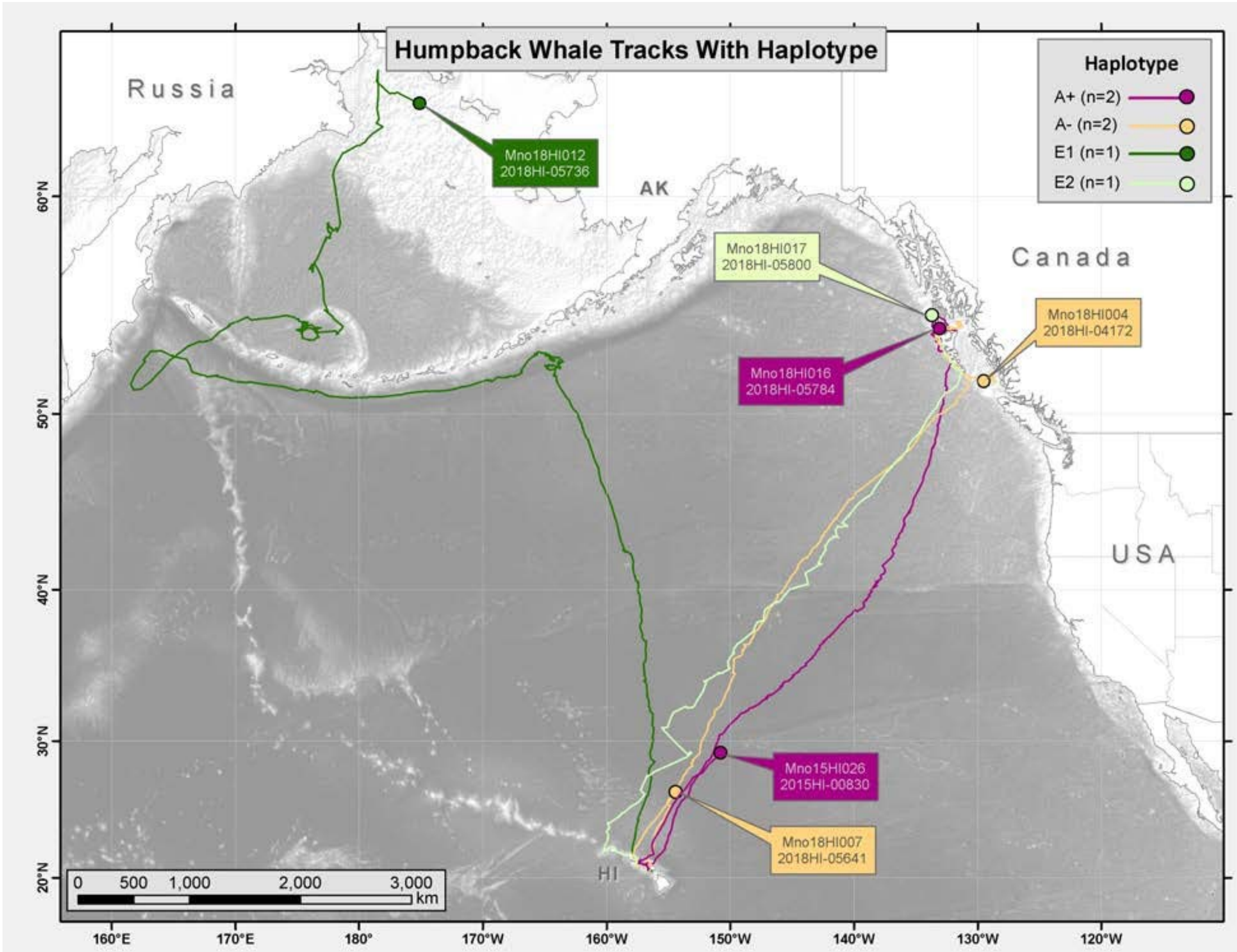


Figure 37. The migratory destinations or trajectories of six individuals sampled in Hawaii during the 2018 tagging effort with known mtDNA haplotypes. Haplotypes are colored according to Figure 34. Note that biopsy sample Mno18HI016 (whale #5784, a female) was also matched by genotypes to a whale identified in Haida Gwaii in 2005 during SPLASH (SPLASH ID 560234).

