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

Final Report for the Pacific Northwest Feeding Area in Summer/Fall 2019, Including Historical Data from Previous Tagging Efforts off the US West Coast

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Commander, U.S. Pacific Fleet

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Abstract

Oregon State University (OSU) conducted a tagging and tracking study on Eastern North Pacific humpback whales (*Megaptera novaeangliae*) to determine their movement patterns, occurrence, and residence times along the West Coast of the United States (US). This report presents results from field efforts conducted off the coast of northern Washington (NWA) in summer and fall 2019, as well as results from previous OSU studies of humpback whales in southern and central California (SCCA), northern California and Oregon (NCA/OR), and NWA from 2004 to 2018. Whale use of US Navy training and testing areas as well as their use of Biologically Important Areas (BIAs) and National Marine Sanctuaries (NMSs) is examined, and assignment to various Distinct Population Segments (DPSs) based on genetic information is discussed. This report also presents detailed analyses of dive behavior, ecological relationships, and photo-identification. Tracking data were obtained for a total of 81 whales, with an overall tracked duration ranging from 0.1 to 164.2 days [d] (mean = 39.1 d, standard deviation [SD] = 33.6 d). The distribution of the tracked animals supported humpback whale affinity for continental shelf and shelf-edge habitat and documented extensive use of the northwestern coast of Washington and the central coast of California, and to a lesser degree, the northern California coast and the Columbia River mouth at the Oregon/Washington border. Complete or partial migrations were documented for eight whales, with recorded or presumed breeding destinations including Mexico, Guatemala, and Hawaii. The most intensively used Navy range was the Northwest Training and Testing Study Area (NWTT), with 73 percent of whales (59 of 81) having locations there and a maximum residency of 86.6 d. The second most intensively used range was Warning Area-237 (W237) of the NWTT, with 47 percent of whales having locations there and a maximum residency of 65.4 d. Only 6.2 percent of whales migrated through the Southern California Range Complex (SOCAL) and only 1.2 percent migrated through the Southern California Anti-submarine warfare Offshore Range (SOAR) subarea. Nine percent of whales had locations within Point Mugu Range Complex (PT MUGU), spending between 6.1 and 33.8 d there. Most of the occupancy in NWTT was by whales tagged in NWA and NCA/OR, and only 13 percent of whales tagged in SCCA had locations in NWTT. The occupancy of US West Coast BIAs and NMSs also suggested spatial separation of whales throughout feeding areas, as there was very little overlap of locations in BIAs or NMSs of whales tagged in the different regions. The most intensively used were the Northern Washington BIA and the Olympic Coast NMS for whales tagged in NWA, the Point St. George BIA and Greater Farallones NMS for whales tagged in NCA/OR, and the Gulf of the Farallones to Monterey Bay BIA and Greater Farallones NMS for whales tagged in SCCA. A total of 79 individual whales were genetically identified from skin biopsy samples collected during tagging efforts (n = 14 from SCCA; n = 15 from NCA/OR; n = 50 from NWA). The composition of haplotype frequencies suggested a differentiation between the SCCA and NCA/OR feeding aggregations that had not been previously recognized. The relative likelihood of individual assignment to each of the four recognized DPSs in the North Pacific based on the genetic profiles indicated that the majority of individuals from SCCA (64 percent) assigned with highest likelihood to the Central America DPS, whereas the largest proportion of individuals from NCA/OR (47 percent) and NWA (48 percent) assigned with highest likelihood to the Hawaii DPS. The remaining individuals assigned to the Mexico and Western North Pacific DPSs.

Executive Summary

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

In 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 along the US West Coast. 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 (MMPA). This report presents detailed results from the tagging, biopsy sampling, and photo-identification efforts conducted off the coast of northern Washington in summer and fall 2019, as well as results from previous OSU studies of humpback whales in California, Oregon, and Washington from 2004 to 2018. Whale use of Navy training and testing areas as well as their use of NMFS-identified Biologically Important Areas (BIAs) and US National Marine Sanctuaries (NMSs) is examined and assignment to various DPSs, based on tracking, genetic, and photographic information, is discussed. This report also presents detailed dive behavior analyses and ecological relationships between whale locations and oceanographic conditions.

Five types of non-recoverable, fully implantable (or "consolidated type") tags were used during this study, all providing long-term tracking information via the Argos satellite system: Telonics ST-15 and ST-21 Location-Only (LO) tags; Telonics Duration Monitoring (DUR) tags, providing locations and dive duration information; Telonics Duration Monitoring Plus (DUR+) tags, providing locations, dive duration, and number of feeding lunges; and Telonics Dive Monitoring (DM) tags, providing locations, dive duration, number of feeding lunges, and depth. Additionally, one Wildlife Computers MK-10 Advanced Dive Behavior (ADB) tag, a partially implantable, recoverable tag, was used in 2018, providing tracking over multiple weeks while recording high-resolution dive profile information (dive duration, depth, and accelerometer and magnetometer data). Twenty-four humpback whales were tagged (all DM tags) in northern Washington (NWA) in September and October 2019. Argos locations were received from 22 of the tags, with tracking periods ranging from 4.2 to 164.2 days (d) (mean = 46.8 d, standard deviation [SD] = 39.0 d). A total of 61 humpback whales were tagged by OSU off the US West Coast prior to 2019, covering the period 2004 to 2005 and 2016 to 2018. Of these, 25 were deployed in southern and central California (SCCA; in 2004, 2005, and 2017); 16 were deployed in northern California and Oregon (NCA/OR; in 2005 and 2016-2018); and 20 were deployed in NWA (in 2018). Tracking data were obtained for 59 whales prior to 2019 (the remaining tags provided no locations), and when combined

with tags from 2019, overall tracking duration ranged from 0.1 to 164.2 d (mean = 39.1 d, SD = 33.6, n = 81). The ADB tag, deployed in WA in 2018, transmitted for 12.5 d but was not recovered.

Switching state-space models (SSSM) were applied to the Argos locations from the tags for the purpose of generating regularly spaced tracks with annotated movement behavior for use in several analyses including home range, dive behavior, and ecological relationships.

The distribution of tracked humpback whales supported humpback whale affinity for continental shelf and shelf-edge habitat, and documented extensive use of the northwestern coast of Washington and the central coast of California, and to a lesser degree, the northern California coast and the Columbia River mouth at the Oregon/Washington border. Both the overall latitudinal ranges in feeding areas and the home ranges calculated from tracks greater than 30 d in length showed overlap in the distribution of humpback whales tagged in NWA and NCA/OR, and between whales tagged in NCA/OR and SCCA, but not between whales tagged in NWA and SCCA. The northernmost locations ranged from Queen Charlotte Sound, British Columbia, Canada, for whales tagged in NWA, the southwest coast of Vancouver Island, British Columbia, for whales tagged in NCA/OR, and off the north-central Oregon coast for whales tagged in SCCA. The southernmost non-migratory locations ranged from the northern Oregon coast for whales tagged in NWA, off Point Sal, central California, for whales tagged in NCA/OR, and in the Santa Barbara Channel for whales tagged in SCCA. Home ranges and core areas of use were significantly smaller for whales tagged in NWA than those tagged in either NCA/OR or SCCA.

Six whales were tracked on their southbound migration, with departure dates ranging from 1 November to 24 December. Migratory destinations were tracked for five of the six whales, with four (two from NWA and two from NCA/OR) migrating to the mainland coast of Mexico and one (from SCCA) migrating to Guatemala. The sixth whale was last located after a 66-d gap in locations off the southwestern coast of Baja California, Mexico. Migration duration was remarkably similar for all five whales, ranging from 27.6 to 31.6 d. Partial migrations were tracked for an additional two whales tagged in NWA in 2019, each with a southwest trajectory toward Hawaii.

The Navy areas considered in this report were: the Southern California Range Complex (SOCAL), the Southern California Anti-submarine warfare Offshore Range subarea (SOAR), the Point Mugu Range Complex (PT MUGU), the Northwest Training and Testing Study Area (NWTT), the Warning Area-237 (W237) within the NWTT, and the Gulf of Alaska Temporary Maritime Activities Area (GOA). The most heavily used Navy range by humpback whales in this study was NWTT, with 73 percent of whales (59 of 81) having locations there (in March and August through December) and a maximum residency of 86.6 d. Most of the occupancy of this range was by whales tagged in NWA and NCA/OR, for which 68 percent of tag deployments occurred within the NWTT range. Only 13 percent of humpbacks tagged in SCCA had locations in NWTT. The second most heavily used range was area W237 of the NWTT, with 47 percent of whales having locations there (August through December) and a maximum residency of 65.4 d. All but one of these whales (tagged in NCA/OR) was tagged in NWA. The southern Navy ranges saw much less use by humpback whales (no whales were tagged within the southern ranges), with only five whales migrating through SOCAL (in January, February, November, and December) and only one migrating through SOAR (in November). Nine percent of whales had locations within PT MUGU, with three whales migrating through the range (in February, November, and December) and the remaining four (one tagged in NCA/OR, three tagged in SCCA) spending between 6.1 and 33.8 d there (in July through November). No tagged humpback whales were located in the GOA training range (and no tagging occurred within this range) in any of the years covered in this report (2004 to 2019).

The occupancy of US West Coast feeding BIAs and NMSs also suggested spatial separation of humpback whales throughout feeding areas, as there was very little overlap of locations in BIAs or NMSs of whales tagged in the different regions. The most important areas (those with the highest proportion of tagged whales having locations there) were the Northern Washington (NOWA) BIA and the Olympic Coast (OC) NMS for humpbacks tagged in NWA, the Point St. George (PSG) BIA and Greater Farallones (GF) NMS for whales tagged in NCA/OR, and the Gulf of the Farallones to Monterey Bay (Farallones) BIA and GFNMS for whales tagged in SCCA.

Dives of DM-tagged humpback whales off Washington in 2019 summarized a median of 65.6 percent of the tracking durations. Dive durations primarily ranged from 3 to 8 minutes with dive depths generally less than 100 meters (m). Feeding effort was higher off Vancouver Island and the southern Washington coast; however, fewer dives were also recorded in those areas. Longer-duration and deeper daytime dives suggest whales were feeding on krill throughout the study area, although dive depths occurring on Swiftsure Bank off Washington were limited by shallow bottom topography.

A cumulative assessment of dive behavior for humpback whales tagged from southern California to Washington from 2016 to 2019 indicated that dive behavior was largely characterized by diel variability, with deeper, longer-duration dives occurring during the day, when more feeding behavior also occurred. Spatial and temporal variability of dive behavior was relatively low across meso-scales (10-100 kilometers [km] and 1-5 d), likely due to the whales' ability to feed on both fish and krill. However, local-scale (< 10 km) differences in behavior did occur in areas like Swiftsure Bank, where dive depths were limited by shallow water depths, and more southerly areas where dive behavior differed with distance to shore, possibly reflecting whales targeting different prey types. Tagged whales throughout the study area spent the majority (over 50 percent) of their reported time at depths < 30 m, which is within the zone of possible impact for deep-drafted vessels transiting the area. Time at depths < 30 m was higher for whales tracked off central California compared to further north, suggesting that regional differences in behavior, in addition to volume of vessel traffic, may influence the level of vessel collision risk for these areas.

The output of the SSSM applied to 78 humpback whale Argos tracks, representing a combination of the 2016-2019 data collected under CESU agreements together with earlier data collected by OSU off the US West Coast during tagging efforts in 2004 and 2005, produced a total of 2,696 daily locations with annotated behavioral mode available for ecological characterization. Of these, 86.4 percent were classified as area-restricted searching (ARS; an indication of foraging behavior), 9.8 percent as uncertain, and 3.8 percent as transiting. These locations occurred across 17 degrees of latitude, spanning from the northern tip of Vancouver Island, British Columbia, Canada, in the north to the Santa Barbara Channel, California, in the south. Ecological characterization indicated that while engaged in ARS behavior, tracked humpback whales moved a median of 12.9 km between daily locations, corresponding to a median speed of 0.54 km/hour [h]. While in ARS, whales occurred at a median depth of 162.0 m, over southwest-facing seafloor with median slope of 0.76°, and at median distances of 3.8 km from the shelf break and 24.8 km from shore. The oceanographic conditions where humpback whales engaged in ARS behavior were characterized by a median sea surface temperature of 13.0°C, median sea surface temperature gradient (a measure of frontal activity) of 0.17°C/deg, and median phytoplankton chlorophyll-*a* content of 1.74 mg/m^3.

Tests of global differences between tagging regions (SCCA, NCA/OR, and NWA) were statistically significant for all variables, being most pronounced for sea surface temperature, seafloor aspect, and distance to the shelf break (robust ANOVA *F*-test with *p*-values < 0.001 in all cases). Post-hoc tests indicated significant differences between tagging regions for most pairwise comparisons (robust Yuen's test with *p*-values < 0.001 in all cases), except for SCCA and NCA/OR, which were less differentiated with respect to mean distance and speed between daily locations, seafloor slope, sea surface temperature gradient, and chlorophyll-*a* content. The strong differentiation of NWA relative to NCA/OR and SCCA was likely driven by the distinct environmental conditions imposed by the Strait of Juan de Fuca and adjacent waters. From this analysis we conclude that the differences in movement characteristics and environmental conditions between tagging regions are consistent with the other results of this study that point at a spatial separation (or at least limited exchange) between BIAs and areas of whale aggregation along the US West Coast. Together, these results provide an improved understanding of the ecological requirements of the humpback whale DPSs that use these regions.

Biopsy samples were collected from 19 tagged whales and from nine untagged humpback whales off the Washington coast during the 2019 season. All samples provided DNA profiles sufficient for subsequent analyses. Mitochondrial deoxyribonucleic acid (mtDNA) sequences of the 28 samples confirmed species identification and resolved seven haplotypes, all of which have been previously described for North Pacific humpback whales and so are in the public domain. The 28 samples were represented by a unique multi-locus genotype of at least 14 loci, sufficient for individual identification. One recapture was identified by photo-identification and confirmed by genotype matching. After removing this replicate, the Washington dataset represented 27 individual whales, nine females and 18 males.

The DNA profiles of the 27 individuals were compared to a reference database of 3,320 individuals sampled previously in the North Pacific, including 1,805 sampled by the ocean-wide survey referred to as the "Structure of Populations, Levels of Abundance, and Status of Humpbacks" program (SPLASH), and to the individuals sampled during previous tagging effort off California, Oregon, and Washington in 2016, 2017 and 2018, under previous CESU agreements. From this comparison, two recaptures were detected; an untagged male was a genotype match to an individual biopsy-sampled, but not tagged, during the OSU tagging effort in Washington in 2018; and a tagged male was a genotype match to an individual biopsy sampled during the SPLASH effort in northern British Columbia in 2005.

The profiles of the 27 individuals identified from the 2019 tagging effort were combined with DNA profiles from 53 individuals identified from previous tagging efforts along the US West Coast. The one recapture between tagging datasets (identified above) was removed, for a total of 79 individual humpback whales identified during tagging efforts from 2016 to 2019 (n = 14 from SCCA; n = 15 from NCA/OR; n = 50 from NWA).

Differences in mtDNA haplotype frequencies were used to investigate the influence of maternal fidelity to both feeding aggregations and breeding grounds, including tagging samples collected previously and the SPLASH reference database. A comparison of haplotype frequencies from the SCCA, NCA/OR, and NWA samples suggested some degree of differentiation between these feeding aggregations, with NCA/OR whales appearing more similar to the NWA aggregation. This differentiation between SCCA and NCA/OR feeding aggregations had not been recognized previously in the limited sampling of the Oregon coast during SPLASH, but was noted in the results of previous tagging efforts, based on smaller sample sizes, under previous CESU agreements in 2016, 2017, and 2018.

The DNA profiles of humpback whales sampled on the feeding grounds were used to calculate the relative likelihood of individual membership in each of the four recognized DPSs in the North Pacific, using a Bayesian assignment procedure and the SPLASH reference database. The proportion of individuals assigned to alternate DPSs differed among the three tagging datasets with SCCA showing the majority of individuals (64 percent) assigning with highest likelihood to the Central America DPS, whereas the largest proportion of individuals from NCA/OR (47 percent) and NWA (48 percent) assigned with highest likelihood to the Hawaii DPS. The genetic assignment of individuals showed some degree of correspondence with the migratory destinations of the tagged whales, suggesting the potential for further improvement in individual assignment to DPSs with larger reference databases.

Of the 104 whales tagged and/or biopsied off the US West Coast from 2004 to 2019, 82 had fluke photos that could be used for identification purposes. Sixty-eight of these have been identified in the Happywhale photo-ID database, with matches to SPLASH-defined regional strata in southern British Columbia/Washington, California/Oregon, Mexico, Hawaii, and Central America. Strong site fidelity was shown to feeding areas, as most matches between feeding seasons were to the feeding areas in which the whales were tagged/biopsied. Most breeding-area matches were to mainland Mexico for whales tagged in SCCA and to Baja California, Mexico, for whales tagged in NCA/OR and NWA. One whale (from SCCA) had matches to both Mexico and Central America.

A total of 578 fluke IDs were also obtained of untagged whales encountered during our tagging efforts. Of these, 449 were identified in Happywhale, with matches to SPLASH strata in southern British Columbia/Washington, California/Oregon, Mexico, Hawaii, and Central America. As with tagged/biopsied whales, most matches between feeding seasons were to the feeding areas in which the whales were photographed. Most breeding-area matches were to mainland Mexico for whales tagged in SCCA and to Baja California for whales tagged in NCA/OR and NWA. Two whales (from SCCA) had matches to both Mexico and Central America, and four whales (from NWA) had matches to both Mexico and Hawaii.

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Acronyms, Abbreviations, and Units

°C	Degrees Celsius
Aleutian BIA	Aleutian Islands Biologically Important Area
ANOVA	Analysis of variance
Area W237	Warning Area-237 within the Northwest Training and Testing Study Area
ARS	Area-restricted searching
ASPECT	Slope aspect
BIA	Biologically Important Area
bp	Base pair
CAU	Core area of utilization
CESU	Cooperative Ecosystem Studies Unit
CINMS	Channel Islands National Marine Sanctuary
CHL	Phytoplankton chlorophyll-*a*
CBNMS	Cordell Bank National Marine Sanctuary
cm	Centimeter
d	Day
deg	Degrees
DEPTH	Depth
DISTSHELF	Distance to the 200-m isobath (or distance to the shelf break)
DISTSHORE	Distance to the nearest shoreline
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)
DUR+	Duration Plus tag (model Telonics RDW-665)
EEZ	Exclusive Economic Zone
ERD	Environmental Research Division
ERDDAP	Environmental Research Division Data Access Program
ESA	Endangered Species Act
Farallones-Monterey BIA	Gulf of the Farallones-Monterey Bay Biologically Important Area

Fort Bragg BIA	Fort Bragg to Point Arena Biologically Important Area
g	Gram
GOA	Gulf of Alaska Temporary Maritime Activities Area
GFNMS	Greater Farallones National Marine Sanctuary
h	Hour
HR	Home range
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 SPOT5 or SPOT6)
m	Meter
mg m^{-3}	Milligrams per cubic meter
min	Minute
mm	Millimeter
MMPA	Marine Mammal Protection Act
mo	Month
MBNMS	Monterey Bay National Marine Sanctuary
Morro Bay BIA	Morro Bay to Point Sal Biologically Important Area
mtDNA	Mitochondrial deoxyribonucleic acid
NAVFAC	Naval Facilities Engineering Command
NMFS	National Marine Fisheries Service
NMS	National Marine Sanctuary
NOAA	National Oceanic and Atmospheric Administration
NOWA BIA	Northern Washington Biologically Important Area
NWTRC	Northwest Training Range Complex
NWTT	Northwest Training and Testing Study Area
OCNMS	Olympic Coast National Marine Sanctuary
OSU	Oregon State University
PCR	Polymerase chain reaction
PDI	Post-dive interval

PSG BIA	Point St. George Biologically Important Area
PT MUGU	Point Mugu Range Complex
PWDIST	Pairwise Distance
PWSPEED	Pairwise Speed
R/V	Research Vessel
s	Second
Santa Barbara BIA	Santa Barbara Channel-San Miguel Biologically Important Area
SD	Standard deviation
SEAK BIA	Southeast Alaska Biologically Important Area (summer and fall)
SLOPE	Slope (or depth gradient)
SOAR	Southern California Anti-submarine warfare Offshore Range subarea
SOCAL	Southern California Range Complex
SPLASH	Structure of Populations, Levels of Abundance and Status of Humpbacks program
SSSM	Conventional switching state-space model
SST	Sea surface temperature
SSTG	Magnitude of the horizontal sea surface temperature gradient
Stonewall BIA	Stonewall and Heceta Bank Biologically Important Area
SWFCS	Southwest Fisheries Science Center
SWS	Saltwater conductivity switch
US	United States
V	Volt

1 Introduction

The purpose of this Cooperative Ecosystem Studies Unit (CESU) agreement between the Department of the Navy (Navy) and Oregon State University (OSU) is to support marine mammal studies in compliance with the Letters of Authorization and Biological Opinions issued by the United States (US) National Marine Fisheries Service (NMFS) to the Navy for activities in all Pacific Ocean testing and training range complexes. From the perspective of the conservation status of humpback whales (*Megaptera novaeangliae*) in 2016 NMFS divided the global population into fourteen Distinct Population Segments (DPS) for purposes of listing under the Endangered Species Act[1] (ESA). Four DPS 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 DPS (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 Southeast Alaska and northern British Columbia; Mexico animals being found off northern Washington-southern British Columbia; and Central America animals being found off California and Oregon (Bettridge et al. 2015). However, some degree of mixing of DPSs occurs in the feeding areas, with Hawaii whales also being found throughout the Gulf of Alaska, the Aleutian Islands, and eastern Russia; and Mexico whales 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). This mixing of DPSs in the feeding areas complicates unequivocal assignment of individuals to breeding stock for management purposes without further information. As a result, there is a need for data on occurrence and habitat use by these different DPSs in the feeding areas, and their overlap with shipping traffic, fishing grounds, and areas of military operation, so that management agencies can prioritize actions and to mitigate potential impacts from these activities.

Since 2016, OSU has been conducting marine species monitoring on behalf of the Navy off the US West Coast and Hawaii under CESU agreements N62473-17-2-0001 and N62473-19-2-0002. The study seeks to provide greater detail on which humpback whale DPSs use the Navy activity areas in the North Pacific Ocean through the use of satellite telemetry, genetic analyses, and photo-identification (photo-ID) (Mate et al. 2018a, 2019, Palacios et al. 2020a, b). Information was also sought on humpback whale use of other areas of special interest to NMFS, such as National Marine Sanctuaries (NMSs) or the Biologically Important Areas (BIAs) for humpback whales in waters of the US Exclusive Economic Zone

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

(EEZ; i.e., the ocean waters extending out to 200 nautical miles of the US coastline) (Calambokidis et al. 2015, Ferguson et al. 2015a, b). Satellite tag deployments occurred in California in 2017, Oregon in 2016, 2017 and 2018, and in Washington in 2018 and 2019 to track the movements of humpback whales off the US West Coast for multiple weeks to multiple months after deployment. Results from the West Coast studies through 2018 were reported by Mate et al. (2018a) and Palacios et al. (2020a). This Final Report provides detailed results from tagging in the Strait of Juan de Fuca and the outer Washington coast in the late summer and early fall of 2019. It includes information on humpback whale use of Navy ranges, BIAs, and NMSs, as well as their feeding-season home range, habitat use, and ecological characteristics. In addition, this Final Report includes information on dive duration, feeding activity, and behavioral characteristics from 2019-tagged whales, as well as genetic and resight results from analyses of biopsy samples and photo-IDs. A cumulative analysis of all the data as a whole is also presented, including results of previous tagging efforts by OSU off California and Oregon in 2004 and 2005.

1.1 Study Goals

With this project, OSU sought to track humpback whale movement between or through Pacific Navy range complexes, and to collect photo-IDs and genetic samples (taken during tag placement) to further help delineate the DPSs, as well as to describe the whales' feeding-season home range, migration to breeding areas, habitat use, and ecological characteristics. Data from tagged whales also provided detail on dive duration, activity levels, and other behavioral characteristics over periods spanning multiple weeks to multiple months. Specifically, the goals of the summer/fall 2019 field efforts in the Pacific Northwest were to:

- Attach 25 Telonics RDW-665 Dive Monitoring (DM) satellite tags (equipped with depth sensors, accelerometers, and event-detection software) to humpback whales to monitor diving behavior and activity levels.

Additionally, through the collection of biopsy samples and genetic analyses of tagged whales, as well as untagged whales sampled during the conduct of fieldwork, this study sought to provide:

- Sex identification.
- 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 genotyping, with population structure analysis including comparison to existing published databases for humpback whales in the Pacific Ocean (i.e., a searchable "DNA register" of genetic profiles).

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 Deployments

Tagging efforts were conducted from small (6.7 to 7.0 meter [m]) rigid-hulled inflatable boats. 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 were extensively covered by external parasites. Satellite tags were deployed using the Air Rocket Transmitter System (Heide-Jørgesen et al. 2001), an air-powered applicator, following the methods described in Mate et al. (2007). Tags were deployed from distances of 1.5 to 5 m with 90- to 120-pound force per square inch in the applicator’s 70 cubic-centimeter (cm) pressure chamber.

2.1.1.1 Washington Tagging (2018 and 2019)

Humpback whale tagging efforts off Washington took place as day trips from Neah Bay, just east of Cape Flattery on the Olympic Peninsula, from 1 to 21 August 2018 (Palacios et al. 2020a) and 18 September to 6 October 2019.

2.1.1.2 Oregon Tagging (2005, 2016, 2017, and 2018)

Humpback whale tagging efforts off Oregon in 2016, 2017, and 2018 funded under CESU agreements (Palacios et al. 2020a) were conducted as day trips from ports along the Oregon coast. Two days of tagging (15 September and 11 October) took place out of Newport, in central Oregon in 2016. In 2017, tagging trips took place on 7 days (d), as follows: 2 d out of Newport; 1 d each out of Charleston, Brookings, and Gold Beach, in southern Oregon; and 2 d out of Clatsop Spit, in northern Oregon. The location of our field efforts varied due to the changing presence of whales, as reported to us by commercial fishermen and one aerial survey we conducted on 7 October 2017 off central Oregon. Tagging efforts off Oregon in 2018 took place as day trips out of Newport, on three days from 6 to 8 September 2018.

Prior to this CESU-funded study, one humpback whale was tagged during a day trip off Port Orford, southern Oregon, on 5 October 2005 as part of the Tagging of Pacific Pelagics (TOPP) study (Mate et al. 2018a).

2.1.1.3 California Tagging (2004, 2005, and 2017)

Humpback whale tagging efforts took place off the southern (Santa Barbara Channel) and central coast of California (off Half Moon Bay) in 2017 during a 31-d cruise aboard the 26-m OSU research vessel (R/V) *Pacific Storm*, from 5 July to 5 August (Mate et al. 2018a). The *Pacific Storm* served as a home base and support vessel for the research crew, from which a rigid-hulled inflatable boat was launched for tagging.

Prior to this CESU-funded study, humpback whales were tagged by OSU off central California (Half Moon Bay, Monterey Bay, and the Gulf of the Farallones) from 28 July to 21 August 2004, and off central (Big Sur and Gulf of the Farallones) and northern California (Cape Mendocino and Point Saint George) between 4 August and 6 October 2005, as part of the TOPP study (Mate et al. 2018a). The August taggings were conducted with support from the R/V *Pacific Storm*, whereas taggings in October were conducted as day trips in the rigid-hulled inflatable boat.

2.2 Satellite Tags

Five types of fully implantable, non-recoverable (“consolidated type;”*sensu* Andrews et al. 2019), Argos-based tags were used from 2004 to 2019 (**Table 1**): (1) Telonics ST-15 tags hereafter referred to as Location-Only or LO tags); (2) Telonics ST-21 tags (also referred to as LO tags); (3) Telonics RDW-640 tags (hereafter referred to as Duration-Only or DUR tags); (4) Telonics RDW-665 Dive-Monitoring tags (hereafter referred to as DM tags); and (5) Telonics RDW-665 Duration-Plus tags (hereafter referred to as DUR+ tags). All tag types were composed of a main body, a penetrating tip, and an anchoring system (**Figure 1**). All tag-specific size dimensions are given in **Table 1**. The main body consisted of a stainless-steel cylinder that housed a certified Argos transmitter and a 6-volt (V) lithium battery pack. A flexible whip antenna and a saltwater conductivity switch (SWS), both made of nitinol cable, were mounted on the distal endcap of this cylinder, while a penetrating tip was screwed onto the other end. The distal endcap had two perpendicular stops 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) for all tag types.

Eight of the tags (four DM, two DUR+, and two DUR) had eight stainless steel wires (3.5 cm long, 0.9 mm gauge) mounted behind the blades on the penetrating tip. These wires provided initial anchorage prior to deployment of the curved metal strip anchors, which were held flush to the tag body with wraps of water-soluble starch fabric (Solvy®) and deployed to their curved position after the Solvy® dissolved. To minimize tissue damage at the tag site, we eliminated the wires from remaining tags. Instead, Solvy® was rolled into ropes and tied around the metal strip anchors to hold them flush for tag deployment. Upon deployment the Solvy® ropes were pushed up the tag body, allowing the anchors to deploy immediately, eliminating the need for additional wire anchors.

Tag cylinders were partially coated with a long-dispersant polymer matrix (Resomer® or Eudragit®) in which a broad-spectrum antibiotic (gentamicin sulfate) was mixed to allow for a continual release of antibiotic into the tag site for an extended period of time to reduce the chances of infection (Mate et al. 2007). The tags were designed to be almost completely implantable (except for the perpendicular stops, antenna, and SWS), and were ultimately shed from the whale probably due to hydrodynamic drag and/or the natural migration of foreign objects out of the tissue (Mate et al. 2007). The operational duration of these tags was almost always limited by issues related to retention on the whale rather than by battery life. To date, the mean duration of the fully implantable tags deployed by OSU on humpback whales worldwide has been 35.1 d [standard deviation (SD) = 34.9 d, median = 25.8 d, n = 278], with a maximum duration of 220 d (OSU, unpublished data).

In addition to the fully implantable tags described above, one partially implantable, recoverable tag was deployed off Washington in 2018, which will hereafter be referred to as the Advanced Dive Behavior (ADB) tag (**Figure 2**; Mate et al. 2017). The ADB tag consisted of a certified Argos transmitter and a Wildlife Computers Time-Depth Recorder, with a three-axis accelerometer and magnetometer, cast in an epoxy tube (2.0 cm in diameter and 11.5 cm long). A FastLoc® geographic positioning system (GPS) receiver, encased in syntactic foam (10.0-cm diameter dome with a maximum height of 4.0 cm), was attached to one end of the epoxy tube. Three light-emitting diode lights were mounted on top of the syntactic foam to facilitate relocation of the tag. The tubular portion of the tag was slid into a cylindrical stainless-steel tag housing (2.6 cm in diameter and 14.5 cm long) for deployment. A circular stainless-steel plate, or collar, was welded onto the distal end of the housing to protect the syntactic foam during deployment. A penetrating tip and anchoring system, similar to that of the implantable tags, was mounted onto the cylindrical end of the tag housing. The cylindrical portion of the tag housing was designed for implantation beneath the whale's skin while the plate and syntactic foam GPS receiver sat atop the whale's back. The ADB tag and housing weighed approximately 470 g (approximately 240 g for the tag and approximately 230 g for the housing). A plastic "D-ring" was mounted on the bottom of the syntactic foam with a corrodible wire. This D-ring passed through a slot in the stainless-steel plate and was secured on the backside of the plate with a screw. After a pre-determined time, an electrical current was activated within the tag, oxidizing the corrodible wire, whereupon the tag was ejected from the housing and floated to the surface for recovery (Mate et al. 2017). For this study, the electro-mechanical connection between the tag and its housing was programmed to release the tag on 15 August 2018, in principle allowing time for tag recovery during our three-week field effort.

2.2.1 LO Tag Programming

In addition to providing transmissions for location calculation, the ST-15 LO tags reported a cumulative count of surfacings (based on the SWS wet/dry sensor) made by the whale (not analyzed for this report). The ST-21 LO tags contained a pressure sensor and were able to record dive depth as well as dive duration, but the sensor data were not reported correctly and are not used in this report. LO tags were programmed to transmit at least 10 s apart only when out of the water during four 1-hour (h) periods per day, coinciding with times when satellites were most likely to be overhead. With such a duty cycle, the life expectancy of the LO tag's battery was estimated at over one year (**Table 2**).

2.2.2 DUR Tag Programing

DUR tags used the status of the SWS (wet/dry) to detect submergence events and to record dive duration for "selected dives". For this study, selected dives were specified as those > 2 minutes (min) in duration (**Table 2**). Argos messages for DUR tags consisted of the start time and duration of a variable number of consecutive selected dives, typically four to six dives depending on data compression. The tag maintained an Argos message buffer that held up to 10 messages in the tag's memory. When enough selected dives were recorded to create a new message, it was added to the buffer. If there were already 10 messages in the buffer, the oldest message was discarded to make space for the new message. Every time the tag transmitted, it randomly selected one of the messages for transmission from the buffer and every third transmission was a diagnostic message, containing the tag's current temperature and voltage. DUR tags were programmed to transmit for five 1-h periods per day coinciding with times when satellites were most likely to be overhead. With such a transmission schedule, the life expectancy of the DUR tag's battery was approximately 220 to 290 d (**Table 2**).

2.2.3 DM Tag Programing

DM tags contained a pressure sensor and tri-axial accelerometers, and were able to record dive depth, dive duration, changes in body orientation, and motion while attached to a whale. As with the DUR tags, DM tags used the status of the SWS (wet/dry) to detect submergence events and to record dive duration for "selected dives". Selected dives were specified as those > 2 min in duration and 10 m in depth. 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. 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. 2018a, Palacios et al. 2020a). When in the breeding areas, the whales typically do not feed, so detected "lunge events" serve as a more general metric of activity level and behavior during the breeding season (Palacios et al. 2020b).

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. Feeding lunges are associated with a peak followed by a minimum in Jerk (Allen et al. 2016), so for the 2019 DM tags we identified feeding lunges as instances when the Jerk value exceeded 1.5 SD above the mean, followed by a value less than 1/2 of the mean within 30 s after the Jerk peak (See **Table 2** for lunge detection specifications of tags deployed prior to 2019). The mean Jerk value was continually updated following each selected dive and therefore represented a "grand mean" across all dives. 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 tags maintained an Argos message buffer like that of the DUR tag (described in **Section 2.2.2**). 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 feeding lunge detection criteria over time. DM tags were programmed to transmit only when out of the water during six 1-h periods every day to coincide with times when satellites were most likely to be overhead. With such a transmission schedule, the life expectancy of the DM tag's battery was approximately 90 to 120 d (See **Table 2** for transmission schedules of tags deployed prior to 2019).

2.2.4 DUR+ Tag Programing

DUR+ tags, used only in Washington in 2018, lacked a pressure sensor but were otherwise configured the same way as the DM tag, with a SWS for submergence detection and tri-axial accelerometers, and onboard processing software to detect behavioral events in the motion data. Argos messages for DUR+ tags consisted of the start date and time of each selected dive (dives > 2 min duration), dive duration, and number of lunges for a variable number of consecutive selected dives, typically four to six depending on data compression. The tag maintained an Argos message buffer like that of the DUR and DM tags, with similar transmission protocols as for the DM tag (described above in **Section 2.2.3**). DUR+ tags were programmed to transmit during six 1-h periods per day coinciding with times when satellites were most likely to be overhead, until 30 September 2018, then transmit during six 1-h periods every other day thereafter. This resulted in an electronic life expectancy of approximately 120 to 180 d.

2.2.5 ADB Tag Programming

The ADB tag was programmed to collect a GPS-quality FastLoc® location every 7 min or as soon thereafter as the whale surfaced from a dive. Dive depth was recorded every 1 s with 2-m vertical resolution. Body orientation (from the accelerometer) and magnetic compass heading (from the magnetometer) were also recorded at 1-s intervals. These data were all archived onboard the tag and accessible only when the tag was recovered. Qualifying dives (those greater than 2 min in duration and 10 m in depth) were also summarized for transmission through the Argos system along with GPS locations recorded by the tag. Summary messages (behavior messages) describing individual qualifying dives were generated by recording dive duration, maximum dive depth, dive shape (U-, V-, or square-shaped- and whether the U- or V-shaped dives were skewed right, left or centered) and the subsequent surfacing duration. Up to four consecutive summarized dives were transmitted in each behavior message (Wildlife Computers PAT-MK10 User Guide [30 November 2015] http://wildlifecomputers.com/wp-content/uploads/manuals/MK10-User-Guide.pdf). A single Argos message from the tag could send either one GPS location, one histogram summary (not used here), or one behavior message (summarizing four dives). Version 3 of the FastLoc® GPS acquisition program was installed in the ADB tag (Mate et al. 2017).

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 assigns 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 accuracy associated with each Argos satellite location was reported as one of six possible location classes (LCs) ranging from less than 200 m (LC = 3) to greater than 5 kilometers (km) (LC = B) (Vincent et al. 2002).

In order to generate a complete track from the Argos location data, OSU implemented a sequential data editing protocol on the received ("raw") locations from each tag to retain the best locations for analysis. First, locations occurring on land were excluded. Then, locations of class Z were removed from analyses because of the unbounded errors (or sometimes invalid locations) associated with them. The remaining locations were further filtered by LC, as follows. Lower-quality LCs (LC = 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 and occurrence in Navy areas and BIAs (see **Sections 2.3.3** and **2.3.4** below).

2.3.2 Track Regularization and Behavioral Annotation with State-Space Models

Some of the analyses covered by this report, such as home range, dive behavior, and ecological relationships (see **Sections 2.3.5, 2.3.6, 2.4, and 2.5** below), further required that track locations be spaced at regular intervals and have a behavioral mode annotation. For tracks from 2016 through 2019, the raw Argos locations (i.e., prior to applying the sequential data editing protocol described in **Section 2.3.1**) of all tracks > 3 d with > 10 locations, were used largely unedited (except for the removal of Z-class 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* add-on packages (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, 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 the 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 retaining every 20th sample 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 previous tagging efforts off Oregon and California in 2004 and 2005, fewer transmission periods were scheduled per day to prolong battery life (four 1-h transmission periods per day every day for the first 90 d and subsequently going to every second day; see Mate et al. 2007), and thus fewer locations were received per day than for the 2016 through 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 (Mate et al. 2018a), and we did not attempt to re-analyze them for purposes of this report using the more modern hSSSM due to the computational cost involved.

2.3.3 Occurrence in Navy Areas and BIAs

The number of filtered locations occurring inside versus outside Navy areas was computed for each 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 were: (1) the Southern California Range Complex (SOCAL), (2) the Southern California Anti-submarine warfare Offshore Range subarea (SOAR), (3) the Point Mugu Range Complex (PT MUGU), (4) the Northwest Training and Testing Study Area (NWTT), (5) the Warning Area-237 (W237) within the NWTT, and (6) the Gulf of Alaska Temporary Maritime Activities Area (GOA; **Figure 3**). Area W237 is located within NWTT, so whale occurrence in W237 is also counted as occurrence in NWTT as the two areas were analyzed separately. Likewise, SOAR is located within SOCAL, so whale occurrence there is also counted as occurrence in SOCAL.

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 (Calambokidis et al. 2015, Ferguson et al. 2015a, b) and NMSs. The BIAs considered for this report were: (1) Santa Barbara Channel-San Miguel (Santa Barbara BIA), (2) Morro Bay to Point Sal (Morro Bay BIA), (3) Gulf of the Farallones-Monterey Bay (Farallones BIA), (4) Fort Bragg to Point Arena (Fort Bragg BIA), (5) Point St. George (PSG BIA), (6) Stonewall and Heceta Bank (Stonewall BIA), and (7) Northern Washington (NOWA BIA) (**Figure 4**). The NMSs considered in this report were: (1) Channel Islands NMS (CINMS), (2) Monterey Bay NMS (MBNMS), (3) Greater Farallones NMS (GFNMS), (4) Cordell Bank NMS (CBNMS), and (5) Olympic Coast NMS (OCNMS) (**Figure 5**).

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

2.3.3.1 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.

2.3.4 Home Range Analysis

Because the focus of this section was on habitat occupation during the feeding season, we removed the migration portion of the tracks prior to analysis. For this purpose, the migration portion was established as the segment of each hSSSM track where behavioral mode remained as transiting during southward movement after which tags either stopped transmitting or reached a breeding area. After removing the migration portion, we created feeding-area kernel home ranges for the remaining portions of track that contained at least 30 d of estimated locations (Seaman et al. 1999), using the least-squares cross-validation bandwidth selection method (Worton 1989, Powell 2000), as implemented in the R package by the *adehabitatHR* v. 0.4.18 package (Calenge 2006, 2017). The 90 percent (home range, HR) and 50 percent (core area of utilization, CAU) isopleths were produced for each track and isopleth portions that overlapped land were removed. The areas of each whale's HR and CAU were then calculated in ESRI® ArcMap v. 10.3. Spatial "hotspots" of whale aggregation were identified based on the amount of overlap between the individual home ranges.

2.3.5 Cumulative Analyses

After conducting the analyses described above for the tracking data from the 2019 tagging season, all field seasons off the US West Coast (2004 through 2019) were combined and similar analyses were conducted on the cumulative dataset. For these analyses, data were grouped according to tagging region, with whales tagged in southern and central California being grouped together (SCCA), those tagged in northern California (Cape Mendocino and north) and Oregon being grouped together (NCA/OR), and those tagged in northern Washington being grouped together (NWA). Results were grouped as such to determine whether there were differences in tracking patterns between different tagging regions, leading to better understanding of DPS assignment of humpback whales along the US West Coast. We tagged only one whale in southern California (south of Point Conception), so this track was combined with those of whales tagged in central California, despite potential differences between movements of whales in the two regions. Whales from northern California were combined with those from Oregon due to the proximity of taggings in southern Oregon and northern California and the extensive movement of whales between these two areas, as shown by the data.

Comparisons between tagging regions were conducted for tracking duration, total distance traveled for each whale, HR and CAU size, residency in Navy areas and BIAs, and distance to shore in Navy areas using the software package R v. 4.0.2. Analysis of variance (ANOVA) was used to test whether there were any significant differences in the region mean values, and multiple range tests using the Fisher's least significant difference procedure determined which means were significantly different from one another. A Kruskal-Wallis test was used to test for differences in medians when the assumption of homogeneity of variance among regions (using Levene's test) was not met. A general linear model was used to compare total distances traveled between tagging regions after accounting for tracking duration. Simple linear regression was used to test for a relationship between HR/CAU size and number of SSSM locations used in their calculation, to rule out the possibility that HR/CAU size was biased by track length.

2.4 Dive Behavior Analyses

The goals of the analyses in this section were to use dive data from DUR, DM, DUR+, and ADB tags to characterize the diving and feeding behavior of tagged whales over their tracked duration prior to migration (weeks to months) and to examine how it changed temporally and spatially. Migratory dives were removed from the received dive behavior summaries by truncating them at the date and time of migration start identified in **Section 2.3.4**. The percent of the tracking duration summarized by reported dives[2] from all tags was calculated as the sum of all received dive durations plus the sum of all received post-dive intervals (PDI; i.e., the time between the end of one selected dive and the start of the next one) divided by the tracking duration. 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

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[2] In the past (e.g., Mate et al. 2018a, b, 2019), DUR, DUR+, and DM tags have occasionally reported abnormally long-duration ("anomalous") dives lasting from 44 min up to the maximum possible value recorded by the tag (4,095 s or 68.3 min). These anomalous dives could be related to times when the whales surfaced in such a way that the tag was not lifted out of the water (e.g., when the whales surface to breathe or rest at the surface), but diagnostic information is limited to conclude this definitively. Whales in this and previous reports were documented regularly diving for 20-25 min, so dives > 30 min in duration were removed as "anomalous" in this report (n = 116 across all years). Three tags from 2019 reported anomalously deep dives (> 500 m). These dives were limited in number for two of the tags (whale #2019WA-5742, n = 50; and whale #2019WA-5803, n = 10) and were distinctly deeper than all other dives made so they were removed as outliers while other dives were retained. Dive depths for whale #2019WA-10827 were much more variable than all other tags, with 157 dives > 500 m and many dives > 200-300 m reported with durations < 3 min suggesting a problem with how dive depth data were recorded. Thus, dive depths from that tag were removed from the analysis.

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- and ADB-tagged whales to assess the potential for 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 near-surface portion of dives that were 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 (from DUR and DUR+ tags) and number of feeding lunges (from DUR+ tags) versus date and versus time of day were generated for each individual tag and for all tags combined to visualize temporal and diel trends in the dive data. Due to the large number of plots generated, only the plots aggregating all tag data are presented to illustrate the trends that are described in the results, unless an individual tag is presented as an example. Similar plots showing maximum dive depth were made for data received from the DM and ADB tags.

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 dives for each whale within a tagging season were then mapped onto a 0.1-degree hexagonal grid and the median dive duration was 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 average dive duration 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 dives and/or 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 (DUR+ and DM) and maximum dive depths for all DM-tagged whales.

2.4.1 Cumulative Analyses

After conducting the described analyses on the 2019 dive data, similar analyses were applied to all previous years of humpback whale dive data collected off the US West Coast from 2016 to 2019. Gridded maps similar to those generated from 2019 data were created using all available dive data to explore the characteristics and spatial distribution of dive behavior across the US West Coast. A similar method was used to examine the spatial distribution of time spent near the surface. A gridded map of the percentage of time spent near the surface was also generated by taking the sum of dive durations for all dives ≤ 30 m depth occurring within a grid cell plus all post-dive intervals, then dividing it by the sum of dive durations for all dives and all post-dive intervals within the cell. This allowed for an assessment of the spatial distribution of time spent near the surface across the study area based on the reported dives for all whales using each grid cell.

2.5 Ecological Relationships

We conducted an ecological characterization of the tracking data by describing the movement behavior and environment used by the tagged whales during the course of their movements. For purposes of this section, the data collected in 2019 are considered together with the previous humpback whale tracking data collected by OSU off the US West Coast from 2004 to 2018, thus allowing for a sufficient sample size for meaningful analysis and interpretation.

We considered environmental variables representing static features of the seascape from digital elevation models of seafloor relief, as well as oceanographic variables representing dynamic processes from remotely sensed measurements and extracted observations that most closely matched the SSSM/hSSSM locations in time and space. Considering that the environmental data products used in this ecological characterization had a temporal resolution of 1 d or coarser (**Table 3**), and to avoid pseudo-replication, the 2016-2019 hSSSM tracks were thinned from three to one location per day (keeping only the first estimated location of each day) prior to extraction. The historical tracking data had been previously modeled at one location per day using the conventional SSSM methodology (as described in **Section 2.3.2**; see also Mate et al. 2018a). We additionally excluded from analysis SSSM/hSSSM locations that were estimated on land, as well as those locations with 95 percent credible limits exceeding 1 degree in longitude and/or in latitude to reduce introducing bias by locations with large estimation uncertainty. Finally, since the focus of this section was on habitat use during the feeding season, we removed the migrating portion of the tracks prior to analysis, as described in **Section 2.3.4** (Home Range Analysis).

The static variables describing the seafloor relief were depth (DEPTH), slope (SLOPE, or depth gradient), aspect (ASPECT, the directional facing of the slope), and distance to the 200-m isobath (DISTSHELF, or distance to the shelf break). Distance to the nearest shoreline (DISTSHORE) was also calculated for each SSSM/hSSSM location (**Table 3**). The dynamic oceanographic variables extracted were sea surface temperature (SST), magnitude of the horizontal sea surface temperature gradient (SSTG, a measure of frontal activity), and phytoplankton chlorophyll-*a* concentration (CHL) (**Table 3**).

Several of these data products were available from the Environmental Research Division (ERD) of the NOAA/NMFS/SWFSC through the web service *Environmental Research Division Data Access Program* (ERDDAP, Simons 2019; http://coastwatch.pfeg.noaa.gov/erddap/index.html), as detailed in **Table 3**. For these variables, the extraction process for matching tracking and environmental data was automated using the package *rerddapXtracto* v. 0.4.5 (Mendelssohn 2019), a collection of functions that permit client-side access to the data sets served by ERDDAP from within the software for statistical computing R v. 3.6.1 (R Core Team 2019). These functions additionally allow the use of a box of arbitrary size to extract the underlying data around each location. Thus, in order to account for the uncertainty in the location estimation by the SSSM/hSSSM, we obtained the median value for the environmental variables closest in time and space to each location occurring within a box defined by the 95 percent credible limits in longitude and in latitude, respectively. The number of values used in this computation was dependent not only on the extent of the credible limits around each location, but also on the spatial resolution of the environmental products used, which varied from 1.11 km (for SST) to 1.39 km (for CHL) (**Table 3**). In addition to reflecting the uncertainty in location estimation, this approach had the benefit of minimizing the number of locations with missing environmental values due to cloud cover in some of the products had we simply obtained the single pixel value nearest to a location.

In addition to behavioral mode (BMODE; see **Section 2.3.2**), for each track we also computed the distance and speed between pairs of SSSM/hSSSM locations (i.e., pairwise distance [PWDIST] and pairwise speed [PWSPEED], respectively) as metrics of the local scales of movement of the tagged whales across the study area. For these calculations we used the R package *trip* v. 1.6.0 (Sumner et al. 2009, Sumner 2011). In this way, we generated fully annotated SSSM/hSSSM tracks with behavioral mode, pairwise distance and speed, and a suite of environmental variables at each estimated location for ecological characterization.

Considering the large latitudinal extent covered by the compiled humpback whale tracking data set, we partitioned the study area into the same tagging region groupings outlined in **Section 2.3.5** above (SCCA, NCA/OR, and NWA) for the purpose of investigating possible regional differences in habitat characteristics that would support the pattern of occupation by the different humpback whale DPSs along the US West Coast during the feeding season. The characteristics of the behavioral and environmental variables associated with the whale tracking data are presented using descriptive statistics. Because in many cases the environmental variables had strongly skewed and/or long-tailed distributions, we report the median and the median absolute deviation (MAD) as more robust metrics compared to the mean and the SD.

Formal comparisons between the regional tagging groupings (SCCA, NCA/OR, NWA) were conducted for the behavioral and environmental variables (after log transformation, if necessary) using statistically robust methods, as implemented in the R package *WRS2* v. 1.1-0 (Mair and Wilcox 2020). For the categorical behavioral mode variable (BMODE), the global hypothesis for differences between discrete multinomial distributions was tested using a one-way ANOVA with an *F*-test statistic, while the post-hoc pairwise comparisons between regional groups were tested via multiple comparisons for independent groups with Hochberg's adjustment (Mair and Wilcox 2020). For the continuous environmental variables these tests were conducted using heteroscedastic trimmed means comparisons (Yuen's test with 20 percent trimming level), both for the omnibus one-way ANOVA and for the post-hoc pairwise tests (with Holm adjustment for multiple *p*-values; Mair and Wilcox 2020).

The statistical comparisons between tagging regions were supplemented with graphical methods using annotated bar plots and box-violin plots, as implemented in R package *ggstatsplot* v. 0.5.0.9000 (Patil 2018).

2.6 Genetics

2.6.1 DNA Extraction and mtDNA Sequencing

Total genomic deoxyribonucleic acid (DNA) was extracted from skin tissue following standard proteinase K digestion and phenol/chloroform methods (Sambrook et al. 1989), as modified for small samples by Baker et al. (1994). An approximate 800-base-pair (bp) fragment of the mitochondrial deoxyribonucleic acid (mtDNA) control region was amplified with the forward primer M13Dlp1.5 and reverse primer Dlp8G (Dalebout et al. 2004) under standard conditions (Baker et al. 2013). These sequences were edited for quality control and trimmed to a 500-bp consensus region in Sequencher v. 4.6. Variations in the control region sequences were used to identify unique haplotypes among the samples collected during each season of the project. The unique haplotypes were then aligned with previously published haplotypes downloaded from the public repository GenBank® to investigate differences in regional haplotype frequencies (Baker et al. 2013). As mtDNA is a maternally inherited genome, unique haplotypes represent maternal lineages and the distribution of haplotypes reflect maternal fidelity to migratory destinations (Baker et al. 2013).

2.6.2 Microsatellite Genotypes

Variation in the nuclear DNA of each sample was investigated by multi-locus genotyping of up to 16 microsatellite loci for each humpback whale sample using previously published conditions (Baker et al. 2013). Unlike mtDNA, the allele frequencies of nuclear DNA genotypes reflect patterns of biparental inheritance, including reproductive isolation considered in the delineation of DPSs. 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 multiplexes for automated sizing on an ABI3730xl (Applied Biosystems™) DNA analyzer. Microsatellite alleles were sized and binned using Genemapper v. 4.0 (Applied Biosystems™) and all peaks were visually inspected.

2.6.3 Sex Identification

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

2.6.4 Individual Identification

Individual whales were identified from the multi-locus genotypes of up to 16 microsatellite loci using CERVUS v. 3.0.3 (Marshall et al. 1998). Mismatches of up to three loci were allowed in initial comparisons 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 16 microsatellite genotypes, sex, and mtDNA control region sequence or haplotype. The expected probability of identity (P_{ID}) for a given number of loci was calculated with GenAlex (Peakall and Smouse 2006). The P_{ID} reflects the probability of a pair of individuals sharing a multi-locus genotype by chance given the frequency of alleles at each microsatellite locus. This probability is typically very low for the loci chosen in this study, providing confidence in the identification of individuals (Baker et al. 2013).

2.6.5 Species and Stock Identification

Species identity from field observations was confirmed by submitting mtDNA haplotype sequence 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 3,320 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 up to 16 loci. Consequently, the mtDNA of humpback whales sampled during this project can be compared 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 NWA, NCA/OR, and SCCA datasets and the 18 regional strata defined during SPLASH for the North Pacific (Baker et al. 2013) were conducted using a permutation procedure implemented in the program Arlequin (Excoffier and Lischer 2010). Assignment of individuals from the NWA, NCA/OR, and SCCA datasets to the four DPSs, as recognized by the ESA (81 FR 62259, 81 FR 93639), was based on multi-locus genotyping using the Bayesian population assignment procedure implemented in the program GeneClass2 (Piry et al. 2004). This program uses multi-locus genotypes and mtDNA haplotypes to calculate the relative likelihood of an individual originating from alternate populations given the frequencies of alleles from a reference dataset representing those populations. The confidence of any individual assignment, as reflected in the relative likelihood score, is the result of several factors, including the sample size of the reference database, the number of variable loci and the true underlying differentiation of the breeding populations (Manel et al. 2005).

For the purposes of this report, reference samples for the four DPSs came from one or more of the eight breeding-area strata defined by SPLASH (Baker et al. 2013), and were combined in the following way: "Western North Pacific" included all individuals sampled from Okinawa, Ogasawara and the Philippines, for a total of n = 245 individuals; "Mexico" included all individuals sampled from the Mexican mainland (MX-ML) and the offshore Revillagigedo Archipelago (MX-AR), for a total of n = 176 individuals; and "Hawaii" and "Central America" were kept as reported in Baker et al. (2013), for a total of n = 230 and n = 39, respectively. The individuals sampled from a third Mexican region, Baja California, were not included in this reference database as this region is considered an area of mixing between a local breeding population and migrating animals from other Mexican breeding areas and the Central American breeding area. The reference dataset for the DPSs (i.e., the revised stratification of the SPLASH

DNA register) included up to 10 microsatellite loci and mtDNA haplotype where available for each individual.

2.7 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, tag-site wound condition, and to identify previously tagged whales during resightings for the purpose of examining tag-site 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 uploaded and compared to Happywhale up to 29 June 2020. Images in Happywhale have different levels of contributor-specified access and use permissions. OSU is a signatory of a Memorandum of Understanding that grants 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 Happywhale resighting information in general terms (i.e., matches to SPLASH-defined strata) that do not identify the specific location or time associated with data provided by other contributors.

Additionally, 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

Twenty-four DM tags were deployed on humpback whales out of Neah Bay, Washington, between 18 September and 6 October 2019. Argos satellite locations were received from 22 tags (**Table 4**); two tags did not transmit at all (one of which was struck by the biopsy dart during deployment and possibly damaged).

3.1 Tagging Rates

A total of 385 humpback whales were approached during 10 d of tagging efforts in Washington in 2019. Twenty-four tags were deployed, for a tagging rate of 2.4 tags per d. Biopsy samples were obtained from

19 tagged whales and nine untagged whales (**Table 4**). Fluke photographs were obtained from 20 tagged whales (not necessarily the same whales that were biopsied) and 130 untagged whales (**Table 4**).

3.2 Behavioral Responses to Tagging

Seventeen of the 24 humpback whales tagged in Washington (71 percent) in 2019 exhibited moderate, short-term startle responses to the tagging/biopsy process. These responses consisted of mild to strong tail flicks and fast dives (**Table 5**). 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. None of 10 whales responded to biopsy darting alone.

3.3 Wound Healing

Whales will hereafter be referred to by their tag number, following the nomenclature "YYYYregion-tagnumber". Three of 24 humpback whales tagged in 2019 were resighted on subsequent days during the field efforts in Washington with their tags still attached and transmitting (**Table 6).** One was seen 5 d after tagging (#2019WA-5679, a male), one was seen 7 d and 11 d after tagging (#2019WA-10823, a male), and one was seen 8 d after tagging (#2019WA-833, a male). No swelling was visible at the tag sites for these three whales. For whale #2019WA-10823, a small amount of white tissue was seen on one side of the tag 7 d after tagging, and 11 d after tagging this tissue encircled the tag. This same sort of tissue response has been observed on non-tag wounds on other whales (OSU unpublished data) and may be a natural response to injury.

