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 2019, 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 areas (“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 2019, 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 the Hawaiian Islands 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 the Hawaiian Islands in 2019, as well as results from previous OSU studies of humpback whales in the Hawaiian Islands from 1995 to 2018. Whale use of Navy training and

testing areas as well as their use of NMFS-identified Biologically Important Areas (BIAs) in the Hawaiian Islands and Alaska is also examined. Fully implantable (or "consolidated type") Telonics Dive Monitoring (DM) tags were used in 2019, providing long-term tracking information via the Argos satellite system as well as dive behavior (duration, depth, and number of lunges per dive). In addition to DM tags, fully implantable Telonics Duration Monitoring Plus (DUR+) tags were used in 2018, the latter providing the same capabilities as the DM tag except for depth. DM and DUR+ tags followed the same general physical design as OSU's earlier fully implantable Location-Only (LO) tag used during previous tagging efforts (1997-2000, and 2015; Mate et al. 2019). Externally mounted (or "anchored type") tags were deployed during the 1995 and 1996 tagging efforts off the islands of Kauai and Hawaii (Mate et al. 1998). Twenty-five humpback whales were tagged off Maui in March 2019. Argos locations were received from 24 of the 25 tags, with tracking periods ranging from 0.1 to 81.3 days (d) (mean = 21.4 d, standard deviation [SD] = 20.2 d, n = 24). A total of 101 humpback whales were tagged by OSU in the Hawaiian Islands prior to 2019, covering the period 1995 to 2000, 2015, and 2018. Of these, 85 were deployed off Maui (in 1997, 1998, 1999, 2000, 2015, and 2018); 10 were deployed off Kauai (in 1995, 1996, and 1997); and six were deployed off Hawaii (in 1996). Tracking data were obtained for 81 whales prior to 2019 (the remaining tags provided no locations), with tracking durations ranging from 0.04 to 160.0 d. Tracking periods (for fully implantable tags deployed from 1995 to 2019) for whales that migrated away from the Hawaiian Islands (median = 38.2, maximum = 160.0 d, n = 36) were longer than for whales that were only tracked within the islands (median = 7.7, maximum = 44.4 d, n = 60). Hierarchical switching state-space models (hSSSM) were applied to the Argos locations from the tags deployed in 2018 and 2019 (duty-cycled at 6 hours (h)/d), and conventional switching state-space models (SSSM) to the Argos locations from the historical LO tags (which were programmed with less frequent duty cycles) for the purpose of generating regularly spaced tracks with annotated behavioral state for use in analyses of movement behavior and identification of migration phases. The aggregate tracking results within the Hawaiian Islands support results of previous photo-ID studies and aerial surveys, showing highest densities of whales in the Maui Nui region (the inner waters of the "four-island region" of Maui, Molokai, Lanai, and Kahoolawe), where most of the whales were tagged, as well as Penguin Bank, and extensive inter-island movements. The results also identify high use of Middle Bank and the Papahanaumokuakea Marine National Monument by some whales in 2019. Mean residence time in the Hawaiian Islands from tagging to departure (for whales with known departure date from the islands) for the aggregate tracking data was 13.1 d (range = 1.1-42.8 d, SD = 9.4 d, n = 39), lending support to earlier studies that found that there is a rapid turnover of individuals in this breeding area during the winter season. Migratory destinations were tracked for 12 humpback whales tagged off Maui, with seven whales going to northern British Columbia and southeastern Alaska, one going to southern British Columbia, and four going to the eastern Aleutian Islands, supporting the findings of previous telemetry, genetic, and photo-ID studies. One of the latter four whales continued on to the Kamchatka Peninsula (Russia), 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. In terms of movement behavior, state-space model output for 86 tracks ≥ 3 d in duration (range = 3-176 d) indicated that locations classified as "area-restricted searching" occurred primarily in the breeding (n = 2,159 SSSM/hSSSM locations; 50.4 percent) as well as feeding (n = 528 SSSM/hSSSM locations; 12.3 percent) areas, while "transiting" locations were the predominant behavioral mode while migrating (n = 1,598 SSSM/hSSSM locations; 37.3 percent). Movement speed was somewhat slower in the feeding areas (mean = 1.42 km/h, median = 0.85 km/h, SD = 1.55 km/h, n = 528 SSSM/hSSSM locations) than in the breeding area (mean = 1.62 km/h, median = 1.20 km/h, SD = 1.38 km/h, n = 2,159 SSSM/hSSSM locations), while it was substantially higher during migration (mean = 4.65 km/h, median = 4.61 km/h, SD = 2.39 km/h, n = 1,598 SSSM/hSSSM locations). However, travel speeds during the migration phase were not sustained but showed variation over time and among individual animals, including both highfrequency oscillations as well as longer periods of increased and decreased speed lasting several days. Five Navy areas within the Hawaii Range Complex (HRC) were considered in this report: Four Island Region Mitigation Area (FIRMA), Humpback Whale Seasonal Special Reporting Area Oahu North (SSRAON), Humpback Whale Seasonal Special Reporting Area Oahu South (SSRA-OS), Humpback Whale Seasonal Special Reporting Area Penguin Bank (SSRA-PB), and Barking Sands Tactical Underwater Range and Underwater Range Expansion, combined (BS-Merge). Of these, FIRMA was the most heavily used by humpback whales, with 95 percent of tracked whales spending time there (maximum residency of 23.1 d). This was unsurprising, as 96 of the 105 tracked whales were tagged within FIRMA. Area SSRA-PB was the next most heavily used, with 66 percent of whales spending time there (maximum residency of 23.8 d), followed by SSRA-OS (25 percent of whales, maximum residency of 1.3 d) and then SSRA-ON (23 percent of whales, maximum residency of 1.5 d). Only 11 percent of tracked whales spent time within BS-Merge (three of five tagged in Kauai, nine of 96 tagged in Maui, none of four tagged in Hawaii), with maximum residency in this area of 1.4 d. This low use was not surprising, given the range's close proximity to Kauai and the small sample size of whales tagged in Kauai. More tagging off Kauai would improve our understanding of BS-Merge use by humpback whales while in the Hawaiian Islands and help determine whether the minimal use noted here is simply a function of tagging location bias. None of the 12 humpback whales tagged in the Hawaiian Islands from 1995 to 2019 that reached a migratory destination were tracked within any Navy training areas along the US West Coast or in the Gulf of Alaska, but our small sample size of migrating whales reaching a feeding destination likely contributed to this finding. Of the three Biologically Important Areas (BIAs) that have been designated for humpback whales in the Hawaiian Islands, two (Kauai-Niihau and Hawaii) did not overlap (completely) with Navy areas. Of these, Kauai was the most heavily used by humpback whales tagged from 1995 to 2019, with 14 percent of tracked whales (15 of 105, five of which were tagged there) having locations there (maximum

residency of 3.5 d). Six percent of tracked whales (six of 105, four of which were tagged there) had locations in the Hawaii BIA, with a maximum residency of 6.2 d. More tagging off the islands of Hawaii and Kauai would further our understanding of BIA use in those areas. Ninety-one percent of tracked whales (96 of 105) had locations in a region surrounding the islands defined by the 200-meter (m) isobath as its inner boundary and 50 km from shore as its outer boundary, with a maximum residency of 30.2 d. Of the seven humpback whales migrating to the northwestern coast of the US and Canada, four were tracked within the Southeast Alaska BIA, with a maximum residency of 70 d. Humpback whale use of feeding-area BIAs outside the Southeast Alaska BIA was minimal (two whales were tracked within the Aleutians BIA and none in the Shumagin or Bristol Bay BIAs), due in part to the small number of whales tracked to these areas, but also to 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. Tags summarized dives for a mean of 62.0 percent of the tracking duration across 2018 and 2019. Dives in the breeding areas were generally shallow (< 100 m), with a mean of 64 percent of recorded dive behavior occurring in the upper 30 m of the water column. Occasional dives reached 400 m; however, maximum dive depth was likely limited by bottom depth in many cases, and there were no discernible spatial patterns to dive behavior. Dive behavior during migration was generally similar to behavior in the breeding areas. However, for the first 7 to 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 of tagged whales in the feeding areas near Haida Gwaii were shallow, with no temporal trends with the exception of one whale from 2019, which made deeper, longer duration dives during the day, suggesting it was employing a different foraging strategy compared to other tagged whales using the area.Biopsy samples were collected from 23 of 25 tagged whales off Maui in 2018 and from 21 of 25 tagged whales and one untagged whale off Maui in 2019. Mitochondrial deoxyribonucleic acid (DNA) sequences of the combined samples resolved seven 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 in 2018 and 11 loci in 2019, indicating that each sample represented an individual whale. The 45 individuals represented five females and 40 males. The DNA profiles of all 45 individuals were compared to an unpublished database of DNA profiles representing 3,351 individual humpback whales from the North Pacific. This "DNA register" represents a shared archival resource held by OSU's Cetacean Conservation and Genomics Laboratory, in collaboration with regional contributors, following the technical standards for DNA profiling used in the SPLASH program (Baker et al. 2013). Five matches (i.e., genotype recaptures) were detected: two to individuals sampled in the Hawaiian Islands in 2004, two to individuals sampled in the northern Gulf of Alaska (one in 2004 and one in 2009), and one to an individual sampled in northern British Columbia in 2005. A sixth genotype recapture was documented between a whale tagged by OSU in the Hawaiian Islands in 1999 and a whale sampled in southeastern Alaska in 2019, 20 years after tagging. Of the 50 whales tagged off Maui in 2018 and 2019, 36 had fluke photos that could be used for identification purposes. Twenty-six of these have been identified in the Happywhale photo-ID database, with matches to the Hawaiian Islands, Mexico (Baja California), western Gulf of Alaska, northern Gulf of Alaska, southeastern Alaska, and northern Washington/southern British Columbia. The ID of a whale that was biopsied but not tagged was matched in Happywhale to the Hawaiian Islands and southeastern Alaska. 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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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With the second year of this CESU agreement to study humpback whales in the Hawaiian Islands through the use of satellite telemetry, dive behavior, genetics, and photo-ID, we have characterized this DPS' breeding-season 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. Field efforts in the Hawaiian Islands 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.

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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
BIA	Biologically Important Area
bp	Base pair
BS-Merge	Barking Sands Tactical Underwater Range and Barking Sands Underwater Range Expansion areas, combined
CESU	Cooperative Ecosystem Studies Unit
cm	Centimeter
d	Day
deg	Degrees of longitude or latitude
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
FIRMA	Four Island Region Mitigation Area

g	Gram
GOA	Gulf of Alaska Temporary Maritime Activities Area
h	Hour
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
SSRA-ON	Humpback Whale Seasonal Special Reporting Area Oahu North
SSRA-OS	Humpback Whale Seasonal Special Reporting Area Oahu South
SSRA-PB	Humpback Whale Seasonal Special Reporting Area Penguin Bank
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 training and testing range complexes. From the perspective of the conservation status of 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 Act[1] (ESA). Four DPSs were designated for the North Pacific based on the location of distinct breeding areas (81 FR 62259, 81 FR 93639): "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) (81 FR 62259, 81 FR 93639).

The available information indicates that three of these DPSs, Hawaii, Mexico, and Central America, are primarily found along the western coast of North America during the summer-fall feeding season. During this season, these DPSs occur in somewhat distinct feeding aggregations, with Hawaii animals being found in southeastern Alaska and northern British Columbia; Mexico animals being found off northern Washington-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, NMFS 2016a, b). Finally, animals from the Western North Pacific DPS may also be present in small numbers in these areas (Bettridge et al. 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 Islands between 1995 and 2000. These studies showed that some whales migrated north from the Hawaiian Islands into the Gulf of Alaska, with some then turning west towards Russia, while others migrated more directly from the Hawaiian Islands to southeastern Alaska and northern British Columbia (Mate et al. 1998, 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

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

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

Within the Hawaiian Islands, the early tagging 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, tagging studies of humpback whales in the Hawaiian Islands 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 of 2018 and 2019 OSU conducted new satellite tag deployments off Maui 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 these new tagging efforts, and also includes comparison with the historical data from previous tagging efforts by OSU in the Hawaiian Islands (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 the Hawaiian Islands to describe their breeding-season occupation, connectivity, and residence time, as well as their migration to feeding areas, including their movement characteristics. 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 off Maui in 2019 included:

- 25 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.

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.

Finally, through the collection, cataloguing, and matching of photo-IDs, this project sought to augment the value of the tracking and genetic data by:

- Establishing movements, migratory connections, and resighting histories for tagged whales through an independent and complementary technique.
- Establishing movements, migratory connections, and resighting histories for additional, untagged whales encountered during the conduct of fieldwork in the vicinity or company of tagged whales.

2 Methods

2.1 Field Efforts

2.1.1 Tag Deployment

All tagging efforts in 2019 were conducted from the 11-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, and boat driver/data recorder. 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. We also did not tag mothers accompanied by neonate calves. 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 3.5 m with 95- to 98-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 the Hawaiian Islands, from 1995 through 2000, and in 2015 and 2018. During these field efforts, 10 whales were tagged off Kauai, six off Hawaii, and 86 off Maui, with deployments taking place from December to April. Details about tag types, tag programming, and data collected during each season are available in Mate et al. (1998, 2007, 2019) and Palacios et al. (2019).

2.2 Satellite Tags

Tags deployed in 2019 were fully implantable, non-recoverable, Argos-based Telonics RDW-665 Dive Monitoring (DM) tags. These tags followed the same design as DM and Duration Monitoring Plus (DUR+) tags deployed off Maui in 2018 (Mate et al. 2019), with 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 housed 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 was 3.2 cm long × 0.6 cm wide) mounted on the main body at the nose cone (proximal) end. Maximum tag weight was 300 grams (g).

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 (*cf*. "type C" or "consolidated type"; *sensu* Andrews et al. 2019), 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 33 d (standard deviation [SD] = 35 d, median = 24 d, n = 246), with a maximum duration of 220 d (OSU, unpublished data).

2.2.1 DM Tag Programing

DM tags contained a pressure sensor and tri-axial accelerometers and were able to record dive depth, dive duration (based on the wet/dry status of the SWS), and rapid changes in body orientation or 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 rapid changes in the accelerometer data, indicative of increased activity levels, such as when animals lunge. When in the foraging areas, lunge-feeding behavior produces stereotypical signatures in the accelerometer data (Calambokidis et al. 2007, Goldbogen et al. 2008), which can be used as a measure of feeding effort (Mate et al. 2018b, c). When in the breeding areas, the whales typically do not feed, so we used detected "lunge events" as a more general metric of activity level and behavior during the breeding season.

The onboard lunge detection algorithm was implemented on the accelerometer 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:

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

The mean Jerk value was continually updated following each selected dive and therefore represented a "grand mean" across all dives. Lunge events during foraging have been associated with a peak followed by a minimum in Jerk (Allen et al. 2016), so we identified lunge events in the 2018 tags as instances when the Jerk value exceeded 3.0 SD above the mean, followed by a value less than 100 percent of the mean within 30 s after the Jerk peak. The algorithm was updated in the 2019 tags to improve event detection, and lunge events were identified as instances when the Jerk value exceeded 1.5 SD above the mean, followed by a value less than 50 percent of the mean within 30 s after the Jerk peak. Lunges for each selected dive were then counted if they occurred more than 30 s from the previous lunge. 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.

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 24th 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 Argos satellites were most likely to be overhead. With such a transmission schedule, the nominal life expectancy of the DM tag's battery was 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 Islands (see **Sections 2.4-2.8** below).

2.3.2 Track Regularization and Behavioral Annotation with State-Space Models

The objective identification of migration phases and analysis of movement speed (see **Section 2.5** 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**) of all tracks $\geq$ 3 d 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 from a set of tracks (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 150,000 iterations, with the first 50,000 iterations being discarded as a burn-in and the remaining iterations being thinned by removing every 20th to reduce autocorrelation, yielding a final 5,000 samples to be used (Jonsen 2016). Included in the model was the classification of locations into two behavioral modes based on move persistence, which is a measure of autocorrelation in both speed and direction of consecutive pairs of locations (Jonsen et al. 2019). In bsam v. 1.1.2 (Jonsen et al. 2017) move persistence is continuously valued from 1 to 2, and we chose values greater than 1.75 to represent low move persistence (i.e., area-restricted searching; ARS) and values lower than 1.25 to represent high move persistence (i.e., transiting), while values in between were considered "uncertain" following Bailey et al. (2009) and Irvine et al. (2014).

For the analysis of historical data from previous tagging efforts in the Hawaiian Islands (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 and 2019 tags. These historical tracks had been already analyzed by OSU using conventional SSSMs (Jonsen et al. 2005) to produce regularized tracks with only one estimated location per day (Bailey et al. 2009, Irvine et al. 2014, Mate et al. 2018a, 2018b), and we did not attempt to re-analyze them for purposes of this report using the more modern hSSSM due to the high computational cost involved.

2.4 Connectivity Between Islands/Areas Within the Hawaiian Islands

To assess connectivity or movement within the Hawaiian Islands we counted the number of islands/areas visited by tagged whales during their tracking period using the edited Argos tracks. Whales were considered to have visited an island/area if any of their locations were located within 5 km of the area. The areas/islands considered were: 1) PMNM, 2) Niihau, 3) Kauai, 4) Oahu, 5) Penguin Bank, 6) Maui Nui, and 7) Hawaii.

2.5 Identification of Migration Phases, Movement Speed and Residence Time in the Hawaiian Islands

In order to objectively identify the different phases of migration from the tracks, we used the behavioral mode annotation associated with each regularized location, as estimated by the state-space models (see **Section 2.3.2**). Examination of the behavioral mode for all tracks (1995-2000, 2015, 2018, 2019) showed that locations in the Hawaii Islands breeding area as well as upon arrival at the high-latitude feeding destinations were primarily classified as ARS (indicative of residence), while locations in between were primarily classified as transiting (indicative of migration) (**Figure 2a**). We determined that all locations had switched from ARS to transiting mode at a distance of 50 km seaward from the coastline in the Hawaiian Islands breeding area, as well as in most feeding areas (see Palacios et al. 2019). Therefore, we used this distance as an empirical criterion to separate the tracks into breeding, migrating, and feeding phases (**Figure 2b**). To further characterize movement behavior, for each migration phase we calculated travel speed between location pairs using package trip v. 1.6.0 (Sumner et al. 2009, Sumner 2011) in R v. 3.6.1 (R Core Team 2019).

The 50-km buffer zone around the Hawaiian Islands included the main Hawaiian Islands and extended into the northwest Hawaiian Islands out to Kure Atoll (**Figure 2**). To avoid discontinuities of the buffer zone where 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 Hawaiian Islands breeding area, interpolated locations were derived from the edited Argos tracks at 10-min intervals between locations, assuming a linear track and a constant speed. We then determined the date and time of the first interpolated location to cross the 50-km buffer for all whales that left the buffer zone, and considered this the time of departure. 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. Arrival at the migratory destination was similarly calculated as the date and time when a track crossed the 50-km buffer boundary at a high-latitude feeding area. Finally, the time spent on migration was estimated as the difference between departure and arrival dates.

2.6 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 the Hawaiian Islands (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 (deg).

Kernel density utilization distributions of Argos locations in the feeding areas 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 southeastern 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 deg given this area's large geographic extent, whereas the cell size used for British Columbia and southeastern Alaska was 0.1 × 0.1 deg.

2.7 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) the Four Island Region Mitigation Area (FIRMA), 2) the Humpback Whale Seasonal Special Reporting Area Oahu North (SSRA-ON), 3) the Humpback Whale Seasonal Special Reporting Area Oahu South (SSRA-OS), 4) the Humpback Whale Seasonal Special Reporting Area Penguin Bank (SSRA-PB), and 5) Barking Sands Tactical Underwater Range and Underwater Range Expansion, combined (BS-Merge). 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 for Kauai and Niihau (Kauai) and Hawaii (Hawaii) are considered in this report. The Oahu-Lanai-Molokai-Maui BIA (Maui) had substantial overlap with the Navy interest areas identified above, so is not reported separately here. The other area of interest considered in this report was the area between the 200-m isobath and the 50-km buffer boundary (see **Section 2.5** Identification of Migration Phases, Movement Speed and Residence Time in the Hawaiian Islands) around the Hawaiian Islands (200 m to 50 km).

Feeding BIAs considered were: 1) spring, summer, and fall Southeast Alaska (SEAK), 2) Bristol Bay (highest densities June through September), 3) Aleutian Islands (Aleutian; highest densities June through September), and 4) 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, BIAs, and other areas of interest, interpolated locations were derived from the edited Argos tracks as described in **Section 2.5** above. 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.

2.8 Calculation of Distance from Shore

The closest point on land was determined for each filtered Argos location within Navy areas 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.

2.9 Cumulative Analyses

After conducting the analyses described above for the tracking data from the 2019 tagging season, all seasons in the Hawaiian Islands (1995 through 2019) were combined and similar analyses were conducted on the cumulative dataset. We present results for the 2019 tagging season followed by the overall, cumulative results.

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 (deployed in 2018; Mate et al. 2019). 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 recorded from the accelerometer data. Tags deployed in the Hawaiian Islands before 2018 were Location-Only (LO) tags (Mate et al. 2019) that did not provide dive information.

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

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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

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).

The percent of the reported tracking period spent in the upper 30 m of the water column (% Near Surface) was calculated for all DM tagged whales to assess possible exposure to vessel interaction (Calambokidis et al. 2019). This was calculated as the sum of all PDIs plus the sum of the duration of all recorded dives with maximum dive depth ≤ 30 m. This number under-represents the amount of time spent near the surface as it does not include any portion of dives deeper than 30 m depth. The calculated value was typically not based on the complete dive records, as it depended on the percent of the tracking period that was summarized. However, the large sample size and temporal coverage of dives received should be reflective of the overall behavior of the tagged whales.

Summary plots showing dive duration versus date and versus time of day were generated for each individual tag and for all tags combined (DM and DUR+) 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 Argos locations (i.e., before and after the start of the dive) to determine where on the line the dive should fall. The estimated dive locations for each whale were then mapped onto a 0.1-deg 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 lunges for all tags (DM and DUR+) and maximum dive depths for all DM-tagged whales.

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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. Whales were documented in the field regularly diving for 20-25 min, so to be conservative, dives > 30-min duration were removed as "anomalous" in this report (n = 65).

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.

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 was 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 an unpublished database of DNA profiles, representing 3,351 individual humpback whales from the North Pacific (D. Steel, personal communication). This "DNA register" represents a shared archival resource held by OSU's Cetacean Conservation and Genomics Laboratory, in collaboration with regional contributors, following the technical standards for DNA profiling used in the Structure of Populations, Levels of Abundance and Status of Humpbacks (SPLASH) program (Baker et al. 2013). This register includes mtDNA haplotypes, sex, and microsatellite genotypes at 10 loci. 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 2019 Maui tagging data set, the 2018 tagging dataset (Mate et al. 2019), 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 for the purpose of 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-ID 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. The best fluke image was one that showed as much of the flukes as possible, with the flukes being closest to a vertical angle and with good focus/sharpness and exposure, and that clearly showed distinguishing marks and serrations along the trailing edge.

Once this process was completed, our photo-IDs were submitted to the online resource "Happywhale" (http://happywhale.com) to determine if the whales we encountered had been seen previously or subsequently. Happywhale is a continually updated global database of photo-IDs contributed by the public and other researchers that provides automated matching using state-of-the-art algorithms and machine learning, which allowed us to know where and when many of our tagged whales have been seen historically as well as after they were tagged. Photo-IDs from this project were submitted and compared to Happywhale up to 9 April 2020. Images in Happywhale have different levels of contributor-specified access and use permissions. OSU is a signatory of a Memorandum of Understanding that gives us the highest level of access to contributed images for the North Pacific Ocean, but that at the same time has a strict data use and sharing policy. Therefore, for purposes of this report, we only provide resighting information and migratory connections determined through matches in Happywhale in general terms that do not identify the specific location or time. Photographs of tagged whales were also provided directly to us by colleagues or naturalists on whale watching vessels who encountered them, and in these cases we include the specific details of the resight.

3 Results

3.1 Tagging Rates

A total of 243 humpback whales were approached during 8 d of tagging efforts off Maui in 2019. Twenty-five tags were deployed, for a tagging rate of 3.1 tags per d.

3.2 Behavioral Responses to Tagging

Ten of the 25 humpback whales tagged off Maui in 2019 exhibited short-term startle responses to the tagging/biopsy process. These responses consisted of mild (five whales) to moderate (three whales) tail flicks, one flinch, and one flinch followed by a quick re-surfacing. 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

Whales will hereafter be referred to by their tag number. Three of 25 humpback whales tagged in 2019 were resighted during the field efforts off Maui. One was seen 2 d after tagging (#825, a male), while the other two (#830, a male, and #847, a male) were both seen 1 d after tagging. Whale #825 had an area of slight swelling surrounding the tag site, approximately 12 cm in diameter and 2 cm in height. The antenna on this tag appeared to be missing. Whale #830 had an area of slight swelling around the tag site, approximately 20 cm in diameter and 2 cm in height. No swelling was seen around the tag site for whale #847.

One whale (#10829, a male), tagged in 2018 off Maui, was resighted during our 2019 field efforts off Maui, exactly one year after it was originally tagged. The tag scar consisted of a shallow divot approximately 15 cm in diameter and 3 cm in depth. No swelling was visible. Skin color in the divot was lighter than that of surrounding skin.

Two whales tagged off Maui in 2018 and one tagged off Maui in 2019 were resighted in Washington State by naturalists on whale watching vessels, who provided photographs that were useful for wound healing assessment. Whale #5685 (a male), tagged in 2018, was seen 581 d after tagging in the Strait of Juan de Fuca. The tag was still attached (but missing its antenna) in a shallow divot approximately 4 cm in diameter and 2 cm in depth, with lighter skin color. Whale #5843 (a male), tagged in 2018, was seen 104 d after tagging also in the Strait of Juan de Fuca. The tag site consisted of a large divot approximately 25 cm in diameter and 10 cm in depth. Finally, whale #1389 (sex unknown), tagged in 2019, was seen 72 d after tagging in the San Juan Islands. The tag site consisted of a small divot approximately 4 cm in diameter and 1 cm in depth. Lighter skin extended around the divot approximately 8 cm in diameter.

One whale (#5655, a male) tagged off Maui in 2018, was seen off Maui by researchers from the Hawaiian Islands Humpback Whale National Marine Sanctuary 670 d after tagging. From the photographs provided, the blade assembly of the tag was still present in a deep divot, approximately 10 cm in diameter and 8 cm in depth.

3.4 2019 Maui Tagging

3.4.1 Tracked Movements

Twenty-five DM tags were deployed on humpback whales off Maui, Hawaii, from 13 to 21 March 2019, between the islands of Maui, Lanai, and Kahoolawe (**Figure 3**). Argos satellite locations were received from all but one of the 25 tags (**Table 1**), and tracking periods ranged from 0.1 to 81.3 d (mean = 21.4 d, SD = 20.2 d, n = 24). Minimum distance traveled averaged 1,978 km (SD = 2,073 km, maximum = 8,062 km, n = 24; **Table 1**). Biopsy samples and fluke photographs were obtained from 21 tagged whales (not necessarily the same 21 whales; see **Table 1**). After an initial presentation of the 2019 results, the results of analyses (including those from humpback tagging dating back to 1995) will be divided into three broad-scale seasonal geographic areas of occupation: breeding areas, migration, and feeding areas.

Locations for humpback whales tagged off Maui in 2019 ranged over 35 deg of latitude, from the south coast of Maui (20.5°N) to the southwest coast of Baranof Island in southeastern Alaska (56.3°N; **Figure 3**). While in Hawaiian waters, the majority of locations were in the Maui Nui region (inner waters between Maui, Molokai, Lanai, and Kahoolawe; **Figure 4**). Penguin Bank was another area heavily frequented by the tagged whales, with 16 humpbacks spending time there. Four whales had locations within the Papahanaumokuakea Marine National Monument (PMNM), with the majority of these located at the eastern edge of the monument near Middle Bank (approximately 125 km northwest of Niihau (**Figure 4**).

A total of 1,537 regularized locations were estimated from the 18 tracks that were modeled with the hSSSM (i.e., raw tracks containing ≥ 3 d of Argos transmissions). Of these, 552 (35.9 percent) were classified as ARS, 284 (18.5 percent) as uncertain, and 701 (45.6 percent) as transiting (**Table 2**). The mean speed of travel between location pairs for these behavioral modes was 1.72 km/h for ARS (median = 1.38 km/h, SD = 1.35 km/h), 2.09 km/h for uncertain (median = 1.56 km/h, SD = 1.64 km/h), and 5.23 km/h for transiting (median = 5.25 km/h, SD = 2.40 km/h) (**Table 2**). The number of regularized locations associated with each phase of migration was 843 (54.8 percent) in the breeding area, 623 (40.5 percent) while migrating, and 71 (4.6 percent) in the feeding area (**Table 2**).

3.4.1.1 Breeding Areas

3.4.1.1.1 Connectivity

Seventeen of the 24 whales (71 percent) tracked in 2019 moved to another island (or to Penguin Bank) during their tracking periods within the Hawaiian Islands (within the 50-km buffer; **Figure 5**). After leaving the Maui Nui region, 94 percent (16 of 17) of those whales traveled to Penguin Bank, 71 percent (12 of 17) were tracked to Oahu, 29 percent (5 of 17) were tracked to Kauai, 24 percent (4 of 17) were tracked to Niihau, and 18 percent (3 of 17) were tracked to PMNM. No whales were tracked southeast to the island of Hawaii. The average number of areas visited by tagged whales while in the Hawaiian Islands breeding area (including the tagging area) was 2.7 (SD = 1.5, range = 1 to 6). The sample size for females was too small (n = 2) to allow for a meaningful statistical comparison of number of areas visited between sexes.

3.4.1.1.2 Movement Speed

While in the Hawaiian Islands breeding area, tagged whales moved at a mean speed of 2.02 km/h (median = 1.58 km/h, SD = 1.52 km/h, n = 843 hSSSM locations; **Table 2**).

3.4.1.1.3 Residency

Residency within the 50-km buffer zone (see Methods **Section 2.6** for details), or the time from tag deployment to departure, ranged from 3.6 to 36.5 d (mean = 14.3 d, SD = 8.8 d, n = 14; **Table 3**). This includes residency for two whales whose tags stopped transmitting shortly after crossing the buffer.

3.4.1.1.4 Kernel Density Utilization Distribution

Thirteen humpback whales tagged in 2019 were tracked for at least 10 d within the 50-km Hawaiian Islands buffer zone. Kernel density utilization distributions computed from the pooled Argos locations of these whales showed highest use in the Maui Nui region, followed by the southwest corner of Penguin Bank (**Figure 6**). The third highest density of locations was found at the eastern edge of PMNM, near Middle Bank (**Figure 6**).

3.4.1.2 Migration

Twelve humpback whales tagged in 2019 began their northbound migration during their tracking periods and three of these whales reached a high-latitude feeding area before their tags stopped transmitting (**Figures 3 and 7**). 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 Molokai (four whales), the north coast of Oahu (five whales), and Middle Bank at the eastern edge of PMNM (two whales). It was unclear whether the departure point for the final whale was Molokai or Oahu, because of a gap in locations just prior to migration. Departure dates, defined as the dates on which whales crossed the 50-km buffer zone around the Hawaiian Islands, ranged from 22 March to 23 April. This includes departure dates for two other whales that crossed the 50-km buffer zone but were not tracked long enough to determine whether they had started migration.

Seven humpback whales followed a northeasterly trajectory toward British Columbia after departing the Hawaiian Islands, with four of them departing from Molokai, two departing from Oahu, and one departing from Middle Bank (**Figure 3**). Two of these whales traveled to Haida Gwaii, reaching the islands on 5 May (whale #843, 29 d after departing the Hawaiian Islands buffer zone near Oahu) and on 27 May (whale #847, 34 d after departing from Middle Bank). A third whale (#1390) traveled to within approximately 100 km west of the northern tip of Vancouver Island before its tag stopped transmitting on 1 May (30 d after departing the Hawaiian Islands buffer zone near Molokai). The remaining four whales with a northeasterly trajectory were not tracked to a feeding area (but appeared to be heading toward British Columbia when their tags stopped), and only partial migratory information is available for them. The approximate distances these whales traveled upon leaving the 50-km Hawaiian Islands buffer zone ranged from 655 to 3,205 km, over periods of time ranging from 6 to 29 d (**Figure 3**).

Three whales departed from the Hawaiian Islands on a north-northeasterly trajectory, with possible destinations in the northern Gulf of Alaska (**Figure 3**). One of these whales (#1387) departed from Oahu and was tracked for 6 d and approximately 610 km after leaving the 50-km Hawaiian Islands buffer zone. Another whale (#2083) departed from Molokai and was tracked for 12 d and approximately 1,760 km. The third whale (#5648) departed from Middle Bank and was tracked for 24 d and approximately 2,615 km (**Figure 3**).

The last two of the migrating whales departed from Oahu and followed a north-northwesterly heading, with possible destinations in the Aleutian Islands (**Figure 3**). Whale #4176 was tracked for 5 d and approximately 880 km after leaving the 50-km Hawaiian Islands buffer zone, and whale #5655 was tracked for 8 d and approximately 1,185 km after leaving the buffer.

While on migration from the Hawaiian Islands to the feeding areas, tagged whales moved at a mean speed of 5.43 km/h (median = 5.42 km/h, SD = 2.41 km/h, n = 623 hSSSM locations; **Table 2**).

3.4.1.3 Feeding Areas

Whale #843 arrived at the west coast of Graham Island (northernmost Haida Gwaii island) and spent 18 d along the west and northwest coast of the island before being last located on the north coast of the island on 23 May (**Figure 7**). Whale #847 arrived at the southwest coast of Moresby Island (southernmost Haida Gwaii island), spending 5 d on the west coast of Haida Gwaii before traveling north to the southwest coast of Baranof Island in southeastern Alaska (**Figure 7**). Whale #847 was tracked for 5 d in this location before its tag stopped transmitting on 7 June.

3.4.1.3.1 Movement Speed

After arrival to the northern British Columbia/southeastern Alaska feeding area, tagged whales moved at a mean speed of 1.78 km/h (median = 1.12 km/h, SD = 1.86 km/h, n = 71 hSSSM locations; **Table 2**).

3.4.1.3.2 Kernel Density Utilization Distributions

Kernel density utilization distributions computed from the pooled Argos locations of the two humpback whales that were tracked within the northern British Columbia feeding area in 2019 showed highest use at the northwest corner of Haida Gwaii, and another concentration of locations off the west coast of Haida Gwaii (**Figure 8**).

3.4.2 Use of Navy Training Areas

All tagging in 2019 took place within FIRMA. All whales spent between 0.1 and 15.3 d within FIRMA, which represented 3 to 100 percent of their total number of locations, and 2.3 to 100 percent of their tracking durations (**Table 4, Figure 9**). Seventy-five percent of humpbacks (18 of 24) spent time in SSRA-PB, spending < 0.1 to 7.1 d there (**Table 4, Figure 10**). This represented 0 to 44.4 percent of total number of locations and < 0.1 to 44.0 percent of total tracking period for these whales. Forty-two percent of whales (10 of 24) spent time in SSRA-ON, from 0.1 to 0.9 d there, representing 0 to 5.3 percent of their total number of locations, and 0.1 to 3.7 percent of their total tracking periods (**Table 4, Figure 10**). Thirty-seven percent of whales (9 of 24) spent time in SSRA-OS, spending < 0.1 to 1.2 d there (**Table 4, Figure 10**). This represented 0 to 4.5 percent of their total number of locations and <0.1 to 3.7 percent of their total tracking periods. Only 21 percent of humpback whales (5 of 24) spent time in BS-Merge, spending from 0.1 to 1.0 d there (**Table 4, Figure 11**). This represented 0.2 to 2.2 percent of the total number of locations for these whales and 0.3 to 4.9 percent of their total tracking periods. A value of zero for percent of total number of locations in any of these areas was the result of one whale's track crossing an area, but no locations occurring there for that animal.

Average distance to shore in Navy areas ranged from 3.2 km (in SSRA-ON) to 20.3 km (in SSRA-PB), with maximums ranging from 4.1 to 33.8 km, in those same areas, respectively (**Table 5**). All humpback whale locations in the Hawaiian Islands training areas occurred during the months of March and April. None of the tagged humpback whales from 2019 were tracked within any Navy training areas along the US West Coast.

3.4.3 Use of Hawaii BIAs and Other Areas

Six humpback whales tagged in 2019 (25 percent) spent time in the Kauai BIA, spending 0.2 to 1.8 d there (**Table 6, Figure 12**). This represented 0.4 to 10.4 percent of their total number of locations and 0.2 to 8.7 percent of their total tracking periods. Humpback locations occurred in the Kauai BIA during March and April. One whale tagged in 2019 was also tracked within the SEAK BIA, spending 0.2 d there during June (**Table 6, Figure 13**). This represented 0.7 percent of this whale's total number of locations and 0.3 percent of its total tracking period. None of the humpback whales tagged off Maui in 2019 had locations in the Hawaii, Aleutians, Shumagin, or Bristol Bay BIAs.

Eighty-three percent of humpbacks tagged in 2019 (20 of 24) spent time in the 200 m to 50 km area around the Hawaiian Islands, for 0.1 to 12.0 d (**Table 6**). This represented 1.2 to 60.0 percent of the total number of locations for these whales and 1.8 to 52.4 percent of their total tracking periods.

3.5 Cumulative Analyses

A total of 101 humpback whales were tagged by OSU in the Hawaiian Islands prior to 2019 (covering the period 1995 to 2000, 2015, and 2018), providing tracking data for 81 whales (the remaining tags provided no locations). Tracking periods for all whales tagged from 1995 through 2019 ranged from 0.04 to 159.9 d (mean = 24.6 d, SD = 31.8 d, n = 105). Tags deployed in 1995 (in Kauai) and 1996 (in Hawaii) were externally mounted (with two bladed attachment posts; Mate et al. 1998) (*cf*. "type A" or "anchored type"; *sensu* Andrews et al. 2019), rather than fully 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 between the two types of attachments (ANOVA of log-transformed tracking period, p-value = 0.03), with external tags lasting an average of 6.2 d (SD = 5.4 d, n = 9) and fully implanted tags lasting an average of 26.3 d (SD = 32.7 d, n = 96). When only fully implanted tags were considered, tracking periods were not significantly different between males and females (ANOVA, p-value = 0.44). Median tracking periods for fully implanted tags were significantly different between whales that were only tracked within the 50-km buffer around the Hawaiian Islands (median = 7.7 d, maximum = 44.4 d, n = 60) and those that traveled beyond the buffer (median = 38.2 d, maximum = 160.0 d, n = 36; Kruskal-Wallis p-value < 0.0001).

There was a positive relationship between tracking period and total distance traveled by individual humpback whales with implanted tags (linear regression using log-transformed variables, p-value <

0.0001). After accounting for this relationship, distance traveled was not significantly different between males and females (general linear model of log-transformed variables, *p*-value = 0.88), but was significantly different between whales that were only tracked within the 50-km buffer around the Hawaiian Islands (mean = 474 km, SD = 445 km, n = 60) and those that traveled beyond the buffer (mean = 4,027 km, SD = 2,772 km, n = 36; general linear model of log-transformed variables, *p*-value <0.001).

The overall range for all humpback whales tagged from 1995 to 2019 extended over 45 deg of latitude and 74 deg of longitude, from south of the island of Hawaii to the Gulf of Anadyr, Russia, in the Bering Sea, and from Queen Charlotte Sound, British Columbia, Canada, to the Kamchatka Peninsula, Russia (**Figure 14**). Within the 50-km buffer around the Hawaiian Islands, humpback whale locations extended over 4 deg of latitude and 8 deg of longitude, from south and east of the island of Hawaii to west of Nihoa Island in the northwestern Hawaiian Islands (**Figure 15**).

A total of 4,285 regularized locations were estimated from the 86 tracks that were modeled with the SSSM/hSSSM (i.e., raw tracks containing ≥ 3 d of Argos transmissions; range = 3-176 d). Of these, 1,690 (39.4 percent) were classified as ARS, 943 (22.0 percent) as uncertain, and 1,604 (37.4 percent) as transiting (**Table 7, Figure 2a**). The mean speed of travel between location pairs for these behavioral modes was 1.35 km/h for ARS (median = 1.01 km/h, SD = 1.27 km/h), 1.67 km/h for uncertain (median = 1.19 km/h, SD = 1.51 km/h), and 4.81 km/h for transiting (median = 4.74 km/h, SD = 2.19 km/h) (**Table 7, Figure 16a**). Although transiting behavior was recorded both inside and outside the buffer zones, it was the predominant behavioral mode while on migration (**Figure 16b**). The number of regularized locations associated with each phase of migration was 2,159 (50.4 percent) in the breeding area, 1,598 (37.3 percent) while migrating, and 528 (12.3 percent) in the feeding areas (**Table 7, Figures 2b and 16b**).

3.5.1.1 Breeding Areas

3.5.1.1.1 Connectivity

Sixty-six (63 percent) of the 105 humpback whales tracked in the Hawaiian Islands from 1995 to 2019 moved to another island (or to Penguin Bank) during their tracking periods within the Hawaiian Islands (within the 50-km buffer; **Table 8, Figure 17**). As with whales tagged only in 2019, the predominant direction of this travel was to the northwest (**Figures 17 and 18**), with animals leaving the Maui Nui area and heading to Penguin Bank, Oahu, and beyond. Sixty-five percent (62 of 96) of the whales tagged in the Maui Nui area were tracked to other areas, with 90 percent (56 of 62) going to Penguin Bank and 40 percent (27 of 62) going to Oahu. Fewer than 20 percent of the whales tagged in the Maui Nui area visited Kauai, Niihau, Hawaii, or PMNM. Seventy-five percent of the whales tracked from the island of Hawaii (three of four) traveled to other areas, with all three of them moving to the Maui Nui region. Only one (whale #10826, tagged in 1995) of the five whales tracked from Kauai (20 percent) visited other areas within the Hawaiian Islands, traveling southeast to Oahu, Penguin Bank, and Maui Nui during its tracking period, as previously documented in Mate et al. (1998). The average number of areas visited in the Hawaiian Islands by whales tracked from 1995 to 2019 (including the tagging area) was 2.0 (SD = 1.1, range = 1 to 6). Females with a calf (tagged off Maui) visited slightly fewer areas (mean = 1.3 areas, SD = 0.96 areas, n = 7) than males (mean = 2.1 areas, SD = 0.96 areas, n = 55), but after accounting for the positive relationship between number of days in the Hawaiian Islands and number of areas visited (general linear model *p*-value < 0.001), this difference was not significant (general linear model *p*-value = 0.12). There was no difference in number of areas visited between females without a calf and either males or females with a calf. Whales tagged off Kauai (n = 5) and Hawaii (n = 4) were not included in the latter analysis due to lack of sex information for these whales.