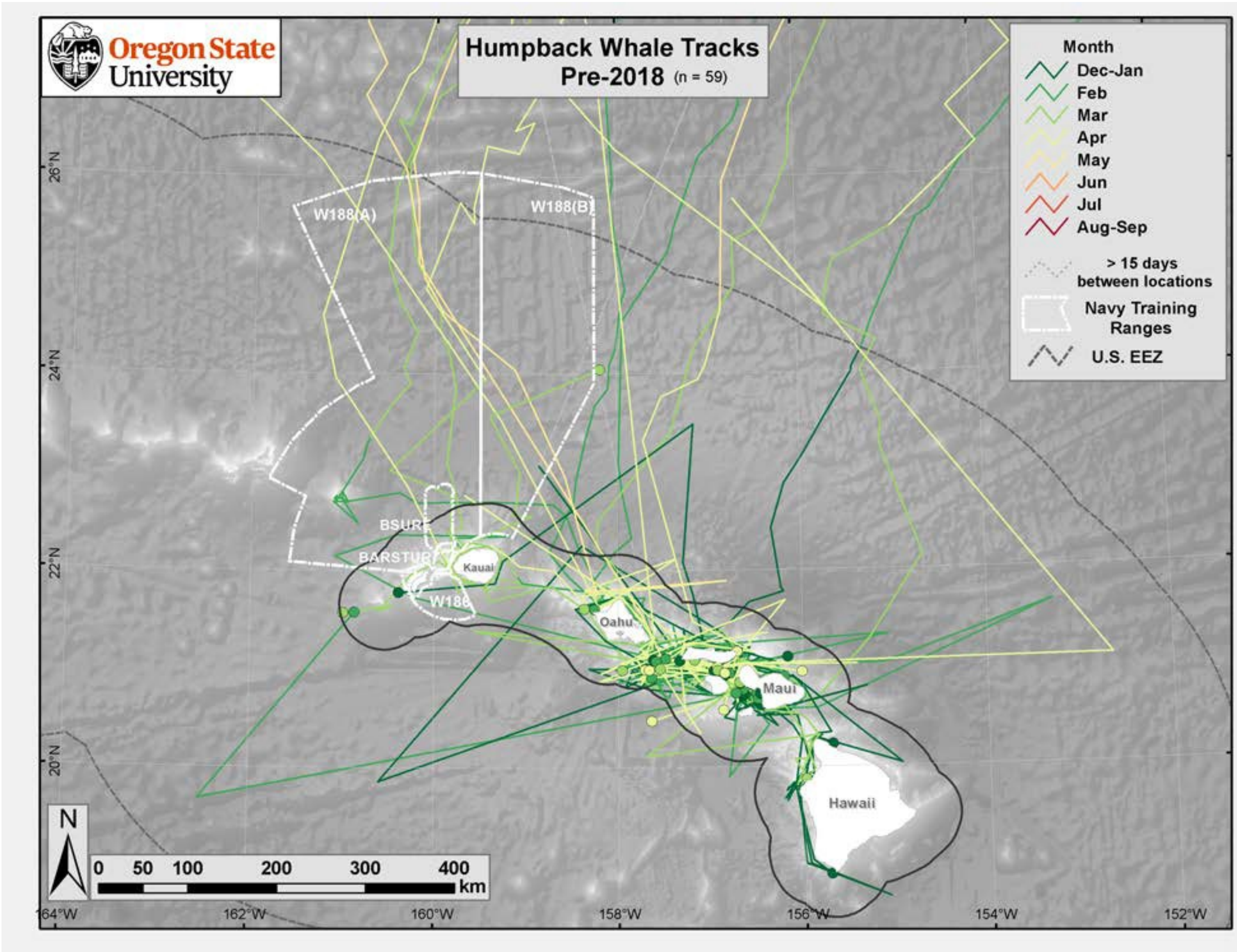


Figure 38. Satellite-monitored tracks for 59 humpback whales tagged in Hawaii from 1995 to 2015, highlighting movement in the breeding grounds and the departure points out of the Hawaiian Archipelago at the start of migration. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding ground (see Section 2.6 for details).

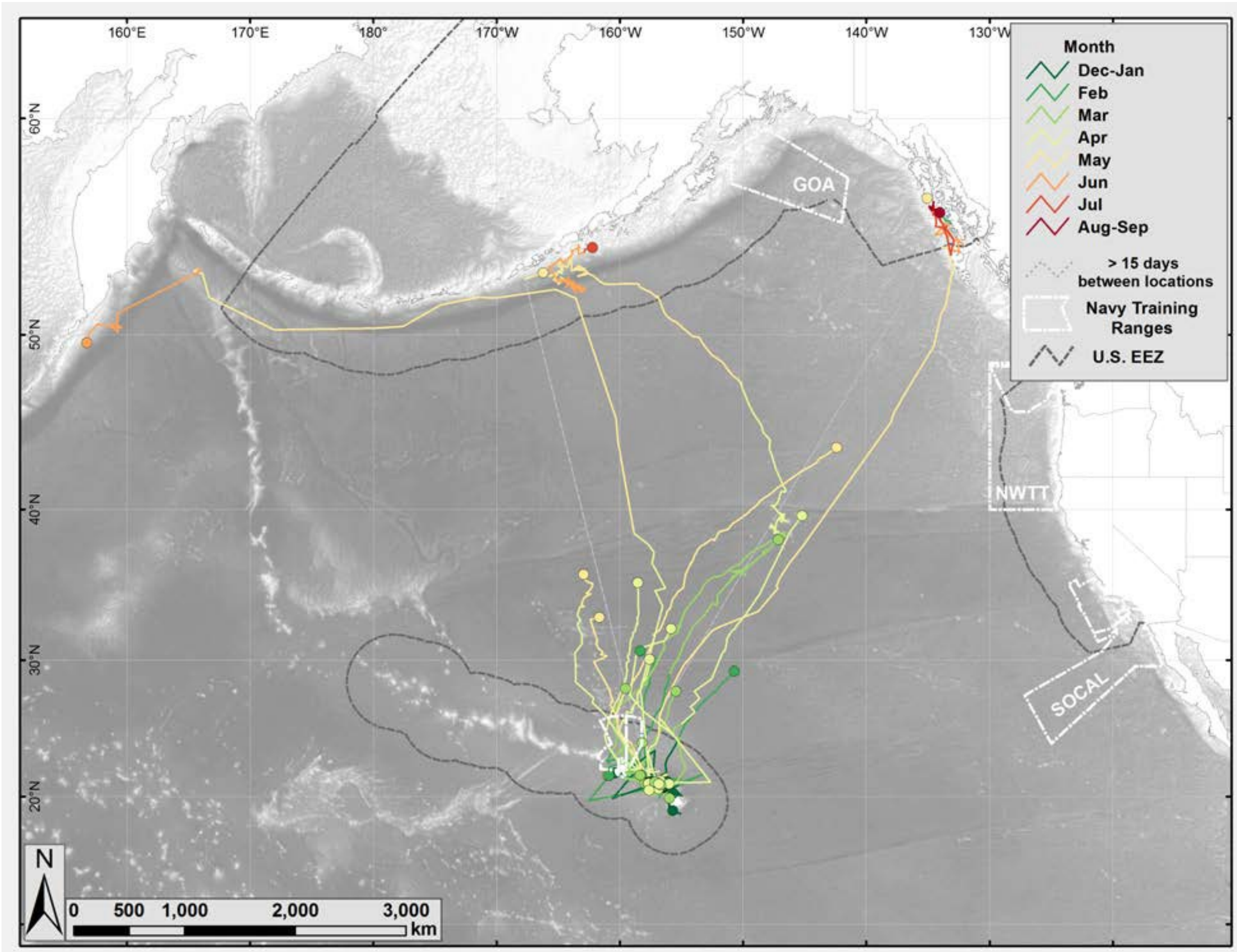


Figure 39. Satellite-monitored tracks for 59 humpback whales tagged in Hawaii from 1995 to 2015, highlighting migration and movement in the feeding grounds.