Seven of the 25 whales tagged in 2018 in Washington were resighted during the 2019 field season. These whales were resighted from 380 to 421 d after tagging and 378 to 400 d after their tag's last transmission (**Table 6**) and no tags were present. Tag scars consisted of divots, ranging in size from approximately 3- to 25-cm diameter and 1- to 8-cm depth, with lighter or discolored skin (**Table 6**). One whale (#2018WA-5838, a male) had a slight bump, approximately 5-cm diameter and 2-cm high, at the tag site rather than a divot. There was no visible swelling at any of the tag sites and all seven whales were in good body condition. One of the whales (#2018WA-23029, a female) was accompanied by a calf.

Five humpback whales tagged in Washington in 2018 (#s 2018WA-5654, 2018WA-5790, 2018WA-5883, 2018WA-5923, 2018WA-23029) were seen and photographed (from 22 to 73 d after tagging) by naturalists aboard commercial whale watching boats and by another researcher. Photographs submitted to us from these encounters showed all tags still attached and no sign of swelling at the tag sites (**Table 6**). In three cases, tag sites consisted of divots, ranging in size from approximately 4- to 20-cm diameter and 2- to 5-cm depth (**Table 6**). There was some white tissue present around the tag site for whale #2018WA-5883 and reddish tissue present around the tag sites for whales #2018WA-23029 and #2018WA-5923.

One whale tagged in Washington in August 2018 (#2018WA-23033) was photographically matched to a dead whale observed by whale watchers floating in the Strait of Juan de Fuca, Washington, on 27 September 2020. The whale was towed ashore on 3 October near Sekiu, Washington, by Cascadia

Research Collective (CRC) scientists. An examination of the whale was conducted on 4 October, led by CRC and aided by a number of organizations and veterinarians including the Marine Mammal Laboratory, Oregon State University, SR3, and the Fiero Marine Life Center. The whale was in an advanced state of decomposition and the cause of death could not be determined conclusively. Its sex was anatomically determined to be male. There was evidence of pre-mortem blunt force trauma to the head, suggestive of a ship strike. The whale was positioned belly-up on the remote beach, making access to and examination of the tag site impossible. The whale was seen active and apparently healthy on 22 September 2020 and had a sighting history in the Strait of Juan de Fuca dating back to 2016. The DPS to which this whale belongs is unknown, however, as there are no known photographic matches to a breeding area and we did not obtain a biopsy sample when the whale was tagged (we had a clean strike, but the dart failed to extract a sample). A skin sample was collected by CRC during the examination and will be analyzed by OSU's Cetacean Conservation and Genomics Lab.

3.4 Tracking Results

3.4.1 Washington 2019 Tagging

Tracking periods ranged from 4.2 to 164.2 d (mean = 46.8 d, standard deviation [SD] = 39.0 d, n = 22; **Table 4**). Minimum distance traveled ranged from 171 to 12,426 kilometers (km) (mean = 2,530 km, SD = 2,833 km, n = 22; **Table 4**).

Locations for humpback whales tagged off Washington ranged over 31 degrees of latitude, from the northwest corner of Vancouver Island, British Columbia, Canada, to approximately 80 km southwest of Puerto Vallarta, Mexico (**Figure 6**). The vast majority of locations occurred between Clallam Bay, 30 km east of Neah Bay, and approximately 100 km west-southwest of Cape Flattery. A smaller cluster of locations occurred approximately 45 to 65 km offshore of Grays Harbor, southern Washington. The densest area of locations occurred over Swiftsure Bank, approximately 16 km northwest of Cape Flattery, where many of the whales were tagged (**Figure 6**).

The whale with tag #2019WA-5743 in 2019 was the same whale that was tagged by OSU with tag #2018WA-4177 in Washington in 2018, where it was photo-ID'd and genetically identified as a male from a biopsy sample (Palacios et al. 2020a). This re-tagging event provided a unique opportunity to compare movements between years for the same individual. In 2018, this whale (hereafter referred to as whale #4177/5743) was tagged in Swiftsure Bank on 3 August, where it spent 2 d before heading approximately 70 km southwest to the shelf edge between Juan de Fuca and Nitinat Canyons (**Figure 7**). The whale remained in the area for 3 d before heading approximately 110 km northwest to Clayoquot Canyon, where it spent another 6 d until its tag stopped transmitting. This tag was an ADB tag that we were unable to recover, presumably because it came off the whale still attached to its housing and sank to the seafloor, where it either failed to release or became lodged on the seafloor after release (see Palacios et al. 2020a). In 2019, whale #4177/5743 was tagged on 20 September, within 10 km of where it was tagged the previous year (**Figure 7**). After spending a couple of days in the tagging area, the whale traveled to the shelf edge between Juan de Fuca and Nitinat Canyons, as in 2018, where it remained for the next 20 d until its tag stopped transmitting (**Figure 7**). Despite a difference of 48 d in tagging date between the two years, the similarities in areas visited by this whale demonstrate the persistent foraging locations of Swiftsure Bank and the offshore canyons to the northwest corner of the Olympic Peninsula for this animal.

Four whales tagged off Washington in 2019 began their fall/winter migration during their tracking periods, and two of these reached a breeding destination before their tags stopped transmitting. Departure dates ranged from 23 November 2019 to 20 January 2020, and time from tagging to departure ranged from 63.1 to 122.6 d (mean = 89.0 d, SD = 24.7 d). Two whales (#2019WA-5742 and #2019WA-5921) headed southwest on a trajectory toward Hawaii (**Figure 8**). Whale #2019WA-5742 (a male) departed from the northwest corner of Vancouver Island on 20 January 2020 and was tracked for 2.5 d and approximately 350 km before its tag stopped transmitting. Whale #2019WA-5921 (a male) departed from the northwest corner of Washington on 17 December 2019 and was tracked for 4 d and approximately 280 km before its tag stopped transmitting.

Two other whales were tracked to breeding areas in Mexico (**Figure 9**). Whale #2019WA-5840 (a female) departed from the Oregon/Washington border on 23 November 2019 and was tracked over a 29-d migration to Bahia de Banderas, Mexico, where it remained for 6 d before its tag stopped transmitting on 29 December. Whale #2019WA-5678 (a female) began migrating from the southern Washington coast on 16 December 2019 and was tracked over a 30-d migration to the Mexican mainland, off the Sinaloa coast. Whale #2019WA-5678 spent approximately 14 d along northern Nayarit and Sinaloa states before heading west-southwest (on 30 January 2020) from Sinaloa across the Gulf of California to the tip of Baja California, on a return migration to the feeding area. Whale #2019WA-5678 continued migrating north and was last located off Cape Mendocino, California, when its tag stopped transmitting on 1 March 2020, 164.2 d after tagging (**Figure 9**). To our knowledge, this is the first documented return migration for a humpback whale tagged in a feeding area after migration to the breeding area.

3.4.1.1 Use of Navy Training Areas

All twenty-two humpback whales tagged in Washington in 2019 spent time in the Navy's NWTT, with percentages of locations in NWTT ranging from 18.8 to 99.6 percent and time spent there ranging from 23.6 to 99.9 percent of their total tracking periods (or 2.8 to 86.6 d; **Table 7, Figure 10**). Eighteen of these whales also had locations in area W237 of the NWTT, with percentages of locations there ranging from 1.0 to 89.9 percent and time spent in W237 ranging from 1.2 to 91.1 percent of their total tracking periods (or 0.5 to 65.4 d; **Table 7, Figure 11**). Two whales had locations in PT MUGU, ranging from 2.3 to 3.7 percent of total locations and from 2.3 to 3.6 percent of total tracking periods there (2.3 to 5.8 d; **Table 7, Figure 12**). These same two whales also had locations in SOCAL, with percentages of locations ranging from 1.3 to 2.5 percent and time spent there ranging from 2.3 to 2.7 percent of their total tracking periods (or 2.3 to 4.4 d; **Table 7, Figure 13**). Distances to shore in NWTT averaged 24.4 km (SD = 11.6 km, maximum = 381 km; **Table 8**). Distances to shore in W237 averaged 53.7 km (SD = 11.6 km, maximum = 319 km; **Table 8**). For the two whales that traveled through PT MUGU and SOCAL, distances to shore averaged 87.5 km (SD = 37.5 km, maximum = 182 km) and 115 km (SD = 4.2 km, maximum = 189 km), respectively (**Table 8**). Humpback whale locations occurred in NWTT during the months of September through December as well as in March (during northbound migration for whale #2019WA-5678), and in W237 during the months of September through December. Locations occurred in MUGU and SOCAL in December (during southbound migration) and February (during northbound migration). None of the humpback whales tagged in Washington in 2019 were tracked within the SOAR or GOA areas.

3.4.1.2 *Use of West Coast BIAs*

All 22 humpback whales tracked in Washington in 2019 had locations in the NOWA BIA, with 5.7 to 82.8 percent of their total number of locations there (**Table 9, Figure 14**). This represented 7.5 to 89.4 percent of their total tracking periods, or 2.7 to 40.1 d (**Table 9**). Humpback whale locations occurred in the NOWA BIA from August through December. Two whales had locations in the Stonewall BIA, with 0.2 percent of their total number of locations and 0.2 percent of their total tracking periods (or 0.4 and 0.2 d, respectively) spent there (**Table 9**, **Figure 15**). One of these whales (#2019WA-5678) also had locations in the Santa Barbara BIA, with 0.4 percent of its total number of locations and 0.2 percent of its total tracking period (0.3 d) spent there (**Table 9**, **Figure 16**). Locations in the Stonewall BIA occurred during November and December and in the Santa Barbara BIA during December. Whale #2019WA-5678's track also crossed the Morro Bay BIA (in December), over a period of 0.1 d (or 0.1 percent of its total tracking period) but had no locations within the BIA (**Table 9; Figure 17**). None of the humpback whales tagged in Washington in 2019 had locations in any other West Coast BIA.

3.4.1.3 *Use of West Coast National Marine Sanctuaries*

All 22 humpback whales tracked in Washington in 2019 had locations in the OCNMS, with 7.2 to 84.9 percent of their total number of locations there (**Table 10, Figure 18**). This represented 10.2 to 86.7 percent of their total tracking periods, or 3.0 to 49.8 d (**Table 10**). Two whales had locations in the MBNMS, ranging from 0.4 to 1.1 percent of their total number of locations for 0.2 to 1.1 percent of their total tracking periods (0.2 to 1.8 d; **Table 10, Figure 19**). One of the latter whales also had locations within the CINMS, with 0.3 percent of its total number of locations there. (**Table 10**). This represented 0.1 percent of this whale's total tracking period, or 0.2 d (**Figure 20**). Humpback whale locations occurred in the OCNMS from September through December, in the MBNMS in December (southbound migration) and February (northbound migration), and in the CINMS in December (southbound migration). None of the humpback whales tagged in Washington in 2019 had locations in any other West Coast NMS.

3.4.1.4 *Home Ranges and Core Areas of Utilization*

Twelve of the humpback whales tagged in Washington in 2019 provided enough locations to calculate feeding area HRs and CAUs (**Table 11, Figures 21 and 22**). HR sizes ranged from 172 to 17,379 km^2 (mean = 3,722 km^2; SD = 4,784 km^2) and extended from the southern end of Queen Charlotte Sound, British Columbia, to Seaside, northern Oregon. The densest location of HRs occurred at the northwest corner of Washington, where HRs overlapped for 10 whales. CAUs ranged in size from 32 to 1,941 km^2 (mean = 513 km^2, SD = 532 km^2), extending from the southern end of Queen Charlotte Sound, British Columbia, to Grays Harbor on the southern Washington coast. The area of highest use, with overlapping CAUs for four whales, occurred at the northwest corner of Washington, approximately 16 km northwest of Cape Flattery, over Swiftsure Bank. Both HR and CAU size were positively related to the number of locations used in the analysis (linear regression of log-transformed variables, *p*-value = 0.006

for HR, *p*-value = 0.015 for CAU). These relationships were largely driven by the large HR and CAU for whale #2019WA-05742, the animal with the longest latitudinal range, traveling up the west coast of Vancouver Island and into Queen Charlotte Sound (**Figure 8**). When this whale was removed from consideration, there was no longer a clear relationship between the number of locations and the size of either HRs or CAUs (linear regression of log-transformed variables, *p*-value = 0.04 for HR, *p*-value = 0.08 for CAU).

3.4.2 Cumulative Analyses

3.4.2.1 Tracked Movements

A total of 61 humpback whales were tagged by OSU off the US West Coast prior to 2019 (covering the period 2004 to 2005 and 2016 to 2018), providing tracking data for 59 whales (the remaining tags provided no locations; **Figure 23**). Different tag styles were deployed in different years: LO tags in 2004 and 2005; DM tags in 2016; DUR and DM tags in 2017; DUR+, DM, and ADB in 2018; and DM in 2019. Tracking periods for all whales tagged from 2004 through 2019 ranged from 0.1 to 164.2 d (mean = 39.3 d, SD = 33.7 d, n = 80). Tracking durations were not significantly different between whales tagged in the three different regions (ANOVA, *p*-value = 0.92; **Table 12**). There was a positive relationship between tracking duration and total distance traveled by individual humpback whales (linear regression using log-transformed variables, *p*-value < 0.0001). After accounting for this relationship, distance traveled was significantly different between humpback whales tagged in NWA (1,382.1 km, standard error [SE] = 1.07 km, n = 41) and those tagged in SCCA (1,027.8 km, SE = 1.02 km, n = 24), with whales tagged in NCA/OR (1,377.4 km, SE = 1.12, n = 15) having intermediate distances (general linear model of log-transformed variables, *p*-value = 0.03; **Table 12**). The latter analyses did not include the tracking duration of the ADB tag deployed in Washington in 2018, because this tag had a planned two-week release for recovery.

The overall range for all humpback whales tagged from 2004 to 2019 extended over 37 degrees of latitude, from Queen Charlotte Sound, British Columbia, Canada, to the southwestern coast of Guatemala. The latitudinal range was almost identical when the three tagging regions were compared; 31.3 degrees for whales tagged in NWA, 30.6 degrees for whales tagged in NCA/OR, and 31.4 degrees for whales tagged in SCCA. The actual northernmost and southernmost points were different between tagging regions, however, with endpoints being furthest north for whales tagged in NWA, furthest south for whales tagged in SCCA, and in between for whales tagged in NCA/OR (**Figure 24**). The northernmost locations were in Queen Charlotte Sound, north of Vancouver Island, British Columbia, for whales tagged in NWA, off Barkley Sound on the southwest coast of Vancouver Island for whales tagged in NCA/OR, and off the north-central Oregon coast for whales tagged in SCCA (**Figure 24**). The southernmost locations were off the Jalisco coast, Mexico, for whales tagged in NWA, off the Michoacan coast, Mexico, for whales tagged in NCA/OR, and off the Guatemalan coast for whales tagged in SCCA (**Figure 24**). When migratory locations were not included (i.e., only considering the tracked locations during the feeding season), latitudinal ranges were much smaller for humpback whales tagged in NWA (5 degrees) than those tagged in NCA/OR (14 degrees) or SCCA (11 degrees). The southernmost feeding season (non-migratory) locations of humpback whales were off the northern Oregon coast, near

Manzanita, for whales tagged in NWA, off Point Sal, California, for whales tagged in NCA/OR, and in the Santa Barbara Channel for whales tagged in SCCA.

Six whales were tracked on their southbound migration, with departure dates ranging from 1 November (for a whale of unknown sex tagged in NCA/OR on 5 October 2005) to 24 December (for a male tagged in NCA/OR on 14 September 2017). Departure points for these whales ranged from the southern Washington coast for two whales tagged in NWA, the northern and central California coast for two whales tagged in NCA/OR, respectively, and the southern California coast for a whale tagged in SCCA. The migratory departure point was unknown for the sixth whale, tagged in NWA, due to a 66-d gap in locations. Migratory destinations were tracked for five of the six whales, with four (two from NWA, two from NCA/OR) migrating to the mainland coast of Mexico and one (from SCCA) migrating to Guatemala (**Figure 25**). Migration duration was remarkably similar for all five whales, ranging from 27.6 to 31.6 d (mean = 29.4 d, SD = 1.5 d). The four whales migrating to Mexico had arrival points off the coasts of Sinaloa, Jalisco, and Michoacan. The sixth whale (from NWA in 2018) was last located after a 66-d gap in locations, off Magdalena Bay, Baja California, Mexico, on 3 December 2018. Partial migrations were tracked for an additional two whales tagged in NWA in 2019 (see **Section 3.4.1** above), each with a southwest trajectory toward Hawaii (**Figure 25**).

3.4.2.2 Use of Navy Training Areas

Seventy-three percent of all humpback whales tagged in Washington, Oregon, and California from 2004 to 2019 (59 of 81) had locations within the NWTT training range (40 of these whales were tagged within the range; **Table 13, Figure 26**). All whales tagged in NWA had locations in NWTT, compared to 93 percent of whales tagged in NCA/OR, and 13 percent of whales tagged in SCCA. The mean number of days spent in the NWTT ranged from a low of 11.4 d (for humpback whales tagged in CA) to 20.3 d (for humpback whales tagged in NWA), with a maximum residency in this area of 86.6 d (for two whales tagged in NCA/OR and NWA, respectively). Eighty-eight percent (37 of 42) of whales tagged in NWA had locations within area W237 of the NWTT, compared to 7 percent (1 of 15) of whales tagged in NCA/OR, and no whales tagged in SCCA (**Table 13**, **Figure 27**). The mean number of days spent in W237 for NWA whales was 12.7 d (maximum of 65.4 d), and the one whale tagged in NCA/OR (#2017OR-1387) spent 14.3 d there. Five percent (2 of 42) of whales tagged in NWA had locations within PT MUGU, compared to 13 percent (2 of 15) of whales tagged in NCA/OR, and 13 percent (3 of 24) of whales tagged in SCCA (**Table 13, Figure 28**). The mean number of days spent in PT MUGU was 4.0 d for whales tagged in NWA, 4.3 d for whales tagged in NCA/OR, and 21.9 d for whales tagged in SCCA, with a maximum of 33.8 d there (for a whale tagged in SCCA). Five percent (2 of 42) of whales tagged in NWA had locations within SOCAL, compared to 13 percent (2 of 15) of whales tagged in NCA/OR, and 4 percent (1 of 24) of whales tagged in SCCA (**Table 13, Figure 29**). The mean number of days spent in SOCAL was 3.3 d for whales tagged in NWA and 1.8 d for whales tagged in NCA/OR, with a maximum of 4.4 d. The one whale from SCCA spent 2.8 d in SOCAL. Only one whale, tagged in NCA/OR, spent time within SOAR, spending 0.4 d there as its track crossed the area (**Table 13, Figure 30**). No whales were tracked within the GOA training area.

Humpback whale locations in the NWTT occurred predominantly in the late summer and fall, with whales tagged in NWA having locations there from August through December, whales tagged in NCA/OR having locations there from September through December, and whales tagged in SCCA having locations there in August and September. One whale, tagged in NWA in 2019, had locations in NWTT in March, on its northbound migration. Humpback locations in W237 of the NWTT occurred from August through December for whales tagged in NWA and in November and December for whales tagged in NCA/OR. No whales tagged in SCCA had locations within W237. Locations in PT MUGU occurred in February and December for whales tagged in NWA, November and December for whales tagged in NCA/OR, and August through November for whales tagged in SCCA. Locations in SOCAL occurred in December (during southbound migration) and February (during northbound migration) for whales tagged in NWA, January and November for whales tagged in NCA/OR, and in November for whales tagged in SCCA. The one whale, tagged in NCA/OR, whose track crossed SOAR, spent time there in November.

Distances to shore for tagged humpback whales in Navy areas ranged from an overall mean of 40 km in NWTT to 176 km in SOCAL (**Table 14**). Maximum distance to shore ranged from 182 km in PT MUGU to 385 km in SOCAL (Table 14). Mean distance to shore in NWTT was significantly different for whales tagged in NWA (mean = 22 km, SD = 11.7 km, n = 42) than whales tagged in NCA/OR (mean = 44 km, SD = 10.4 km, n = 14; ANOVA, p-value < 0.001). Whales tagged in SCCA were not included in the former analysis, as only three of them had locations in NWTT. Sample sizes were also not large enough to permit meaningful statistical comparisons of distance to shore between field seasons in any other Navy training areas.

3.4.2.3 Use of West Coast BIAs

With the exception of one humpback whale tagged in NCA/OR spending 7.4 d in the NOWA BIA, only whales tagged in NWA had locations in the NOWA BIA (**Table 15**, **Figure 31**). Forty-one of 42 whales (98 percent) tagged in NWA had locations in the NOWA BIA, with a mean residency of 11.7 d (maximum residency of 40.1 d). Fifty-three percent (8 of 15) humpbacks tagged in NCA/OR spent time in the Stonewall BIA, compared to five percent (2 of 42) whales tagged in NWA, and four percent (1 of 24) whales tagged in SCCA (**Table 15, Figure 32**). The overall mean time spent in the Stonewall BIA was 1.6 d, with a maximum of 9.9 d. With the exception of one humpback whale spending 0.1 d and 0.3 d in the Morro Bay and Santa Barbara BIAs, respectively, as it migrated south, humpback whales tagged in NWA were not found in any other West Coast BIA during their tracking periods. Sixty percent (9 of 15) humpback whales tagged in NCA/OR spent time in the PSG BIA, compared to four percent (1 of 24) whales tagged in SCCA, with mean residency of 2.2 d (maximum 11.3 d; **Table 15, Figure 33**). The Fort Bragg, Farallones, and Morro Bay BIAs were used by higher proportions of whales from SCCA than from NCA/OR, with 21 percent (5 of 24), 96 percent (23 of 24), and 13 percent (3 of 24) of whales from SCCA spending time in Fort Bragg, Farallones, and Morro Bay, respectively, compared to 13 percent (2 of 15), 20 percent (3 of 15), and seven percent (1 of 15) of whales from NCA/OR (**Table 15, Figures 34 through 36**). Mean residencies were 2.3 d (maximum of 4.5 d) for Fort Bragg, 14.6 d (maximum of 71.6 d) for Farallones, and 3.9 d (maximum of 11.7 d) for Morro Bay. Thirteen percent (2 of 15) of humpback whales tagged in NCA/OR were tracked in the Santa Barbara BIA (mean of 0.3 d, maximum of 0.4 d) compared to four percent (1 of 24) of whales tagged in SCCA (for 3.3 d; **Table 15, Figure 37**).

Humpback whale locations in the NOWA BIA occurred in August through December for whales tagged in NWA and in November for the NCA/OR whale. Occupancy in the Stonewall BIA occurred during November and December for whales tagged in NWA, from September through November for whales tagged in NCA/OR, and in August for one whale tagged in SCCA. Humpback locations in the PSG BIA occurred there from September through December for whales tagged in NCA/OR, and in September for whales tagged in SCCA. Whales tagged in NCA/OR spent time in the Fort Bragg BIA in October and November, whereas whales tagged in SCCA spent time there in August and September. Occupancy in the Farallones BIA occurred during September through November for whales tagged in NCA/OR and from July through October for whales tagged in SCCA. The one humpback whale tagged in NWA that spent time in the Morro Bay and Santa Barbara BIAs did so in December. Whales tagged in NCA/OR had locations in the Morro Bay and Santa Barbara BIAs in November and December. Whales tagged in SCCA had locations in the Morro Bay BIA in August, October, and November, and in the Santa Barbara BIA in July and August.

3.4.2.4 Use of West Coast National Marine Sanctuaries

Except for one humpback whale tagged in NCA/OR spending 8.6 day in the OCNMS, only whales tagged in NWA had locations in the OCNMS (**Table 16**, **Figure 38**). All 42 whales tagged in NWA had locations in the OCNMS, with a mean residency of 12.6 d (maximum residency of 49.8 d). No humpback whales tagged in NWA had location within the GFNMS or the CBNMS. Eighty-three percent (20 of 24) of humpback whales tagged in SCCA had locations in the GFNMS, compared to 27 percent (4 of 15) of whales tagged in NCA/OR (**Table 16, Figure 39**). Mean residency in GFNMS was 7.7 d, with a maximum residency of 35.2 d. Sixty-three percent (15 of 24) of whales tagged in SCCA had locations in the CBNMS, compared to 20 percent (3 of 15) of whales tagged in NCA/OR, with mean residency of 5.7 d (maximum of 42.7 d; **Table 16, Figure 40**). Thirty-three percent (8 of 24) of whales tagged in SCCA had locations in the MBNMS, compared to 13 percent (2 of 15) of whales tagged in NCA/OR, and five percent (2 of 42) of whales tagged in NWA (**Table 16, Figure 41**). Mean residency in MBNMS was 8.7 d, with a maximum of 45.3 d. Only one whale from each of the NWA and SCCA tagging regions (two and four percent, respectively) spent time within the CINMS, compared to 13 percent (2 of 15) of whales from the NCA/OR region (**Table 16, Figure 42**). Mean residency in CINMS was 0.2 d, with a maximum of 0.4 d.

Humpback whale locations in the OCNMS occurred from August through December for whales tagged in NWA and in November and December for one whale tagged in NCA/OR. Humpback locations occurred in the GFNMS in September through November for whales tagged in NCA/OR and from July through October for whales tagged in SCCA. Whales tagged in NCA/OR had locations in the CBNMS during September through November, while whales tagged in SCCA had locations there from August through October. Occupancy in the MBNMS occurred during February and December for whales tagged in NWA, during October and November for whales tagged in NCA/OR, and during July through October for whales tagged in SCCA. Locations in the CINMS occurred during December for whales tagged in NWA, during November and December for whales tagged in NCA/OR, and during August for whales tagged in SCCA.

3.4.2.5 Home Ranges and Core Areas of Utilization

Feeding-area HRs (90 percent kernel isopleths) were significantly different in size between humpback whales tagged in NWA (mean = 3,346 km^2, SD = 3,622 km^2, n = 21) than either those tagged in NCA/OR (mean = 18,352 km^2, SD = 21,777 km^2, n = 8) or SCCA (mean = 17,069 km^2, SD = 30,338 km^2, n = 12) (ANOVA of log-transformed HR, *p*-value = 0.001; **Table 12, Figure 43**). Feeding-area CAUs (50 percent kernel isopleths) were also significantly different in size between whales tagged in NWA (mean = 494 km^2, SD = 416 km^2, n = 21) and those tagged in NCA/OR (mean = 2,449 km^2, SD = 2,965 km^2, n = 8) or SCCA (mean = 2,348 km^2, SD = 2,734 km^2, n = 12) (ANOVA of log-transformed HR, *p*-value = 0.001; **Table 12, Figure 44**). There was no relationship between the number of locations used in the analysis and the size of either HRs or CAUs (linear regression of log-transformed variables, *p*-values > 0.09).

There was modest overlap in HRs for whales tagged in NWA and those tagged in NCA/OR, from the northwest corner of Washington to the northern Oregon coast, but no overlap in HRs between whales tagged in NWA and those tagged in SCCA (**Figure 43**). There was considerably more overlap in HRs for whales tagged in NCA/OR and those tagged in SCCA, with HRs for whales in both regions extending from the central Oregon coast to the Santa Barbara Channel in southern California (**Figure 43**). CAUs of whales tagged in NWA did not overlap with whales tagged in the other regions and there was very little overlap in CAUs between whales tagged in NCA/OR and those tagged in SCCA (two whales tagged in northern California had CAUs extending to the central CA coast; **Figure 44**). Areas of highest use (where CAUs overlapped for the greatest number of whales) for humpback whales tagged in NWA were located at the western end of the Strait of Juan de Fuca extending out to Swiftsure Bank off the northwest corner of Washington (**Figure 44**). The area of highest use for whales tagged in NCA/OR occurred off the northern California coast near Trinidad, and the area of highest use for whales tagged in SCCA occurred off Half Moon Bay in central California (**Figure 44**).

3.5 Dive Behavior

3.5.1 2019 Washington Tags

The 22 DM-tagged whales in 2019 provided a median of 3,116 dive summaries (range = 542 to 12,349; **Table 17**). Reported dives summarized a median of 65.6 percent of the tracking durations (range = 37.7 to 90.6 percent). Dive depths were generally less than 100 m; however, two tags recorded dives > 300-m depth with the deepest reaching to 361 m (**Figure 45**). Dive durations were very consistent across all tags, primarily ranging from 3 to 8 min (**Figure 46**). Dive durations were slightly longer during the day, although the longest-duration dives occurred at all hours of the day (**Figure 47**). Dive depths were deeper during the day, though generally remained shallower than 150 m and typically less than 75 m at night (**Figure 47**). A median of 57.0 percent of reported time was spent within 30 m of the surface (**Table 17**). Lunges were recorded across all hours of the day but were more common during daylight hours, occurring during deeper dives and in larger numbers per dive at those times (**Figures 48 and 49)**. Dives of Washington-tagged whales in 2019 were predominantly recorded near the tagging area at the mouth of the Strait of Juan de Fuca and offshore of the Washington coast (**Figure 50**). Temporal variability of dive behavior was limited, although shallower, shorter-duration, daytime dives occurred in the area of Swiftsure Bank, west of the Strait of Juan de Fuca, and further west, offshore of the Olympic Peninsula, compared to the rest of the area used (**Figure 50**). More lunges per dive were recorded off Vancouver Island and the southern Washington coast. However, those areas also recorded fewer dives overall suggesting the results may be biased (**Figure 50**).

3.5.2 Cumulative Dive Analysis

Diel differences in dive behavior occurred throughout the study area, with deeper, longer duration dives occurring during the day. However, there were some regions where this did not occur, including the area near Swiftsure Bank and near shore off central California, where dive depths were limited by shallow water (see **Section 4.2** for further detail). Median daytime maximum dive depths were consistent across the waters off Washington and Vancouver Island with the exception of the area near Swiftsure Bank, where dives were shallower (**Figure 51**). Median daytime dive depths off Oregon and northern California were shallower than off Washington; however, the sample size of depth data was much more limited. Daytime dive depths were shallowest near shore off central California but were deeper for dives further offshore in that area near the continental slope (**Figure 51**). Median dive durations were longest off Vancouver Island and Washington and declined to the south, reaching their lowest values off southern California (**Figure 52**). Over 50 percent of recorded dive behavior (dive duration and post-dive interval) occurred within 30 m of the surface across the majority of the study area (**Figure 53**). Areas with the highest percentage of time spent near the surface were near shore off San Francisco, California, and northern California, and were also areas with the lowest median maximum daytime dive depths (**Figure 51**).

3.6 Ecological Relationships

A total of 78 tracks from humpback whales tagged in waters of California, Oregon, and Washington over the period 2004-2019 was available for SSSM/hSSSM modeling. For the feeding season off the US West Coast this analysis generated a total of 2,696 SSSM/hSSSM daily locations with annotated behavioral mode and environmental values, covering an extent of 10 degrees of longitude and 17 degrees of latitude (**Table 18, Figure 54**).

A map of the behavioral classification of the locations in each tagging year/season is shown in **Figure 54** and in each tagging region (SCCA, NCA/OR, NWA) in **Figure 55**. Of the total 2,696 locations analyzed for the study area, 86.4 percent were classified as ARS mode by the SSSM/hSSSM, 9.6 percent as uncertain, and 3.8 percent as transiting (**Table 19**). For a given tagging year/season, behavioral classification as ARS mode ranged from as low as 50.0 percent (2005NCA/OR season) to as high as 92.6 percent (2019WA); uncertain classification ranged from 4.9 percent (2019WA) to 100 percent (2016OR); and transiting mode ranged from 0.4 percent (2004CA) to 9.6 percent (2018OR) (**Table 19, Figure 54**). Within the three tagging regions, behavioral classification as ARS mode ranged from a low of 65.6 percent of the locations (NCA/OR) to 92.1 percent (NWA), while the proportion of transiting locations ranged from a low of 2.7 percent (NWA) to 6.7 percent (NCA/OR) (**Table 19, Figures 55 and 56**).

The results of testing for differences in BMODE across tagging regions indicated that the discrete distributions differed significantly for the global hypothesis ($F = 0.035$, p-value < 0.001) as well as for all pairwise comparisons (p-value ≤ p-critical): SCCA-NCA/OR (p-value = 0.002 ≤ p-critical = 0.025), NCA/OR-

NWA (p-value = 0.002 $\leq$ p-critical = 0.017), and SCCA-NWA (p-value = 0.004 $\leq$ p-critical = 0.05) (**Figure 56**).

Considering the small sample size for locations classified as transiting by the SSSM/hSSSM, along with the fact that further interpretation of analyses involving locations classified as uncertain is (by nature) not possible, for the remainder of this section we only report results for locations classified as ARS, which were the vast majority. The overall median distance and speed between SSSM/hSSSM location pairs (ARS mode only) were 12.9 km (MAD = 10.9 km) and 0.54 km/h (MAD = 0.45 km/h), respectively (**Table 20**). Within the three tagging regions, median PWDIST was lowest for NWA (10.6 km; MAD = 8.9 km), while it was similar for SCCA and NCA/OR (median = 16.2 and 16.5 km, MAD = 13.0 and 13.2 km, respectively; **Table 20**). Consequently, PWSPEED reflected the same pattern across regions (**Table 20**).

The tests of differences across tagging regions indicated that the distributions of PWDIST and PWDSPEED differed significantly for the global hypothesis (F = 55.51, p-value < 0.001 for both variables; **Table 23**), while the pairwise comparisons indicated no statistically significant differences between SCCA and NCA/OR only (p-value < 0.001 for both variables; **Table 24, Figure 57**). While engaged in ARS behavior, tracked humpback whales occurred at a median depth of 162.0 m (MAD = 91.9 m), over seafloor with a median slope of 0.76° (MAD = 0.84°) and a median aspect of 220.9° (MAD = 60.9°), and at median distances of 3.8 km (MAD = 3.8 km) from the shelf break and 24.8 km (MAD = 21.0 km) from shore (**Table 21**). The oceanographic conditions where humpback whales engaged in ARS behavior were characterized by a median sea surface temperature of 13.0°C (MAD = 2.2°C), median sea surface temperature gradient of 0.17°C/deg (MAD = 0.11°C/deg), and median phytoplankton chlorophyll-*a* content of 1.74 mg/m^3 (MAD = 1.52 mg/m^3) (**Table 22**).

Tests of global differences between tagging regions were statistically significant for all environmental variables (robust ANOVA F-test with p-values < 0.001 in all cases; **Table 23**). These differences were most pronounced for SST, ASPECT, and DISTSHELF (effect sizes = 0.73, 0.62, and 0.44, respectively; **Table 23**). Post-hoc tests indicated significant differences between tagging regions for most pairwise comparisons (robust Yuen's test with p-values < 0.001; **Table 24**), except between SCCA and NCA/OR, which were less differentiated with respect to mean SLOPE, SSTG, and CHL (**Table 24, Figures 58-60**).

3.7 Genetics

3.7.1 2019 Washington Tagging

Biopsy samples were collected from 19 tagged whales and from nine untagged humpback whales. All samples provided DNA profiles sufficient for subsequent analyses. The mtDNA sequences of the 28 samples resolved seven haplotypes (**Table 25**), all of which have been previously described for North Pacific humpback whales (**Figure 61**; Baker et al. 2013) and so are in the public domain.

The 28 samples were represented by a unique multi-locus genotype of at least 14 loci with an average of 14.9 loci across the dataset. The probability of identity for any given set of 14 loci ranged from $P_{ID} = 1.3 \times 10^{-14}$ to 5.5×10^{-15}. One recapture was identified by photo-identification and confirmed by genotype matching. After removing this replicate, the Washington dataset represented 27 individuals. These 27 individuals included nine females and 18 males. The DNA profiles of the 27 individuals were compared to profiles from previous tagging samples and to an unpublished reference database of 3,320 individuals sampled previously in the North Pacific (including the 1,805 individuals sampled by the program SPLASH as reported in Baker et al. (2013)). From this comparison, two recaptures were detected: an untagged male (biopsy code Mno19WA009) that was a genotype match to an individual biopsy-sampled, but not tagged, during the tagging effort in Washington in 2018 (Genetic ID gWAS18WA002); and a tagged male (biopsy code Mno19WA016, whale #2019WA-5742) that was a genotype match to an individual biopsy sampled during the SPLASH effort in northern British Columbia in 2005 (Genetic ID gNBS05-53091, SPLASH ID 700379).

3.7.2 Cumulative Genetic Analyses

The profiles of the 27 individuals identified from the 2019 tagging effort were combined with profiles from 53 individuals identified from previous tagging efforts along the West Coast of the US. The one recapture between tagging datasets (identified above) was removed for a total of 79 individual humpback whales identified during tagging surveys from 2016 to 2019 (n = 14 from SCCA, n = 15 from NCA/OR, n = 50 from NWA).

Pairwise comparisons of mtDNA haplotype frequencies showed significant differentiation between the tagging samples from SCCA and the tagging samples from both NCA/OR and NWA (**Figure 62**). Similar pairwise comparisons also showed significant differences between the SCCA and NWA tagging samples to all 10 SPLASH feeding areas except the Western Aleutians (WAL; likely due to small sample size for the WAL) and the SPLASH strata they are geographically located in (California/Oregon [CA/OR] and Southern British Columbia/Washington [BC/WA], respectively; **Table 26**). In contrast, pairwise tests of differentiation between the NCA/OR tagging samples and SPLASH showed significant differences to only three of the 10 feeding areas described in Baker et al. (2013; **Table 26**); Russia, South East Alaska and Northern British Columbia. The difference between the NCA/OR tagging samples and the CA/OR strata of SPLASH approached significance (F_{ST} = 0.0345, *p*-value = 0.0611).

A similar pattern is present when looking at pairwise comparisons of mtDNA haplotype frequencies between the three tagging datasets and the eight SPLASH breeding areas described in Baker et al. (2013). The NWA and SCCA tagging samples were significantly different to all or almost all (SCCA was not significantly different to Central America) of the eight breeding areas, whereas the NCA/OR tagging samples were significantly different to only three of the eight breeding areas; the Philippines, Okinawa and Central America (**Table 26**).

The proportion of individuals assigned to different DPSs using the program GeneClass2 differed among the three tagging datasets with SCCA showing the majority of individuals (64 percent) assigning with highest likelihood to the Central America DPS, whereas the largest proportion of individuals from NCA/OR (47 percent) and NWA (48 percent) assigned with highest likelihood to the Hawaii DPS (**Table 27, Figure 63**). There were six tagged individuals whose tag lasted either until the whale had reached a breeding destination or was on a migratory trajectory to indicate a breeding destination (**Figure 64**). Two of these individuals, Mno19WA013 (whale #2019WA-5678) and Mno19WA018 (whale #2019WA-5840), migrated to the Mexican mainland and had a genetic assignment to the MX-AR/ML DPS. Two individuals, Mno19WA016 (whale #2019WA-5742) and Mno19WA019 (whale #2019WA-5921), appeared to initiate their migration toward Hawaii when the tags stopped transmitting. Both of these individuals had a genetic assignment to the Hawaii DPS. However, for Mno19WA019 (whale #2019WA-5921) the assignment was very weak with an almost equal apportionment to the MX-AR/ML DPS (**Table 27, Figure 63**). The remaining two individuals Mno18WA020 (whale #2018WA-5790) and Mno17OR004 (whale #2017NCA/OR-1387) both migrated to Mexico but had a genetic assignment to the Hawaii DPS.

3.8 Photo-identification

3.8.1 Washington 2019

A total of 13,775 photographs were taken of humpback whales in Washington during the 2019 field season. From these photographs, 150 individuals were identified and added to OSU's photo-ID catalog. Of the 24 whales tagged, 20 fluke photos were obtained, 15 of which have been identified in the Happywhale photo-ID database (**Table 28**). Fourteen whales had been seen prior to tagging; six in Washington, one in California, four in Mexico, and three in both Mexico and Washington. Six whales were seen after tagging; one in Hawaii and five in Mexico. Fluke photos were obtained of four of the nine whales that were biopsied without being tagged and three were matched in Happywhale. All three of the biopsied whales had been seen previously in Washington and one was seen after in Mexico. For the whales seen in Mexico (both tagged and biopsied-only) three were seen in mainland Mexico, two in Baja California, and four in both Baja California and mainland Mexico.

Of the remaining 126 identified whales (untagged or unbiopsied), 80 had matches to Happywhale (**Table 28**). In addition to 33 matches to southern British Columbia and Washington, there were 47 matches to other SPLASH strata; 31 in Mexico, 11 in Hawaii, three in California, and two in Oregon. The whales seen in Mexico included five in mainland Mexico, ten in Baja California, 12 in both mainland Mexico and Baja California, one in the Revillagigedo Archipelago and mainland Mexico, one in mainland Mexico and Hawaii, and two in Baja California and Hawaii.

3.8.2 Cumulative Photo-identification

The photo-IDs of the 150 individuals identified in the 2019 tagging effort were combined with IDs from 510 individuals identified from previous tagging efforts by OSU along the US West Coast, for a total of 660 individual humpback whales identified during tagging efforts from 2004 to 2019 (243 from SCCA, 132 from NCA/OR, 285 from NWA; **Table 28**).

Of the 82 tagged and/or biopsied whales with photo-IDs, 68 had matches in Happywhale to SPLASH-defined regional strata. Eighty-two percent (56 of 68) of these whales were matched to the feeding areas in which they were tagged/biopsied (**Table 29**). Forty-four percent (four of nine) of the whales tagged in NCA/OR were also seen in the southern British Columbia/Washington feeding area, and three percent (one of 31) of the whales tagged in NWA were also seen in the California/Oregon feeding area (**Table 29**). No whales tagged in SCCA were matched to other SPLASH-defined feeding areas. Forty-seven of the 68 resighted whales also had matches to SPLASH-defined breeding areas, including Hawaii, Mexico, and Central America (**Table 29 and Figure 65**). The majority of matches for whales tagged in SCCA were to mainland Mexico (14 whales), followed by Baja California (five whales), and Central

America (one whale; **Table 29**). Most matches for whales tagged in NCA/OR and NWA were to Baja California (eight from NCA/OR, 12 from NWA), followed by mainland Mexico (six from NCA/OR, nine from NWA), and Hawaii (two from NCA/OR, five from NWA; **Table 29**). Thirteen of these whales had matches to more than one breeding area; 12 in both Baja California and mainland Mexico (six from NWA, three from NCA/OR, three from SCCA), and one in both mainland Mexico and Central America (from SCCA).

Of the 578 untagged whales with IDs, 449 were matched in Happywhale to SPLASH-defined regional strata. Ninety-four percent (423 of 449) of these whales had matches to the areas in which they were photographed during our tagging seasons. Twelve percent (10 of 84) of whales photographed in NCA/OR were also matched to the southern British Columbia/Washington feeding area, and two percent (three of 154) of whales photographed in NWA were also matched to the California/Oregon feeding area (**Table 30**). A total of 333 of the 449 resighted whales also had matches to breeding areas, and as with tagged whales, these included matches to Hawaii, Mexico, and Central America (**Table 30** and **Figure 66**). The majority of matches for whales tagged in SCCA were to mainland Mexico (108 whales), followed by Baja California (89 whales), and Central America (11 whales; **Table 30**). Most matches for whales tagged in NCA/OR were to Baja California (45 whales), followed by mainland Mexico (37 whales), Hawaii (three whales), and Central America (one whale; **Table 30**). Most matches for whales tagged in NWA were to Baja California (57 whales), followed by mainland Mexico (41 whales), Hawaii (35 whales), and the Revillagigedo Archipelago, Mexico (two whales; **Table 30**). One hundred and thirteen of these whales had matches to more than one breeding area; 102 in both Baja California and mainland Mexico (59 from SCCA, 18 from NCA/OR, 25 from NWA), four to both mainland Mexico and Central America (from SCCA), one to Baja California and Central America (from SCCA), one to Baja California, mainland Mexico, and Central America (from SCCA), one to Baja California and the Revillagigedo Archipelago (from NWA), two to Baja California and Hawaii (from NWA), one to mainland Mexico and Hawaii (from NWA), and one to Baja California, mainland Mexico, and Hawaii (from NWA).

4 Discussion

4.1 Tracked Movements

A total of 24 humpback whales were tagged by OSU in feeding areas off Washington State in the summer and fall of 2019, providing tracks for 22 whales. This tracking data expands our understanding of the localized and long-distance movements of humpback whales in the Pacific Northwest, and when combined with tracking data obtained from our previous tag deployments in Oregon and California, provides valuable insight into feeding group structure along the US West Coast. Generally, the locations obtained from the California, Oregon, and Washington tag deployments align well with sightings of humpback whales off the US West Coast recorded during NOAA ship surveys (summer and fall 1991-2009, 2014) as well as Cascadia Research Collective small-boat surveys (1986-2011) and tagging studies (2011, 2012, 2018), and further support reported humpback whale affinity for continental shelf and shelf edge habitat (Schorr et al. 2013, Calambokidis et al. 2015, 2019, Becker et al. 2019).

The tagging of humpback whales in northern Washington in 2019 represents the second year of Washington deployments as part of this CESU agreement (the first being in 2018), the results of which provide some of the first long-term tracking information of humpback whales from this area (earlier satellite tag deployments on humpback whales off Washington by Schorr et al. [2013] and Calambokidis et al. [2019] only yielded short tracked durations). Previous tag deployments by OSU off Oregon (2005, 2016 to 2018) and California (2004-2005, 2017) allow for comparisons among three tagging regions along the US West Coast, here defined as; 1) northern Washington (NWA), 2) northern California (Cape Mendocino northward) and Oregon (NCA/OR), and 3) southern and central California (SCCA). Both the overall latitudinal ranges in feeding areas and the HRs calculated from tracks greater than 30 d in length showed overlap in the distribution of humpback whales tagged in NWA and NCA/OR, and between whales tagged in NCA/OR and SCCA, but not between whales tagged in NWA and SCCA. Humpback whales feeding in southern British Columbia/northern Washington have been considered a separate feeding aggregation to humpbacks feeding in California and Oregon (Calambokidis et al. 2015, Wade et al. 2016). This distinction results from the little interchange reported between the two groups (Calambokidis et al. 2008, 2015, Wade et al. 2016), an apparent genetic differentiation between them (Baker et al. 2013), as well as an apparent gap in sightings between central Oregon and central Washington (Calambokidis et al. 2008). Our tracking results support the distinction of whales from southern British Columbia/northern Washington from California, but not from Oregon, and instead provide evidence of some degree of mixing between Oregon whales and those from adjacent areas. The movement of a humpback tagged off central Oregon in 2017 to Cape Flattery, northern Washington, and Vancouver Island, British Columbia, the overlap in locations along the northern Oregon and southern Washington coast of whales tagged in both NWA and NCA/OR, and the genetic results of humpbacks tagged in the two regions (described more fully in **Section 4.4** below) support the mixing of Oregon and southern British Columbia/northern Washington whales.

Genetic and photographic identification information suggest that the majority of humpback whales in southern British Columbia/northern Washington migrate there from breeding areas in Hawaii or Mexico, with a smaller number coming from Central America (Calambokidis et al. 2008, Wade et al. 2016). The majority of humpback whales in California and Oregon are from Mexico, with a smaller number from Central America (Wade et al. 2016). While limited in sample size, our tracking results provide further evidence for these migratory connections. Two whales tagged in NWA were tracked to mainland Mexico, while two others tagged in NWA were tracked on the beginning of their migration, with trajectories toward Hawaii. Two whales tagged in NCA/OR were tracked to mainland Mexico, and one whale tagged in SCCA was tracked to Guatemala, in Central America. One additional humpback tagged in NWA was last located off the coast of Baja California, Mexico, after a large gap in transmissions, but because only a single transmission was received in Baja California we cannot confirm whether the whale was destined for a breeding area in Mexico or transiting through on its way to Central America. To more fully understand the extent of mixing or separation of humpback whale DPSs on the feeding grounds, obtaining additional migratory routes and destinations is desirable. Longer tag attachments, tagging later in the feeding season, and/or tagging on the breeding grounds would help us achieve this goal.

The high density of locations as well as the overlapping CAUs for seven whales in the Strait of Juan de Fuca provides further evidence that humpback whales have returned to the Salish Sea (i.e., the waters encompassing the Strait of Juan de Fuca, Strait of Georgia, and Puget Sound), as reported by Calambokidis et al. (2017). Humpbacks were largely eliminated in the waters of southern British Columbia and northern Washington through commercial whaling in the early 1900s (Calambokidis et al. 2017). Over 5,600 whales were taken from British Columbia whaling stations from 1908 to 1967, the majority of which were killed by 1917 (Calambokidis et al. 2017). Most sightings of humpback whales in the 1990s and early 2000s were from waters outside the Salish Sea (Calambokidis et al. 2015) but beginning in the late 2000s sightings inside the Salish Sea have increased dramatically, most notably in 2015 (Calambokidis et al. 2017). CAUs for NWA whales in this study occurred both inside and outside the Strait of Juan de Fuca, with much of the inside use taking place in 2018 (Palacios et al. 2020a) and much of the outside use taking place in 2019. Humpbacks in both years were observed lunge-feeding at the surface around Swiftsure Bank, presumably on krill, as surface aggregations of krill and red defecations from the whales were observed. While no such observations occurred within the Strait of Juan de Fuca, anecdotal reports from Makah fishermen targeting sockeye salmon noted the occurrence of humpback whales near their gillnets, presumably targeting the same prey (krill) as the salmon. The inside versus outside the Strait difference between 2018 and 2019 likely reflected different distribution of krill between the two years, or a seasonal difference, as tagging took place in August in 2018 and in late September/early October in 2019. The majority of locations from our NWA deployments in 2018 were concentrated in the western part of the Strait of Juan de Fuca, whereas many of the sightings noted by Calambokidis et al. (2017) occurred in the central Strait of Juan de Fuca and also extended far into Puget Sound. This could also represent inter-annual variation in movements in this area, or perhaps a preponderance of sighting effort closer to population centers in the earlier studies. In any case, there is great potential for overlapping distributions of whales, ship traffic, and fishing operations throughout the Salish Sea, as well as at the mouth of the Strait of Juan de Fuca, putting the whales at increased risk for ship strikes, entanglements in fishing gear, and noise impacts.

Despite a small sample size of whales tagged in NCA/OR (only eight whales qualified for home range analysis), overlapping CAUs identified the northern California coast, particularly near Trinidad and Point St. George, as an area of high use for these whales. This supports studies that show the northern California coast to have high predicted densities of both humpback whales (Calambokidis et al. 2015, Becker et al. 2019) and their krill prey (*Thysanoessa spinifera*) in some years (Cimino et al. 2020). CAUs also overlapped for two whales off the Columbia River mouth, an area noted by Calambokidis et al. (2017) with an increase in sightings in recent years, including sightings part way up the Columbia River and around the town of Chinook, Washington, in 2015 and 2016; areas in which locals had previously not seen humpback whales. This contrasts with past studies (Calambokidis et al. 2008), which reported a gap in sightings of humpback whales between central Oregon and central Washington. Humpback whales have been shown to switch their dominant prey type (from krill to fish and vice versa) in response to changing oceanographic conditions and prey availability (Fleming et al. 2016), and Calambokidis et al. (2017) report that shifts in prey, especially when targeting nearshore concentrations of fish like anchovies, has sometimes brought whales closer to shore and into new areas. The humpback whales documented in the Columbia River by Calambokidis et al. (2017) appeared to have been feeding on anchovies. It is unclear whether the use of the Columbia River mouth by humpback whales is a temporary occurrence, or whether this area will continue to be important for feeding humpbacks. Although the anchovy season is relatively short and the numbers of whales there presently is apparently low, their location in the river mouth (with a busy up-river port) could represent an increased risk to humpback whales from potential collisions with vessels if their numbers continue to grow in the future.

For whales tagged in SCCA, the concentration of tracks, HRs, and CAUs around San Francisco aligns well with past visual sightings of humpback whales and predicted distributions from habitat-based density models (Calambokidis et al. 2015, Becker et al. 2019). While this may also partly reflect the high number of tag deployments in that area, the area is undoubtedly an important feeding habitat for humpbacks, as evidenced by approximate residencies in the area between Bodega Bay and Monterey Bay ranging from 19 to 82 d for 10 tagged whales, as well as high residencies recorded in the Farallones BIA (see **Sections 3.4.2.3 and 4.1.2**). The track of the humpback whale tagged in the Santa Barbara Channel (whale #2017CA-830, a male with genetic assignment to the Central America DPS) did not intersect with other whales tagged off central California in 2017 despite a 44-d tracking period for this whale, which would have been ample time to travel to the latter area. This may signify a separation of humpback whales from southern and central California during the feeding season or the more southern whale simply finding adequate forage in the area, but a larger sample size of whales from both regions would be required to fully address these interpretations.

4.1.1 Use of Navy Training Areas

All but one of the humpback whales tagged in NWA and NCA/OR had locations within the NWTT. This is not surprising, as 68 percent of tag deployments took place within NWTT, and the remaining 39 percent took place within 14 km of the range. With a mean residency in NWTT of 16.8 d for all whales, and maximum residencies of 86.6 d for both NWA and NCA/OR whales, NWTT clearly represents important feeding habitat for humpback whales from the Pacific Northwest. Area W237, within the NWTT, was predominantly used by humpback whales tagged in NWA, with 88 percent of these whales having locations there, compared to only one humpback whale tagged in NCA/OR having locations there. This may represent spatial separation of humpback whales from NCA/OR and NWA, but it may also reflect the timing and duration of tracking periods. As our NCA/OR tag deployments have always taken place in August, September, or October, and we haven’t tracked these whales into the spring and summer, we cannot rule out the possibility that NCA/OR whales may also use more northerly parts of the NWTT or area W237 earlier in the feeding season. Tagging more whales in NCA/OR and Washington earlier in the feeding season or longer tag attachments would improve our understanding of Navy range use and potential spatial separation of these whales. No humpback whales tagged in SCCA (out of 24 tracks) spent time in area W237, and only 13 percent of whales tagged in SCCA had locations in the NWTT, with most of the locations occurring in the southern half of the range, again demonstrating a spatial separation between whales tagged in NWA and SCCA.

With the exception of three migrating whales transiting through PT MUGU and SOCAL, only one whale from NCA/OR or NWA spent time in southern California training ranges (a whale tagged in northern California in 2005 spent approximately 6.1 d in PT MUGU). Presumably, humpback whales migrating to and from breeding areas in Mexico or Central America would pass briefly through SOCAL, and to a lesser extent PT MUGU, in winter and spring, as the ranges extend approximately 1,200 and 210 km offshore, respectively. Otherwise we have very little evidence of NCA/OR or NWA whales spending extended periods of time in the southern ranges during the feeding season. Even for whales tagged in SCCA, there was very little use of the southern ranges, with only one whale migrating through SOCAL, and only three whales spending time in PT MUGU. These latter three whales (including the one tagged in southern California) spent extended periods of time in PT MUGU, however, with residencies ranging from 9.0 to 33.8 d, highlighting the importance of this range for some feeding humpback whales. If, as mentioned above, there is some degree of separation of humpback whales in California during the feeding season, then our sample of only one whale tagged in southern California (compared to 23 tagged in central California) may contribute to this apparent lack of use of southern ranges. The management implications of southern Navy ranges being used primarily by southern California humpback whales is significant, as these likely represent more whales from the endangered Central America DPS (Calambokidis et al. 2017). Additional tagging in southern California during the feeding season or in Central America during the breeding season would help address this potential separation.

4.1.2 Use of BIAs

The occupancy of US West Coast feeding BIAs also suggests spatial separation of humpback whales throughout feeding areas, as there was no overlap in the BIAs most important to whales from different tagging regions (as indicated by the BIAs with the highest proportion of tagged whales having locations there): NOWA for whales tagged in NWA, PSG for whales tagged in NCA/OR, and Farallones for whales tagged in SCCA. Also, only two of 42 humpbacks tagged in NWA spent time in BIAs south of Washington (during migration), and only one whale tagged in SCCA was found in a BIA north of California, spending less than one day in the Stonewall BIA in Oregon. Such spatial separation was not as clear for whales tagged in NCA/OR, with one whale spending time in the NOWA BIA in northern Washington, and locations for others occurring in all other BIAs. It is worth noting that the NCA/OR whales with non-migrating locations in the more southern BIAs (Fort Bragg, Farallones, Morro Bay) were animals tagged in southern Oregon or northern California, whereas the southernmost BIA used by whales tagged in central or northern Oregon was PSG. These results further support, not only a potential separation of humpbacks from NWA with those from SCCA, but also a decline in connectivity with latitudinal separation as reported by Calambokidis et al. (2017).

The extensive use of the NOWA BIA by whales tagged in NWA reflects not only the location of tag deployments in Washington, within or very close to the BIA, but also speaks to the whales' affinity for the region, as evidenced by the substantial residency (average 9.6 d, maximum 40.1 d in NOWA) and the seasonal extent (August through December) of locations there. In 2018, areas of highest use for humpbacks tagged in NWA (where CAUs overlapped for a maximum number of whales) extended east of the western edge of the NOWA BIA, throughout the Strait of Juan de Fuca, and in both 2018 and 2019 these areas extended north of the NOWA boundary into Canadian waters (north of the US Exclusive Economic Zone; Palacios et al. 2020a). The high density of locations at the southwestern tip of Vancouver Island, especially around Swiftsure Bank, reveals this area to be of importance to feeding humpback whales, and were it not for international boundaries, inclusion of this area as part of a BIA seems reasonable.