3.5.1.1.2 Movement Speed

While in the Hawaiian Islands breeding area, tagged whales moved at a mean speed of 1.62 km/h (median = 1.20 km/h, SD = 1.38 km/h, n = 2,159 SSSM/hSSSM locations; **Table 7**).

3.5.1.1.3 Residency

The tracks of 39 humpback whales tagged in the Hawaiian Islands from 1995 to 2019 crossed the 50-km buffer as they departed on migration (including two whales whose tags stopped transmitting shortly after crossing the buffer). The 39 whales consisted of 17 males, 5 females, and 17 whales of unknown sex (**Table 3**). Departure dates for these whales were as early as 20 December (for whale #4177, of unknown sex tagged off Maui in December 1999) and as late as 3 May (for whale #828, a female with a calf tagged off Maui in April 1997). The residence time inside the 50-km buffer for these 39 whales ranged from 1.1 to 42.8 d (mean = 13.1 d, SD = 9.4 d; **Table 3**).

Mean residence time in the Hawaiian Islands from tagging to departure was slightly lower for mothers with calves (mean = 10.4 d, SD = 10.7 d, n = 3) than for females without calves (mean = 11.3 d, SD = 10.9 d, n = 2), which in turn was lower than the residence time for males (mean = 15.9 d, SD = 10.4 d, n = 17), but sample sizes were too small for a meaningful statistical comparison.

3.5.1.1.4 Kernel Density Utilization Distributions

When all humpback whales tagged in the Hawaiian Islands from 1995 to 2019 were combined, a total of 52 whales spent at least 10 d in the 50-km Hawaiian Islands buffer zone. The results of kernel density estimation of the pooled locations for these whales were very similar to the results from the 2019 locations alone, with the exception of locations extending to the island of Hawaii where tagging took place in 1996. The areas of highest use were at the southwest tip of Penguin Bank and within the Maui Nui region (**Figure 19**). The area of next highest density of locations was near Middle Bank at the eastern edge of the PNMN (**Figure 19**).

3.5.1.2 Migration

When all humpback whales tagged in the Hawaiian Islands from 1995 to 2019 were combined, a total of 37 began their northbound migration and 12 of these whales reached a high-latitude feeding area during their tracking periods (**Table 3, Figure 14**). Departure dates ranged from 20 December (for a whale of unknown sex tagged on 11 December 1999) to 3 May (for a female with a calf tagged on 9 April 1997). Departure points for these whales ranged throughout the islands; 14 from Oahu, seven from Molokai, four from Kauai, three from Middle Bank, northwest of Kauai, two from Maui, and one from Niihau. Migratory departure points were unknown for six other whales, due to gaps in tracking information.

Of the 12 whales that were tracked to a feeding area, seven were tracked to northern British Columbia/southeastern Alaska, one was tracked to southern British Columbia, and four were tracked to the eastern Aleutian Islands (**Figure 14**). 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. Migration duration ranged from 28.0 to 44.8 d (mean = 34.2 d, SD = 5.5 d, n = 10; **Table 2**). Migration duration could not be calculated for two whales that traveled to southeastern Alaska for which no locations were obtained during migration.

Partial migrations were tracked for 25 whales, of which 22 presumed destinations could be identified based on the whale's trajectory (**Figure 14**). Of these, eight whales were on a trajectory toward the eastern Aleutian Islands, six were headed toward northern British Columbia/southeastern Alaska, five were headed toward the Gulf of Alaska, and three were headed toward Southern British Columbia/Northern Washington. Too few locations were received during the partial migration of the remaining two whales to determine a trajectory.

While on migration from the Hawaiian Islands to the feeding areas, tagged whales moved at a mean speed of 4.65 km/h (median = 4.61 km/h, SD = 2.39 km/h, n = 1,598 SSSM/hSSSM locations; **Table 7**). Travel speeds during the migration phase for the 10 tracks that lasted until arrival at the feeding areas and that reported locations during migration were not sustained but showed variation over time, including both high-frequency oscillations as well as periods of increased and decreased speed lasting several days (**Figure 20**). There was also some individual variation, with some whales migrating at slower speeds (e.g., mean = 2.08 km/h for whale #10828 from 1999; mean = 3.93 km/h for whale #5784 from 2018) and others at consistently faster speeds (e.g., mean = 5.73 km/h for whale #10826 from 1998; mean = 5.59 km/h for whale #4172 from 2018) (**Figure 20**).

3.5.1.3 Feeding Areas

3.5.1.3.1 Movement Speed

After arrival to the feeding areas, tagged whales moved at a mean speed of 1.42 km/h (median = 0.85 km/h, SD = 1.55 km/h, n = 528 SSSM/hSSSM locations; **Table 7**).

3.5.1.3.2 Kernel Density Utilization Distributions

When the 2019 whales were combined with humpback whales tagged in the Hawaiian Islands from 1995 to 2018, a total of seven whales were tracked within the northern British Columbia/southeastern Alaska feeding area (**Figure 21**). The results of kernel density estimation of the pooled locations for these whales were similar to the results from the 2019 locations alone, with the area of highest density of locations at the northwest corner of Haida Gwaii, British Columbia (**Figure 22**). The area of next highest density was at the southern tip of Kuiu Island, Alaska (**Figure 22**), at the southern end of Chatham Strait.

Kernel density utilization distributions for the four whales tracked to the Aleutian Islands prior to 2019 showed areas of use along the southern side of the Aleutian Island chain stretching from Unimak Pass to the Kamchatka Peninsula and up into the northwestern Bering Sea to the Gulf of Anadyr, Russia. The area of highest density was approximately 160 km south of Akutan Island and Unimak Pass in the eastern Aleutians (**Figure 23**), followed by a much smaller density of locations in Bowers Basin, Bering Sea (from one whale tagged in 2018), approximately 175 km northeast of Attu Island.

3.5.2 Use of Navy Training Areas

All humpback whale tagging off Maui from 1997 to 2019 took place within FIRMA, and as such, 100 percent of the tracked whales from Maui had locations there (**Table 9, Figure 24**). Twenty percent of the whales tracked from Kauai (one of five) and 75 percent of the whales tracked from Hawaii (three of four) also had locations within FIRMA (**Table 9**). For all whales, mean number of days spent in FIRMA was 2.4 d, with a maximum residency of 23.1 d, for a whale tagged off Maui (**Table 9**). Area SSRA-PB was the next most heavily used Navy area for humpback whales, with 66 percent of tracked whales (69 of 105) having locations there (**Table 9, Figure 25**). Number of days spent in SSRA-PB averaged 1.6 d, with a maximum residency of 23.8 d. Twenty-five percent of tracked whales (26 of 105) had locations within SSRA-OS, with a mean of 0.2 d spent there (maximum residency of 1.3 d; **Table 9, Figure 25**). Twenty-three percent of tracked whales (24 of 105) had locations within SSRA-ON, for a mean number of days of 1.0 d and maximum residency of 1.5 d (**Table 9, Figure 25**). Area BS-Merge saw the least use by humpback whales, with 11 percent of tracked whales (12 of 105) having locations there. Number of days spent in BS-Merge averaged 0.7 d, with a maximum residency of 1.4 d (**Table 9, Figure 26**). Sample sizes were not large enough to permit meaningful statistical comparisons of residency in Navy areas between whales tagged at different islands. None of the humpback whales tagged in the Hawaiian Islands from 1995 to 2019 were tracked within any Navy training areas along the US West Coast or in the Gulf of Alaska.

Humpback whale locations occurred in Hawaiian Islands Navy training areas during winter and spring for whales tagged in all years (**Figure 27**). Humpback locations occurred during five months in FIRMA and SSRA-PB (December through April), during four months in SSRA-ON (January through April), and during three months in both SSRA-OS and BS-Merge (February through April).

Overall, mean distance to shore in Navy areas ranged from a low of 3.3 km (in SSRA-ON) to a high of 29.8 km (in BS-Merge; **Table 10**). Maximum distances to shore in Navy areas ranged from 6.8 (in SSRA-ON) to 72.1 (in BS-Merge). The whales with the greatest distances to shore in Navy areas were those individuals that were migrating north to feeding areas. Sample sizes in Navy areas were not large enough to permit meaningful statistical comparisons between whales tagged at different islands.

3.5.3 Use of BIAs

Of the BIAs in the Hawaiian Islands that did not overlap with Navy areas, the Kauai BIA was the most heavily used by humpback whales tagged from 1995 to 2019, with 14 percent of tracked whales (15 of 105, five of which were tagged there) having locations there (**Table 11, Figure 28**). Average time spent in the Kauai BIA was 0.9 d, with a maximum of 3.5 d. Six percent of tracked whales (six of 105, four of which were tagged there) had locations in the Hawaii BIA (**Table 11, Figure 29**). The average number of days spent in the Hawaii BIA was 2.3 d, with a maximum residency of 6.2 d. Four percent of tracked whales (four of 105) had locations in the SEAK BIA, spending an average of 27.8 d there (maximum 70.0 d; **Table 11, Figure 30**). Two percent of tracked whales (two of 105) had locations in the Aleutians BIA, averaging 0.6 d there (maximum 1.0 d, **Table 11, Figure 30**). No humpback whales tagged in the Hawaiian Islands had locations in the Bristol Bay or Shumagin BIAs. Ninety-one percent of tracked whales (96 of 105) had locations in the 200 m to 50 km region around the Hawaiian Islands, for an average of 2.8 d (maximum 30.2 d; **Table 11**).

Locations of humpback whales tagged in the Hawaiian Islands from 1995 to 2019 were found within the Kauai BIA during three months (February through April) and within the Hawaii BIA during two months (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). Locations within the 200 m to 50 km region occurred during six months (December through May).

3.5.4 Dive Behavior

Dive behavior of whales tagged in 2019 was similar to those tagged in 2018 so cumulative results across both years are presented unless otherwise specified (as stated in Methods **Section 2.10**, tags deployed prior to 2018 did not record dive information). Whales in this section are referred to by their tagging year and tag number. Of the 46 tagged whales that provided dive data in 2018 and 2019, 35 were males, six were females, and five were of unknown sex (**Table 12**). Four tags failed to transmit any dive data and one was not successfully deployed. Tags provided a mean of 1,839 dive summaries (range = 15 to 13,983; **Table 12**) and the number of dives reported summarized a mean of 62.0 percent of the tracking duration (range = 28.4 to 100.0 percent). Lunges were more numerous during 2019, likely due to the modified lunge detection algorithm (see **Section 2.2.1**), so direct comparisons of the number of lunges recorded were not made across years.

3.5.4.1 Breeding Areas

DM-tagged whales in the breeding areas generally dove to depths of less than 100 m. However, over half of the DM-tagged whales (25 of 46) made occasional dives exceeding 200 m and nine dove to depths > 300 m (**Figure 31)**. Whale #2019_831 recorded numerous deep dives including 81 at the maximum possible depth recorded by the tag (511 m). At least some of these dives were likely due to a failure of the tag as the deepest dives occurred in areas like Penguin Bank, where the dives would have exceeded the reported water depth. However, dive durations did not appear to be affected. Thus dives > 500 m were removed from the data record (n = 85) and other deep dives recorded by that tag should be treated with caution. Tags summarized a mean of 61.6 percent of the tracking period, and a mean of 64.1 percent of the recorded dive behavior occurred in the upper 30 m of the water column **(Table 13).** Dive durations during both years were highly variable across individuals, generally ranging from 3 to 15 min in duration with occasional dives lasting over 30 min (n = 68). Due to the limited number of very long duration dives, duration figures were truncated at 30 min to better visualize dominant trends (**Figure 32**). Dive depths, durations, and lunges were generally similar across all hours of the day, although dives were slightly deeper during daylight hours **(Figures 33 and 34).** Spatial distribution of dive depths and lunges was relatively uniform across the areas used **(Figure 35)** and there were no discernable temporal patterns in dive depth or duration either within or across individuals**.** Dives were of three general types: short-duration (< 15 min) dives to depths < 100 m, long-duration (> 15 min) dives to depths < 50 m, and dives > 100 m depth **(Figure 36).** Lunging activity was concentrated in short-duration dives and dives > 100 m depth. Four tagged whales were tracked to Middle Bank at the east end of the PMNM. Dive behavior from these whales while in the area of Middle Bank was similar to other parts of the breeding area; however, it suggests the whales spent the majority of time over the bank as their dive depth was limited to ~60 m **(Figure 37).**

Dive behavior was generally similar between male and female tagged whales although the substantially smaller number of female whales tracked means inferences should be made with caution **(Figure 38).** Dive durations of female whales spanned almost the entire range of dive durations made by other tagged whales and the spatial distribution of dive behavior was also very similar despite the more limited number of dives recorded (data not shown).

3.5.4.2 Migration

Whales #2019_827 and #2019_834 were not included in migration analysis due to a limited number of locations outside the 50-km buffer and uncertainty as to whether they had begun migration.

Overall dive behavior of the 18 whales tracked during migration was similar to behavior in the breeding areas. Dive depths were typically less than 100 m and fell into the three categories of: dives < 100 m depth, long-duration dives < 50 m, and dives > 100 m depth (**Figure 39**). Dives made by female whales were generally deeper, but shorter in duration compared to male whales **(Figure 39)**. Unlike in the breeding areas, there was a noticeable diel trend with deeper, longer duration dives occurring at night than during the day (**Figure 40**). This trend was driven by dives occurring during the first two weeks of migration with dives subsequently returning to more typical ranges of depths < 100 m and durations < 10 min with no strong diel pattern **(Figure 41).**

Lunges were recorded by all but one whale tracked during migration (no lunges for whale #2018_5736) but the number was highly variable across individuals within each year, with some whales making five to 10 times more lunges than others **(Table 14)**. Lunges occurred during extended periods (5 to 7 d) of the migration while the whales made limited, or no deviation in heading. Lunges occurred across all dive types, although they were less frequent during long-duration shallow dives and there was no apparent variation between sexes **(Figure 39).**

3.5.4.3 Feeding Areas

Six tags functioned long enough to track whales to their migratory destination (four from 2018 and two from 2019). Five whales traveled to the area near Haida Gwaii, while the other (whale #2018_5736, a male) traveled to the Aleutian Islands, west to near the Kamchatka Peninsula, and then north into the Bering Sea. One of the two tags (whale #2019_843) that reached Haida Gwaii in 2019 suffered a tag malfunction and reported numerous suspiciously deep dives (> 300 m) over short time periods (< 3 min) after an 11.8-d gap in transmissions. Thus, dive depths from this tag were not included in this analysis.

Dive depths of tagged whales near Haida Gwaii were generally very shallow, with the majority to depths < 50 m (**Figure 42**), and tagged whales spent a median of 77.0 percent of their time at depths < 30 m (**Table 15**). Most dives were recorded near the northwest part of Haida Gwaii but there was little spatial variability in dive behavior **(Figure 43**). However, dive behavior of whale #2019_847 was noticeably different from other whales tracked near Haida Gwaii. Whale #2019_847 made deeper and longer-duration dives compared to other tagged whales in the area and also showed a diel trend in dive behavior with deeper, longer dives occurring at night **(Figure 44)**. All whales arrived from migration in a similar part of southern Haida Gwaii; however, whale #2019_847 progressed northwest to waters off southeastern Alaska, while other whales remained near Haida Gwaii (**Figure 44**). While dive depths for whale #2019_843 were unreliable, dive durations appeared to be unaffected and were more similar to durations from 2018 tracks compared to those of whale 2019_847.

Whale # 2018_5736 made deeper, longer-duration dives during the day, with more lunge events compared to tagged whales near Haida Gwaii (**Figures 42 and 45**). 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 46 and 47**). 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. Lunges during dives made by tagged whales near Haida Gwaii and whale # 2018_5736 were concentrated during deeper dives (**Figures 48 and 49**).

3.5.5 Genetics

Biopsy samples were collected from 21 of the 25 tagged whales and one untagged whale in 2019 and all samples provided DNA profiles sufficient for subsequent analyses. The mtDNA sequences of the 22 samples resolved seven haplotypes for the consensus region of 500 bp (**Table 16**). 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 16**).

The 22 samples were represented by a unique multi-locus genotype of at least 11 loci with an average of 14.32 loci across the dataset. The probability of identity for any given set of 11 loci ranged from PID = 3.6× 10-9 to 3.3 × 10-12, providing confidence that the 22 unique multi-locus genotypes represent 22 individual whales. These 22 individuals included two females and 20 males. The DNA profiles of the 22 individuals were compared to the 23 individuals (three females and 20 males) sampled during the 2018 tagging effort and to an unpublished database of DNA profiles, representing 3,351 individual humpback whales from the North Pacific (D. Steel, personal communication). This "DNA register" represents a shared archival resource held by the OSU's Cetacean Conservation and Genomics Laboratory, in collaboration with regional contributors, following the technical standards for DNA profiling used in the SPLASH program (Baker et al. 2013). Three recaptures of whales tagged in 2019 were detected. The first (biopsy sample Mno19HI007, whale #838, a male), was matched by genotyping to an individual sampled in the Hawaiian Islands on 4 March 2004 (SPLASH ID 430211). This sample was linked through photo-ID from the SPLASH project to a previous sighting in the Hawaiian Islands on 11 February 2004 and to three sightings in southeast Alaska on the 17 July, 21 July, and 2 August 2004. The second (biopsy sample Mno19HI021, whale #5648, a male) was matched by genotyping to an individual sampled in the northern Gulf of Alaska on 4 June 2004 (SPLASH ID 472569). This sample was linked through photo-ID from the SPLASH project to a resighting the following year (19 July 2005), also in the northern Gulf of Alaska. Although the tag on this individual stopped transmitting before it reached its feeding area, the trajectory suggested it could be returning to the northern Gulf of Alaska region (**Figure 2**). The third (biopsy sample Mno19HI018, whale #2083, a female), was matched by genotyping to an individual sampled in Prince William Sound, northern Gulf of Alaska, on 3 March 2009 (biopsy sample Mno09PWS013), and photographically matched to Prince William Sound on 24 and 28 January 2008 (photo-IDs GWAK-P177 and NMFS-JRM-20080124-1-057). A fourth genotype match was found between a whale tagged by OSU off Maui in 1999 and an individual sampled in southeastern Alaska (biopsy Mno19SEA037) on 16 June 2019. The third and fourth whales were matched to samples in the DNA register provided by Janice M. Straley (University of Alaska Southeast Sitka), who was notified of these matches.

The DNA profiles of the 23 individual humpback whales tagged during the 2018 field effort were also compared to the SPLASH database, and as reported in Mate et al. (2019), two recaptures were detected. The first of these (biopsy sample Mno18HI007, whale #5641, a male), was matched by genotyping to an individual sampled in the Hawaiian Islands on 22 April 2004 (SPLASH ID 430296). The sample was linked through photo-ID from the SPLASH project to a resighting 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 2019 Maui tagging samples did not differ from the mtDNA frequencies of the 2018 Maui tagging samples or from the samples collected from the Hawaiian Islands during SPLASH. However, they did differ significantly in pairwise comparisons with the other seven SPLASH breeding areas described in Baker et al. (2013) (**Figure 50a** and **Table 17**). The Maui tagging samples also differed significantly from seven of the 10 SPLASH feeding areas described in Baker et al. (2013). The haplotype frequencies of the tagging samples were not significantly different from the northern Gulf of Alaska, southeastern Alaska, and northern British Columbia (**Table 17**).

The mtDNA haplotype frequencies of the 2018 Maui tagging samples differed significantly in pairwise comparisons with each of the SPLASH breeding areas described in Baker et al. (2013), except Hawaii. The 2018 Maui 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 (**Table 17**).

The distribution of mtDNA haplotypes in the feeding areas in SPLASH was also reflected in the migratory destinations of the tagged whales (**Figure 51**). The two haplotypes of the three individuals from 2019 migrating towards southeastern Alaska or northern British Columbia (whales #843, 847, and 1385) were consistent with the haplotypes common to those regions ("A-"and "A+"). The three haplotypes of the five individuals from 2018 migrating towards southeastern Alaska or northern British Columbia (whales #4172, 5784, and 5800) were also consistent with the haplotypes common to those regions ("A-", "A+" and "E2"). The haplotype of the one individual from 2018 migrating to the Aleutian Islands and continuing on to Russia (whale #5736) was consistent with a haplotype common to that region ("E1").

3.5.6 Photo-Identification

A total of 25,708 photographs were taken of humpback whales off Maui during the 2018 and 2019 field seasons. From these photographs, 194 unique individuals were identified and added to our Hawaiian Islands humpback whale photo-ID catalog. Five of these 194 individuals were photographed in both years, including one that was tagged in 2018 (#10829, a male). Of the 50 tagged whales (25 in both 2018 and 2019), 36 had fluke photos that could be used for ID purposes. We also obtained a fluke photo of one whale in 2019 that was biopsied and not tagged. Out of the 36 tagged whales, 26 have been identified in the Happywhale photo-ID database as of 9 April 2020. Thirteen of these were identified in the Hawaiian Islands before tagging, three were identified in the Hawaiian Islands after tagging, and eight were seen in the Hawaiian Islands both before and after tagging. Four of the whales seen in the Hawaiian Islands were also seen in feeding areas: one sighted in southeastern Alaska both before and after tagging; one sighted off Washington State and Vancouver Island before and after tagging; one sighted in Kachemak Bay and Prince William Sound in the northern Gulf of Alaska before tagging; and one sighted in the Shumagin Islands, western Gulf of Alaska, after tagging. Two other whales were only sighted outside of the Hawaiian Islands: one after tagging in Washington and southern British Columbia, and one before tagging in Baja California, Mexico. The whale in 2019 that was biopsy-sampled only had been seen in the Hawaiian Islands before tagging and in southeastern Alaska after tagging. The Hawaiian Islands resights included 18 among-year resights and seven within-year resights.

Of the remaining 157 identified whales (untagged or unbiopsied), 93 had matches to whales in Happywhale. Of these matches, 60 were seen only in the Hawaiian Islands, nine were only seen outside of the Hawaiian Islands, and 24 were seen both in the Hawaiian Islands and elsewhere. The Hawaiian Islands resights included 71 among-year resights and 13 within-year resights. For the 33 whales seen outside of the Hawaiian Islands, matches included: five in Russia (two in the Chukchi Sea, one in the Commander Islands, one in the Gulf of Anadyr and the Chukchi Sea, and one in the northwestern Bering Sea); two in the eastern Aleutian Islands (north of Unalaska Island); two in the western Gulf of Alaska (Shumagin Islands); one in the western Gulf of Alaska (Shumagin Islands) and the northern Gulf of Alaska (Kodiak Island); seven in the northern Gulf of Alaska (Kachemak Bay, Prince William Sound, Kodiak Island); six in southeastern Alaska (Glacier Bay and Frederick Sound); three in northern British Columbia; one in both northern British Columbia and Washington; three in Washington; one in both Washington and mainland Mexico; and two in Oregon. The two whales seen in Oregon were sighted by OSU during our 2017 field season.

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 2019, as well as a cumulative analysis including results from humpback whales tagged by OSU in the Hawaiian Islands in prior years (1995-2000, 2015, 2018). 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, speeds, 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 and 2019 allowed for a characterization of diving behavior, with a comparison between breeding and feeding areas and during migration. The biopsy samples collected provided genetic 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 fully implantable tags on humpback whales in this study (mean = 26.3, n = 96) was quite a bit shorter than tracking periods for similar tags deployed by OSU on blue (mean = 73.4 d, n = 82) and fin whales (mean = 55.4 d, n = 25) (Mate et al. 2018). 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, or 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 in their breeding areas. 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 in their breeding areas. 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 fully implantable tags deployed by OSU on humpback whales in their feeding areas, 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 (behavioral or otherwise) rather than the proposed behavioral or tissue composition differences between breeding and feeding seasons.

4.1.1 Breeding Area

The tracking results within the Hawaiian Islands 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.

After Maui Nui and Penguin Bank, the next area of highest density for tagged humpback whales was near Middle Bank, a seamount on the eastern boundary of PMNM, in the northwestern Hawaiian Islands. Most of this was driven by locations of whales tagged in 2019; only one whale tagged previously off Maui (in 2000) was tracked within PMNM. Acoustic detections (Lammers et al. 2011) and habitat modeling (Johnston et al. 2007) suggest that PMNM may represent an extension of humpback whale wintering habitat (Baird et al. 2015). Henderson et al. (2018) reported four of seven humpback whales tagged off Kauai in March 2017 traveling to Middle Bank, with one also continuing northwest to the island of Nihoa. Four of the 25 humpbacks tagged off Maui in this study (in 2019) had locations within

PMNM, ranging from Middle Bank to approximately 70 km northwest of Nihoa, with residency ranging up to four days in the monument itself and up to eight days around Middle Bank, suggesting that this area could represent important wintering habitat for humpback whales as their population in the Hawaiian Islands grows. Humpback whales have been documented spending time at shallow seamounts in the western South Pacific during the breeding season, perhaps for purposes related to breeding activities, resting, navigation, or supplemental feeding (Garrigue et al. 2015, Derville et al. 2020).

4.1.1.1 Connectivity

While the predominant direction of travel within the islands was to the northwest for whales tagged off Maui and Hawaii, our sample size for Kauai (n = 5) was too small (and zero for other islands) to adequately address directionality more comprehensively. However, we note that two whales tagged off Kauai in 1995 followed the opposite pattern, with one traveling to Oahu and the other traveling to Oahu, Penguin Bank, and the Maui Nui area during their tracking periods (Mate et al. 1998). Henderson et al. (2019) also reported southeastward movement from Kauai to Oahu for one of six humpback whales tagged off Kauai in 2018. Migration departure occurred from most islands (except Kahoolawe, Lanai, and Hawaii) and Middle Bank. 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 (14 of 26 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.

4.1.1.2 Residency

Since we cannot know a whale's initial arrival time in the Hawaiian Islands prior to tagging, we expect our satellite-telemetry-derived residence times from tagging to departure (mean = 13.1 d, SD = 9.4 d, n = 39) to represent the minimum. Our results are almost identical to those for humpback whales tagged at the Socorro Island breeding area off Mexico (mean = 13.6 d, SD = 9.3 d, n = 8; Lagerquist et al. 2008). Photo-ID studies have concluded that there is a rapid turnover of individuals within the same Hawaiian island throughout the winter breeding season, with an overall within-island residency estimated at two weeks or less (Craig et al. 2001). Craig et al. (2001) reported that the average inter-island residency was 36.2 d, however. It is reasonable to assume that at the time of tagging some whales had just arrived in the Hawaiian Islands 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, the overall true residence time is likely longer than the satellite-telemetry-based mean minimum value we report. OSU recently documented for the first time the complete residency from arrival to departure in a breeding area at 14 d for a female whale tagged in a feeding area at the Strait of Juan de Fuca, Washington, that undertook a round-trip migration to the Mexican breeding area during winter (Mate et al. 2020).

For whales identified in Maui, Craig et al. (2001) found significant differences in within-island residency between age and sex classes, with residence time being shorter for females without a calf than for males or adults of unknown sex. While limited by sample size, our sex-specific results also support this notion (mean minimum residence: 11.3 d for females without a calf and 15.9 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. Females with a calf in our study had the shortest minimum residence times, with a mean of 10.4 d. However, one potential source of bias in our residence time estimates is that we only considered females with older calves as candidates for tagging, so residence time for this reproductive class may be biased downward, as females with older calves would be closer to departure than females with neonate calves.

4.1.2 Migration

The migratory destinations of humpbacks tagged in the Hawaiian Islands support previous telemetry, genetic, and photo-ID studies, which show the majority of humpbacks wintering in the Hawaiian Islands traveling to feeding areas in northern British Columbia and southeastern Alaska, with fewer numbers going to the Gulf of Alaska, the Aleutian Islands and Bering Sea, and fewer numbers still going to northern Washington/southern British Columbia (Mate et al. 2007, Baird et al. 2015, Calambokidis et al. 2008, Wade et al. 2016). Of the 12 tagged whales that were tracked to a feeding area (1995 to 2019 combined; two of which had large gaps in coverage *en route*), the majority migrated to northern British Columbia/southeastern Alaska (seven whales), followed by the Aleutian Islands and Bering Sea (four whales), and southern British Columbia (one whale). The presumed destinations of an additional 22 humpback whales that were tracked during partial migrations showed different tendencies than those just mentioned, with the majority projected to arrive in the Aleutian Islands (eight whales), followed by northern British Columbia/southeastern Alaska (six whales), the Gulf of Alaska (five whales), and finally northern Washington/southern British Columbia (three whales). Mate et al. (2007), however, documented that initial migratory heading is not necessarily an indication of final destination, showing one whale tagged off Maui in 1999 (#10828, of unknown sex) heading initially toward British Columbia but ending up in the Aleutian Islands.

4.1.3 Feeding Areas

In northern British Columbia/southeastern Alaska, the area of highest use identified through the kernel density utilization distributions was located at the northwest corner of Haida Gwaii, British Columbia, followed by the southern tip of Kuiu Island, Alaska, at the southern end of Chatham Strait. Humpback occurrence in northern British Columbia and southeastern Alaska included locations from the same individuals (one whale tagged in 1998, one in 2018, and one in 2019). These connections are reinforced by the lack of significant genetic differentiation between humpback whales in northern British Columbia and southeastern Alaska (Baker et al. 2013) and support the treatment of northern British Columbia and southeastern 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 (Calambokidis et al. 2008), a lack of genetic differentiation (Baker et al. 2013), and the proximity of the areas. The track of a whale tagged in 2018 supports this connection and details extensive long-range movements throughout the entire Aleutian Island chain (also demonstrated by a whale tagged in 1997) and much of the Bering Sea. All of the Aleutian locations of humpbacks tracked from the Hawaiian Islands 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 of our 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 the Hawaiian Islands and Mexico (Calambokidis et al. 2008, Titova et al. 2017). Whale #5736, tagged in 2018, 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 d of its tracking period. These results suggest that there may be more movement among Russian feeding areas than once thought.

4.1.4 Migration Phases and Movement Speed

While mean travel speed was much slower during ARS than during transit (1.35 versus 4.81 km/h), there was significant spread (especially in transiting) and also some overlap (**Figure 16a**), indicating that speed alone is not a perfect indicator of activity. Both turning angle and speed are considered in the calculation of the move persistence metric that underlies the estimation of behavioral mode by state-space models (Jonsen 2016, Jonsen et al. 2019). Uncertain mode was most similar to ARS, suggesting that locations classified as uncertain may have had characteristics more similar to ARS behavior than to transiting (**Figure 16a**).

It is not surprising that most locations classified as transiting occurred while in migration, while those classified as ARS occurred in the breeding and feeding areas (**Figure 16b**), as that was the criterion used to designate the of the 50-km buffer zones and to separate movement phases. However, travel speed was somewhat slower in the feeding areas (mean = 1.42 km/h; **Table 7**) than in the breeding area (mean = 1.62 km/h; **Table 7**), as had been previously reported by Palacios et al. (2019), suggesting that the activities that the whales engage in during the breeding and feeding phases have different energetic requirements despite both having similar movement characteristics. It should also be noted that in this study we only report migration speeds between breeding and feeding areas (4.65 km/h), and Palacios et al. (2019) reported faster mean speeds for the migration between the southeastern Alaska feeding area and breeding areas in the Hawaiian Islands and Mexico (5.51 km/h) than for the reverse migration between the Hawaiian Islands breeding area and the feeding areas in northern British Columbia and throughout Alaska (4.44 km/h).

The travel speeds reported in this study for the different migration phases based on a robust number of tracks for animals moving between a breeding area and feeding areas in the North Pacific were consistent with what has been reported in the literature. Within Hawaiian waters and during early departure, Henderson et al. (2019) estimated travel speeds of 0.9-1.1 km/h during milling behavior and 6.6-6.8 km/h during directed travel for animals tagged off Kauai. Mate et al. (1998) reported average travel speeds of 4.5 km/h and 6.2 km/h for two whales migrating between the Hawaiian Islands and the Aleutian Islands. Lagerquist et al. (2008) reported average speeds of 1.2 km/h in the breeding areas and 2.2 km/h in feeding areas for animals tagged in the Revillagigedo Islands, Mexico, and tracked to feeding destinations in the North Pacific, while the average speed during migration was 4.0 km/h. While in feeding areas in the eastern Aleutians and the Bering Sea, Kennedy et al. (2014) reported travel speeds of 0.94-2.15 km/h for seven whales that spent most of their time foraging, and 4.57 km/h for a whale that spent most of its time transiting. For humpback whales migrating from breeding to feeding grounds in the southern hemisphere, Horton et al. (2011) reported travel speeds of 2.8 to 6.5 km/h during long-distance, constant-course track segments in the western South Atlantic and the western South Pacific, while Félix and Guzmán (2014) reported travel speeds of 2.72 to 7.04 km/h in the eastern South Pacific. Finally, Kennedy et al. (2013) reported a mean travel speed of 1.7 km/h while in the breeding grounds for humpback whales tagged in the Caribbean, and mean travel speed of 4.3 km/h while migrating to feeding areas in the eastern and western North Atlantic. Together, the above information indicates that humpback whales can have quite variable travel speeds, but generally they are above 4.5 km/h while migrating, and about a third of that speed when in the feeding or breeding areas.

Finally, the delineation of a 50-km buffer zone around the breeding and feeding areas based on behavioral classification (see **Figure 2** and Palacios et al. 2019) facilitated the objective estimation of residence time and movement speeds during the different phases of the migration (breeding, migrating, feeding), based on the portion of the tracks that occurred inside or outside of them. However, there are limitations to this approach, as previously discussed in Palacios et al. (2019). Of primary relevance, some migratory destinations may occur at distances farther away than 50 km from land, as exemplified by the whales that arrived in the eastern Aleutians and initiated ARS behavior over the Aleutian Trench, more than 160 km south of Akutan Island and Unimak Pass. In these cases, subjective decisions or more complex criteria for the identification of migration phases are required.

4.1.5 Use of Navy Training and Testing Areas

The tracking data obtained from humpback whales tagged in the Hawaiian Islands from 1995 through 2019 also contribute to our understanding of whale use of Navy training and testing areas in the Hawaiian Islands. Navy area FIRMA encompasses almost all of the Maui Nui region, and with Maui Nui being an area of high use for tagged whales and all whales tagged off Maui being within FIRMA, it is not surprising that FIRMA was the most heavily used Navy area (95 percent of tracked whales had locations there). Area SSRA-PB was the next most heavily used Navy area by humpback whales (66 percent of tracked whales), followed by SSRA-OS (25 percent of tracked whales), and SSRA-ON (23 percent of tracked whales). Area BS-Merge saw the least use by humpback whales, with only 11 percent of tracked whales having locations there. More tagging off Kauai would improve our understanding of the use of the more westerly Navy areas by humpback whales in the Hawaiian Islands 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). Tagging earlier in the year would also improve our understanding of the seasonality of humpback occurrence in Navy ranges, as the seasonality observed in this study is largely driven by the timing of deployment (the majority of which took place in February or March) and duration of tag attachment.

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, given the small percentage (11 percent) of whales tagged in the Hawaiian Islands that were 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.

None of the humpback whales tagged in the Hawaiian Islands were tracked within any Navy training and testing areas along the US West Coast. There was also no use of the Navy's NWTT range by humpback whales tagged in the Hawaiian Islands. However, as outlined below in the photo-ID section, humpback whales from the Hawaiian Islands have been sighted off the coasts of Oregon, Washington, and southern British Columbia (Palacios et al. 2020), which would result in time spent within the NWTT area. Our small sample of migrating whales may again be the reason for this apparent lack of use of the NWTT area.

4.1.6 Use of BIAs

Because of the almost complete overlap of the Oahu-Lanai-Molokai-Maui BIA with FIRMA and the three Navy Humpback Whale Seasonal Special Reporting Areas already discussed, Kauai and Hawaii are the only breeding area BIAs considered here. Neither of these BIAs were used heavily by tracked whales, with only 14 percent and 6 percent spending time in the Kauai and Hawaii BIAs, respectively. This is in part due to the small number of tag deployments in those areas, as well as the timing. More tagging off the islands of Kauai and Hawaii and tagging earlier in the winter season would further our understanding of BIA use in those areas. A northwest progression through the Hawaiian Island chain is evident in whales' use of BIAs, with 10 percent of the whales tracked from Maui traveling to the Kauai BIA and only 2 percent moving southeast to the Hawaii BIA. The island of Hawaii may represent an arrival point for some humpback whales migrating from northern feeding areas, as demonstrated by the tracking of two tagged humpback whales from southeastern Alaska to the island (Palacios et al. 2019). If a significant proportion of humpback whales arrive at the southeastern corner of the Hawaiian Archipelago and then progress northwest through the islands, our later-season tagging (in February, March, and April) off Maui and Kauai may underestimate the importance of the Hawaii BIA.

While only four 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 southeastern Alaska feeding areas, 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 southeastern Alaska, such as the Aleutian BIA, was minimal, due in part to the small number of whales tracked to these areas, but also to 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.

4.2 Dive Behavior

Tags summarized a similar percentage of the tracking duration across both years (mean = 61.6 percent) while 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 (Breed et al. 2011, Quick et al. 2019). The large number of dives reported per tag (mean = 1,839) and consistency of dive behavior reported across years suggests a representative sample of dives was received. The larger number of lunge events recorded by tags in 2019 was likely due to changes in the lunge detection algorithm and makes comparisons across years more difficult. Thus, additional effort with tags that have dive-monitoring capabilities may be needed to better understand how activity levels are distributed across various types of dives.

4.2.1.1 Breeding Areas

Information about humpback whale diving behavior in the Hawaiian Islands has typically been generated from either short-duration archival tags or surface-based observations (Chu 1988, Baird et al. 2000, Herman et al. 2007), with the exception of one recent study using Argos-transmitting tags (Henderson et al. 2018). Humpback whales are not feeding while in the Hawaiian Islands breeding areas, 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, dive behavior was very consistent across years. 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 2017). The purpose of the occasional deeper dives (> 300 m in some cases) made by some whales is unclear but similar deep dives have been reported in humpback breeding areas in New Caledonia (Derville et al. 2020) suggesting they are a feature of behavior in the breeding areas. As previously observed (Henderson et al. 2018, Mate et al. 2019), maximum dive depths off the

Hawaiian Islands were likely limited by seafloor depth in many cases, as the most used areas generally ranged in depth from 50 to 150 m. Competitive behavior has been observed down to depths of almost 300 m (Herman et al. 2007), thus, the deeper dives may be related to aspects of competitive behavior that occur at a lower rate due to the generally shallow seafloor and that are very poorly known.

Tagged whales spent over 65 percent of their reported time near the surface (< 30 m depth) while occupying waters that are heavily used by a wide range of commercial, military, and recreational vessels. Ship strikes of large whales are a growing concern globally (Panigada et al. 2006, Silber et al. 2012, Redfern et al. 2013, Pirotta et al. 2018) and the number of reported whale/vessel collisions in Hawaiian waters have been increasing more rapidly than can be explained by increased whale abundance (Lammers et al. 2013). Whales submerged at one to two times the depth of a vessel's draft are at an increased probability of being impacted by the vessel (Silber et al. 2010). Thus, the high proportion of time spent near the surface and high occupancy of the Maui Nui region, an area of high vessel concentration (Lammers et al. 2013), suggests the tagged whales are at an elevated risk of potential collision with vessels in the area. Unlike in the feeding areas, where diel variation in dive behavior can reduce exposure to vessel collision during part of the day (Calambokidis et al. 2019, Palacios et al. 2019), tagged whales in the Hawaiian Islands were near the surface across all hours of the day making possible exposure dependent on vessel traffic patterns.

Dive durations were more variable across individuals than dive depths, and long-duration dives (> 20 min) were relatively common in the data, especially at depths < 50 m when little activity ("lunges") was recorded. Male humpback whales are known to make long-duration dives while they are vocalizing/singing (Herman 2017) 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 after tag deployment, making dives lasting > 20 min. Female tagged whales also made these long-duration dives. The purpose behind this behavior is unclear, but it is likely a strategy to conserve energy or rest in the breeding area. 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 areas 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, while our tracks were heavily biased toward males, no sex-based differences in dive behavior were observable, which corresponds with published work from New Caledonia (Derville et al. 2020).

4.2.1.2 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 whales' 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), deviations in heading were minimal, suggesting the purpose was not related to feeding, or that prey abundance was too low to justify extended occupancy. 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 providing navigational cues (Horton et al. 2017). Recent work has correlated gray whale strandings to increases in solar activity, suggesting this may have confused the whales' ability to navigate (Granger et al. 2020). Solar impacts on the earth would presumably be lowest during the night so these deep dives may represent the whales descending to avoid surface noise or to improve their sensing of the geomagnetic signal. In large epipelagic fish, the function of deep dives may be related to obtaining bathymetric and/or geomagnetic cues to aid navigation, as a heat dissipation mechanism, or to escape predators (Andrzejaczek et al. 2019).