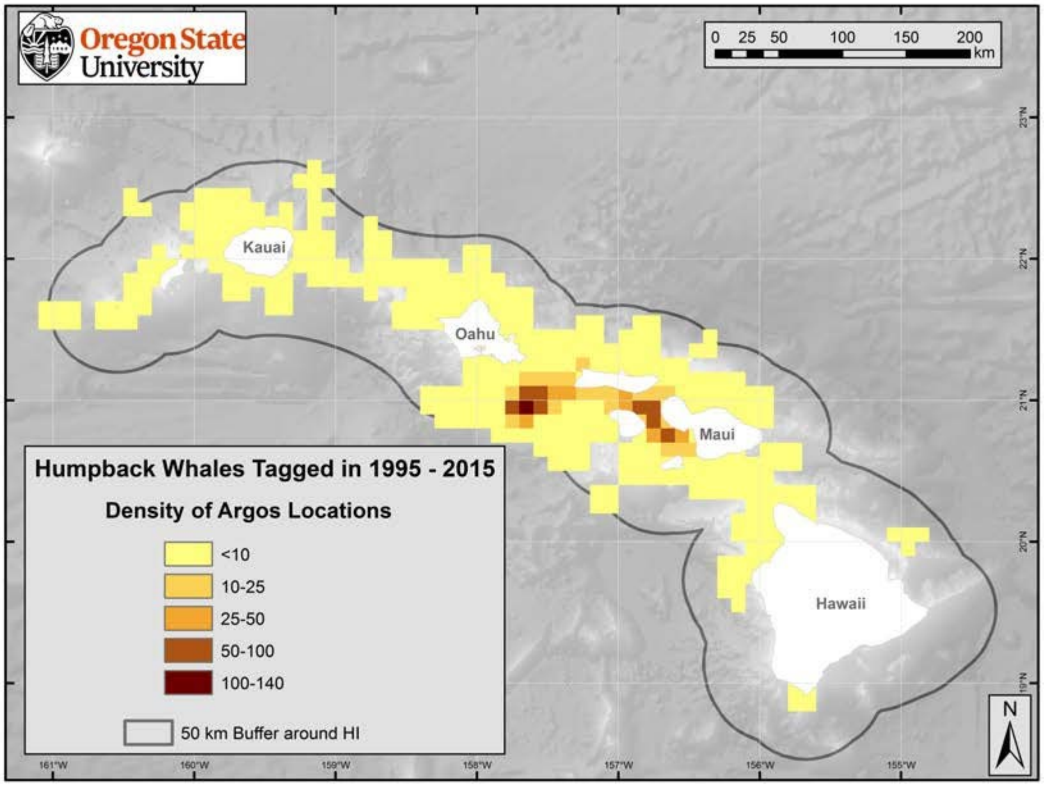


Figure 40. Kernel density utilization distribution for Argos locations in Hawaii of 29 humpback whales with at least 10 days within the 50-km buffer zone tagged off Maui (28 tags) and Kauai (1 tag) from 1995 to 2015. Grid cell size is 0.1 × 0.1 degrees. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding ground (see Section 2.6 for details).

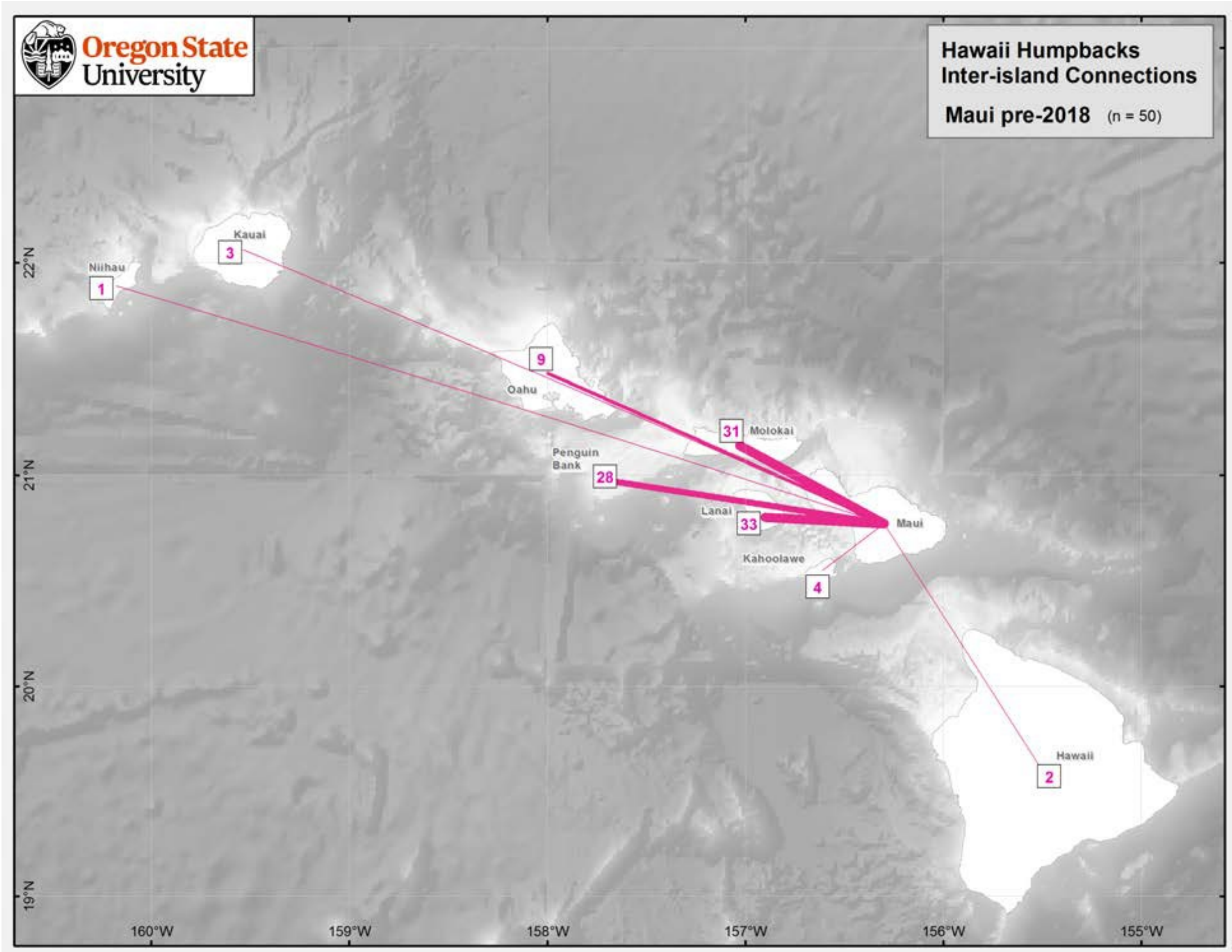


Figure 41. The number of whales (shown in boxes) out of 50 tagged off Maui, Hawaii, from 1997 to 2015 that had locations within 5 km of the other main Hawaiian Islands and Penguin Bank.