For humpback whales tagged in NCA/OR, CAUs overlapped with the PSG, Stonewall, and Fort Bragg BIAs, but the area of highest use occurred outside of BIAs near Trinidad, northern California. While the sample size was small for HR and CAU analysis, this does highlight the importance of this area for humpback whales. More tagging in NCA/OR could help determine whether inclusion of this area in the BIAs is warranted.

The areas of highest use for humpback whales tagged in SCCA was completely contained within the Farallones BIA, supporting the designation of this area as important to humpback whales. The minimal use of the Santa Barbara BIA by humpback whales tagged in SCCA is likely more a reflection of tagging location than low importance of the area, as only one of the 24 deployments in SCCA occurred in southern California (in the Santa Barbara Channel).

4.1.3 Use of NMSs

Humpback whale use of NMSs mimics the latitudinal or feeding-region separation of locations shown above for Navy ranges and BIAs, with all humpbacks tagged in NWA having locations within OCNMS, and 83 percent of humpbacks tagged in SCCA having locations with GFNMS. While this partly reflects the large numbers of tagging locations within these NMSs, average residency of 11.9 d and 12.6 d (and maximum residencies of 35.2 d and 49.8 d) in GFNMS and OCNMS, respectively, attest to the important feeding habitat within these NMSs for humpback whales. While smaller percentages of SCCA whales had locations within CBNMS and MBNMS, residencies were also quite high for these areas (averages of 9.7 d and 19.1 d, maximums of 42.7 d and 45.3 d, for CBNMS and MBNMS respectively). Over a quarter of the humpback whales tagged in NCA/OR spent time in GFNMS, with a maximum residency of 8.6 d, demonstrating that proximity of tagging location to a sanctuary is not the only factor contributing to NMS use by humpbacks.

4.2 Dive Behavior

Dive behavior of tagged whales was broadly similar across the US West Coast, suggesting whales were feeding in a similar way, or on a similar prey, despite regional differences in movement patterns. The diel trend observed in dive behavior across much of the study area is characteristic of rorqual krill-feeding behavior, with lunges and deeper, long-duration dives occurring during the day (Calambokidis et al. 2007, Goldbogen et al. 2008, Mate et al. 2017). For whales tagged off Washington, the diel effect was least pronounced for dives that occurred near Swiftsure Bank, where daytime dives were typically < 75 m depth, while dives across the rest of the area, including within the Strait of Juan de Fuca, were > 125 m depth. This difference in dive behavior raises the possibility that tagged whales were targeting different prey near Swiftsure Bank, as they are known to be capable of feeding on both fish and krill (Clapham et al. 1997, Fleming et al. 2016). However, water depths at Swiftsure Bank are < 100 m, compared to > 200 m for other parts of the area occupied by Washington-tagged whales, including within the Strait of Juan de Fuca. Thus, daytime dive depths of tagged whales using Swiftsure Bank were limited by bottom depth, reducing the possibility of an observable diel change in dive behavior in that area. Additionally, aggregations of surface feeding whales were observed on multiple occasions in the area of Swiftsure, coincident with observations of krill in the water and red defecation from whales in the area. Thus, tagged whales off Washington appear to have been feeding on krill throughout their range, while the topography of Swiftsure Bank may have acted to concentrate prey at shallower depths in that area (Genin 2004), giving the appearance of a regional difference in behavior.

Local-scale variability of dive behavior was also observed in humpback whales tagged off central California in 2017. Deeper dives with more numerous lunges per dive were recorded further from shore, mostly driven by data from one tagged whale (whale #2017CA-4175). This whale recorded deeper dive depths and more lunges per dive than other DM-tagged whales off California. The deeper dives were made during the day, making the behavior of whale #2017CA-4175 characteristic of rorqual krill-feeding behavior (Calambokidis et al. 2007, Goldbogen et al. 2008, Mate et al. 2017). The whale also spent most of the tracking period further west over the continental slope, where krill aggregations are higher (Santora et al. 2011), compared to the other tagged whales, and recorded high numbers of lunges per dive on multiple consecutive dives to the same depth range, indicating feeding bouts (Mate et al 2017). While dives made by other DM-tagged whales off California were closer to shore, they were made to very shallow depths (mean = 36.6 m) in waters > 75 m deep, suggesting they were not limited by bottom depth as were dives near Swiftsure Bank off Washington (Mate et al 2018a). The generally shallow dive depth and consistent low levels of lunges per feeding dive recorded by other tagged whales suggests that these whales were feeding on fish. Lunges were recorded more intermittently for these whales, with singular lunges recorded during multiple consecutive dives to a specific depth. It is possible that these whales were feeding at a lower rate, although humpbacks display much more kinematic variability when feeding on fish compared to krill (Cade et al. 2016, 2020), so the tags may not have detected all lunge-feeding events made on fish. While the sample size was small, these results suggest that humpback whale behavior off California may be more variable at local scales compared to areas further north.

The ability of humpback whales to forage on both krill and fish may drive the spatial homogeneity of observed tagged whale dive behavior. The smaller size of humpback whales makes energetic costs of transport higher compared to larger rorqual species like blue whales, suggesting there is selection pressure for humpback whales to maximize the intake of nearby resources, rather than searching for new ones. Humpback whales in Monterey Bay, California, are able to exploit the greatest available prey abundances by feeding on both krill and fish (Fossette et al. 2017). This allows them to occupy a broad spatial distribution and remain in the feeding area for longer than blue whales, which are limited to only areas with high abundances of krill (Fossette et al. 2017). The relatively consistent spatial and temporal distribution of tagged humpback whale dive behavior in this study suggests this trend may extend to other parts of the US West Coast and implies that humpback whales may be expected to occur in areas for longer periods of time than other rorqual species.

Tagged whales spent over half of their reported time near the surface (< 30 m depth) and, off Washington and California, they occupied waters that are heavily used by a wide range of commercial, military, and recreational vessels. Ship strikes of large whales are a growing concern (Silber et al*.* 2012, Panigada et al*.* 2006, Redfern et al*.* 2013), and the Strait of Juan de Fuca is used to access the fifth (Port of Vancouver) and seventh (Port of Seattle) largest commercial shipping ports in North America while San Francisco Bay is also home to the tenth largest US port (Port of Oakland). The draft of the type of medium to large container ships using these areas is 14 to16 m (Calambokidis et al. 2019) and 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 suggests the tagged whales in these places are at an elevated risk of potential collision with large vessels moving through the area. Additionally, diel differences in dive behavior, similar to those observed in this study, have been shown to increase the vulnerability of whales to vessel collision at specific times of day, as they spend more time near the surface at night (Calambokidis et al. 2019). The shallower water depth of Swiftsure Bank may also act to increase the chance of vessel collision as whales are forced to occupy portions of the water column closer to the surface. Humpback whales tagged off central California spent more time at < 30 m depth compared to tagged whales off Oregon (73 versus 63 percent), which matches the findings of a different study of humpback whales off central and southern California (69 to 88 percent of their time during the day and night, respectively; Calambokidis et al. 2019). The greater time spent at shallow depth by California whales may be related to behavioral differences associated with local variation in the distribution and type of prey between Washington and California waters. Further work is needed to more accurately examine the potential risk of ship strikes for humpback whales off the US West Coast.

4.3 Ecological Relationships

SSSM/hSSSM analysis of 78 humpback whale tracks from three tagging regions off the US West Coast (SCCA, NCA/OR, NWA) over the period 2004-2019 revealed that whales occurred throughout this environment during the feeding season, from the northern tip of Vancouver Island at the north to the Santa Barbara Channel at the south (**Figure 55**), and that ARS mode was the predominant behavior (86.4 percent overall classification). However, the composition of behavioral mode was significantly different between regions and implied that whales tagged off NCA/OR spent less time foraging (66.0 percent in ARS) compared to whales tagged off SCCA (87.5 percent) or NWA (92.1 percent). For ARS location pairs, significant differences between the regions for variables describing movement patterns (PWDIST, PWSPEED) additionally indicated shorter distances and slower speeds for whales tagged off NWA than for whales tagged off SCCA or NCA/OR (p-value < 0.001; **Table 24**).

With respect to the physiography of the seafloor, humpback whales occurred predominantly over continental shelf waters (median depth = 162.0 m) but generally closer to the shelf break (median distance = 3.8 km) than to shore (median distance = 24.8 km). Statistical comparisons indicated significant differences between tagging regions for all seafloor variables (**Table 23**), with seafloor slope being steeper and more southward-facing for whales tagged off NWA and gentler and more westward-facing for whales tagged off NCA/OR, and with distance to the shelf break being small for whales tagged off WA and becoming progressively larger for whales tagged off NCA/OR and SCCA (**Table 21**). Off NWA these differences reflected the semi-enclosed conditions imposed by the Strait of Juan de Fuca and adjacent waters. In the open waters further to the south, humpback whales tagged off NCA/OR occurred significantly closer to the shelf break and farther from shore than whales tagged off SCCA (**Table 21**).

The extent to which prey type and availability may be influencing these differences between tagging regions is unknown at this point, but the diving patterns reported in **Section 3.5** suggest that this is likely the case.

In terms of oceanographic conditions where humpback whales engaged in ARS behavior, the strongest difference between regions was in SST, with waters being notably warmer for whales tagged off SCCA (median = 15.0°C) and cooler for whales tagged off NCA/OR and NWA (median = 12.0 and 12.2°C, respectively; **Table 22**). These differences are a reflection of the well-known global latitudinal temperature gradient (Becker et al. 2019, Palacios et al. 2019a), as well as of local variations in wind-driven upwelling processes along the western coast of North America (Checkley and Barth 2009), and probably not indicative of differential temperature preferences by the whales using these regions. Pairwise comparisons between regions for the other two oceanographic variables examined (SSTG and CHL) were either not significant (SSTG *p*-value = 0.387; **Table 24**) or had a significant but comparatively high *p*-value (CHL *p*-value = 0.014; **Table 24**) for whales tagged off SCCA and NCA/OR, while all comparisons with whales tagged off NWA were highly significant, indicating that NWA was the most differentiated of the three regions.

The combination of tracking data across multiple years allowed us to conduct a comprehensive characterization of the ecological relationships and habitat requirements of humpback whales during the feeding season at the ecosystem scale. One caveat is that interannual effects (Fleming et al. 2016, Becker et al. 2019) may also have had an effect on some of the observed variations (e.g., in the years covered by this study, SST was anomalously warm in 2004, 2005, and 2017), but these remain unaccounted for at this point. Additionally, our analyses focused on ARS mode and did not consider comparisons with the other two behavioral modes (transiting and uncertain). While in principle a two-way or multi-factorial ANOVA approach including region, behavioral mode, and year would be desirable, the sample sizes for some of these factors are currently too small for this type of analysis. Additional years of tagging would help address this deficiency.

4.4 Genetics

4.4.1 Population Structure of Feeding Areas

The significant difference in mtDNA haplotype frequencies between the tagging samples from SCCA and the tagging samples from both NCA/OR and NWA indicates a degree of differentiation between feeding areas not previously accounted for within the SPLASH program (Baker et al. 2013). Previously, whales feeding off Oregon were considered to be more closely affiliated with California, referred to in SPLASH as CA/OR (see **Figure 61**). There was no significant difference between the tagging samples from NCA/OR and those from NWA. However, this could be due to the small sample size and the high proportion of the four most common haplotypes within the NCA/OR dataset. A larger samples size for NCA/OR and finer-scale analyses are needed to delineate the most appropriate boundary for feeding areas along the US West Coast.

4.4.2 Individual Assignment to DPS

The individual assignment procedures provided evidence of the genetic affinity of each individual to each of the four DPSs. The relative likelihood scores of these assignments for the 14 whales sampled in SCCA were generally consistent with the expectation of mixing between individuals from the Mexico and Central America DPSs, as reported previously from photo-identification (Calambokidis et al. 2008, 2017) and from the comparisons of mtDNA haplotype frequencies (Baker et al. 2013). The strength of these assignments was high, with assignment likelihoods for all but one individual above 70 percent and the majority (10 of 14 individuals) above 90 percent. In contrast, the relative likelihood scores of assignments for the whales tagged in NCA/OR and NWA showed a greater diversity of affinities for the different DPSs, including a greater proportion of ancestry from Hawaii and the Western North Pacific. In addition, the strength of these assignments was weaker than for the SCCA tagging sample, with only 25 of 65 sampled individuals having an assignment likelihood over 90 percent. The difference in DPS assignment between the SCCA tagging dataset and the NCA/OR and NWA datasets is consistent with the test of differentiation showing a significant difference in mtDNA haplotypes for these datasets (i.e., the haplotype characteristics of the Central America DPS are less frequent off the coasts of NCA/OR and NWA). This is presumably due to differences in migratory connections and habitat use between the different DPSs (see Calambokidis et al. 2017). The difference in the strength of assignment among the tagging datasets is likely due to genetic differentiation among the DPSs. Individuals will assign with a higher likelihood to a DPS that is strongly differentiated, such as Central America, whereas assignment will be weaker for DPSs with more shared genetic diversity, such as Mexico and Hawaii.

Although the results of the assignment procedure are encouraging and provide a useful covariate for analysis of the tagging results, it is important to note that the accuracy of the assignments is dependent on the quality of the reference data set; in this case, as described from samples collected during the SPLASH program (Baker et al. 2013). These samples were collected more than a decade ago, and more importantly, were limited in number of microsatellite loci and in population sampling for the two DPSs of greatest concern, Central America and Mexico (see **Table 27**). The confidence in individual assignments of whales on the feeding areas could be improved by increasing the number of loci in the reference data set using genomic methods (e.g., RADseq or similar, Andrews et al. 2016) and by increasing the population sampling using available samples collected in Mexico during SPLASH (Calambokidis et al. 2008). For Central America, however, there is a need to collect new samples, preferably from throughout the breeding range of this DPS.

4.5 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 off the US West Coast. By including photo-IDs of both tagged as well as 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. Photo-ID results provided further evidence for strong fidelity to feeding areas, as 100 percent of whales resighted in feeding areas had matches to the regions in which they were tagged/photographed. There was also good general agreement in migratory connections between feeding and breeding areas between tracking and photo-ID results.

Probabilistic genetic assignment of biopsy-sampled individuals to DPS is a promising approach in areas where DPSs mix, such as the feeding area off US West Coast, as demonstrated in this study. However, the general proportions of assignment to DPS did not always agree with the proportion of matches between feeding and breeding areas based on photo-ID. Specifically, the genetic assignment suggested that 52 percent of the animals sampled in NWA and 47 percent of the animals sampled in NCA/OR had a likelihood of assignment to the Hawaii DPS, while the photo-ID results (from tagged and untagged animals) indicated that only about eight percent of whales photographed off NCA/OR and 29 percent of whales photographed off NWA had matches to Hawaii. The majority of matches to a breeding area for whales photographed off NCA/OR and NWA were to Mexico. Although differences in methodology, sample size, and robustness of the reference database used for these matches preclude a more formal comparison, such a difference suggests the possibility that humpback whales with Hawaii heritage may be spreading to breeding grounds in Mexico as the Hawaii DPS recovers. Indeed, photo-ID matches have been found in the past between Hawaii and Mexico (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker et al. 1986, Forestell and Urbán-R 2007). However, any suggestion that such movement is operating more in one direction (i.e., from Hawaii to Mexico), is complicated by the recent resighting of a humpback whale in Mexico in 2014 and then in Hawaii in 2015 (Palacios et al. 2019b). Additional work is needed to improve the genetic reference database currently in use, as described in the previous section, and photo-ID can serve as an independent data source to validate this approach.

Photo-ID results were also not in complete accordance with genetic results in the proportion of SCCA whales assigned to the Central America and Mexico DPSs, with the vast majority of photo-ID matches of SCCA whales to Mexico, compared to over 70 percent of genetic assignments of SCCA whales to Central America. Some of this discrepancy may be explained by a larger photo-ID effort in Mexico compared to Central America. As some of the whales we photographed were resighted in both mainland Mexico and Central America, we cannot be certain that whales photographed only in Mexico were definitively members of the Mexico DPS. It is unclear where the boundary lies between the Mexico and Central America DPSs, with recent results suggesting that parts of the southern Mexico mainland should fall within the Central America DPS region (International Whaling Commission 2020). A more detailed examination of the specific locations of our photo-ID matches in the breeding areas could help our understanding of this boundary.

Photo-ID is a powerful tool for identifying whales over time and space but is limited by the amount of cooperation between researchers in sharing their catalogs and the amount of time needed to review IDs for matches, compile, and exchange the results. By using Happywhale, which combines a growing citizen-science base with state-of-the-art machine learning algorithms and automation, we have been able to overcome some of these limitations to make more connections between areas. As the number of photo-ID catalogs submitted to Happywhale by other researchers continues to increase at a rapid pace, our capacity to expand the overall interpretation and significance of our tagging and genetic results will also improve.

5 Recommendations

The results of this study significantly expanded our understanding of the local and long-distance movements of humpback whales along the US West Coast and provide valuable insight into the population structure of the feeding aggregations that use this productive ecosystem. But these results also open up new questions and avenues for research. Throughout this report we have indicated how additional work could help address these questions. However, in this section we provide a compilation of the key recommendations arising from this study.

1. Our tracking results support the distinction of whales from southern British Columbia/northern Washington from southern and central California, but not from northern California/Oregon, and instead provide evidence of some degree of mixing between northern California/Oregon whales and those from adjacent areas. To more fully understand the degree of this mixing or separation, especially in the context of whale use of the NWTT range, we recommend **conducting additional tagging in Oregon waters**. Additionally, as all our tag deployments took place in late summer and early fall**, tagging earlier in the feeding season (late spring and early summer) might reveal new details about the pattern of whale movements between feeding areas along the US West Coast**.
2. Similarly, the single whale tagged in southern California during this study did not intersect with other whales tagged off central California, suggesting a separation between these two areas. Under this premise, the southern Navy ranges of SOCAL and PT MUGU would be presumably used primarily by southern California humpback whales from the endangered Central America DPS during summer, while whales migrating to/from feeding areas in central California, Oregon, and Washington from/to breeding areas in Mexico or Central America would pass through southern California (and consequently through SOCAL and PT MUGU) in winter and spring. We recommend **obtaining a larger sample size of tagged whales from southern California**, and also conducting **tagging in Central America** during the breeding season **to fully address this potential separation between southern and central California whales**.
3. The high use by tagged humpback whales of the Strait of Juan de Fuca and adjacent waters in northern Washington in both 2018 and 2019 support the results from recent studies documenting a repopulation of the Salish Sea. However, there is great potential for overlap between whales, ship traffic, and fishing operations in this area, putting the whales at increased risk for ship strikes, entanglements in fishing gear, and noise impacts. We recommend **conducting additional analyses of the tagging data already in hand to characterize the degree of overlap between these activities and whale distribution, both horizontally as well as with respect to vertical use of the water column, taking advantage of the dive data collected by our DM tags**.
4. Similarly, this study suggested an apparent high use of the Columbia River mouth by tagged humpback whales that is consistent with an increase in sightings in recent years reported by other studies. Considering the busy up-river port of Portland, the associated shipping and port operation activities at the river's mouth could represent an increased risk to humpback whales from potential collisions with vessels if their numbers continue to grow. We recommend

conducting a dedicated tagging study around the Columbia River mouth to obtain further data on the pattern of humpback whale use of this area.

5. The extensive use of the Olympic Coast National Marine Sanctuary and the Northern Washington BIA revealed the importance of northern Washington waters for whales tagged in Washington, with areas of highest use extending east into the Strait of Juan de Fuca and north into Canadian waters, as shown by a high density of locations at the southwestern tip of Vancouver Island, especially around Swiftsure Bank. Given that this area is bisected by the international boundary, **further analysis of the data collected during this study could inform plans for coordinated transboundary management of humpback whales by the US and Canada**.
6. For whales tagged in northern California and Oregon, the area of highest use occurred off Trinidad, outside of the three established BIAs in this region (Fort Bragg, Point St. George, and Stonewall Bank). Therefore, we recommend **obtaining a larger sample size of tagged whales from northern California and Oregon to determine whether inclusion of the area off Trinidad in the existing BIAs is warranted**.
7. A significant difference in mtDNA haplotype frequencies between the biopsy samples from southern and central California and those from both northern California/Oregon and northern Washington indicated a degree of differentiation between feeding areas off the US West Coast not previously accounted for within the SPLASH program. No similar difference in mtDNA haplotype frequencies between northern California/Oregon and northern Washington samples was found, although this could be due to a small sample size. We recommend **obtaining a larger sample size of skin tissues for northern California and Oregon and conducting finer-scale analyses in order to delineate the most appropriate boundary for feeding aggregations along the US West Coast**.
8. The results of the probabilistic genetic assignment procedure of whales on the feeding areas to breeding DPS are encouraging but are currently limited in number of microsatellite loci and in population sampling for the two DPSs of greatest conservation concern (Central America and Mexico). Indeed, the genetic assignment results did not always agree with the proportion of matches between feeding and breeding areas based on photo-ID. **We recommend increasing the number of biopsy samples for the Central America and Mexico DPSs in order to improve the confidence in individual genetic assignments by increasing the number of loci in the reference dataset**.
9. Photo-ID results were also not in complete accordance with genetic results in the proportion of southern and central California whales assigned to the Central America and Mexico DPSs, with the vast majority of photo-IDs of southern and central California whales matching to Mexico, compared to over 70 percent of genetic assignments of southern and central California whales matching to Central America. As some of the whales we photographed were resighted in both mainland Mexico and Central America, we cannot be certain that whales photographed only in Mexico were definitively members of the Mexico DPS. **To increase our confidence in photo-ID assignment for these two DPSs, we recommend increasing photo ID efforts in Central America**.

10. Finally, in addition to the need for an improved delineation between feeding aggregations along the US West Coast, at present it is unclear where the boundary lies between the Mexico and Central America breeding DPSs. It has been recently suggested that parts of the southeastern Mexico mainland should fall within the Central America DPS region, which could change the results of our DPS assignments (either through genetics or photo-ID). **To help our understanding of where this DPS's boundary lies, we recommend a more detailed analysis of the specific locations of our photo-ID matches to the Mexican and Central American breeding areas**.

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Table 1. Dimensions of tags deployed on humpback whales by OSU in Washington, Oregon, and California from 2004 to 2019.

Tag Type	Housing Dimensions	Antenna Dimensions	Saltwater Switch Dimensions	Endcap and Stop Material	Stop Dimensions
LO (Telonics ST-15)	1.9 cm diameter x 19.0 cm length	3.0 mm diameter x 13.5 cm length	1.5 mm diameter x 6.0 cm length	Delrin®	1.5 cm long x 0.9 cm wide x 0.8 cm thick
LO (Telonics ST-21)	1.9 cm diameter x 19.0 cm length	3.0 mm diameter x 19.0 cm length	Saltwater Switch was incorporated into the antenna	Delrin®	1.5 cm long x 0.9 cm wide x 0.8 cm thick
DUR (Telonics RDW-640)	1.9 cm diameter x 15.9 cm length	1.3 mm diameter x 15.8 cm length	1.3 mm diameter x 2.2 cm length	Polycarbonate	1.5 cm long × 0.9 cm wide × 0.6 cm thick
DUR+ (Telonics RDW-665)	1.9 cm diameter x 20.7 length	1.3 mm diameter x 15.8 cm length	1.3 mm diameter x 2.2 cm length	Polycarbonate	1.5 cm long × 0.9 cm wide × 0.6 cm thick
DM (Telonics RDW-665)	1.9 cm diameter x 20.7 length	1.3 mm diameter x 15.8 cm length	1.3 mm diameter x 2.2 cm length	Polycarbonate	1.5 cm long × 0.9 cm wide × 0.6 cm thick

Table 2. Programming details for tags deployed by OSU on humpback whales in Washington (WA), Oregon (OR), and California (CA) from 2004 to 2019.

Season and Tag Type	Selected Dive Criteria	Event Detection			Transmit Hours	Expected Battery Life
		High Threshold	Low Threshold	Minimum Time Between Events		
2004CA – LO	-	-	-	-	4/d	> 1 year
2005CA/OR – LO	-	-	-	-	4/d	> 1 year
2016OR – DM	Dives > 2 min & > 10 m	3.5 SD	100% of mean	30 s	6/d	90-120 d
2017CA – DUR	Dives > 2 min	-	-	-	5/d	220-290 d
2017CA – DM	Dives > 2 min & >10 m	1.5 SD	50% of mean	35 s	6/d until 1 Sep 2017 then 6 every other day	100-160 d
2017OR – DUR	Dives > 2 min	-	-	-	5/d	220-290 d
2018WA – DUR+	Dives > 2 min	1.5 SD	50% of mean	30 s	6/d until 30 Sep 2018 then 6 every other day	120-180 d
2018WA – DM	Dives > 2 min & > 10 m	1.5 SD	50% of mean	30 s	6/d	90-120 d
2018OR – DM	Dives > 2 min & > 10 m	1.5 SD	50% of mean	30 s	6/d	90-120 d
2019WA – DM	Dives > 2 min & > 10 m	1.5 SD	50% of mean	30 s	6/d	90-120 d

Key: % = percent.

Table 3. List of environmental data products used in the characterization of ecological relationships. Depth and the three dynamic oceanographic variables were obtained from ERDDAP[†] with the R package *rerddapXtracto* v. 0.4.5, while the derived static variables plus distance to shore were generated in ArcGIS. Columns include variable name (and abbreviation), measurement unit, data set and parameter names required by *rerddapXtracto*, satellite sensor or data product, and temporal and spatial resolution.

Variable	Unit	Data set	Parameter name	Sensor/Product	Temporal resolution	Spatial resolution
Depth (DEPTH)	m	ETOPO360	altitude	ETOPO1 global relief model of Earth's surface	NA	0.0167 deg (1.85 km)
Slope (SLOPE)[‡]	degrees	NA	NA	ETOPO1	NA	0.0167 deg (1.85 km)
Aspect (ASPECT)[‡]	degrees	NA	NA	ETOPO1	NA	0.0167 deg (1.85 km)
Distance to 200-m isobath (DISTSHELF)[‡]	km	NA	NA	ETOPO1	NA	0.0167 deg (1.85 km)
Distance to shore (DISTSHORE)[§]	km	cntry_06.shp	NA	ESRI World Countries 2006	NA	50 m
Sea surface temperature (SST)	°C	jplMURSST41SST	analysed_sst	Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1	1 d	0.01 deg (1.11 km)
Magnitude of sea surface temperature gradient (SSTG)[*]	°C/deg	erdMurFront41USWest	magnitude_gradient	Estimated MUR SST v4.1 gradient magnitude, US West Coast	1 d	0.01 deg (1.11 km)
Chlorophyll-*a* concentration (CHL)	mg m^{-3}	erdMWchla8day[***]	chlorophyll	Moderate Resolution Imaging Spectroradiometer (MODIS) on Aqua satellite	8 d[†]	0.0125 deg (1.39 km)

Key: NA = Not Applicable; °C = degrees Celsius.

[†] The base URL for the ERDDAP server in all *rerddapXtracto* calls was: https://upwell.pfeg.noaa.gov/erddap

[‡] The variables SLOPE, ASPECT, and DISTSHELF were not available on ERDDAP. They were derived from the bathymetry available in ArcGIS.

[§] The variable DISTSHORE was not available from ERDDAP. It was computed from the World Countries 2006 shoreline available in ArcGIS.

[*] SSTG is derived from MUR SST data as part of the procedures implemented for SST frontal edge detection on ERDDAP (van der Walt et al. 2014; https://rmendels.github.io/canny_doc.html)

[†] Although this CHL product covers 8-d periods, it is computed as a running composite, such that it provides a value for every day.

Table 4. Deployment and performance data for 24 satellite-monitored radio tags (Telonics DM tags) deployed on humpback whales off Washington in September and October 2019. Genetic analysis of biopsy samples provided sex and mitochondrial DNA (mtDNA) haplotype information. Deployment dates are represented as UTC dates.

Tag #*	Deployment Date	Date of Last Location	Biopsy Collected	Fluke Photo-ID Collected	Sex	mtDNA Haplotype	# Days Tracked	# Filtered Locations	Total Distance (km)
833	18-Sep-2019	8-Oct-2019	Yes	Yes	Male	A+	19.9	180	873
4173	19-Sep-2019	20-Oct-2019	Yes	Yes	Female	E10	30.9	224	1,478
5670	19-Sep-2019	10-Nov-2019	Yes	No	Male	E6	51.2	296	3,227
5678	19-Sep-2019	1-Mar-2020	Yes	Yes	Female	A+	164.2	1,122	12,426
5679	19-Sep-2019	29-Sep-2019	Yes	Yes	Male	E4	9.9	91	515
5701**	19-Sep-2019	-	Yes	No	Male	A+	-	-	-
5742	19-Sep-2019	23-Jan-2020	Yes	No	Male	A-	125.2	834	5,174
5743***	20-Sep-2019	15-Oct-2019	No	Yes	Male	A-	24.0	208	1,054
5803	20-Sep-2019	2-Nov-2019	No	Yes	Unknown	-	42.1	245	2,148
5826	20-Sep-2019	6-Nov-2019	Yes	Yes	Male	A-	46.7	307	3,345
5840	21-Sep-2019	29-Dec-2019	Yes	Yes	Female	E10	99.1	483	7,550
5921	24-Sep-2019	21-Dec-2019	Yes	No	Male	A+	87.9	490	4,909
10820	24-Sep-2019	21-Oct-2019	Yes	No	Female	A+	26.8	236	1,472
10823	24-Sep-2019	4-Nov-2019	Yes	Yes	Female	A-	40.8	233	1,286
10826	24-Sep-2019	29-Sep-2019	Yes	Yes	Male	E4	4.2	44	171
10827	30-Sep-2019	26-Oct-2019	Yes	Yes	Male	A+	25.4	238	1,147
10830	30-Sep-2019	14-Nov-2019	No	Yes	Unknown	-	44.8	319	2,385
10833	5-Oct-2019	14-Nov-2019	Yes	Yes	Male	A+	40.0	299	1,417
10838	5-Oct-2019	30-Oct-2019	Yes	Yes	Male	A+	24.4	129	903
10840	5-Oct-2019	1-Nov-2019	No	Yes	Unknown	-	26.2	244	896
10842	5-Oct-2019	24-Oct-2019	Yes	Yes	Female	A+	18.7	181	861
23031	5-Oct-2019	20-Nov-2019	Yes	Yes	Female	E4	45.6	397	1,621
23038	7-Oct-2019	8-Nov-2019	Yes	Yes	Male	E4	32.2	195	1,312
23043**	7-Oct-2019	-	No	Yes	Unknown	-	-	-	-
Mean							**46.8**	**318**	**2,553**
Median							**36.1**	**241**	**1,445**

KEY: # = number; * tags are reported here with just their tag number rather than the full nomenclature to save space in the table; ** these tags did not provide any location and are not included in calculation of summary statistics; *** this represents a re-tagging of a whale tagged in Washington in 2018 (whale 2018WA-4177).

Table 5. Responses to tagging and/or biopsy darting by humpback whales tagged and biopsy sampled in Washington in 2019.

Response	Number of whales
Tagging/biopsy darting	
No response	7
Strong tail flick	5
Medium tail flick	5
Mild tail flick	4
Fast dive	3
Biopsy darting alone	
No response	10

Table 6. Resight information and tag site descriptions for humpback whales tagged off Washington, Oregon, and California from 2004 to 2019. Wound size estimates are approximate.

Tag # (Sex)	Tagging Date	Resighting Dates	Resight Location (Source)	# Days Post-Tagging	Tag Present/ Tag Transmitting	Body Condition	Tag Site Condition
2019WA-5679 (Male)	9/19/19	9/24/19	NW of Cape Flattery (OSU)	5	Yes/Yes	Good	No swelling.
2019WA-10823 (Male)	9/24/19	10/1/19 10/5/19	NW of Cape Flattery (OSU) NW of Cape Flattery (OSU)	7 11	Yes/Yes Yes/Yes	Good Good	Small amount of white tissue. No swelling. White tissue surrounding tag. No swelling
2019WA-833 (Male)	9/24/19	10/2/19	W Strait of Juan de Fuca (OSU)	8	Yes/Yes	Good	No Swelling.
2018WA-4177 (Male)	8/3/18	9/20/19	W Strait of Juan de Fuca (OSU)	413	No/No	Good	Small divot ~ 3-cm diameter and 1-cm deep. No swelling
2018WA-5801 (Male)	8/6/18	9/19/19	NW of Cape Flattery (OSU)	409	No/No	Good	Divot ~10-cm diameter and 2-cm deep. Some skin discoloration. No swelling.
2018WA-5838 (Male)	8/6/18	9/19/19	NW of Cape Flattery (OSU)	409	No/No	Good	Slight bump ~5-cm diameter and 2-cm high Slight skin discoloration. No swelling.
2018WA-5883 (Female)	8/7/18	9/14/18	Clallam Bay (Jeff Harris)	38	Yes/No	Good	Small divot ~4-cm diameter and 2-cm deep with some white tissue visible. No Swelling.
2018WA-10839 (Female)	8/10/18	9/30/19 10/5/19	W Strait of Juan de Fuca (OSU)	416 421	No/No No/No	Good Good	Divot ~4-cm diameter and 2-cm deep. Some skin discoloration. No swelling.

2018WA-23029 (Female)	8/10/18	9/2/18	San Juan Island (Erin Johns Gless)	23	No/No	Good	Red tissue ~8-cm diameter around tag. No divot and no swelling.
2018WA-23029 (Female)	8/10/18	10/1/19	Cape Flattery (OSU)	417	No/No	Good	Divot ~8-cm diameter and 1-cm deep. No swelling
2018WA-5654 (Unknown)	8/12/18	8/13/18 8/14/18	W Strait of Juan de Fuca (OSU W Strait of Juan de Fuca (OSU)	1 2	Yes/Yes Yes/Yes	Good Good	Area of rough skin around tag site ~5-cm diameter.
2018WA-5654 (Unknown)	8/12/18	9/14/18 10/19/18 10/24/18	Clallam Bay (Jeff Harris) Race Rocks (Althea Leddy) Race Rocks (Selena Rhodes Scofield)	33 68 73	Yes/No Yes/No Yes/No	Good Good Good	Divot ~20-cm diameter and 4-cm deep. No swelling
2018WA-5700 (Female)	8/13/18	8/16/18	W Strait of Juan de Fuca OSU	3	Yes/Yes	Good	Some rough skin around tag ~4-cm diameter. No swelling.
2018WA-5700 (Female)	8/13/18	9/19/19	W Strait of Juan de Fuca (OSU)	402	No/No	Good	Deep divot ~25-cm diameter and 8-cm deep. No swelling.
2018WA-5709 (Male)	8/13/18	9/19/19	NW of Cape Flattery (OSU)	402	No/No	Good	Divot ~10-cm diameter and 3-cm deep. No swelling.
2018WA-5790 (Male)	8/14/18	9/19/18	Port Angeles (Erin Johns Gless)	36	Yes/Yes	Good	Tag surrounded by divot ~20-cm diameter and 5-cm deep. No swelling.
2018WA-5823	8/17/18	8/20/18	W Strait of Juan de Fuca (OSU)	3	Yes/Yes	Good	Some rough skin within ~5-cm diameter around tag. No swelling.
2018WA-5923 (Male)	8/18/18	9/14/18	Clallam Bay (Jeff Harris)	27	Yes/Yes	Good	Drone footage shows red area ~10-cm wide near tag, but not surrounding tag. No swelling obvious from photo.

KEY: NW = northwest; W = west; # = number.

Table 7. Percentage of filtered locations (including the deployment location) and time spent inside the NWTT and W237 areas for humpback whales tagged off Washington in 2019. See Section 2.3.1 for location filtering method.

Tag #	Total		NWTT			W237			PT MUGU			SOCAL		
	# Locs	# Days	% Locs	% of Days	# Days	% Locs	% of Days	# Days	% Locs	% of Days	# Days	% Locs	% of Days	# Days
833	181	19.9	74.0	70.2	14.0	3.3	2.7	0.5	0	0	0	0	0	0
4173	225	30.9	99.6	99.9	30.8	60.9	67.8	20.9	0	0	0	0	0	0
5670	297	51.2	94.9	96.0	49.2	54.2	56.6	29.0	0	0	0	0	0	0
5678	1123	164.2	18.8	26.0	42.6	12.2	17.5	28.7	3.7	3.6	5.8	1.3	2.7	4.4
5679	92	9.9	91.3	90.7	9.0	45.7	41.3	4.1	0	0	0	0	0	0
5742	835	125.2	39.6	34.1	42.7	33.1	30.0	37.6	0	0	0	0	0	0
5743	209	24.0	96.7	97.7	23.5	88.0	91.1	21.9	0	0	0	0	0	0
5803	246	42.1	96.3	95.8	40.3	89.8	89.4	37.6	0	0	0	0	0	0
5826	308	46.7	39.9	33.0	15.4	1.0	1.2	0.6	0	0	0	0	0	0
5840	484	99.1	68.2	71.3	70.7	43.4	47.7	47.3	2.3	2.3	2.3	2.5	2.3	2.3
5921	491	87.9	98.0	98.6	86.6	70.9	74.5	65.4	0	0	0	0	0	0
10820	237	26.8	73.8	76.7	20.5	31.2	36.0	9.6	0	0	0	0	0	0
10823	234	40.8	46.2	33.2	13.5	0	0	0	0	0	0	0	0	0
10826	45	4.2	64.4	66.6	2.8	0	0	0	0	0	0	0	0	0
10827	239	25.4	50.6	54.3	13.8	28.9	31.0	7.9	0	0	0	0	0	0
10830	320	44.8	97.2	98.9	44.3	77.8	74.7	33.5	0	0	0	0	0	0
10833	300	40.0	22.3	23.6	9.4	0	0	0	0	0	0	0	0	0
10838	130	24.4	66.9	80.0	19.5	36.9	65.7	16.0	0	0	0	0	0	0
10840	245	26.2	28.2	30.0	7.9	0	0	0	0	0	0	0	0	0
10842	182	18.7	94.5	96.5	18.0	58.2	61.0	11.4	0	0	0	0	0	0
23031	398	45.6	85.4	85.6	39.1	8.0	8.3	3.8	0	0	0	0	0	0
23038	196	32.2	54.6	70.4	22.7	27.0	44.4	14.3	0	0	0	0	0	0
Mean	**319**	**46.8**	**68.3**	**69.5**	**28.9**	**42.8**	**46.7**	**21.7**	**3.0**	**2.9**	**4.1**	**1.9**	**2.5**	**3.3**
Median	**242**	**36.1**	**71.0**	**74.0**	**21.6**	**40.2**	**46.1**	**18.5**	**3.0**	**2.9**	**4.1**	**1.9**	**2.5**	**3.3**

KEY: Locs = Locations; # = number; % = percentage.

Table 8. Geodesic distances (km) to nearest point on shore in Navy training ranges for humpback whales tagged off Washington in 2019 (including mean, standard deviation [SD], and maximum [Max] distance to shore). The number of locations includes filtered locations (see Section 2.3.1 for filtering method) plus deployment location (when the deployment location occurred in a Navy range).

Tag #	NWTT				W237				PT MUGU				SOCAL			
	n	Mean	SD	Max	n	Mean	SD	Max	n	Mean	SD	Max	n	Mean	SD	Max
833	128	17	6	30	6	30	2	33	0	-	-	-	0	-	-	-
4173	87	40	18	77	137	43	13	65	0	-	-	-	0	-	-	-
5670	121	43	17	88	161	49	12	91	0	-	-	-	0	-	-	-
5678	74	40	21	125	137	56	13	79	42	114	46	182	15	118	53	189
5679	42	19	9	37	42	60	17	81	0	-	-	-	0	-	-	-
5742	55	17	8	57	276	66	16	89	0	-	-	-	0	-	-	-
5743	18	22	10	39	184	68	10	81	0	-	-	-	0	-	-	-
5803	16	28	15	61	221	70	11	90	0	-	-	-	0	-	-	-
5826	120	18	5	29	3	32	6	38	0	-	-	-	0	-	-	-
5840	120	54	35	171	210	47	15	101	11	61	16	84	12	112	23	140
5921	133	44	51	381	348	52	40	319	0	-	-	-	0	-	-	-
10820	101	18	6	31	74	57	18	87	0	-	-	-	0	-	-	-
10823	108	17	4	28	0	-	-	-	0	-	-	-	0	-	-	-
10826	29	18	3	24	0	-	-	-	0	-	-	-	0	-	-	-
10827	52	17	5	31	69	55	8	76	0	-	-	-	0	-	-	-
10830	63	22	6	36	249	54	19	100	0	-	-	-	0	-	-	-
10833	67	16	4	26	0	-	-	-	0	-	-	-	0	-	-	-
10838	39	21	12	55	48	59	11	92	0	-	-	-	0	-	-	-
10840	69	16	3	26	0	-	-	-	0	-	-	-	0	-	-	-
10842	66	18	14	61	106	65	18	93	0	-	-	-	0	-	-	-
23031	308	18	5	30	32	41	6	53	0	-	-	-	0	-	-	-
23038	54	15	4	27	53	63	13	85	0	-	-	-	0	-	-	-
Mean	**85**	**24.4**		**66.8**	**131.0**	**53.7**		**91.8**	**26**	**87.5**		**133.0**	**13**	**115.0**		**164.5**
SD	**61**	**11.6**		**79.1**	**100**	**11.6**		**59.9**	**22**	**37.5**		**69.3**	**2**	**4.2**		**34.6**

KEY: n = number of locations (sample size) within the area; # = number.

Table 9. Percentage of filtered locations (including the deployment location) and time spent inside humpback whale Biologically Important Areas (BIAs) for humpback whales tagged off Washington in 2019. See Section 2.3.1 for location filtering method.

Tag #	Total		Northern WA			Stonewall-Heceta			Morro Bay			Santa Barbara		
	# Locs	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days
833	181	19.9	63.0	63.3	12.6	-	-	-	-	-	-	-	-	-
4173	225	30.9	13.3	8.7	2.7	-	-	-	-	-	-	-	-	-
5670	297	51.2	11.4	8.4	4.3	-	-	-	-	-	-	-	-	-
5678	1123	164.2	5.7	7.5	12.3	0.2	0.2	0.4	0	0.1	0.1	0.4	0.2	0.3
5679	92	9.9	52.2	57.5	5.7	-	-	-	-	-	-	-	-	-
5742	835	125.2	28.0	23.4	29.3	-	-	-	-	-	-			
5743	209	24.0	71.3	77.3	18.6	-	-	-	-	-	-	-	-	-
5803	246	42.1	52.4	50.9	21.4	-	-	-	-	-	-	-	-	-
5826	308	46.7	36.0	29.	13.7	-	-	-	-	-	-	-	-	-
5840	484	99.1	26.4	29.9	29.7	0.2	0.2	0.2	-	-	-	-	-	-
5921	491	87.9	36.3	31.6	27.7	-	-	-	-	-	-	-	-	-
10820	237	26.8	65.8	63.2	16.9	-	-	-	-	-	-	-	-	-
10823	234	40.8	47.0	36.7	15.0	-	-	-	-	-	-	-	-	-
10826	45	4.2	71.1	71.8	3.0	-	-	-	-	-	-	-	-	-
10827	239	25.4	46.4	51.6	13.1	-	-	-	-	-	-	-	-	-
10830	320	44.8	82.8	89.4	40.1	-	-	-	-	-	-	-	-	-
10833	300	40.0	26.7	25.6	10.2	-	-	-	-	-	-	-	-	-
10838	130	24.4	50.0	55.6	13.5	-	-	-	-	-	-	-	-	-
10840	245	26.2	31.4	33.2	8.7	-	-	-	-	-	-	-	-	-
10842	182	18.7	46.2	46.0	8.6	-	-	-	-	-	-	-	-	-
23031	398	45.6	78.9	81.8	37.3	-	-	-	-	-	-	-	-	-
23038	196	32.2	29.6	23.1	7.4	-	-	-	-	-	-	-	-	-
Mean	**319**	**46.8**	**44.2**	**43.9**	**16.0**	**0.2**	**0.2**	**0.3**	-	-	-	-	-	-
Median	**242**	**36.1**	**46.3**	**41.4**	**13.3**	**0.2**	**0.2**	**0.3**	-	-	-	-	-	-

KEY: Locs = Locations; # = number; % = percentage.

Table 10. Percentage of filtered locations (including the deployment location) and time spent inside National Marine Sanctuaries for humpback whales tagged off Washington in 2019. See Section 2.3.1 for location filtering method.

Tag #	Total		Olympic Coast			Monterey Bay			Channel Islands		
	# Locs	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days	% Locs	% Days	# Days
833	181	19.9	72.9	77.4	15.4	-	-	-	-	-	-
4173	225	30.9	44.9	38.3	11.8	-	-	-	-	-	-
5670	297	51.2	32.7	28.6	14.7	-	-	-	-	-	-
5678	1123	164.2	7.2	10.2	16.8	1.1	1.1	1.8	0.3	0.1	0.2
5679	92	9.9	45.7	48.9	4.8	-	-	-	-	-	-
5742	835	125.2	16.4	10.8	13.5	-	-	-	-	-	-
5743	209	24.0	37.8	39.1	9.4	-	-	-	-	-	-
5803	246	42.1	23.2	18.1	7.6	-	-	-	-	-	-
5826	308	46.7	38.6	31.9	14.9	-	-	-	-	-	-
5840	484	99.1	32.0	34.9	34.5	0.4	0.2	0.2	-	-	-
5921	491	87.9	62.1	56.7	49.8	-	-	-	-	-	-
10820	237	26.8	62.0	60.5	16.2	-	-	-	-	-	-
10823	234	40.8	47.4	36.5	14.9	-	-	-	-	-	-
10826	45	4.2	71.1	71.3	3.0	-	-	-	-	-	-
10827	239	25.4	47.3	51.3	13.0	-	-	-	-	-	-
10830	320	44.8	74.1	82.1	36.8	-	-	-	-	-	-
10833	300	40.0	27.7	26.1	10.4	-	-	-	-	-	-
10838	130	24.4	48.5	40.8	9.9	-	-	-	-	-	-
10840	245	26.2	32.2	33.5	8.8	-	-	-	-	-	-
10842	182	18.7	47.3	45.3	8.5	-	-	-	-	-	-
23031	398	45.6	84.9	86.7	39.6	-	-	-	-	-	-
23038	196	32.2	35.2	25.6	8.2	-	-	-	-	-	-
Mean	**319**	**46.8**	**45.1**	**43.4**	**16.5**	**0.7**	**0.7**	**1.0**	-	-	-
Median	**242**	**36.1**	**45.3**	**38.7**	**13.3**	**0.7**	**0.7**	**1.0**	-	-	-

KEY: Locs = Locations; # = number; % = percentage.

Table 11. Sizes of HRs and CAUs calculated from hierarchical state-space modeled (hSSSM) locations for humpback whales tagged off Washington in 2019. In the sex column, unknown sex whales are cases where no biopsy sample was collected. hSSSM locations were calculated at three per day.

Tag #	# hSSSM Locations	Sex	HR Size (km²)	CAU Size (km²)
4173	93	Female	2,093	313
5670	154	Male	3,207	638
5678	262	Female	5,910	515
5742	364	Male	17,379	1,941
5803	127	Unknown	1,344	267
5826	141	Male	624	148
5840	186	Female	4,066	460
5921	250	Male	6,276	993
10823	123	Female	181	41
10830	135	Unknown	2,781	645
10833	120	Male	172	32
23031	138	Female	627	161
Mean (SD)			3,722 (4,784)	513 (532)

KEY: # = number.

Table 12. Mean (and SD) tracking duration, total distance traveled, home range, and core area for 80 humpback whales tagged by OSU off southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA) from 2016 to 2018. Tracking results from the recoverable ADB tag deployed off Washington in 2018 are not included here because that tag was programmed to release from the whale after two weeks. SD in the final row represents the SD of the overall mean for all three regions.

Region	Tracking Duration (d)			Total Distance (km)			Home Range (km^2)			Core Area (km^2)		
	n	Mean	SD	n	Mean	SE*	n	Mean	SD	n	Mean	SD
NWA	41	40.4	33.6	41	1,382.1	1.07	21	3,346	3,622	21	494	416
NCA/OR	15	40.5	38.2	15	1,377.4	1.12	8	18,352	21,777	8	2,449	2,965
SCCA	24	37.0	32.1	24	1,027.8	1.02	12	17,069	30,338	12	2,348	2,734
All Regions	**80**	**39.3**	**2.0**	**80**	**1,262.4**	**1.07**	**41**	**12,922**	**8,318.1**	**41**	**1,763.7**	**1,100.7**

KEY: n = number of whales (sample size); # = number; * = standard error is reported for the results of the general linear model used to test for differences in total distance between tagging regions after accounting for tracking duration

Table 13. Mean and maximum (Max) number of days spent inside the NWTT, W237, PT MUGU, SOCAL, and SOAR areas for 81 humpback whales tagged off southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA), from 2004 to 2019. Area W237 is located within area NWTT, so whale occurrence in W237 is also counted as occurrence in NWTT, as the two areas were analyzed separately.

	# Days														
Region (n Whales Tracked)	**NWTT**			**W237**			**PT MUGU**			**SOCAL**			**SOAR**		
	n	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**
NWA (42)	42	20.3	86.6	37	12.7	65.4	2	4.0	5.8	2	3.3	4.4	0	-	-
NCA/OR (15)	14	18.3	86.6	1	14.3	14.3	2	4.3	6.1	2	1.8	1.8	1	0.4	0.4
SCCA (24)	3	11.4	28.4	0	-	-	3	21.9	33.8	1	2.8	2.8	0	-	-
All Regions (81)	**59**	**16.7**	**86.6**	**38**	**13.5**	**65.4**	**7**	**10.1**	**33.8**	**5**	**2.6**	**4.4**	**1**	**0.4**	**0.4**

KEY: n = number of whales (sample size)

Table 14. Geodesic distances (km) to nearest point on shore in Navy training ranges for humpback whales tagged off southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington from 2004 to 2019 (including mean of individual means and overall maximum [Max] distances to shore).

Region (n Whales Tracked)	NWTT			W237			PT MUGU			SOCAL			SOAR		
	n	Mean	Max	n	Mean	Max	n	Mean	Max	n	Mean	Max	n	Mean	Max
NWA (42)	42	22	381	37	50	319	2	88	182	2	115	189	0	-	-
NCA/OR (15)	14	44	183	1	73	175	2	36	86	1	317	385	0	-	-
SCCA (24)	3	55	201	0	-	-	3	42	106	1	95	115	0	-	-
All Regions (81)	**59**	**40**	**381**	**38**	**62**	**319**	**7**	**55**	**182**	**4**	**176**	**385**	**0**	**-**	**-**

KEY: n = number of whales (sample size).

Table 15. Mean and maximum (Max) number of days spent inside the West Coast BIAs for 81 humpback whales tagged off southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA) from 2004 to 2019.

	# Days																				
Region (n tracked)	**Northern Washington**			**Stonewall and Heceta Bank**			**Point St. George**			**Fort Bragg to Point Arena**			**Gulf of the Farallones - Monterey Bay**			**Morro Bay to Point Sal**			**Santa Barbara Channel -San Miguel**		
	n	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**
NWA (42)	41	11.7	40.1	2	0.3	0.4	0	-	-	0	-	-	0	-	-	1	0.1	0.1	1	0.3	0.3
NCA/OR (15)	1	7.4	7.4	8	3.9	9.9	9	3.9	11.3	2	1.8	2.2	3	4.6	5.7	1	3.7	3.7	2	0.3	0.4
SCCA (24)	0	-	-	1	0.7	0.7	1	0.4	0.4	5	2.7	4.5	23	24.5	71.6	3	7.8	11.7	1	3.3	3.3
All Regions (81)	**42**	**9.6**	**40.1**	**11**	**1.6**	**9.9**	**10**	**2.2**	**11.3**	**7**	**2.3**	**4.5**	**26**	**14.6**	**71.6**	**5**	**3.9**	**11.7**	**4**	**1.3**	**3.3**

KEY: n = number of whales (sample size).

Table 16. Mean and maximum (Max) number of days spent inside the West Coast National Marine Sanctuaries for 81 humpback whales tagged off southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA) from 2004 to 2019.

	# Days														
Region (n Whales Tracked)	**Olympic Coast**			**Greater Farallones**			**Cordell Bank**			**Monterey Bay**			**Channel Islands**		
	n	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**	**n**	**Mean**	**Max**
NWA (42)	42	12.6	49.8	0	-	-	0	-	-	2	1.0	1.8	1	0.2	0.2
NCA/OR (15)	1	8.6	8.6	4	3.4	8.6	3	1.7	2.9	2	6.1	8.8	2	0.4	0.4
SCCA (24)	0	-	-	20	11.9	35.2	15	9.7	42.7	8	19.1	45.3	1	0.1	0.1
All Regions (81)	**43**	**10.6**	**49.8**	**24**	**7.7**	**35.2**	**18**	**5.7**	**42.7**	**12**	**8.7**	**45.3**	**4**	**0.2**	**0.4**

KEY: n = number of whales (sample size).

Table 17. Dive data summarized by 64 DM, DUR, and DUR+ tags and one ADB tag deployed on humpback whales in the southern and central California (SCCA), northern California/Oregon (NCA/OR), and northern Washington (NWA) tagging regions during August to October 2016-2019.

Tag #	Year	Region	TagType	Summary period (days)	# Dives	% Track summarized	% Near surface	Mean dives per day	Minimum dives per day	Maximum dives per day
830	2017	SCCA	DUR	33	2019	35.3	-	59.4	7	100
833	2017	SCCA	DM	14.2	1476	57.1	74.1	98.4	19	188
834	2017	SCCA	DUR	78.8	4914	38.4	-	62.2	4	181
838	2017	SCCA	DM	1.9	195	67.4	85.7	65	20	139
848	2017	SCCA	DM	2.9	369	87.2	65	92.2	19	142
1389	2017	SCCA	DUR	50.4	2452	25	-	50	8	117
1390	2017	SCCA	DUR	68.5	3282	27.6	-	46.9	7	96
4173	2017	SCCA	DM	8.9	997	56.9	72.8	110.8	56	146
4175	2017	SCCA	DM	51.4	2985	40.3	65.2	67.8	1	160
10822	2017	SCCA	DUR	76.8	1003	6.7	-	25.1	9	86
10842	2017	SCCA	DUR	38.6	2853	44	-	73.2	26	153
23038	2017	SCCA	DUR	26.9	2205	53.5	-	78.8	9	168
			Median	**35.8**	**2112.0**	**42.2**	**72.8**	**66.4**	**9.0**	**144.0**
5838	2016	NCA/OR	DM	7.2	551	72.1	76.8	68.9	31	105
5923	2016	NCA/OR	DM	18.8	1090	46.9	78	64.1	4	128
1387	2017	NCA/OR	DUR	149.8	6156	23.6	-	42.5	9	137
4174	2017	NCA/OR	DUR	31.1	2152	61.5	-	67.2	9	131
10838	2017	NCA/OR	DUR	32.2	3296	55	-	99.9	21	191
23034	2017	NCA/OR	DUR	32.3	1784	37.2	-	54.1	21	108
10834	2018	NCA/OR	DUR+	18	2356	85.1	-	124	31	203
23030	2018	NCA/OR	DUR+	16.1	1522	76.3	-	89.5	26	143
23032	2018	NCA/OR	DUR+	12.3	1745	100	-	124.6	9	171
23035	2018	NCA/OR	DUR+	60.1	7135	89.4	-	118.9	4	200
23041	2018	NCA/OR	DUR+	9.1	1263	100	-	114.8	9	178
			Median	**18.8**	**1784.0**	**72.1**	**77.4**	**89.5**	**9.0**	**143.0**

Tag #	Year	Region	TagType	Summary period (days)	# Dives	% Track summarized	% Near surface	Mean dives per day	Minimum dives per day	Maximum dives per day
4177	2018	NWA	DM	12.4	320	22.5	87.1	24.6	10	45
5640	2018	NWA	DUR+	39.2	5418	97.8	-	132.1	4	202
5650	2018	NWA	DUR+	13.2	1712	100	-	122.3	40	170
5654	2018	NWA	DUR+	44.9	5293	85.2	-	115.1	30	177
5700	2018	NWA	DUR+	38.7	5069	84.6	-	126.7	19	187
5709	2018	NWA	DUR+	16.4	2088	100	-	116	20	168
5719	2018	NWA	DUR+	13.8	1650	95.8	-	110	32	174
5726	2018	NWA	DUR+	25.2	2912	73.4	-	107.9	9	166
5790	2018	NWA	DUR+	110.5	3492	30.9	-	85.2	1	144
5801	2018	NWA	DM	17	1609	96.8	75.2	89.4	21	154
5823	2018	NWA	DUR+	73.7	7107	67.3	-	103	6	211
5838	2018	NWA	DM	30.6	2555	77.7	71.3	79.8	2	134
5883	2018	NWA	DM	15	1726	100	69.3	107.9	33	144
5923	2018	NWA	DUR+	33.8	4718	100	-	134.8	20	172
10825	2018	NWA	DM	51.9	4648	91.7	68.3	87.7	20	143
10836	2018	NWA	DM	19	2277	85.2	69.9	113.8	7	179
10839	2018	NWA	DM	35.3	3039	78.6	67.1	82.1	3	139
23029	2018	NWA	DM	28.4	3017	90	64.8	100.6	16	156
23033	2018	NWA	DM	6.3	448	90.3	72	56	3	93
23039	2018	NWA	DM	11.3	1306	93	69.3	100.5	15	133
833	2019	NWA	DM	19.9	1818	80.8	59.9	86.6	36	143
4173	2019	NWA	DM	31.2	3260	72.6	52.7	101.9	30	160
5670	2019	NWA	DM	51.2	5162	67.7	50.4	99.3	26	184
5678	2019	NWA	DM	153.1	12349	77.6	68.6	80.2	7	135
5679	2019	NWA	DM	9.3	734	69	49	73.4	17	122
5742	2019	NWA	DM	129	9585	60.5	56.9	75.5	6	147
5743	2019	NWA	DM	29.3	2296	90.6	75.2	88.3	10	140

Tag #	Year	Region	TagType	Summary period (days)	# Dives	% Track summarized	% Near surface	Mean dives per day	Minimum dives per day	Maximum dives per day
5803	2019	NWA	DM	44	3441	71.5	68.7	80	8	140
5826	2019	NWA	DM	46.7	3819	50.1	46.5	81.3	5	161
5840	2019	NWA	DM	100	7175	71.1	71.9	71.8	1	160
5921	2019	NWA	DM	86.8	7622	63.7	71.4	86.6	5	144
10820	2019	NWA	DM	26.4	1822	60.9	58.8	65.1	13	117
10823	2019	NWA	DM	40.8	4124	64.9	32.3	98.2	16	159
10826	2019	NWA	DM	3.8	542	88.1	56.7	108.4	15	147
10827	2019	NWA	DM	25.3	1711	66.2	61.7	63.4	9	128
10830	2019	NWA	DM	44.7	3887	70.4	57.1	84.5	9	164
10833	2019	NWA	DM	39.8	3573	54.1	53.2	87.1	27	156
10838	2019	NWA	DM	28.1	1812	55	67.5	90.6	1	167
10840	2019	NWA	DM	26.1	1996	48.5	47	71.3	2	136
10842	2019	NWA	DM	18.6	1585	57.6	47.5	79.2	10	141
23031	2019	NWA	DM	45.6	2971	60.1	57.3	64.6	4	128
23038	2019	NWA	DM	40.6	2403	37.7	50.8	89	2	157
		Median2018		**26.8**	**2733.5**	**90.2**	**69.6**	**105.5**	**15.5**	**161.0**
		Median2019		**40.2**	**3115.5**	**65.6**	**57.0**	**82.9**	**9.0**	**145.5**
		Median All WA		**30.9**	**2941.5**	**73.0**	**63.3**	**88.0**	**10.0**	**150.5**

KEY: # = number; % = percent.