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 increased activity (as measured by detected 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 areas, whales in both years recorded lunges across a relatively long time period in the middle of their migration. These whales did not suspend their migrations to feed as has been observed with other whales (Mate et al. 2007, Stamation et al. 2007), possibly indicating that some whales attempted to supplement energy reserves prior to arrival in the feeding areas. It is also possible the increased lunging activity may reflect an unknown social aspect of migratory behavior.

4.2.1.3 Feeding Areas

Five of six tagged whales that reached the feeding areas traveled to the area near Haida Gwaii, while the last one went to the western Aleutian Islands and Bering Sea. Dives near Haida Gwaii were generally closely associated with the western and northern coastline of the island, and lunges typically occurred during deeper dives. This suggests the whales may have been feeding on prey attracted to topographically driven productivity (Whitney et al. 2005). The dive behavior of tagged whales near Haida Gwaii was very consistent both temporally and spatially with the exception of whale #2019_847, which arrived at the southern end of Haida Gwaii but traveled north to waters off southeastern Alaska. Despite passing through waters heavily used by other tagged whales off Haida Gwaii, whale #2019_847 was the only one whose track showed a diel difference in behavior with deeper, longer duration dives occurring during the day. This difference in dive behavior suggests tagged whales may have been employing different foraging strategies despite occupying similar areas. 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 #2019_847 was characteristic of rorqual krill-feeding behavior (Calambokidis et al. 2007, Goldbogen et al. 2008) and was most similar to whale #2018_5736, which traveled to the Aleutian Islands and into the Bering Sea. Both of those tagged whales appeared to feed while moving, rather than remaining in a localized area, suggesting that they were able to find consistent levels of forage as they moved, or that the deeper daytime dives also represented food-searching behavior.

4.3 Genetics

4.3.1 Population Structure of Feeding Areas

The DNA profiles, combined with the tagging and photo-ID records 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 45 whales tagged off Maui in 2018 and 2019 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 50**) and quantitatively by the pairwise FST value in the test of differentiation (**Table 17**). In comparisons to breeding areas characterized by SPLASH, the tagging samples from both years showed the greatest similarity (i.e., the lowest FST) with the SPLASH samples from the Hawaiian Islands and the greatest differences with those from Okinawa, the Philippines, and Central America. In comparisons to feeding areas, the Maui tagging samples showed the greatest similarity to the SPLASH samples from the northern Gulf of Alaska (in 2018) and southeastern Alaska and northern British Columbia (in 2019) and the greatest differences with California/Oregon and with Russia (both years).

It is well established from previous studies using telemetry, photo-ID, and genetic markers, that the migratory connections of the Hawaiian Islands breeding areas to feeding areas is complex (Baker et al. 2013). Although migratory fidelity is strong in both seasonal habitats, there is no simple relationship between breeding and feeding areas. Instead, the Hawaii DPS includes individuals with fidelity to feeding areas extending from British Columbia to Russia, 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 Islands whales tagged in this study and their feeding area destinations. The tagged individuals migrating to, or toward southeastern Alaska and northern British Columbia had either "A-", "A+", or "E2" haplotypes which are the most common haplotypes for these feeding areas, as characterized in SPLASH, indicating a good agreement in describing the population from both lines of evidence. In contrast, the tagged individual from 2018 with an "E1" haplotype migrated to the Aleutians and on to Russia. This haplotype is relatively widespread among feeding areas, except southeastern Alaska, where it is absent in the SPLASH samples (Baker et al. 2013).

As reported previously (Mate et al. 2019), genotype matching and photo-ID have the potential to enhance information on the migratory fidelity and life history of tagged whales by integrating long-term sighting records. Here, comparing the genotype of one of the tagged whales from 2018 (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. Two of the 21 whales tagged in 2019 also provided genotype recaptures with whales sampled previously during SPLASH, one with both genotype and photo-ID records in the Hawaiian Islands and southeastern Alaska (SPLASH ID 430211), and one with both genotype and photo-ID records from the northern Gulf of Alaska (SPLASH ID 472569). Comparison of humpback whale samples collected in the North Pacific after the SPLASH program provided genotype recaptures for two more whales, one between the Hawaiian Islands in 2019 and the northern Gulf of Alaska in 2009 and one between the Hawaiian Islands in 1999 and southeastern Alaska in 2019, the latter providing an example of 20-year post-tagging survival (Janice Straley, University of Alaska Southeast Sitka, pers. comm.). These specific examples of data integration are further evidence of the potential for improved modeling of cumulative exposure to local stressors, including Naval activity, on both feeding and breeding habitat.

4.4 Photo-Identification

Photo-ID provided a useful complement to the tracking and genetic data for the purpose of better understanding the movements and migratory destinations of humpback whales in the Hawaiian Islands. By including photo-IDs of both tagged and untagged whales, we have obtained a more complete picture of the migratory connections, not only for whales whose tags did not last until arrival at a migratory destination, but also for whales seen in the vicinity of tagged whales. The proportions of photo-ID matches of Hawaiian Islands whales to different feeding areas agrees with genetic results in this study as well as past photo-ID and genetic studies (Calambokidis et al. 2008, Baker et al. 2013), with the strongest connections to southeastern Alaska (21 percent of matches) and the northern Gulf of Alaska (21 percent of matches). The next highest proportion of matches (16 percent) was between the Hawaiian Islands and southern British Columbia/Washington, followed by Russia, western Gulf of Alaska, northern British Columbia, eastern Aleutian Islands, and Oregon. Higher proportions of Hawaiian Islands humpback whales feeding in southern British Columbia/Washington than in some other feeding areas in the North Pacific could be a reflection of larger numbers of photo-IDs in Happywhale from that feeding area compared to other areas, or could reflect an increase in the number of humpbacks migrating to southern British Columbia/Washington as the Hawaiian Islands population grows. Calambokidis et al. (2017) reported an increase in humpback whale abundance in Washington and southern British Columbia from 1993 through 2014, with a dramatic return of humpbacks in the Salish Sea, where they once occurred prior to early 20th Century whaling.

Our 2018 and 2019 photo-ID results provide further evidence for strong migratory fidelity in both breeding and feeding areas, with all but two of the 91 Hawaiian Islands whales that were matched to a breeding area in another year being matched to the Hawaiian Islands, and all but three of 39 whales with matches to SPLASH feeding areas being matched to a single feeding area. The exceptions include two Hawaiian Islands whales being matched to Mexico (one to the mainland and one to Baja California), one matched to both the Shumagin Islands (western Gulf of Alaska) and Kodiak Island (northern Gulf of Alaska), one tracked to northern British Columbia and southeastern Alaska (as well as being photographically matched to southeastern Alaska), and the final matched to both Washington and northern British Columbia. The latter three whales had matches to adjacent feeding areas that are known to have higher rates of between-season interchange among them than other areas (Calambokidis et al. 2008). Changes in breeding destinations for individual whales have also been documented previously, with animals from the Hawaiian Islands being seen in the Japan (Darling and Cerchio 1993, Salden et al. 1999) and Mexico (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker et al. 1986, Forestell and Urbán-R 2007) breeding areas.

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Table 1. Deployment and performance data for 25 satellite-monitored radio tags deployed on humpback whales off Maui, Hawaii, during March 2019. In the Sex column, Unknown refers to cases when no biopsy sample was collected. See Section 2.3.1 for location filtering method.

Tag #	Sex	Deployment Date	Date of Last Location	Biopsy/Fluke Photo Collected	Days Tracked	Filtered Locations	Total Distance (km)
825*	Male	14-Mar-19	-	Yes/Yes	-	-	-
827	Male	14-Mar-19	8-Apr-19	Yes/Yes	24.5	114	1,404
830	Male	14-Mar-19	4-Apr-19	Yes/Yes	20.8	88	1,186
831	Male	16-Mar-19	2-Apr-19	Yes/Yes	17.0	116	916
834	Unknown	16-Mar-19	2-Apr-19	No/Yes	16.5	129	1,105
835	Male	16-Mar-19	6-Apr-19	Yes/Yes	20.4	120	1,946
836	Unknown	16-Mar-19	5-Apr-19	No/Yes	19.9	128	2,388
838	Male	16-Mar-19	30-Mar-19	Yes/No	13.4	71	604
839	Male	16-Mar-19	17-Mar-19	Yes/Yes	0.3	4	49
840	Male	17-Mar-19	17-Mar-19	Yes/No	0.1	1	18
843	Male	17-Mar-19	23-May-19	Yes/No	67.8	368	6,046
845	Male	17-Mar-19	18-Mar-19	Yes/Yes	0.6	7	39
847	Male	17-Mar-19	7-Jun-19	Yes/Yes	81.3	567	8,062
848	Male	19-Mar-19	21-Mar-19	Yes/No	2.7	14	123
1385	Female	19-Mar-19	21-Apr-19	Yes/Yes	33.0	252	3,822
1386	Male	19-Mar-19	1-Apr-19	Yes/Yes	13.0	70	1,122
1387	Male	19-Mar-19	2-Apr-19	Yes/Yes	13.8	87	1,258
1389	Unknown	19-Mar-19	14-Apr-19	No/Yes	25.4	179	1,612
1390	Unknown	19-Mar-19	1-May-19	No/Yes	42.1	343	4,956
2082	Male	20-Mar-19	20-Mar-19	Yes/Yes	0.2	3	14
2083	Female	20-Mar-19	21-Apr-19	Yes/Yes	31.4	244	3,223
4175	Male	21-Mar-19	21-Mar-19	Yes/Yes	0.3	2	11
4176	Male	21-Mar-19	12-Apr-19	Yes/Yes	22.8	151	2,074
5648	Male	21-Mar-19	21-Apr-19	Yes/Yes	30.7	185	3,614
5655	Male	22-Mar-19	5-Apr-19	Yes/Yes	14.7	83	1,878
Mean (SD)					**21.4 (20.2)**	**139 (137)**	**1,978 (2,073)**

KEY: km = kilometer(s); SD = Standard Deviation; # = number; * = not included in the computation of Mean or SD.

Table 2. Summary statistics for travel speed (in km/h) between location pairs for 18 humpback whale tracks from tag deployments in 2019 in Maui, Hawaii on which state-space models were run. Values are reported by estimated behavioral mode (upper part of the table) and by migration phase, as determined by occurrence inside or outside the 50-km buffer zones (lower part of the table). Also reported are the 95th sample quantile (qtl) and the lower- and upper-95 percent confidence intervals (CI) around the mean.

Behavioral mode	**N**	**Mean**	**Median**	**SD**	**95th qtl**	**Lower CI**	**Upper CI**
ARS	552	1.72	1.38	1.35	4.38	1.61	1.83
Uncertain	284	2.09	1.56	1.64	5.50	1.90	2.28
Transiting	701	5.23	5.25	2.40	9.29	5.05	5.40
Phase	**N**	**Mean**	**Median**	**SD**	**95th qtl**	**Lower CI**	**Upper CI**
Breeding	843	2.02	1.58	1.52	5.16	1.92	2.12
Migration	623	5.43	5.42	2.41	9.34	5.24	5.62
Feeding	71	1.78	1.12	1.86	5.51	1.35	2.21

Table 3. Residence time in the Hawaiian Islands (Hawaii) for 39 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 island 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). Eleven of the tags lasted at least until arrival to a feeding area (last two columns).

Tag #	Sex	Deployment Island	Deployment Date	Date of Last Location	Days Tracked	Total Distance (km)	Hawaii Departure	Hawaii Residency (d)	Migration Duration (d)	Destination	Complete Migration
10822	U	Kauai	27-Mar-1995	7-Apr-1995	11.0	1,223	29-Mar-1995	1.2		(*Western Gulf of Alaska*)	No
10824	F/C	Kauai	26-Mar-1995	31-Mar-1995	4.5	451	29-Mar-1995	2.7		-	No
23038	U	Kauai	2-Apr-1995	19-Apr-1995	17.0	1,631	3-Apr-1995	1.1		(*Western Gulf of Alaska*)	No
828	F/C	Maui	9-Apr-1997	21-May-1997	42.7	3,339	3-May-1997	22.6		*(Aleutians)*	No
830	U	Maui	5-Apr-1997	23-Jun-1997	79.0	7,255	9-Apr-1997	3.7	30.8	Aleutians and Kamchatka	Yes
831	U	Maui	5-Apr-1997	24-Apr-1997	18.2	2,418	13-Apr-1997	1.2		-	No
847	U	Maui	14-Apr-1998	23-May-1998	38.3	3,390	20-Apr-1998	6.0		(*Southern British Columbia/Northern Washington*)	No
848	U	Maui	8-Apr-1998	4-May-1998	25.9	2,215	13-Apr-1998	4.9		*(Aleutians)*	No
10826	M	Maui	15-Apr-1998	10-Aug-1998	117.0	7,884	26-Apr-1998	10.8	30.4	Northern British Columbia/southeastern Alaska	Yes
10828	U	Maui	11-Feb-1999	3-Jul-1999	142.6	10,279	23-Feb-1999	12.5	41.6	Aleutians (via KRS)	Yes
10830	M	Maui	10-Feb-1999	6-Mar-1999	23.9	1,626	1-Mar-1999	18.8		*(Southeastern Alaska)*	No
10836	M	Maui	10-Feb-1999	17-Apr-1999	65.4	4,621	25-Mar-1999	42.8		*(Northern British Columbia/southeastern Alaska)*	No
10842	U	Maui	14-Feb-1999	8-Mar-1999	21.7	1,588	2-Mar-1999	15.4		*(Aleutians)*	No

Tag #	Sex	Deployment Island	Deployment Date	Date of Last Location	Days Tracked	Total Distance (km)	Hawaii Departure	Hawaii Residency (d)	Migration Duration (d)	Destination	Complete Migration
4177	U	Maui	11-Dec-1999	12-May-2000	152.8	4,675	20-Dec-1999	8.4	<51*	Southeastern Alaska	Yes
835	U	Maui	5-Feb-2000	25-Mar-2000	49.7	3,651	19-Feb-2000	14.1		*(Southern British Columbia/Northern Washington)*	No
843	U	Maui	4-Feb-2000	5-May-2000	91.1	3,991	13-Feb-2000	9.5	<69*	Aleutians	Yes
830	M	Maui	20-Jan-2015	5-Feb-2015	16.2	1,541	29-Jan-2015	9.5		(*Southern British Columbia/Northern Washington*)	No
5746	U	Maui	15-Jan-2015	22-Feb-2015	38.0	2,487	13-Feb-2015	29.3		*(Aleutians)*	No
843	U	Maui	15-Mar-2018	17-May-2018	63.0	3,294	8-Apr-2018	23.2		*(Aleutians)*	No
4172	M	Maui	14-Mar-2018	6-May-2018	53.7	6,296	17-Mar-2018	3.3	29.8	Northern British Columbia	Yes
5641	M	Maui	16-Mar-2018	2-Apr-2018	17.2	1,019	29-Mar-2018	13.5		Northern British Columbia	No
5736		Maui	18-Mar-2018	12-Aug-2018	147.2	11,302	31-Mar-2018	13.7	28.0	Aleutians/Kamchatka/ Bering Sea	Yes
5800	M	Maui	19-Mar-2018	17-May-2018	58.2	6,259	3-Apr-2018	14.4	34.5	Northern British Columbia	Yes
5784	F/C	Maui	19-Mar-2018	1-Jul-2018	104.5	8,065	25-Mar-2018	5.9	44.8	Northern British Columbia	Yes
10833	U	Maui	21-Mar-2018	6-May-2018	59.5	860	11-Apr-2018	20.5		(Aleutians)	No
827	M	Maui	14-Mar-19	8-Apr-2019	24.5	1,404	8-Apr-2019	24.4			No
834	U	Maui	16-Mar-2019	2-Apr-2019	16.5	1,105	2-Apr-2019	16.2			No
835	M	Maui	16-Mar-2019	6-Apr-2019	20.4	1,946	27-Mar-2019	12.2			No
836	U	Maui	16-Mar-2019	5-Apr-2019	19.9	2,388	24-Mar-2019	6.9			No

Tag #	Sex	Deployment Island	Deployment Date	Date of Last Location	Days Tracked	Total Distance (km)	Hawaii Departure	Hawaii Residency (d)	Migration Duration (d)	Destination	Complete Migration
843	M	Maui	17-Mar-2019	23-May-2019	67.8	6,046	5-Apr-2019	19.9	36.8	Northern British Columbia	Yes
847	M	Maui	17-Mar-2019	7-Jun-2019	81.3	8,062	23-Apr-2019	36.5	34.3	Northern British Columbia	Yes
1385	F	Maui	19-Mar-2019	21-Apr-2019	33.0	3,822	22-Mar-2019	3.6			No
1386	M	Maui	19-Mar-2019	1-Apr-2019	13.0	1,122	26-Mar-2019	7.2			No
1387	M	Maui	19-Mar-2019	2-Apr-2019	13.8	1,258	27-Mar-2019	8.2			No
1390	U	Maui	19-Mar-2019	1-May-2019	42.1	4,956	31-Mar-2019	11.5	30.6	Southern British Columbia	Yes
2083	F	Maui	20-Mar-2019	21-Apr-2019	31.4	3,223	9-Apr-2019	19.0			No
4176	M	Maui	21-Mar-2019	12-Apr-2019	22.8	2,074	7-Apr-2019	17.3			No
5648	M	Maui	21-Mar-2019	21-Apr-2019	30.7	3,614	29-Mar-2019	10.8			No
5655	M	Maui	22-Mar-2019	5-Apr-2019	14.7	1,878	28-Mar-2019	6.9			No
Mean					**48.5**	**3,699**		**13.1**	**34.2**		
SD					**39.7**	**2,727**		**9.4**	**5.5**		

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

* Whales 4177 and 843 provided no locations during migration, so migration duration could not be accurately calculated. The number reported here is from the time they left the Hawaiian Islands until their next location was received. These numbers are not included in the calculation of summary statistics.

Table 4. Percentage of filtered Argos locations and time spent inside Navy activity areas BS-Merge, SSRA-ON, SSRA-OS, SSRA-PB, and FIRMA for 24 humpback whales tagged off Maui, Hawaii, 2019. See Section 2.3.1 for location filtering method.

Tag #	Total		BS-Merge			SSRA-ON			SSRA-OS			SSRA-PB			FIRMA		
	# Locs	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days
827	115	24.5	1.7	0.3	0.1	0.9	3.4	0.8	0	1.1	0.3	2.6	2.2	0.5	44.3	37.1	9.1
830	89	20.8	2.2	4.9	1.0	0	0	0	0	0.1	0.03	0	5.9	1.2	32.6	29.8	6.2
831	117	17.0	0	0	0	0	0	0	0	0	0	33.3	30.6	5.2	59.8	57.0	9.7
834	130	16.5	1.5	1.9	0.3	0	0	0	0.8	0.04	0.01	20.8	17.0	2.8	46.2	43.6	7.2
835	121	20.4	0	0	0	0	0	0	0	0	0	29.8	34.7	7.1	13.2	7.4	1.5
836	129	19.9	0	0	0	1.6	3.2	0.6	1.6	1.1	0.2	3.9	3.4	0.7	14.7	16.2	3.2
838	72	13.4	0	0	0	0	0	0	0	0	0	44.4	44.0	5.9	37.5	44.0	5.9
839	5	0.3	0	0	0	0	0	0	0	0	0	0	0	0	100	100	0.3
840	1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	100	100	0.1
843	370	67.8	0	0	0	0.8	0.4	0.3	0	0.1	0.1	10.0	10.0	6.8	12.7	12.9	8.8
845	8	0.6	0	0	0	0	0	0	0	0	0	0	0	0	100	98.6	0.6
847	568	81.3	0.2	0.4	0.3	0	0.1	0.1	0	0.2	0.2	6.3	6.7	5.4	18.8	18.8	15.3
848	15	2.7	0	0	0	0	0	0	0	0	0	0	0	0	100	100	2.7
1385	253	33.0	0	0	0	0	0	0	0	0	0	0.4	0.02	0.01	8.3	8.9	2.9
1386	71	13.0	0	0	0	0	0	0	0	0	0	23.9	19.9	2.6	18.3	25.0	3.3
1387	88	13.8	0	0	0	0	1.6	0.2	0	0	0	21.6	21.6	3.0	21.6	22.1	3.0
1389	181	25.4	0	0	0	3.9	2.8	0.7	1.7	1.5	0.4	25.4	20.9	5.3	48.6	53.0	13.5
1390	344	42.1	0	0	0	0	0	0	0	0	0	5.2	5.0	2.1	14.2	19.2	8.1
2082	4	0.2	0	0	0	0	0	0	0	0	0	0	0	0	100	100	0.2
2083	245	31.4	0	0	0	5.3	2.8	0.9	4.5	3.7	1.2	16.3	20.8	6.5	14.3	17.5	5.5
4175	3	0.3	0	0	0	0	0	0	0	0	0	0	0	0	100	81.3	0.3
4176	152	22.8	0	0	0	1.3	0.4	0.1	0	0	0	6.6	8.4	1.9	53.9	56.5	12.9
5648	186	30.7	1.1	1.0	0.3	1.6	1.0	0.3	0	0	0	2.2	2.2	0.7	3.2	2.3	0.7
5655	84	14.7	0	0	0	3.6	3.7	0.5	0	0.3	0.05	13.1	10.3	1.5	17.9	19.0	2.8
Mean	**146**	**27.6**	**1.4**	**1.7**	**0.4**	**1.9**	**2.0**	**0.5**	**0.9**	**0.9**	**0.3**	**14.8**	**14.6**	**3.3**	**45.0**	**44.6**	**5.1**
SD			**0.8**	**1.9**	**0.4**	**1.8**	**1.4**	**0.3**	**1.5**	**1.2**	**0.4**	**12.9**	**12.5**	**2.4**	**35.7**	**34.3**	**4.5**

KEY: Locs = Locations; # = number; + Summary statistics do not include zero values in their calculation.

Table 5. Geodesic distances (km) to nearest point on shore in Navy activity areas for 24 humpback whales tagged off Maui, Hawaii, in 2019 (including mean, standard deviation [SD], and maximum [Max] 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 #	BS-MERGE				SSRA-ON				SSRA-OS				SSRA-PB				FIRMA			
	n	**Mean**	**SD**	**Max**	**n**	**Mean**	**SD**	**Max**	**n**	**Mean**	**SD**	**Max**	**n**	**Mean**	**SD**	**Max**	**n**	**Mean**	**SD**	**Max**
827	2	4.4	0.2	4.5	1	3.6	-	3.6	0	-	-	-	3	15.1	2.3	16.9	51	4.3	2.6	13.5
830	2	10.5	1.7	11.7	0	-	-	-	0	-	-	-	0	-	-	-	29	7.0	3.0	19.2
831	0	-	-	-	0	-	-	-	0	-	-	-	39	20.0	10.5	35.6	70	4.1	2.8	12.8
834	2	5.7	0.4	6.0	0	-	-	-	1	5.1	-	5.1	27	24.1	8.8	31.8	60	5.6	2.7	15.7
835	0	-	-	-	0	-	-	-	0	-	-	-	36	23.0	12.1	40.0	16	6.1	3.7	16.0
836	0	-	-	-	2	1.1	0.01	1.1	2	4.7	0.7	5.3	5	16.8	8.9	22.6	19	5.5	3.7	17.0
838	0	-	-	-	0	-	-	-	0	-	-	-	32	31.8	9.4	43.2	27	6.5	4.4	18.7
839	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	5	9.3	6.7	20.6
840	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
843	0	-	-	-	3	2.5	0.5	3.0	0	-	-	-	37	23.8	12.6	45.8	47	6.4	4.8	19.8
845	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	8	8.6	3.4	14.1
847	1	20.1	-	20.1	0	-	-	-	0	-	-	-	36	22.2	13.7	40.3	106	5.5	3.7	20.1
848	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	15	4.9	2.9	10.4
1385	0	-	-	-	0	-	-	-	0	-	-	-	1	4.3	-	4.3	21	4.9	2.9	10.7
1386	0	-	-	-	0	-	-	-	0	-	-	-	17	27.4	10.4	40.3	13	4.0	1.7	6.6
1387	0	-	-	-	0	-	-	-	0	-	-	-	19	21.5	11.6	38.1	19	4.7	2.3	8.5
1389	0	-	-	-	7	2.4	1.5	4.4	3	3.4	0.9	3.9	46	18.2	14.2	38.5	88	5.3	3.4	17.3
1390	0	-	-	-	0	-	-	-	0	-	-	-	18	16.2	13.4	35.4	49	5.5	3.4	18.5
2082	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	4	6.9	2.8	8.6
2083	0	-	-	-	13	3.9	1.9	6.5	11	5.5	2.2	10.0	40	19.5	12.9	42.7	35	5.6	3.8	15.5
4175	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	3	5.6	3.0	9.0
4176	0	-	-	-	2	3.1	0.2	3.3	0	-	-	-	10	27.5	14.3	40.8	82	4.7	2.6	12.9
5648	2	10.9	4.3	13.9	3	5.2	1.4	6.8	0	-	-	-	4	23.6	9.9	32.1	6	3.5	2.9	7.7
5655	0	-	-	-	3	3.5	0.8	4.4	0	-	-	-	11	9.5	8.0	25.2	15	7.0	4.3	19.2
Mean*	**1.8**	**10.3**		**11.2**	**4.3**	**3.2**		**4.1**	**4.3**	**4.7**		**6.1**	**22.4**	**20.3**		**33.8**	**34.3**	**5.7**		**14.4**
SD*	**0.4**	**6.2**		**6.3**	**4.0**	**1.2**		**1.9**	**4.6**	**0.9**		**2.7**	**15.1**	**6.7**		**10.9**	**29.7**	**1.4**		**4.5**

KEY: n = number of locations in that particular Navy area; # = number; * Summary statistics do not include zero values in their calculation.

Table 6. Percentage of filtered Argos locations and time spent inside BIAs for 24 humpback whales tagged off Maui, Hawaii, during March 2019. See Section 2.3.1 for location filtering method.

Tag #	Total		Kauai			Hawaii			SEAK			Aleutians			200m to 50km		
	# Locs	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days
827	115	24.5	10.4	7.2	1.8	0	0	0	0	0	0	0	0	0	36.5	41.4	10.1
830	89	20.8	2.2	8.7	1.8	0	0	0	0	0	0	0	0	0	50.6	52.4	10.9
831	117	17.0	0	0	0	0	0	0	0	0	0	0	0	0	9.4	12.9	2.2
834	130	16.5	4.6	7.4	1.2	0	0	0	0	0	0	0	0	0	20.0	27.8	4.6
835	121	20.4	0	0	0	0	0	0	0	0	0	0	0	0	7.4	18.3	3.7
836	129	19.9	0	0	0	0	0	0	0	0	0	0	0	0	7.8	7.2	1.4
838	72	13.4	0	0	0	0	0	0	0	0	0	0	0	0	34.7	26.2	3.5
839	5	0.3	0	0	0	0	0	0	0	0	0	0	0	0	60.0	31.6	0.1
840	1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	100	100	0.1
843	370	67.8	0	0	0	0	0	0	0	0	0	0	0	0	8.6	8.3	5.6
845	8	0.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
847	568	81.3	0.4	0.2	0.2	0	0	0	0.7	0.3	0.2	0	0	0	14.1	14.8	12.1
848	15	2.7	0	0	0	0	0	0	0	0	0	0	0	0	6.7	5.4	0.1
1385	253	33.0	0	0	0	0	0	0	0	0	0	0	0	0	1.2	1.8	0.6
1386	71	13.0	0	0	0	0	0	0	0	0	0	0	0	0	18.3	14.9	1.9
1387	88	13.8	0	0	0	0	0	0	0	0	0	0	0	0	13.6	13.4	1.8
1389	181	25.4	1.1	2.2	0.6	0	0	0	0	0	0	0	0	0	17.7	18.2	4.6
1390	344	42.1	0	0	0	0	0	0	0	0	0	0	0	0	3.5	4.7	2.0
2082	4	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2083	245	31.4	0	0	0	0	0	0	0	0	0	0	0	0	12.2	11.9	3.8
4175	3	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4176	152	22.8	0	0	0	0	0	0	0	0	0	0	0	0	14.5	15.0	3.4
5648	186	30.7	3.2	2.4	0.7	0	0	0	0	0	0	0	0	0	18.8	17.1	5.3
5655	84	14.7	0	0	0	0	0	0	0	0	0	0	0	0	15.5	14.8	2.2
Mean	**146**	**27.6**	**3.7**	**4.7**	**1.0**	**0**	**0**	**0**	**0.7**	**0.3**	**0.2**	**0**	**0**	**0**	**22.4**	**3.8**	**21.8**
SD			**3.6**	**3.5**	**0.7**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**23.3**	**3.5**	**21.7**

KEY: Locs = Locations; SEAK = Southeast Alaska BIAs; # = number; * Summary statistics do not include zero values in their calculation.

Table 7. Summary statistics for travel speed (in km/h) between location pairs for 86 humpback whale tracks from previous OSU tag deployments in the Hawaiian Islands (1995-2000, 2015, 2018, 2019) on which state-space models were run. Values are reported by estimated behavioral mode (upper part of the table) and by migration phase, as determined by occurrence inside or outside the 50-km buffer zones (lower part of the table). Also reported are the 95th sample quantile (qtl) and the lower- and upper-95 percent confidence intervals (CI) around the mean.

Behavioral mode	N	Mean	Median	SD	95th qtl	Lower CI	Upper CI
ARS	1690	1.35	1.01	1.27	3.73	1.28	1.41
Uncertain	943	1.67	1.19	1.51	4.92	1.57	1.77
Transiting	1604	4.81	4.74	2.19	8.53	4.70	4.92
Missing*	48	1.93	1.45	1.75	5.30	1.44	2.43
Phase	**N**	**Mean**	**Median**	**SD**	**95th qtl**	**Lower CI**	**Upper CI**
Breeding	2159	1.62	1.20	1.38	4.47	1.56	1.68
Migration	1598	4.65	4.61	2.39	8.58	4.53	4.76
Feeding	528	1.42	0.85	1.55	4.90	1.29	1.55

KEY: * = Missing corresponds to the last location of each track, which did not receive a behavioral classification by the conventional SSSM, and are included here for completeness.

Table 8. Connectivity between islands/areas for 105 humpback whales satellite-tagged in the Hawaiian Islands from 1995 to 2019. 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 "Number of whales visiting other areas 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 three other areas during its tracking period. Shaded cells refer to the number of whales tagged and subsequently tracked from that area.

Deployment Location (# tags tracked)	**Number of whales visiting other areas after tagging**						
	PMNM	**Niihau**	**Kauai**	**Oahu**	**Penguin Bank**	**Maui Nui**	**Hawaii**
Kauai (5)	0	0	5	1	1	1	0
Maui Nui (96)	4	6	9	27	56	96	2
Hawaii (4)	0	0	0	0	0	1	4

KEY: # = number.

Table 9. Mean (standard deviation [SD]) and maximum (Max) number of days spent inside Hawaiian Island Navy areas for 105 humpback whales tagged in Hawaii from 1995 to 2019. 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 maximum.

	# Days														
Deployment Island (# Whales Tracked	**BS-Merge**			**SSRA-ON**			**SSRA-OS**			**SSRA-PB**			**FIRMA**		
	n	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**
Kauai (5)	3	1.0 (0.4)	1.4	1	1.4	1.4	0	--	--	1	0.7	0.7	1	1.0	1.0
Maui (96)	9	0.4 (0.4)	1.0	23	0.5 (0.4)	1.5	26	0.2 (0.3)	1.3	67	4.2 (4.2)	23.8	96	5.3 (4.6)	23.1
Hawaii (4)	0	--	--	0	--	--	0	--	--	1	0.03	0.03	3	1.0 (1.0)	2.0
All Islands (105)	**12**	**0.7 (0.4)**	**1.4**	**24**	**1.0 (0.6)**	**1.5**	**26**	**0.2**	**1.3**	**69**	**1.6 (2.3)**	**23.8**	**100**	**2.4 (2.5)**	**23.1**

KEY: n = number of whales with time spent in that Navy area; # = number.

Table 10. Summary statistics (mean, standard deviation [SD], and maximum [Max]) for distance to shore (km) inside Navy areas in the Hawaiian Islands for 105 humpback whales tagged in the Hawaiian Islands from 1995 to 2019. 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.

Deployment Island (# Whales Tracked	BS-Merge			SSRA-ON			SSRA-OS			SSRA-PB			FIRMA		
	n	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**
Kauai (5)	3	38.0 (24.3)	65.1	1	3.2 (1.2)	4.0	0	-	-	1	28.3 (-*)	28.3	1	4.9 (1.4)	6.2
Maui (96)	8	21.5 (22.1)	72.1	16	3.3 (1.1)	6.8	8	5.4 (3.1)	10.4	60	22.3 (7.3)	47.4	96	6.0 (2.2)	20.6
Hawaii (4)	0	-	-	0	-	-	0	-	-	0	-	-	3	4.7 (2.7)	15.8
All Islands (105)	**11**	**29.8 (11.6)+**	**72.1**	**17**	**3.3 (0.1)**	**6.8**	**8**	**5.4 (3.1)**	**10.4**	**61**	**25.3 (4.3)**	**47.4**	**100**	**5.2 (0.7)**	**20.6**

KEY: n = number of whales having locations within that Navy area; # = number; * SD not reported here because only one location was received for this whale in this area; + Summary statistics do not include zero values in their calculation.

Table 11. Mean, SD, and maximum (Max) number of days spent inside BIAs in the Hawaiian Islands, Southeast Alaska (SEAK), and the Aleutian Islands, and in the waters from the 200-m isobaths around the Hawaiian Islands out to the 50-km buffer zone around the islands, for 105 humpback whales tagged in the Hawaiian Islands from 1995 to 2019.

	# Days														
Deployment Island (# Whales Tracked	**BIA-Kauai**			**BIA-Hawaii**			**BIA-SEAK**			**BIA-Aleutians**			**200m to 50km**		
	n	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**	**n**	**Mean (SD)**	**Max**
Kauai (5)	5	0.5 (0.2)	0.8	0	--	--	0	--	--	0	-	-	5	2.6 (1.7)	5.3
Maui (96)	10	1.3 (1.0)	3.5	2	3.8 (3.4)	6.2	4	27.8 (33.5)	70.0	2	0.6	1.0	88	4.4 (5.5)	30.2
Hawaii (4)	0	--	--	4	0.7 (0.4)	1.1	0	--	--	0	-	-	3	1.5 (0.3)	1.7
All Islands (105)	**15**	**0.9 (0.6)**	**3.5**	**6**	**2.3 (2.2)**	**6.2**	**4**	**27.8**	**70.0**	**2**	**0.6**	**1.0**	**96**	**2.8 (1.5)**	**30.2**

KEY: km = kilometers; m = meters; n = sample size; SD = standard deviation; # = number.

Table 12. Summary of dive data reported by 51 DM and DUR+ tags deployed on humpback whales off Maui, Hawaii, during March 2018 and 2019. Depth data were not available for DUR+ tags so % Near Surface is not reported for those tags.

Tag #	Year	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	% Near Surface	Mean Dives Per Day	Min Dives Per Day	Max Dives Per Day
832	2018	DM	Male	0.4	22	79.7	80.0	22	22	22
836	2018	DM	Male	12.0	1268	60.7	45.3	97.5	7	127
839	2018	DM	Male	15.1	1213	62.4	55.4	75.8	13	123
843	2018	DM	Female	62.8	3538	33.2	43.9	55.3	6	103
849	2018	DM	Female	11.3	599	28.4	56.9	46.1	8	72
4172	2018	DM	Male	53.5	3728	79.0	85.3	69.0	2	159
4177	2018	DUR+	Male	2.1	329	94.9	NA	82.3	2	162
5641	2018	DM	Male	22.8	717	38.8	73.0	37.7	4	65
5644	2018	DUR+	Male	10.9	957	47.1	NA	79.8	29	122
5655	2018	DM	Male	4.2	174	31.9	69.3	29.0	7	52
5685	2018	DM	Male	4.6	454	53.5	48.9	75.7	4	125
5701	2018	DM	Male	-	-	-	-	-	-	-
5736	2018	DM	Male	159.8	13188	66.6	64.0	82.4	4	152
5742	2018	DM	Male	4.4	355	51.7	69.8	71.0	27	105
5743	2018	DM	Male	2.4	152	49.4	60.2	38.0	6	98
5746	2018	DM	Male	7.9	565	44.5	68.9	62.8	7	103
5784	2018	DUR+	Female	104.4	13983	73.1	NA	133.2	56	258
5800	2018	DM	Male	57.8	1651	63.8	92.9	28.5	1	88
5826	2018	DUR+	Male	4.0	297	45.7	NA	49.5	1	95
5843	2018	DM	Male	0.1	15	107.5	39.5	15.0	15	15
5878	2018	DM	Female	1.0	121	89.4	80.8	60.5	15	106
5938	2018	DM	Male	11.0	877	71.2	34.8	73.1	24	130
10827	2018	DM	Male	7.2	534	65.2	63.5	59.3	1	108
10829	2018	DM	Male	3.9	381	58.7	55.3	76.2	34	102
10833	2018	DUR+	Unknown	20.0	2089	65.2	NA	99.5	27	174
825	2019	DM	Male	-	-	-	-	-	-	-

Tag #	Year	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	% Near Surface	Mean Dives Per Day	Min Dives Per Day	Max Dives Per Day
826	2019	DM	Unknown	-	-	-	-	-	-	-
827	2019	DM	Male	24.3	1459	41.7	61.3	66.3	7	147
830	2019	DM	Male	20.7	1458	41.0	64.9	72.9	2	175
831	2019	DM	Male	15.8	1131	56.9	70.9	66.5	29	110
834	2019	DM	Unknown	16.3	1942	79.5	48.8	107.9	12	151
835	2019	DM	Male	20.3	1540	48.3	55.5	73.3	3	128
836	2019	DM	Unknown	19.5	1259	48.8	73.7	60.0	10	100
838	2019	DM	Male	12.7	642	46.6	74.0	45.9	7	102
839	2019	DM	Male	0.3	61	86.4	77.6	30.5	3	58
840	2019	DM	Male	-	-	-	-	-	-	-
843	2019	DM	Male	67.7	3006	37.8	60.1	52.7	15	123
845	2019	DM	Male	0.6	119	94.6	64.8	59.5	50	69
847	2019	DM	Male	80.8	6811	68.5	61.8	84.1	5	157
848	2019	DM	Male	2.6	251	77.5	77.3	83.7	60	118
1385	2019	DM	Female	32.9	2347	82.2	82.6	71.1	29	149
1386	2019	DM	Male	12.3	636	31.8	64.2	45.4	6	76
1387	2019	DM	Male	13.7	1041	67.5	74.6	69.4	15	113
1389	2019	DM	Unknown	25.3	2286	69.6	65.4	84.7	12	150
1390	2019	DM	Unknown	42.0	2986	72.8	74.8	67.9	3	123
2082	2019	DM	Male	0.2	19	100.6	67.4	19.0	19	19
2083	2019	DM	Female	31.3	3381	81.1	50.2	102.5	10	156
4175	2019	DM	Male	-	-	-	-	-	-	-
4176	2019	DM	Male	22.6	2252	72.0	66.4	97.9	31	147
5648	2019	DM	Male	27.0	1951	48.4	69.8	92.9	4	191
5655	2019	DM	Male	14.4	797	36.1	61.2	56.9	8	158
		Mean*	**2018**	**24.3**	**1967**	**60.9**	**54.3**	**63.3**	**13.4**	**111.1**
			2019	**22.9**	**1699**	**63.2**	**66.7**	**68.7**	**15.5**	**123.6**
*** Tags that transmitted**			**Cumulative**	**23.6**	**1839**	**62.0**	**60.2**	**65.9**	**14.4**	**117.1**

Table 13. Summary of dive data in the breeding areas reported by 51 DM and DUR+ tags deployed on humpback whales off Maui, Hawaii, during March 2018 and 2019. Depth data were not available for DUR+ tags so % Near Surface is not reported for those tags.