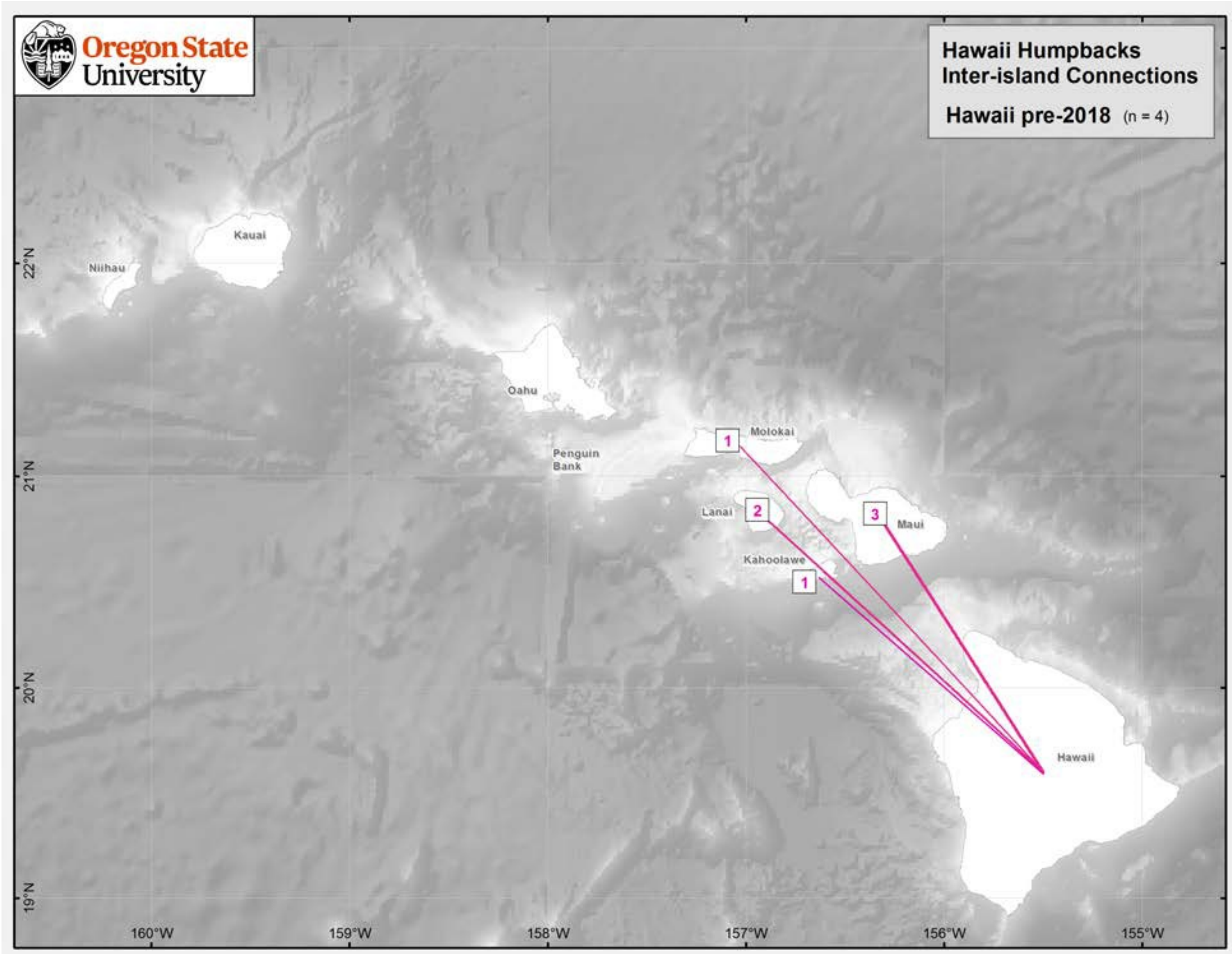


Figure 42. The number of whales (shown in boxes) tagged off the island of Hawaii in 1996 (out of a total of 4 tagged whales) that had locations within 5 km of the other main Hawaiian Islands and Penguin Bank.