Table 18. Summary of the number of tracks used in SSSM/hSSSM analyses, the number of generated locations, and the geographic extent covered by the modeled locations for each tagging year/season (CA = California, OR = Oregon, WA = Washington) and for each tagging region (SCCA = southern and central California, NCA/OR = northern California/Oregon, NWA = northern Washington). The migrating portions of tracks, as well as locations that occurred on land and those with high estimation uncertainty were removed prior to analysis.

Season	Number of tags	Number of locations	Minimum longitude	Maximum longitude	Minimum latitude	Maximum latitude
2004CA	6	253	-124.9	-120.7	34.9	42.9
2005CA	3	92	-124.5	-120.9	34.3	40.7
2005NCA/OR	3	91	-125.4	-123.9	39.6	42.8
2016OR	2	25	-124.8	-124.2	40.7	44.6
2017CA	13	476	-126.5	-119.7	34.3	45.1
2017OR	4	198	-126.4	-123.9	38.5	48.7
2018OR	5	115	-124.8	-124.1	40.9	46.2
2018WA	20	565	-128.3	-123.4	45.8	50.2
2019WA	22	881	-129.6	-124.2	45.7	51.3
Region	**Number of tags**	**Number of locations**	**Minimum longitude**	**Maximum longitude**	**Minimum latitude**	**Maximum latitude**
SCCA	21	814	-126.5	-119.7	34.3	45.1
NCA/OR	15	436	-126.4	-123.1	37.7	48.7
NWA	42	1446	-129.6	-123.4	45.7	51.3
Total	**78**	**2607**	**-129.6**	**-119.7**	**34.3**	**51.3**

Table 19. Summary of the number of SSSM/hSSSM locations with their behavioral classification, and the percentage of the total (%), for each tagging year/season (CA = California, OR = Oregon, WA = Washington) and **for each tagging region (SCCA = southern and central California, NCA/OR = northern California/Oregon, NWA = northern Washington). The migrating portions of tracks, as well as locations that occurred on land and those with high estimation uncertainty were removed prior to analysis.**

	Total		Transiting		Uncertain		ARS	
Season	**# tags**	**# locs**	**# locs**	**% locs**	**# locs**	**% locs**	**# locs**	**% locs**
2004CA	6	253	1	0.4	33	13.0	219	86.6
2005CA	3	92	1	1.1	9	9.8	82	89.1
2005NCA/OR	3	91	5	5.5	32	35.2	54	59.3
2016OR	2	25	0	0.0	25	100.0	0	0.0
2017CA	13	476	31	6.5	31	6.5	414	87.0
2017OR	4	198	13	6.6	46	23.2	139	70.2
2018OR	5	115	11	9.6	14	12.2	90	78.3
2018WA	20	565	17	3.0	32	5.7	516	91.3
2019WA	22	881	22	2.5	43	4.9	816	92.6
Region	**# tags**	**# locs**	**# locs**	**% locs**	**# locs**	**% locs**	**# locs**	**% locs**
SCCA	21	814	33	4.1	69	8.5	712	87.5
NCA/OR	15	436	29	6.7	121	27.8	286	65.6
NWA	42	1446	39	2.7	75	5.2	1332	92.1
Total	**78**	**2696**	**101**	**3.7**	**265**	**9.8**	**2330**	**86.4**

KEY: locs = locations; # = number; % = percentage.

Table 20. Summary statistics (median and MAD) for PWDIST and PWSPEED computed for the SSSM/hSSSM locations in each tagging region (SCCA = southern and central California, NCA/OR = northern California/Oregon, NWA = northern Washington). The total number of modeled locations (ARS mode only) and the number of locations available for the calculations are given. The migrating portions of tracks, as well as locations that occurred on land and those with high estimation uncertainty were removed prior to analysis.

	Total		PWDIST (km)			PWSPEED (km/h)		
Region	**# tags**	**# locs**	**# locs**	**Median**	**MAD**	**# locs**	**Median**	**MAD**
SCCA	18	712	699	16.21	12.96	699	0.68	0.54
NCA/OR	13	286	280	16.50	13.21	280	0.69	0.55
NWA	42	1332	1291	10.66	8.89	1291	0.44	0.37
Total	**73**	**2330**	**2270**	**12.90**	**10.80**	**2270**	**0.54**	**0.45**

KEY: locs = locations; MAD = median absolute deviation; # = number.

Table 21. Summary statistics (median and MAD) for the seafloor relief variables obtained for the SSSM/hSSSM locations in each tagging region (SCCA = southern and central California, NCA/OR = northern California/Oregon, NWA = northern Washington). The total number of modeled locations (ARS mode only) and the number of locations that received an annotated value for the different variables are given. The migrating portions of tracks, as well as locations that occurred on land and those with high estimation uncertainty were removed prior to analysis.

	Total		DEPTH (m)			SLOPE (deg)			ASPECT (deg)			DISTSHELF (km)			DISTSHORE (km)		
Region	**# tags**	**# locs**	**# locs**	**Median**	**MAD**	**# locs**	**Median**	**MAD**	**# locs**	**Median**	**MAD**	**# locs**	**Median**	**MAD**	**# locs**	**Median**	**MAD**
SCCA	18	712	698	115	68.20	698	0.51	0.60	698	233.84	31.07	698	8.00	9.09	698	27.64	15.50
NCA/OR	13	286	284	152	57.08	284	0.58	0.58	284	268.19	40.31	284	4.88	4.79	284	33.26	16.26
NWA	42	1332	1324	183	83.03	1324	0.97	0.98	1324	195.05	64.99	1324	2.74	2.54	1315	18.97	18.95
Total	**73**	**2330**	**2306**	**162**	**91.92**	**2306**	**0.76**	**0.84**	**2306**	**220.85**	**60.86**	**2306**	**3.75**	**3.79**	**2297**	**24.79**	**21.02**

KEY: locs = locations; MAD = median absolute deviation; # = number.

Table 22. Summary statistics (median and MAD) for the remotely sensed oceanographic variables obtained for the SSSM/hSSSM locations in each tagging region (SCCA = southern and central California, NCA/OR = northern California/Oregon, NWA = northern Washington). The total number of modeled locations (ARS mode only) and the number of locations that received an annotated value for the different variables are given. The migrating portions of tracks, as well as locations that occurred on land and those with high estimation uncertainty were removed prior to analysis.

	Total		SST (°C)			SSTG (°C/deg)			CHL (mg/m³)		
Region	**# tags**	**# locs**	**# locs**	**Median**	**MAD**	**# locs**	**Median**	**MAD**	**# locs**	**Median**	**MAD**
SCCA	18	712	712	15.01	1.22	712	0.19	0.10	661	1.52	1.44
NCA/OR	13	286	286	12.65	1.53	286	0.18	0.11	282	1.16	0.77
NWA	42	1332	1317	12.19	1.48	1317	0.15	0.10	1233	1.91	1.60
Total	**73**	**2330**	**2315**	**12.97**	**2.18**	**2315**	**0.17**	**0.11**	**2176**	**1.74**	**1.52**

KEY: locs = locations; MAD = median absolute deviation; °C = degrees Celsius; # = number.

Table 23. Results of the robust (heteroscedastic) one-way ANOVA tests for global differences between tagging regions (southern and central California, northern California/Oregon, and northern Washington) for variables describing movement behavior (PWDIST, PWSEED) as well as the underlying static (DEPTH, SLOPE, ASPECT, DISTSHELF, DISTSHORE) and dynamic (SST, SSTG, CHL) environmental conditions associated with SSSM/hSSSM locations in ARS mode only. All variables except ASPECT and SST were log-transformed prior to analysis. These multiple-group comparisons were based on trimmed means (20 percent trimming level) and effect size based on Yuen's test, as implemented in R package *WRS2* (Mair and Wilcox 2020).

Variable	*F*-statistic	df1‡	df2‡	*p*-value	Effect size†
PWDIST	55.51	2	444.27	< 0.001	0.28
PWSPEED	55.51	2	444.27	< 0.001	0.29
DEPTH	61.16	2	406.54	< 0.001	0.33
SLOPE	41.79	2	446.17	< 0.001	0.23
ASPECT	255.89	2	495.74	< 0.001	0.62
DISTSHELF	156.86	2	434.42	< 0.001	0.44
DISTSHORE	46.52	2	596.59	< 0.001	0.31
SST	956.45	2	453.02	< 0.001	0.73
SSTG	33.46	2	465.26	< 0.001	0.20
CHL	19.17	2	439.21	< 0.001	0.20

Key: †Effect size values of 0.10, 0.30, and 0.50 correspond to thresholds for small, medium, and large effect sizes, respectively. ‡df1 and df2 correspond to the degrees of freedom associated with the test statistic.

Table 24. Results of the robust post-hoc pairwise comparisons between tagging regions (SCCA = southern and central California, NCA/OR = northern California/Oregon, NWA = northern Washington) for variables describing movement behavior (PWDIST, PWSEED) as well as the underlying static (DEPTH, SLOPE, ASPECT, DISTSHELF, DISTSHORE) and dynamic (SST, SSTG, CHL) environmental conditions associated with SSSM/hSSSM locations in ARS mode only. All variables except ASPECT and SST were log-transformed prior to analysis. These post-hoc tests were based on trimmed means (20 percent trimming level) using linear contrasts and Yuen's test with Holm adjustment for multiple *p*-values, as implemented in R package *WRS2* (Mair and Wilcox 2020).

Variable	Group 1	Group 2	$\Psi^{\dagger}$	*p*-value
PWDIST	SCCA	NCA/OR	-0.037	0.587
PWDIST	SCCA	NWA	0.413	< 0.001
PWDIST	NCA/OR	NWA	0.450	< 0.001
PWSPEED	SCCA	NCA/OR	-0.037	0.587
PWSPEED	SCCA	NWA	0.413	< 0.001
PWSPEED	NCA/OR	NWA	0.450	< 0.001
DEPTH	SCCA	NCA/OR	-0.278	< 0.001
DEPTH	SCCA	NWA	-0.384	< 0.001
DEPTH	NCA/OR	NWA	-0.107	0.006
SLOPE	SCCA	NCA/OR	-0.193	0.046
SLOPE	SCCA	NWA	-0.608	< 0.001
SLOPE	NCA/OR	NWA	-0.415	< 0.001
ASPECT	SCCA	NCA/OR	-31.284	< 0.001
ASPECT	SCCA	NWA	39.263	< 0.001
ASPECT	NCA/OR	NWA	70.547	< 0.001
DISTSHELF	SCCA	NCA/OR	0.460	< 0.001
DISTSHELF	SCCA	NWA	1.069	< 0.001
DISTSHELF	NCA/OR	NWA	0.609	< 0.001
DISTSHORE	SCCA	NCA/OR	-0.166	< 0.001
DISTSHORE	SCCA	NWA	0.272	< 0.001
DISTSHORE	NCA/OR	NWA	0.438	< 0.001
SST	SCCA	NCA/OR	2.248	< 0.001
SST	SCCA	NWA	2.862	< 0.001
SST	NCA/OR	NWA	0.614	< 0.001
SSTG	SCCA	NCA/OR	0.040	0.387
SSTG	SCCA	NWA	0.232	< 0.001
SSTG	NCA/OR	NWA	0.192	< 0.001
CHL	SCCA	NCA/OR	0.197	0.014
CHL	SCCA	NWA	-0.198	< 0.001
CHL	NCA/OR	NWA	-0.395	< 0.001

Key: $^{\dagger}\Psi$ = the value of the linear contrast expression used as a post-hoc test for each pairwise comparison.

Table 25. Frequency and identity of 16 mtDNA haplotypes, including GenBank codes, for the 79 whales sampled off southern and central California, northern California and Oregon, and northern Washington during 2016-2019.

Haplotype code	GenBank code	Southern and central California tagging (2017)	Northern California and Oregon tagging (2016-2018)	Northern Washington tagging (2018-2019)
A+	KF477244	-	4	17*
A-	KF477245	-	2	15*
A3	KF477246	-	-	1
E1	KF477249	1	2	3*
E2	KF477256	-	1	-
E4	KF477258	2	2	6*
E5	KF477259	-	-	2
E6	KF477260	-	-	1*
E7	KF477261	-	1	2*
E10	KF477250	-	-	2*
E13	KF477253	1	-	-
E15	KF477255	1	-	-
F1	KF477265	-	1	1
F2	KF477266	3	2	-
F3	KF477271	4	-	-
F6	KF477267	2	-	-
Total		**14**	**15**	**50**

Key: * = haplotypes identified from the 2019 Washington tagging samples.

Table 26. Results of pairwise tests of differentiation of mtDNA haplotype frequencies between the southern and central California, northern California and Oregon, and northern Washington tagging samples and the 18 regional strata (feeding areas and breeding areas) defined in SPLASH (Baker et al. 2013). The sample sizes refer to the number of individuals with associated haplotypes. Rows in italics indicate low sample numbers for comparisons with Western Aleutians and the Philippines.

		Southern and central California tagging n = 14		**Northern California and Oregon tagging n = 15**		**Northern Washington tagging n = 50**	
Population	**n**	**F_{ST}**	***p*-value**	**F_{ST}**	***p*-value**	**F_{ST}**	***p*-value**
Feeding Areas							
Russia (RUS)	70	0.1159	0.0004	0.0473	0.0295	0.1102	<0.0001
Western Aleutians (WAL)	*8*	*0.0385*	*0.1385*	*0.0000*	*0.7721*	*0.0476*	*0.1074*
Bering (BER)	114	0.1298	0.0005	0.0026	0.3567	0.0492	0.0009
Eastern Aleutians (EAL)	36	0.0929	0.0019	0.0000	0.6679	0.0344	0.0294
Western Gulf of Alaska (WGOA)	96	0.1065	0.0010	0.0000	0.5558	0.0383	0.0030
Northern Gulf of Alaska (NGOA)	233	0.1540	0.0003	0.0163	0.1920	0.0144	0.0591
Southeast Alaska (SEA)	183	0.3964	<0.0001	0.2318	0.0006	0.1199	0.0001
Northern British Columbia (NBC)	104	0.3321	<0.0001	0.1542	0.0035	0.0650	0.0037
Southern British Columbia/Washington (SBC/WA)	51	0.1144	0.0007	0.0000	0.8210	0.0000	0.4029
California/Oregon (CA/OR)	123	0.0378	0.0557	0.0345	0.0611	0.1471	<0.0001
Breeding Areas							
Philippines (PHI)	*13*	*0.1961*	*0.0010*	*0.1330*	*0.0093*	*0.2297*	*<0.0001*
Okinawa (OK)	72	0.2290	<0.0001	0.1537	0.0004	0.2260	<0.0001
Ogasawara (OG)	159	0.1068	0.0004	0.0320	0.0555	0.0845	<0.0001
Hawaii (HI)	227	0.1979	0.0001	0.0404	0.0772	0.0201	0.0404
Mexico-Revillagigedo Archipelago (MX-AR)	106	0.0998	0.0009	0.0000	0.4515	0.0475	0.0004
Mexico-Baja California (MX-BC)	110	0.0740	0.0020	0.0000	0.6892	0.0439	0.0003
Mexico-Mainland (MX-ML)	62	0.0678	0.0043	0.0000	0.8329	0.0451	0.0014
Central America (CENTAM)	36	0.0559	0.0602	0.0772	0.0178	0.2025	<0.0001

Key: n = sample size.

Table 27. The relative likelihood of assignment for each biopsy-sampled individual to the four DPSs based on the program GeneClass2 and using the published SPLASH dataset as reference samples (Baker et al. 2013). The highest likelihood for each individual is indicated in bold.

Tag #	Lab ID	Sex	Assignment Likelihood to DPS			
			Western North Pacific	Hawaii	Mexico-ML/AR	Central America
Southern and central California						
830	Mno17CA001	Male	0.00	0.00	0.00	**100.00**
833	Mno17CA002	Male	0.51	5.19	3.48	**90.82**
834	Mno17CA003	Female	0.27	0.44	**96.62**	2.67
838	Mno17CA004	Male	5.39	0.40	**94.19**	0.02
10822	Mno17CA005	Male	0.00	0.01	0.03	**99.96**
840	Mno17CA006	Male	0.01	0.00	1.21	**98.78**
10842	Mno17CA007	Female	0.00	0.01	1.42	**98.57**
848	Mno17CA008	Male	0.01	**71.41**	19.66	8.92
1389	Mno17CA009	Female	1.17	**81.92**	12.46	4.45
2083	Mno17CA010	Male	0.00	0.00	48.39	51.61
1390	Mno17CA011	Female	0.00	0.00	16.94	**83.06**
4173	Mno17CA012	Female	0.00	0.68	1.29	**98.03**
23038	Mno17CA013	Female	0.11	0.00	0.80	**99.09**
4175	Mno17CA014	Female	0.00	0.01	0.01	**99.99**
Northern California and Oregon						
5801	Mno16OR001	Male	0.01	**99.73**	0.02	0.24
5923	Mno16OR002	Male	1.35	**94.82**	3.84	0.00
5838	Mno16OR003	Female	3.52	10.34	**86.14**	0.00
untagged	Mno17OR001	Male	0.02	**62.86**	37.12	0.00
untagged	Mno17OR002	Female	0.01	0.00	9.39	**90.60**
untagged	Mno17OR003	Male	0.00	0.01	14.35	**85.64**
1387	Mno17OR004	Male	0.44	**66.42**	33.14	0.00
4174	Mno17OR005	Female	36.07	0.33	**61.97**	1.63
23043	Mno18OR006	Female	**74.06**	0.11	19.36	6.47
untagged	Mno18OR001	Male	0.00	0.02	0.13	**99.84**
10834	Mno18OR002	Male	1.72	**83.78**	14.48	0.01
23030	Mno18OR003	Male	0.72	**53.03**	46.24	0.02
23032	Mno18OR004	Male	0.02	0.03	**95.78**	4.17
23035	Mno18OR005	Male	0.00	**91.49**	8.44	0.07
23041	Mno18OR006	Male	0.08	15.56	**83.28**	1.08
Northern Washington						
untagged	Mno18WA001	Male	0.55	**96.69**	2.76	0.00
untagged	Mno18WA002	Male	0.00	**99.42**	0.58	0.00
untagged	Mno19WA009*					
untagged	Mno18WA003	Female	8.01	3.33	**85.84**	2.82
untagged	Mno18WA006*					
untagged	Mno18WA004	Male	0.03	**85.74**	14.22	0.01
untagged	Mno18WA005	Male	31.00	18.33	**50.66**	0.02
untagged	Mno18WA007	Male	1.57	2.06	**96.35**	0.03
10825	Mno18WA008	Male	0.00	0.01	34.69	**65.31**
10836	Mno18WA009	Male	1.71	**93.00**	5.30	0.00
10839	Mno18WA010	Female	8.86	**63.27**	27.87	0.00
23029	Mno18WA011	Female	8.60	**66.09**	25.31	0.00
23039	Mno18WA012	Male	2.21	**89.94**	7.85	0.00
4177	Mno18WA013	Male	2.87	**89.24**	7.89	0.00

Tag #	Lab ID	Sex	Assignment Likelihood to DPS			
			Western North Pacific	Hawaii	Mexico-ML/AR	Central America
5640	Mno18WA014	Male	2.49	**96.95**	0.57	0.00
5650	Mno18WA015	Male	0.00	0.00	1.74	98.26
5700	Mno18WA016	Female	12.67	0.66	18.20	68.48
5709	Mno18WA017	Male	11.98	**49.00**	39.00	0.01
5719	Mno18WA018	Female	0.33	**89.75**	9.93	0.00
5726	Mno18WA019	Male	11.28	**47.84**	40.88	0.00
5790	Mno18WA020	Male	0.97	**90.40**	8.60	0.02
5801	Mno18WA021	Male	3.49	**61.02**	35.45	0.04
5823	Mno18WA022	Male	0.05	**81.05**	18.90	0.00
5838	Mno18WA023	Male	**89.81**	2.20	7.04	0.95
5883	Mno18WA024	Female	0.23	3.76	**96.01**	0.01
5923	Mno18WA025	Male	0.00	0.00	0.01	**99.99**
untagged	Mno19WA001	Female	4.73	5.45	**89.73**	0.09
untagged	Mno19WA002	Male	1.00	19.31	**79.69**	0.00
untagged	Mno19WA003	Male	**68.00**	0.30	30.28	1.43
untagged	Mno19WA005*					
untagged	Mno19WA004	Male	2.66	**79.84**	17.50	0.00
untagged	Mno19WA006	Female	**95.60**	0.05	2.37	1.98
untagged	Mno19WA007	Male	13.36	**69.31**	17.34	0.00
untagged	Mno19WA008	Male	0.38	**98.30**	1.32	0.00
833	Mno19WA010	Male	5.13	**87.31**	7.56	0.00
4173	Mno19WA011	Female	0.05	0.07	**99.57**	0.32
5670	Mno19WA012	Male	0.87	0.00	44.11	**55.03**
5678	Mno19WA013	Female	0.00	0.88	**99.12**	0.00
5679	Mno19WA014	Male	0.15	0.04	30.70	**69.11**
5701	Mno19WA015	Male	29.27	13.62	**57.11**	0.00
5742	Mno19WA016	Male	9.67	**67.01**	23.28	0.05
5826	Mno19WA017	Male	6.64	**83.90**	9.45	0.00
5840	Mno19WA018	Female	0.00	0.01	**83.65**	16.34
5921	Mno19WA019	Male	8.12	**47.53**	44.34	0.02
10820	Mno19WA020	Female	1.48	**94.63**	3.90	0.00
10823	Mno19WA021	Female	0.10	**97.05**	2.85	0.00
10826	Mno19WA022	Male	0.00	0.00	18.06	**81.93**
10827	Mno19WA023	Male	0.71	**92.07**	7.22	0.00
10833	Mno19WA024	Male	17.24	13.92	**68.83**	0.01
10838	Mno19WA025	Male	0.05	7.90	**92.05**	0.00
10842	Mno19WA026	Female	3.93	**50.49**	45.58	0.00
23031	Mno19WA027	Female	0.00	0.00	0.79	**99.21**
23038	Mno19WA028	Male	0.00	0.00	3.19	**96.81**

Key: ID = Identifier; ML/AR = Mainland Mexico and Revillagigedo Archipelago; # = number; * = a genotype match with the preceding individual.

Table 28. The results of OSUs photo-identification (ID) efforts during each humpback whale tagging season in California (CA), northern California (NCA), Oregon (OR), and Washington (WA) from 2004 to 2019, showing number of IDs obtained and matched in the Happywhale online database to SPLASH-defined strata for both tagged and/or biopsied whales and untagged/unbiopsied whales.

		Tagged and/or biopsied whales				Untagged/unbiopsied whales		
Season	**# photos taken**	**# whales tagged and/or biopsied**	**# IDs**	**# IDs matched in Happywhale**	**# IDs matched to a breeding area**	**# IDs**	**# IDs matched in Happywhale**	**# IDs matched to a breeding area**
2004CA	594	8	5	4	4	50	37	29
2005CA	690	4	2	2	2	22	17	15
2005NCA/OR	82	3	2	2	2	36	31	27
2016CA	565	0	0	0	0	24	18	16
2016OR	932	3	0	0	0	16	13	11
2017CA	10,982	14	13	12	10	127	113	85
2017OR	4,694	8	8	7	5	46	30	22
2018OR	5,166	6	6	5	5	18	14	11
2018WA	15,565	26	22	18	10	113	96	61
2019WA	13,775	32	24	18	9	126	80	56
Total	**53,045**	**104**	**82**	**68**	**47**	**578**	**449**	**333**

Key: # = number.

Table 29. Photo-identification (ID) matches to the 18 regional strata (feeding areas and breeding areas) defined in SPLASH (Baker et al. 2013) between humpback whales tagged and/or biopsied in southern and central California, northern California and Oregon, and northern Washington from 2004 to 2019 and the Happywhale online photo-ID database.

	Southern and central California (20 IDs)	Northern California and Oregon (16 IDs)	Northern Washington (46 IDs)
Region	**# Matches**	**# Matches**	**# Matches**
Feeding Areas			
Russia (RUS)	0	0	0
Western Aleutians (WAL)	0	0	0
Bering (BER)	0	0	0
Eastern Aleutians (EAL)	0	0	0
Western Gulf of Alaska (WGOA)	0	0	0
Northern Gulf of Alaska (NGOA)	0	0	0
Southeastern Alaska (SEA)	0	0	0
Northern British Columbia (NBC)	0	0	0
Southern British Columbia/Washington (SBC/WA)	0	4	36
California/Oregon (CA/OR)	18	14	1
Total Whales*	**18**	**14**	**36**
Breeding Areas			
Philippines (PHI)	0	0	0
Okinawa (OK)	0	0	0
Ogasawara (OG)	0	0	0
Hawaii (HI)	0	2	5
Mexico-Revillagigedo Archipelago (MX-AR)	0	0	0
Mexico-Baja California (MX-BC)	5	8	12
Mexico-Mainland (MX-ML)	14	6	9
Central America (CENTAM)	1	0	0
Total Whales*	**16**	**12**	**19**

Key: # = number; * Totals here do not equal the sum of matches to feeding and breeding areas because some individual whales have matches to multiple areas.

Table 30. Photo-identification (ID) matches to the 18 regional strata (feeding areas and breeding areas) defined in SPLASH (Baker et al. 2013) between untagged/unbiopsied humpback whales photographed in southern and central California, northern California and Oregon, and northern Washington from 2004 to 2019 and the Happywhale online photo-ID database.

	Southern and central California (223 IDs)	**Northern California and Oregon (116 IDs)**	**Northern Washington (239 IDs)**
Region	**# Matches**	**# Matches**	**# Matches**
Feeding Areas			
Russia (RUS)	0	0	0
Western Aleutians (WAL)	0	0	0
Bering (BER)	0	0	0
Eastern Aleutians (EAL)	0	0	0
Western Gulf of Alaska (WGOA)	0	0	0
Northern Gulf of Alaska (NGOA)	0	0	0
Southeastern Alaska (SEA)	0	0	0
Northern British Columbia (NBC)	0	0	0
Southern British Columbia/Washington (SBC/WA)	0	10	154
California/Oregon (CA/OR)	185	84	3
Total Whales*	185	84	154
Breeding Areas			
Philippines (PHI)	0	0	0
Okinawa (OK)	0	0	0
Ogasawara (OG)	0	0	0
Hawaii (HI)	0	3	35
Mexico-Revillagigedo Archipelago (MX-AR)	0	0	2
Mexico-Baja California (MX-BC)	89	45	57
Mexico-Mainland (MX-ML)	108	37	41
Central America (CENTAM)	11	1	
Total Whales*	**167**	**49**	**117**

Key: # = number; * Totals here do not equal the sum of matches to feeding and breeding areas because some individual whales have matches to multiple areas.

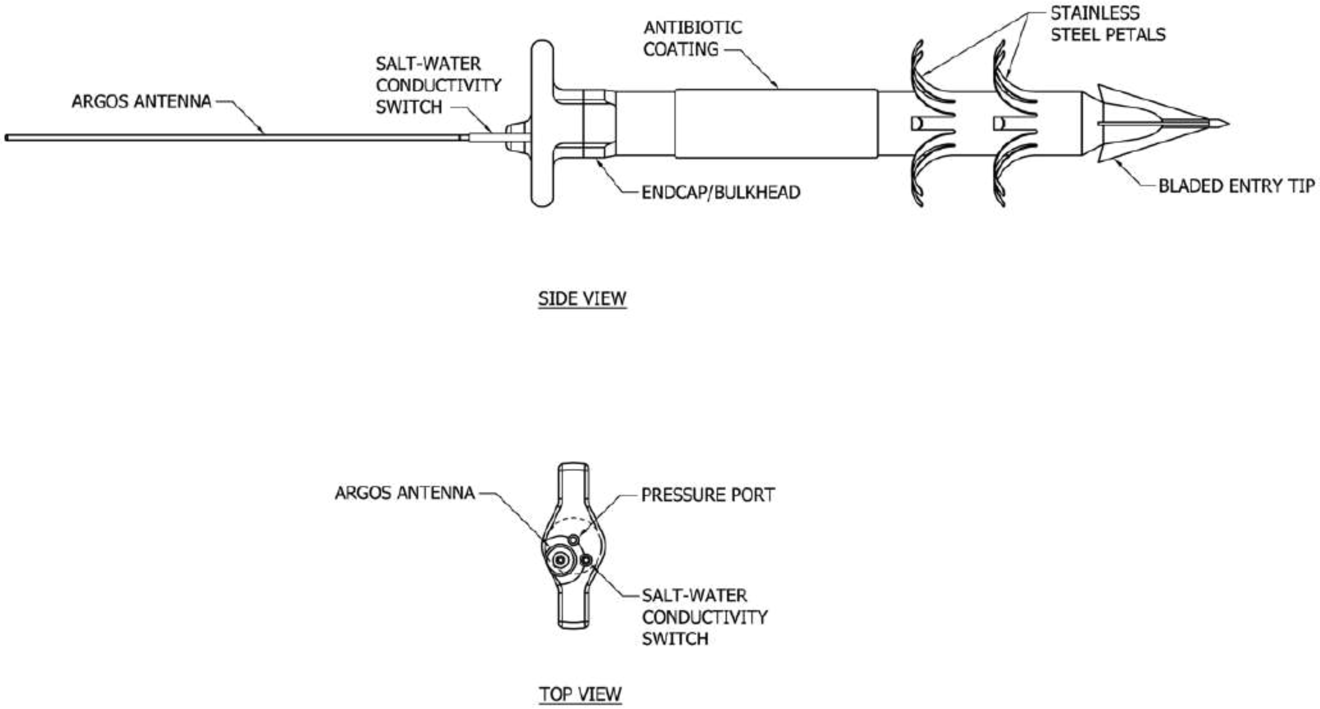


Figure 1. Schematic diagram of the non-recoverable Telonics RDW-665 DM tag showing the main body, the distal endcap with the antenna and saltwater conductivity switch, as well as the penetrating tip and anchoring system.

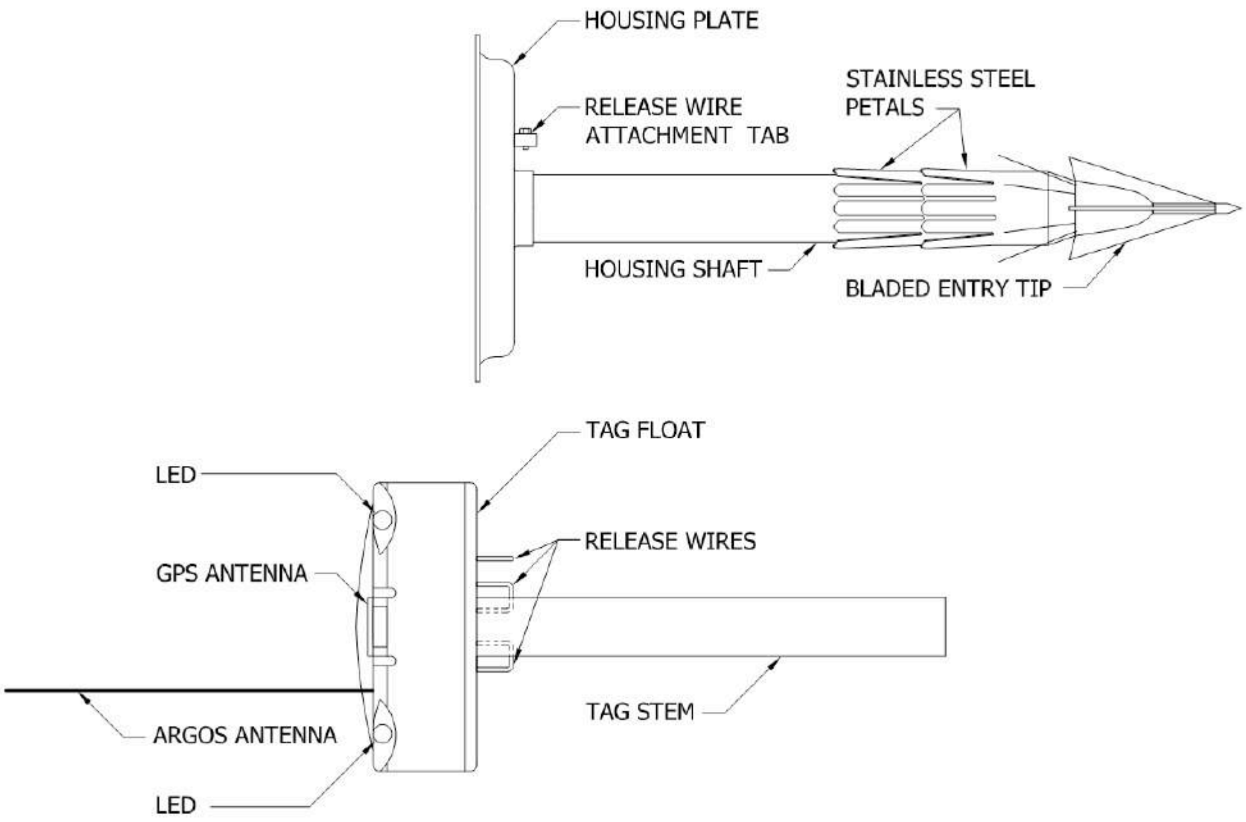


Figure 2. Schematic diagram of the recoverable Wildlife Computers MK10 Advanced Dive Behavior (ADB) tag (bottom) with the OSU-designed housing (top). The housing shaft is designed for implantation beneath the whale’s skin while the plate and tag float sit atop the whale’s back.

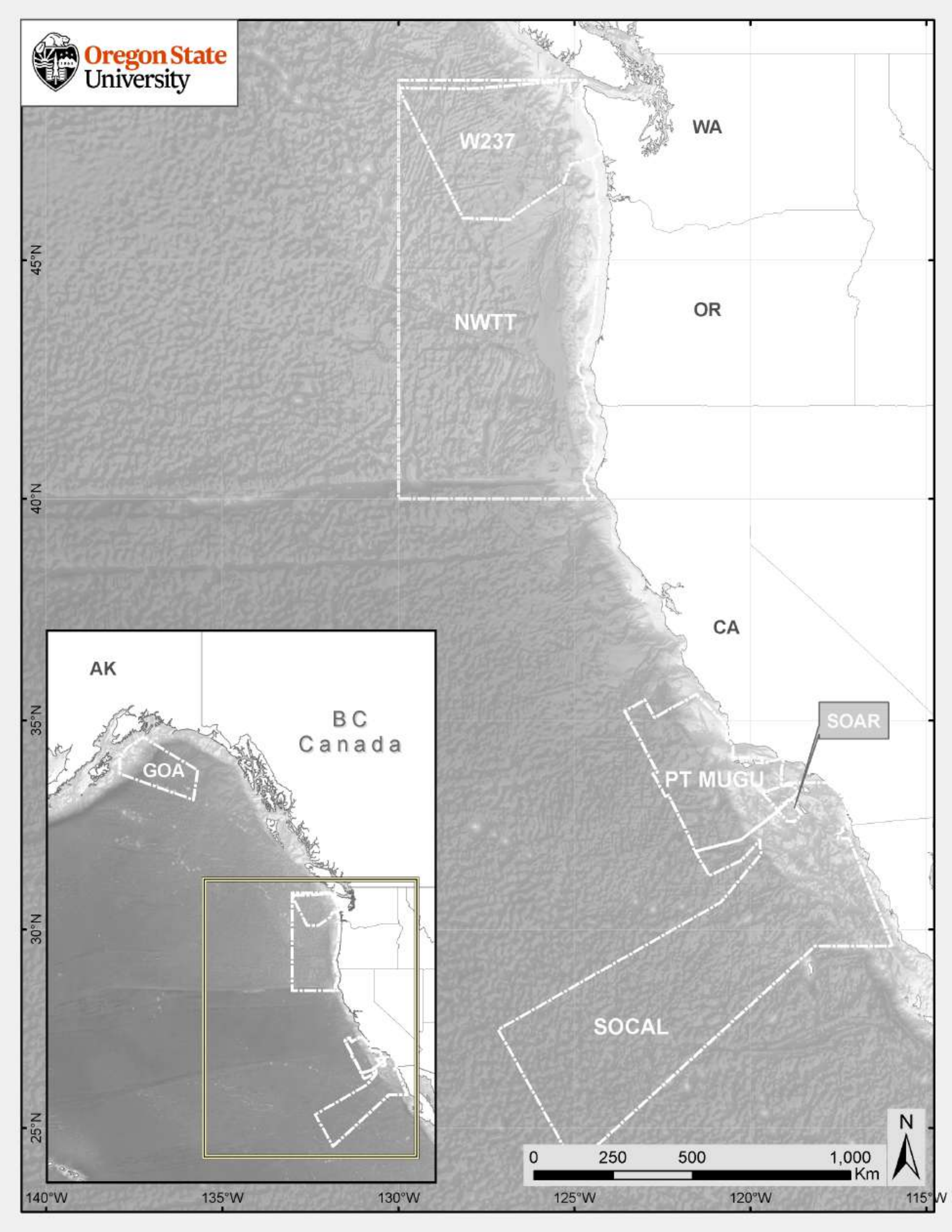


Figure 3. Map of the study area showing the six US Navy Training Areas considered in this report.

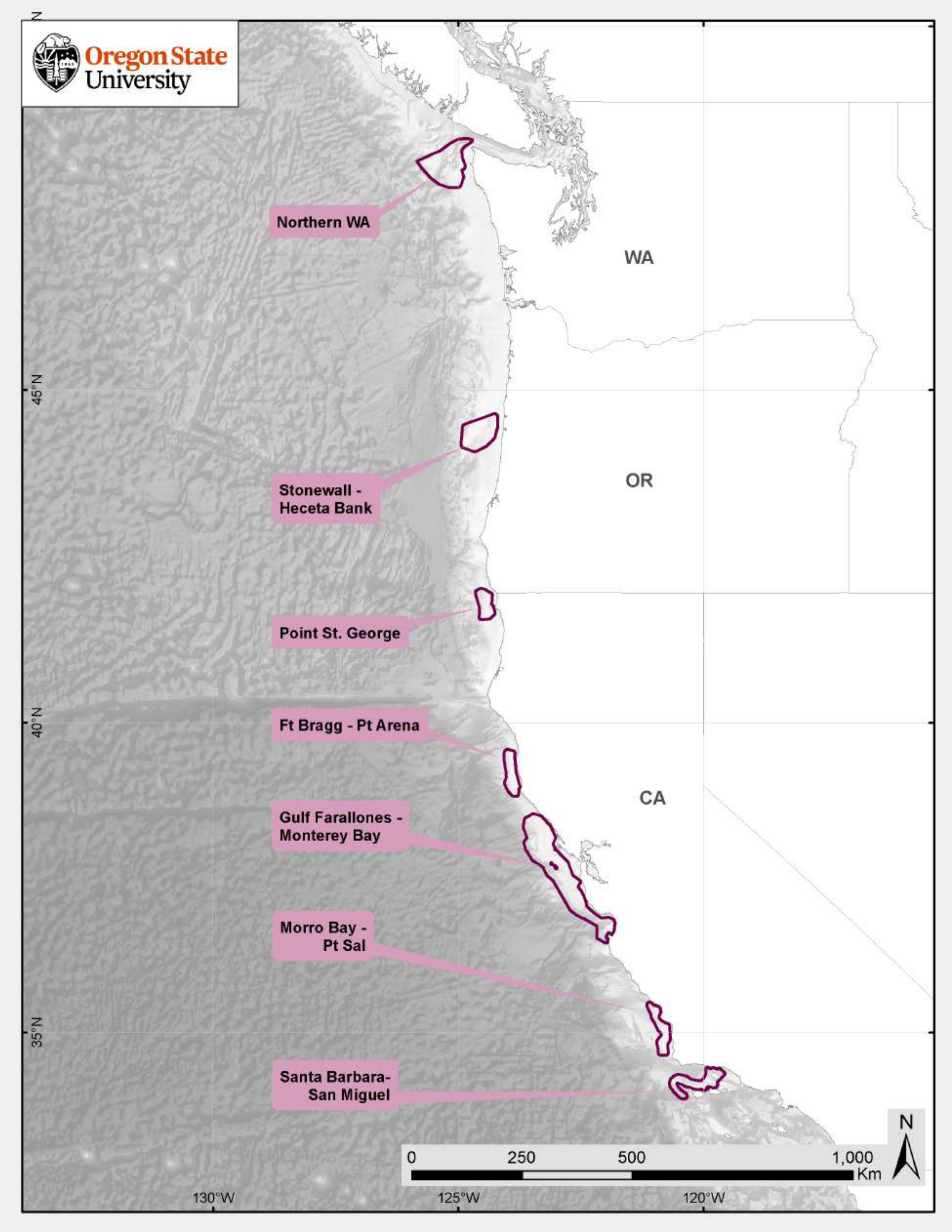


Figure 4. Map of the study area showing the seven Biologically Important Areas (BIAs) for humpback whales considered in this report.

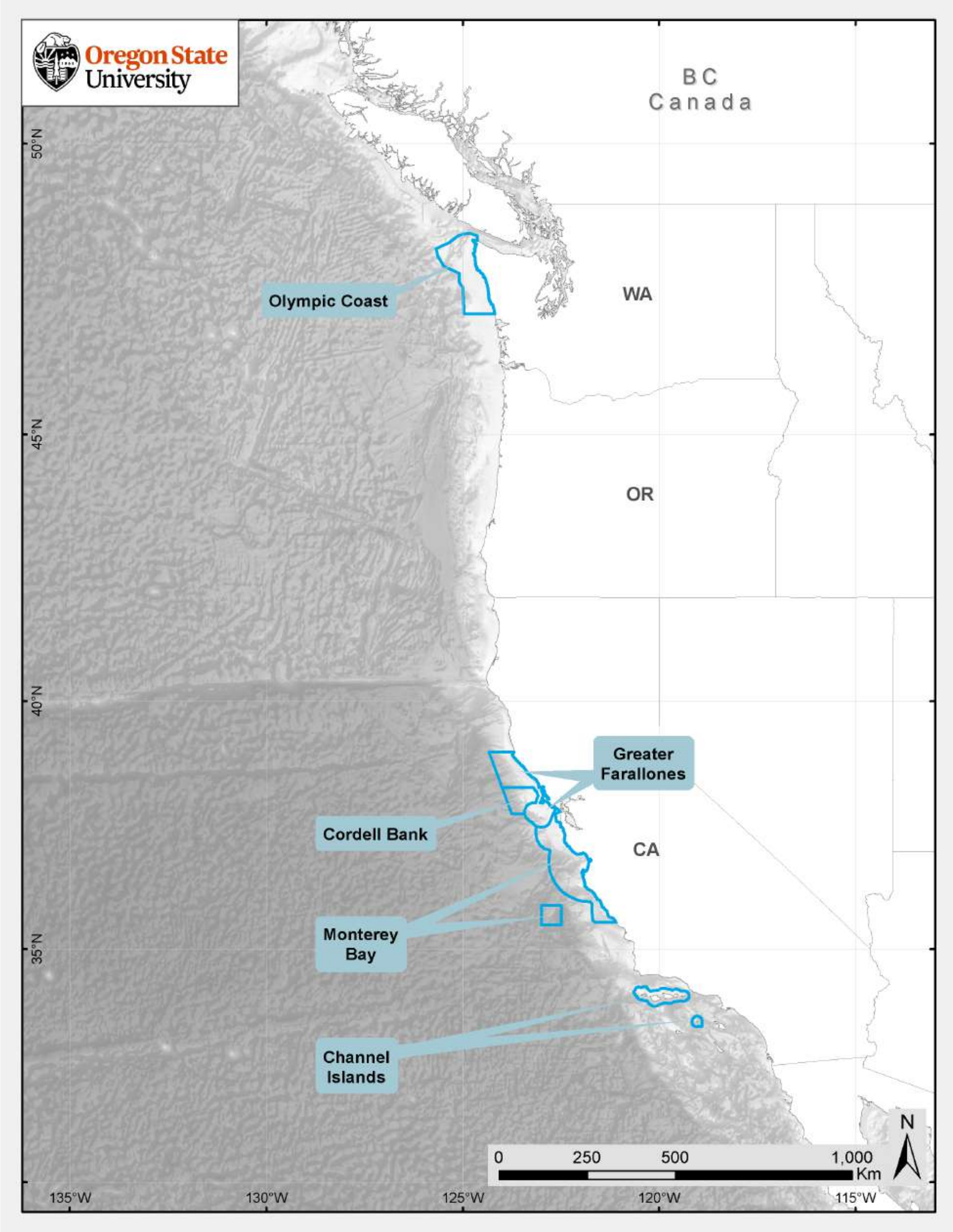


Figure 5. Map of the study area showing the five National Marine Sanctuaries (NMSs)off the US West Coast considered in this report.

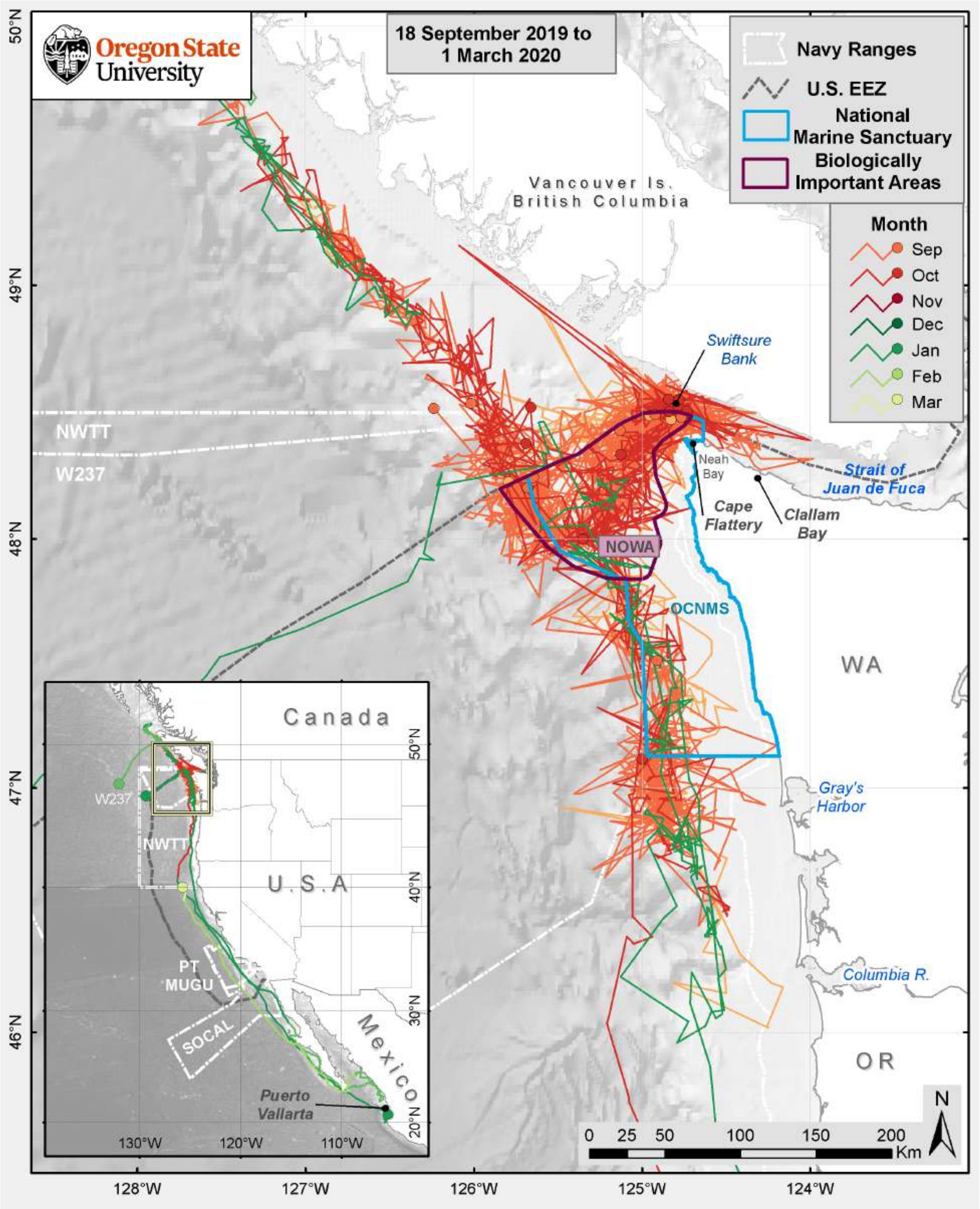


Figure 6. Satellite-monitored tracks for humpback whales tagged off Washington in September and October 2019 (24 DM tags).

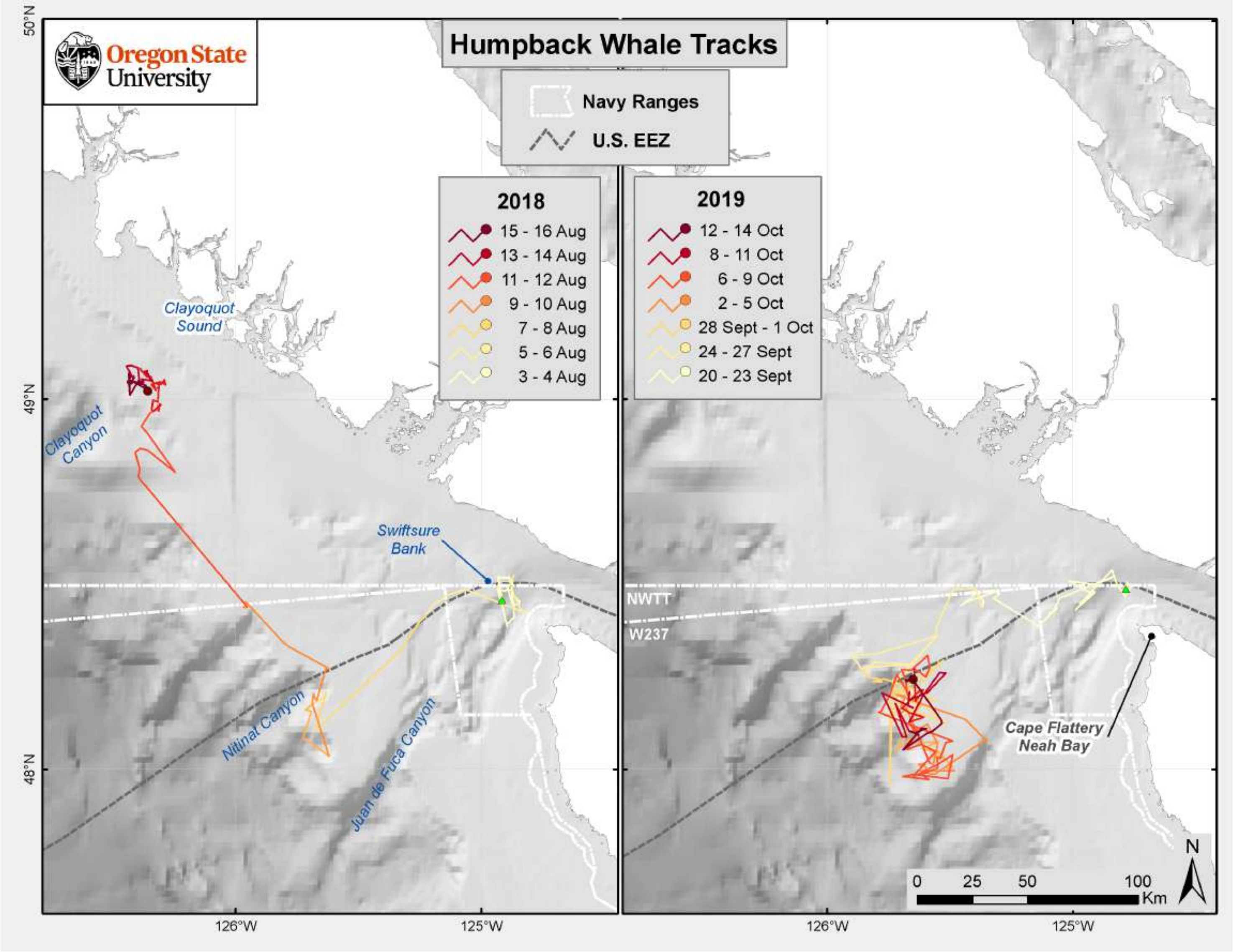


Figure 7. Satellite-monitored tracks of a humpback whale tagged off Washington in August 2018 (ADB tag #2018-4177, genetically identified as a male; left) and again in September 2019 (DM tag #2019-5743; right). The green triangles represent the tagging location and circles indicate each track's last location.

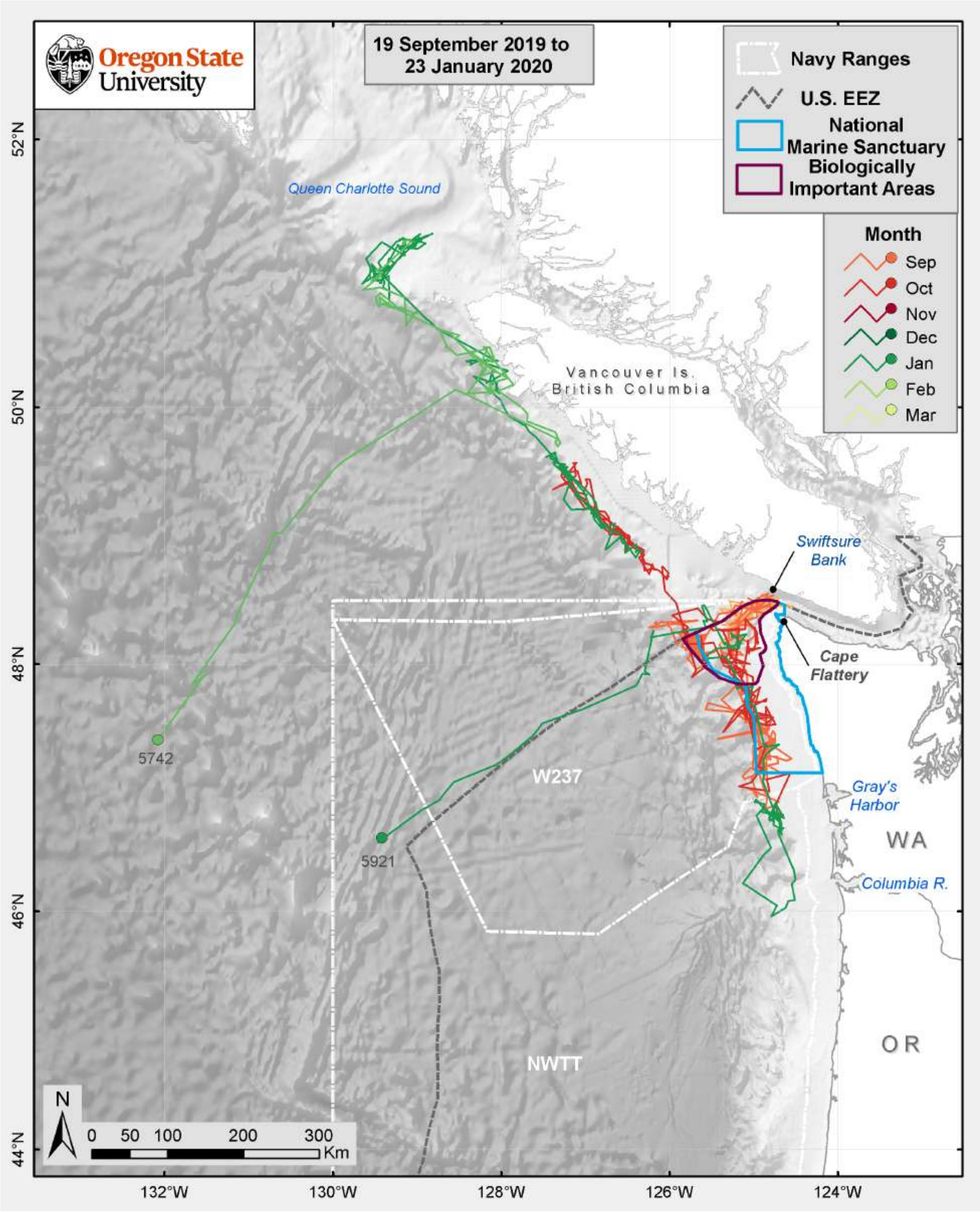


Figure 8. Satellite-monitored tracks of humpback whales tagged off Washington in September and October 2019, highlighting two whales (#2019-5742 and #2019-5921) that began their fall/winter migration toward Hawaii. Circles indicate each track's last location and circle color corresponds to a month, as shown in the legend.