Tag #	Year	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	% Near Surface	Mean Dives Per Day	Min Dives Per Day	Max Dives Per Day
832	2018	DM	Male	0.4	22	79.7	80	22	22	22
836	2018	DM	Male	12.0	1268	60.7	45.3	97.5	7	127
839	2018	DM	Male	15.1	1213	62.4	55.4	75.8	13	123
843	2018	DM	Female	22.8	1237	37.5	39.6	51.5	6	101
849	2018	DM	Female	11.3	599	28.4	56.9	46.1	8	72
4172	2018	DM	Male	3.3	281	71.2	80.5	70.3	32	117
4177	2018	DUR+	Male	2.1	329	94.9	NA	82.3	2	162
5641	2018	DM	Male	13.7	537	47.2	71.6	38.4	14	65
5644	2018	DUR+	Male	10.9	957	47.1	NA	79.8	29	122
5655	2018	DM	Male	4.2	174	31.9	69.3	29.0	7	52
5685	2018	DM	Male	4.6	454	53.5	48.9	75.7	4	125
5701	2018	DM	Male	-	-	-	-	-	-	-
5736	2018	DM	Male	13.0	958	51.7	59.3	68.4	12	115
5742	2018	DM	Male	4.4	355	51.7	69.8	71.0	27	105
5743	2018	DM	Male	2.4	152	49.4	60.2	38.0	6	98
5746	2018	DM	Male	7.9	565	44.5	68.9	62.8	7	103
5784	2018	DUR+	Female	5.5	638	72.5	NA	106.3	67	146
5800	2018	DM	Male	14.0	410	34.2	88.7	27.3	5	54
5826	2018	DUR+	Male	4.0	297	45.7	NA	49.5	1	95
5843	2018	DM	Male	0.1	15	107.5	39.5	15.0	15	15
5878	2018	DM	Female	1.0	121	89.4	80.8	60.5	15	106
5938	2018	DM	Male	11.0	877	71.2	34.8	73.1	24	130
10827	2018	DM	Male	7.2	534	65.2	63.5	59.3	1	108
10829	2018	DM	Male	3.9	381	58.7	55.3	76.2	34	102

Tag #	Year	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	% Near Surface	Mean Dives Per Day	Min Dives Per Day	Max Dives Per Day
10833	2018	DUR+	Unknown	20.0	2089	65.2	NA	99.5	27	174
825	2019	DM	Male	-	-	-	-	-	-	-
826	2019	DM	Unknown	-	-	-	-	-	-	-
827	2019	DM	Male	24.3	1459	41.7	61.3	66.3	7	147
830	2019	DM	Male	20.7	1458	41.0	64.9	72.9	2	175
831	2019	DM	Male	15.8	1131	56.9	70.9	66.5	29	110
834	2019	DM	Unknown	16.3	1942	79.5	48.8	107.9	12	151
835	2019	DM	Male	11.3	752	40.3	60.5	62.7	3	125
836	2019	DM	Unknown	6.6	513	60.7	76.9	64.1	10	100
838	2019	DM	Male	12.7	642	46.6	74.0	45.9	7	102
839	2019	DM	Male	0.3	61	86.4	77.6	30.5	3	58
840	2019	DM	Male	-	-	-	-	-	-	-
843	2019	DM	Male	19.9	1254	47.5	56.7	62.7	15	123
845	2019	DM	Male	0.6	119	94.6	64.8	59.5	50	69
847	2019	DM	Male	36.5	3598	69.0	54.4	94.7	31	157
848	2019	DM	Male	2.6	251	77.5	77.3	83.7	60	118
1385	2019	DM	Female	3.6	171	60.5	81.6	42.8	18	81
1386	2019	DM	Male	7.2	373	34.3	70.4	46.6	31	59
1387	2019	DM	Male	8.2	586	69.4	82.1	58.6	7	92
1389	2019	DM	Unknown	25.3	2286	69.6	65.4	84.7	12	150
1390	2019	DM	Unknown	11.5	936	68.7	64.6	72.0	3	104
2082	2019	DM	Male	0.2	19	100.6	67.4	19.0	19	19
2083	2019	DM	Female	19.0	2026	81.6	43.9	101.3	10	156
4175	2019	DM	Male	-	-	-	-	-	-	-
4176	2019	DM	Male	17.3	1810	76.1	68.2	100.6	25	147
5648	2019	DM	Male	9.6	1046	58.9	61.0	104.6	41	191
5655	2019	DM	Male	6.5	623	50.6	66.8	89.0	26	158

Tag #	Year	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	% Near Surface	Mean Dives Per Day	Min Dives Per Day	Max Dives Per Day
		Mean*	**2018**	**8.1**	**602.6**	**59.2**	**61.5**	**61.5**	**16.0**	**101.6**
			2019	**12.5**	**1048.0**	**64.2**	**66.4**	**69.8**	**19.1**	**117.8**
*** Tags that transmitted**			**Cumulative**	**10.2**	**815.6**	**61.6**	**64.1**	**65.5**	**17.5**	**109.4**

Table 14. Summary of dive data during migration reported by 18 DM and DUR+ tags deployed on humpback whales off Maui, Hawaii, during March 2018 and 2019. Depth data were not available for DUR+ tags so % Near Surface is not reported for that tag.

Tag #	Year	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	% Near Surface	Mean Dives Per Day	Mean Lunges Per Day
843	2018	DM	Female	39.7	2301	31.0	46.9	56.1	4.8
4172	2018	DM	Male	29.3	1692	81.3	86.2	56.4	0.1
5641	2018	DM	Male	9.1	180	26.2	76.8	30.0	4.2
5736	2018	DM	Male	27.3	1723	62.9	77.0	61.5	0.0
5784	2018	DUR+	Female	45.6	5795	75.7	-	123.3	1.6
5800	2018	DM	Male	35.6	830	79.5	94.1	23.1	0.5
835	2019	DM	Male	7.9	788	65.9	51.1	87.6	23.3
836	2019	DM	Unknown	12.3	746	44.7	71.3	57.4	17.7
843	2019	DM	Male	26.7	1134	47.8	65.5	40.5	24.3
847	2019	DM	Male	34.3	2316	65.3	67.5	68.1	34.3
1385	2019	DM	Female	29.2	2176	85.0	82.6	72.5	13.3
1386	2019	DM	Male	5.1	263	28.4	53.8	37.6	9.9
1387	2019	DM	Male	5.5	455	64.9	62.6	75.8	16.7
1390	2019	DM	Unknown	30.5	2050	74.4	78.3	64.1	23.4
2083	2019	DM	Female	12.2	1355	80.5	60.2	96.8	3.3
4176	2019	DM	Male	5.3	442	58.7	59.0	73.7	6.3
5648	2019	DM	Male	10.1	905	73.6	76.5	82.3	0.5
5655	2019	DM	Male	6.0	174	31.3	51.5	24.9	0.7
		Mean	**2018**	**31.1**	**2086.8**	**59.4**	**67.6**	**58.4**	**1.9**
			2019	**15.4**	**1067.0**	**60.0**	**65.0**	**65.1**	**14.5**
			Cumulative	**20.7**	**1406.9**	**59.8**	**65.8**	**62.9**	**10.3**

Table 15. Summary of dive data while in the feeding areas reported by six DM and DUR+ tags deployed on humpback whales off Maui, Hawaii, during March 2018 and 2019. Depth data were not available for DUR+ tags so % Near Surface is not reported for that tag.

Tag #	Year	Tag Type	Sex	Summary Period (days)	# Dives	% Track Summarized	% Near Surface	Mean Dives Per Day	Mean Lunges Per Day
843	2019	DM	Male	9.3	618	36.2	*	61.8	3.9
847	2019	DM	Male	9.9	897	79.0	69.4	81.5	40.1
4172	2018	DM	Male	20.7	1755	77.7	84.7	79.8	0.5
5736	2018	DM	Male	119.5	10507	69.0	61.6	87.6	2.8
5784	2018	DUR+	Female	53.2	7550	71.0	-	139.8	11.9
5800	2018	DM	Male	7.4	411	50.3	89.1	51.4	0.9
		Median	**2018**	**37.0**	**4653**	**70.0**	**84.7**	**83.7**	**1.9**
			2019	**9.6**	**758**	**57.6**	**69.4**	**71.7**	**22.0**
*** Suspicious dive depths so not included**			**Cumulative**	**15.3**	**1326**	**70.0**	**77.0**	**80.7**	**3.4**

Table 16. The identity and frequency of the six mtDNA haplotypes, including GenBank codes, resolved for the 23 whales sampled off Maui, Hawaii, during 2018, and the 22 whales sampled off Maui during 2019.

Haplotype code	GenBank code	Number of tagged Maui whales in 2018 with haplotype	Number of tagged Maui whales in 2019 with haplotype
A+	KF477244	4	5
A-	KF477245	10	12
A3	KF477246	-	1
E1	KF477249	2	1
E2	KF477256	2	1
E5	KF477258	2	1
F2	KF477266	3	1
Total		23	22

Table 17. Results of pairwise tests of differentiation of mtDNA haplotype frequencies between the Maui 2018 (n = 23) and 2019 (n = 22) tagging samples and the 18 regional strata (feeding and breeding areas) defined in SPLASH (Baker et al. 2013). The regional abbreviations and associated sample sizes are consistent with Figure 1a and b. The sample sizes refer to the number of individuals with associated haplotypes in each region. Rows in italics indicate low sample numbers for comparisons with western Aleutians and the Philippines.

		2018 Maui Tagging n = 23		**2019 Maui tagging n = 22**	
Region	**n**	**F_{ST}**	***p*-value**	**F_{ST}**	***p*-value**
Feeding Areas					
Russia (RUS)	70	0.1070	<0.0001*	0.1597	<0.0001*
Western Aleutians (WAL)	*8*	*0.0263*	*0.2222*	*0.0987*	*0.0403**
Bering (BER)	114	0.0801	0.0011*	0.1161	<0.0001*
Eastern Aleutians (EAL)	36	0.0354	0.0701	0.0767	0.0101*
Western Gulf of Alaska (WGOA)	96	0.0359	0.0325*	0.0733	0.0026*
Northern Gulf of Alaska (NGOA)	233	0.0075	0.2385	0.0153	0.1589
Southeastern Alaska (SEA)	183	0.0664	0.0251*	0.0000	0.3313
Northern British Columbia (NBC)	104	0.0366	0.0804	0.0000	0.5217
Southern British Columbia/Washington (SBC/WA)	51	0.0476	0.0260*	0.0711	0.0087*
California/Oregon (CA/OR)	123	0.1242	<0.0001*	0.1971	<0.0001*
Breeding Areas					
Philippines (PHI)	*13*	*0.2326*	*0.0002**	*0.3145*	*<0.0001**
Okinawa (OK)	72	0.2365	<0.0001*	0.2997	<0.0001*
Ogasawara (OG)	159	0.0857	<0.0001*	0.1377	<0.0001*
Hawaii (HI)	227	0.0056	0.2784	0.0058	0.2731
Maui Tagging 2018	23	-	-	0.0000	0.8034
Mexico-Archipelago Revillagigedo (MX-AR)	106	0.0601	0.0023*	0.0980	0.0002*
Mexico-Baja California (MX-BC)	110	0.0451	0.0062*	0.0850	0.0001*
Mexico-Mainland (MX-ML)	62	0.0626	0.0027*	0.1142	<0.0001*
Central America (CENTAM)	36	0.1702	0.0002*	0.2588	<0.0001*

KEY: * = significant difference.

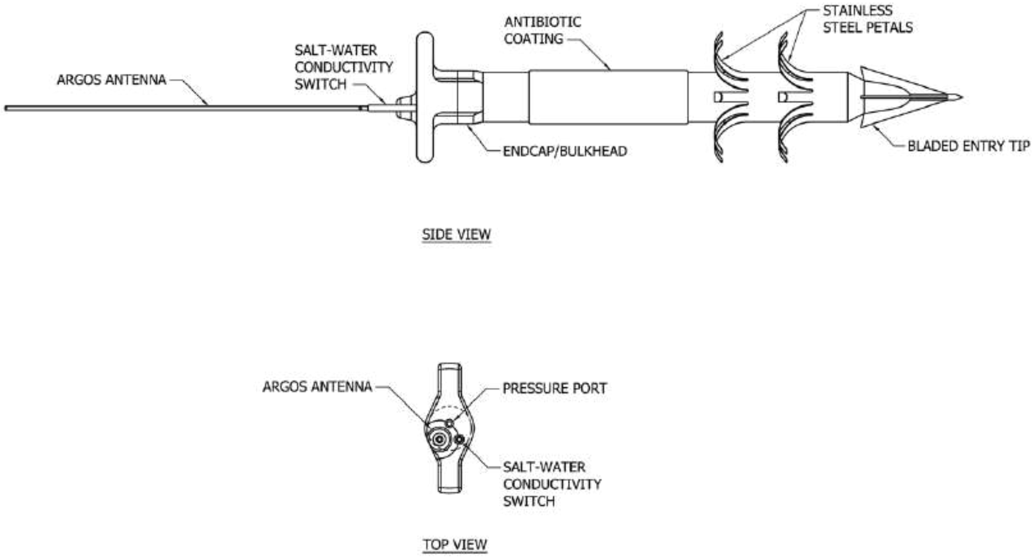

Figure 1. Schematic diagram of the Telonics RDW-665 DM tag showing the main body, the distal endcap with the antenna and saltwater conductivity switch endcap, as well as the penetrating tip and anchoring system.

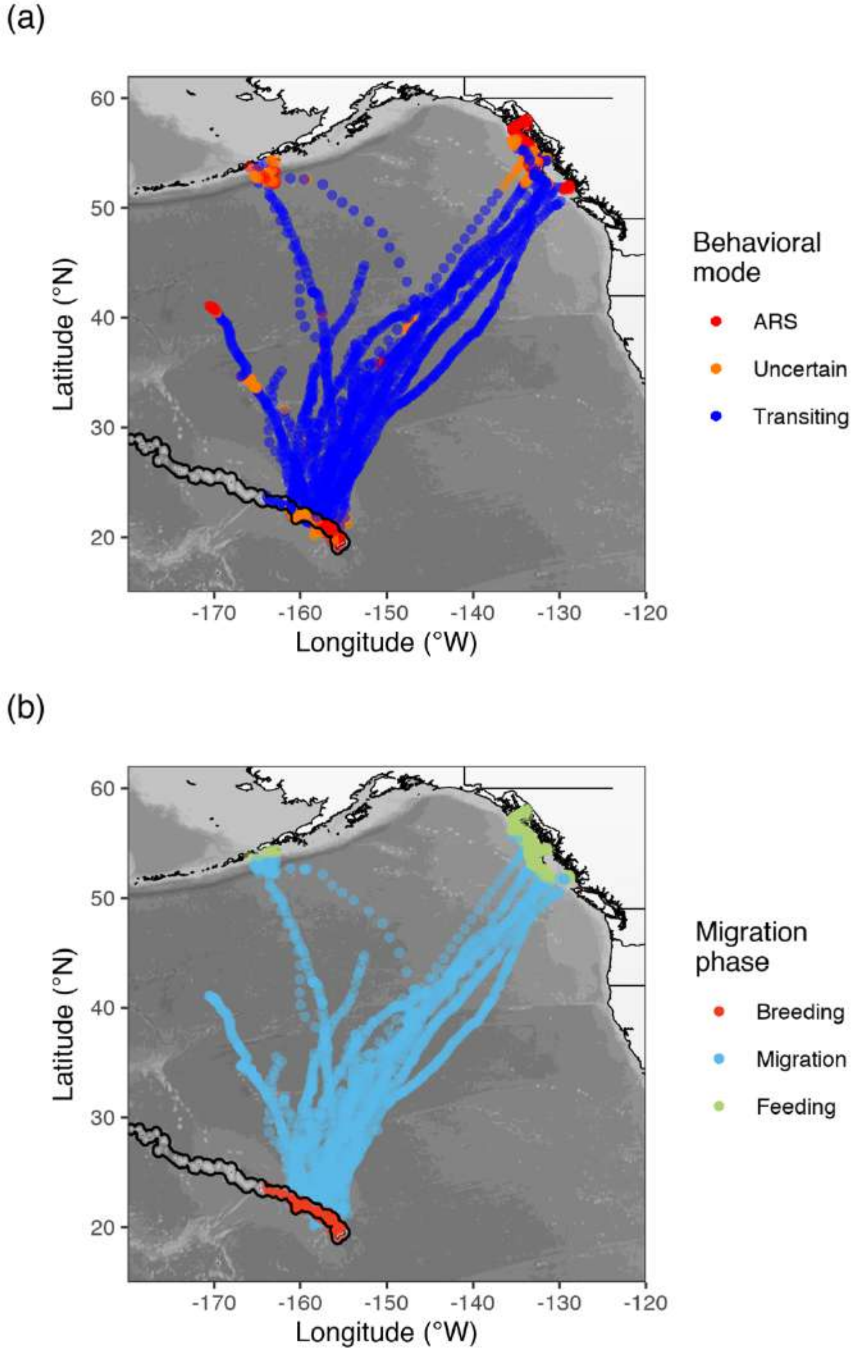

Figure 2. Map of the North Pacific basin showing regularized locations estimated by state-space models for 86 Argos tracks of humpback whales tagged by OSU in the Hawaiian Islands (1995-2000, 2015, 2018, 2019). Locations are colored by: a) annotated behavioral mode, and b) migration phase identified based on occurrence within or beyond a 50-km buffer zone from the coastline. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding area. Maps are truncated at the dateline to emphasize the region where most tracks occurred.

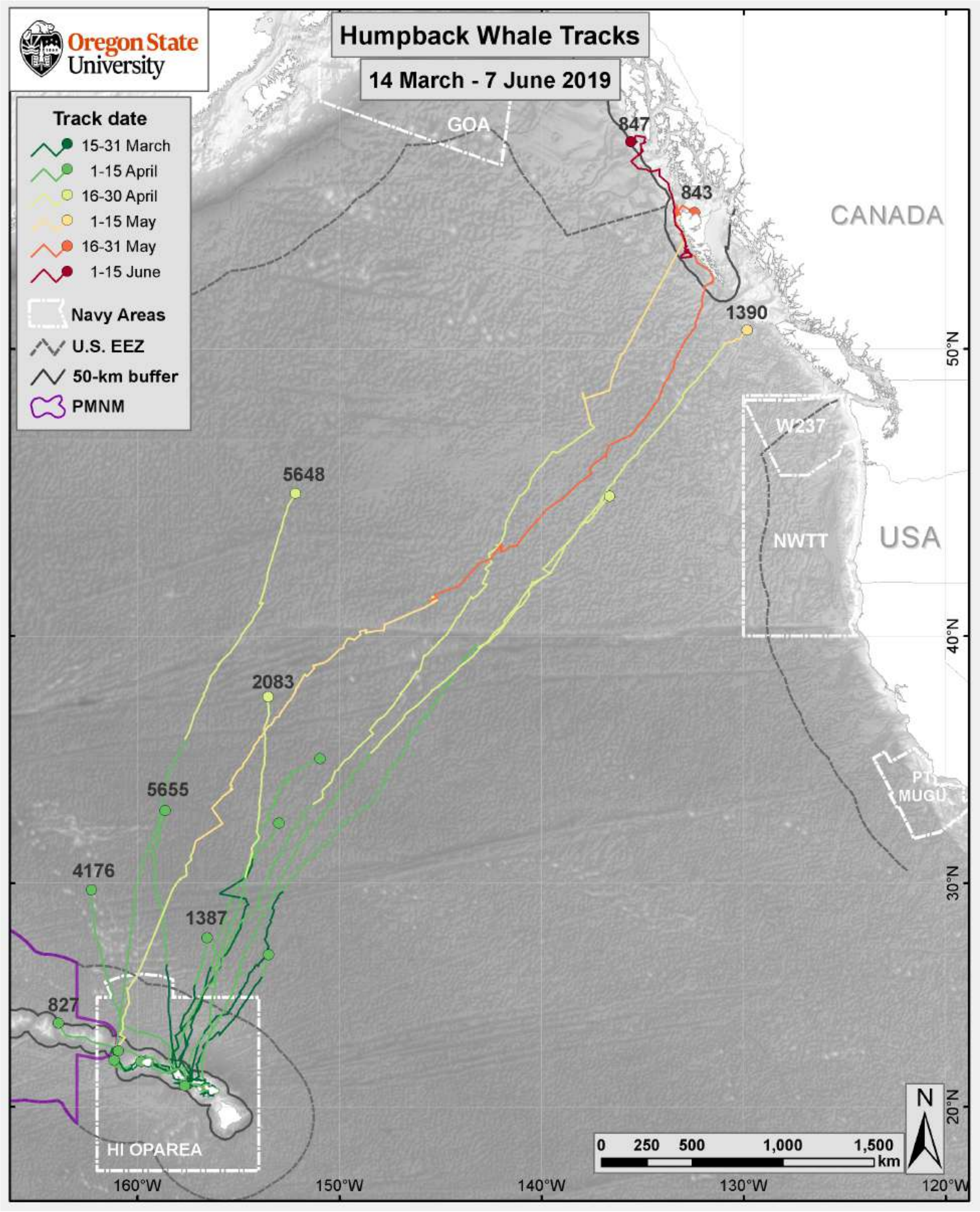

Figure 3. Satellite-monitored tracks for humpback whales tagged off Maui, Hawaii, in March 2019 (24 whales). The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding area (see Methods Section 2.6 for details).

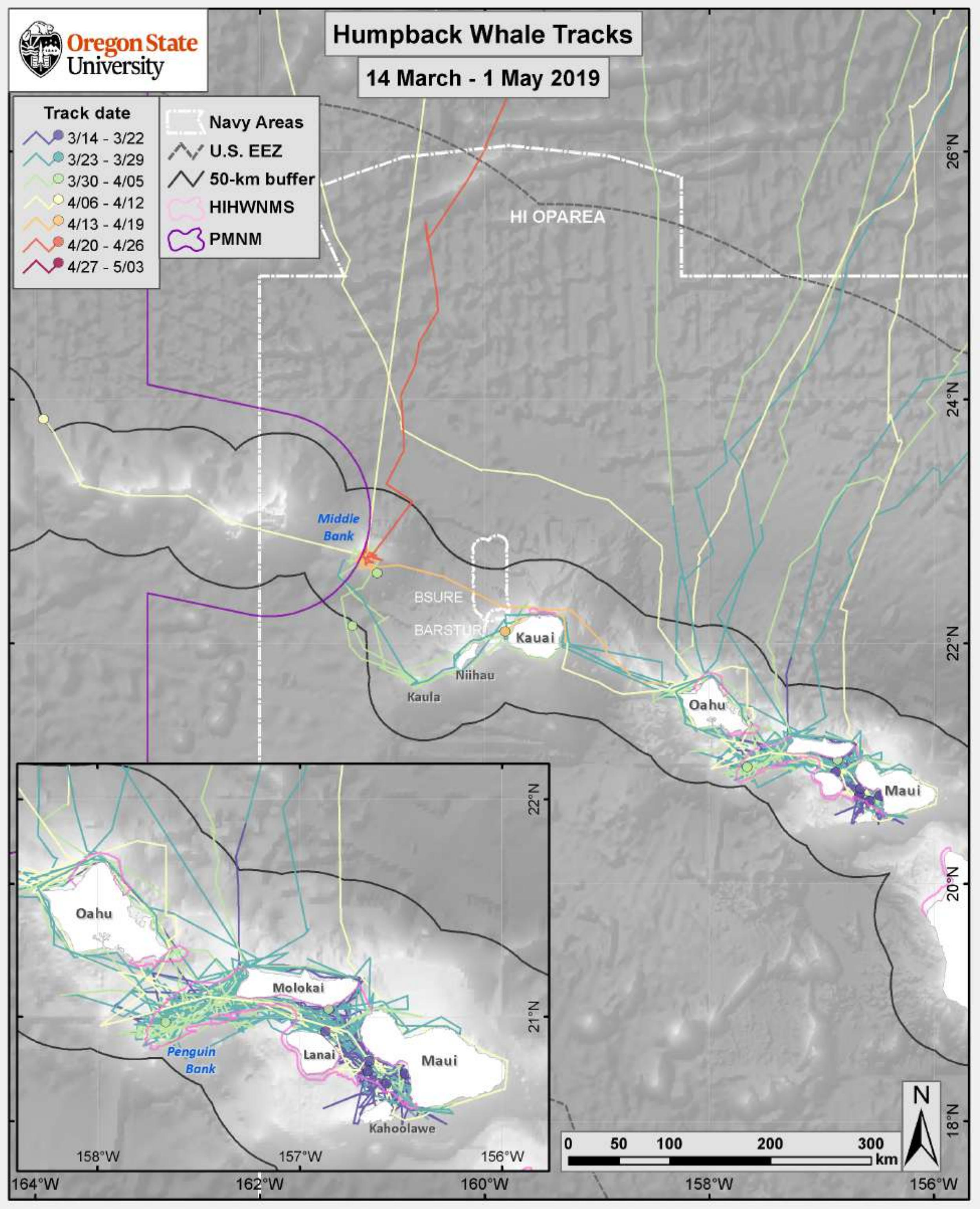

Figure 4. Satellite-monitored tracks for humpback whales tagged off Maui, Hawaii, in March 2019 (24 whales), highlighting movements within the Hawaiian Islands and during the beginning of migration. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding area (see Methods Section 2.6 for details).

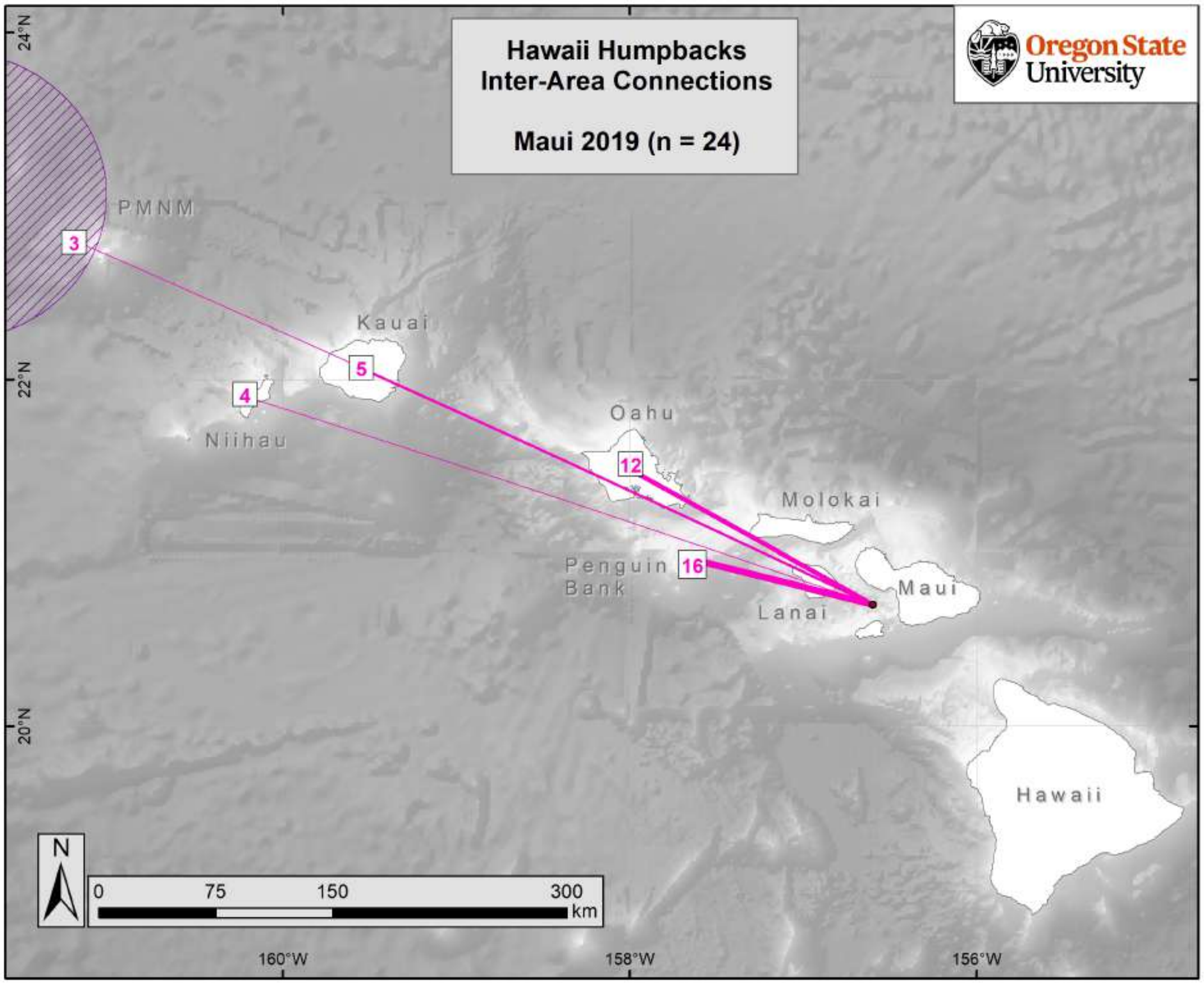

Figure 5. The number of whales (shown in boxes) tagged off Maui, Hawaii, in 2019 that were tracked to other areas in the Hawaiian Islands.

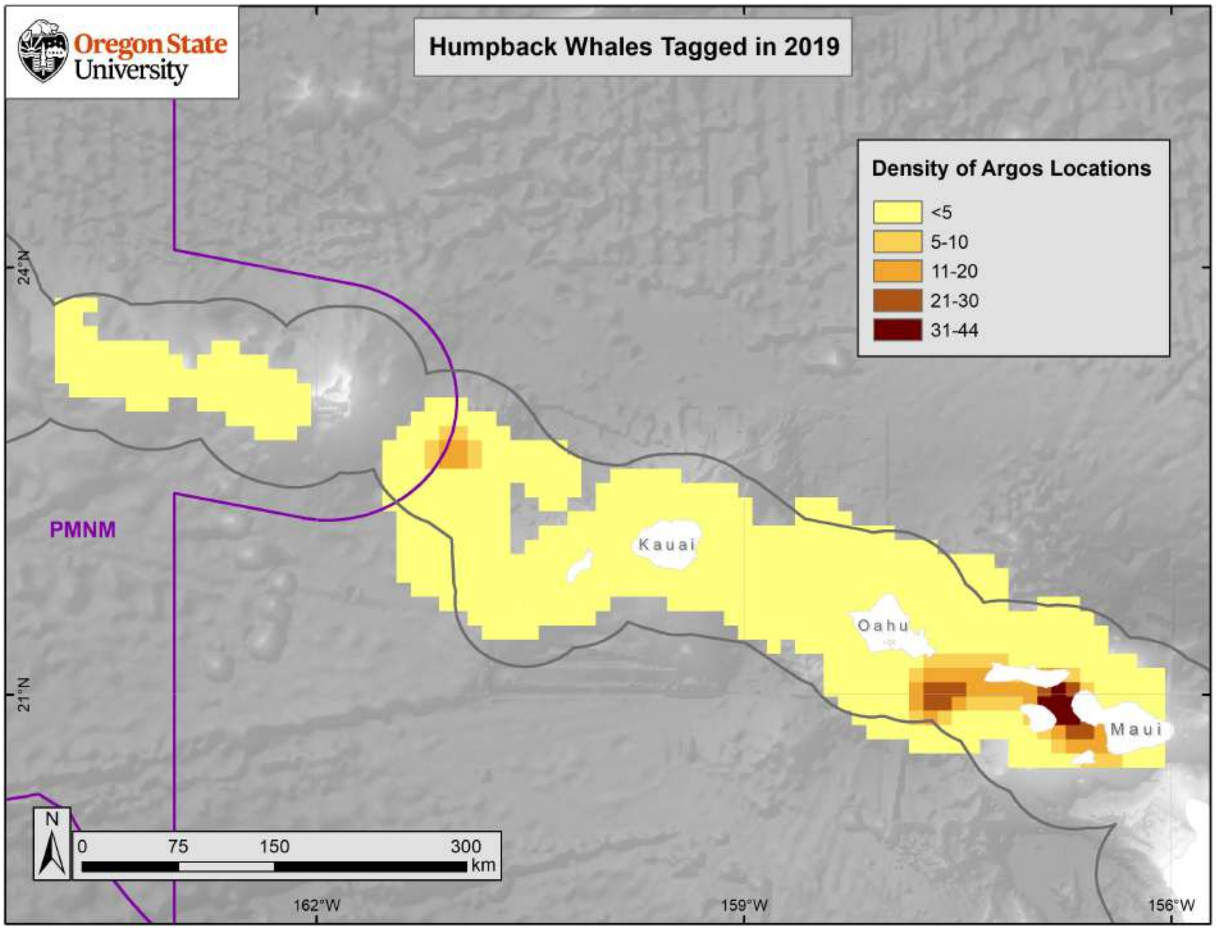

Figure 6. Kernel density utilization distribution for Argos locations in the Hawaiian Islands of humpback whales tagged off Maui, Hawaii, in March 2019 (24 whales). Grid cell size is 0.1 × 0.1 deg. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding area (see Methods Section 2.6 for details). The purple polygon corresponds to the Papahanaumokuakea Marine National Monument (PMNM).

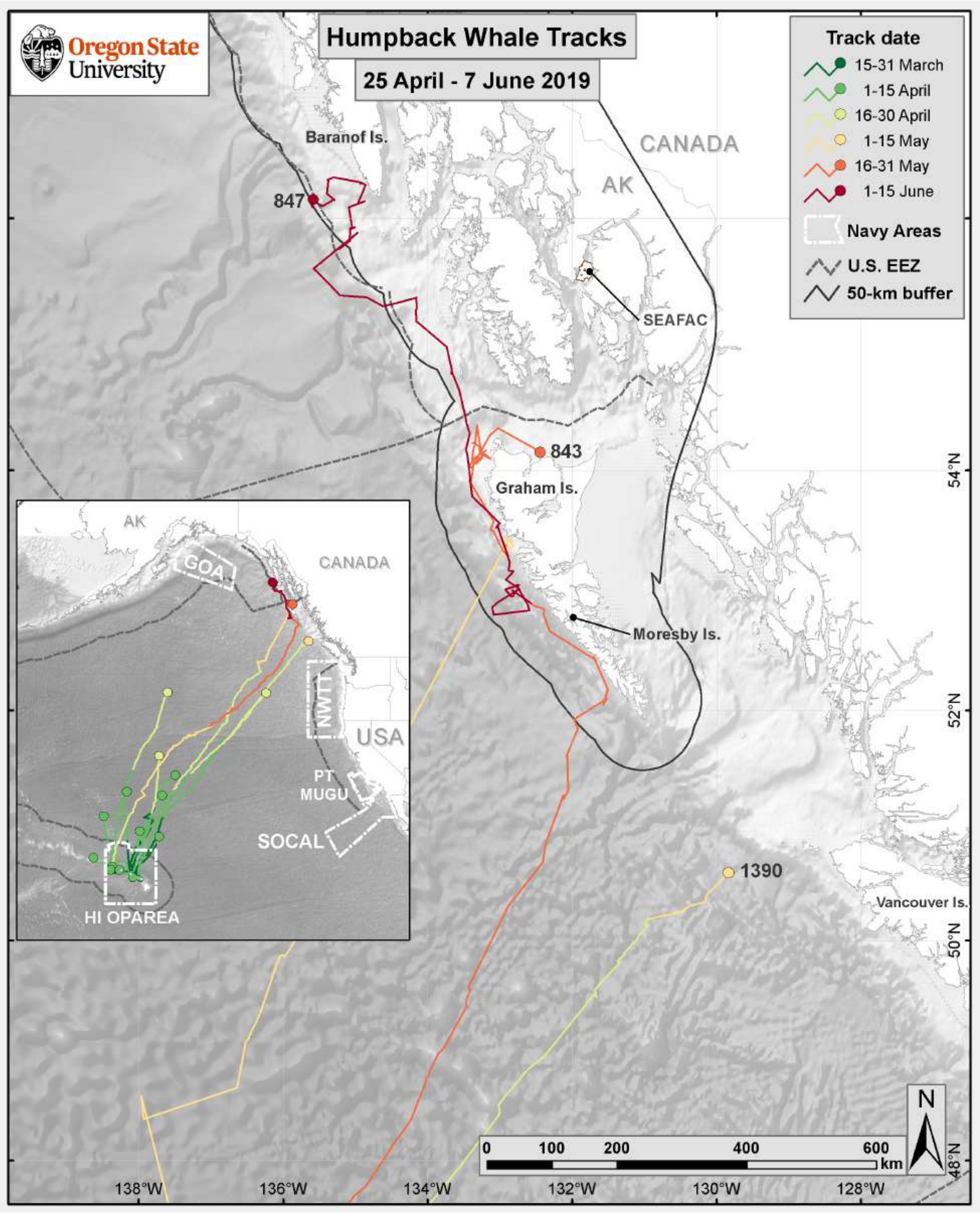

Figure 7. Satellite-monitored tracks for humpback whales tagged off Maui, Hawaii, in March 2019 (24 whales), highlighting migration and movement in feeding areas. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the northern British Columbia and southeastern Alaska feeding area (see Methods Section 2.6 for details).

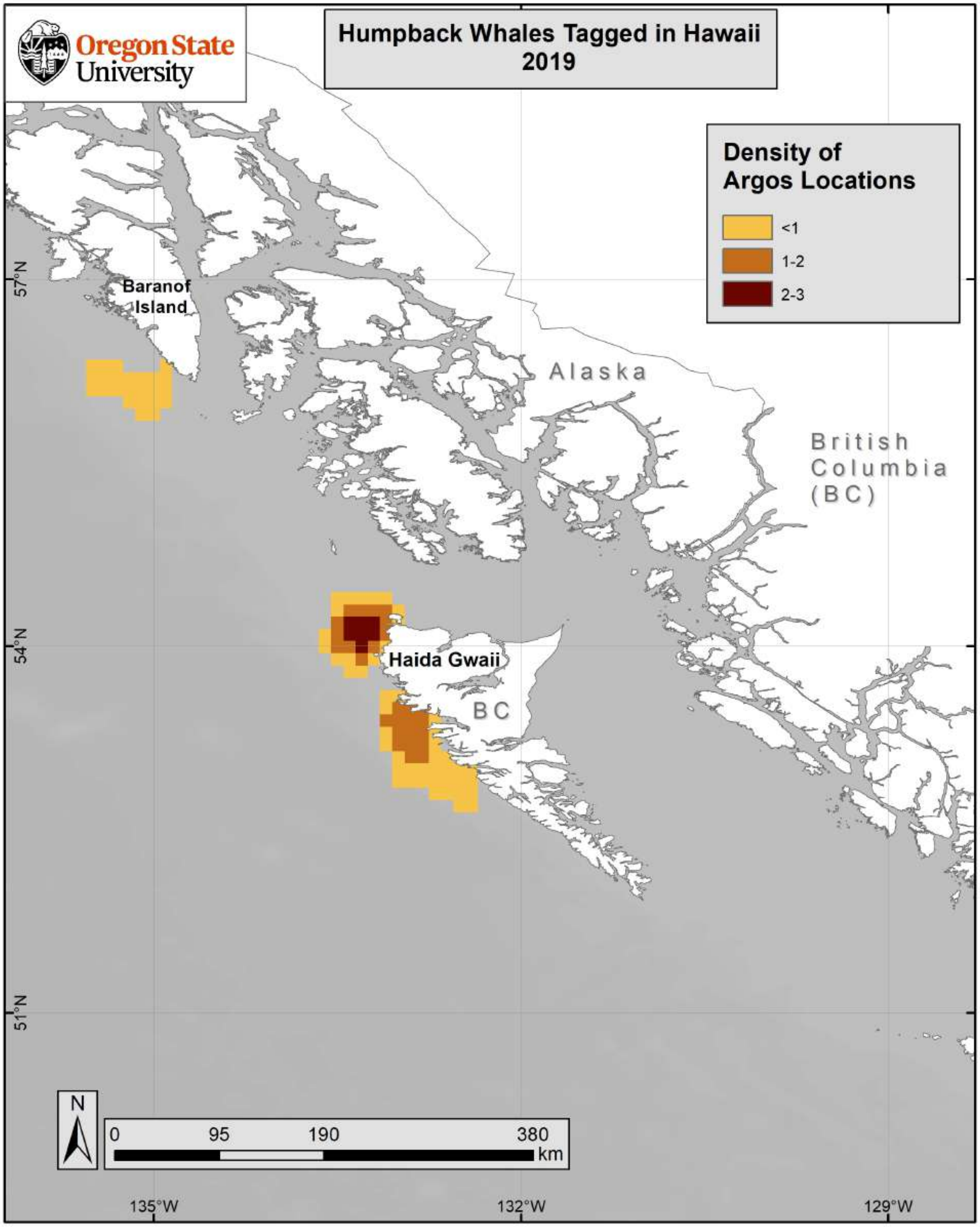

Figure 8. Kernel density utilization distribution for Argos locations in northern British Columbia and southeastern Alaska of humpback whales tagged off Maui, Hawaii, in March 2019 (two whales). Grid cell size is 0.1 × 0.1 deg.

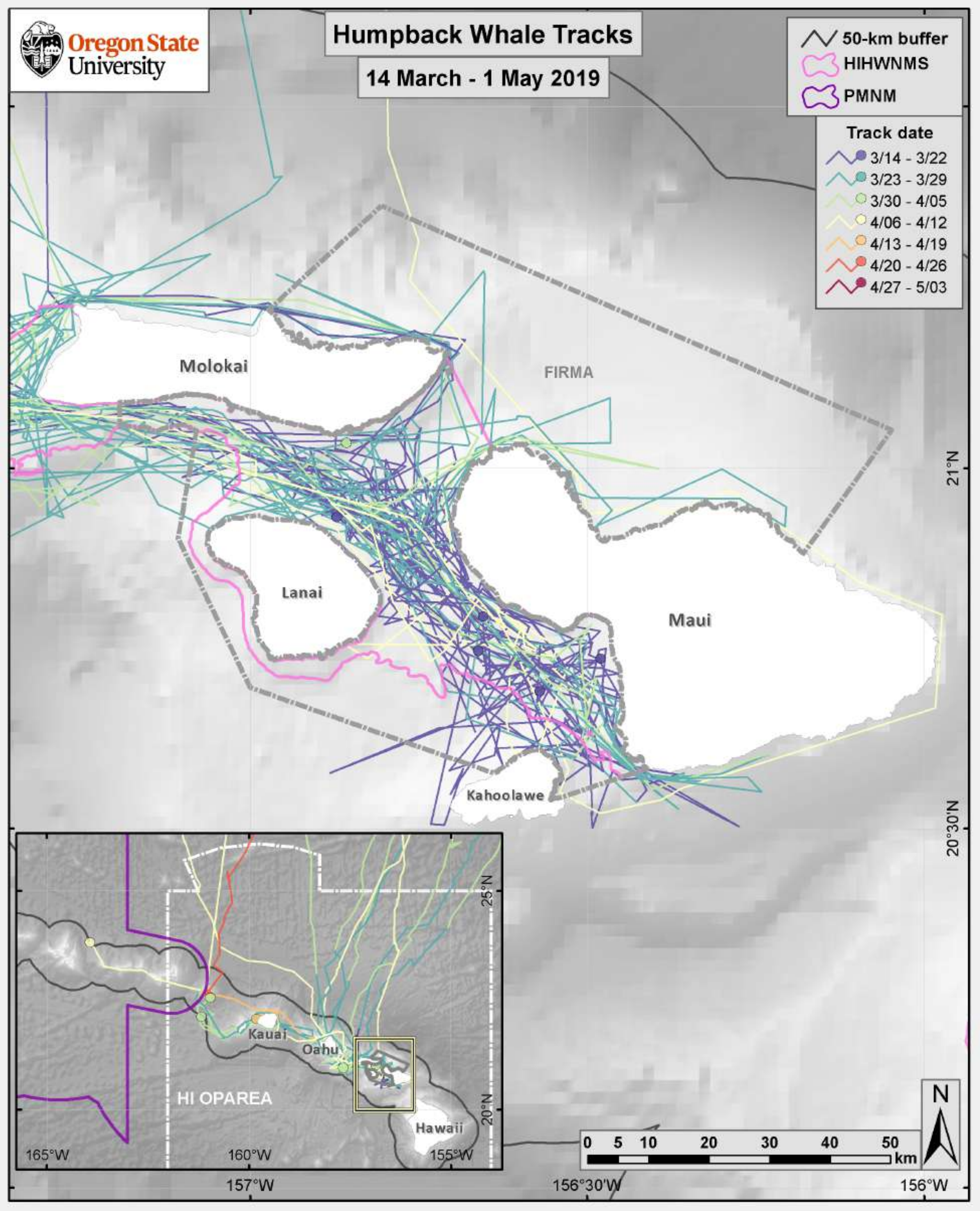

Figure 9. Satellite-monitored tracks in FIRMA for humpback whales tagged off Maui, Hawaii, in March 2019 (24 whales).