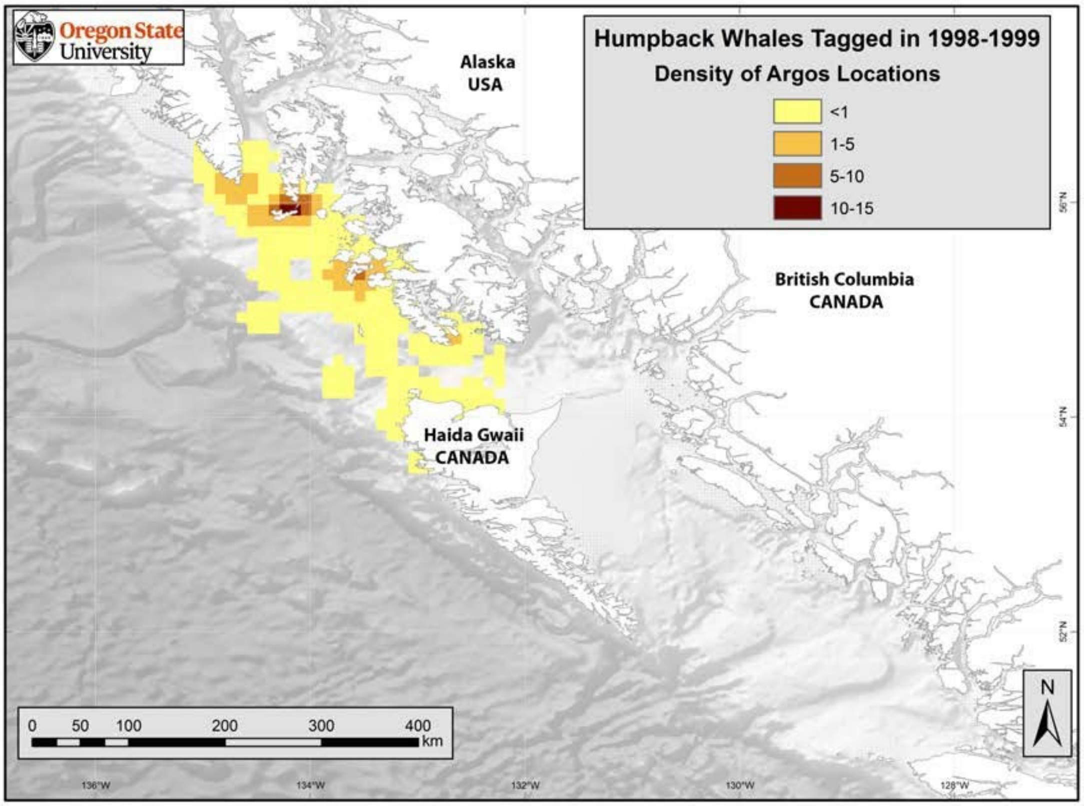


Figure 43. Kernel density utilization distribution for Argos locations in northern British Columbia and Southeast Alaska of two humpback whales tagged off Maui (one in 1998, one in 1999). Grid cell size is 0.1 × 0.1 degrees.

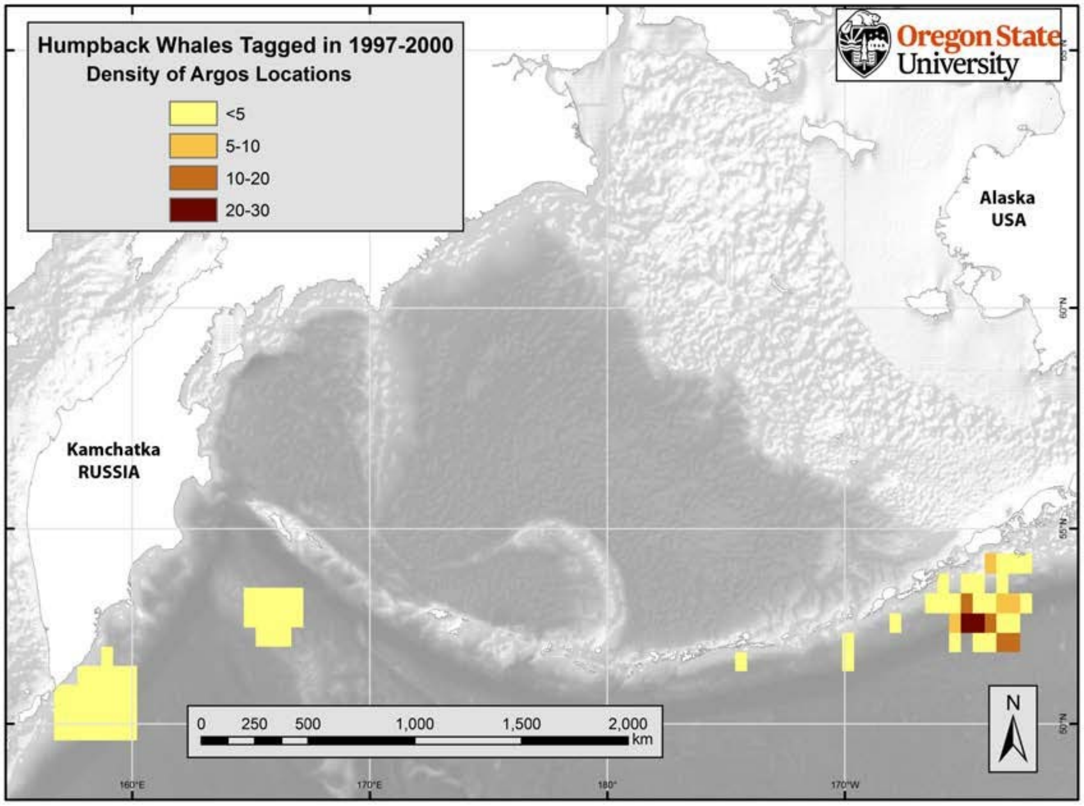


Figure 44. Kernel density utilization distribution for Argos locations in the Aleutian Islands and Kamchatka Peninsula of three humpback whales tagged off Maui (one in 1997, one in 1999, one in 2000). Note that the grid cell size is 0.5 × 0.5 degrees in this representation.