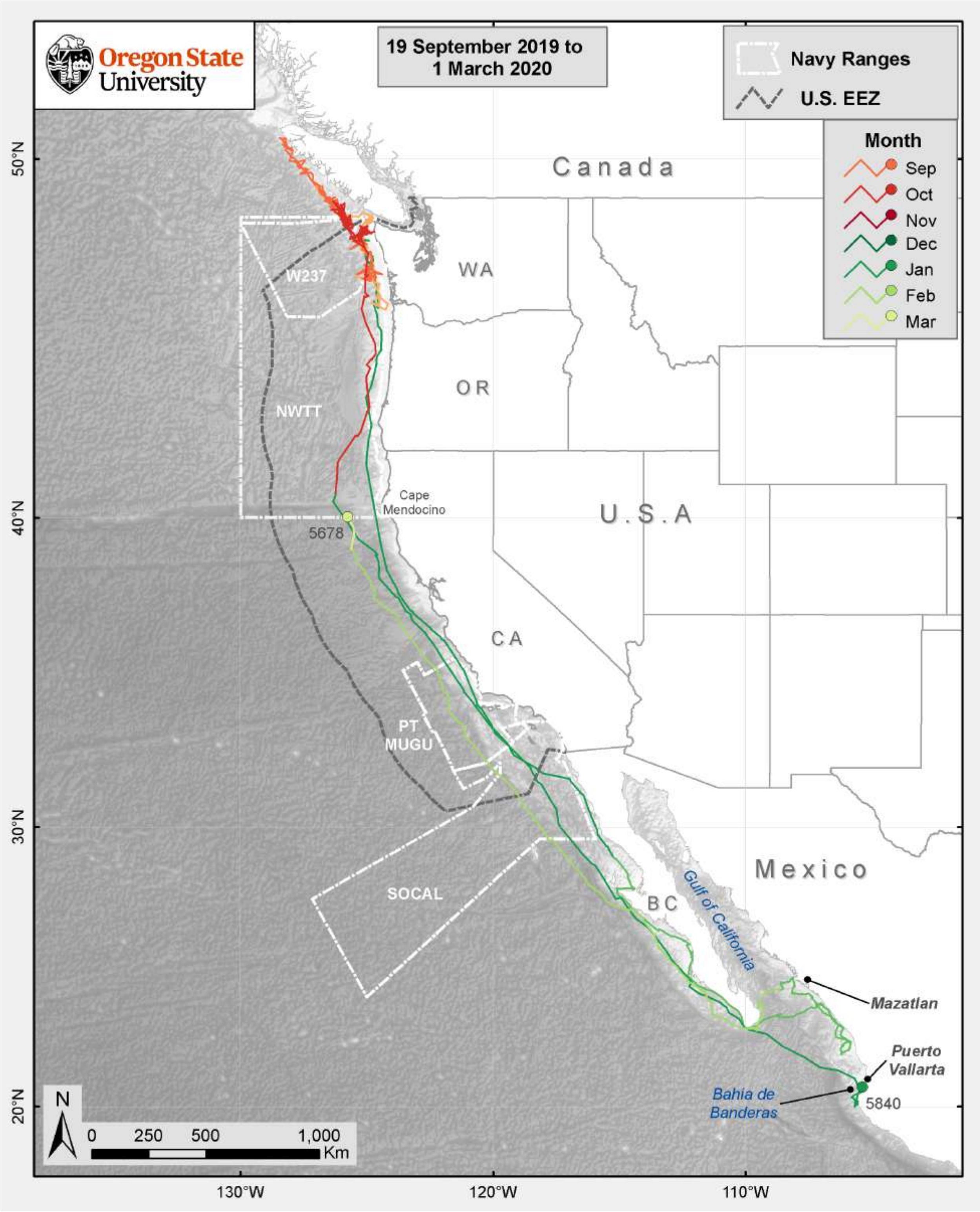


Figure 9. Satellite-monitored tracks of humpback whales tagged off Washington in September 2019, highlighting migration to Mexico for two whales (#2019-5678 and #2019-5840). Circles indicate each track's last location and circle color corresponds to a month, as shown in the legend. Notice the return migration back to the feeding area for whale #2019-5678 through its arrival to NWTT.

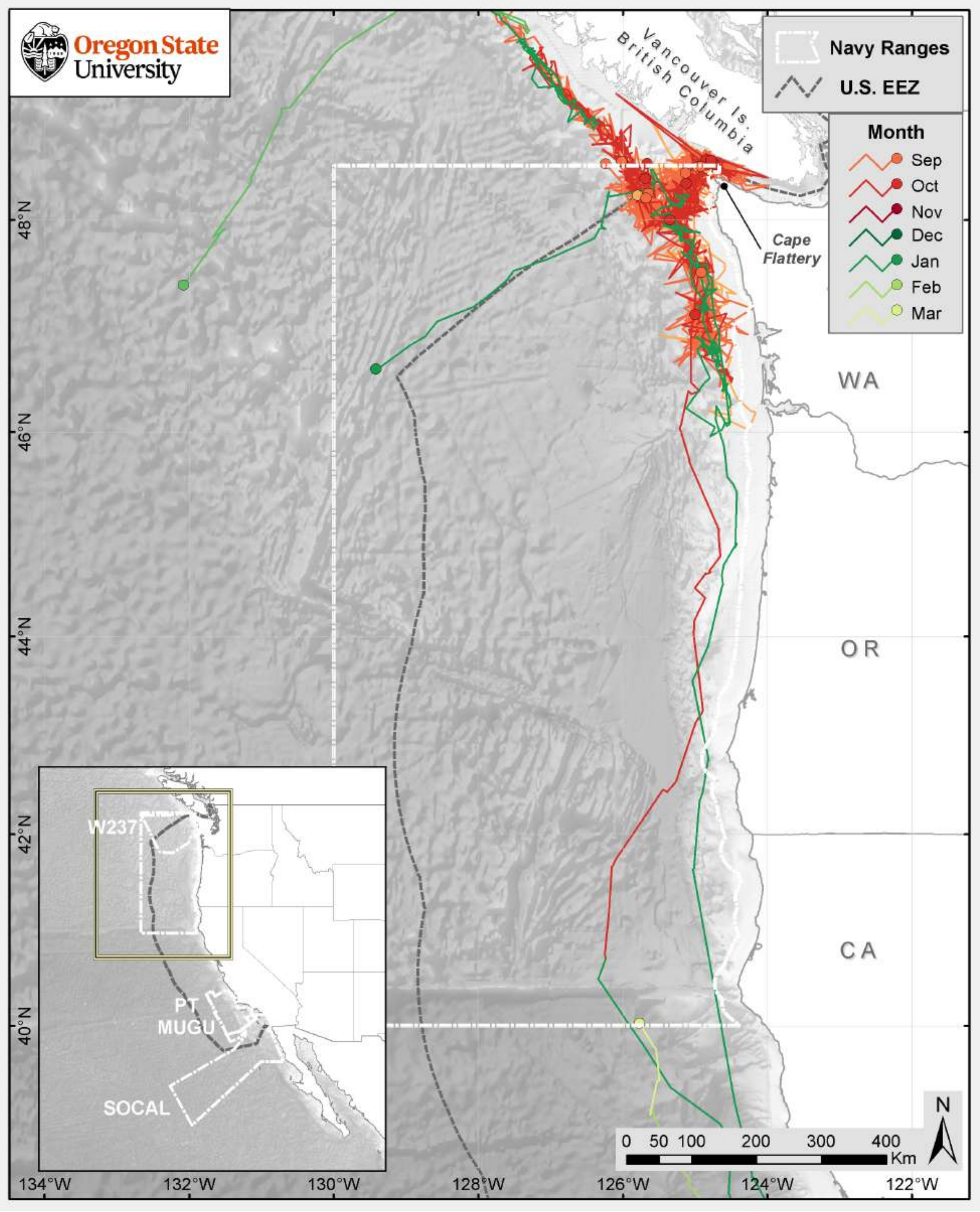


Figure 10. Satellite-monitored tracks in NWTT for humpback whales tagged off Washington in September and October 2019 (22 DM tags).

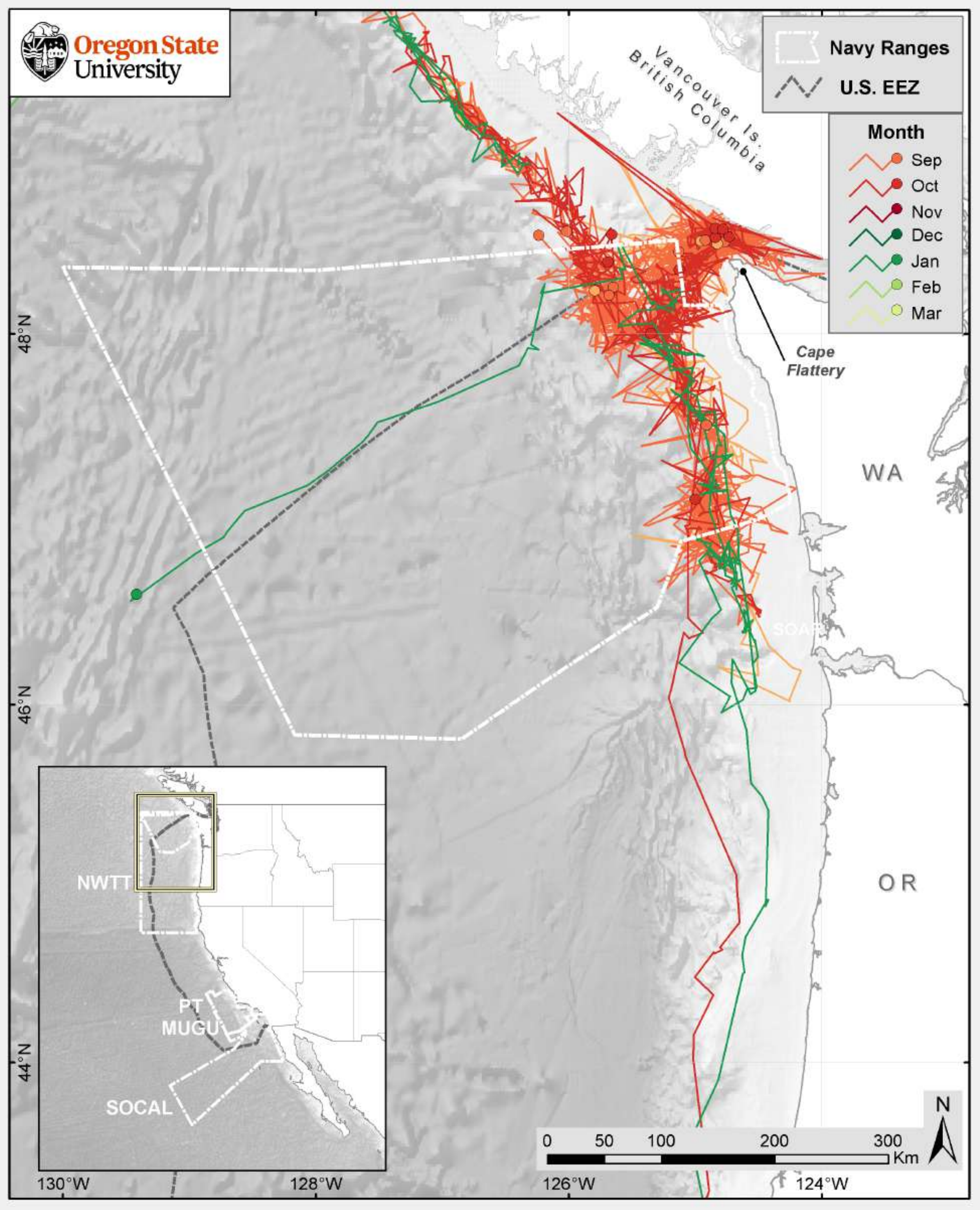


Figure 11. Satellite-monitored tracks in Area W237 of the NWTT for humpback whales tagged off Washington in September and October 2019 (18 DM tags).

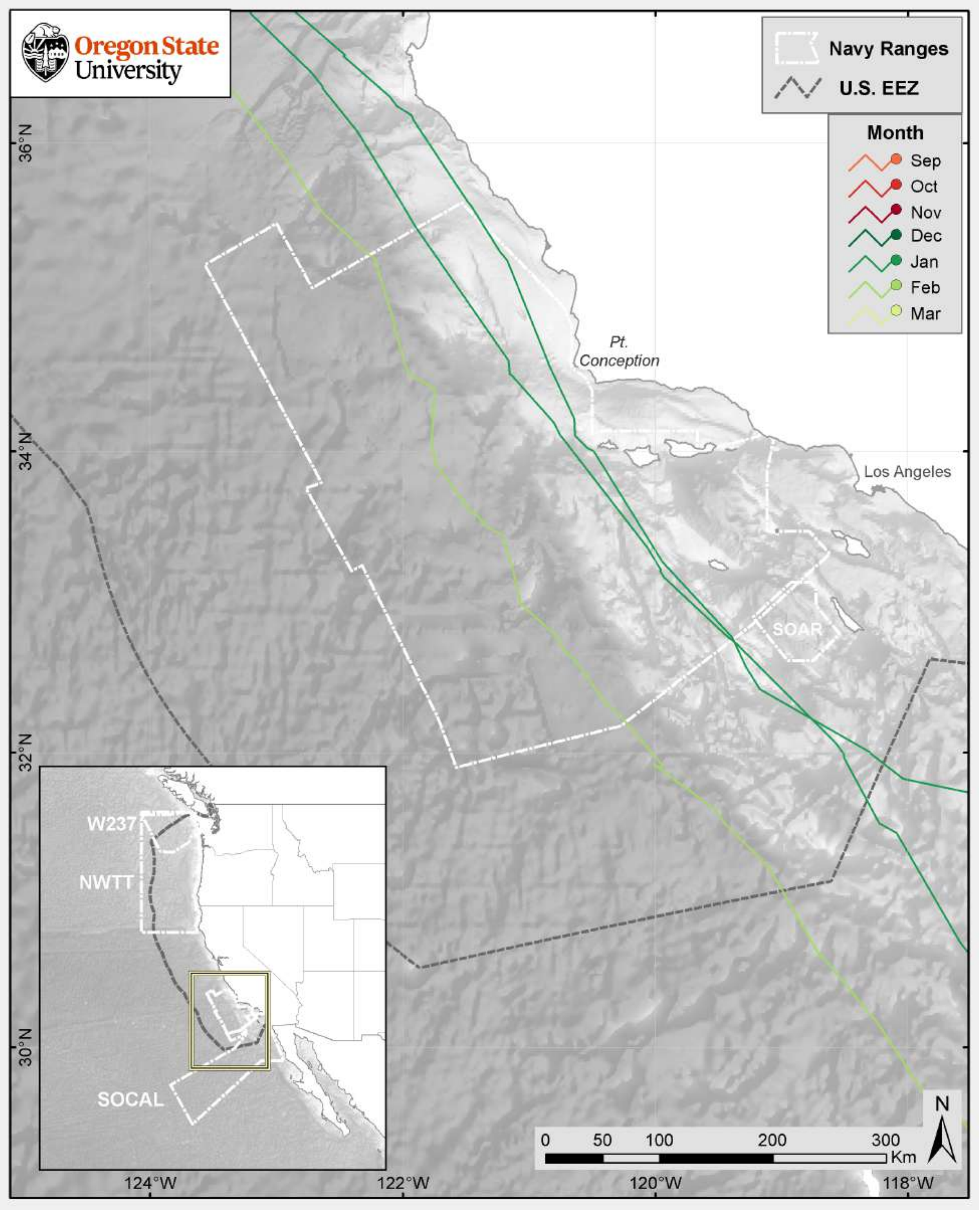


Figure 12. Satellite-monitored tracks in PT MUGU for humpback whales tagged off Washington in September 2019 (2 DM tags).

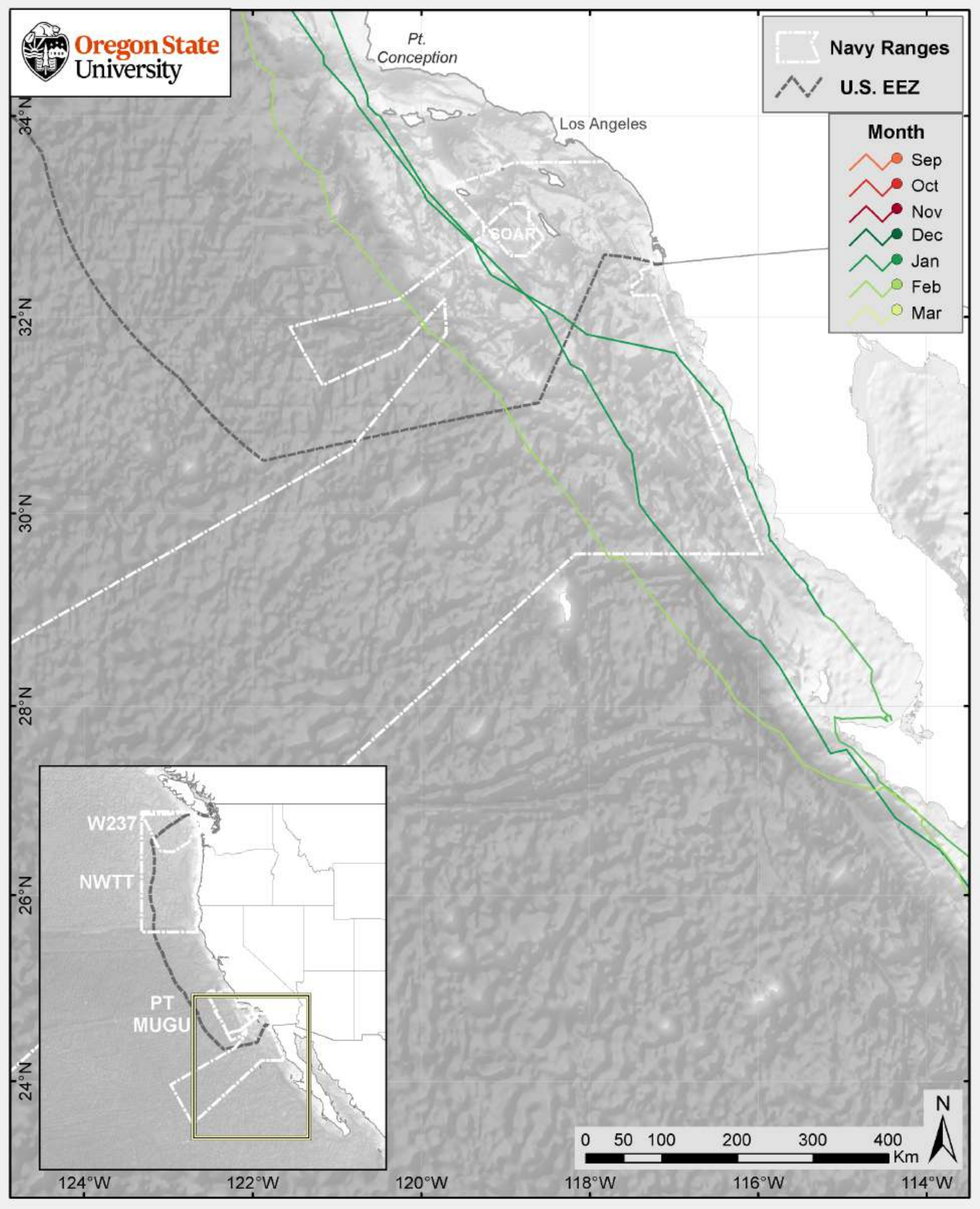


Figure 13. Satellite-monitored tracks in SOCAL for humpback whales tagged off Washington in September 2019 (2 DM tags).

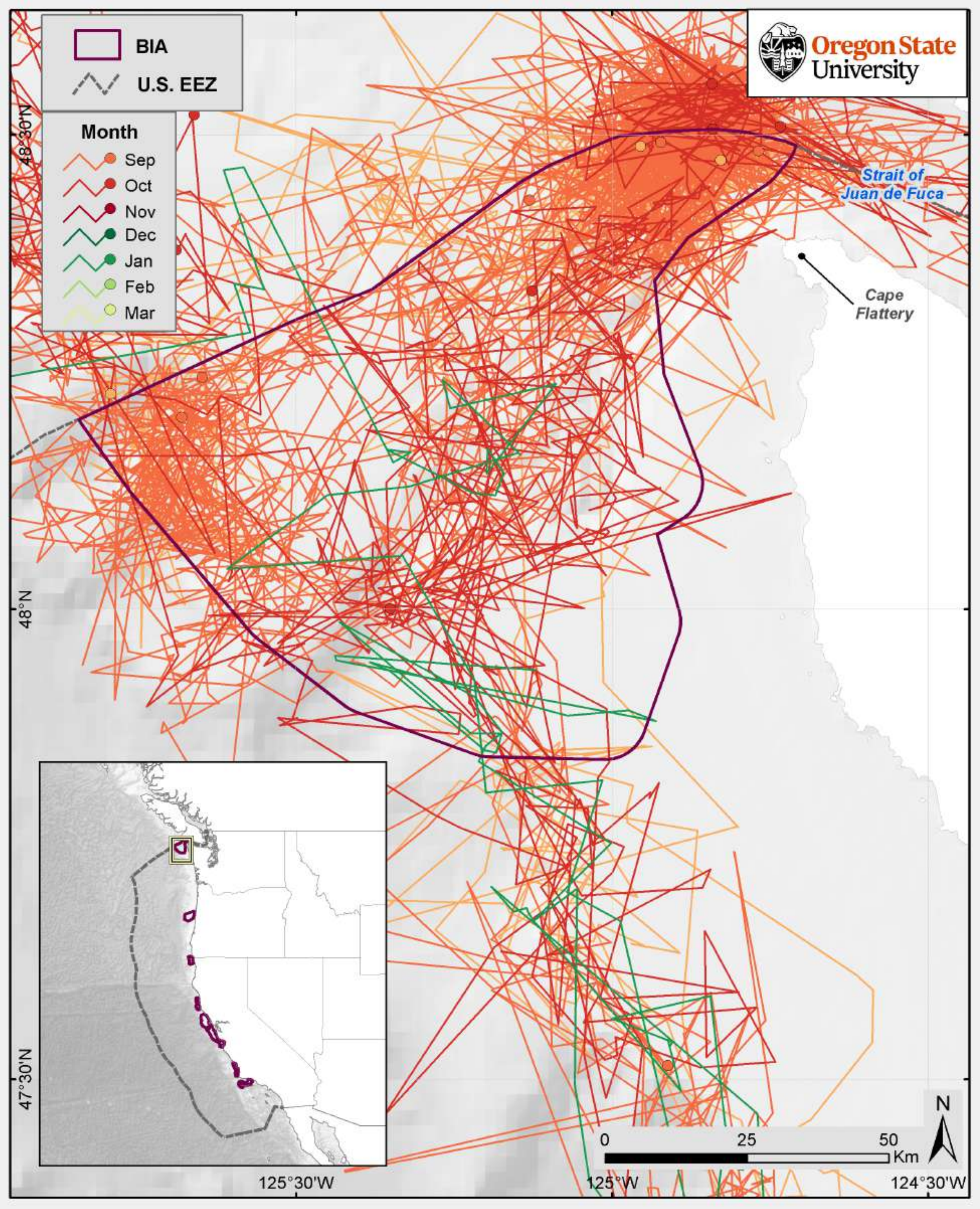


Figure 14. Satellite-monitored tracks in the Northern Washington BIA for humpback whales tagged off Washington in September and October 2019 (22 DM tags).

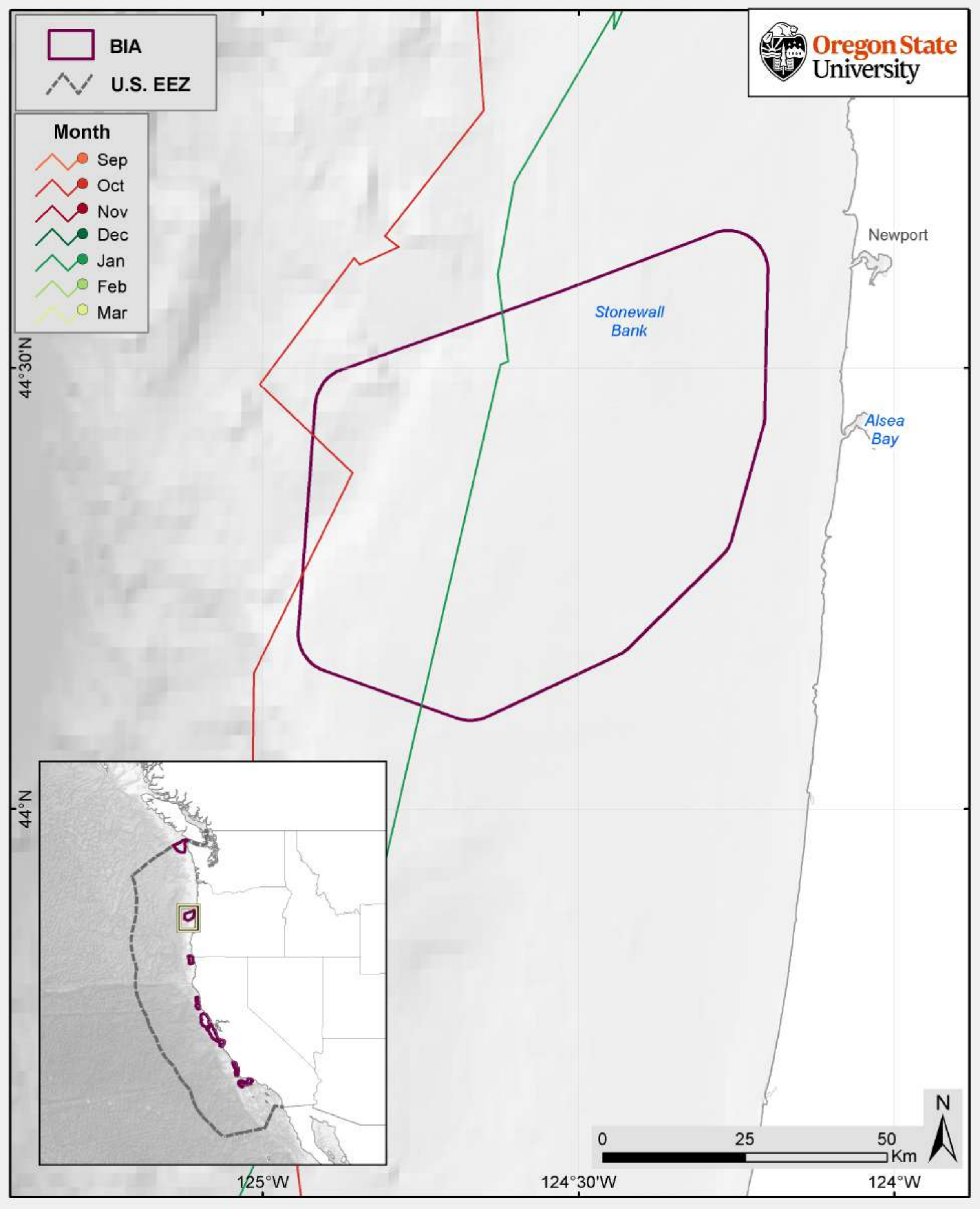


Figure 15. Satellite-monitored tracks in the Stonewall and Heceta Bank BIA for humpback whales tagged off Washington in September 2019 (2 DM tags).

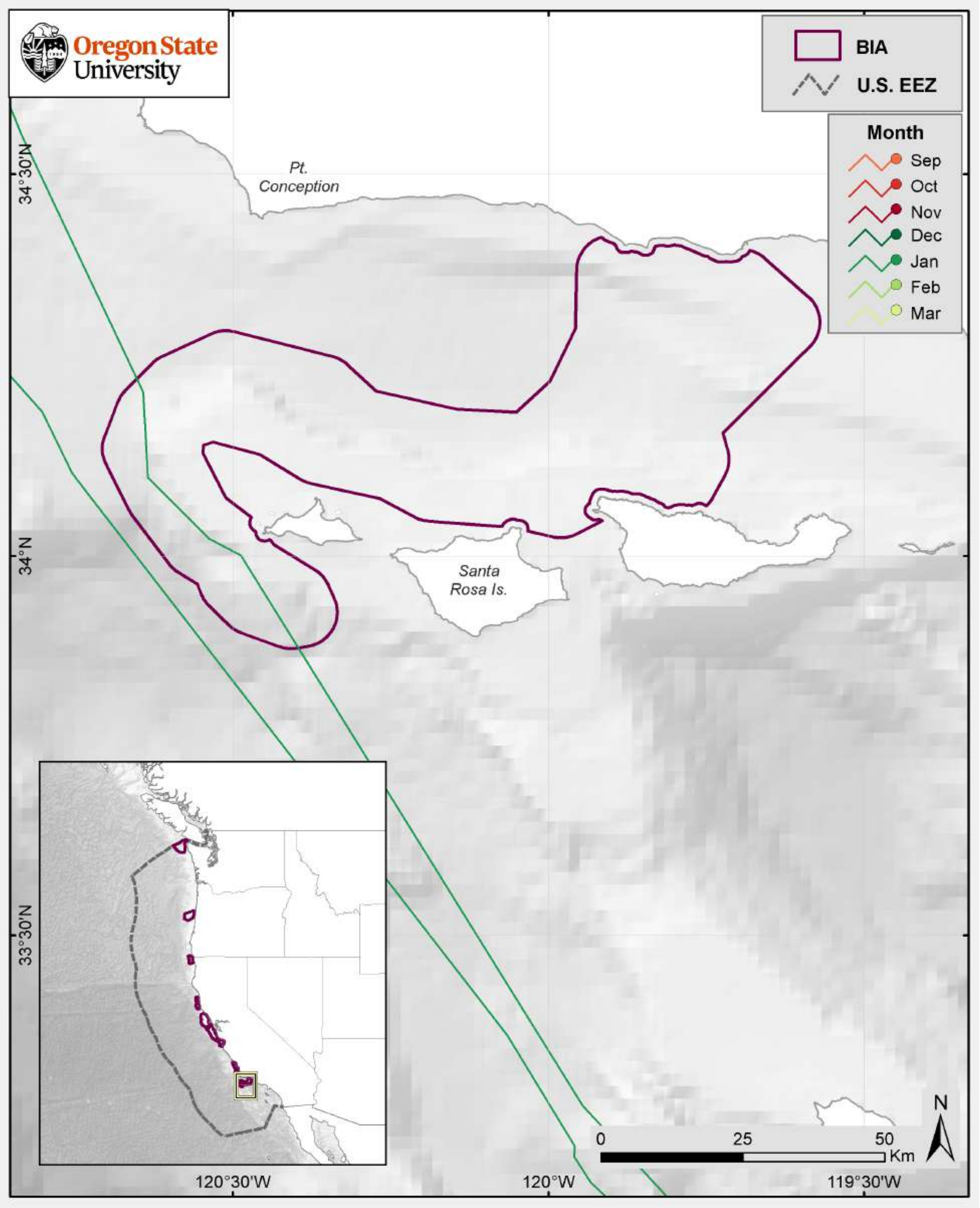


Figure 16. Satellite-monitored track in the Santa Barbara Channel-San Miguel BIA for a humpback whale tagged off Washington in September 2019 (1 DM tag).

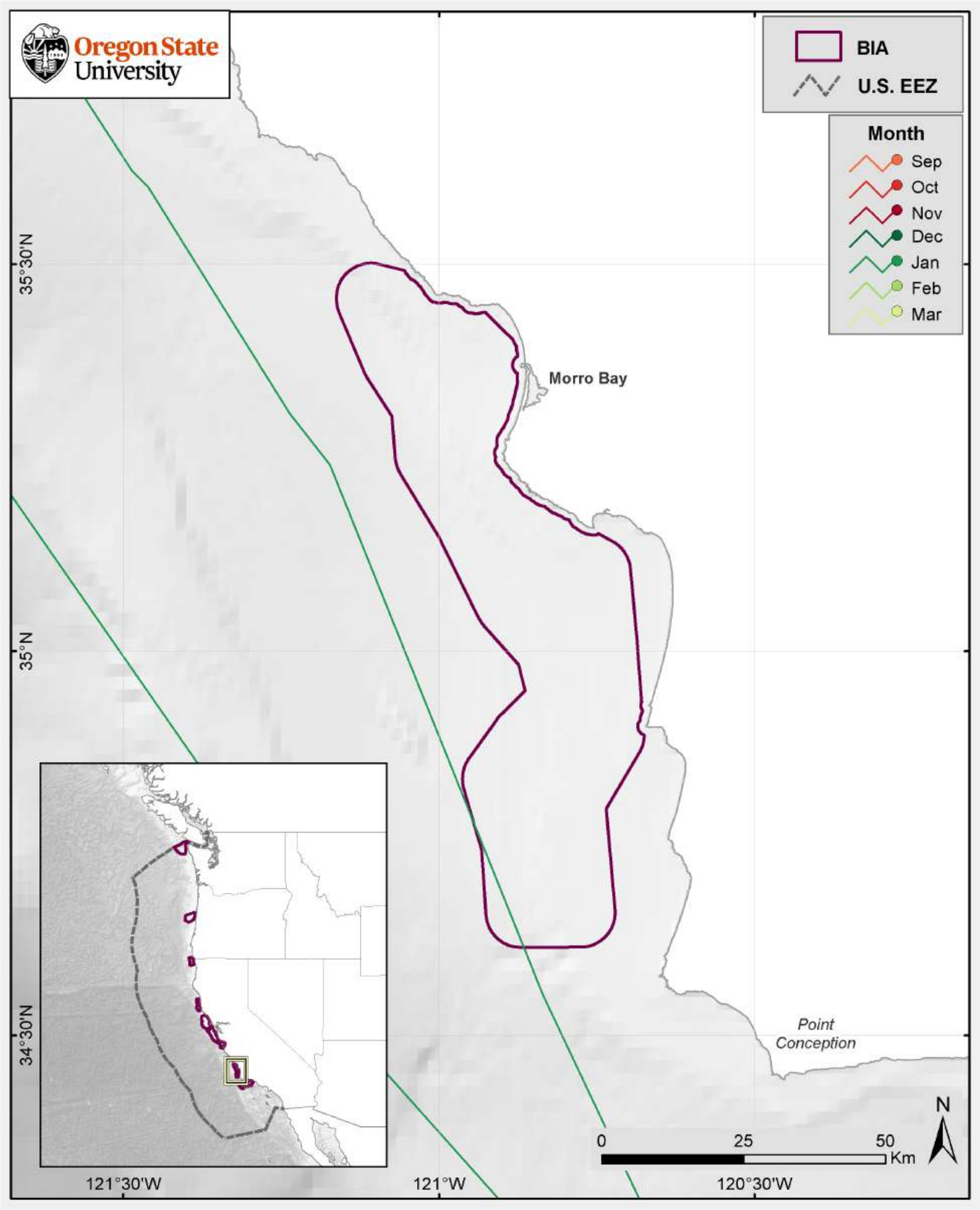


Figure 17. Satellite-monitored track in the Morro Bay to Point Sal BIA for a humpback whale tagged off Washington in September 2019 (1 DM tag).

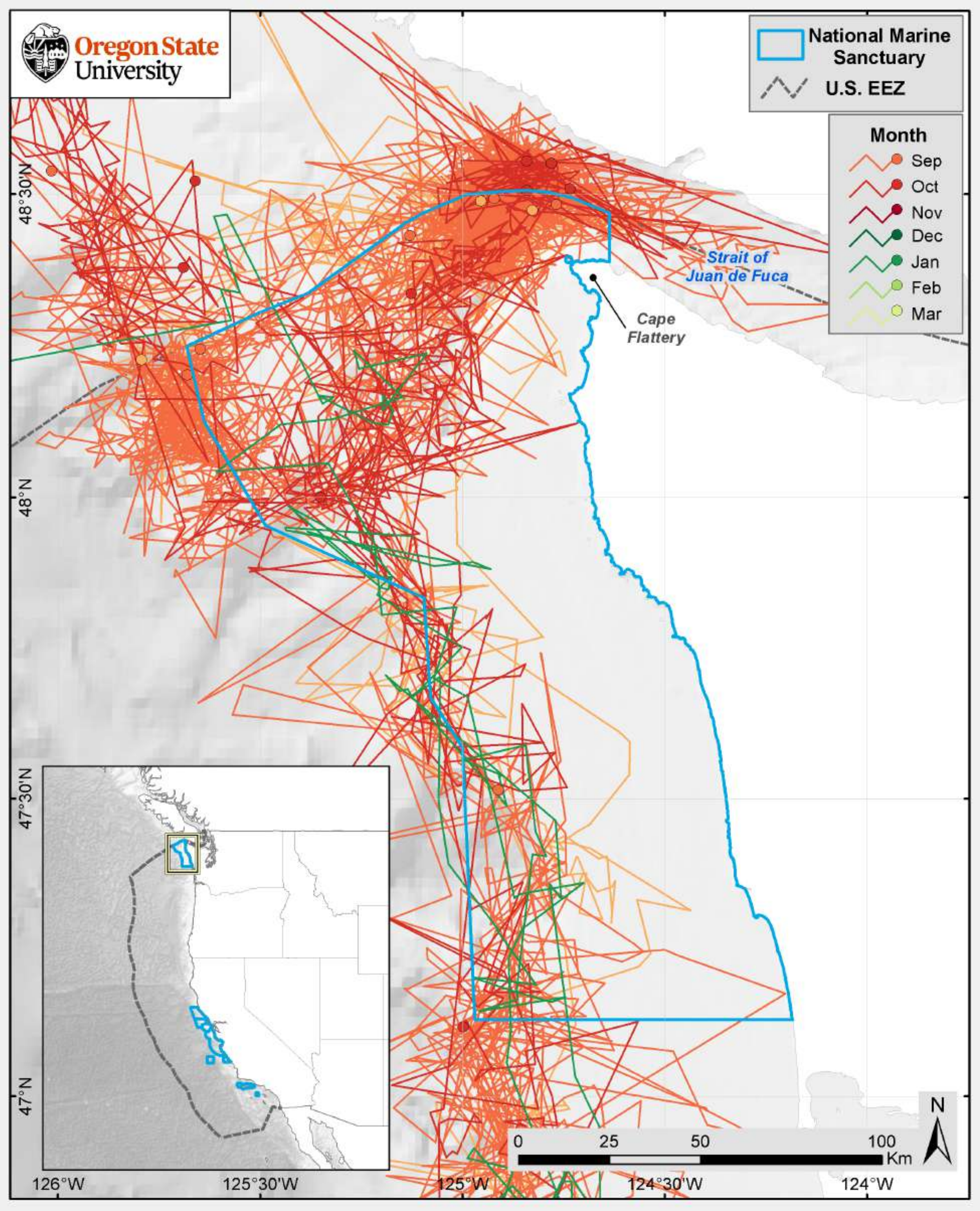


Figure 18. Satellite-monitored tracks in the Olympic Coast NMS for humpback whales tagged off Washington in September and October 2019 (22 DM tags).

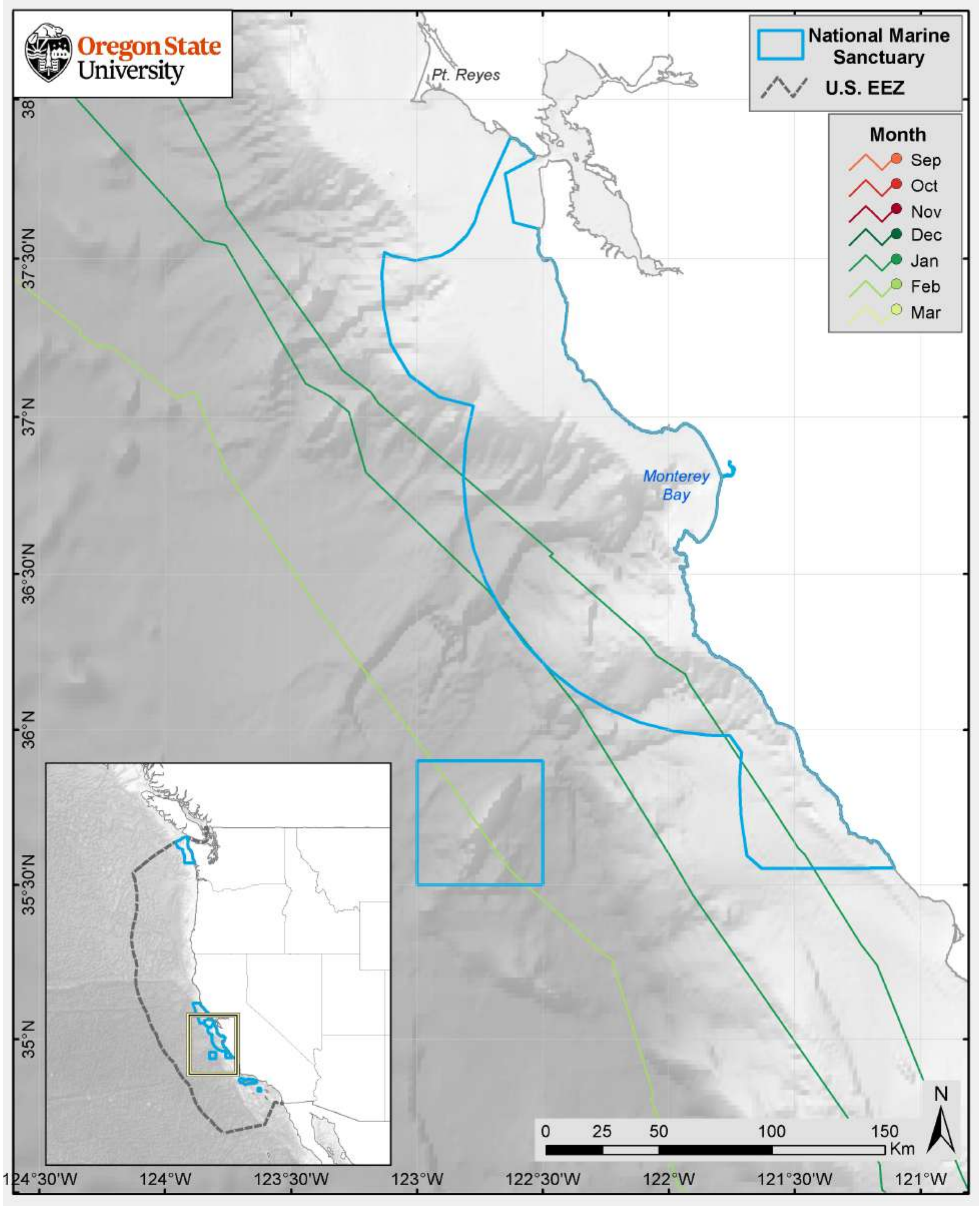


Figure 19. Satellite-monitored tracks in the Monterey Bay NMS for humpback whales tagged off Washington in September 2019 (2 DM tags).

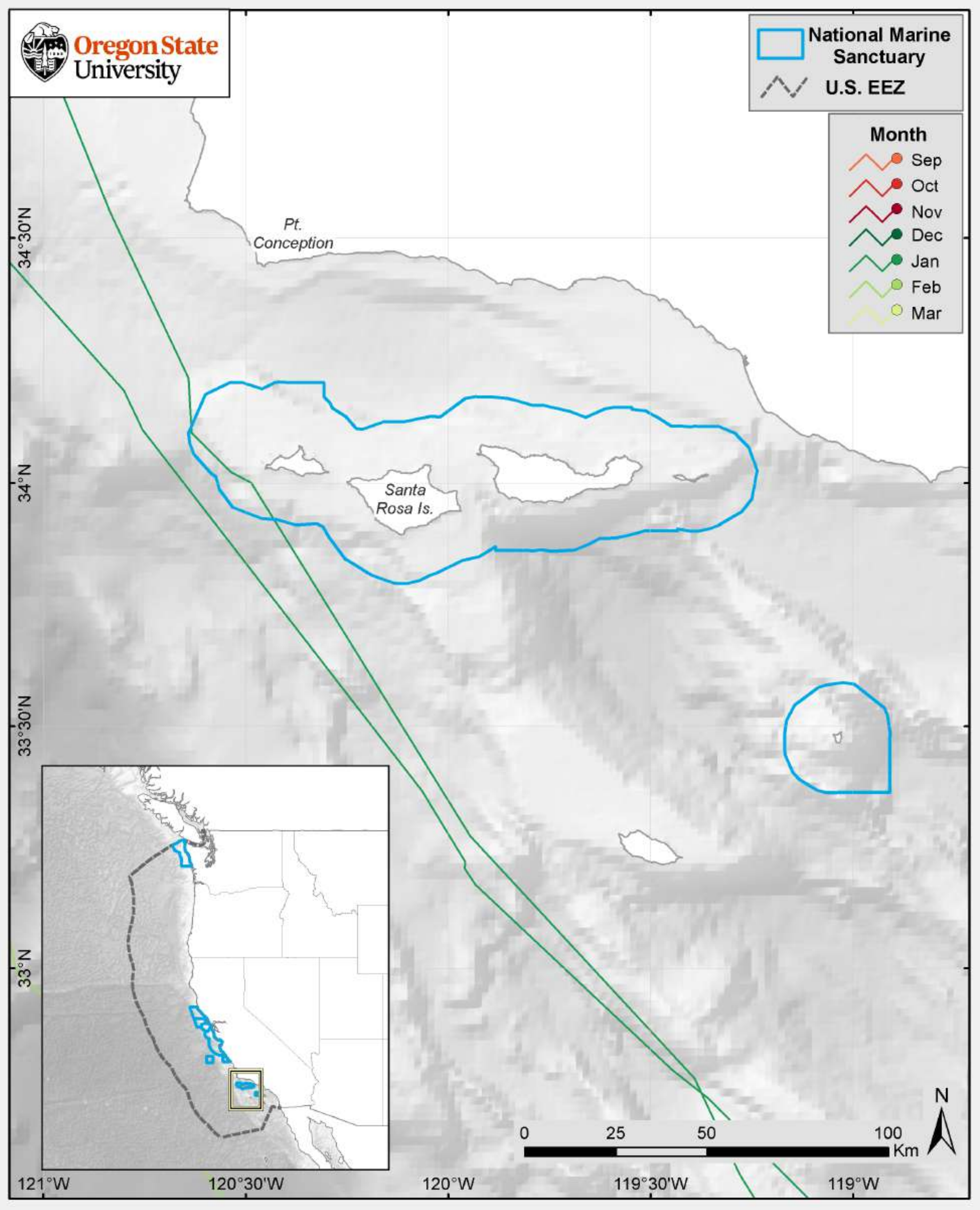


Figure 20. Satellite-monitored tracks in the Channel Islands NMS for a humpback whale tagged off Washington in September 2019 (1 DM tag).

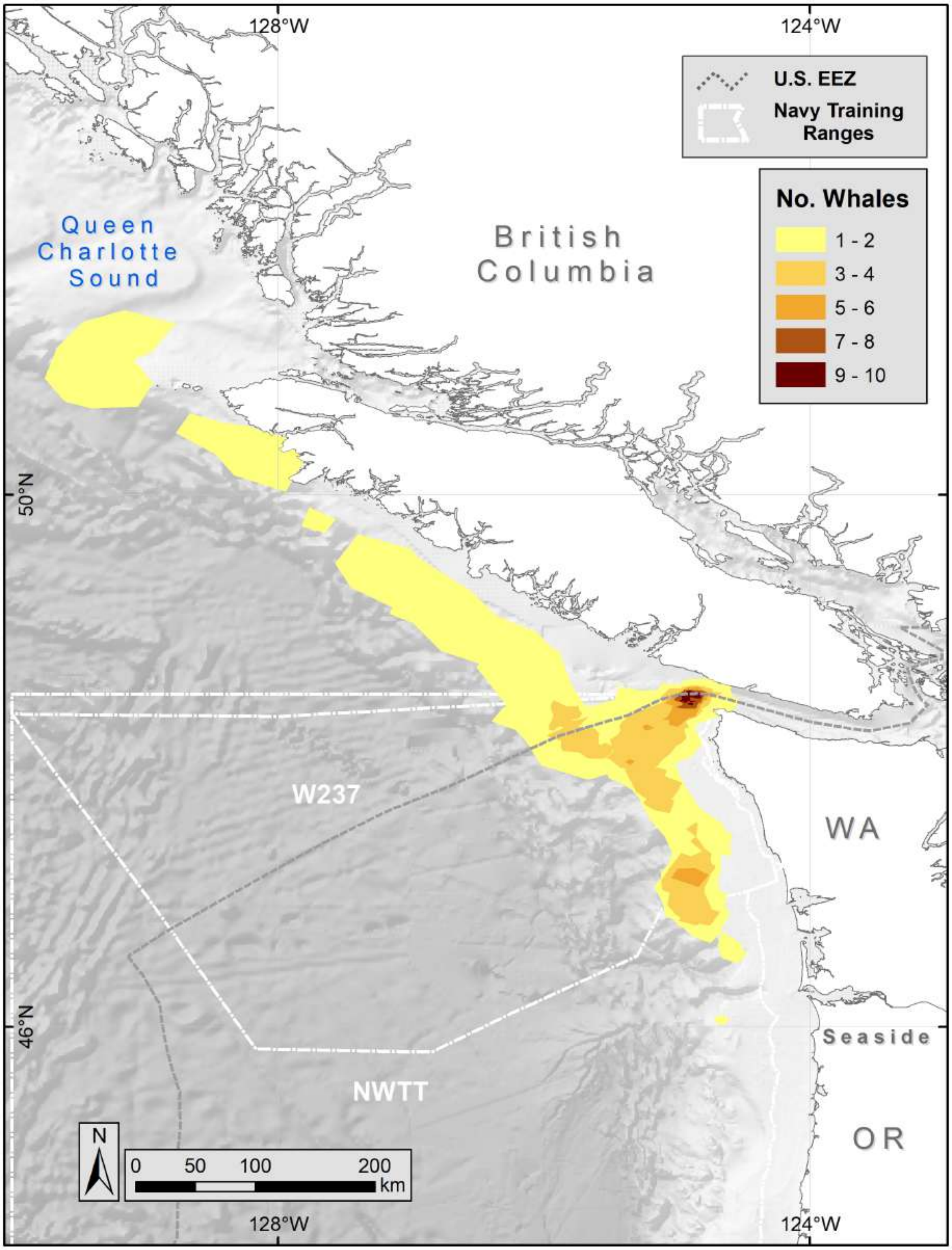


Figure 21. Feeding area HRs for 12 humpback whales tagged off Washington in September and October 2019. Shading represents the number of individual whales with overlapping HRs.

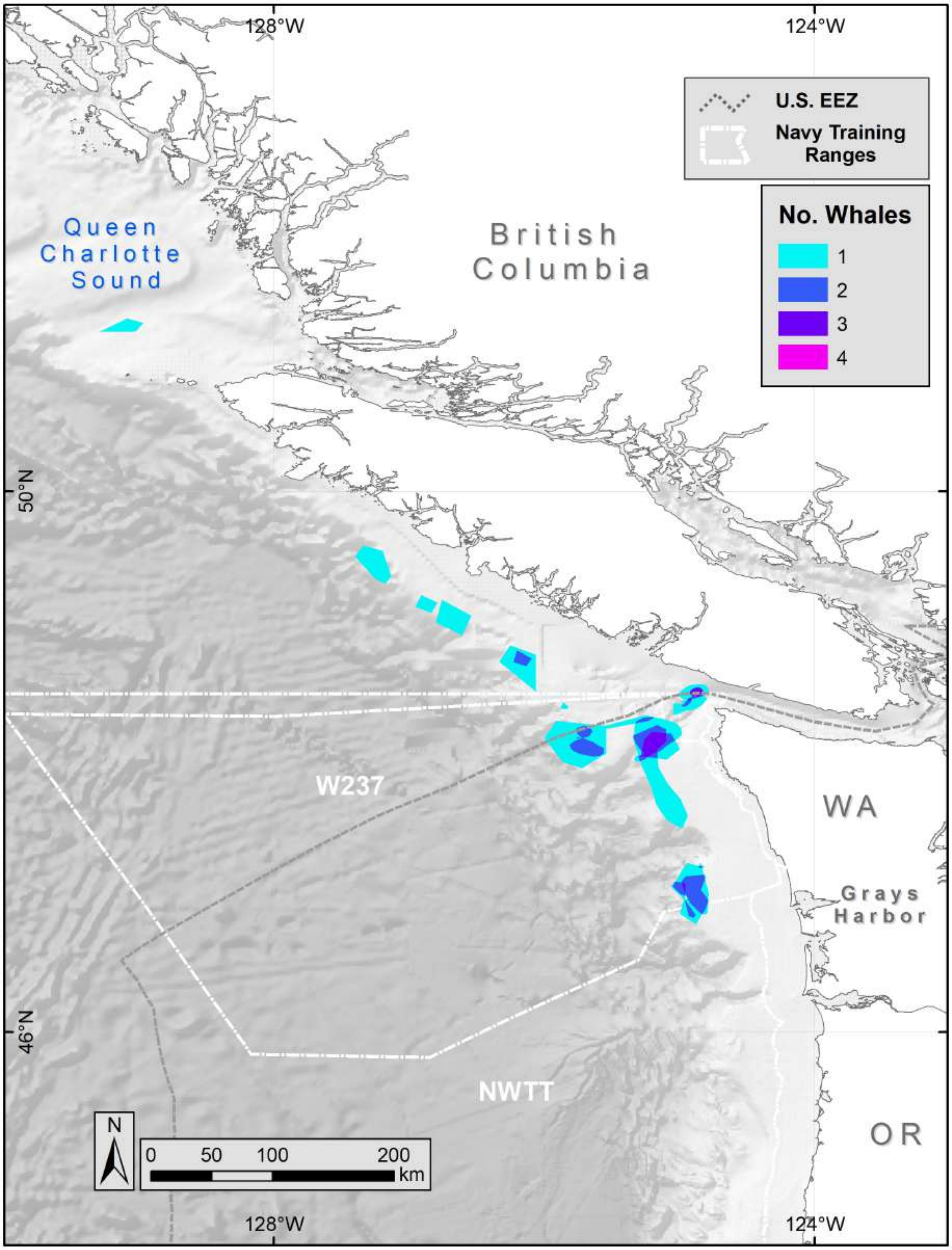


Figure 22. Feeding area CAUs for 12 humpback whales tagged off Washington in September and October 2019. Shading represents the number of individual whales with overlapping CAUs.