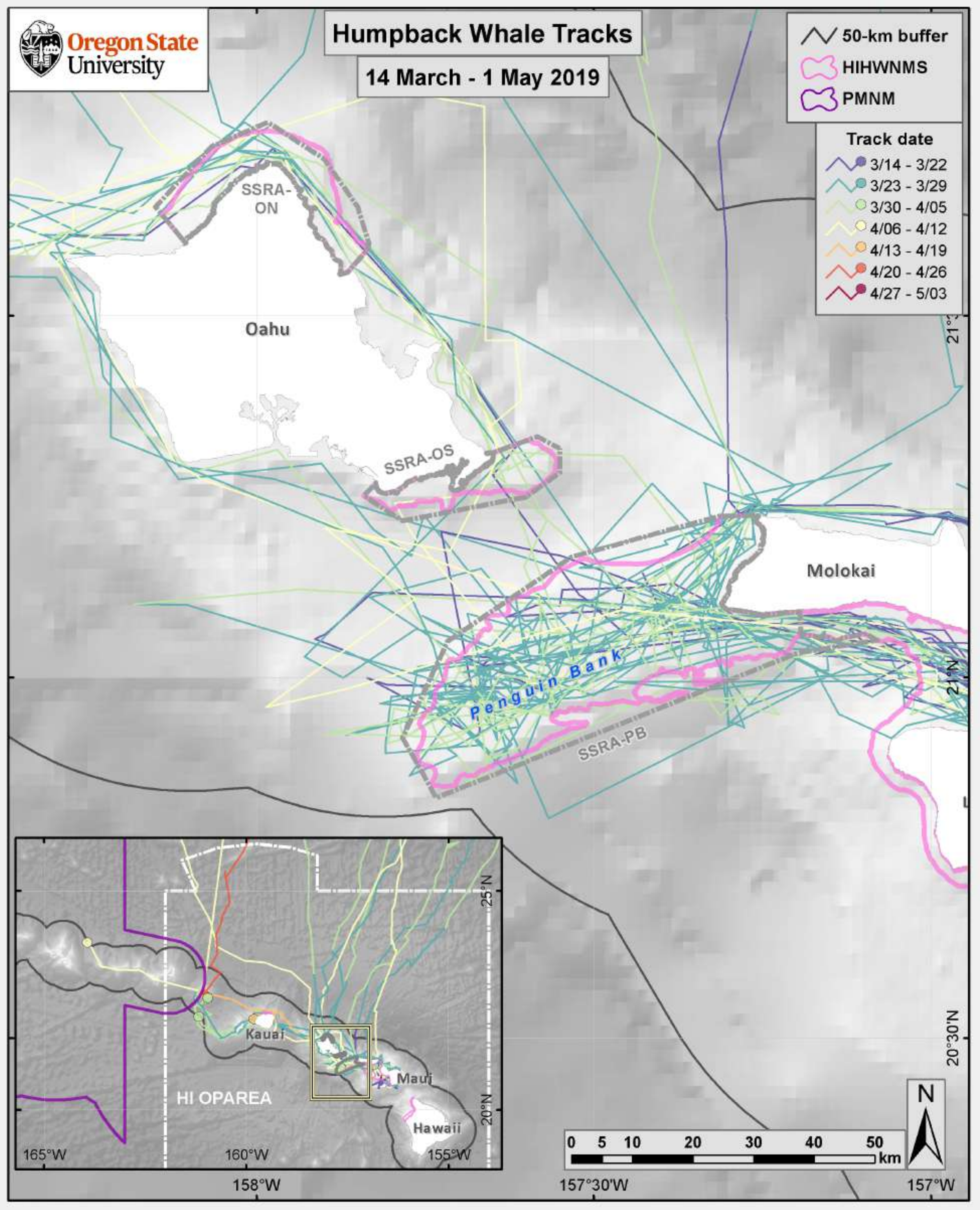

Figure 10. Satellite-monitored tracks in SSRA-PB (18 whales), SSRA-ON (10 whales), and SSRA-OS (nine whales) for humpback whales tagged off Maui, Hawaii, in March 2019.

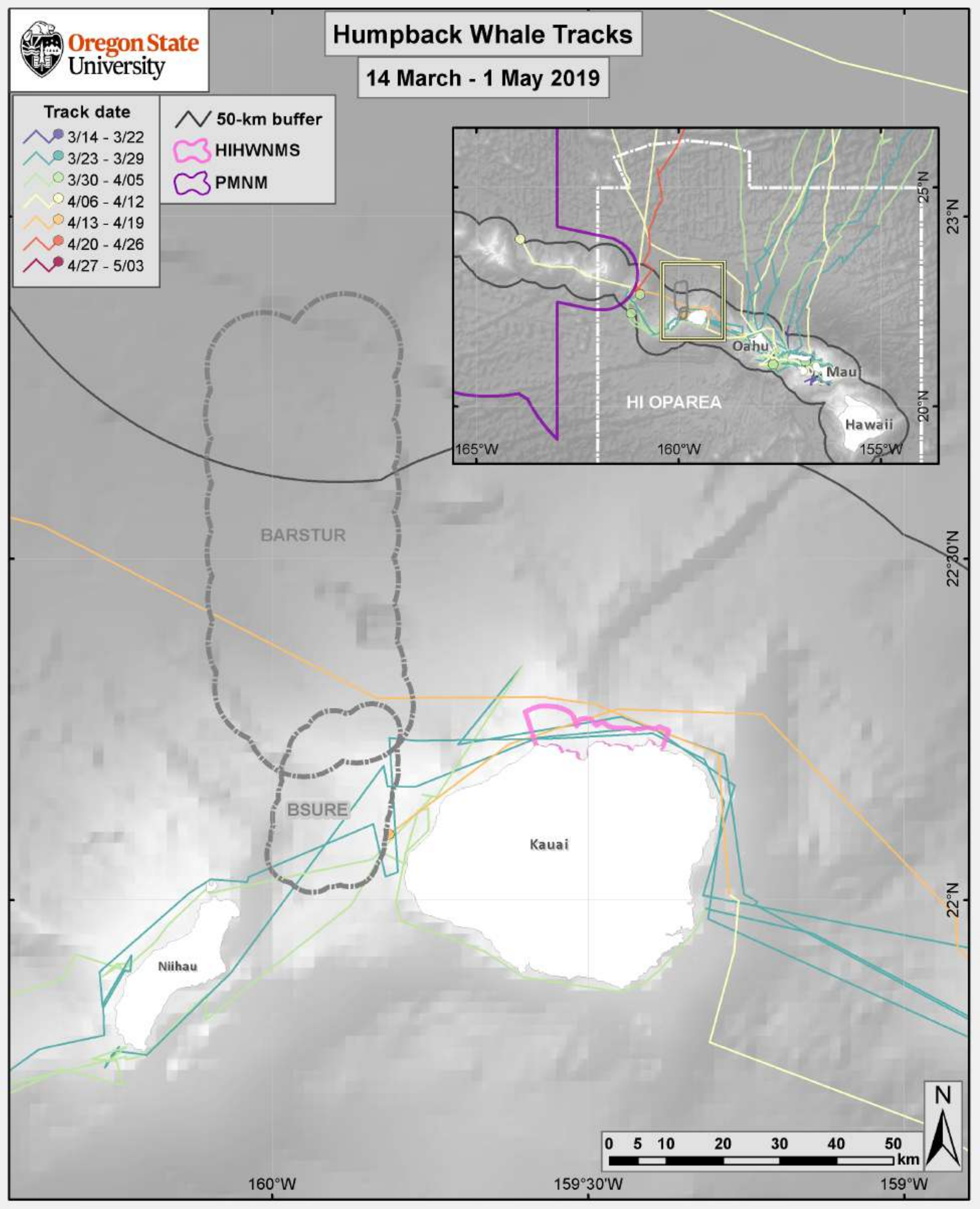

Figure 11. Satellite-monitored tracks in BS-Merge (BARSTUR and BSURE combined) for humpback whales tagged off Maui, Hawaii, in March 2019 (five whales).

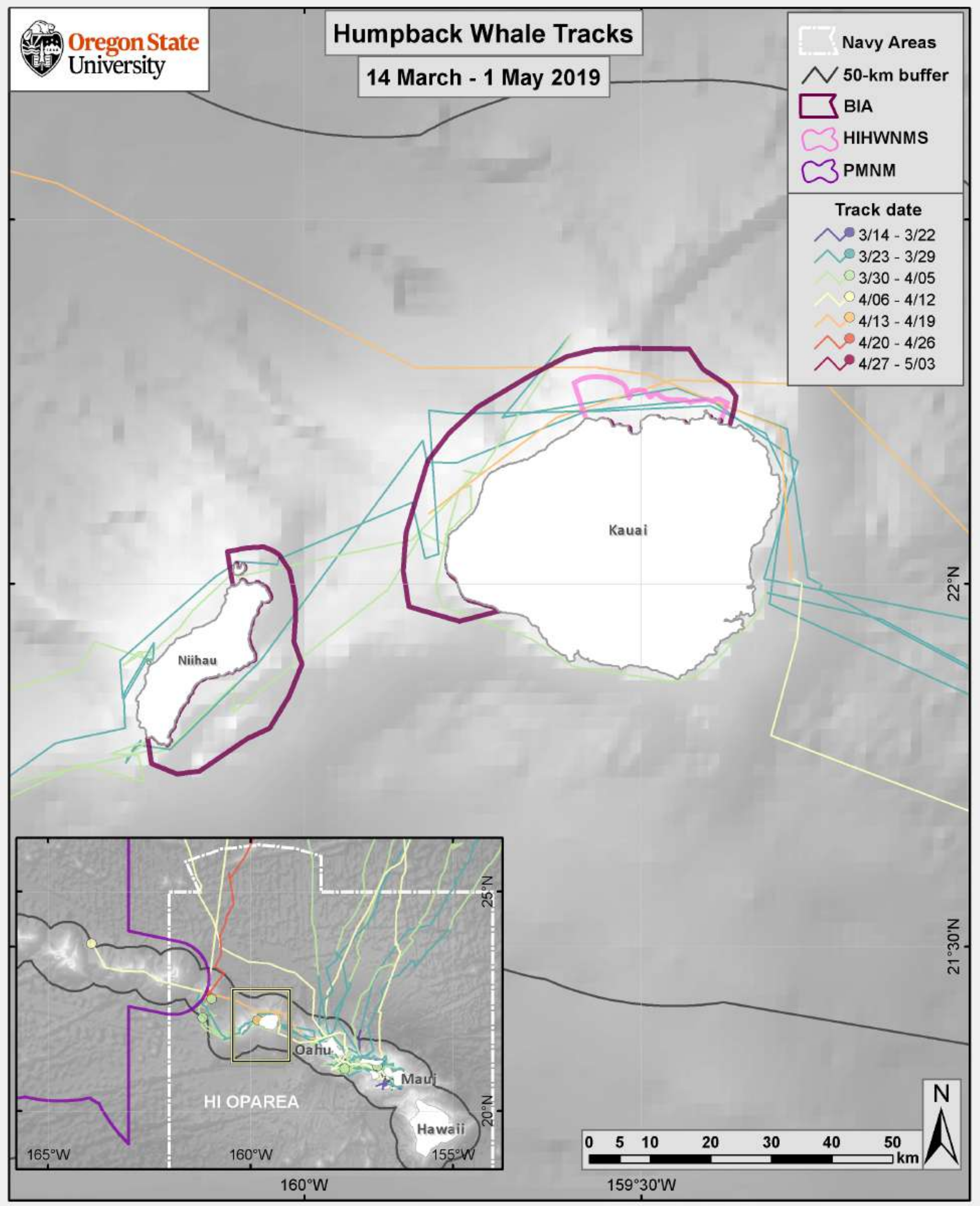

Figure 12. Satellite-monitored tracks in the Kauai BIA for humpback whales tagged off Maui, Hawaii, in March 2019 (six whales).

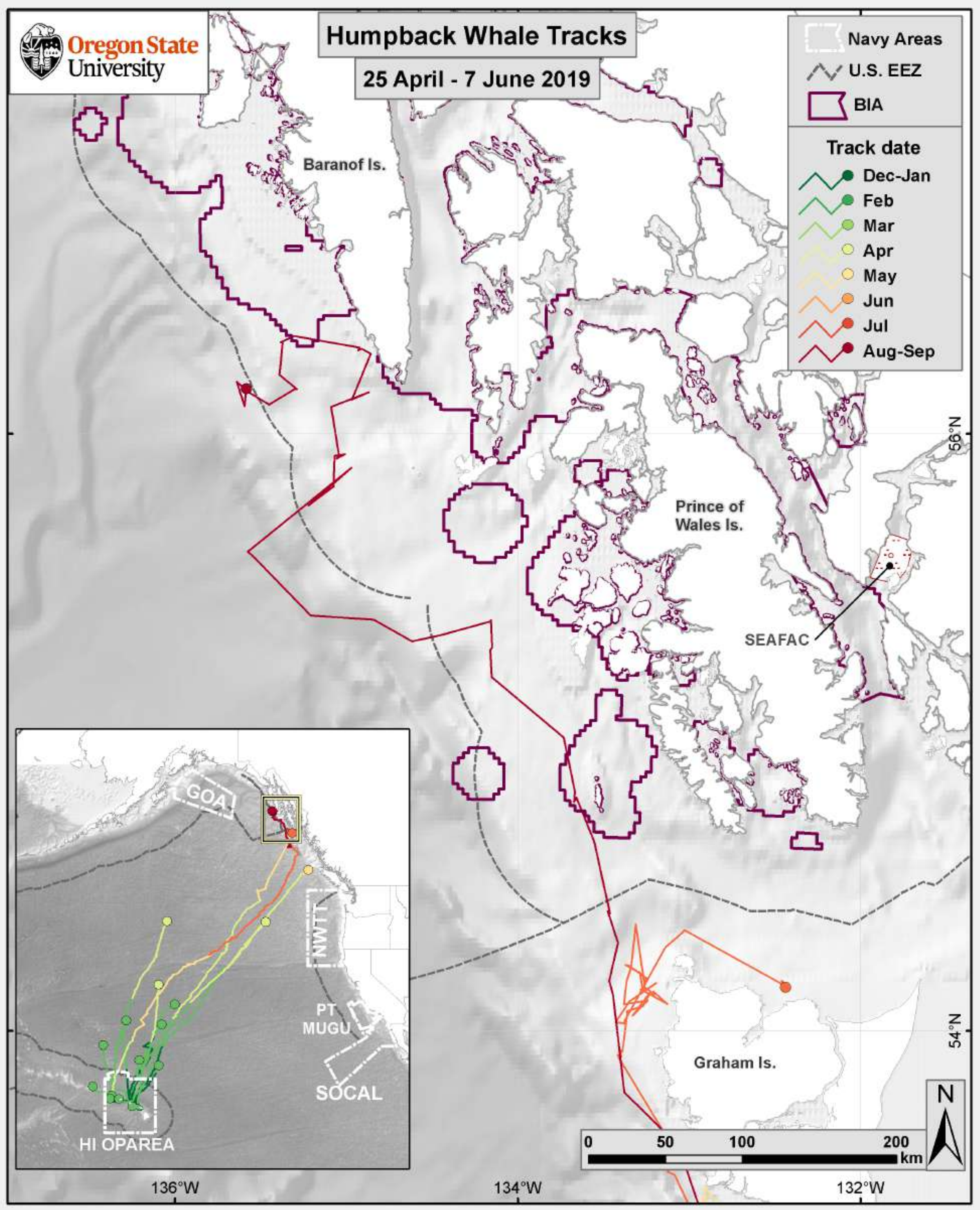

Figure 13. Satellite-monitored track in the Southeast Alaska BIA for a humpback whale tagged off Maui, Hawaii, in March 2019.

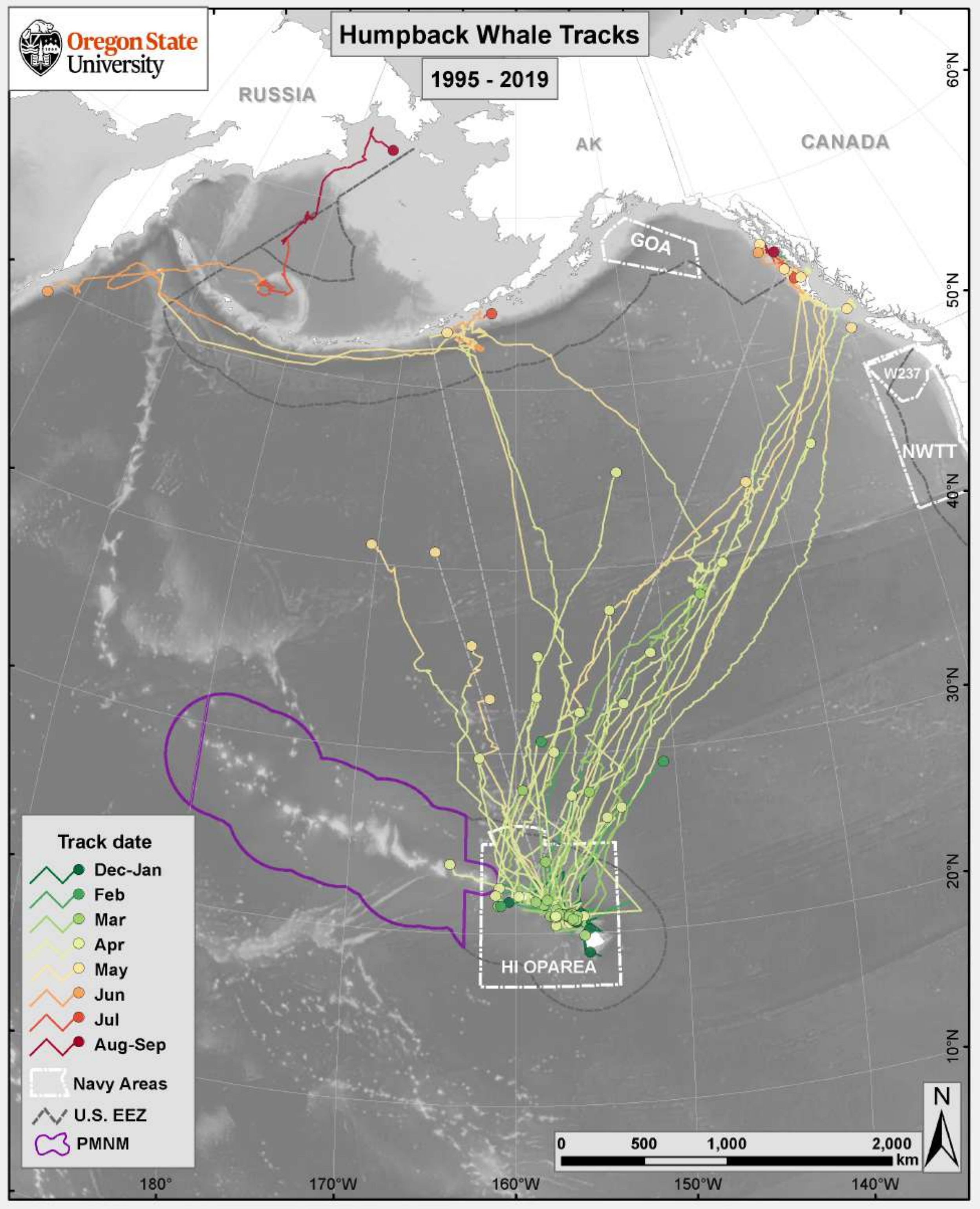

Figure 14. Satellite-monitored tracks for humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (105 whales).

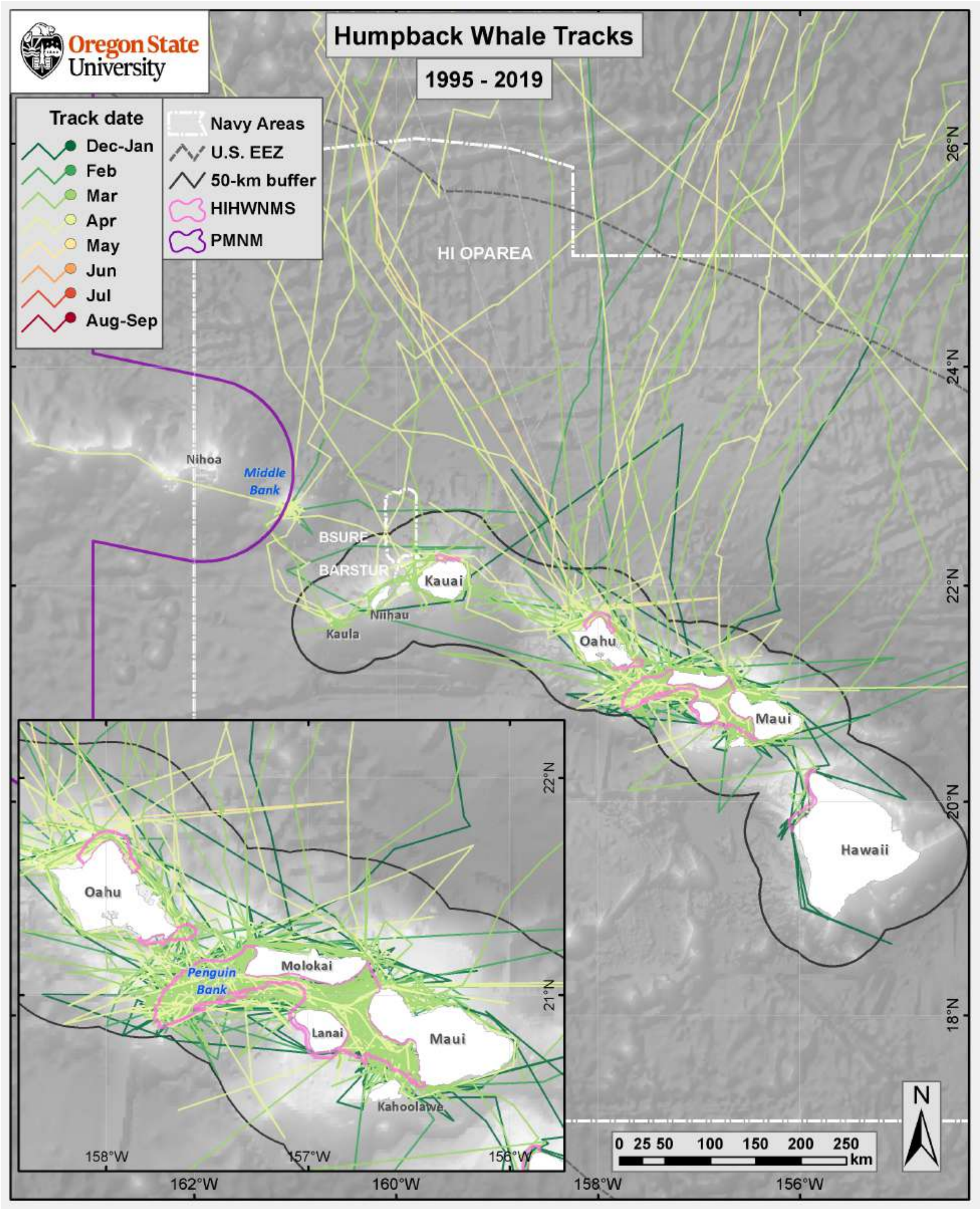

Figure 15. Satellite-monitored tracks for humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (105 whales). The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding area (see Methods Section 2.6 for details).

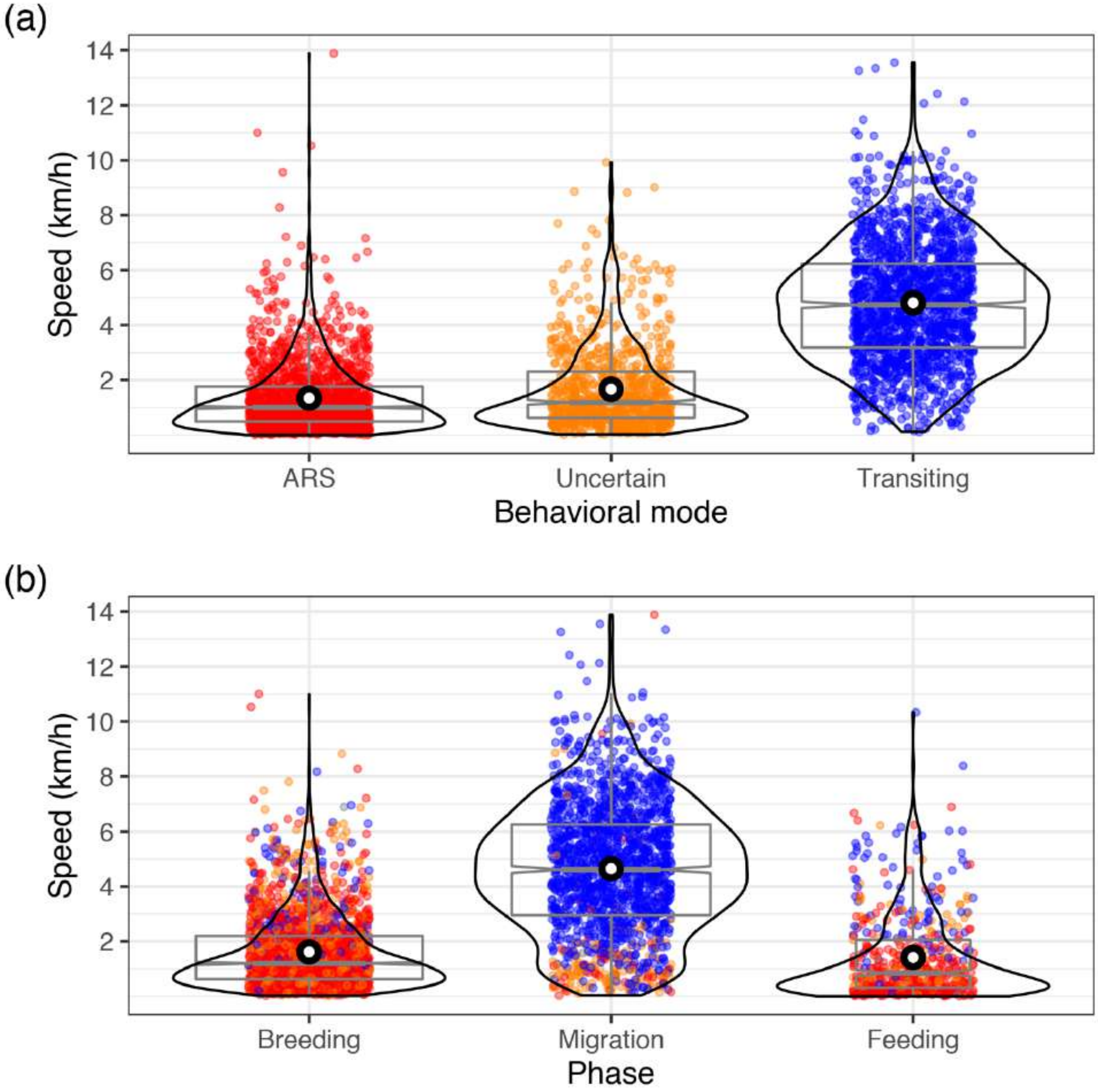

Figure 16. Violin plots of travel speed (in km/h) between location pairs for 86 Argos tracks of humpback whales tagged by OSU in the Hawaiian Islands (1995-2000, 2015, 2018, 2019) on which state-space models were run. Top panel (a) shows the data by behavioral mode, and bottom panel (b) by migration phase, as determined by occurrence inside or outside the 50-km buffer zones. In both panels, locations are colored by their behavioral mode classification (red = ARS, orange = uncertain, blue = transiting). Horizontal lines inside the violins correspond to the sample quartiles and the black circle corresponds to the mean. Violin areas are scaled proportionally to the number of observations in each grouping, as reported in Table 7.

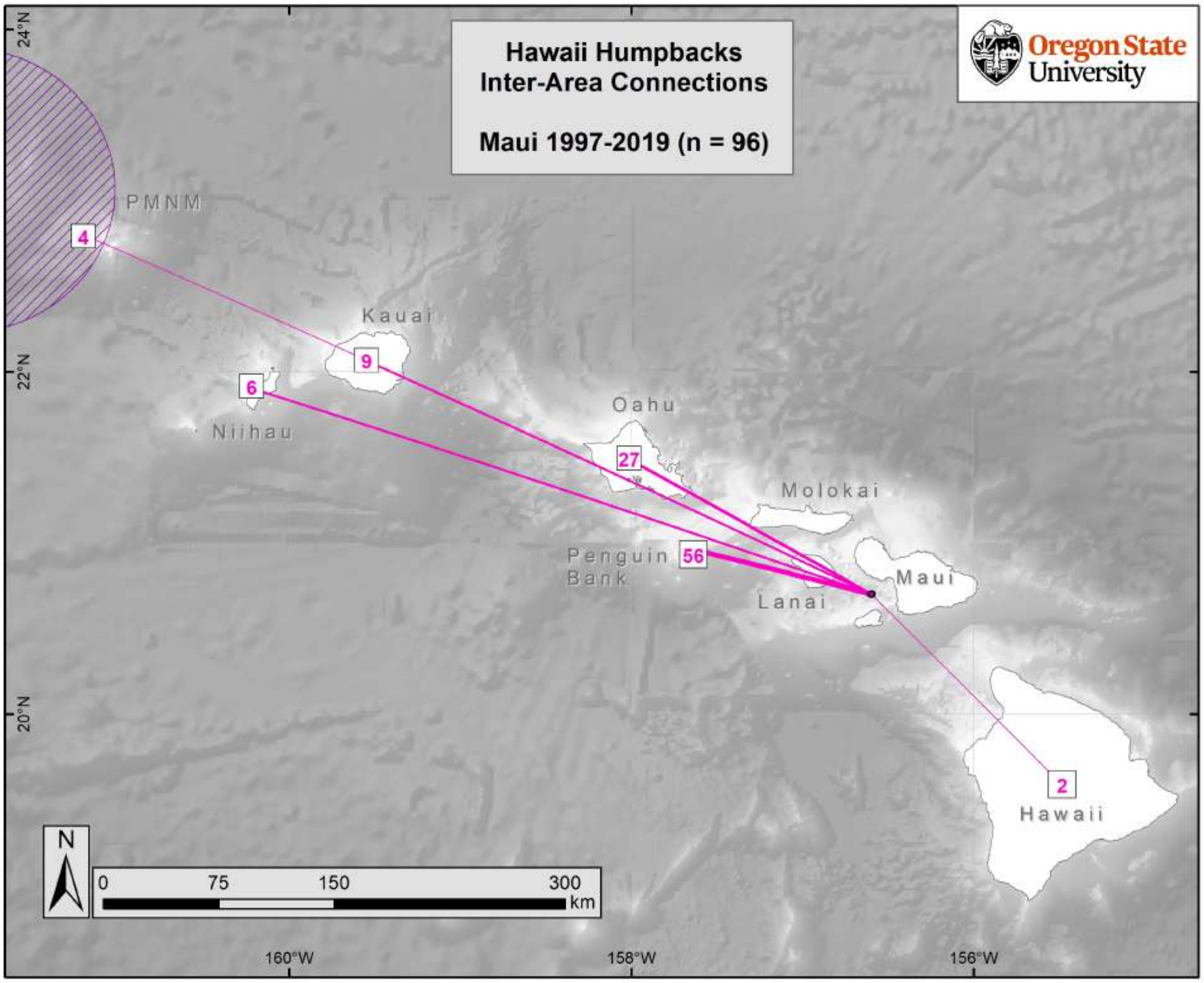

Figure 17. The number of whales (shown in boxes) tagged off Maui, Hawaii, from 1997 to 2019 that were tracked to other areas in the Hawaiian Islands.

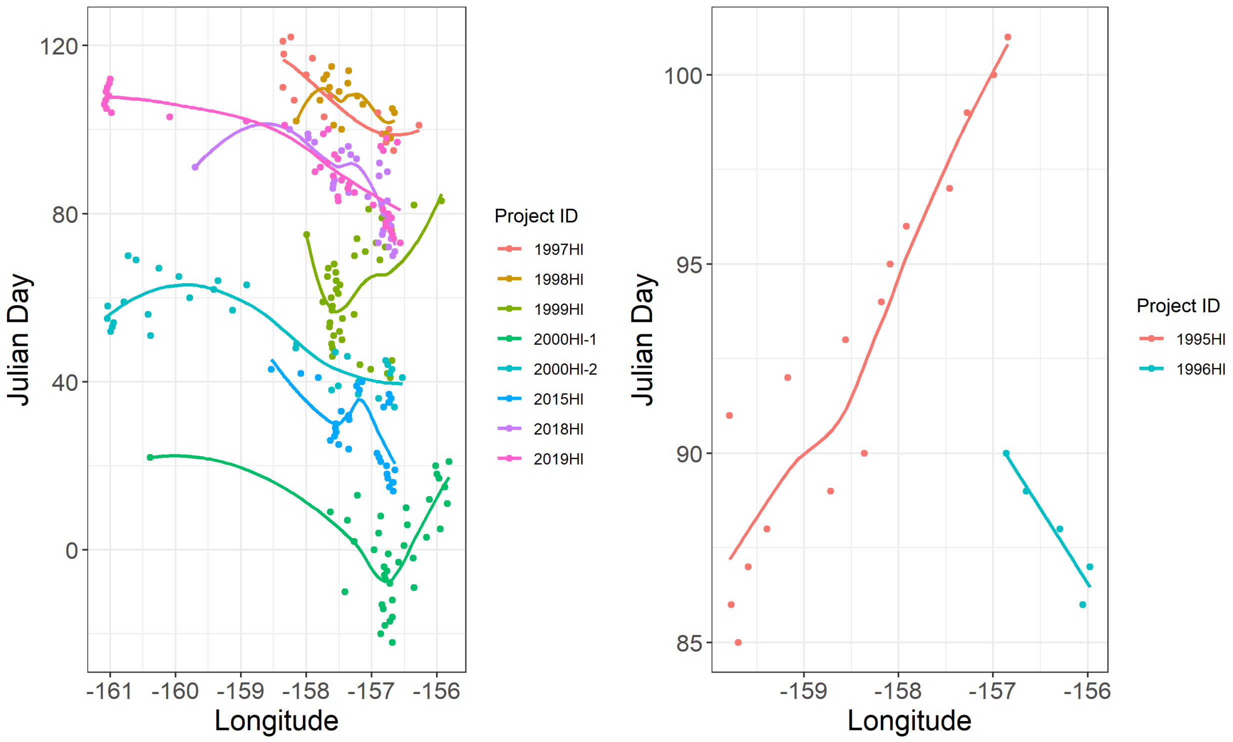

Figure 18. Plots of Argos location longitude versus Julian day for satellite-monitored humpback whales tagged off Maui from 1997 to 2019 (left panel) and off Kauai (1995) and Hawaii (1996; right panel). The curved lines represent loess smoothing functions (left panel) and gam smoothing functions (right panel) intended to guide the eye through the point clouds of matching color.

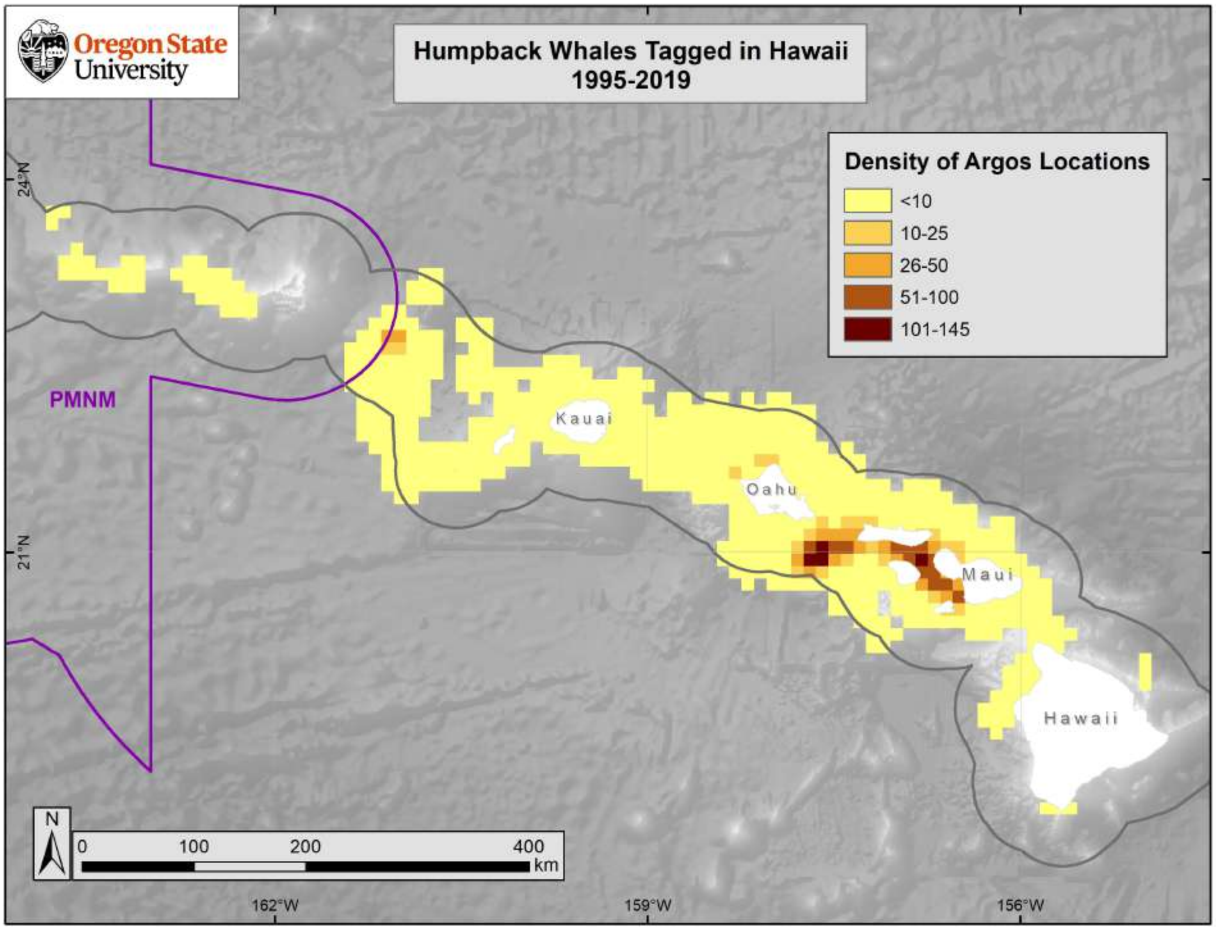

Figure 19. Kernel density utilization distribution for Argos locations in the Hawaiian Islands of humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (105 whales). Grid cell size is 0.1 × 0.1 deg. The black polygon corresponds to the boundary of the 50-km buffer zone delineating the Hawaiian breeding area (see Methods Section 2.6 for details). The purple polygon corresponds to the Papahanaumokuakea Marine National Monument (PMNM).

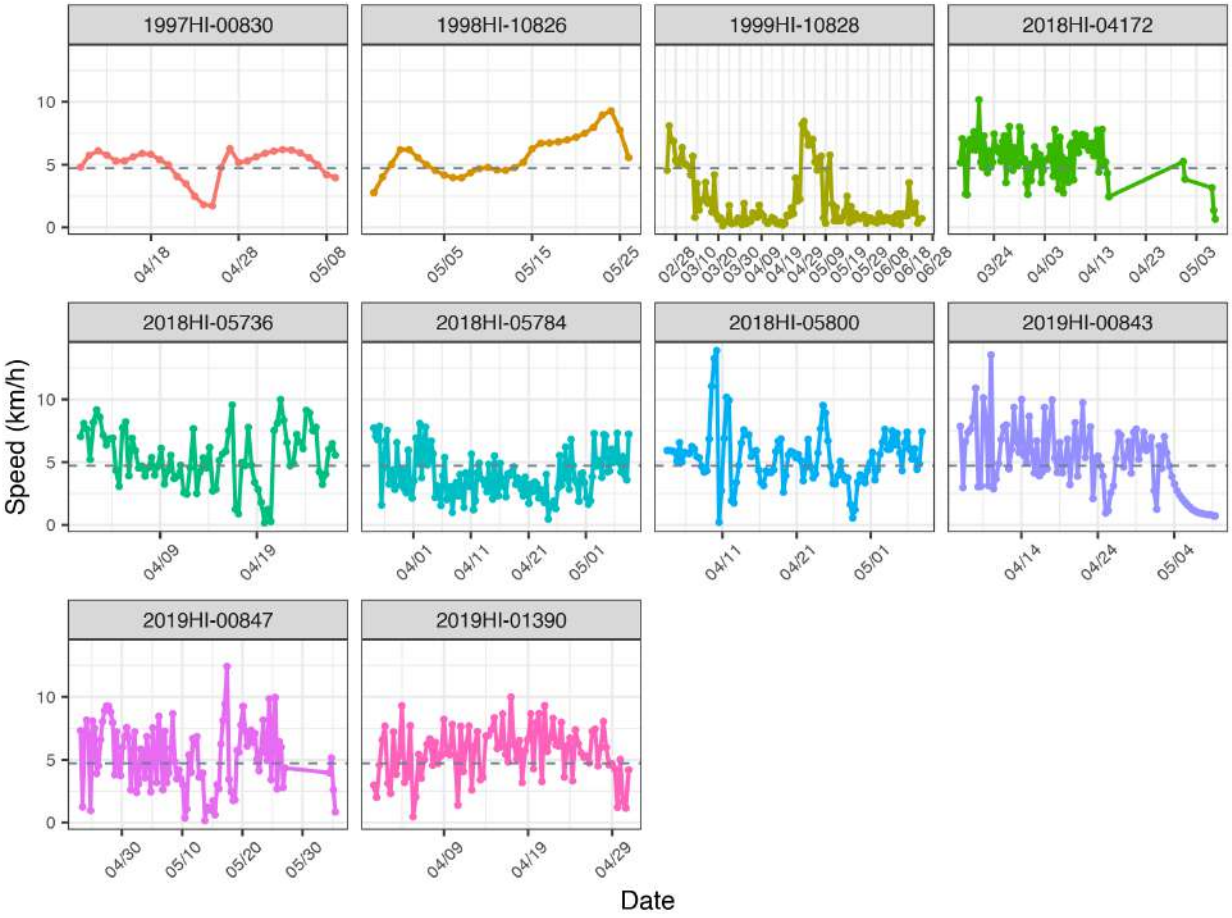

Figure 20. Travel speed (in km/h) between regularized locations estimated by state-space models during migration from the Hawaiian Islands for the 10 tracks that lasted until arrival at the feeding areas and that reported locations during migration, as listed in Table 7. Tag numbers are shown above each panel along with year. The horizontal dashed line inside each panel corresponds to the mean travel speed during migration for all 10 tracks (4.71 km/h).