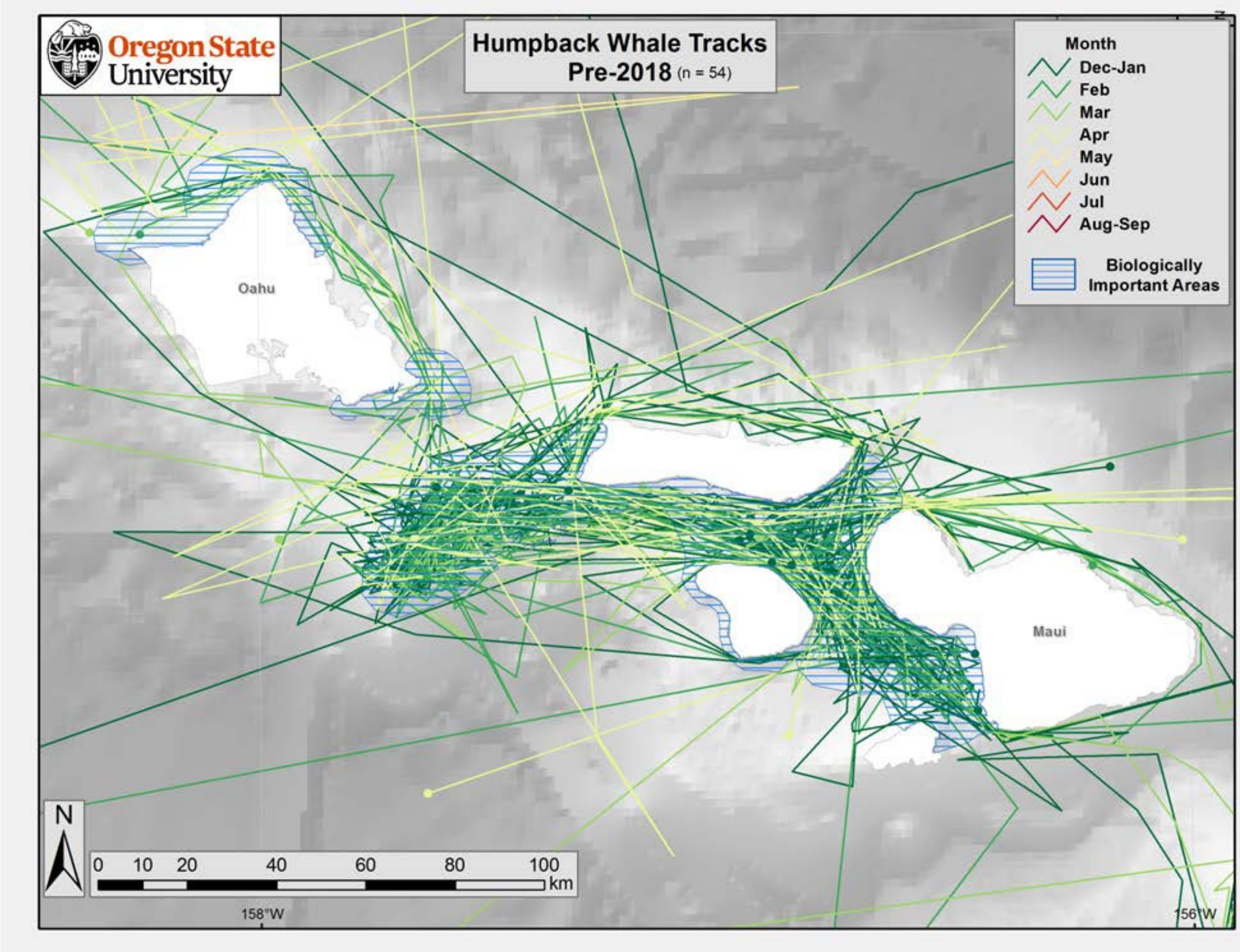


Figure 45. Satellite-monitored tracks in the Maui BIA for humpback whales tagged off Maui (50 tags), Kauai (1 tag), and Hawaii (3 tags) from 1995 to 2015.

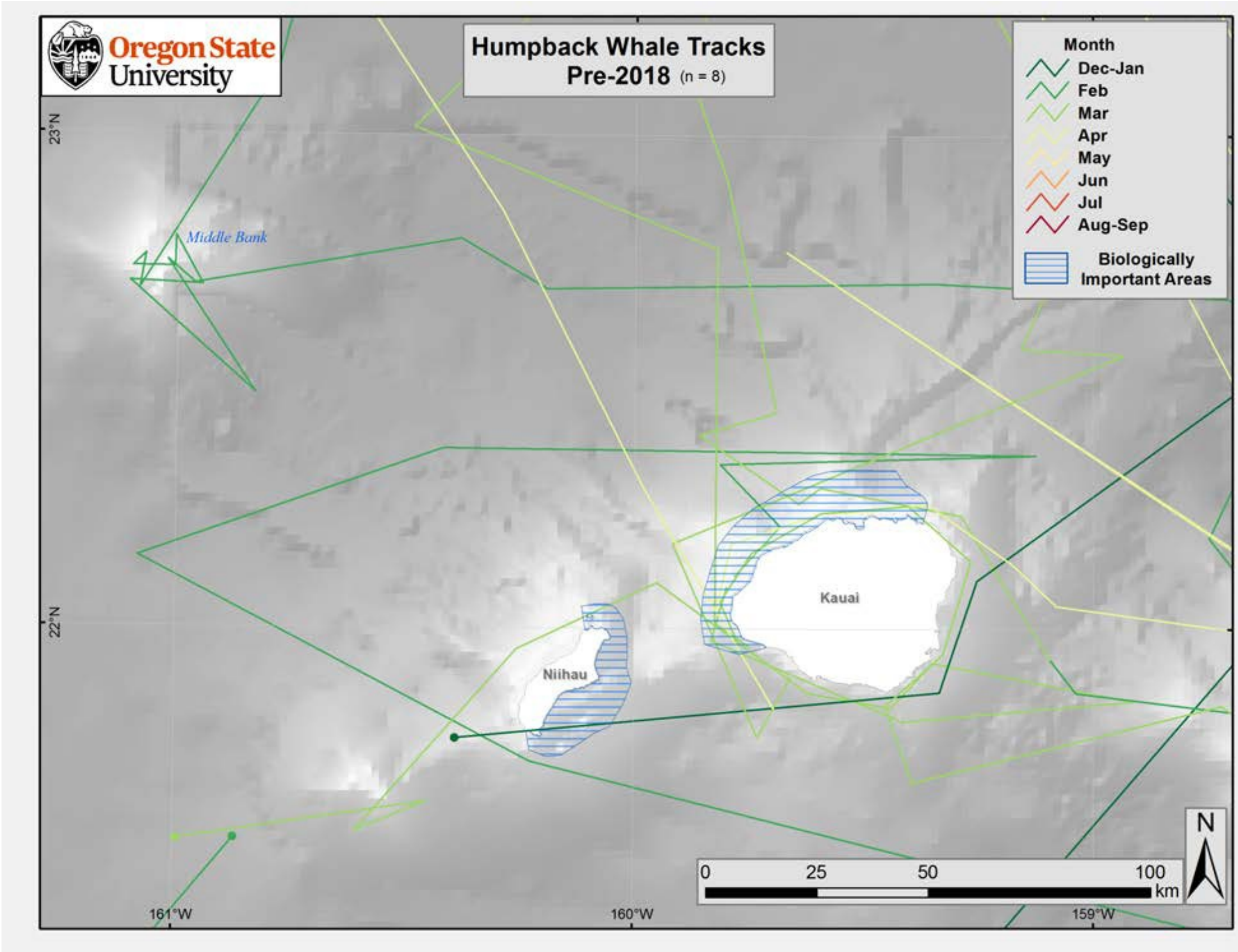


Figure 46. Satellite-monitored tracks in the Kauai BIA for humpback whales tagged off Maui (3 tags) and Kauai (5 tags) from 1995 to 2015.