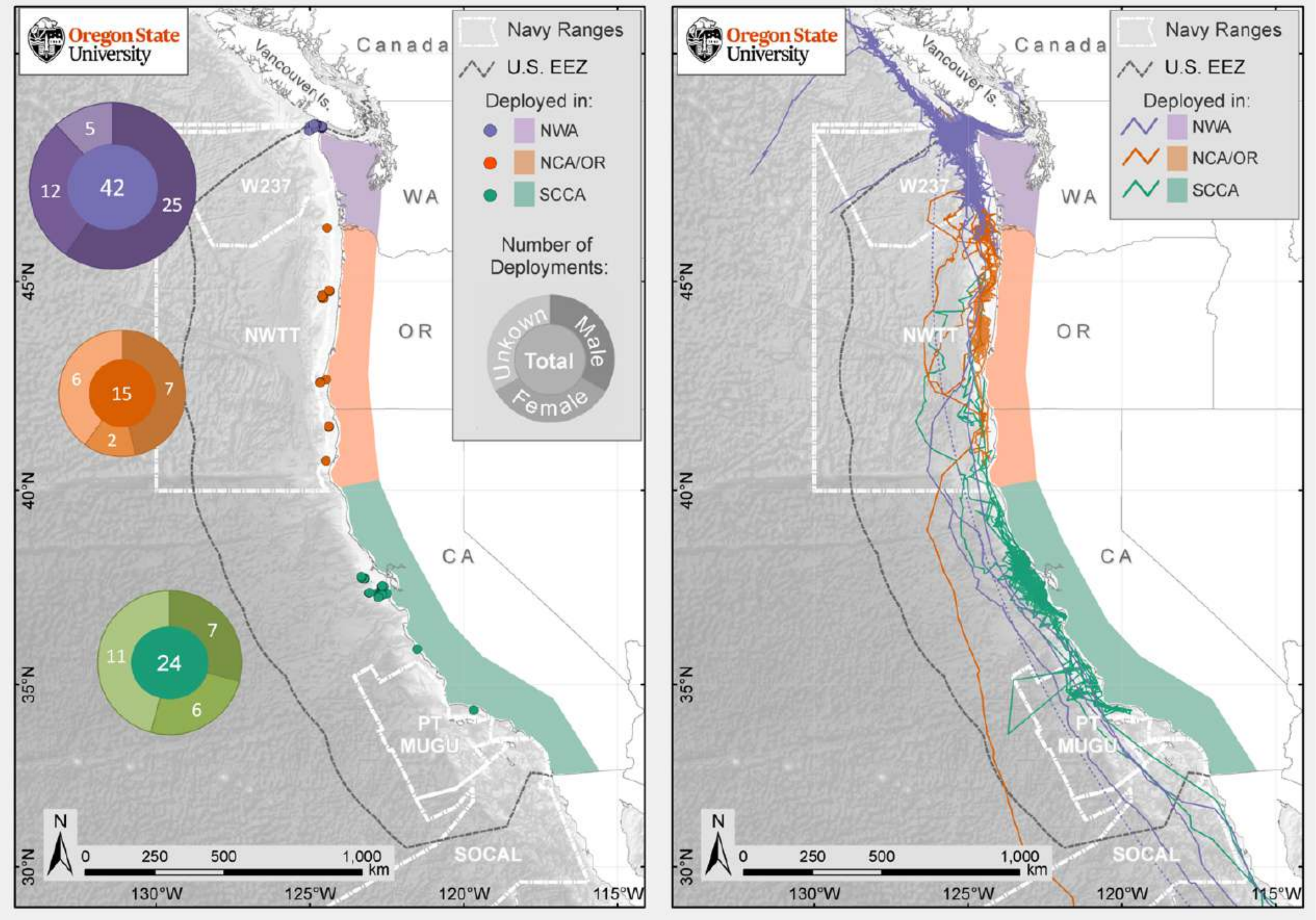


Figure 23. Locations of tag deployments by region and sex (left panel) and satellite-monitored tracks by tagging region (right panel) for humpback whales tagged by OSU in southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA) from 2004 to 2019.

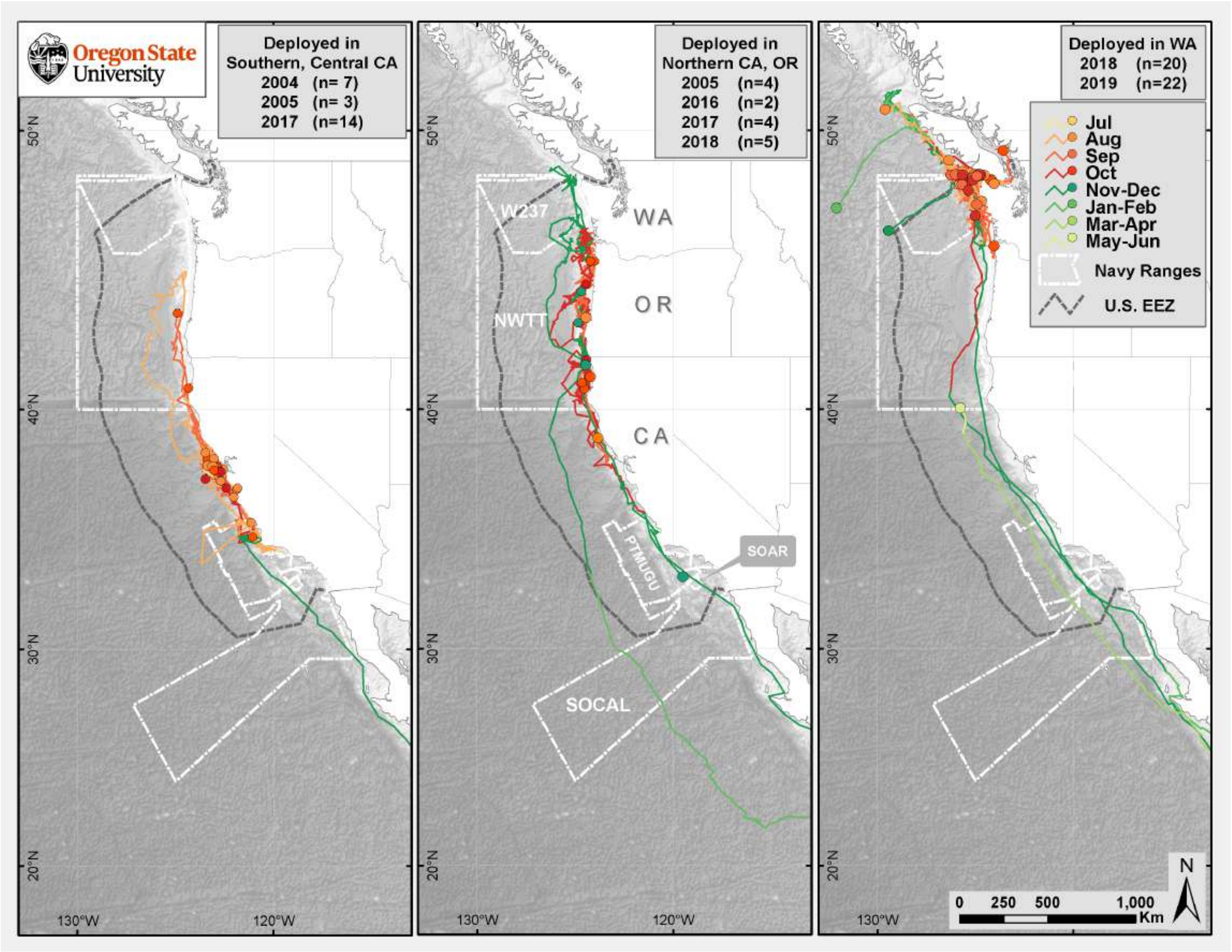


Figure 24. Satellite-monitored tracks for humpback whales tagged in SCCA in 2004, 2005, and 2017 (24 tags; left panel), in NCA/OR in 2005, and 2016 to 2018 (15 tags; middle panel), and in NWA in 2018 to 2019 (42 tags; right panel).

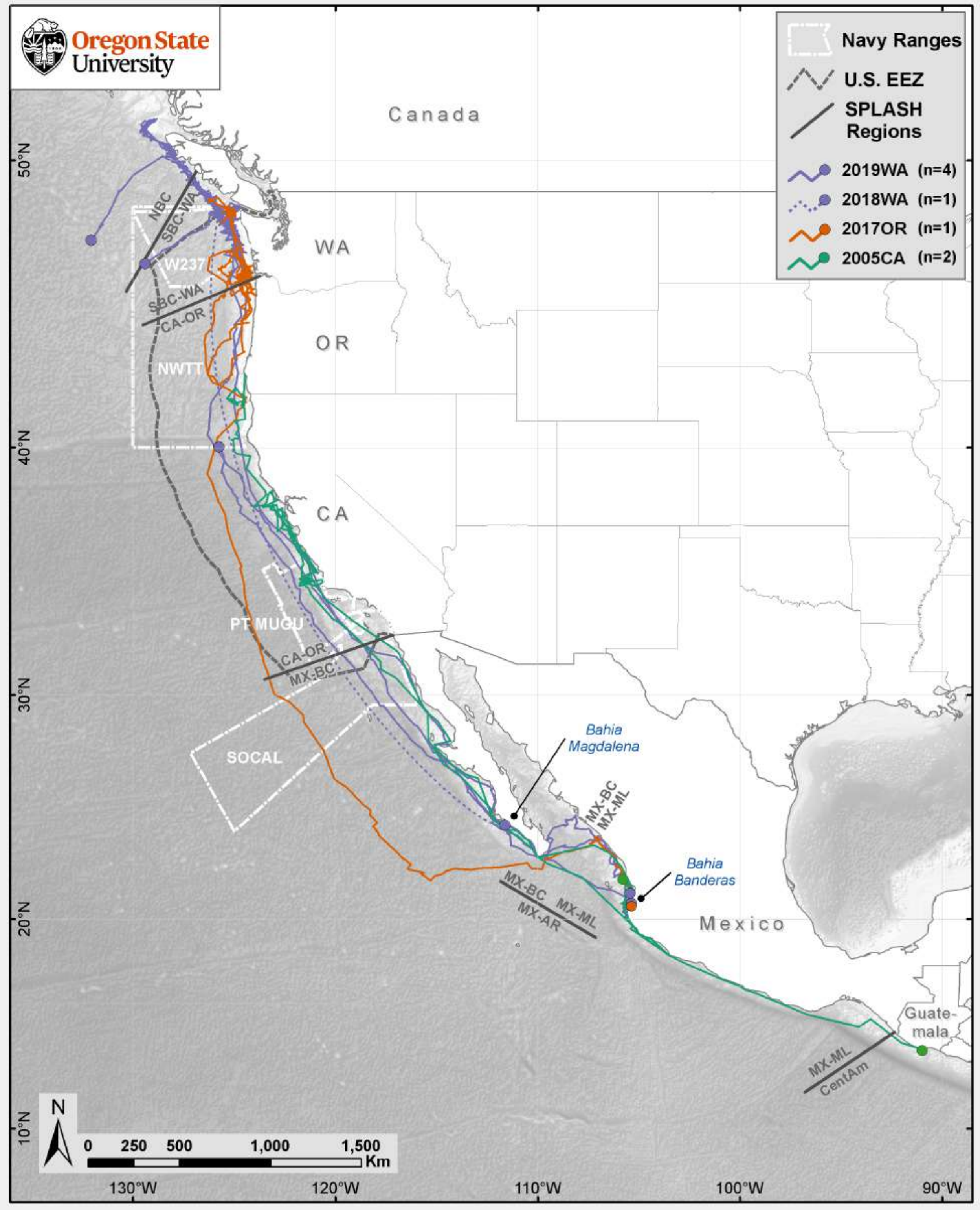


Figure 25. Satellite-monitored tracks of humpback whales tagged off the US West Coast from 2005 to 2019, highlighting migration routes and destination. Circles indicate each track's last location.

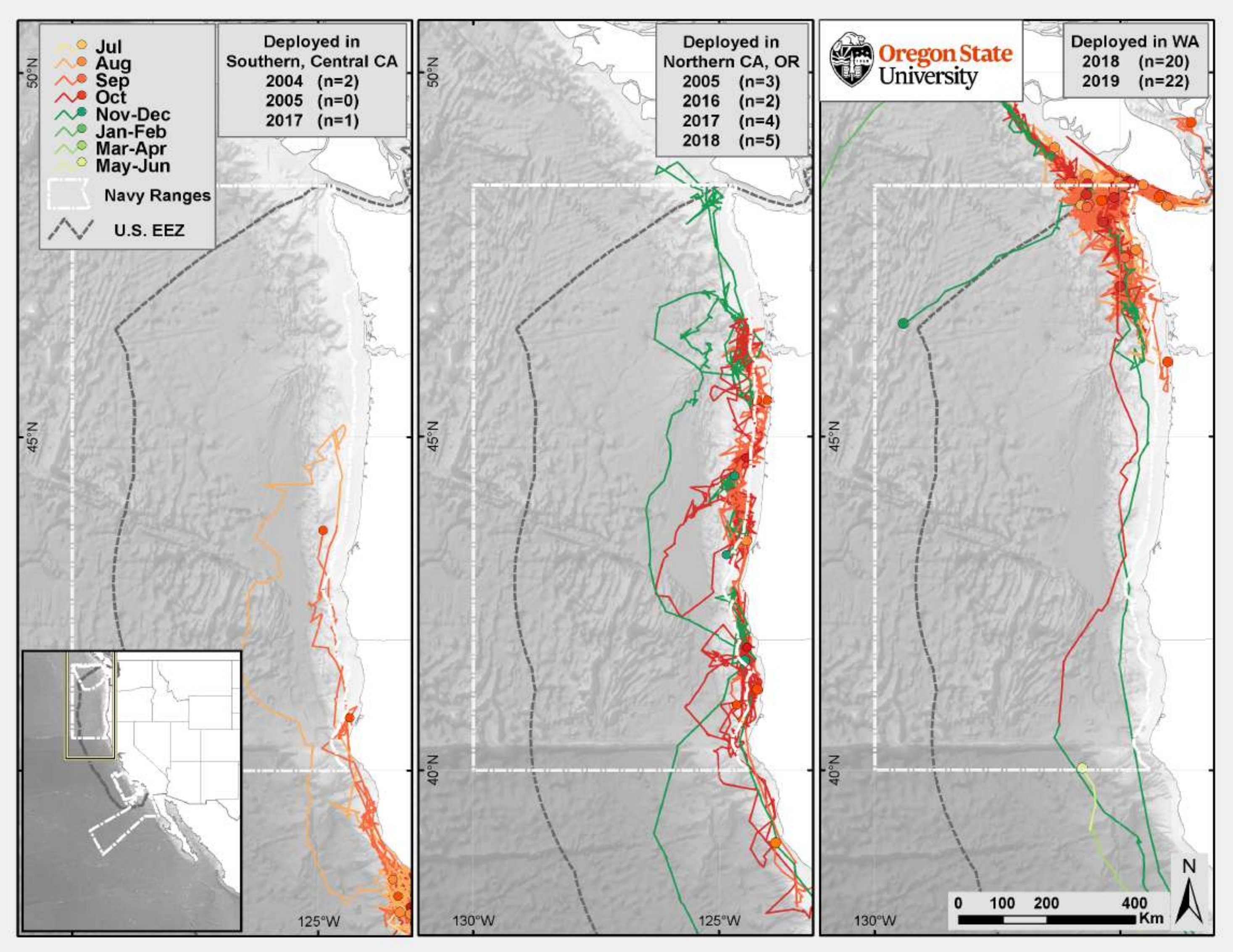


Figure 26. Satellite-monitored tracks in NWTT for humpback whales tagged in SCCA in 2004, 2005, and 2017 (3 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (14 tags; middle panel), and in NWA in 2018 and 2019 (42 tags; right panel).

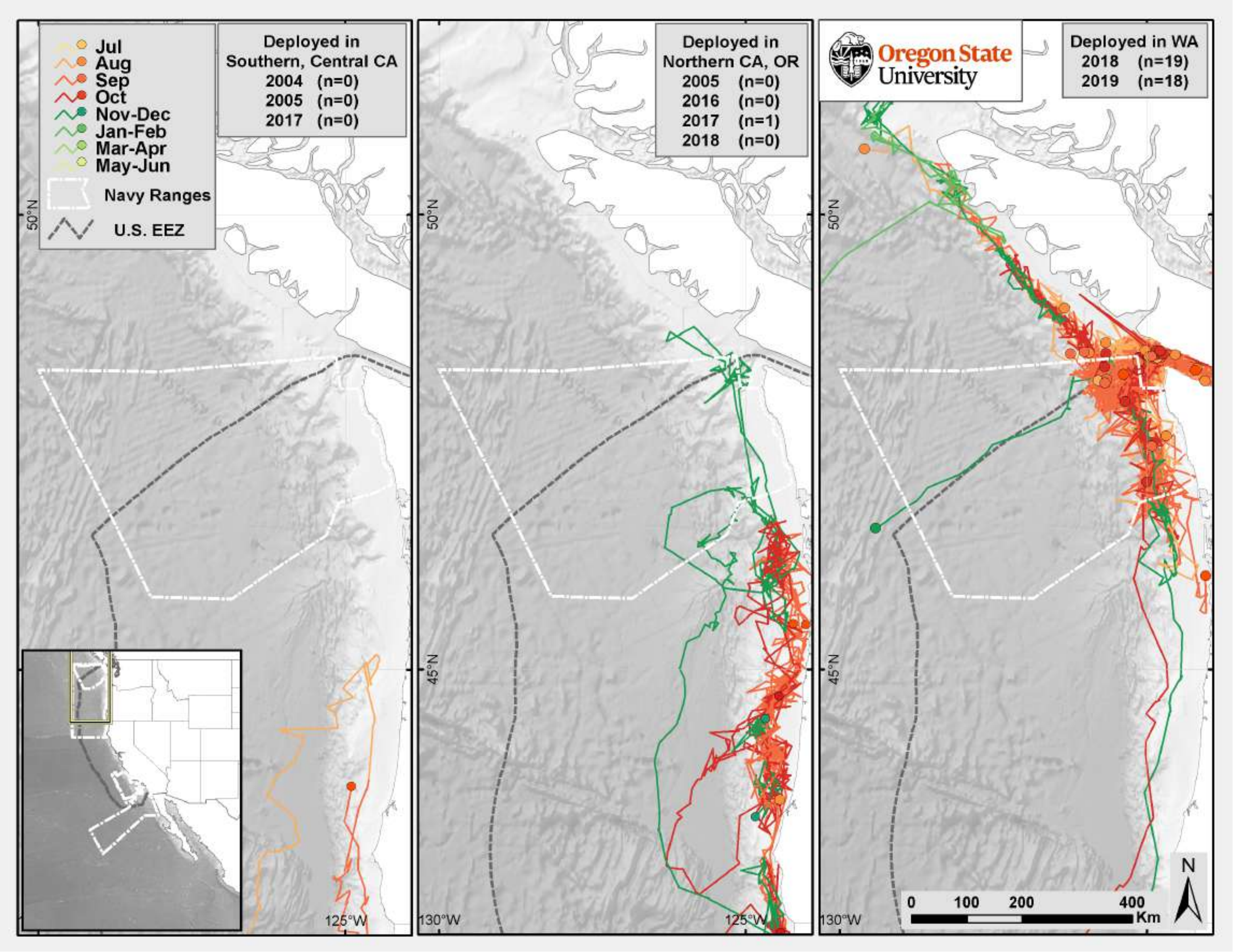


Figure 27. Satellite-monitored tracks in area W237 of the NWTT for humpback whales tagged in SCCA in 2004, 2005, and 2017 (0 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (1 tag; middle panel), and in NWA in 2018 and 2019 (37 tags; right panel).

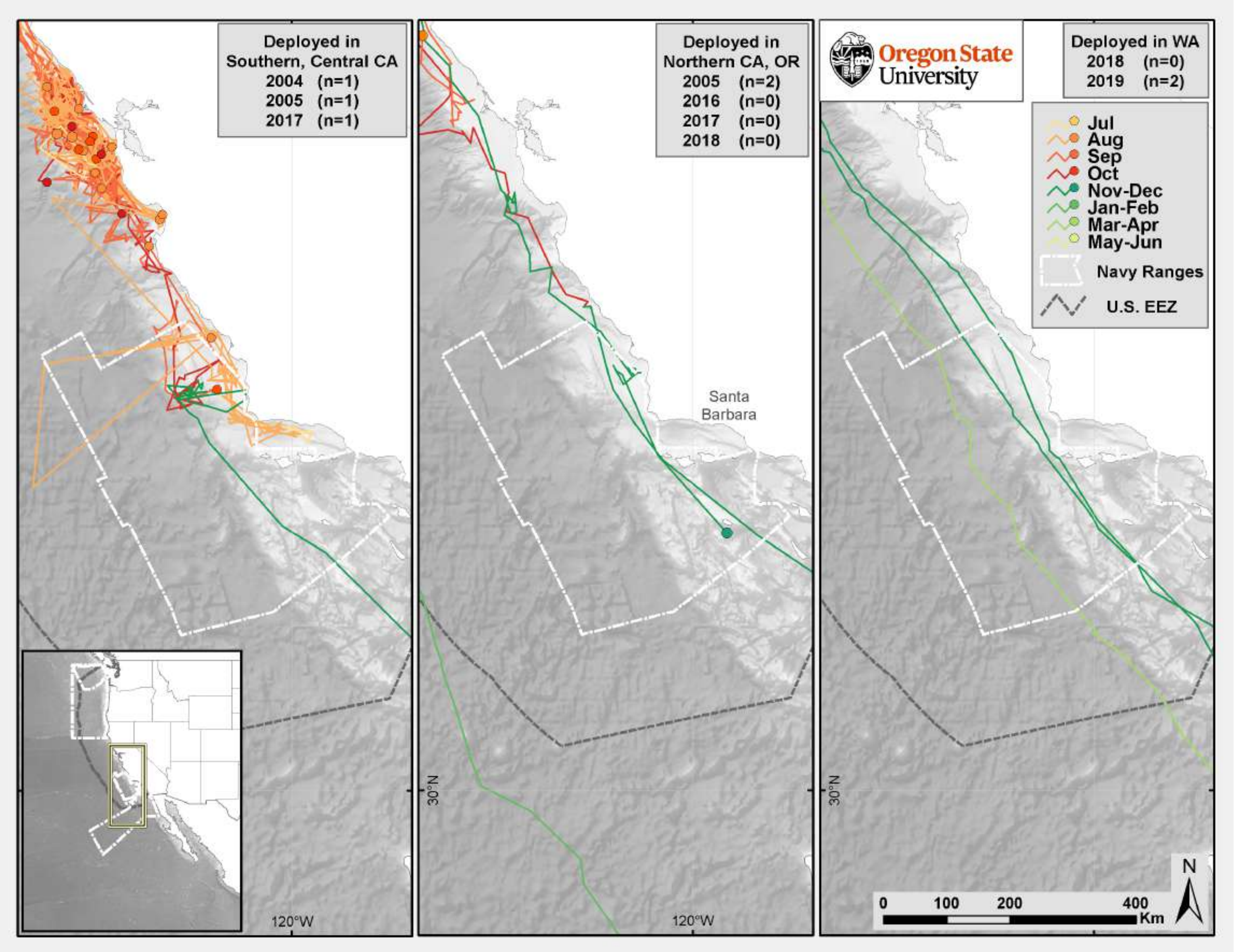


Figure 28. Satellite-monitored tracks in PT MUGU for humpback whales tagged in SCCA in 2004, 2005, and 2017 (3 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (2 tags; middle panel), and in NWA in 2018 and 2019 (2 tags; right panel).

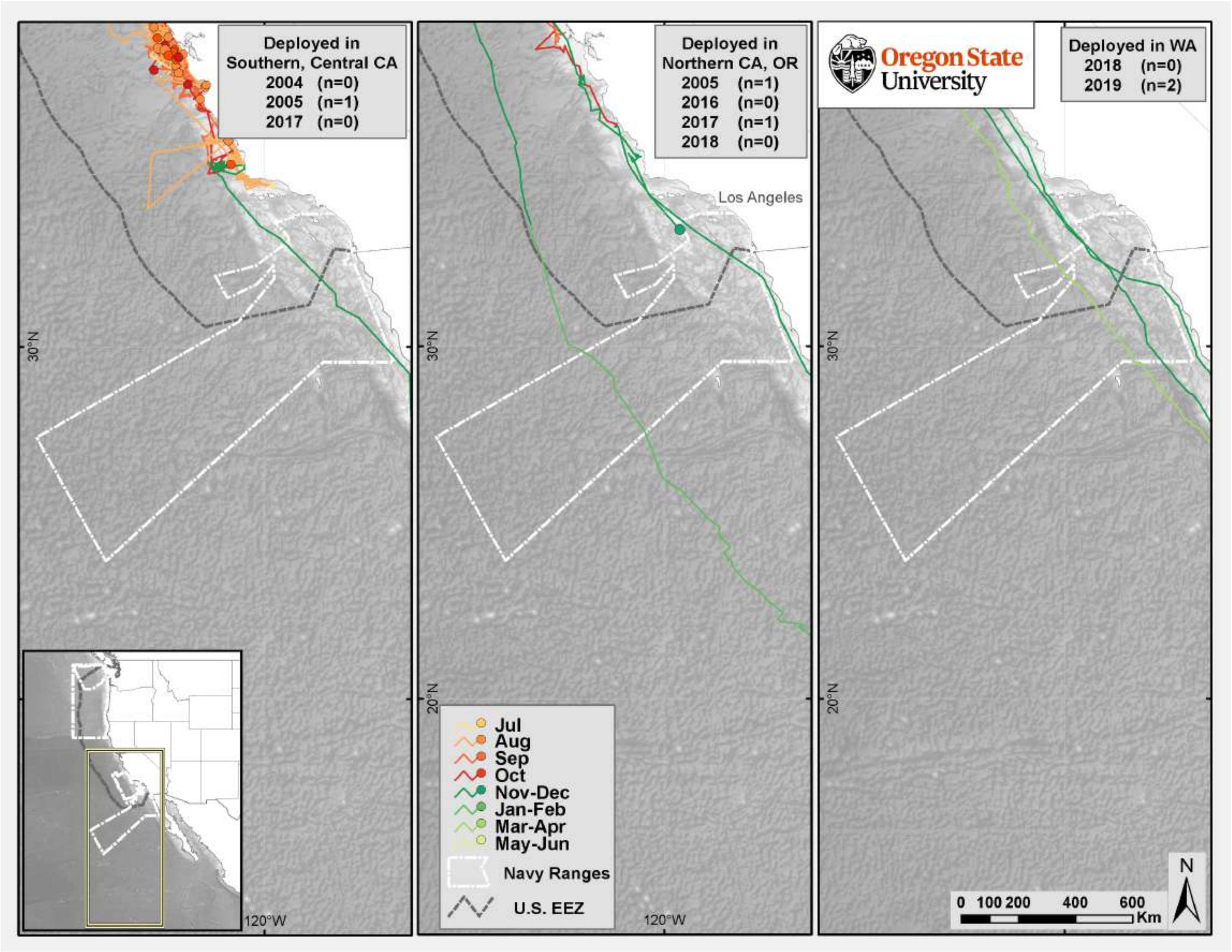


Figure 29. Satellite-monitored tracks in SOCAL for humpback whales tagged in SCCA in 2004, 2005, and 2017 (1 tag; left panel), in NCA/OR in 2005 and 2016 to 2018 (2 tags; middle panel), and in NWA in 2018 and 2019 (2 tags; right panel).

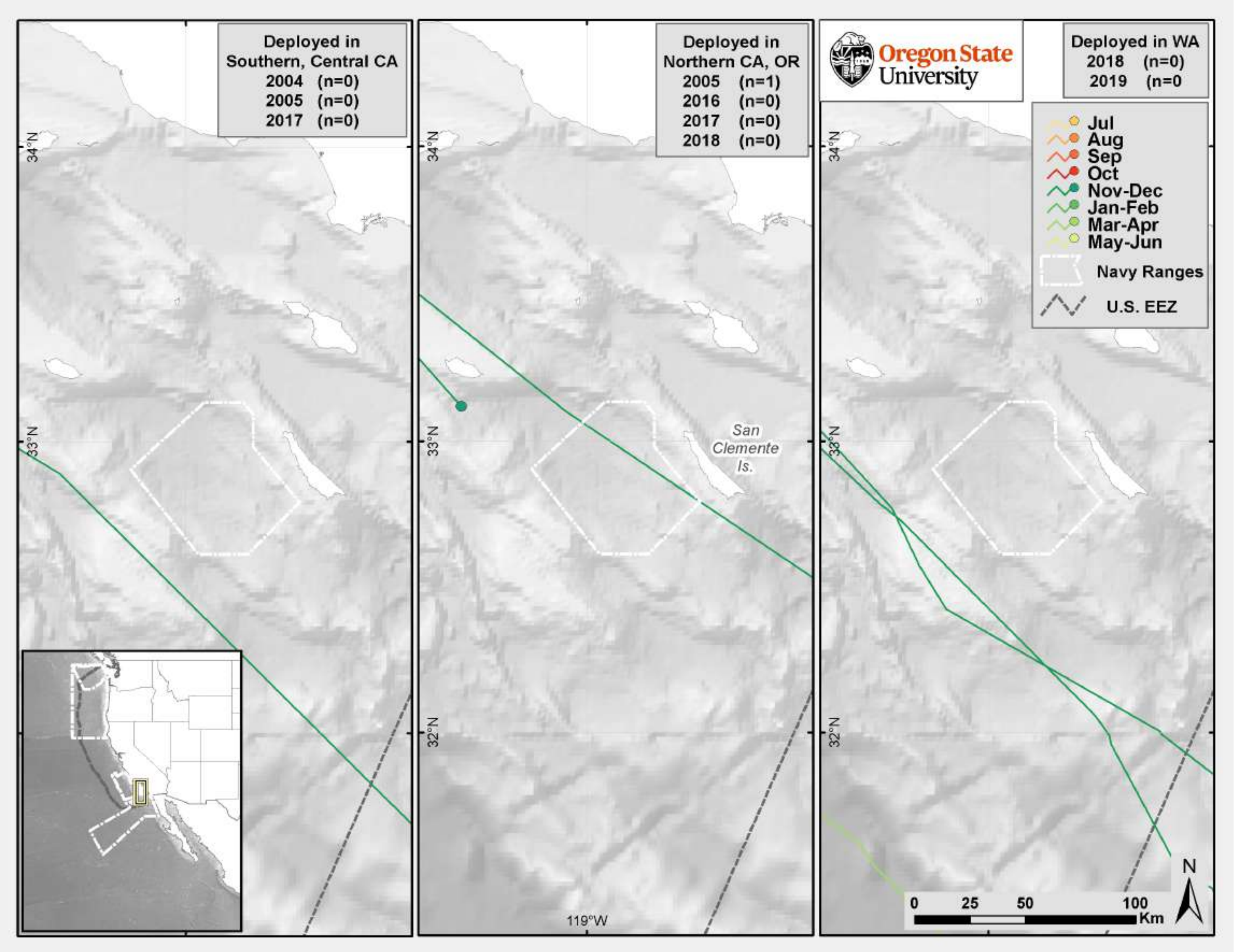


Figure 30. Satellite-monitored tracks in SOAR for humpback whales tagged in SCCA in 2004, 2005, and 2017 (0 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (1 tag; middle panel), and in NWA in 2018 and 2019 (0 tags; right panel).

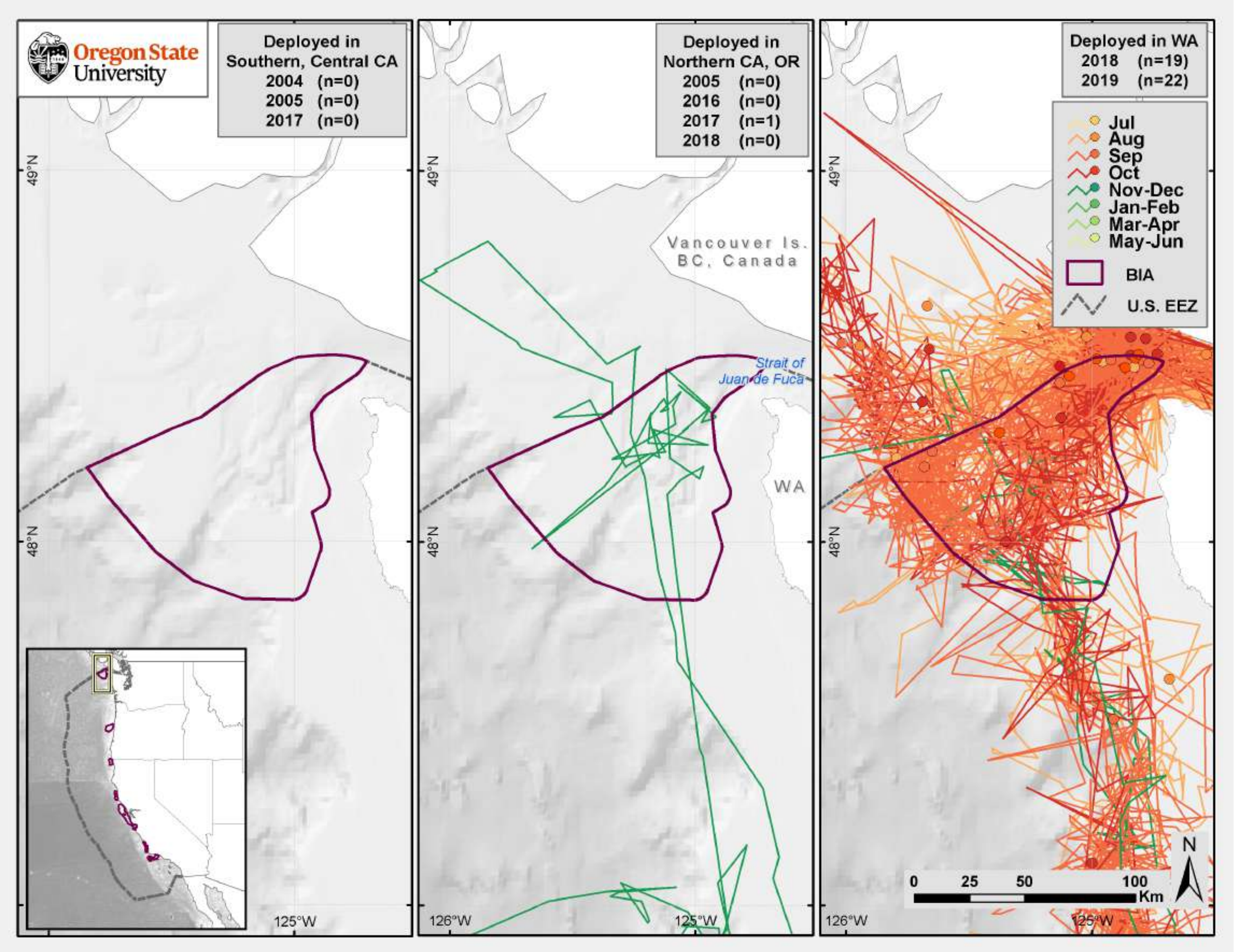


Figure 31. Satellite-monitored tracks in the Northern Washington BIA for humpback whales tagged in SCCA in 2004, 2005, and 2017 (0 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (1 tag; middle panel), and in NWA in 2018 and 2019 (41 tags; right panel).

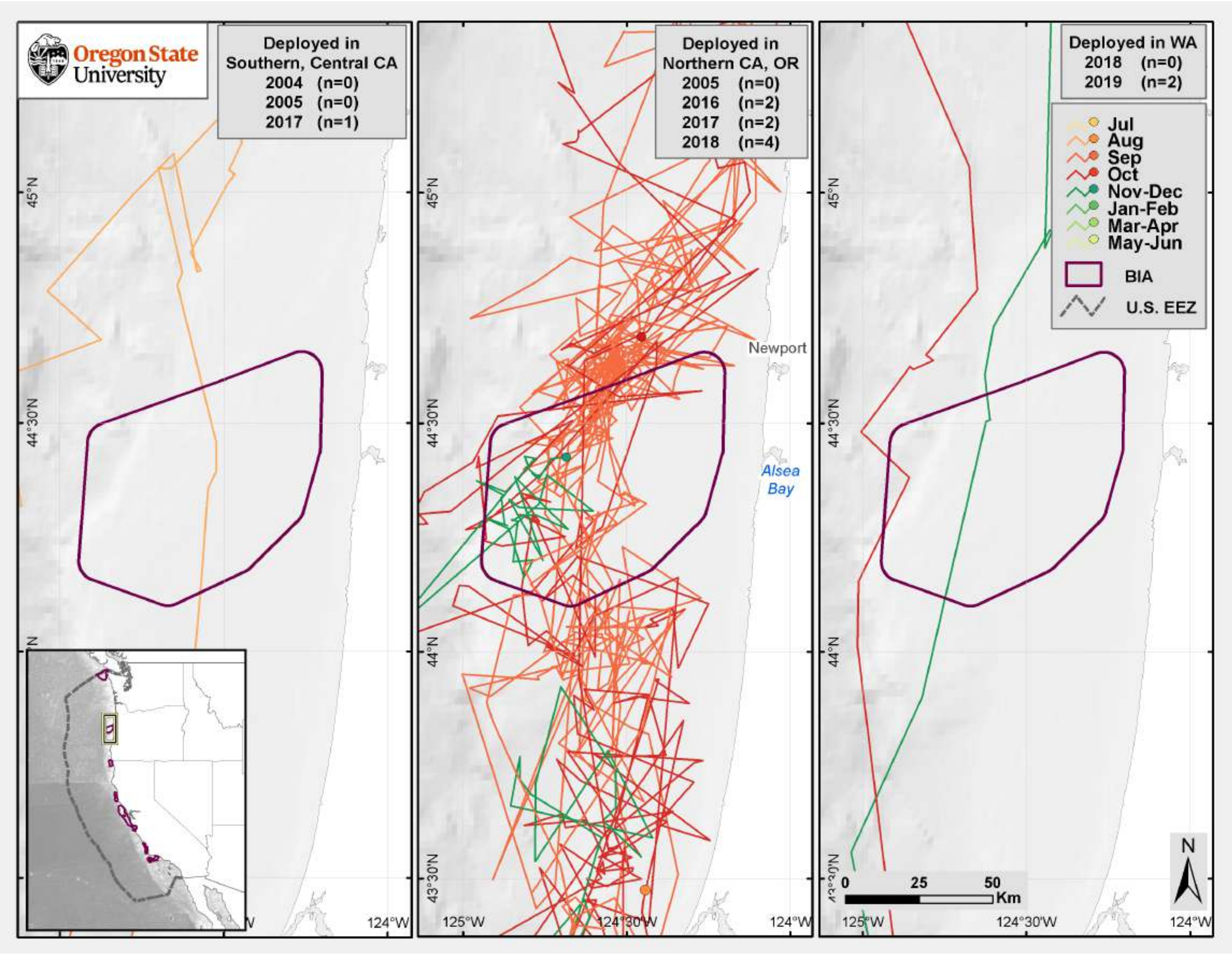


Figure 32. Satellite-monitored tracks in the Stonewall and Heceta Bank BIA for humpback whales tagged in SCCA in 2004, 2005, and 2017 (1 tag; left panel), in NCA/OR in 2005 and 2016 to 2018 (8 tags; middle panel), and in NWA in 2018 and 2019 (2 tags; right panel).

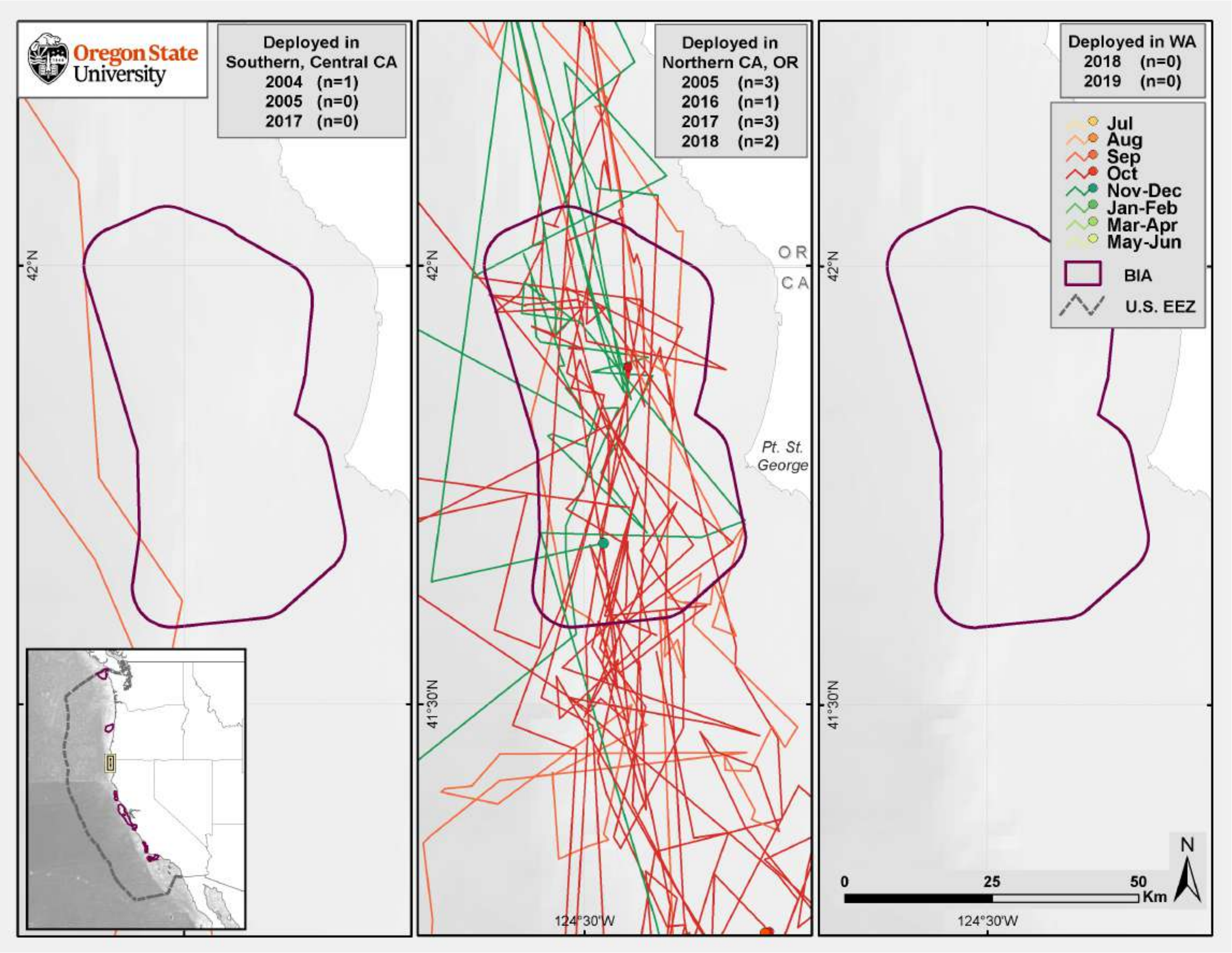


Figure 33. Satellite-monitored tracks in the Point St. George BIA for humpback whales tagged in SCCA in 2004, 2005, and 2017 (1 tag; left panel), in NCA/OR in 2005 and 2016 to 2018 (9 tags; middle panel), and in NWA in 2018 and 2019 (0 tags; right panel).

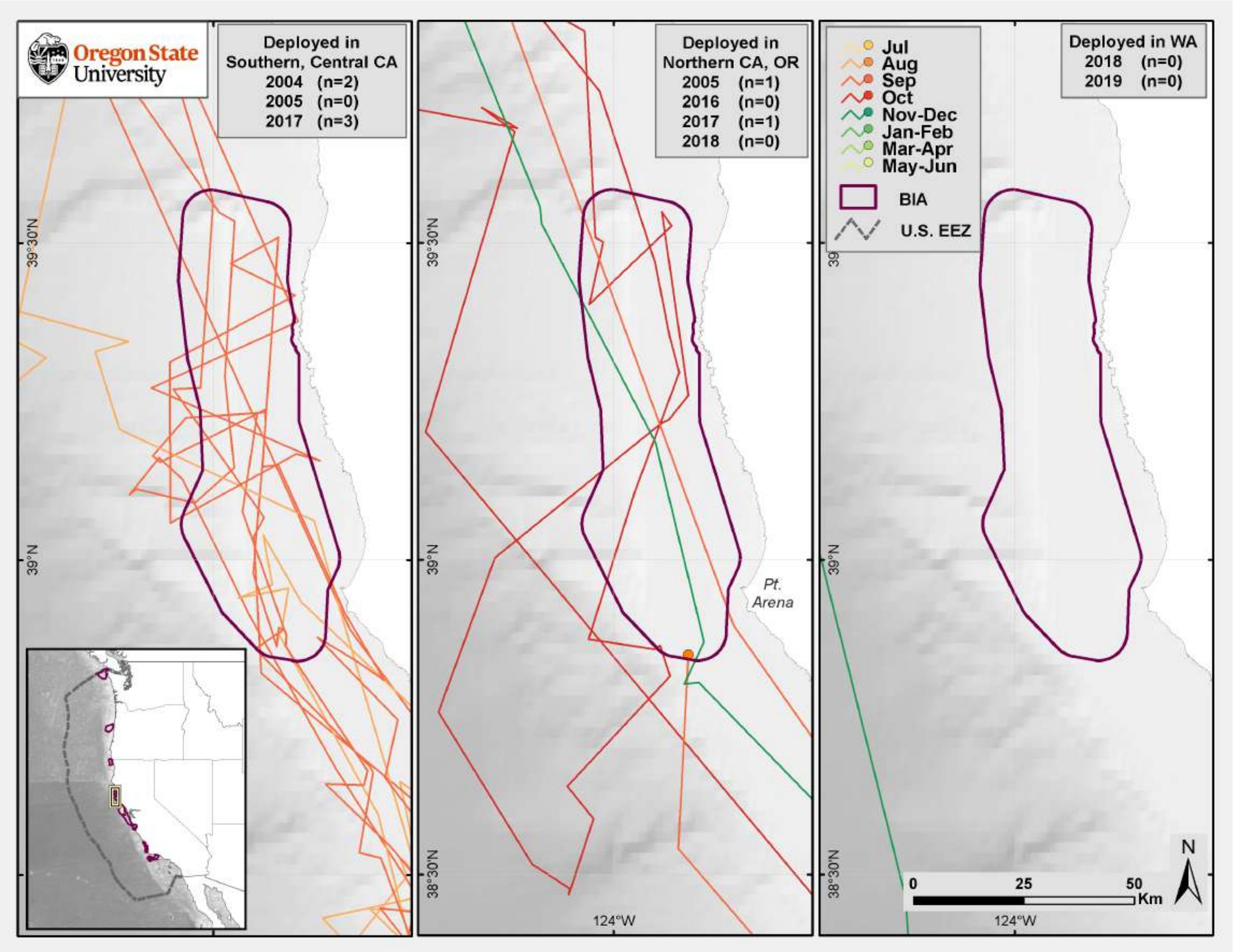


Figure 34. Satellite-monitored tracks in the Fort Bragg to Point Arena BIA for humpback whales tagged in SCCA in 2004, 2005, and 2017 (5 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (2 tags; middle panel), and in NWA in 2018 and 2019 (0 tags; right panel).

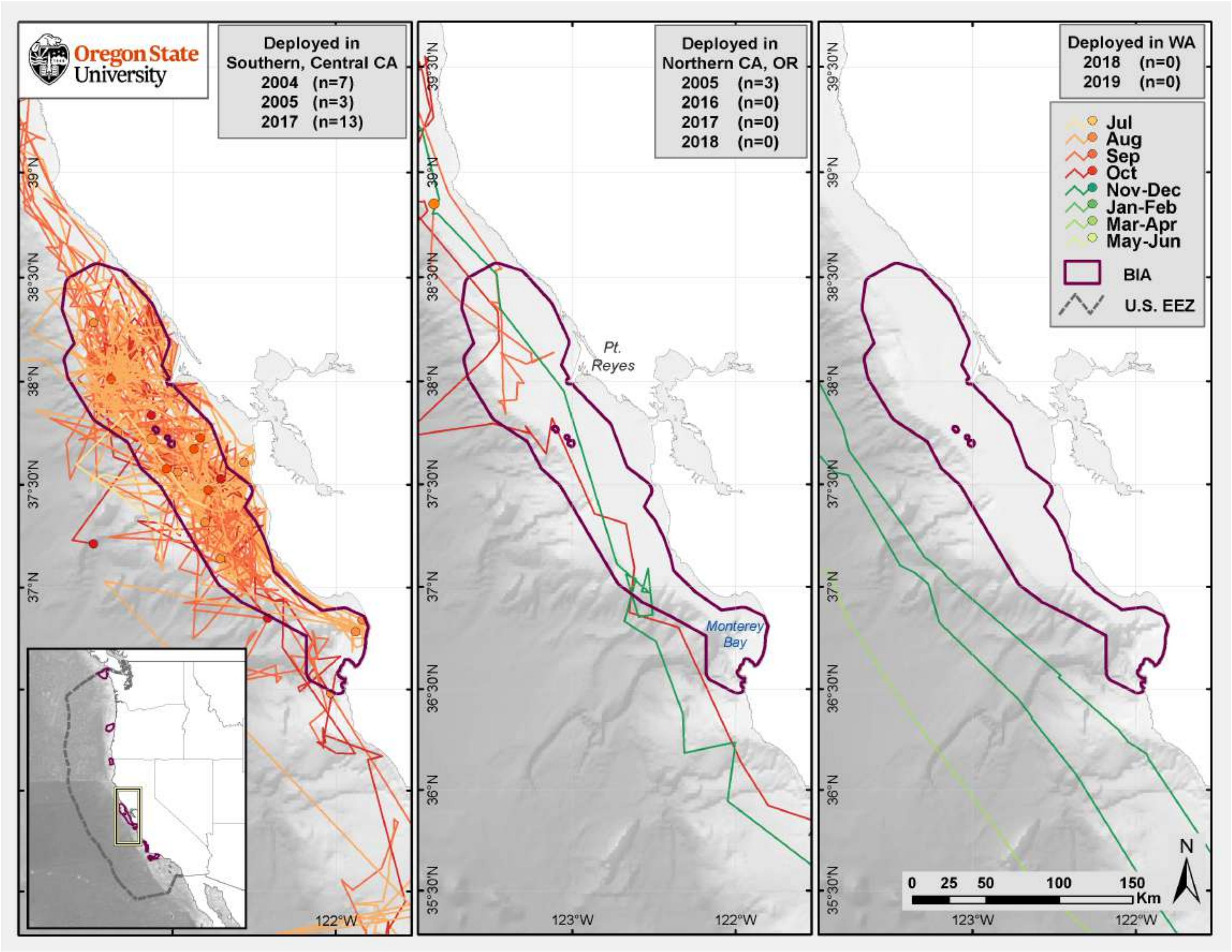


Figure 35. Satellite-monitored tracks in the Gulf of the Farallones-Monterey Bay BIA for humpback whales tagged in SCCA in 2004, 2005, and 2017 (23 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (3 tags; middle panel), and in NWA in 2018 and 2019 (0 tags; right panel).

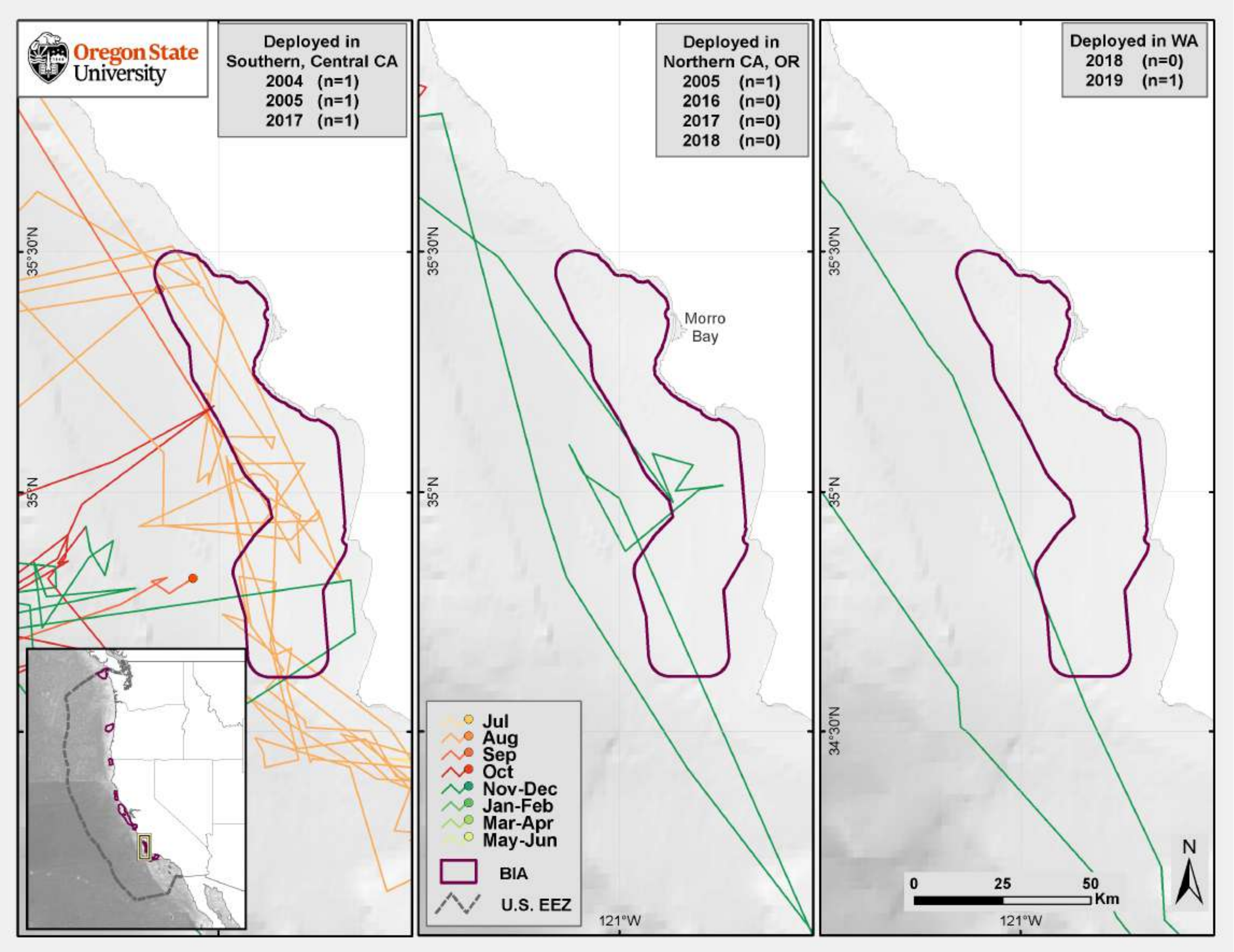


Figure 36. Satellite-monitored tracks in the Morro Bay to Point Sal BIA for humpback whales tagged in SCCA in 2004, 2005, and 2017 (3 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (1 tag; middle panel), and in NWA in 2018 and 2019 (1 tag; right panel).

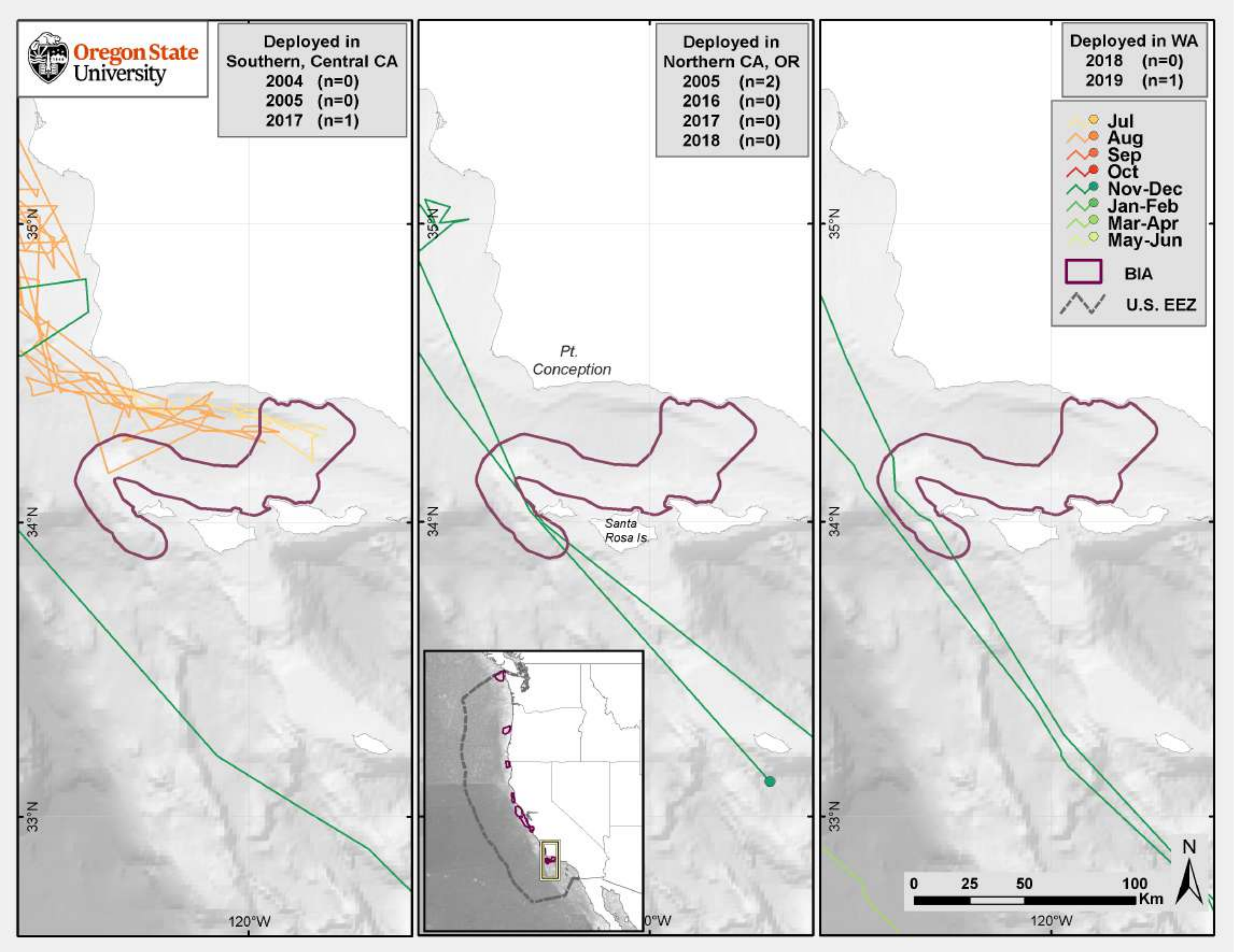


Figure 37. Satellite-monitored tracks in the Santa Barbara Channel-San Miguel BIA for humpback whales tagged in SCCA in 2004, 2005, and 2017 (1 tag; left panel), in NCA/OR in 2005 and 2016 to 2018 (2 tags; middle panel), and in NWA in 2018 and 2019 (1 tag; right panel).