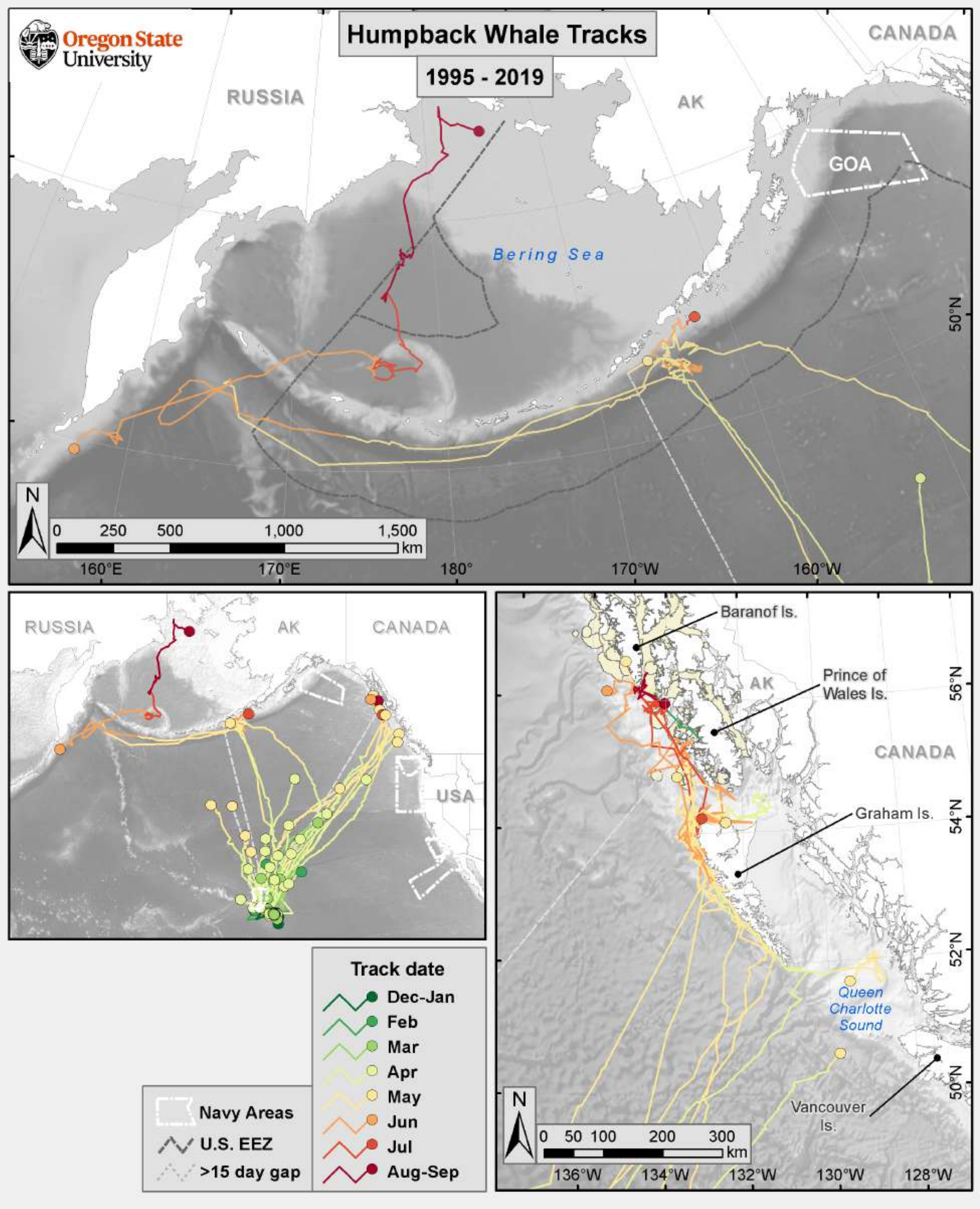

Figure 21. Satellite-monitored tracks for humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (37 whales), highlighting migration and movement in feeding areas.

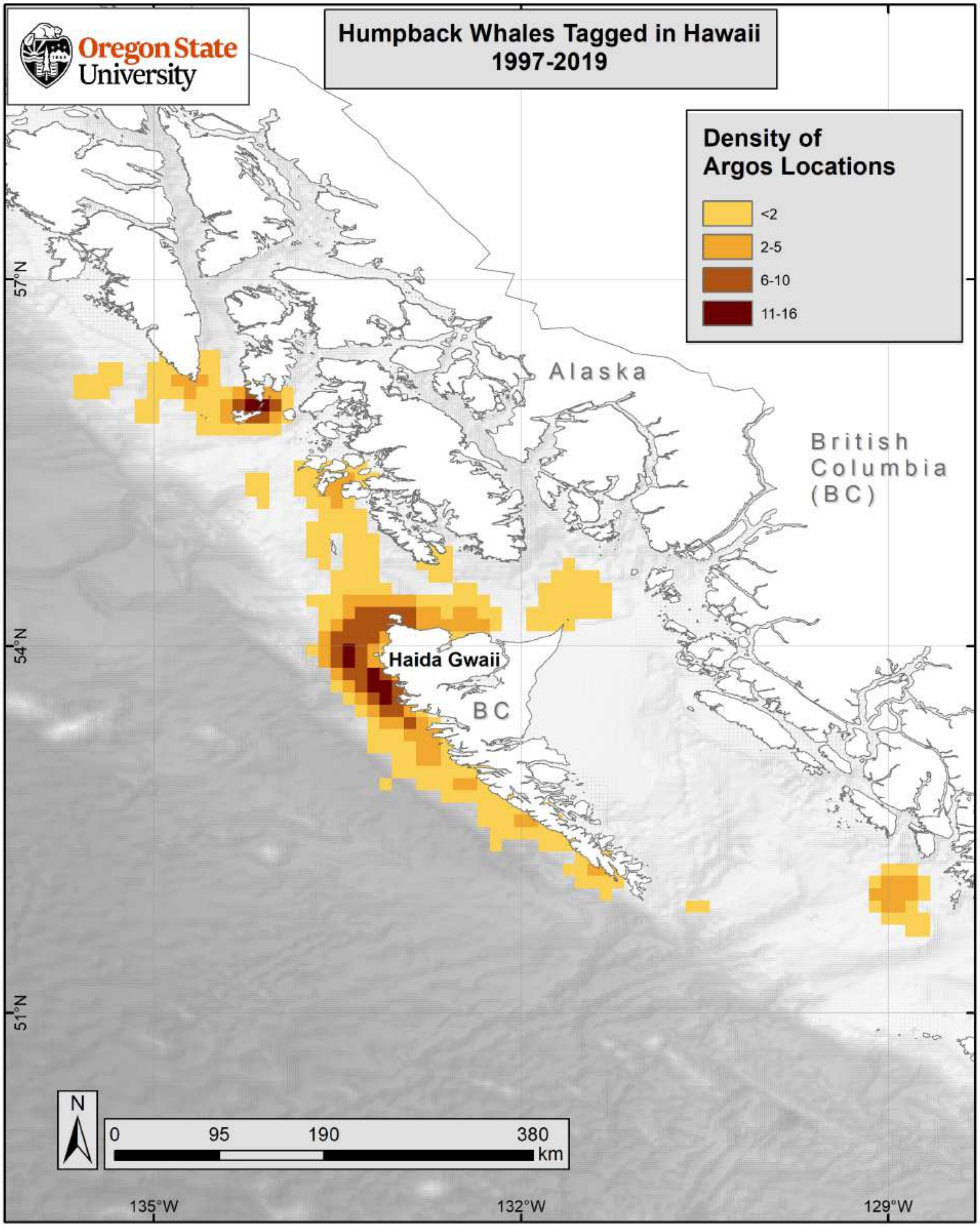

Figure 22. Kernel density utilization distribution for Argos locations in northern British Columbia and southeastern Alaska of humpback whales tagged in the Hawaiian Islands from 1997 to 2019 (seven whales). Grid cell size is 0.1 × 0.1 deg.

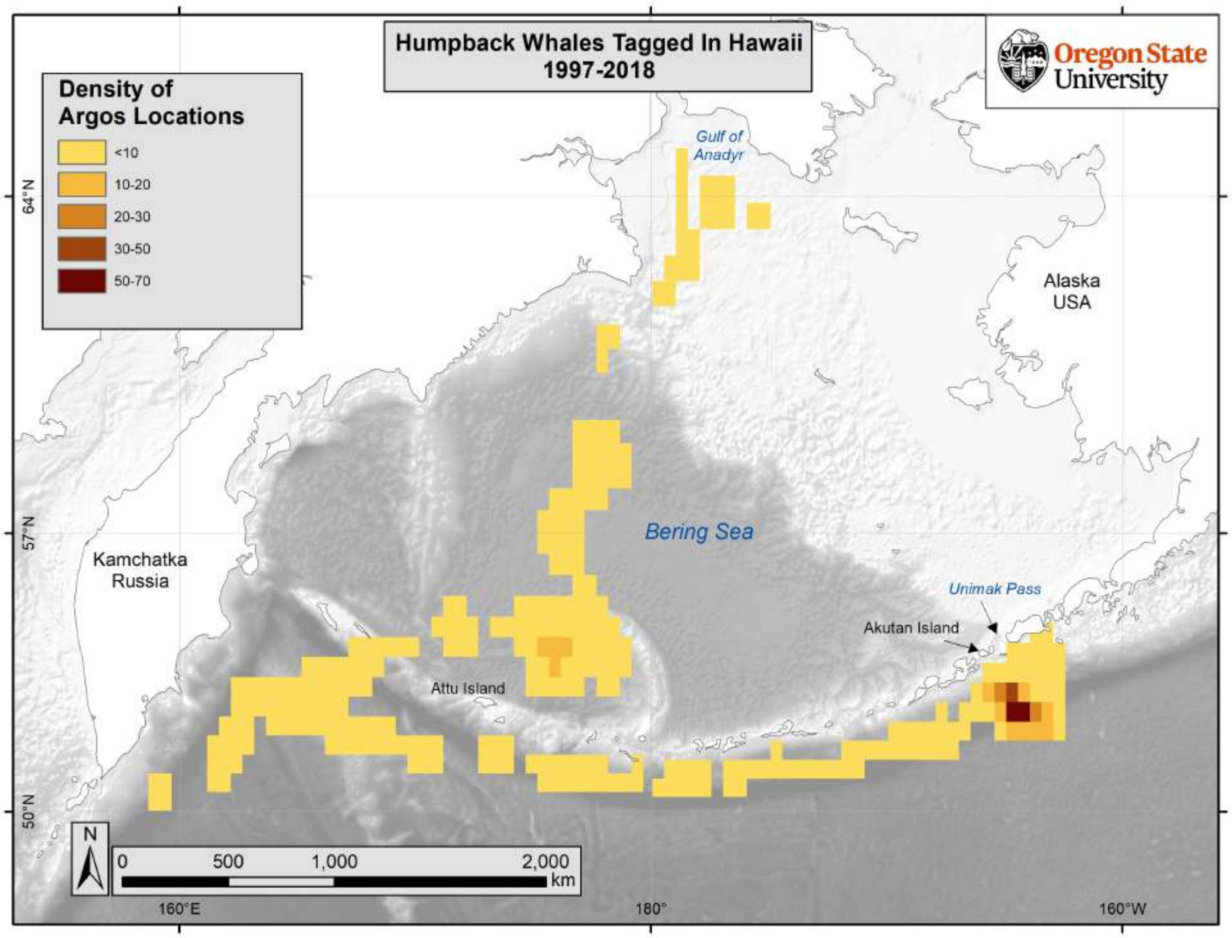

Figure 23. Kernel density utilization distribution for Argos locations in the Aleutian Islands and Bering Sea of humpback whales tagged in the Hawaiian Islands from 1997 to 2018 (four whales). Grid cell size is 0.1 × 0.1 deg.

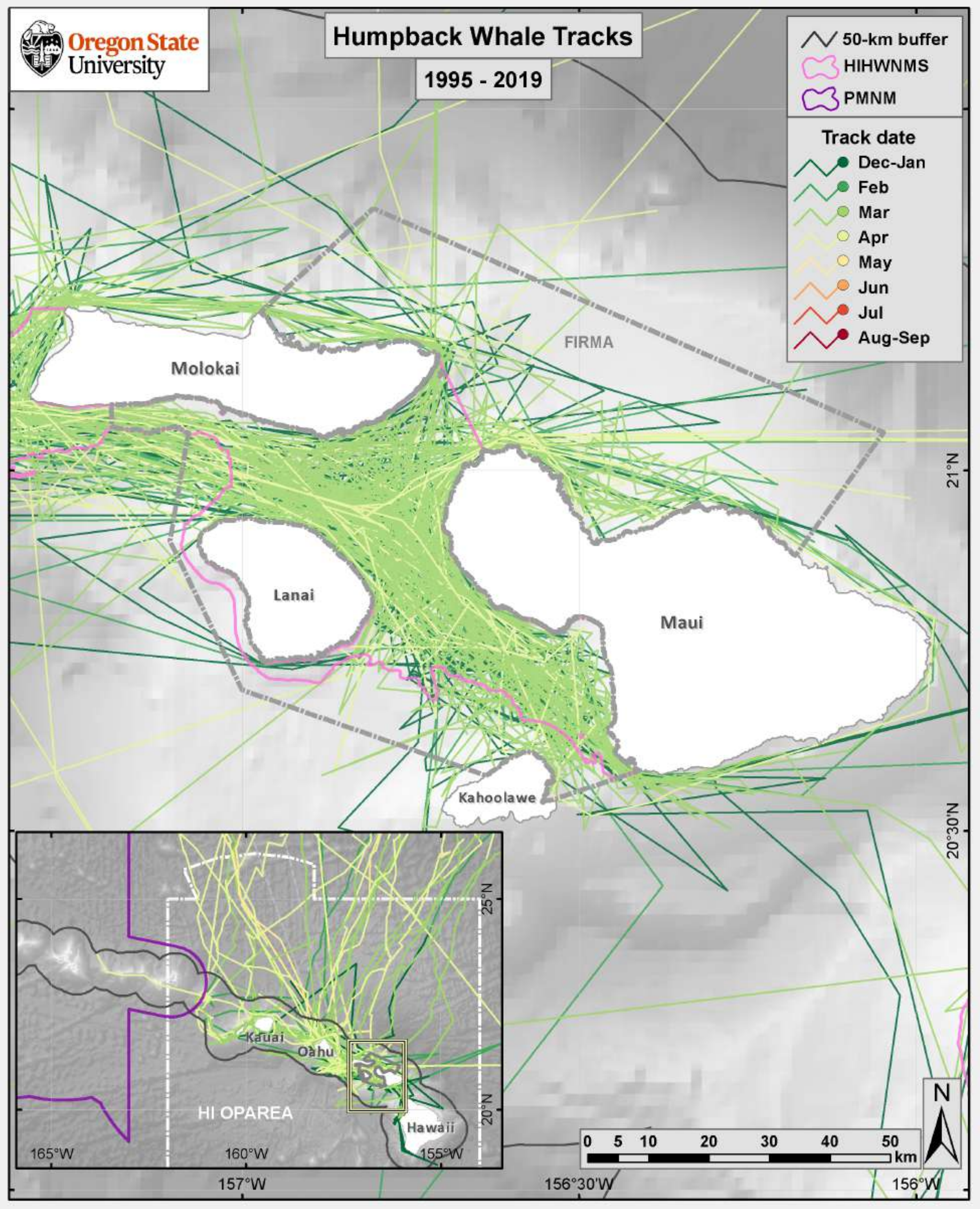

Figure 24. Satellite-monitored tracks in FIRMA for humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (100 whales).

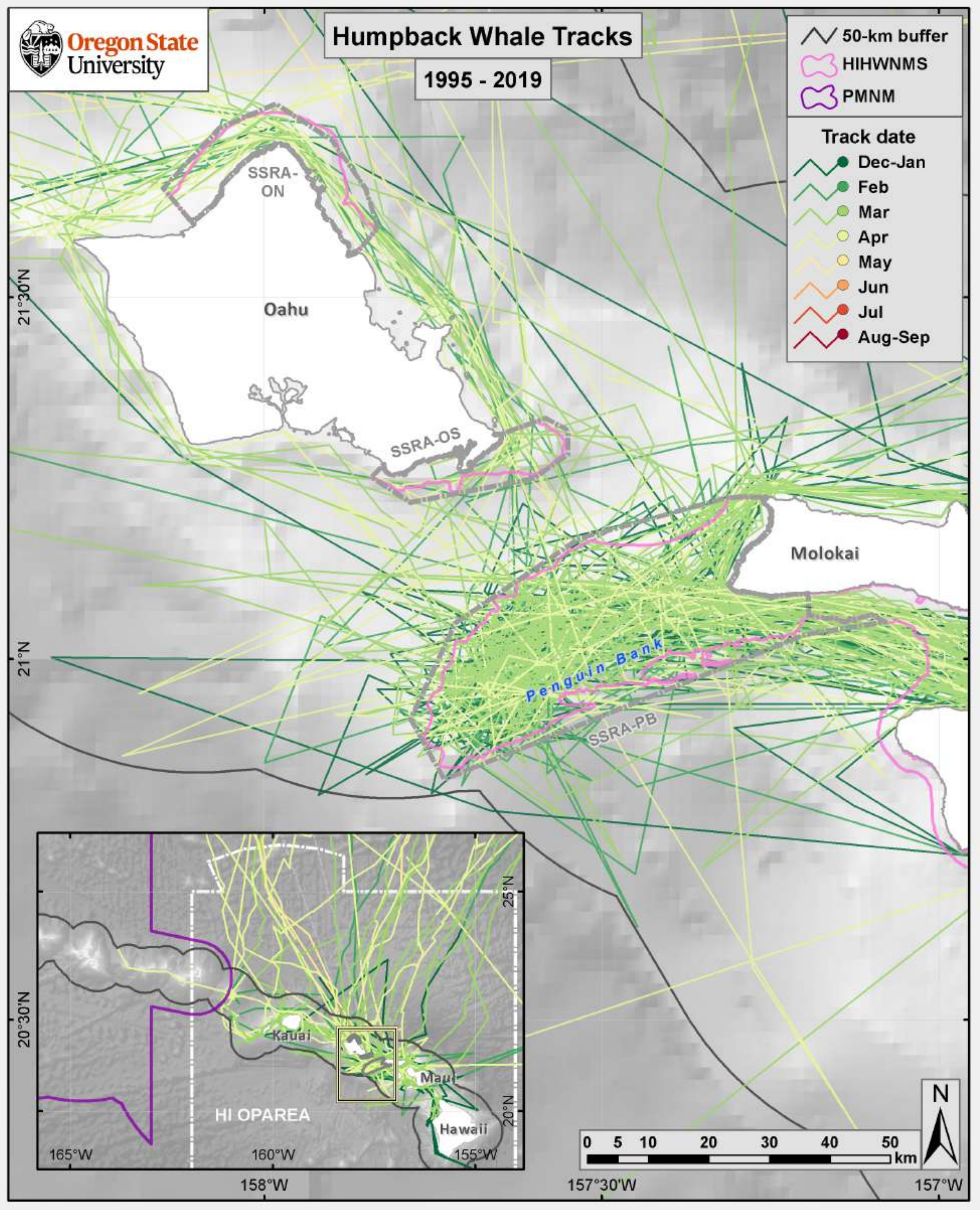

Figure 25. Satellite-monitored tracks in SSRA-PB (69 whales), SSRA-ON (24 whales), and SSRA-OS (26 whales) for humpback whales tagged in the Hawaiian Islands from 1995 to 2019.

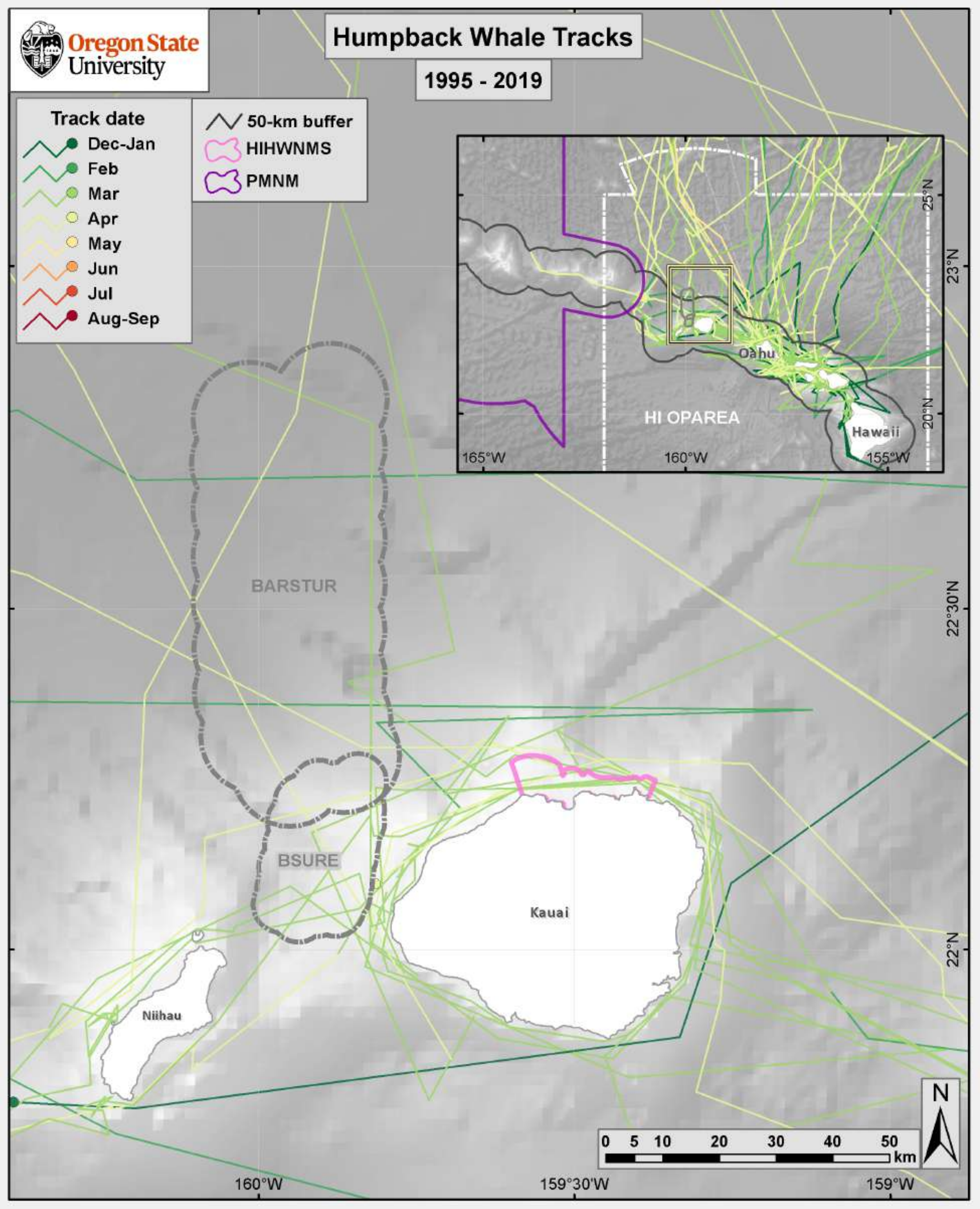

Figure 26. Satellite-monitored tracks in BS-Merge (BARSTUR and BSURE combined) for humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (12 whales).

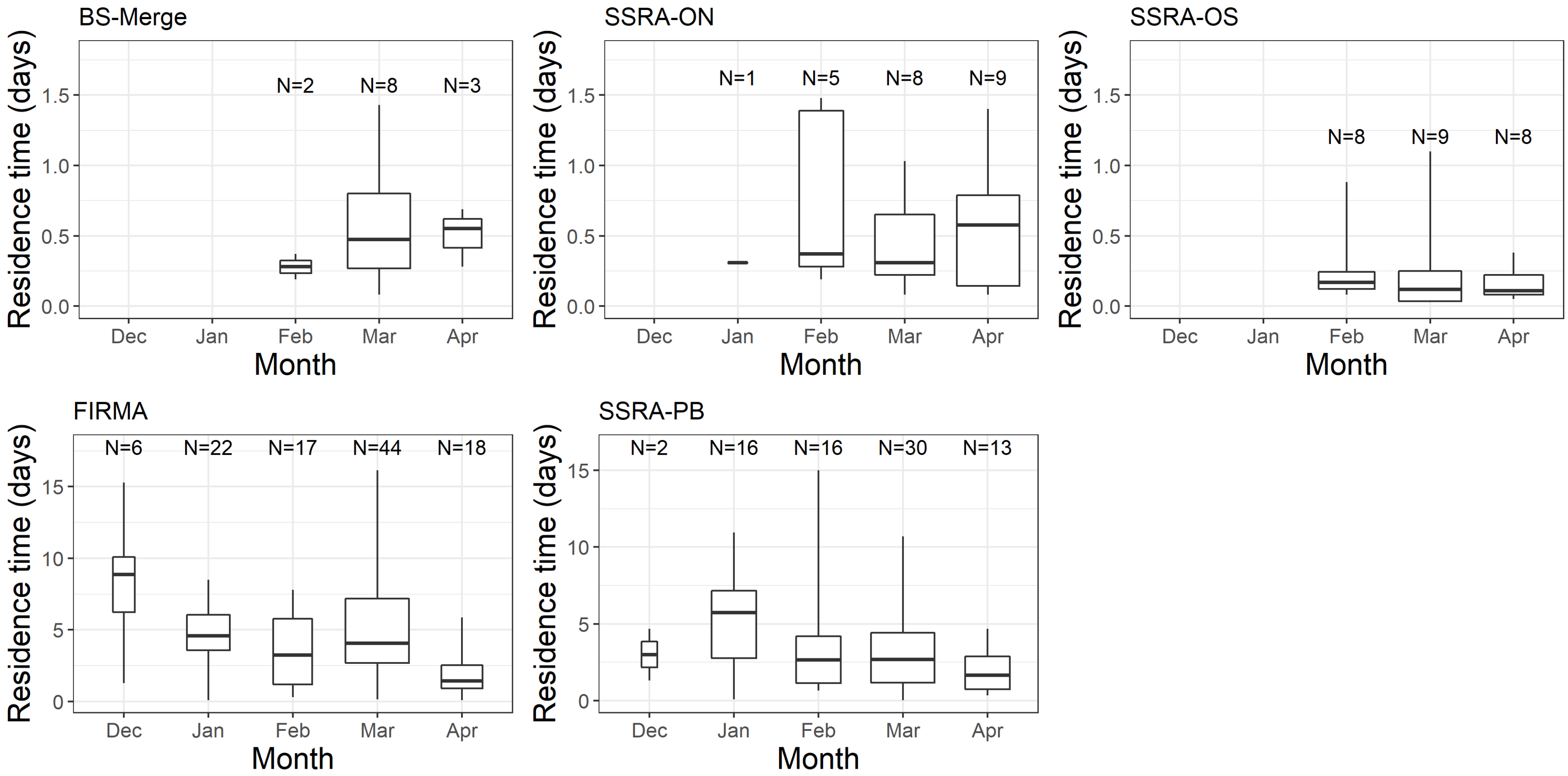

Figure 27. Boxplots of residence time (number of days in the Hawaiian Islands 50 km buffer zone) per month in each of the Navy areas for satellite-monitored humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (105 whales). Note the different scale of the y-axes between the upper and lower plots.

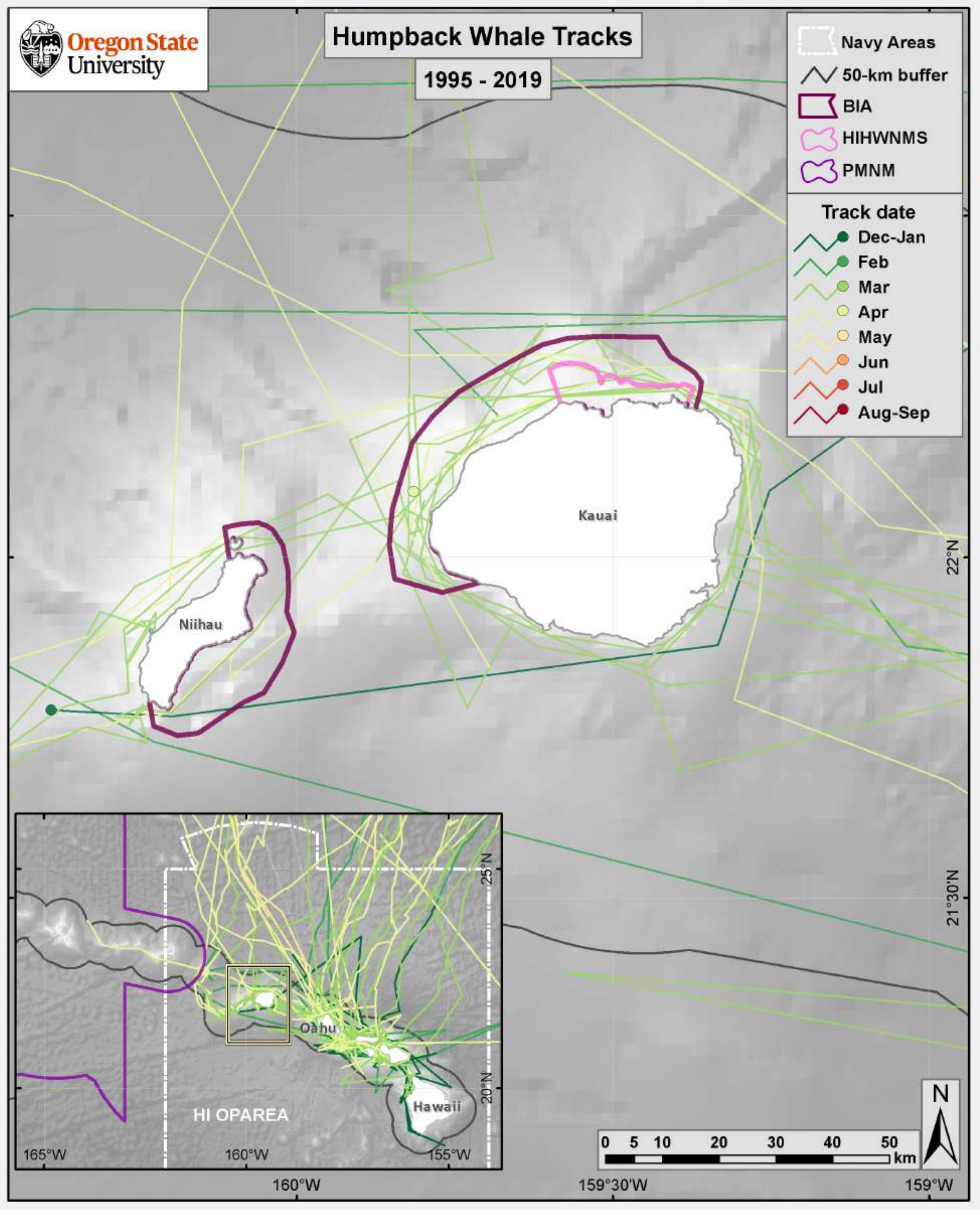

Figure 28. Satellite-monitored tracks in the Kauai BIA for humpback whales tagged in the Hawaiian Islands from 1995 to 2019 (15 whales).

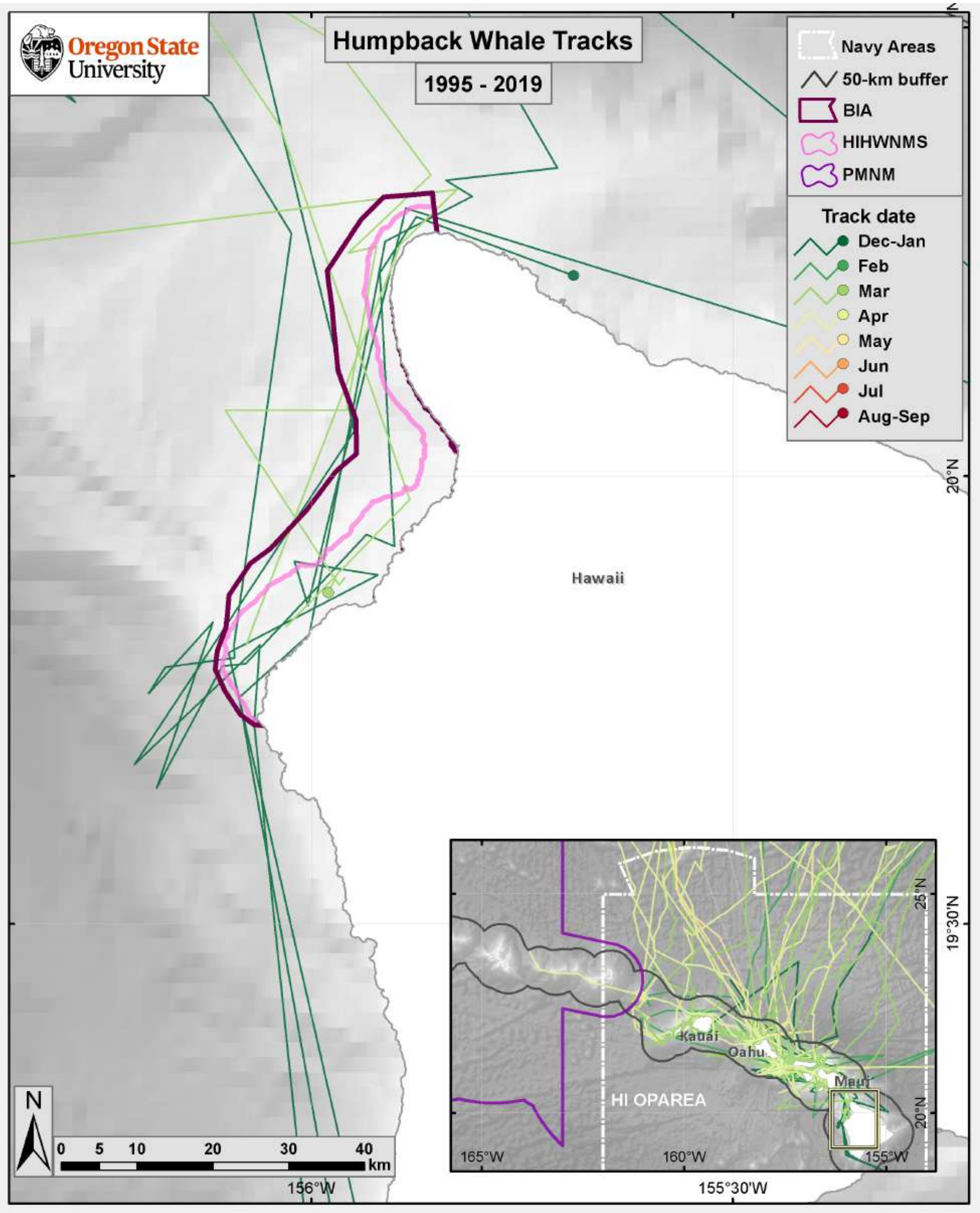

Figure 29. Satellite-monitored tracks in the Hawaii BIA for humpback whales tagged in the Hawaiian Islands from 1996 to 2019 (six whales).

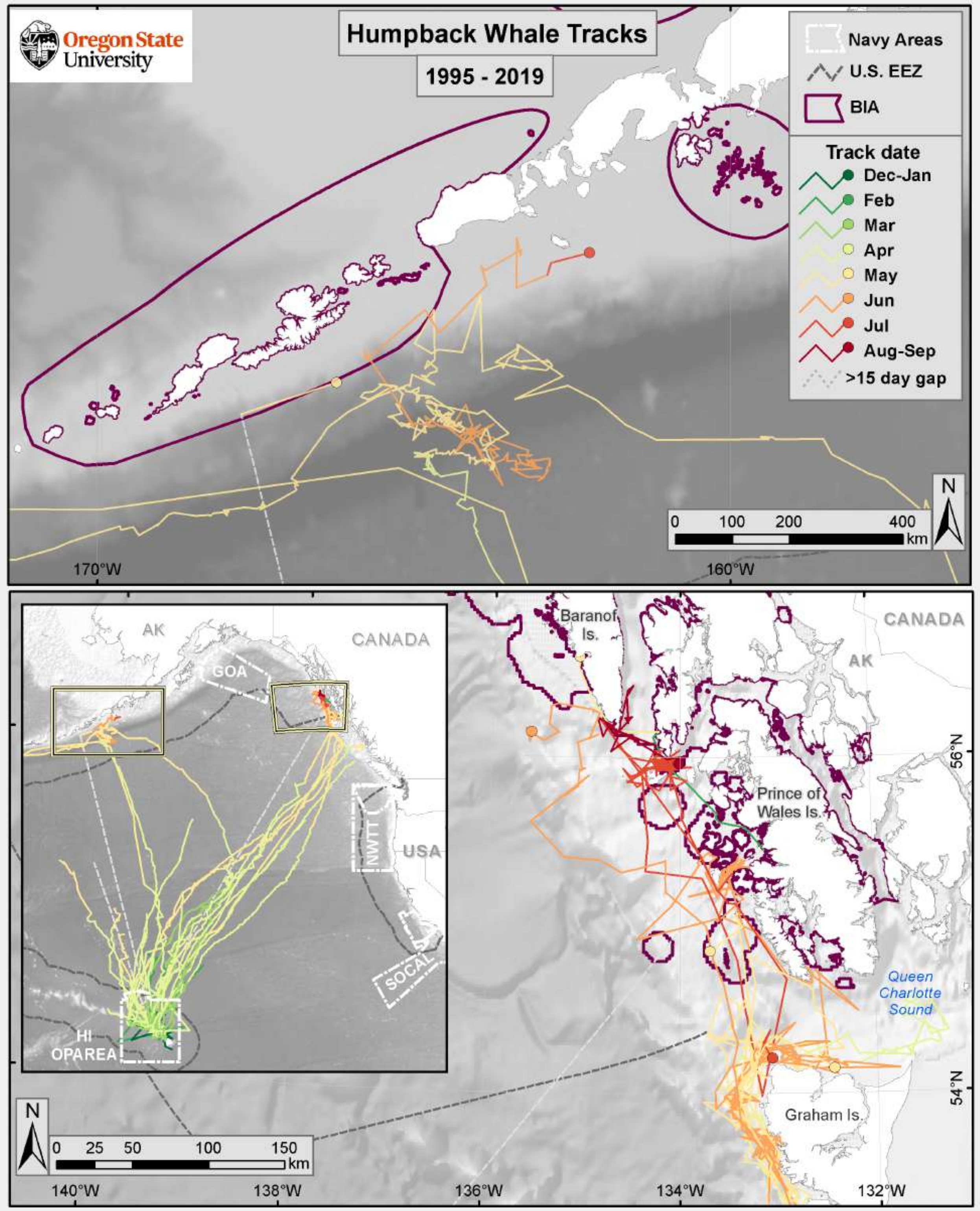

Figure 30. Satellite-monitored tracks in the SEAK (four whales) and Aleutians (two whales) BIAs for humpback whales tagged in the Hawaiian Islands from 1997 to 2019.