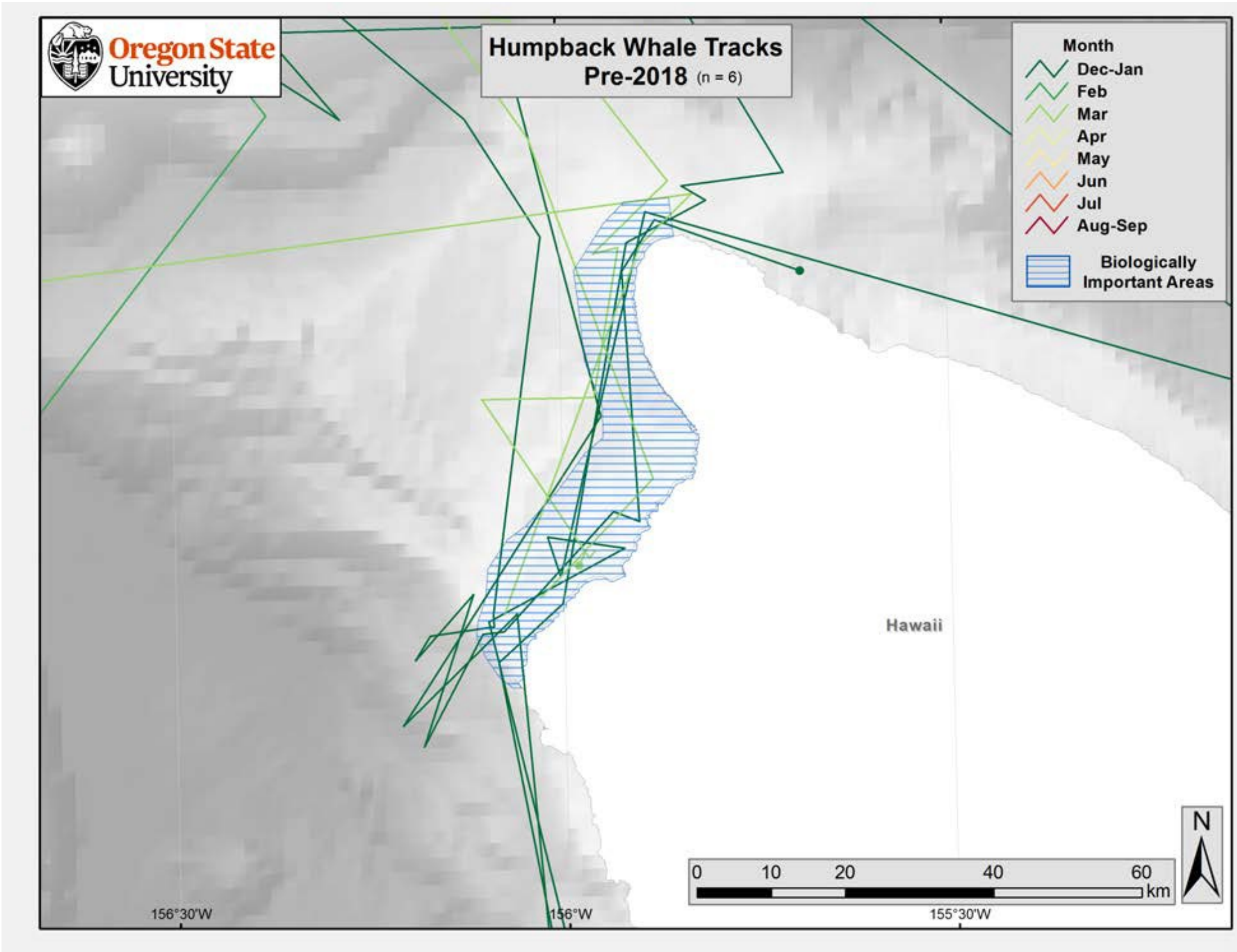


Figure 47. Satellite-monitored tracks in the Hawaii BIA for humpback whales tagged off Maui (2 tags) and Hawaii (4 tags) from 1995 to 2015.