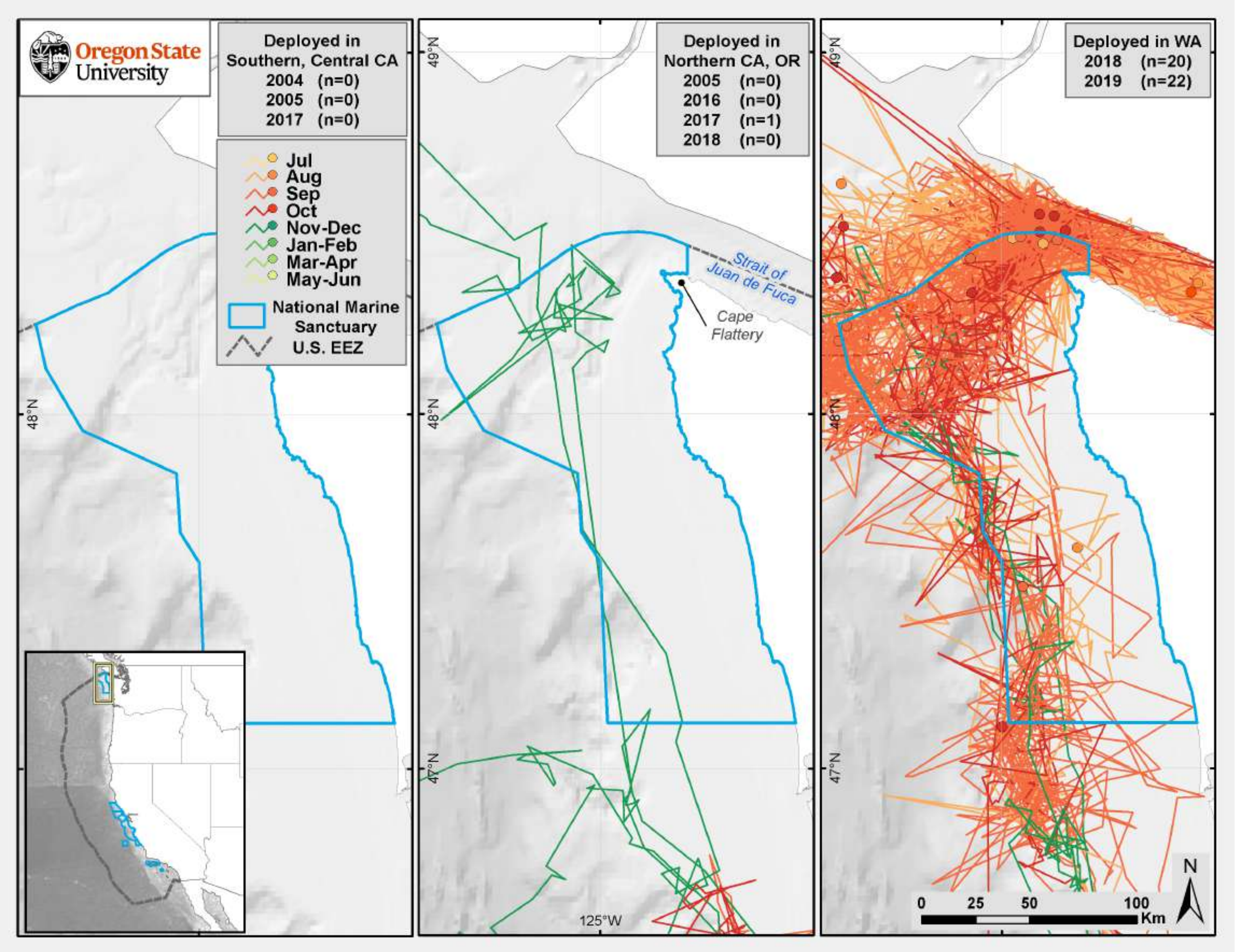


Figure 38. Satellite-monitored tracks in the Olympic Coast NMS for humpback whales tagged in SCCA in 2004, 2005, and 2017 (0 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (1 tag; middle panel), and in NWA in 2018 and 2019 (42 tags; right panel).

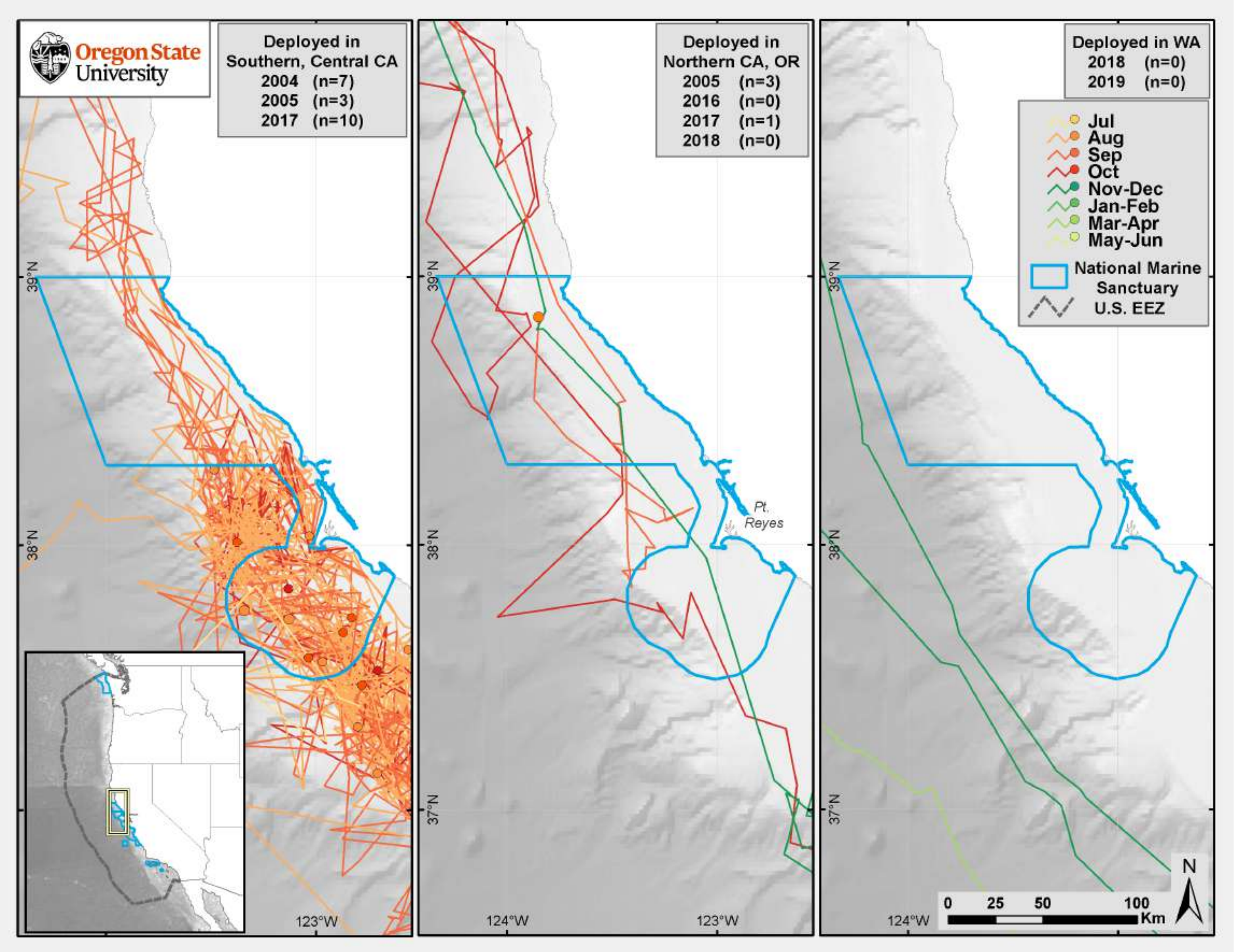


Figure 39. Satellite-monitored tracks in the Greater Farallones NMS for humpback whales tagged in SCCA in 2004, 2005, and 2017 (20 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (4 tags; middle panel), and in NWA in 2018 and 2019 (0 tags; right panel).

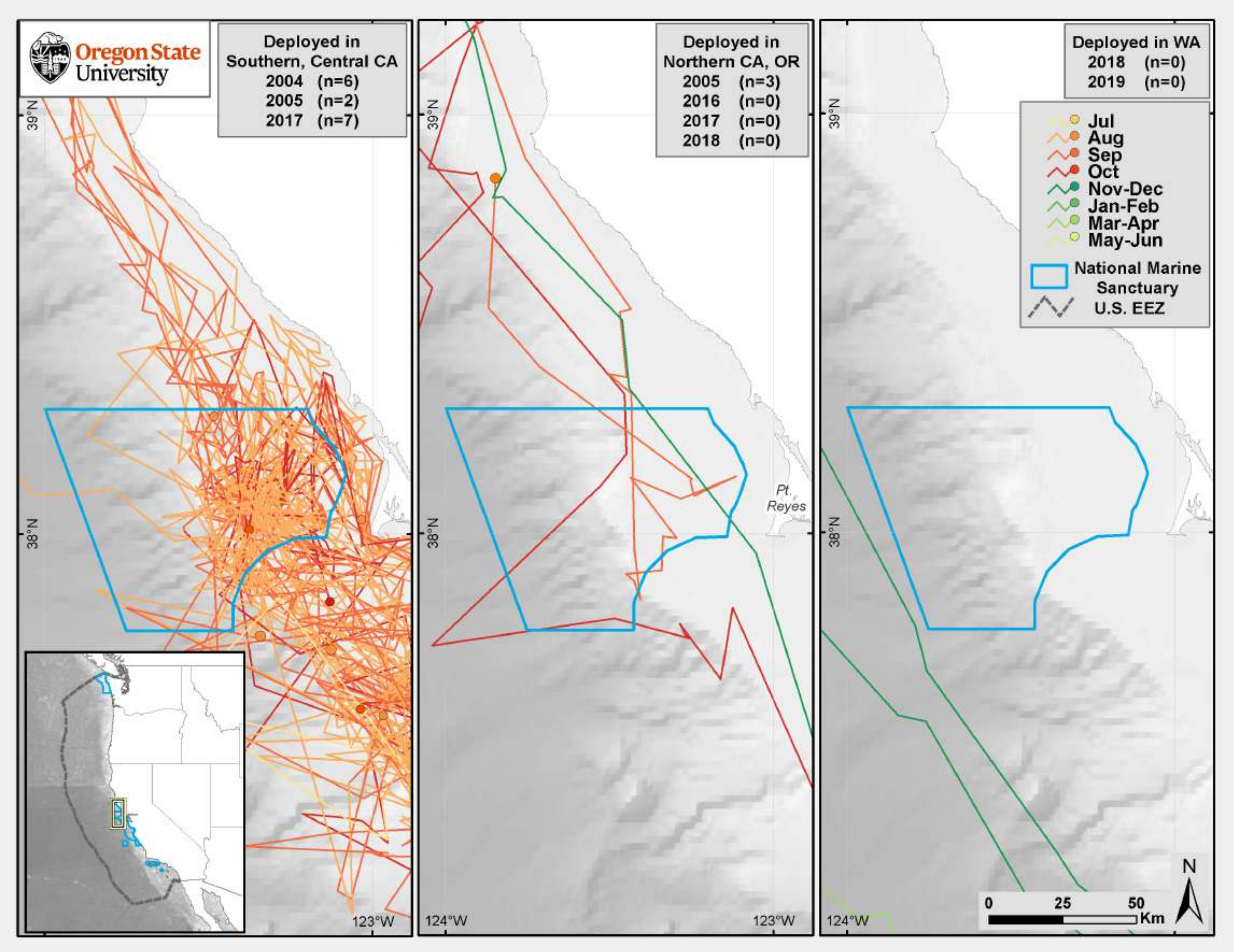


Figure 40. Satellite-monitored tracks in the Cordell Bank NMS for humpback whales tagged in SCCA in 2004, 2005, and 2017 (15 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (3 tags; middle panel), and in NWA in 2018 and 2019 (0 tags; right panel).

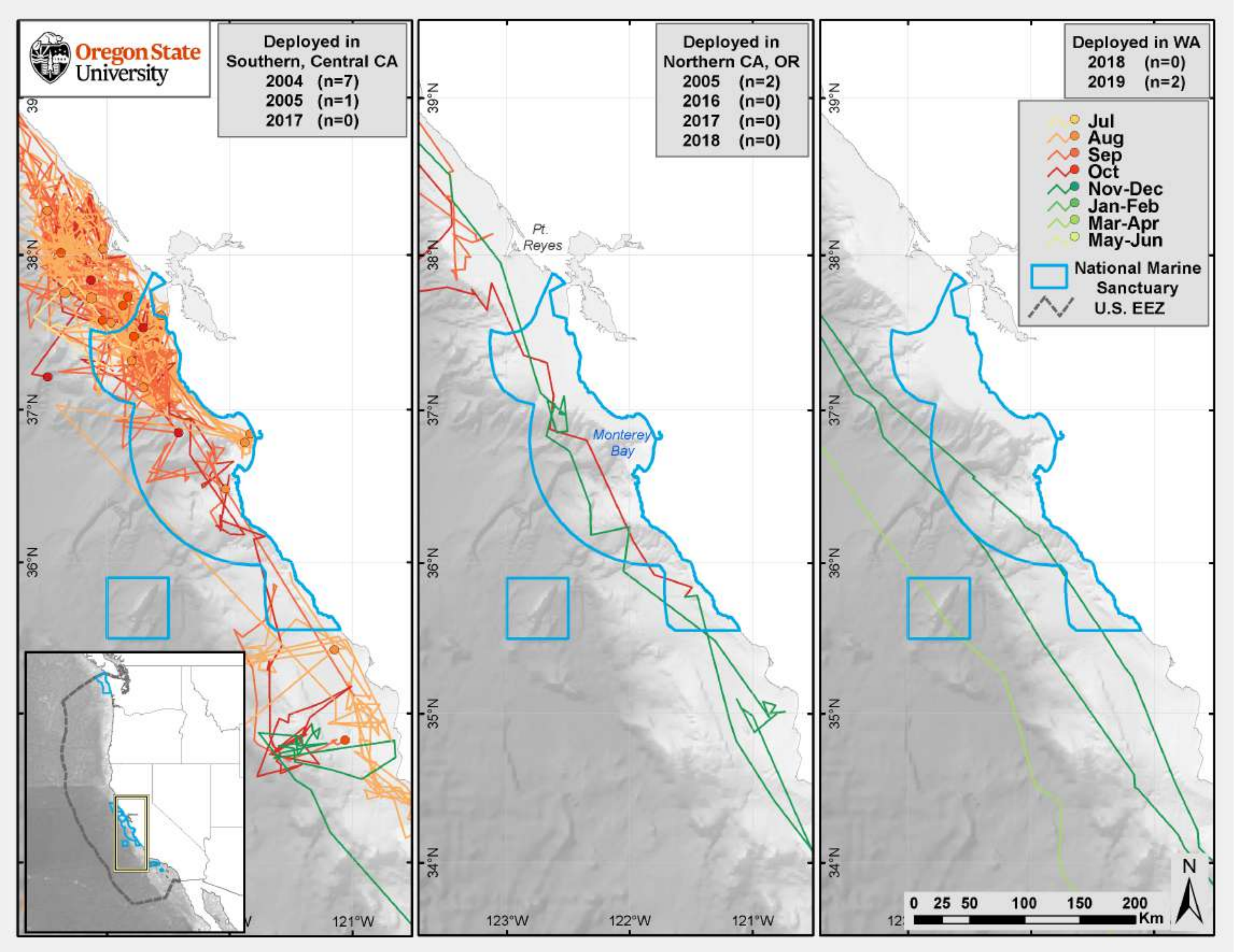


Figure 41. Satellite-monitored tracks in the Monterey Bay NMS for humpback whales tagged in SCCA in 2004, 2005, and 2017 (8 tags; left panel), in NCA/OR in 2005 and 2016 to 2018 (2 tags; middle panel), and in NWA in 2018 and 2019 (2 tags; right panel).

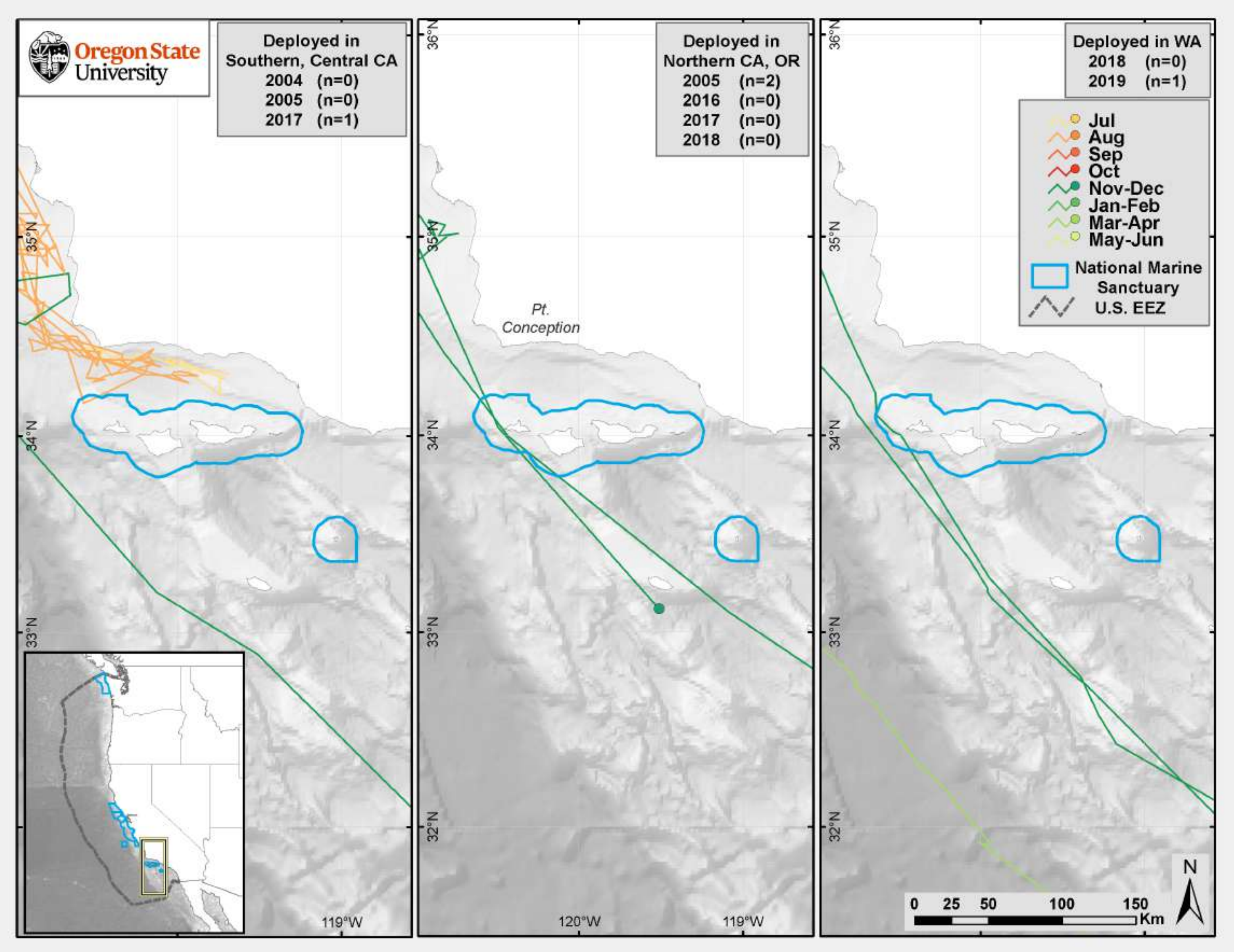


Figure 42. Satellite-monitored tracks in the Channel Islands NMS for humpback whales tagged in SCCA in 2004, 2005, and 2017 (1 tag; left panel), in NCA/OR in 2005 and 2016 to 2018 (2 tags; middle panel), and in NWA in 2018 and 2019 (1 tag; right panel).

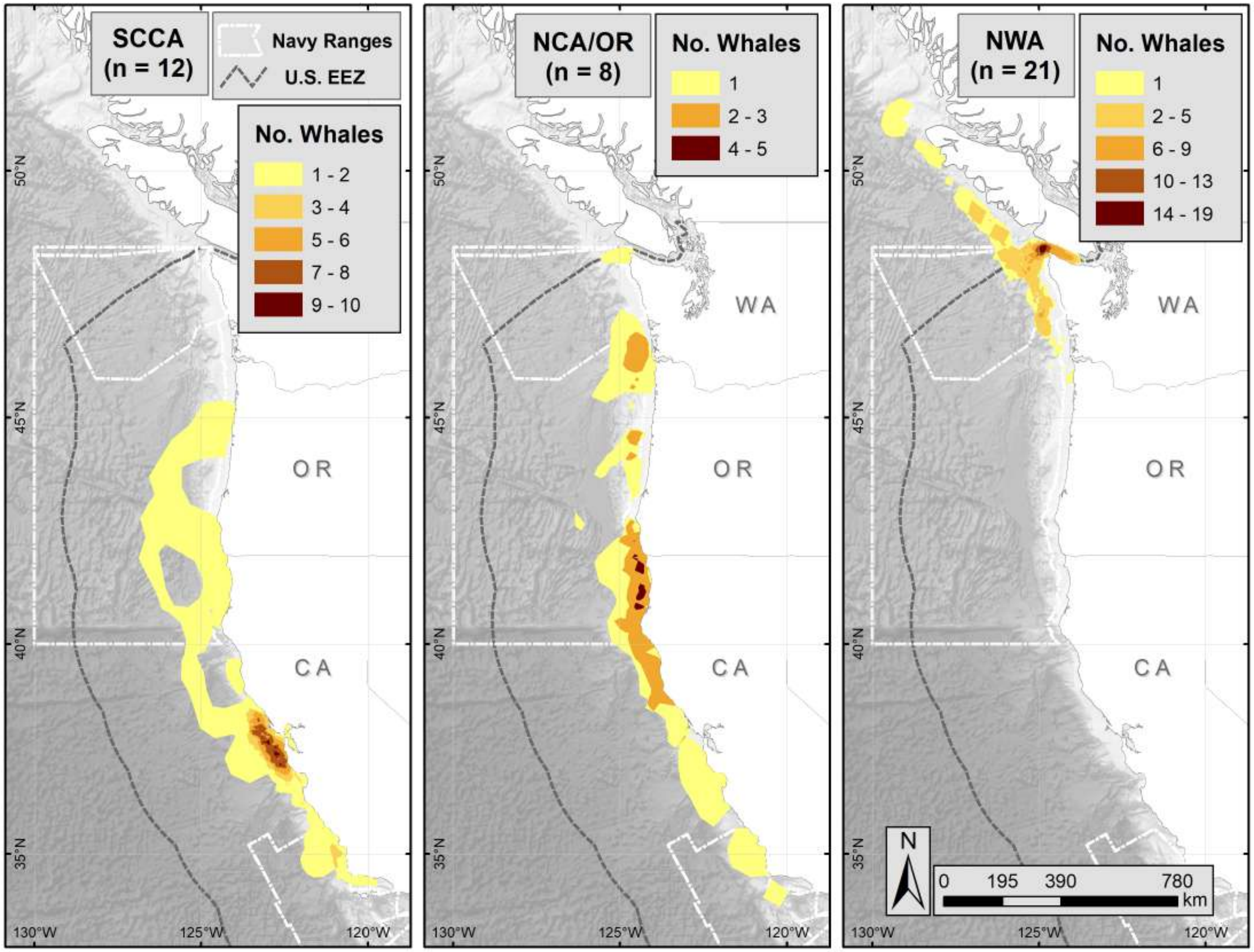


Figure 43. Feeding area HRs for humpback whales tagged off southern and central California (SCCA) in 2004-2005 and 2017 (12 whales; left panel), off northern California and Oregon (NCA/OR) in 2005, 2016-2018 (8 whales, middle panel), and northern Washington (NWA) in 2018-2019 (21 whales; right panel). Shading represents the number of individual whales with overlapping HRs.

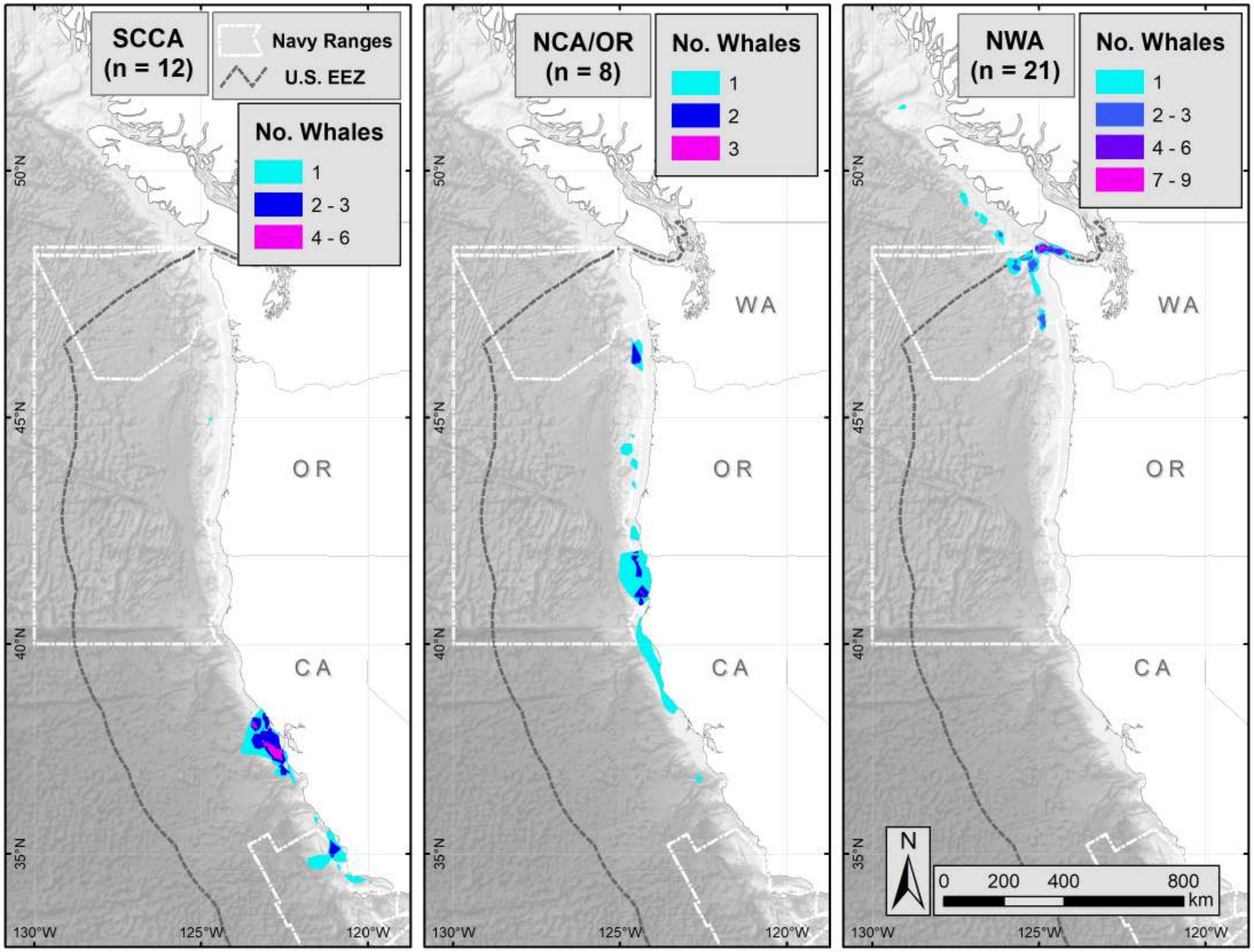


Figure 44. Feeding area CAUs for humpback whales tagged off southern and central California (SCCA) in 2004-2005 and 2017 (12 whales; left panel), off northern California and Oregon (NCA/OR) in 2005, 2016-2018 (8 whales, middle panel), and northern Washington (NWA) in 2018-2019 (21 whales; right panel). Shading represents the number of individual whales with overlapping CAUs.

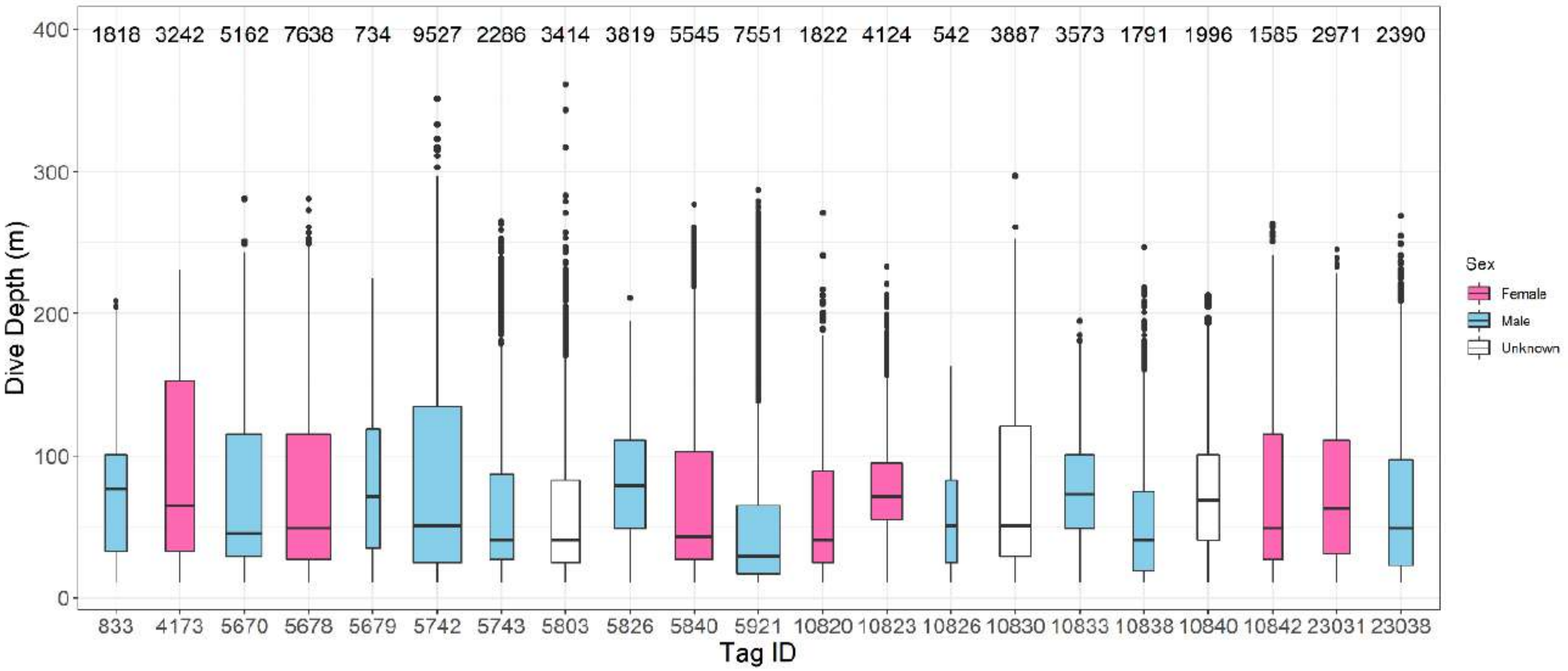


Figure 45. Dive depth in feeding areas of DM-tagged humpback whales (n = 21) tagged off Northern Washington, during September and October 2019. Boxes represent first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box. Sex of the animals are indicated by color. Note: tag #2019WA-10827 is not shown due to suspicious depth readings from that tag (see Methods Section 2.4).

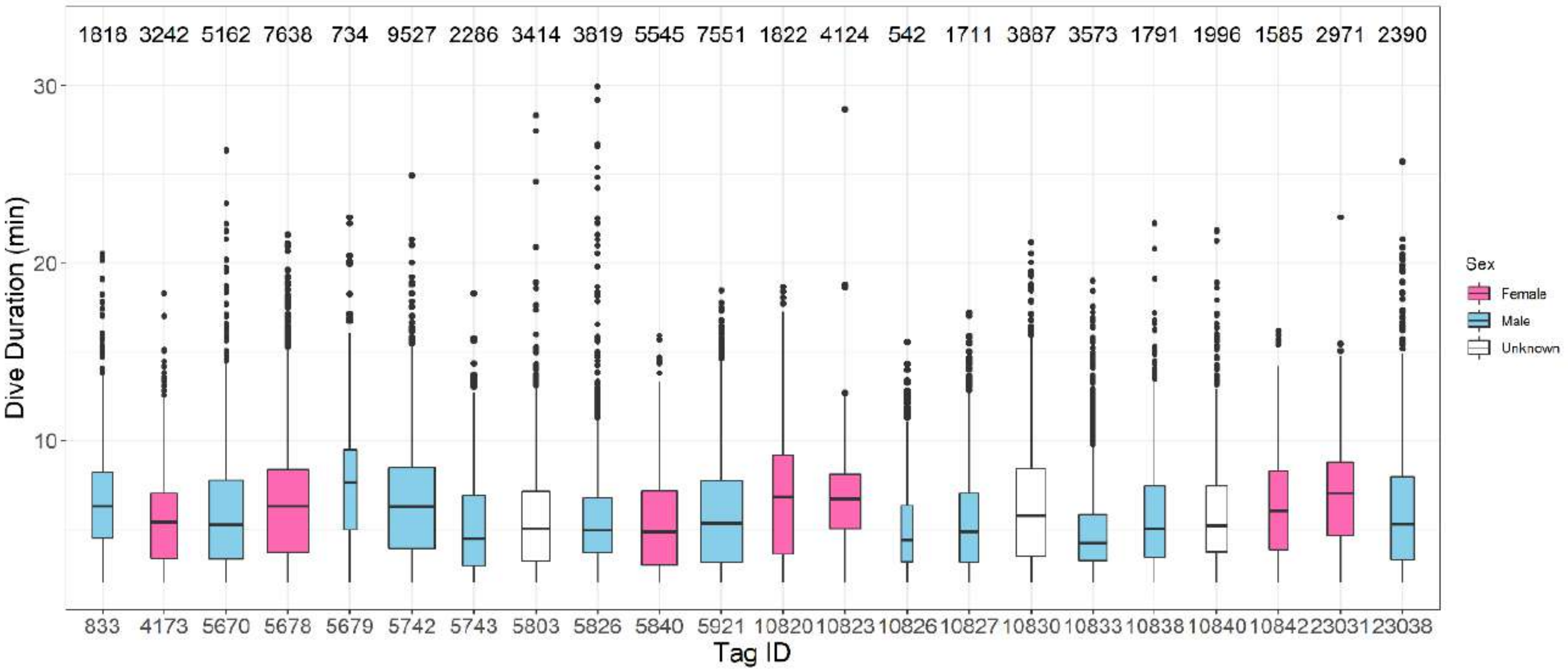


Figure 46. Dive duration in feeding areas of DM-tagged humpback whales (n = 22) tagged off Northern Washington, during September and October 2019. Boxes represent first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Box widths are proportional to the sample size, which is listed above each box. Sex of the animals are indicated by color.

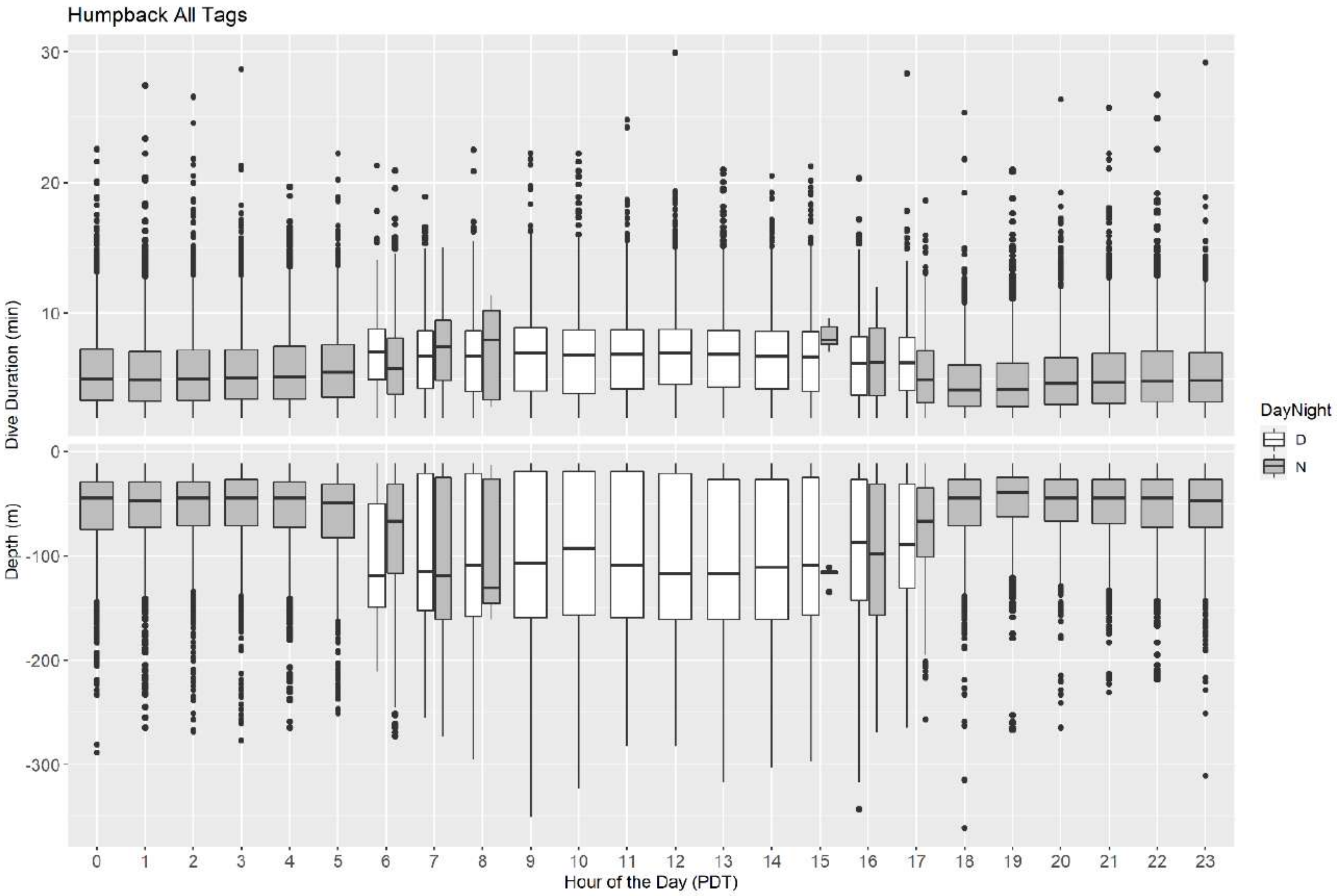


Figure 47. Hourly distributions of dive durations (top) and maximum dive depths (bottom) for DM-tagged humpback whales (n = 21) tagged off Northern Washington, in September and October 2019. Boxes represent first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range. Note: Hours with both day and night values are due to the changing time of sunrise/sunset over the course of the tracking period and at different latitudes occupied by tagged whales.

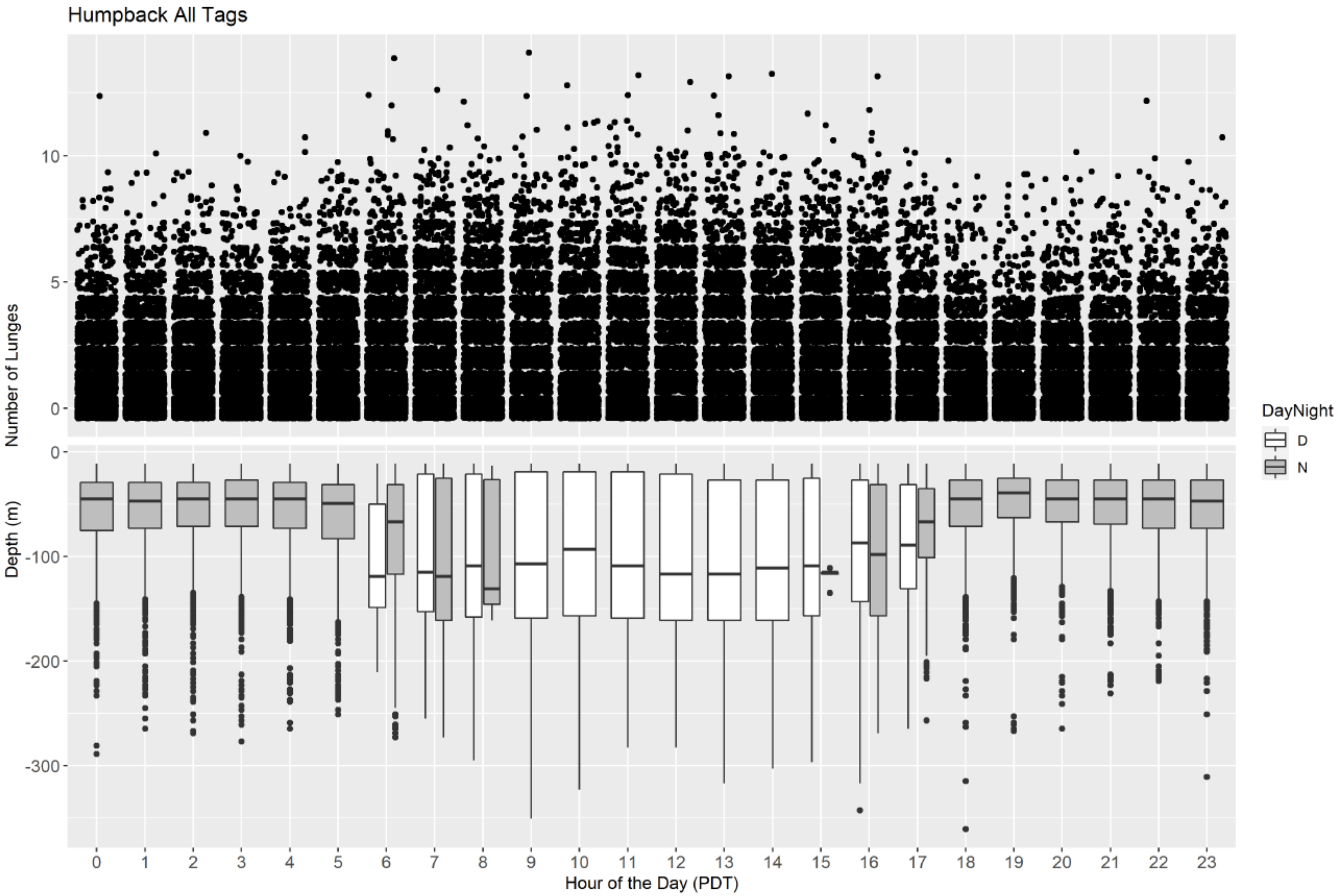


Figure 48. Hourly distributions of number of lunges (top) and maximum dive depths (bottom) for DM-tagged humpback whales (n = 21) tagged off Northern Washington during September and October 2019. Points in the upper panel are jittered for better visibility. Boxes represent first and third quartiles of the data, while points represent values exceeding 1.5 times the inter-quartile range.

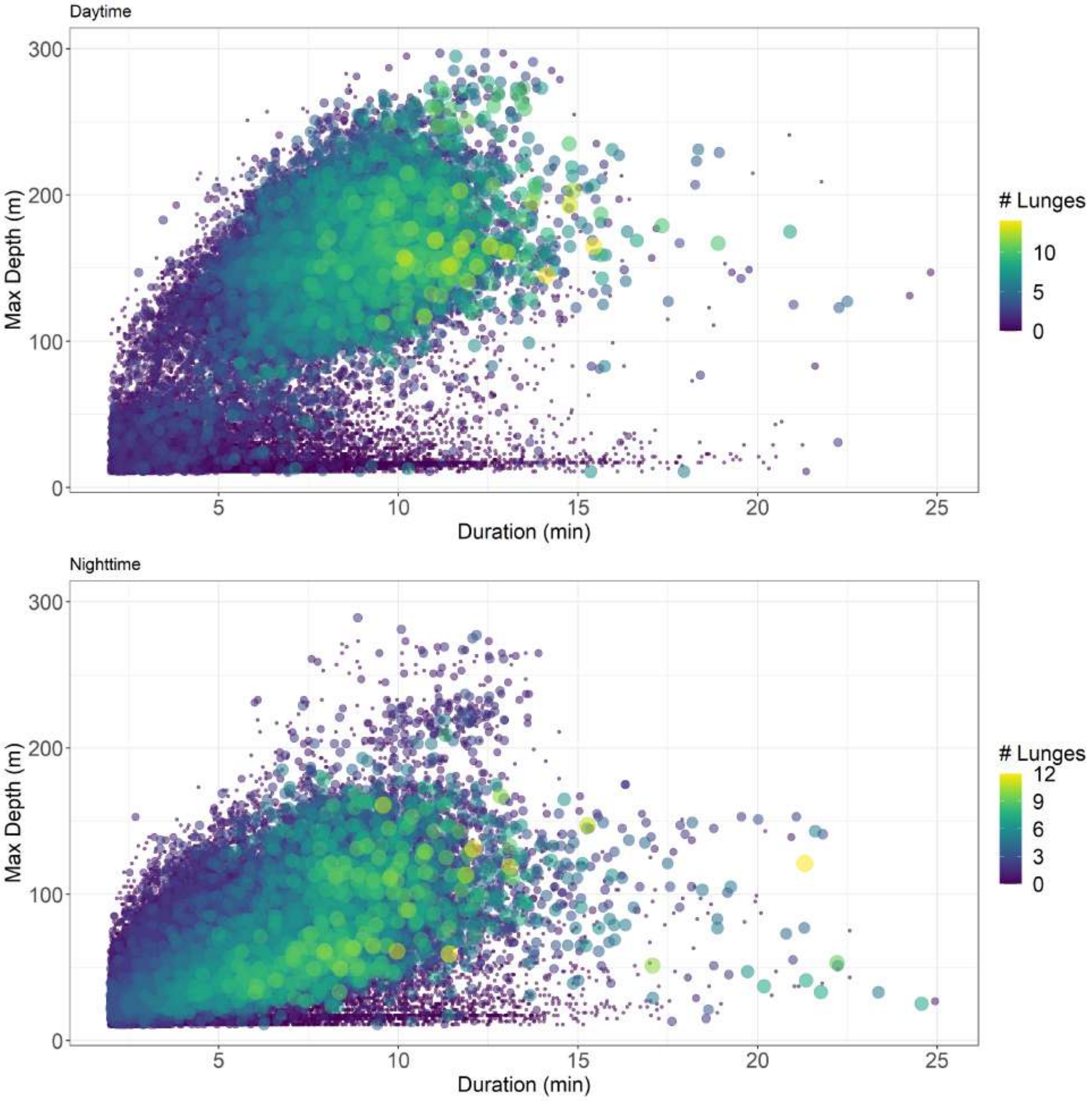


Figure 49. Depth and duration of dives made during the day (top panel) and night (bottom panel) by DM-tagged humpback whales tagged off northern Washington, during September and October 2019. Color and size of the circles represent the number of lunges recorded during each dive.

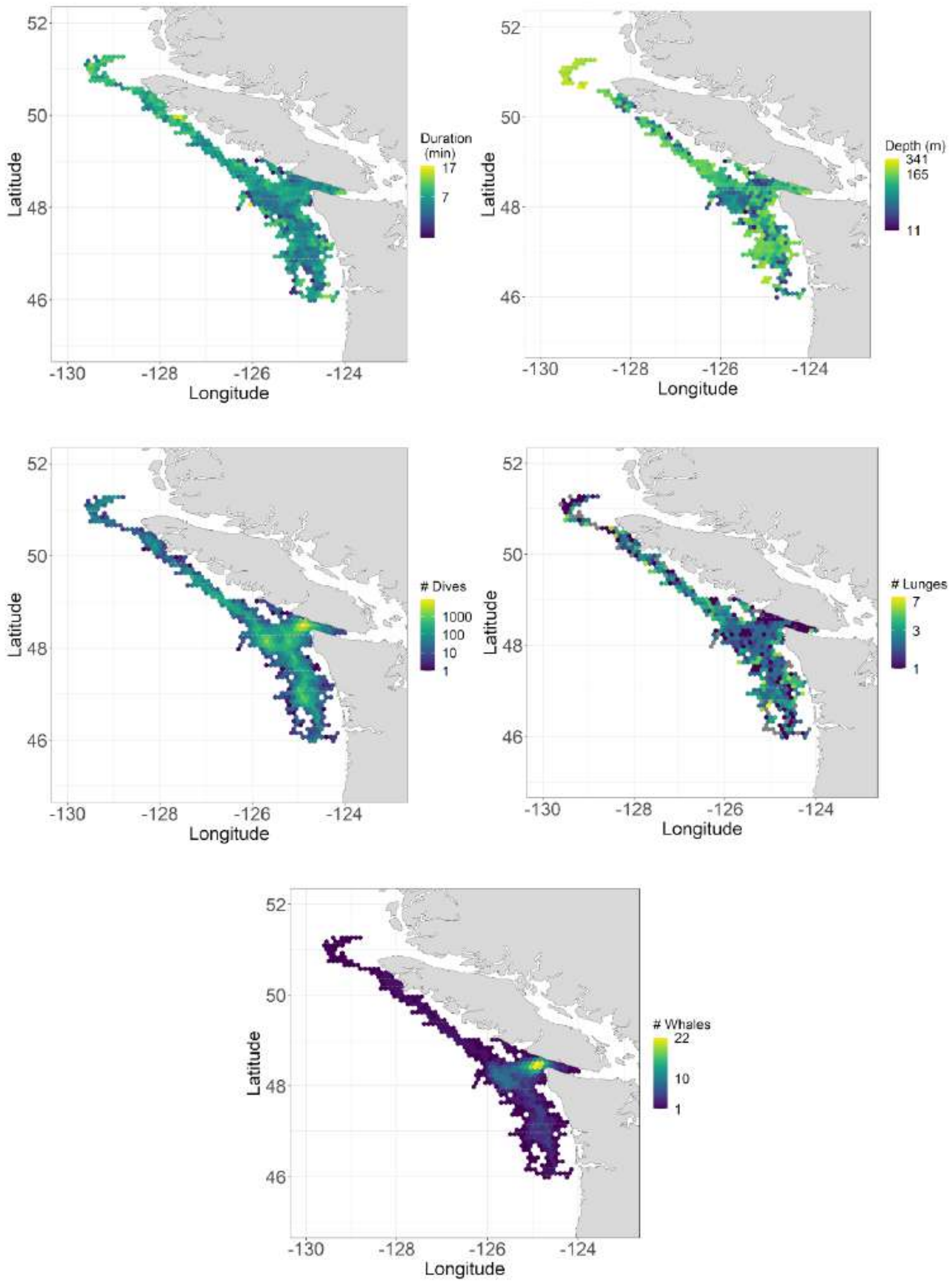


Figure 50. Data from DM-tagged humpback whales tagged off Northern Washington, during September and October 2019 summarized in 0.1-degree hexagonal grids showing the median dive duration (top left), median maximum daytime dive depth (top right), number of dives (middle left), median number of lunges (middle right), and number of tagged whales (bottom) recorded in each grid cell.

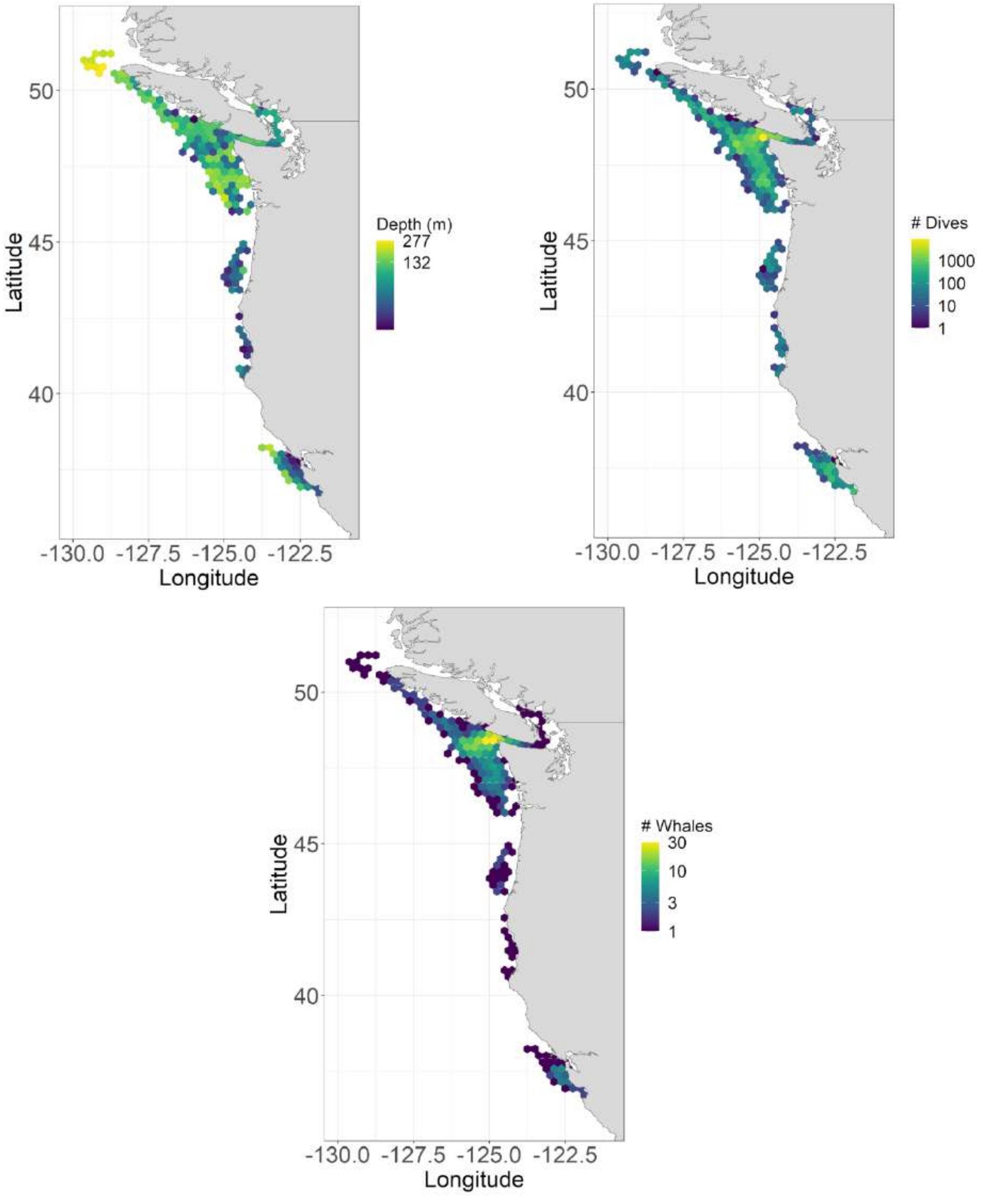


Figure 51. Data from DM-tagged humpback whales summarized in 0.25-degree hexagonal grids showing the median maximum daytime dive depth (top left), number of dives (top right), and number of tagged whales (bottom) recorded in each grid cell. Whales were tagged off Oregon in September and October 2016 (n = 2), California in July and August 2017 (n = 5), and Washington in August 2018 (n = 20) and September and October 2019 (n = 21).

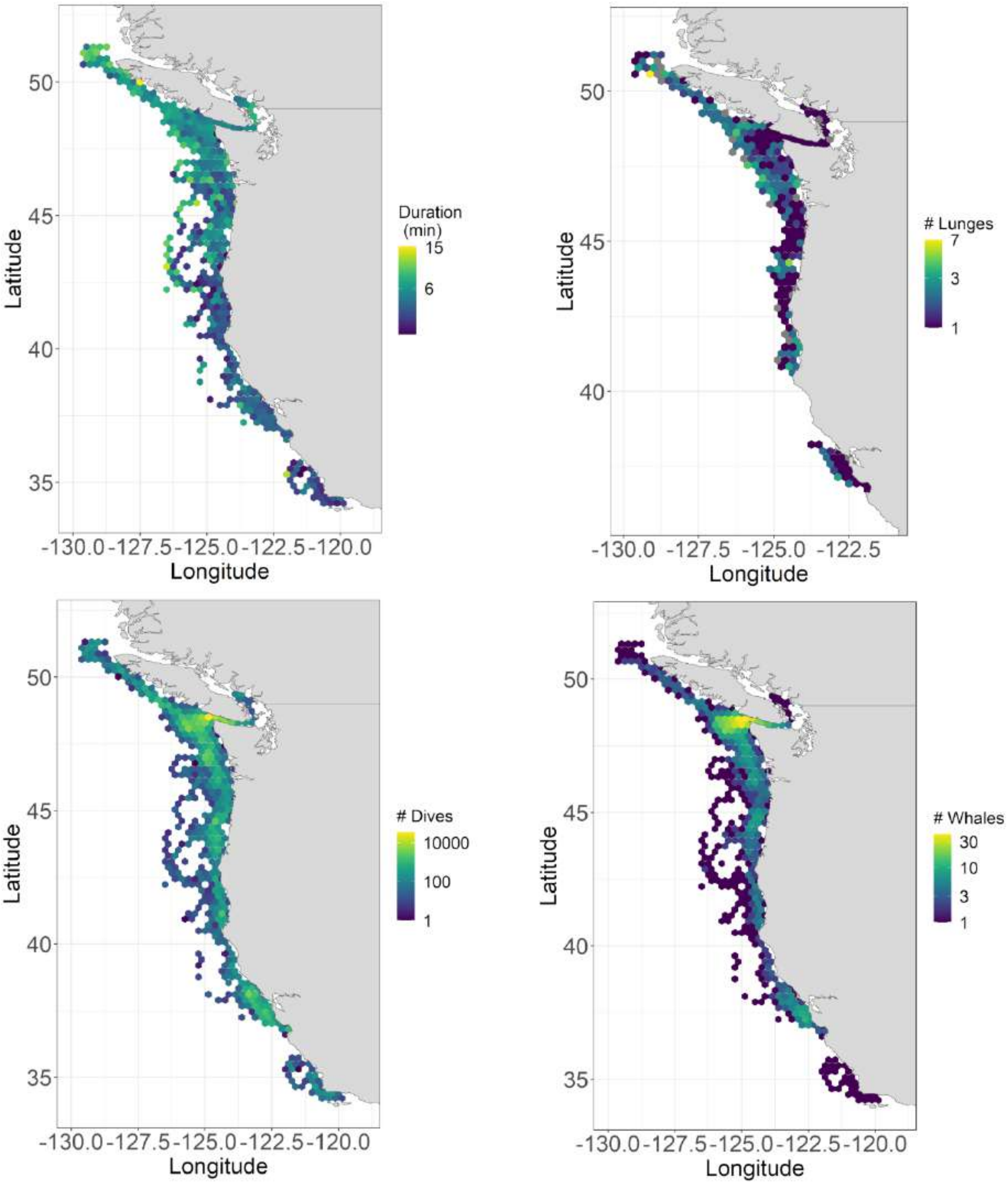


Figure 52. Data from DM-, DUR- and DUR+-tagged humpback whales summarized in 0.25-degree hexagonal grids showing the median dive duration (top left), median number of lunges (top right), number of dives (bottom left), and number of tagged whales (bottom right) recorded in each grid cell. Whales were tagged off Oregon in September and October 2016 (n = 2), California and Oregon in July to October 2017 (n = 16), Oregon and Washington in August and September 2018 (n = 25) and Washington in September and October 2019 (n = 21).