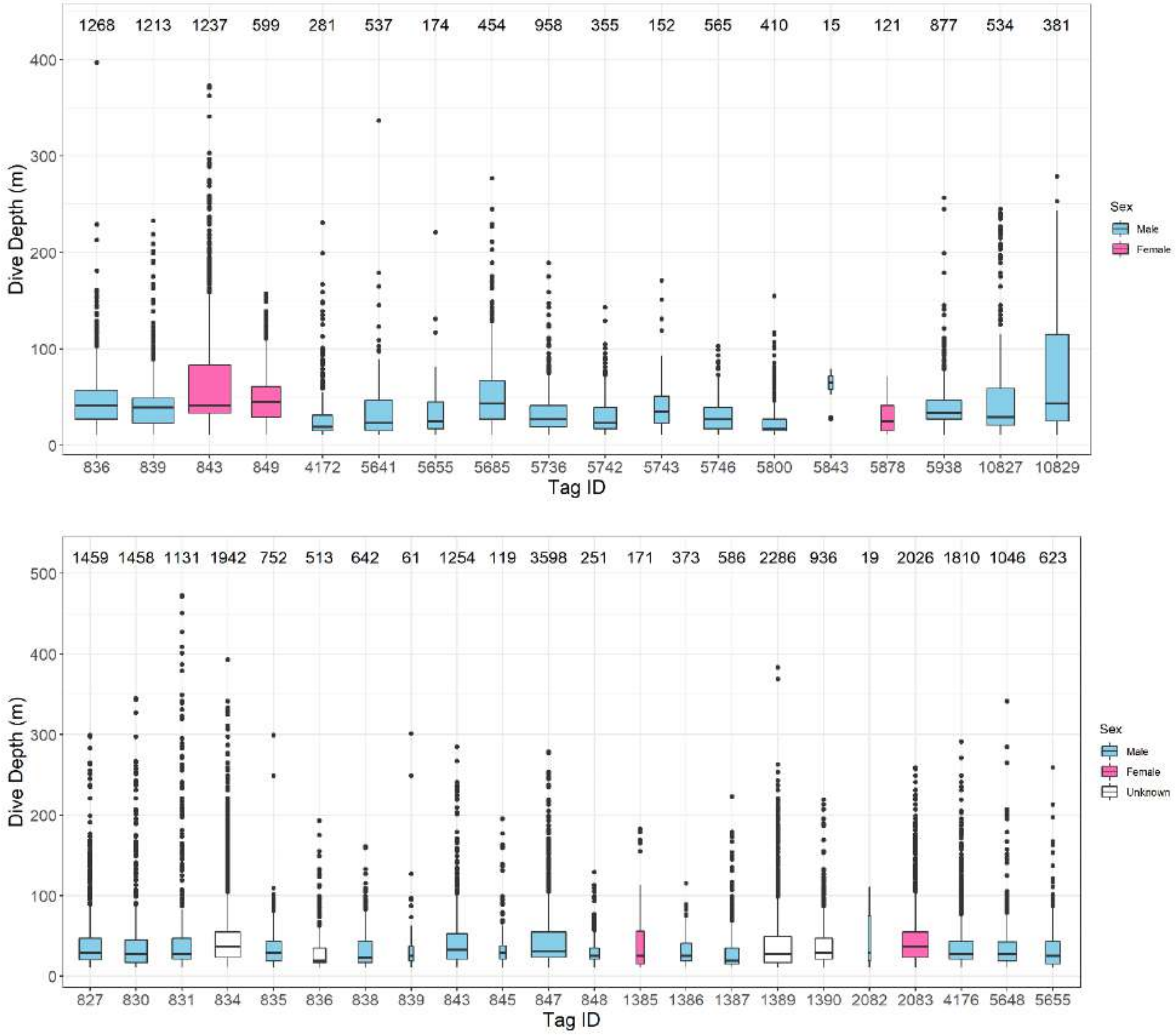

Figure 31. Dive depth while in the breeding areas of DM-tagged humpback whales tagged off Maui, Hawaii, during March 2018 (top panel; n = 18) and March 2019 (bottom panel; n = 22). Boxes represent first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box. Sex of the animals are indicated by color.

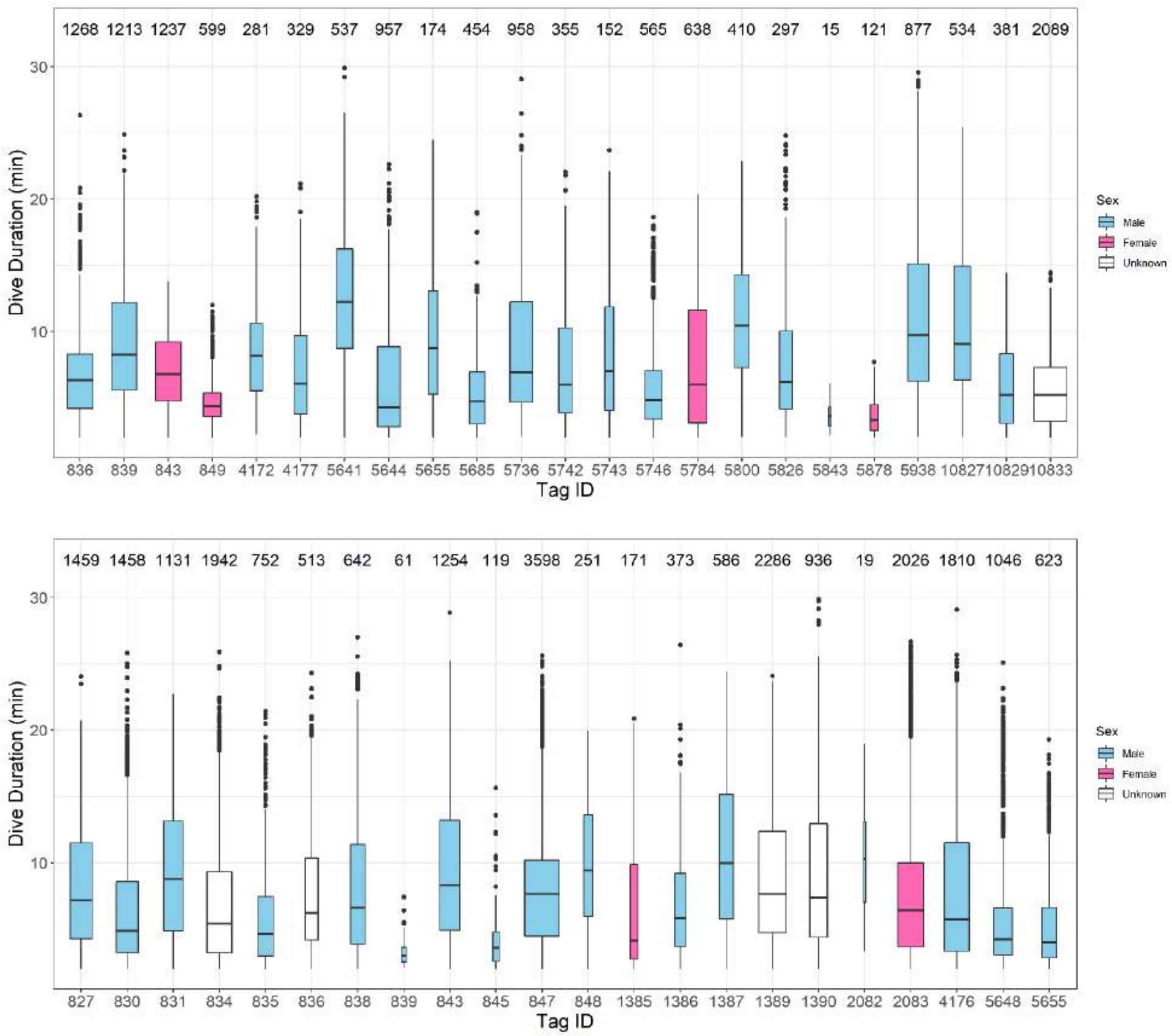

Figure 32. Dive duration while in the breeding areas of DM- and DUR+-tagged humpback whales tagged off Maui, Hawaii, during March 2018 (top panel; n = 23) and March 2019 (bottom panel; n = 22, all DM tags). Boxes represent the first and third quartiles of the data, while points represent values exceeding 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.

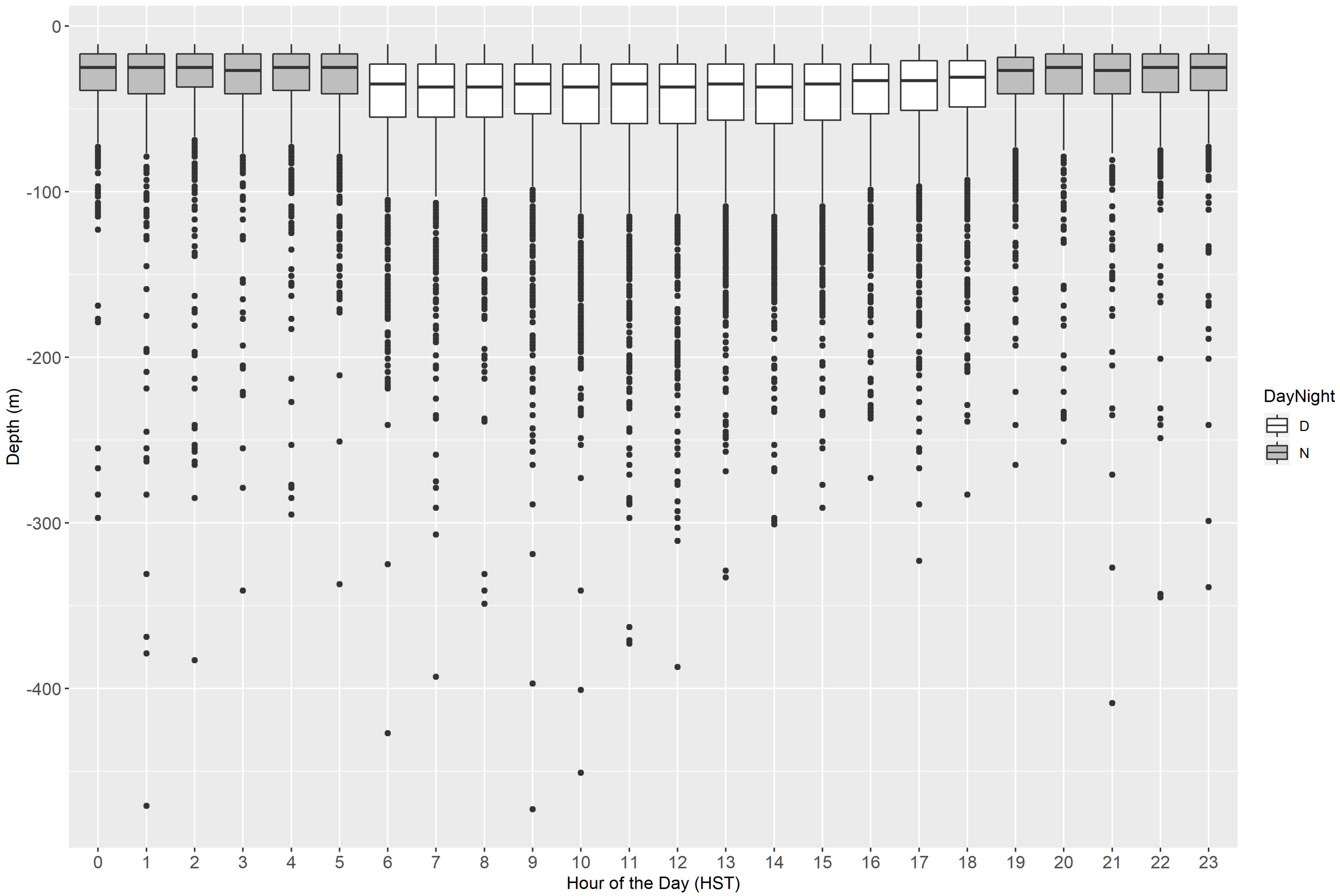

Figure 33. Hourly distribution of dive depth while in the breeding areas of DM-tagged humpback whales (n = 41) tagged off Maui, Hawaii, during March 2018 and 2019. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

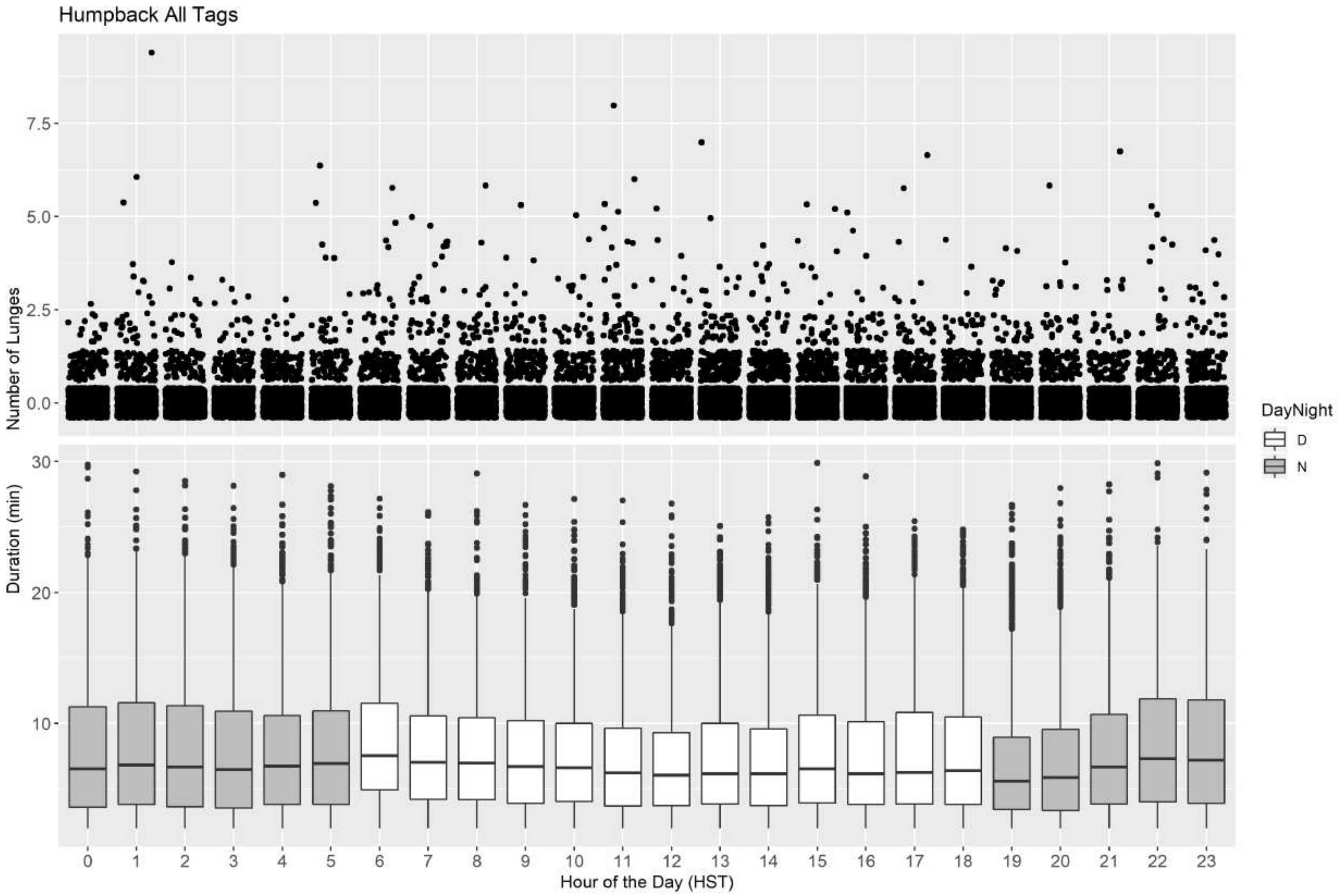

Figure 34. Hourly distributions of number of lunges (top) and dive durations (bottom) while in the breeding areas for DM- and DUR+-tagged humpback whales (n = 46) tagged off Maui, Hawaii, during March 2018 and 2019. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

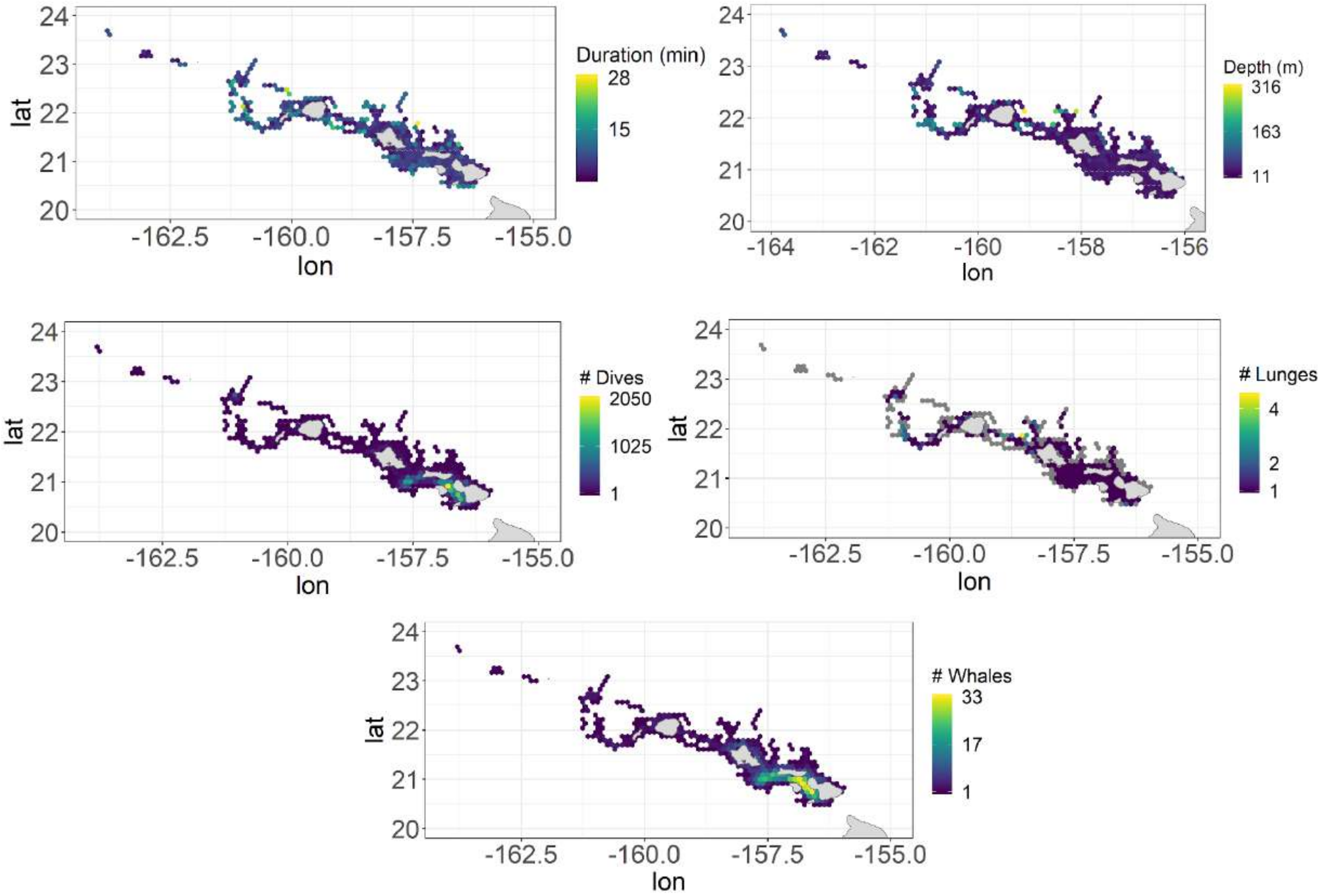

Figure 35. Data from DM- and DUR+-tagged humpback whales tagged off Maui, Hawaii, in March 2018 and 2019 summarized in 0.1-deg hexagonal grids showing the median dive duration (top left), median maximum dive depth (top right), median number of dives (middle left), median number of lunges (middle right), and number of tagged whales (bottom) recorded in each grid cell while in the breeding areas.

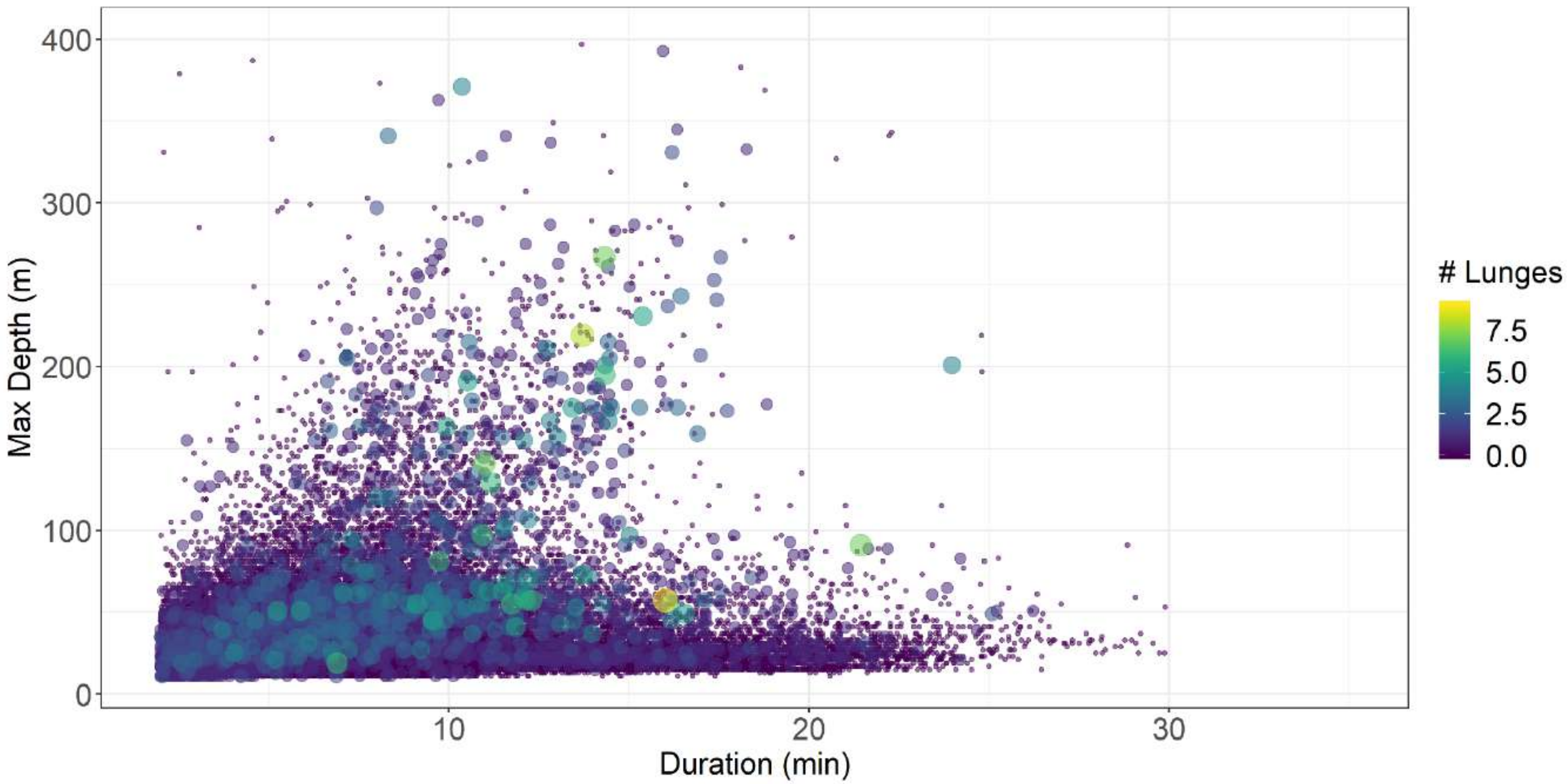

Figure 36. Depth and duration of dives made by DM-tagged humpback whales tagged off Maui, Hawaii, during March 2018 and 2019. Color of the circles represent the number of lunges recorded during each dive.

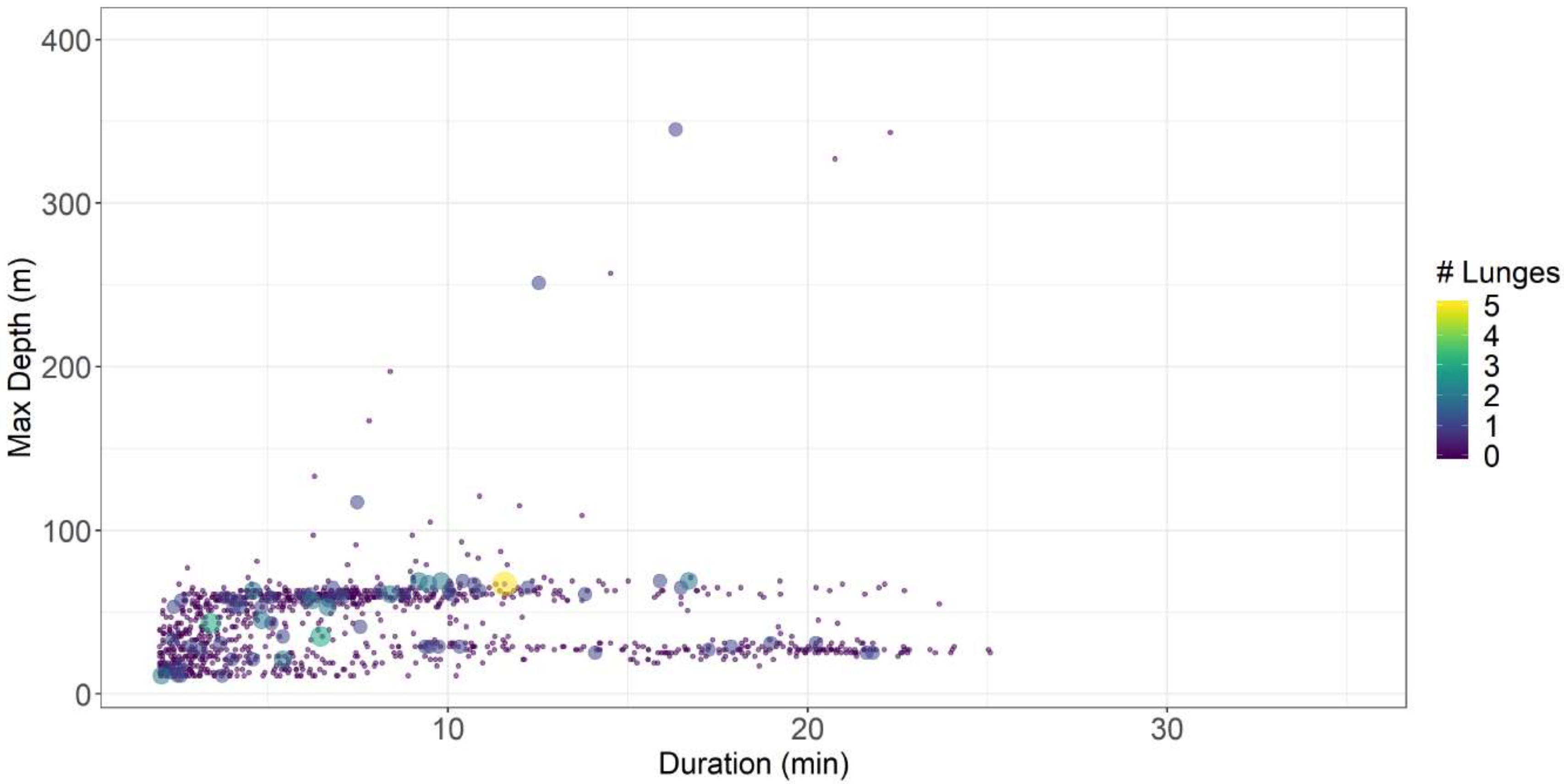

Figure 37. Depth and duration of dives made by four DM-tagged humpback whales near Middle Bank (eastern Papahanaumokuakea Marine National Monument) during late March to April 2019. Color of the circles represent the number of lunges recorded during each dive.

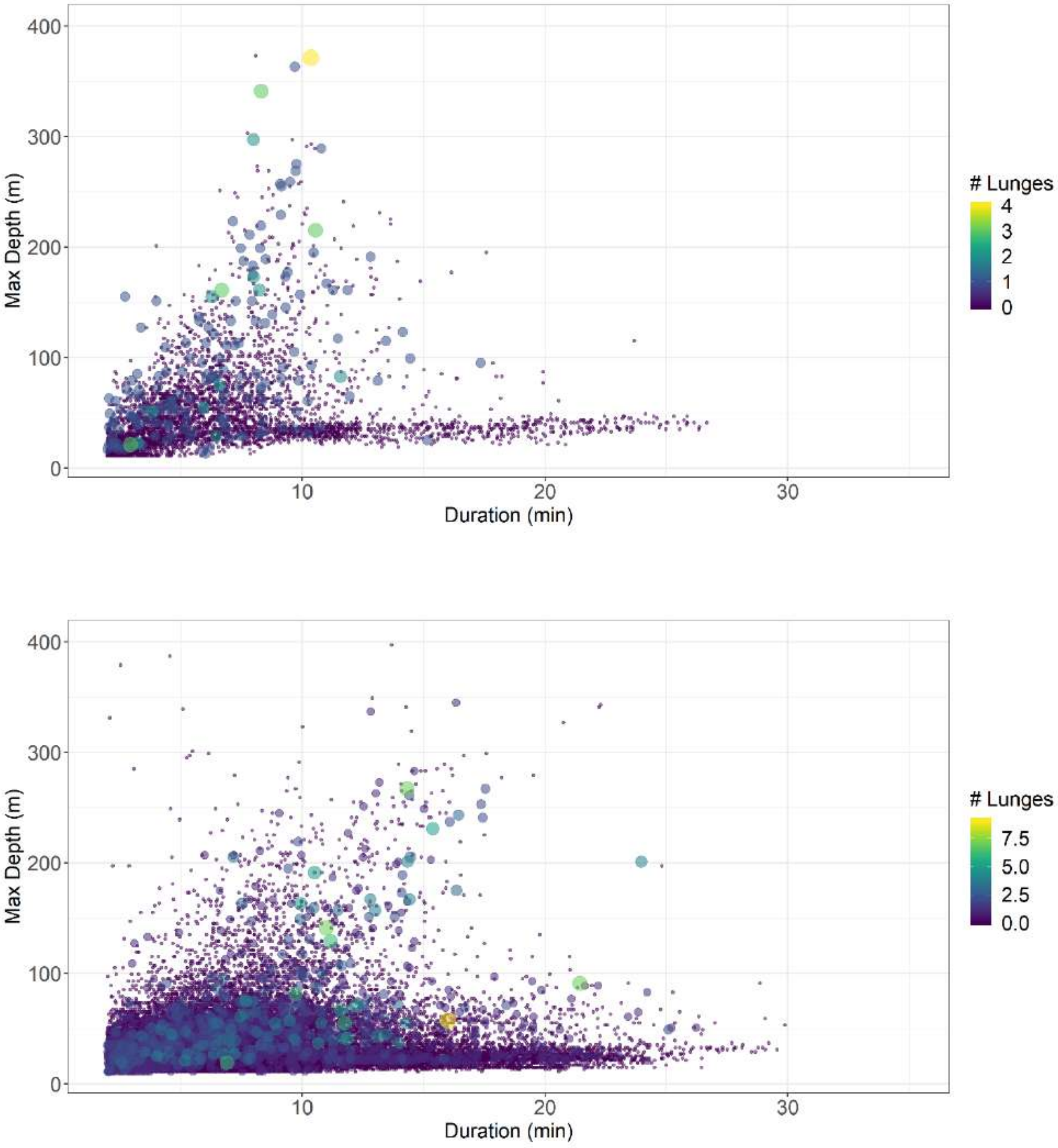

Figure 38. Depth and duration of dives made by DM-tagged female (top) and male (bottom) humpback whales tagged off Maui, Hawaii, during March 2018 and 2019. Color of the circles represent the number of lunges recorded during each dive.

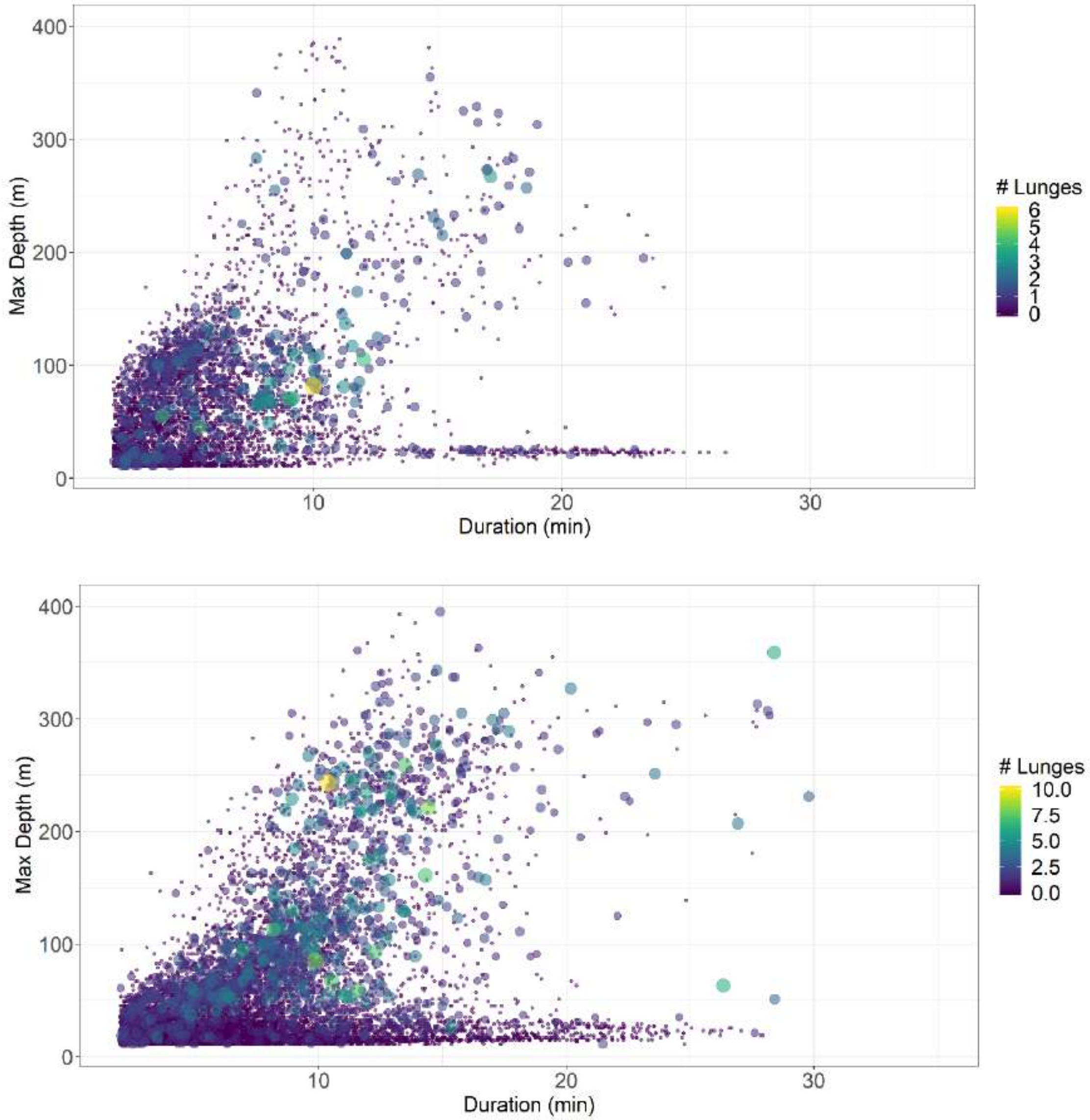

Figure 39. Depth and duration of dives made during migration by DM-tagged female (top) and male (bottom) humpback whales tagged off Maui, Hawaii, during March 2018 and 2019. Color of the circles represent the number of lunges recorded during each dive.

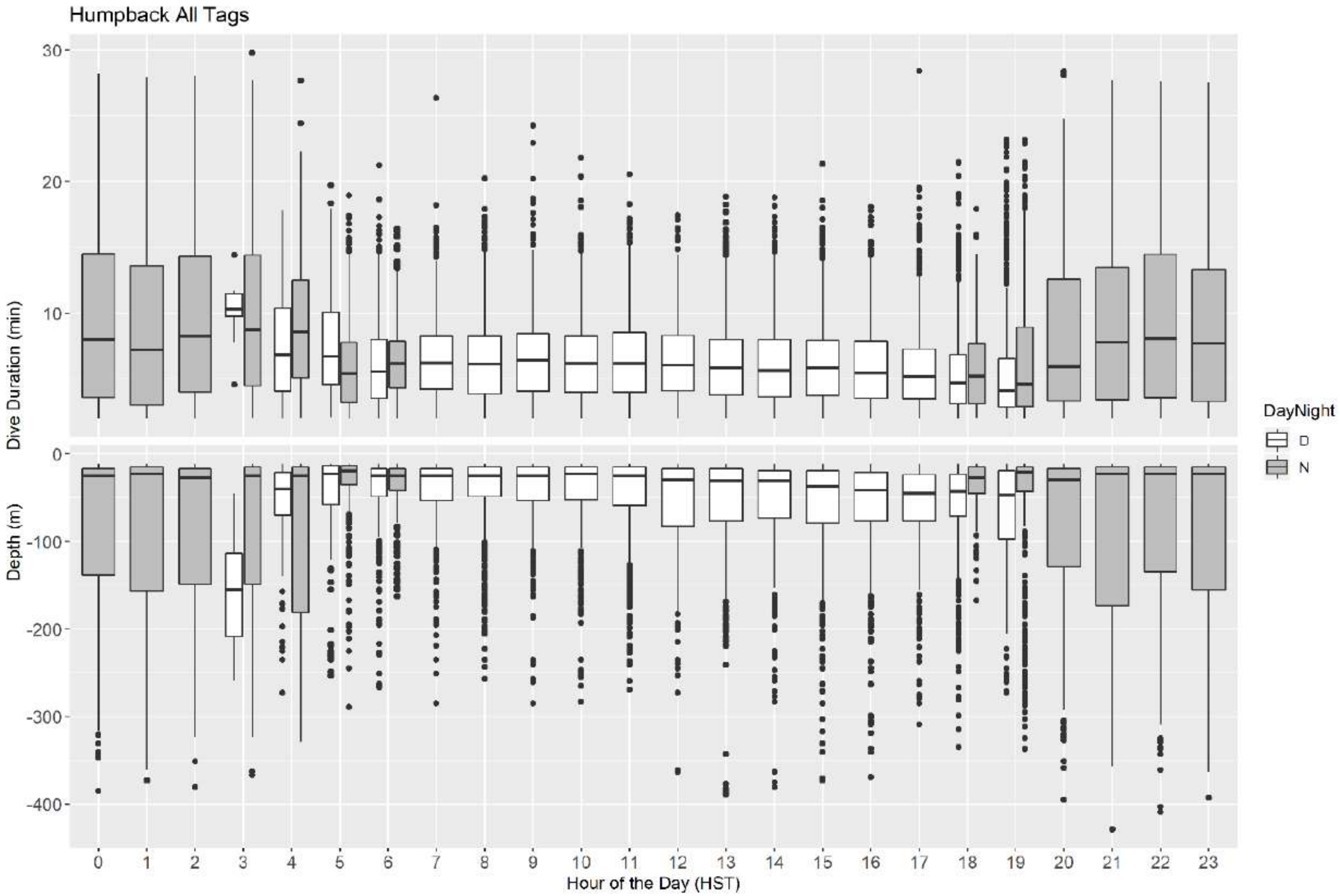

Figure 40. Hourly distributions of number of dive duration (top) and maximum dive depth (bottom) during migration for DM-tagged humpback whales (n = 18) tagged off Maui, Hawaii, during March 2018 and 2019. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Some hours show data for both day and night due to differences in daylight hours across wide latitudinal ranges crossed during migration.

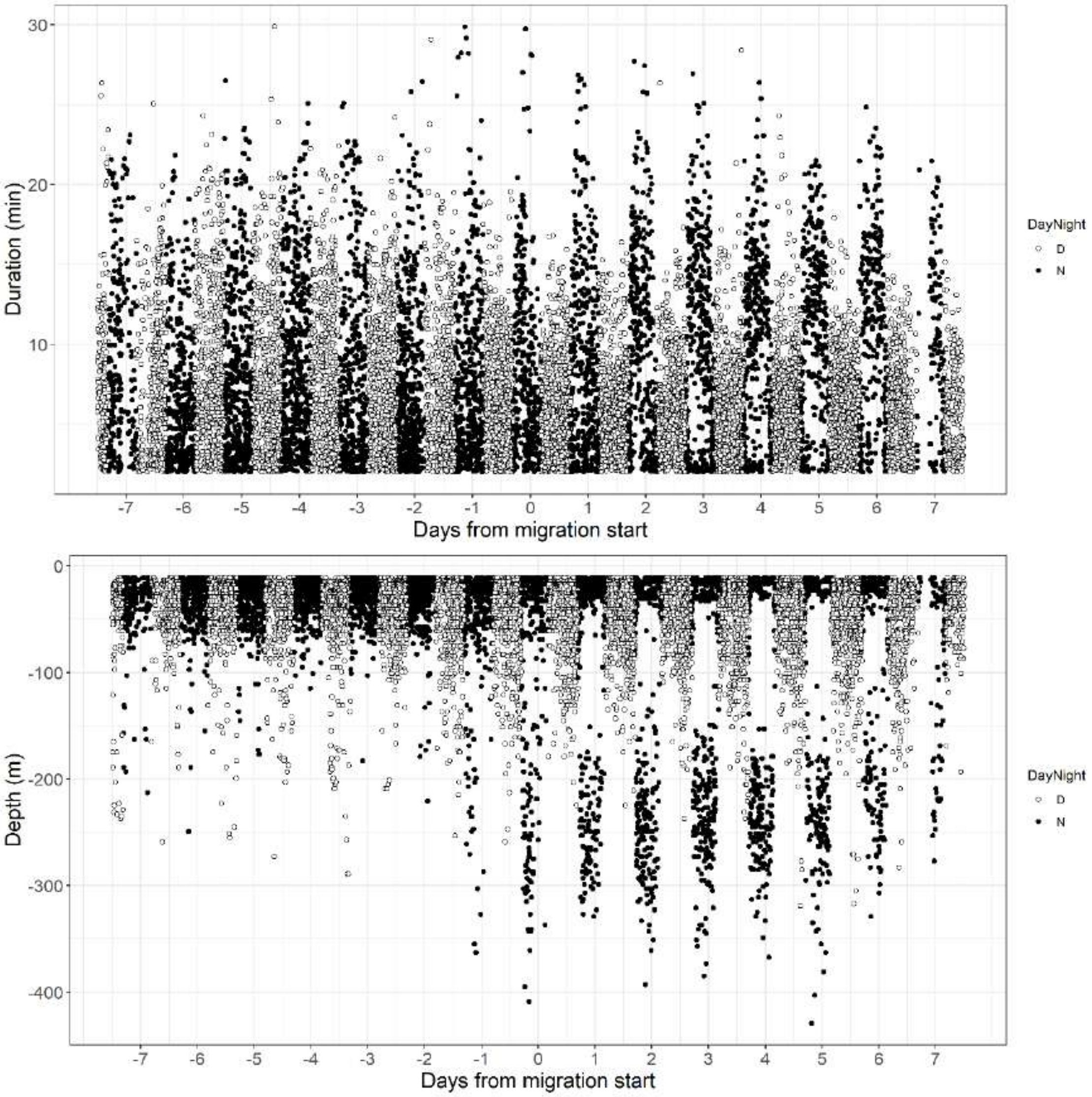

Figure 41. Dive duration (top) and depth (bottom) of DM-tagged humpback whales tagged off Maui, Hawaii, during March 2018 and 2019. Data are presented for the seven days before and after the start of migration with date for all tags (n = 18) scaled to the start of migration (0 days from migration start) when the tagged whales first left a 50-km buffer around the Hawaiian Islands.