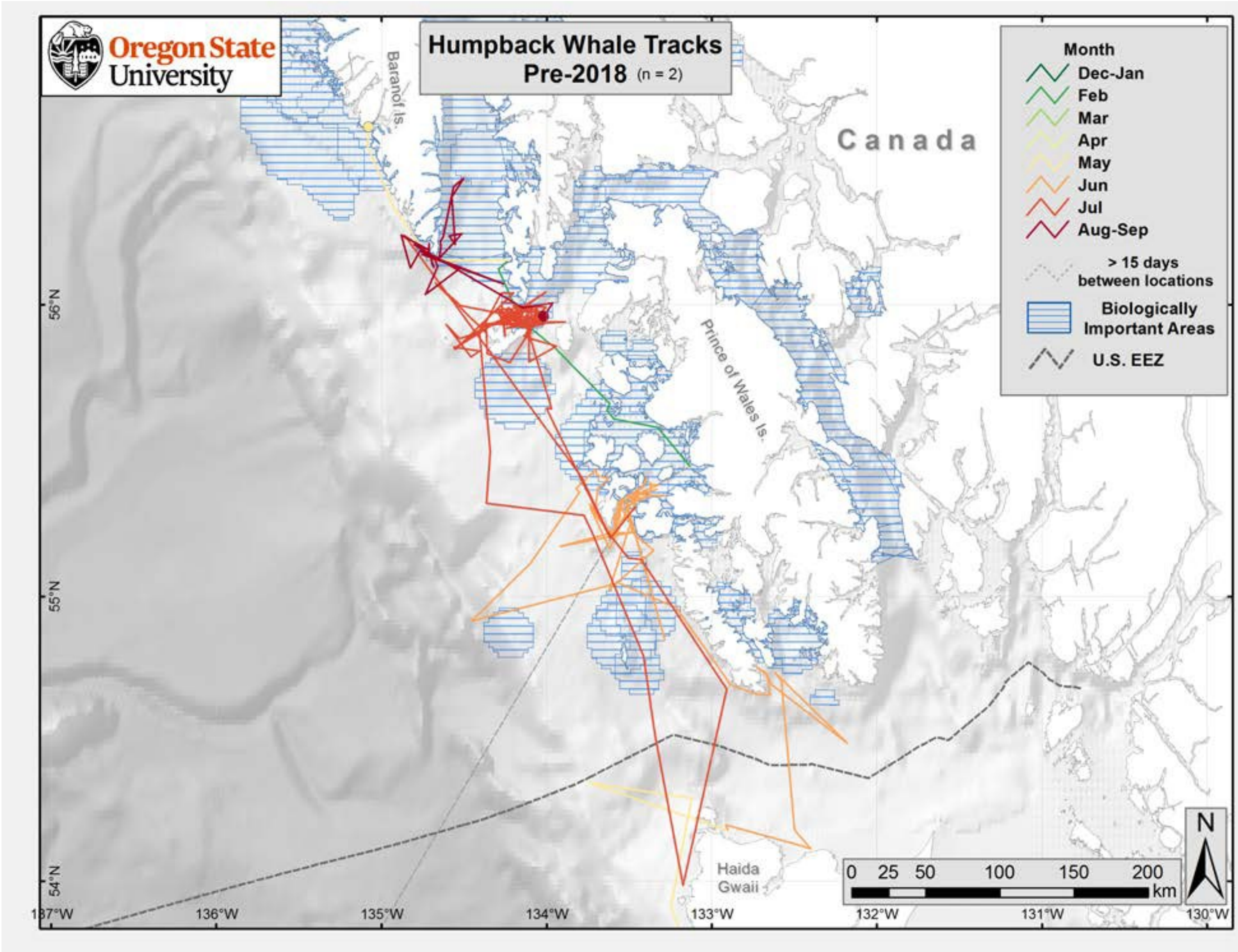


Figure 48. Satellite-monitored tracks in the Southeast Alaska BIA for humpback whales tagged off Maui (2 tags) from 1995 to 2015.

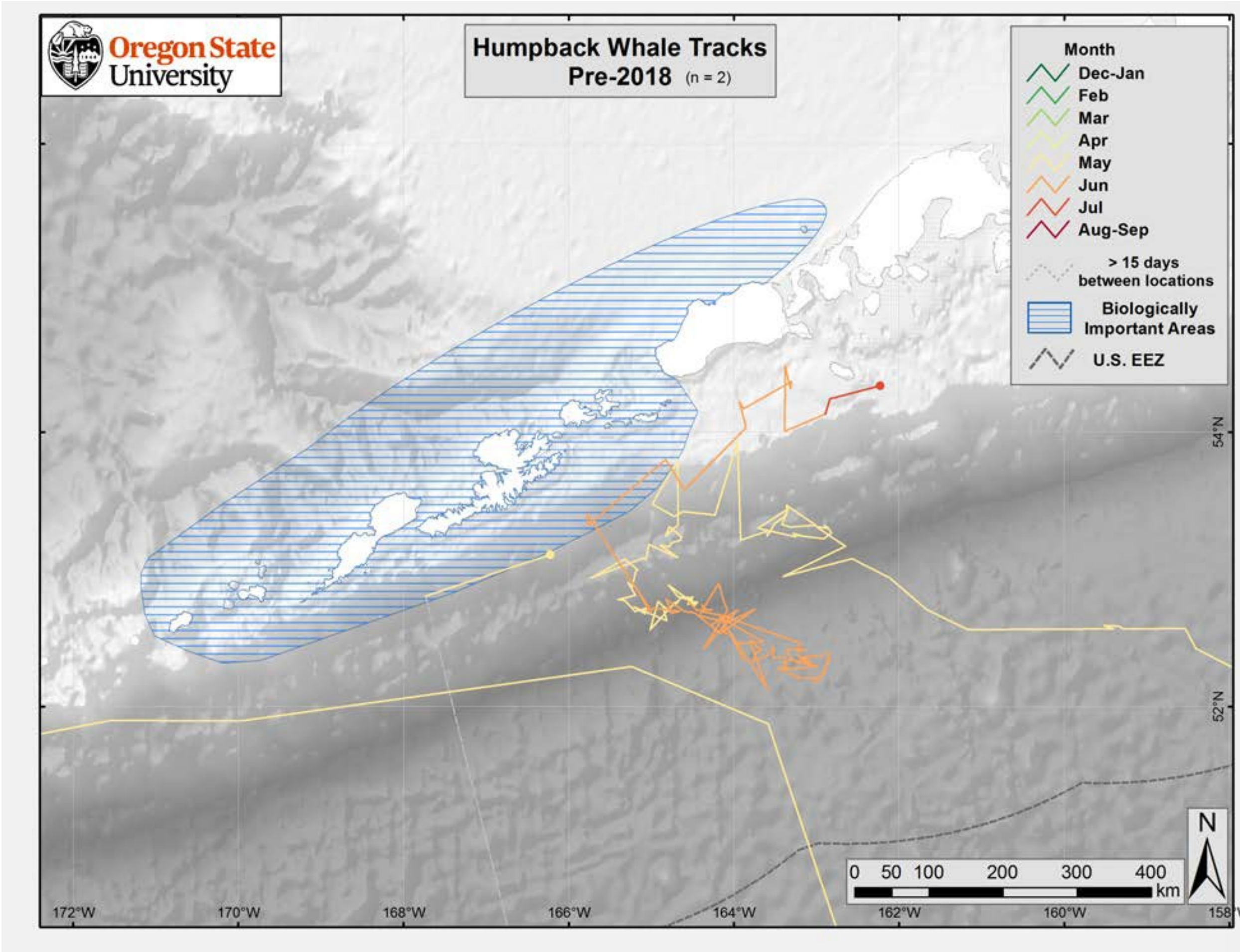


Figure 49. Satellite-monitored tracks in the Aleutian Islands BIA for humpback whales tagged off Maui (2 tags) from 1995 to 2015.