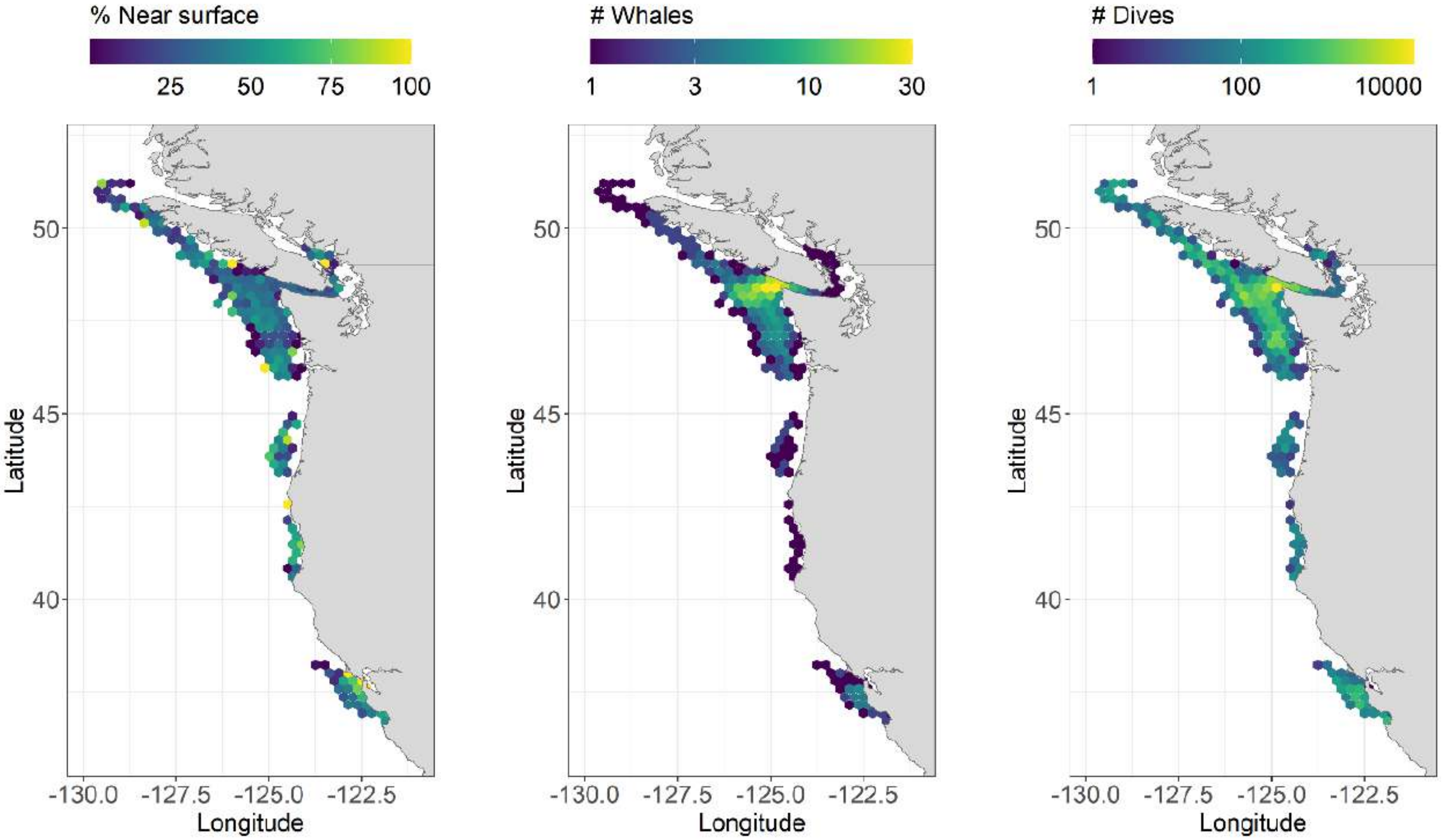


Figure 53. Data from DM-tagged humpback whales summarized in 0.25-degree hexagonal grids showing the percentage of recorded time (dive duration plus post-dive interval) spent at < 30 m depth (left), number of tagged whales (middle), and number of dives (right) recorded in each grid cell. Whales were tagged off Oregon in September and October 2016 (n = 2), California in July and August 2017 (n = 5), and Washington in August 2018 (n = 20) and September and October 2019 (n = 21).

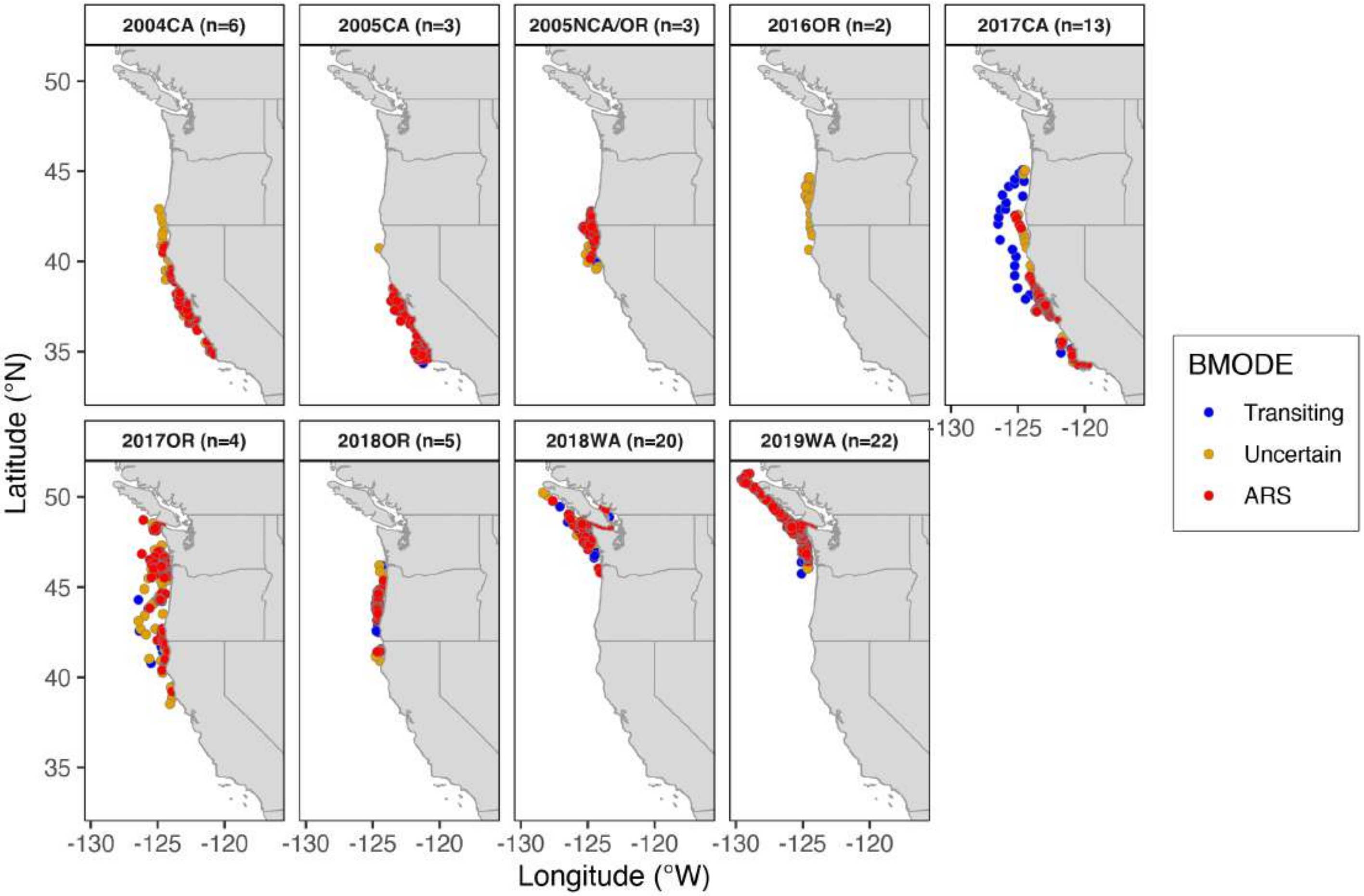


Figure 54. The geographic distribution of SSSM/hSSSM locations colored by behavioral mode (BMODE) for each tagging year/season for 78 humpback whales tagged by OSU in feeding areas off the US West Coast from 2004 to 2019 (CA = California, OR = Oregon, WA = Washington). The number of SSSM/hSSSM tracks available in each year/season is indicated above each panel.

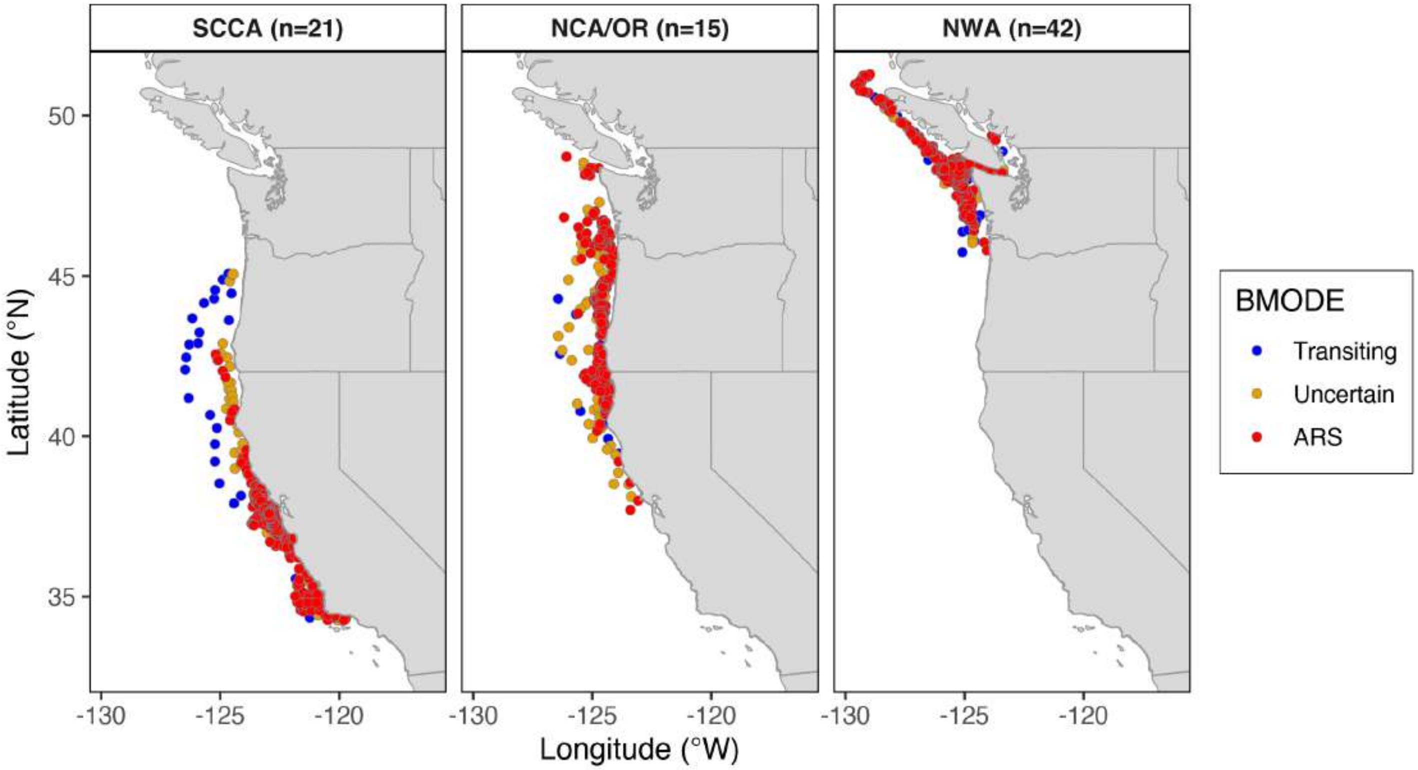


Figure 55. The geographic distribution of SSSM/hSSSM locations colored by behavioral mode (BMODE) for each tagging region (SCCA = southern and central California, NCA/OR = northern California/ Oregon, NWA = northern Washington) for 78 humpback whales tagged by OSU in feeding areas off the US West Coast from 2004 to 2019. The number of SSSM/hSSSM tracks available in each region is indicated above each panel.

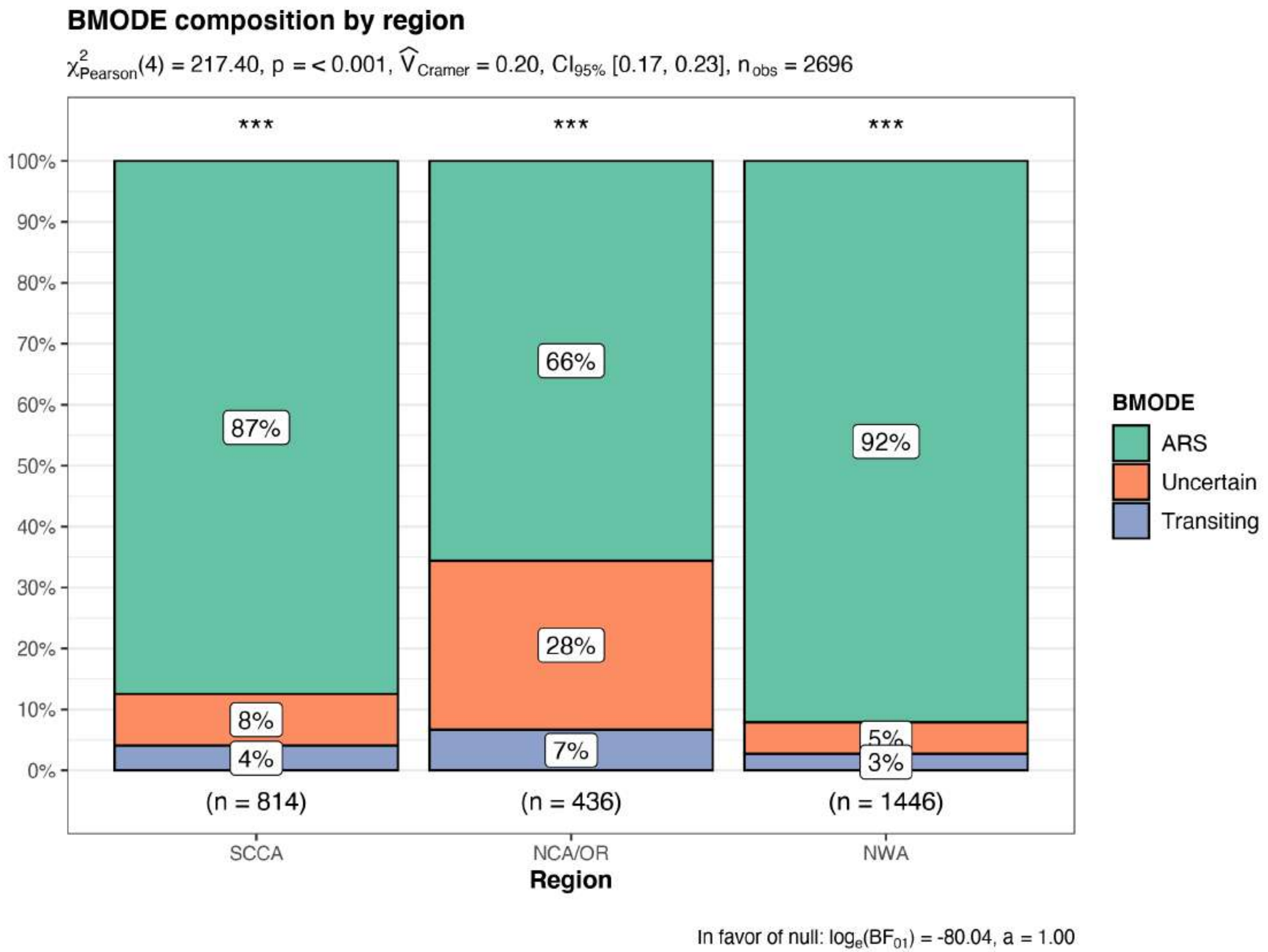
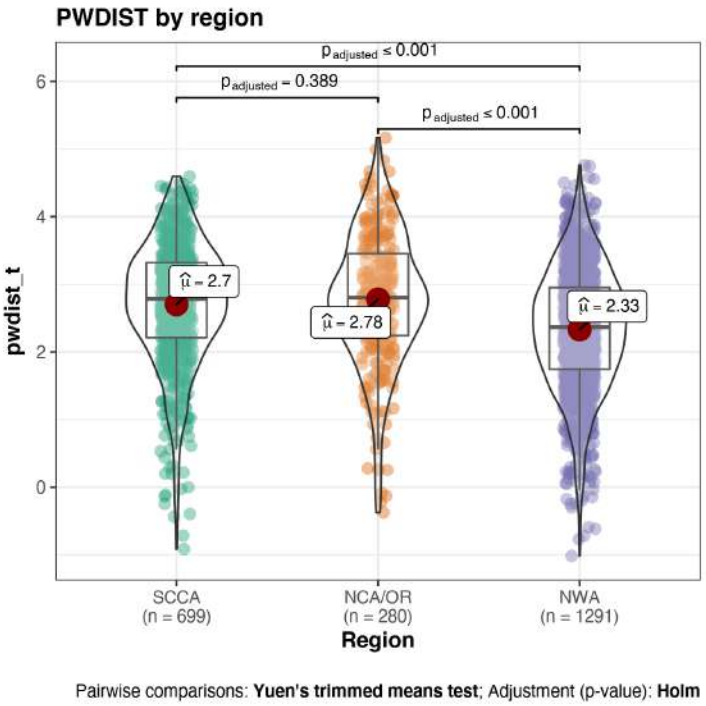


Figure 56. Bar plot showing the behavioral classification of SSSM/hSSSM locations into area-restricted searching (ARS), uncertain, or transiting behavioral modes, as a percentage of the total number of locations in each tagging region, as depicted in Figure 54 (SCCA = southern and central California, NCA/OR = northern California/ Oregon, NWA = northern Washington). Also shown are the results of a parametric one-way ANOVA test for global differences between tagging regions for the discrete distributions of BMODE, including effect size and intra-region proportion tests (*** = p-value < 0.001), as implemented in R package *ggstatsplot* v. 0.5.0.9000 (Patil 2018).



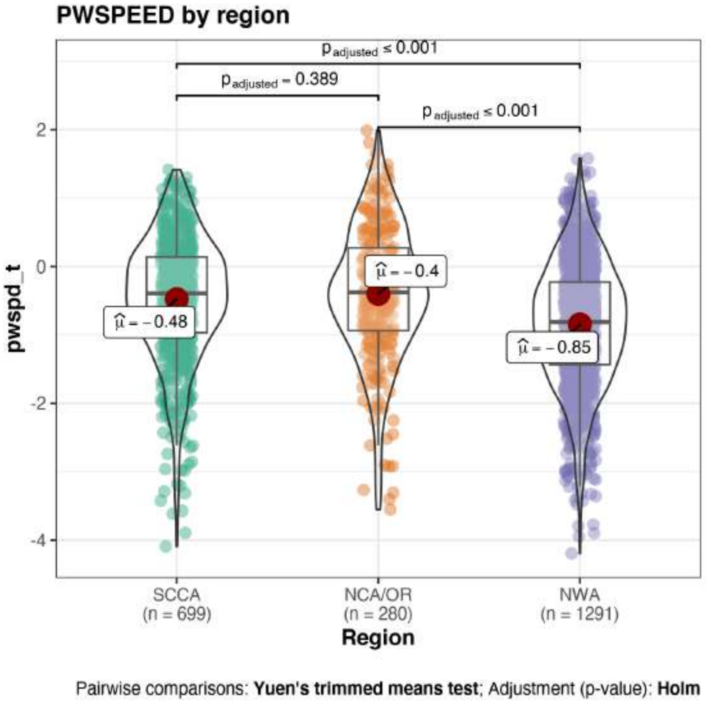


Figure 57. Box-violin plots showing the distributional characteristics of PWDIST (km) and PWSPEED (km/h) for SSSM/hSSSM locations (ARS mode only) in each tagging region (SCCA = southern and central California, NCA/OR = northern California/ Oregon, NWA = northern Washington). Red circles indicate the mean. The y-axis has been log-transformed to enhance visualization and for formal statistical testing. Pairwise comparisons based on Yuen's test on trimmed means and adjusted for multiple *p*-values are shown, as implemented in R package *ggstatsplot* v. 0.5.0.9000 (Patil 2018).

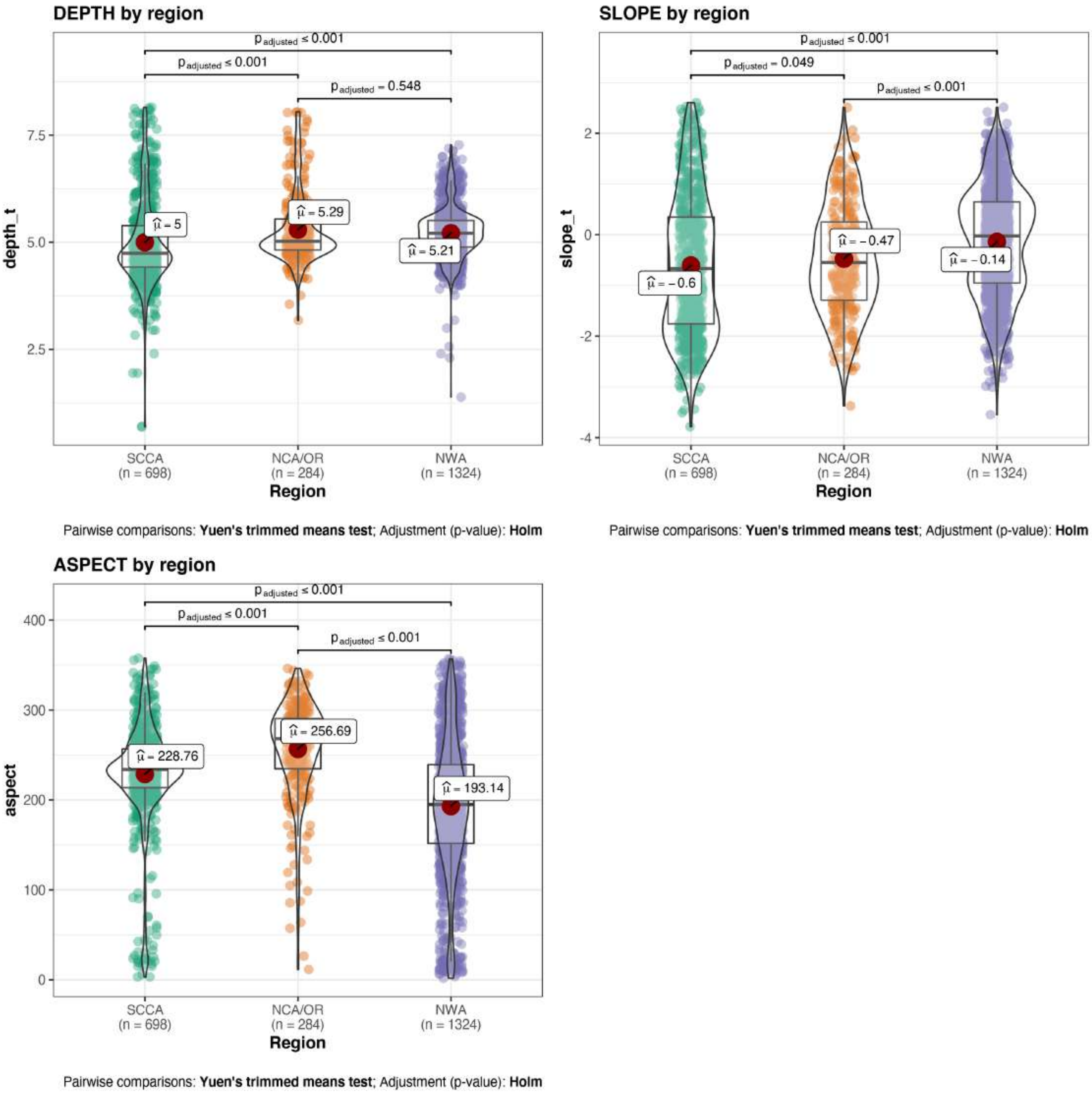


Figure 58. Box-violin plots showing the distributional characteristics of DEPTH (m), SLOPE (deg), and ASPECT (deg) for SSSM/hSSSM locations (ARS mode only) in each tagging region (SCCA = southern and central California, NCA/OR = northern California/ Oregon, NWA = northern Washington). Red circles indicate the mean. The y-axis has been log-transformed for DEPTH and SLOPE to enhance visualization and for formal statistical testing. Pairwise comparisons based on Yuen's test on trimmed means and adjusted for multiple *p*-values are shown, as implemented in R package *ggstatsplot* v. 0.5.0.9000 (Patil 2018).

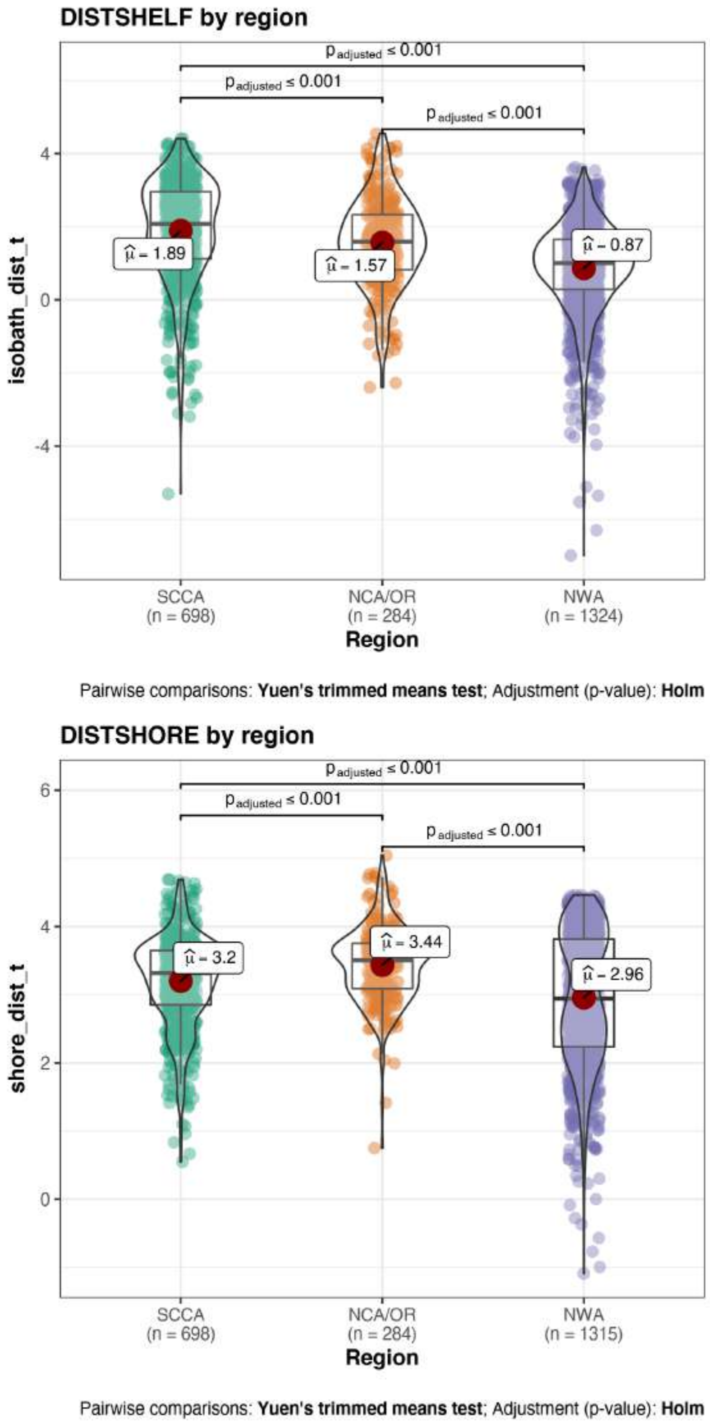


Figure 59. Box-violin plots showing the distributional characteristics of DISTSHELF (km) and DISTSHORE (km) for SSSM/hSSSM locations (ARS mode only) in each tagging region (SCCA = southern and central California, NCA/OR = northern California/ Oregon, NWA = northern Washington). Red circles indicate the mean. The y-axis has been log-transformed to enhance visualization and for formal statistical testing. Pairwise comparisons based on Yuen's test on trimmed means and adjusted for multiple *p*-values are shown, as implemented in R package *ggstatsplot* v. 0.5.0.9000 (Patil 2018).

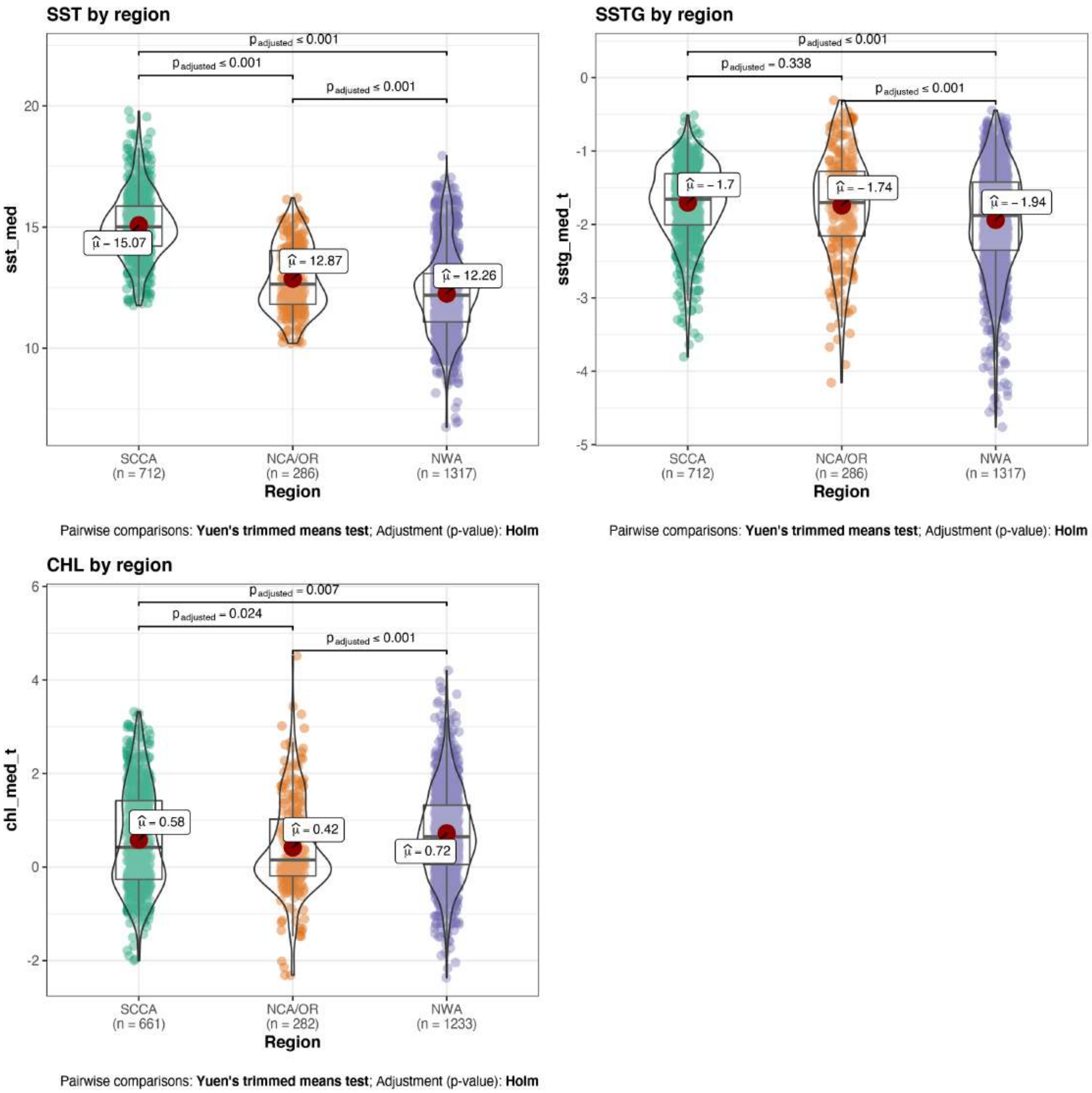


Figure 60. Box-violin plots showing the distributional characteristics of SST (°C), SSTG (°C/deg), and CHL (mg/m³) for SSSM/hSSSM locations (ARS mode only) in each tagging region (SCCA = southern and central California, NCA/OR = northern California/ Oregon, NWA = northern Washington). Red circles indicate the mean. The y-axis has been log-transformed for SSTG and CHL to enhance visualization and for formal statistical testing. Pairwise comparisons based on Yuen's test on trimmed means and adjusted for multiple *p*-values are shown, as implemented in R package *ggstatsplot* v. 0.5.0.9000 (Patil 2018).

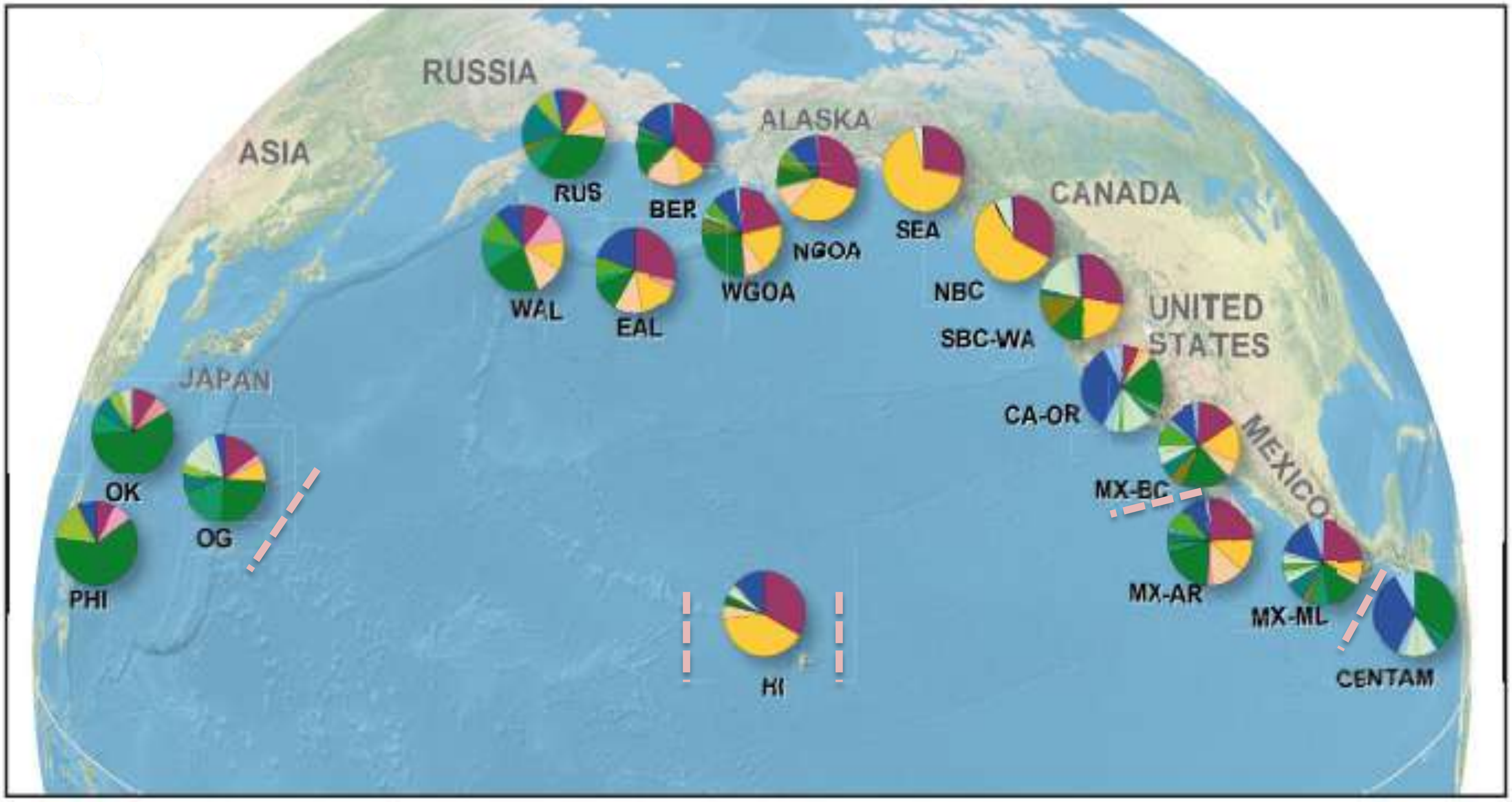


Figure 61. Pie charts of mtDNA frequency for the 10 feeding areas and eight breeding areas sampled during the SPLASH program, as modified from Figure 2 in Baker et al. (2013). The dashed lines indicate the stratification used to represent the reference database of the four DPSs: Central America, Mexico (MX-ML and MX-AR), Hawaii, and the Western North Pacific (OK, OG, and PHI).

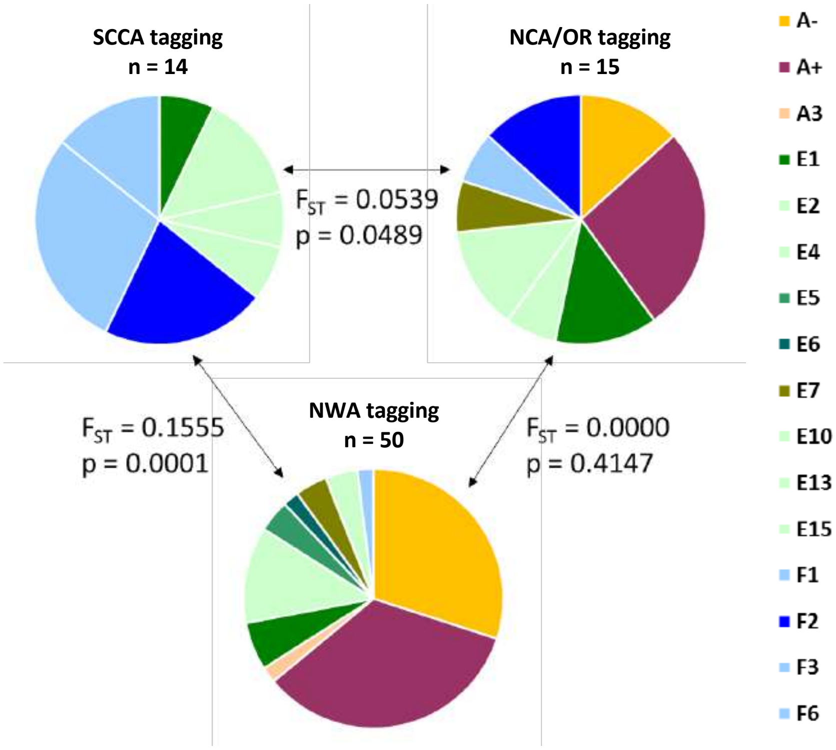


Figure 62. Pie charts of mtDNA haplotype frequencies for the California, Washington, and Oregon tagging samples. The size of the slice reflects the relative frequency of each haplotype for each data set. Arrows and corresponding numbers represent results of pairwise comparisons in mtDNA haplotype frequencies between samples from the three tagging regions: southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA).

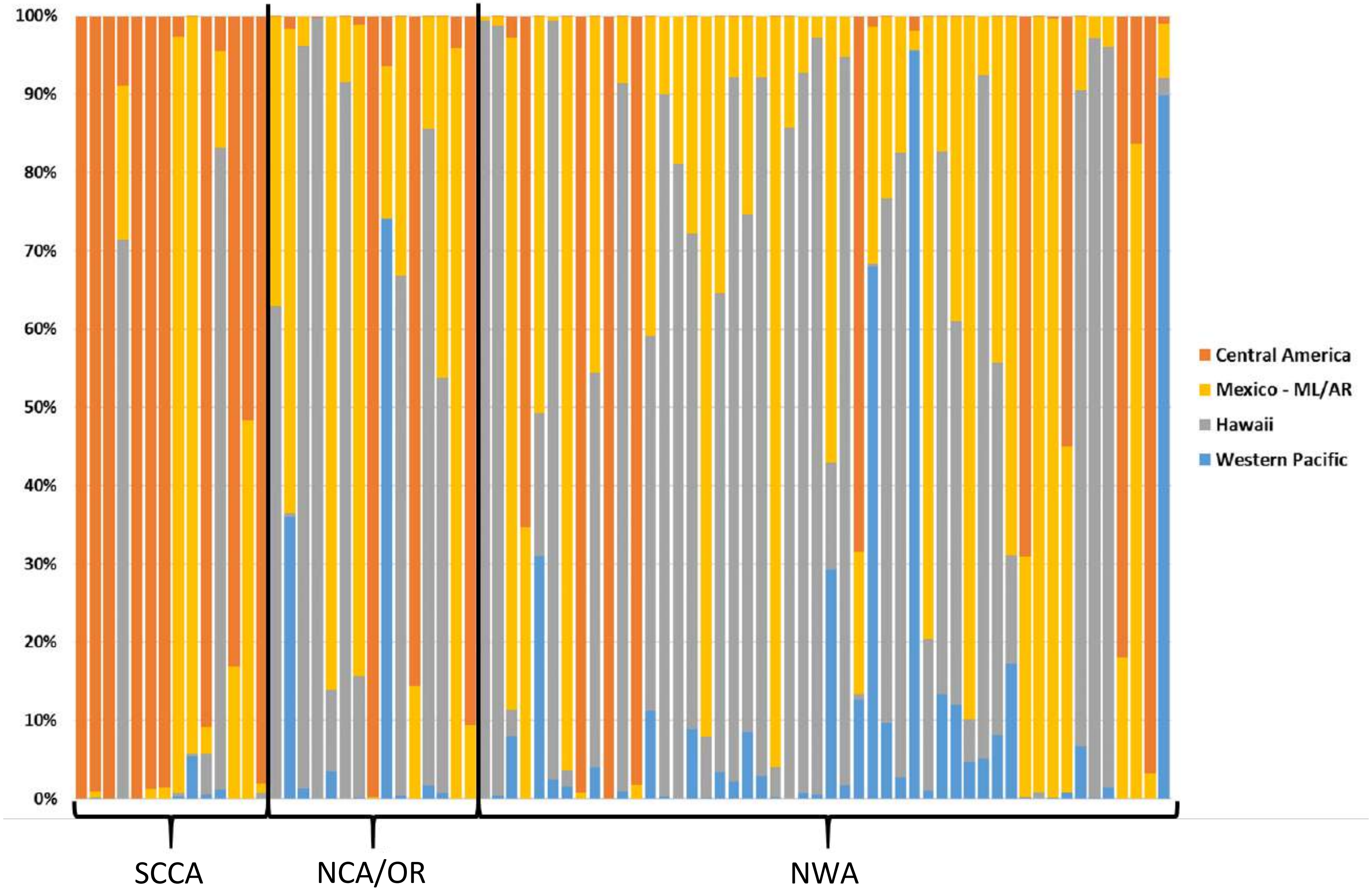


Figure 63. Individual assignment of the southern and central California (SCCA), northern California/Oregon (NCA/OR), and northern Washington (NWA) tagging samples to the four Distinct Population Segments (DPS) recognized by the US Endangered Species Act. The stacked bars represent the relative likelihood of assignment for each whale to the four DPSs based on the program GeneClass2 and using the published SPLASH dataset as reference samples (Baker et al. 2013).

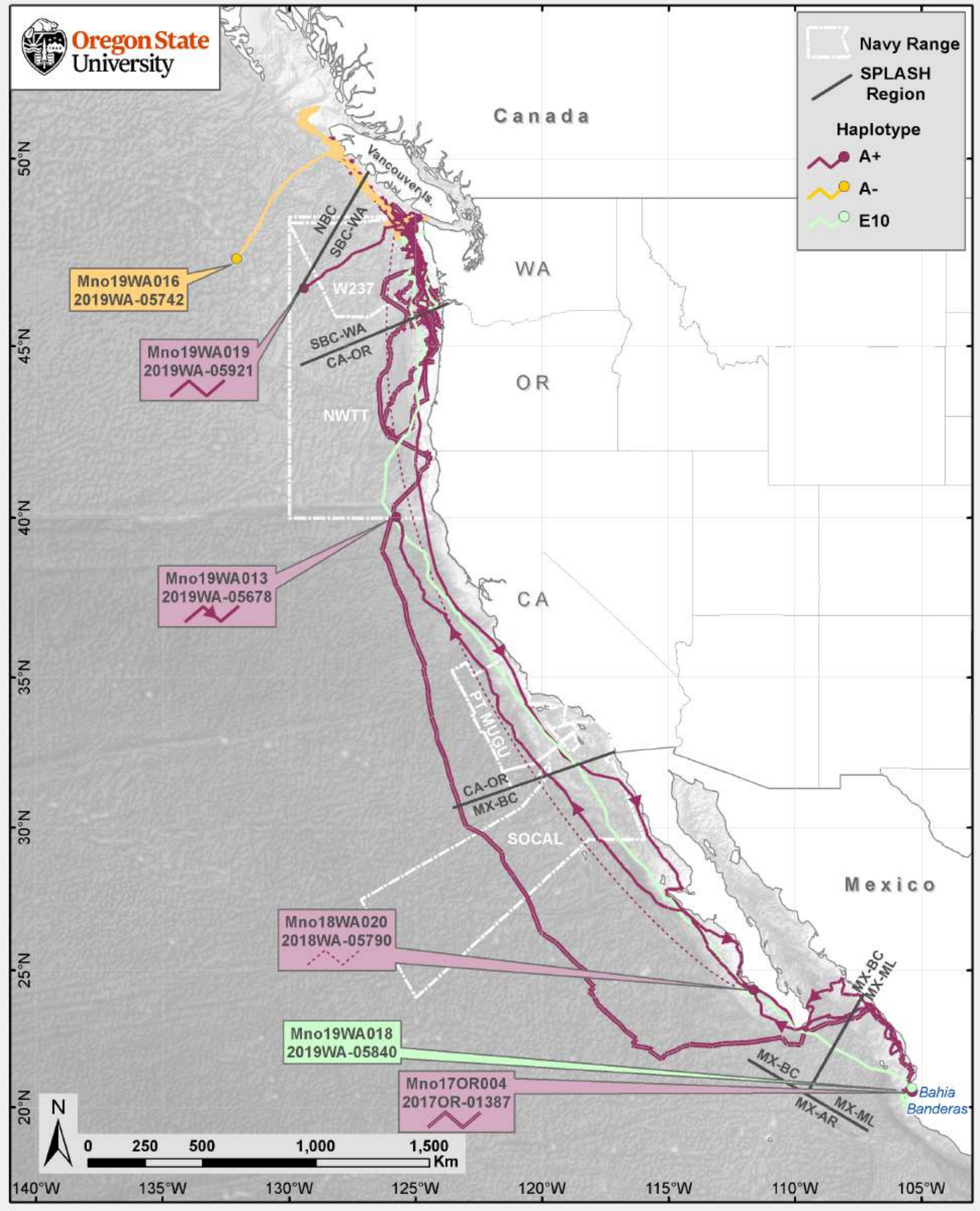


Figure 64. The migratory destinations or trajectories of six individuals sampled in Oregon and Washington from 2017 to 2019 with known mtDNA haplotypes. Haplotypes are colored according to Figure 62.

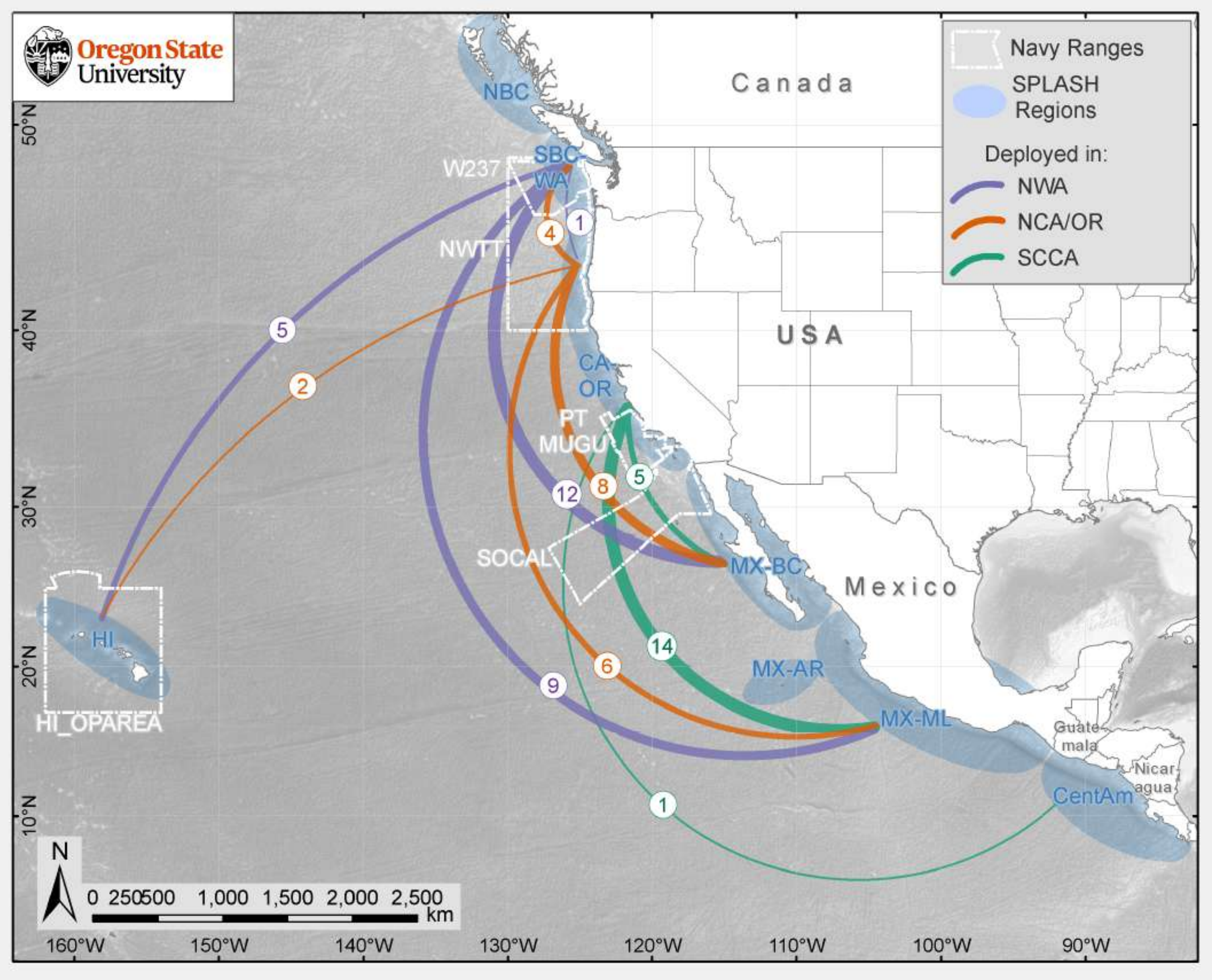


Figure 65. Photo-identification matches between humpback whales tagged and/or biopsied in southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA) from 2004 to 2019 and breeding areas identified in the SPLASH project as revealed by comparison with the Happywhale online photo-identification database. Numbers in circles represent the number of matches between areas connected by the corresponding lines.

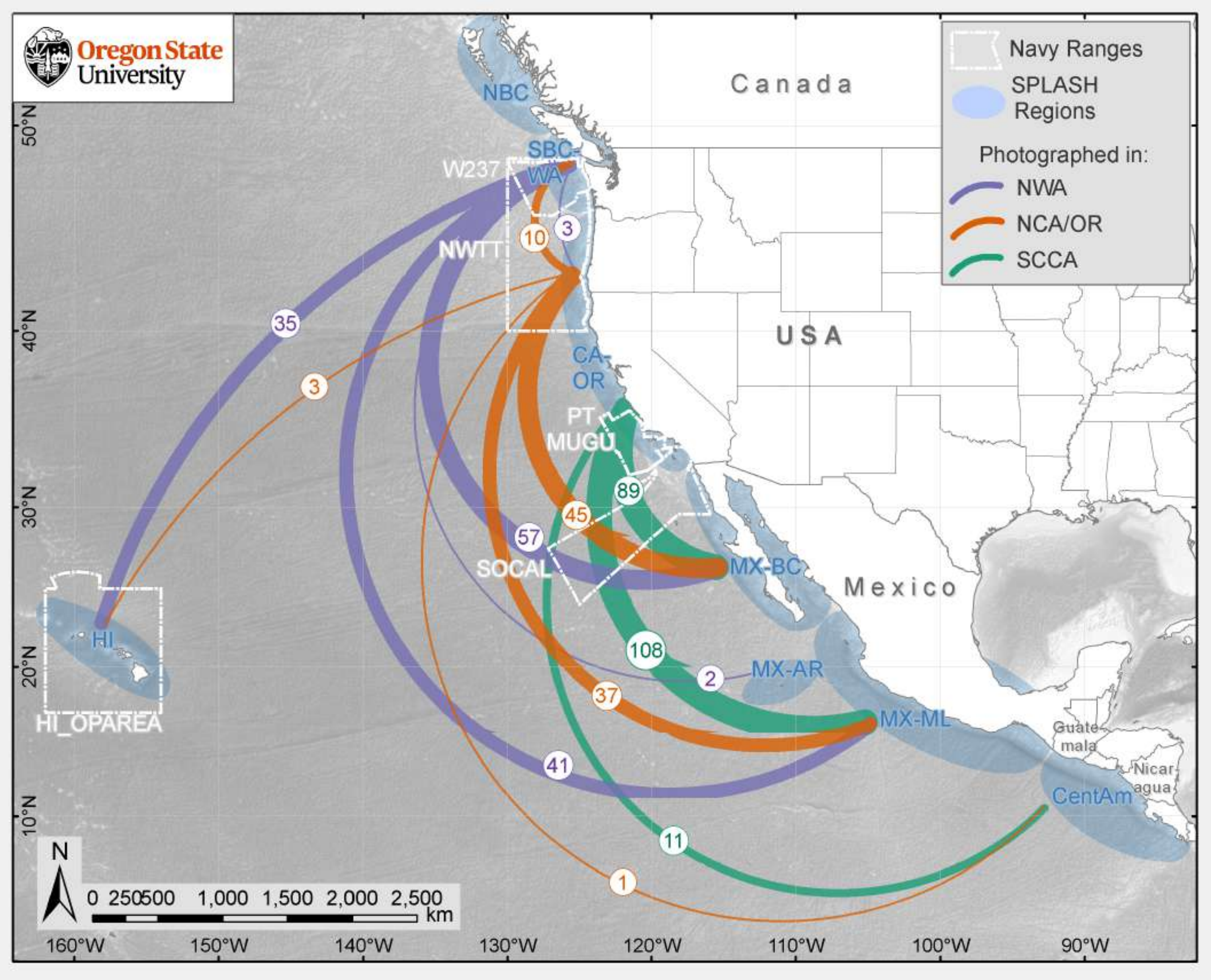


Figure 66. Photo-identification matches between humpback whales photographed in southern and central California (SCCA), northern California and Oregon (NCA/OR), and northern Washington (NWA) from 2004 to 2019 and breeding areas identified in the SPLASH project as revealed by comparison with the Happywhale online photo-identification database. Numbers in circles represent the number of matches between areas connected by the corresponding lines.