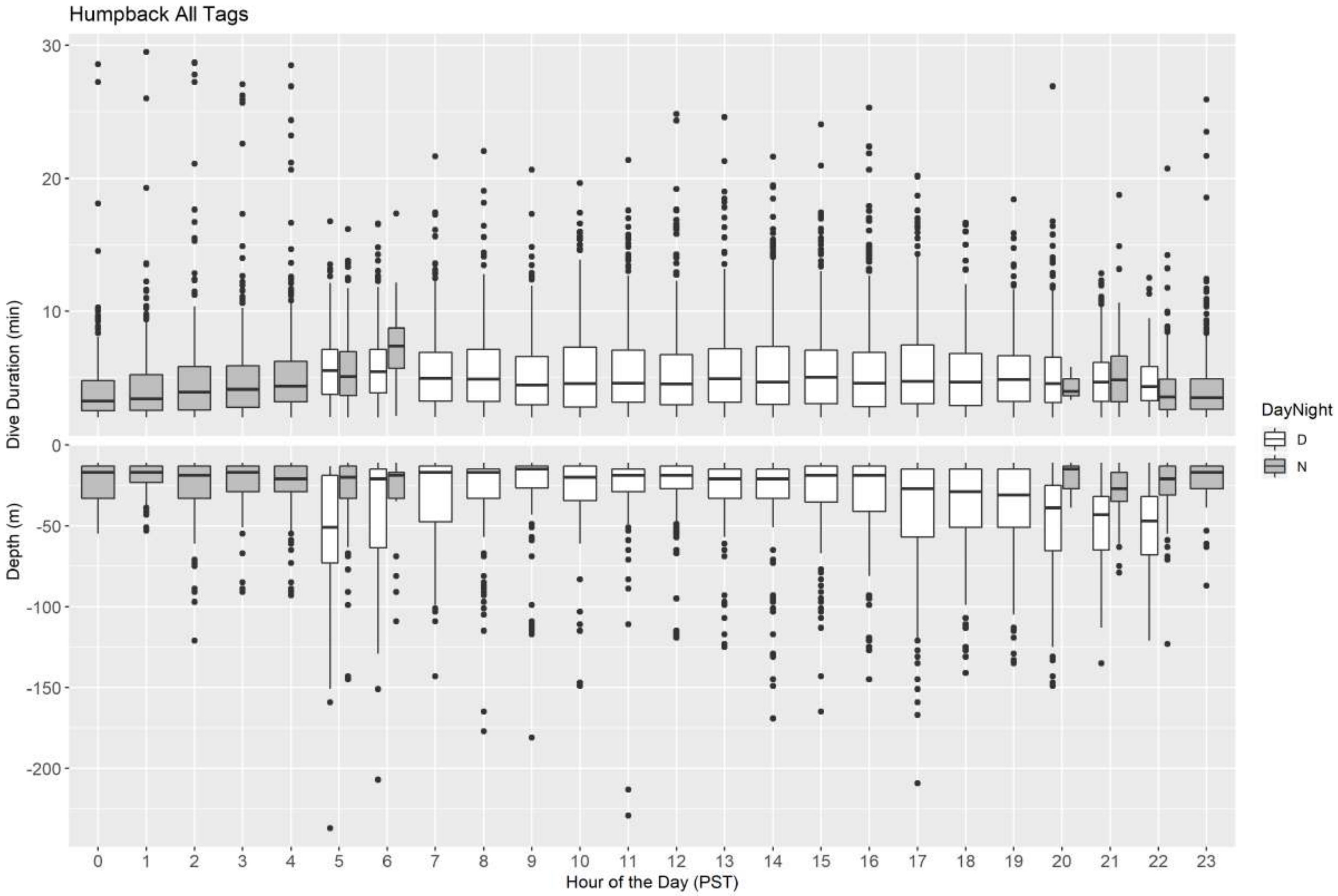

Figure 42. Hourly distributions of dive duration (top) and maximum dive depth (bottom) while in the feeding areas (near Haida Gwaii and SE Alaska) for DM-tagged humpback whales (n = 18) tagged off Maui, Hawaii, during March 2018 and 2019. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Some hours show data for both day and night due to differences in daylight hours across the latitudinal and longitudinal ranges occupied.

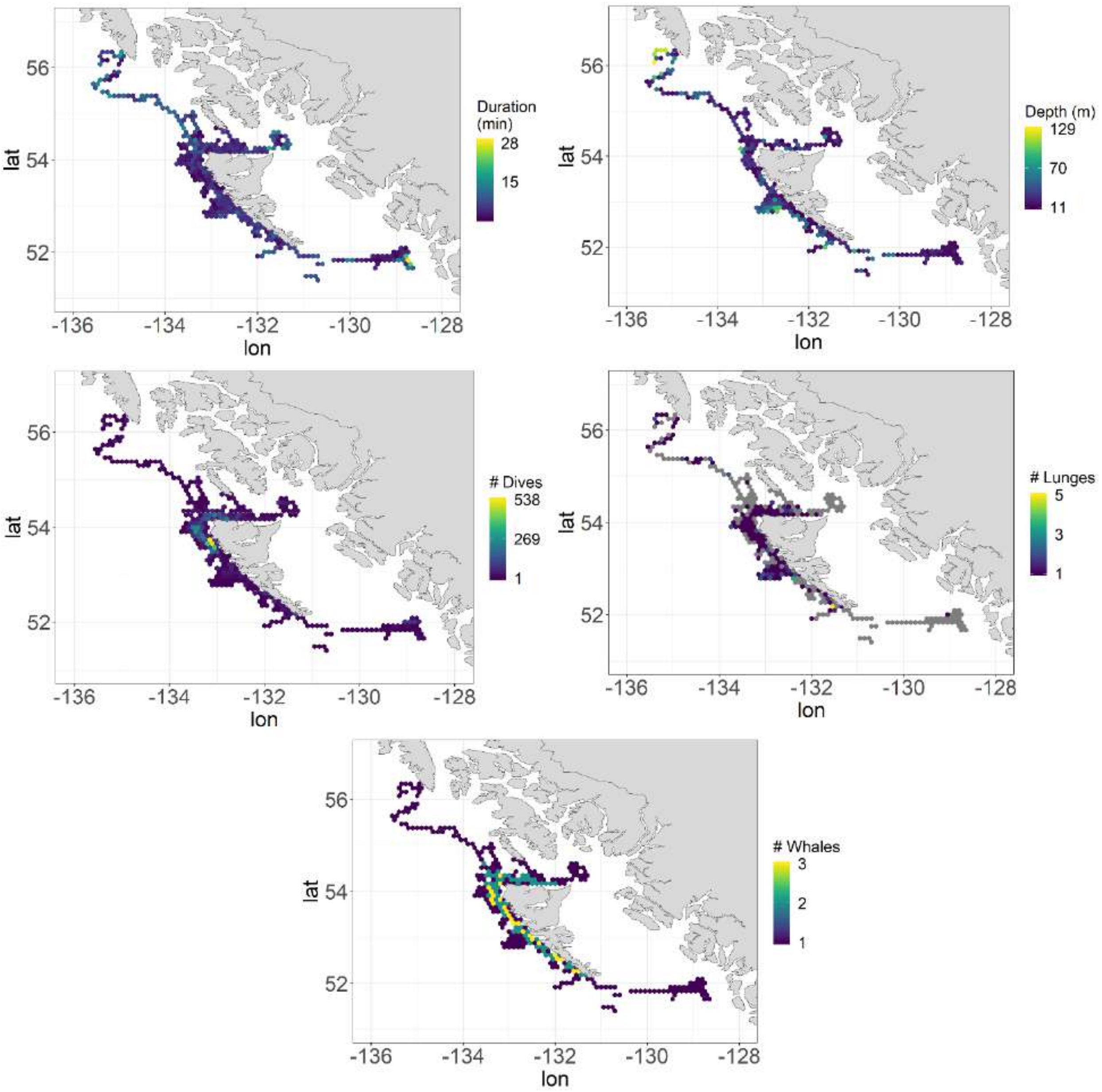

Figure 43. Data from DM- and DUR+-tagged humpback whales tagged off Maui, Hawaii, in March 2018 and 2019 summarized in 0.1-deg hexagonal grids showing the median dive duration (top left), median maximum dive depth (top right), median number of dives (middle left), median number of lunges (middle right), and number of tagged whales (bottom) recorded in each grid cell while in the breeding areas.

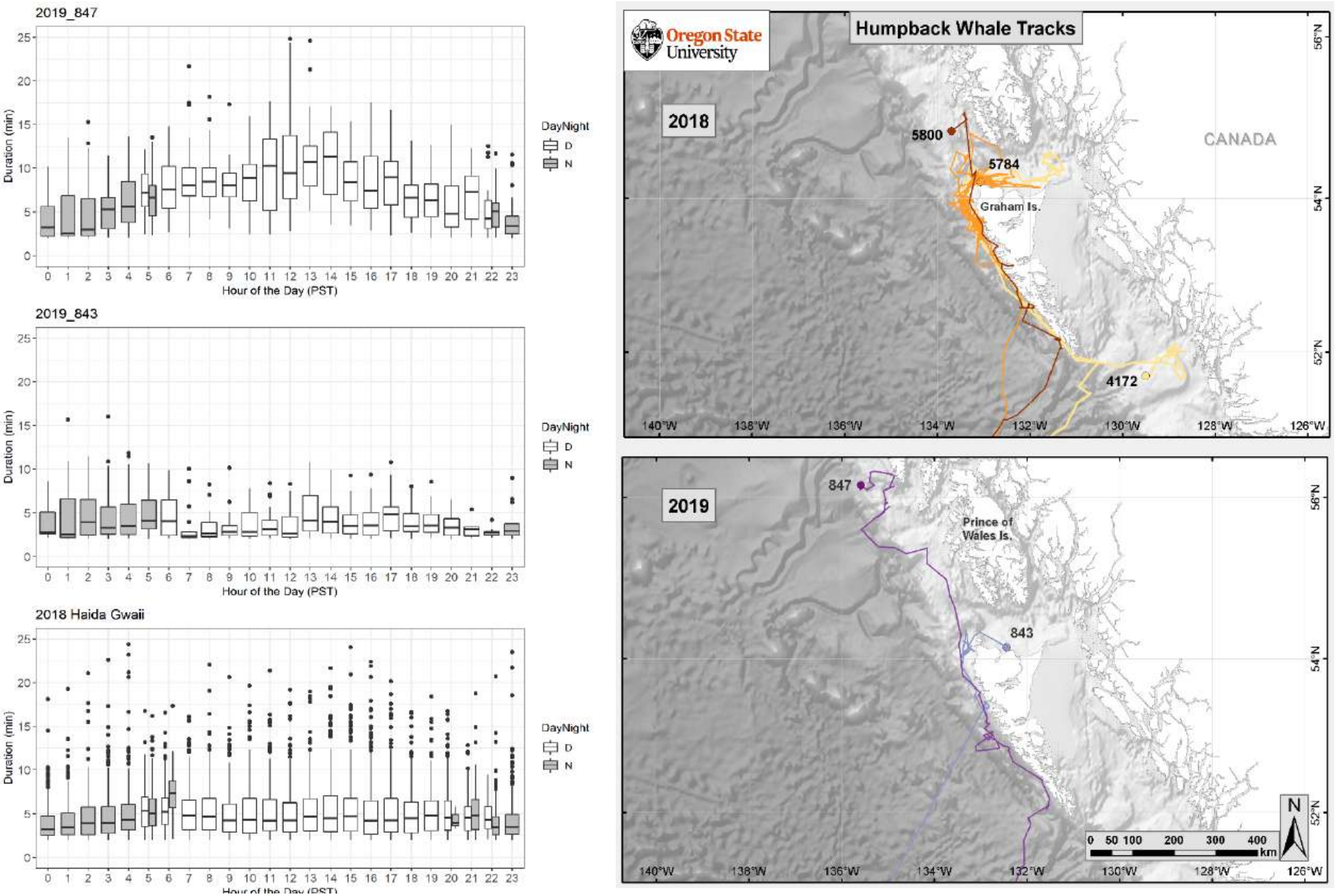

Figure 44. Left panels: Hourly distributions of dive duration while on the feeding grounds (near Haida Gwaii and SE Alaska) for DM- and DUR+-tagged humpback whales (n = 5) tagged off Hawaii during March 2018 (bottom panel; n = 3) and 2019 (top and middle panels). Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Some hours show data for both day and night due to differences in daylight hours across the latitudinal and longitudinal ranges occupied. Right panels: Tracks of tagged humpback whales after arriving at the feeding grounds off Haida Gwaii in 2018 (top panel) and 2019 (bottom panel).

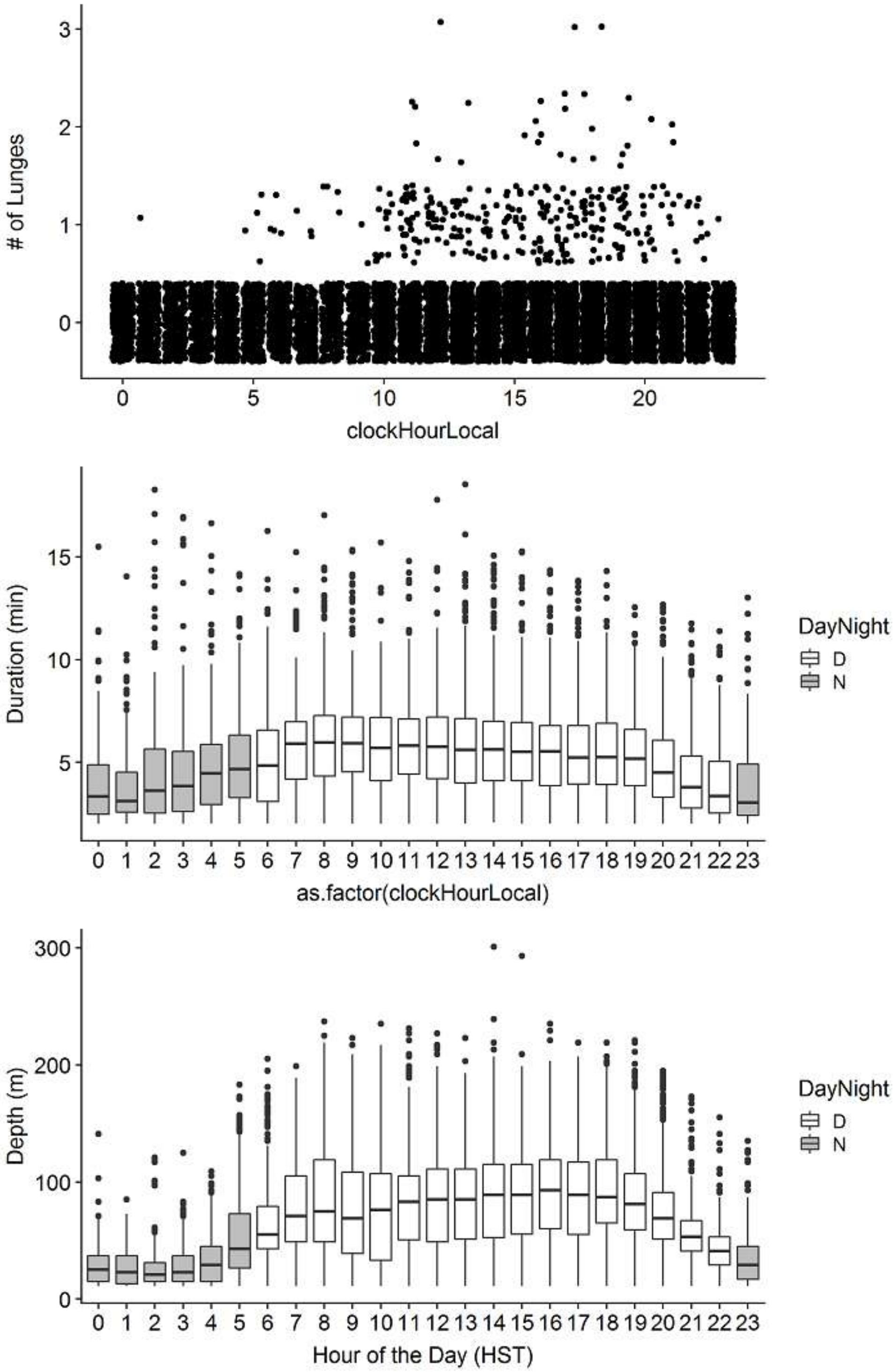

Figure 45. Hourly distribution of the number of lunges (top panel), dive duration (middle panel), and dive depth (bottom panel) while on feeding grounds near the western Aleutian Islands and Bearing Sea for a DM-tagged humpback whale (#5736, a male) tagged off Maui, Hawaii, during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

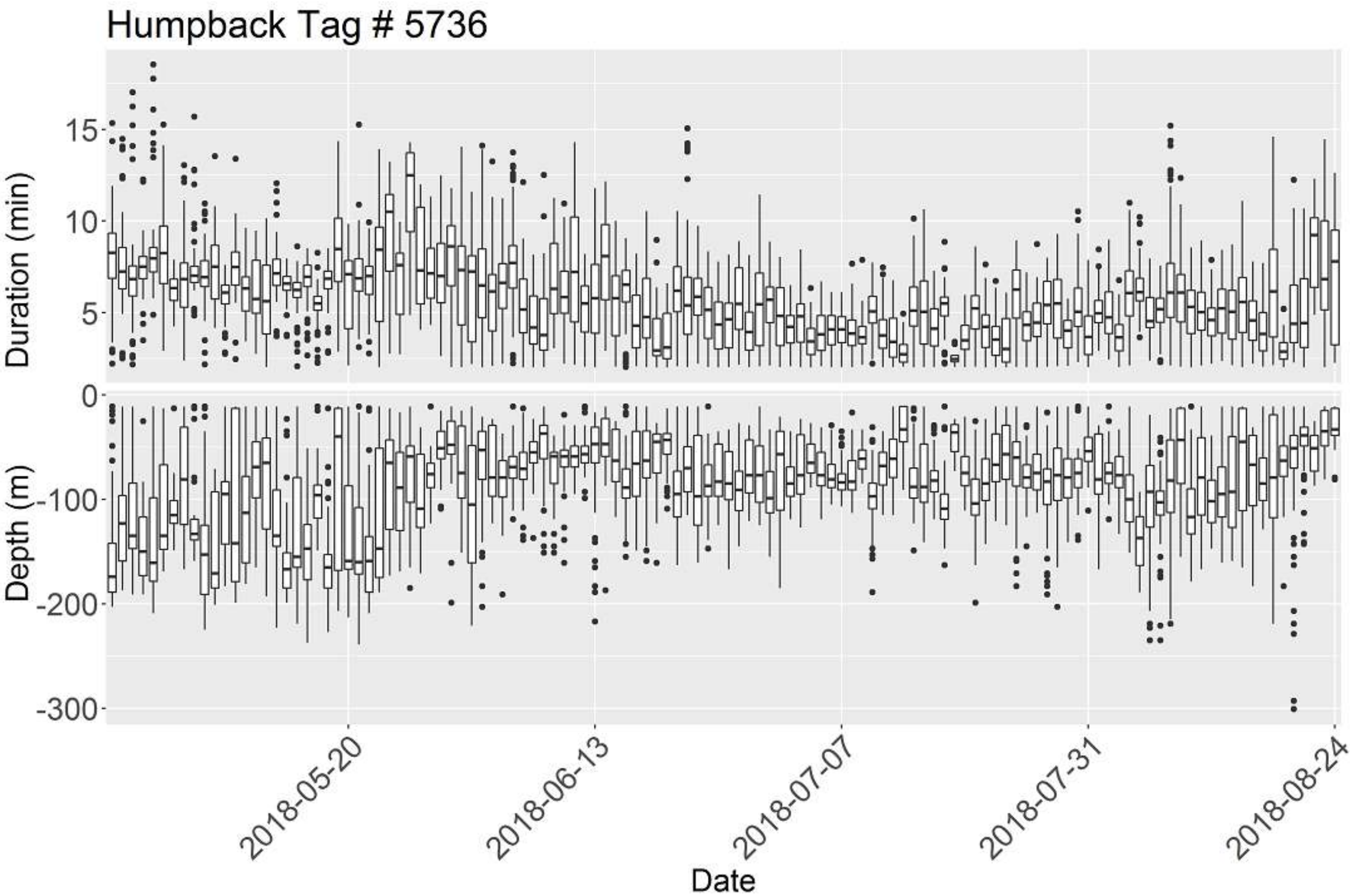

Figure 46. Distribution of daytime dive duration (top panel) and dive depth (bottom panel) during movements on the feeding grounds near the western Aleutian Islands and Bering Sea of a DM-tagged humpback whale (#5736, a male) tagged off Maui, Hawaii, during March 2018.

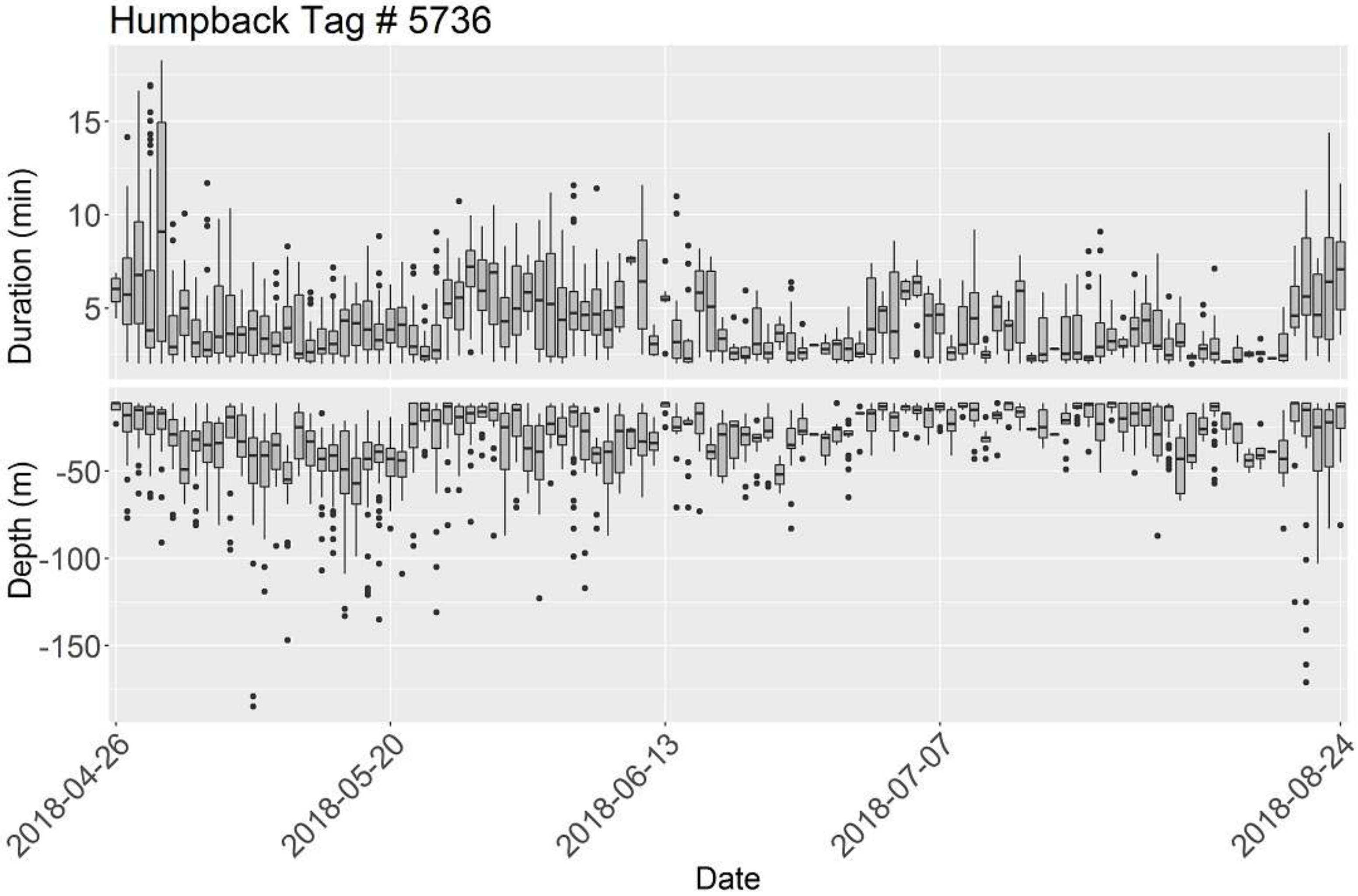

Figure 47. Distribution of nighttime dive duration (top panel) and dive depth (bottom panel) during movements on the feeding grounds near the western Aleutian Islands and Bering Sea of a DM-tagged humpback whale (#5736, a male) tagged off Maui, Hawaii, during March 2018. Boxes represent the first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

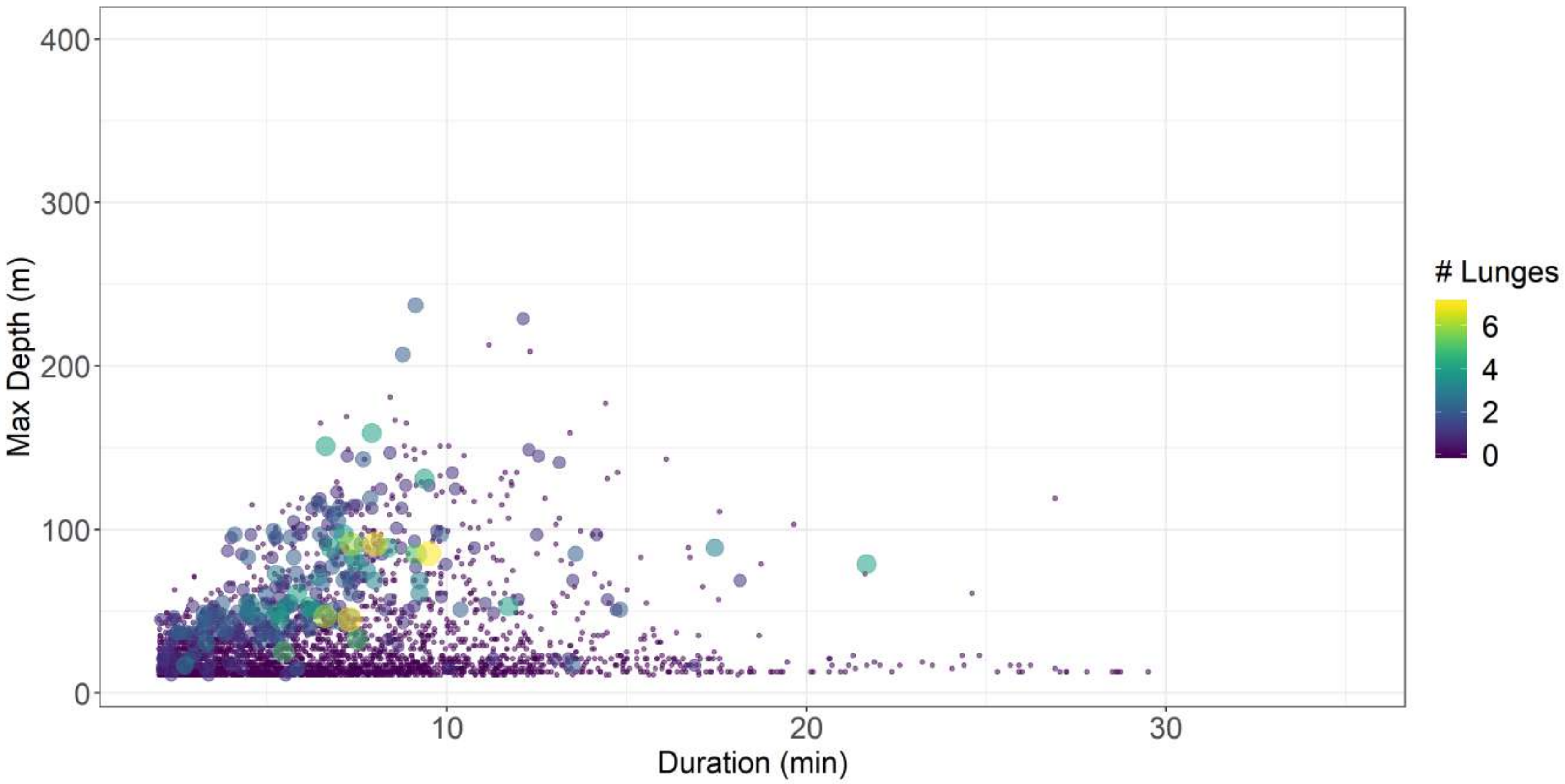

Figure 48. Depth and duration of dives made by DM-tagged humpback whales tracked on the feeding grounds off Haida Gwaii and SE Alaska. Whales were tagged off Maui, Hawaii, during March 2018 and 2019. Color of the circles represent the number of lunges recorded during each dive.

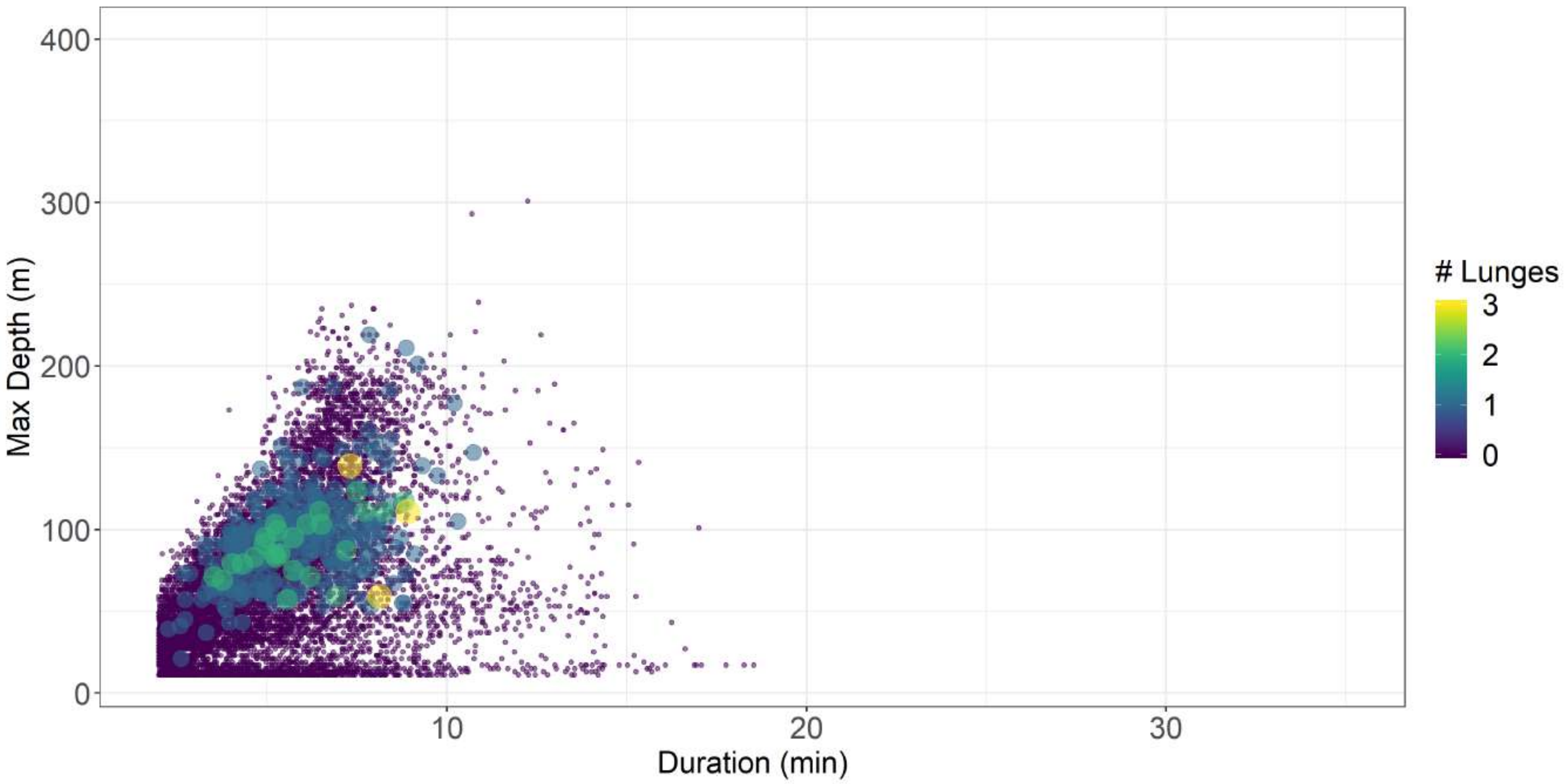

Figure 49. Depth and duration of dives made by a DM-tagged humpback whale (#5736, a male) on the feeding grounds near the western Aleutian Islands and Bearing Sea. The whale was tagged off Maui, Hawaii, during March 2018. Color of the circles represent the number of lunges recorded during each dive.

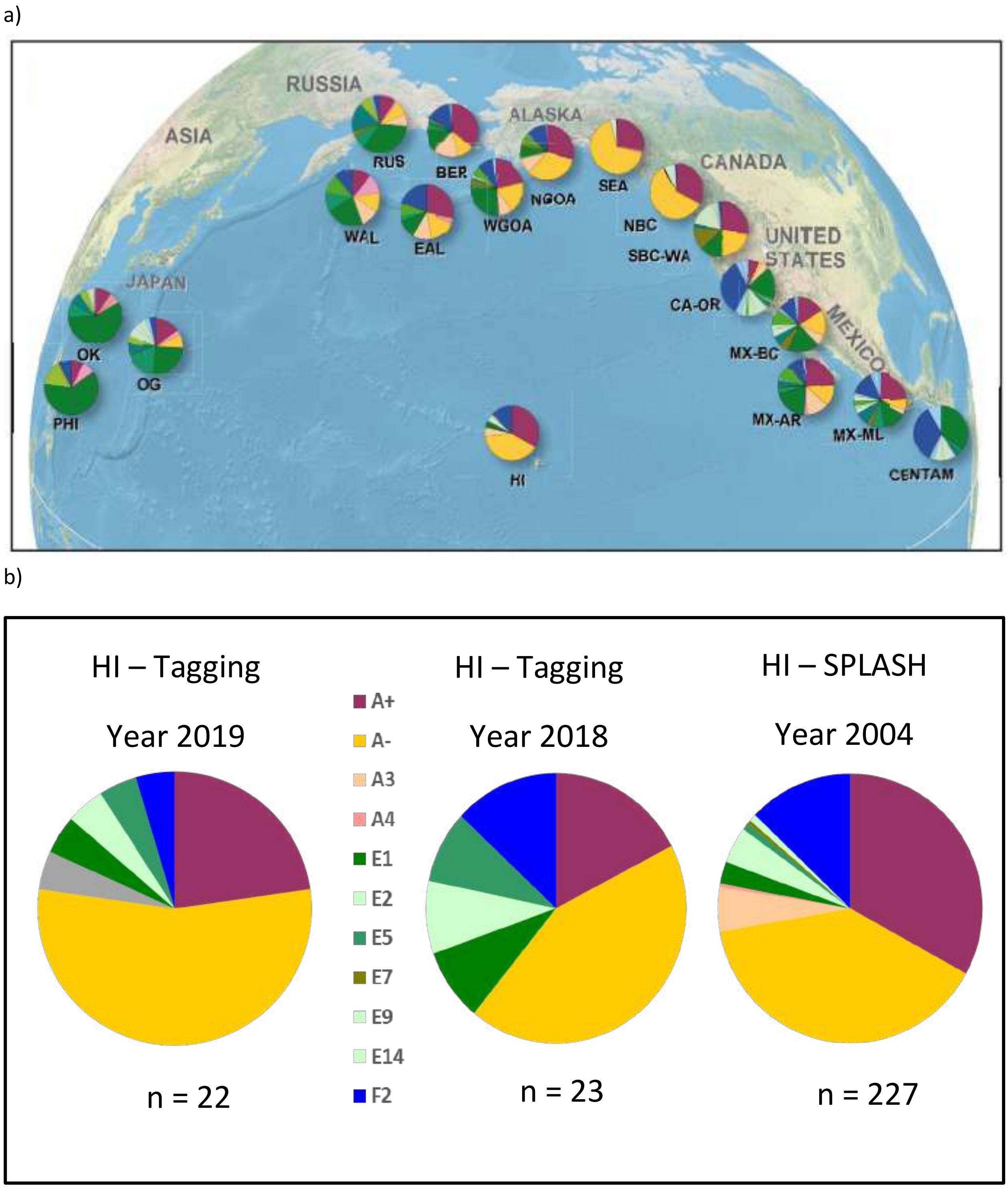

Figure 50. a) The proportion of mtDNA haplotypes for individual humpback whales sampled in the 10 feeding areas and in the eight breeding areas in the North Pacific during the SPLASH program, as modified from Figure 2 in Baker et al. (2013). b) Proportion of mtDNA haplotypes for individual humpback whales sampled off Maui, Hawaii, during the 2019 tagging effort (left), during the 2018 tagging effort (middle), and during SPLASH (right).

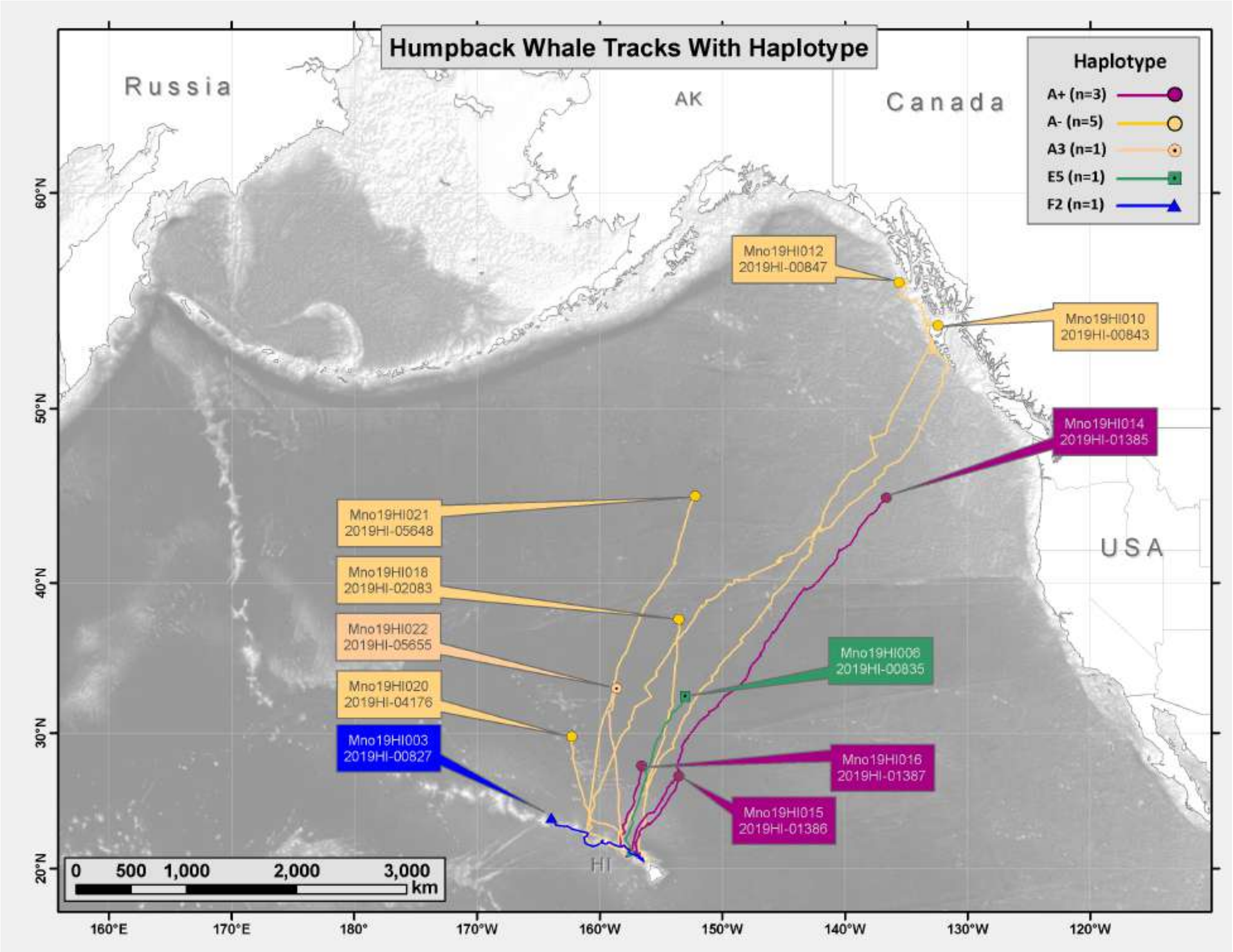

Figure 51. The migratory destinations or trajectories of 11 individuals sampled in Hawaii during the 2019 tagging effort with known mtDNA haplotypes. Haplotypes are colored according to Figure 28.