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Research Article

Feeding Home Ranges of Pacific Coast Feeding Group Gray Whales

BARBARA A. LAGERQUIST,[1] *Oregon State University Marine Mammal Institute and Department of Fisheries and Wildlife, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA*

DANIEL M. PALACIOS, *Oregon State University Marine Mammal Institute and Department of Fisheries and Wildlife, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA*

MARTHA H. WINSOR, *Oregon State University Marine Mammal Institute and Department of Fisheries and Wildlife, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA*

LADD M. IRVINE, *Oregon State University Marine Mammal Institute and Department of Fisheries and Wildlife, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA*

THOMAS M. FOLLETT, *Oregon State University Marine Mammal Institute and Department of Fisheries and Wildlife, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA*

BRUCE R. MATE, *Oregon State University Marine Mammal Institute and Department of Fisheries and Wildlife, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA*

ABSTRACT There is a lack of detailed information about the range and habitat use of gray whales (*Eschrichtius robustus*) during their seasonal occupation off the Pacific Northwest (PNW) coast from northern California to southeast Alaska, USA. These data are important for management because of anthropogenic pressures (e.g., indigenous harvesting, fishing gear entanglements, ship strikes, naval exercises, siting of marine renewable energy facilities). We applied satellite tags to 35 gray whales in the eastern north Pacific (ENP) off the coasts of Oregon and northern California from September to December 2009, 2012, and 2013. These whales are members of the Pacific Coast Feeding Group (PCFG), a subset of gray whales in the ENP that feed off the PNW, during summer and fall. Tracking periods for the satellite-tagged whales in this study ranged from 3 days to 383 days. We applied a Bayesian switching state-space model (SSSM) to locations for each whale track to provide a regularized track with 2 estimated locations per day and associated movement behavior (either transiting or area-restricted searching [ARS]). We isolated the portion of the SSSM track in the feeding area for each whale by removing all southward and northward migration locations. We calculated home ranges (90% isopleths) and core areas (50% isopleths) for these non-migrating, feeding-area tracks with >50 SSSM locations using local convex hull utilization distributions. Feeding-area home ranges for the resulting 23 whales covered most of the near-shore waters from northern California to Icy Bay, Alaska, and ranged in size from 81 km^2 to 13,634 km^2. Core areas varied widely in size (11–3,976 km^2) and location between individuals, with the highest-use areas off Point St. George in northern California, the central coast of Oregon, and the southern coast of Washington, USA. Nearshore waters off Point St. George were a hot spot for whales in the PCFG in late fall, close to where most of the whales were tagged; 19 whales had overlapping home ranges and 15 whales had overlapping core areas there. One whale, a male tracked for 383 days, did not migrate, spending the entire winter off Point St. George and the California-Oregon border. Residence times (portions of the track with a minimum of 3 successive locations in ARS behavioral mode) ranged from 1 day to 142.5 days; 19 whales had residencies >30 days in some areas. Because most of the whales in this study were tagged in the fall in the southern portion of the feeding area, off northern California, results are weighted toward fall and winter movements. Although some whales were tracked into the spring and summer, additional tagging earlier in the year and in more northerly locations would provide an even clearer picture of gray whale use of feeding areas in the PNW. Nevertheless, these results constitute valuable information about high-use areas for gray whales in this region, providing baseline home range data for future comparisons with regard to year-to-year variability, potential responses to climate change, and exposure to anthropogenic activities in the marine environment. © 2019 The Authors. *Journal of Wildlife Management* Published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS anthropogenic risk, *Eschrichtius robustus*, gray whale, home ranges, Pacific Coast Feeding Group, satellite-telemetry.

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[1]*E-mail: barb.lagerquist@oregonstate.edu*

Gray whales (*Eschrichtius robustus*) in the Pacific Coast Feeding Group (PCFG), with an estimated 197 animals (Carretta et al. 2016), are a small (~1%) subset of the gray whale population in the Eastern North Pacific (ENP). Rather than migrating to the Bering, Chukchi, and Beaufort seas with the rest of the ENP population, whales in the PCFG feed in the coastal waters of the Pacific Northwest (PNW) from northern California through southeast Alaska, USA, from May through November (Calambokidis et al. 2002). According to recent genetic studies, gray whales feeding in the PNW and areas north of the Aleutian Islands, Alaska, likely represent a single interbreeding population, although matrilineal site fidelity appears to play a role in creating structure among feeding grounds (Lang et al. 2014). Gray whales in the PCFG may thus represent a demographically independent group and therefore a separate management unit from the rest of the ENP population (Frasier et al. 2011, Lang et al. 2014).

The designation of gray whales in the PCFG as separate from the rest of the ENP population has significant implications for the management of subsistence whaling by the Makah Tribe of Washington, USA. The management plan proposed by the Makah Tribe contains efforts to minimize risk to gray whales in the PCFG while still meeting the needs of the Tribe, including time and area restrictions to reduce the probability of killing a whale in the PCFG (Scordino et al. 2013, Lang et al. 2014). Detailed knowledge about the seasonal distribution and high-use areas of whales in the PCFG is important for reaching this goal. Such information is also valuable in risk assessments and minimizing effects from other anthropogenic activities throughout the PNW (e.g., military training activities; installation, testing, and operation of marine hydrokinetic energy facilities; Henkel et al. 2014). Detailed information about whale residency, migration paths, and high-use areas can also aid in reducing risk of ship strike or entanglement in fishing gear, which may be especially elevated for gray whales because of their nearshore migrations and feeding behavior (Ford et al. 2013, Scordino et al. 2017).

Long-term photo-identification studies have revealed important information about gray whale occurrence and movements in their PNW feeding grounds (Darling 1984, Calambokidis et al. 2002) and have shown seasonal variability in distribution, with whales tending to feed in the northern part of the range in early spring and summer and moving southward as the season progresses (Calambokidis et al. 2002). Detailed movements between photographic recaptures and accurate residence times are missing, however, as is information outside June to September, when most photographic identification effort occurs.

The goal of this descriptive study was to track gray whales in the PCFG with satellite-tags to collect more detailed information about their movements on the summer and fall feeding grounds in the PNW. We hypothesized that there are multiple areas of high use within the PNW feeding grounds and that individual gray whales use >1 of these areas during their feeding season.

STUDY AREA

Our study area, the west coast of North America from the central California coast (~36°N) to Icy Bay, Alaska (~60°N), was delimited by the gray whale locations obtained from satellite-monitored radio-tags covering September 2009 through September 2010, and October 2012 through May 2014. Locations were predominantly over continental shelf waters <10 km from shore, in depths <50 m, covering an area of approximately 150,000 km^2. The benthic habitat is characterized by a patchy distribution of rock outcrops, pinnacles, and boulder fields surrounded by low-relief sand, mud, and cobbles, with kelp (*Nereocystis leutkeana*, *Macrocystis* species) forests in the nearshore area (National Marine Fisheries Service 2015). The oceanography is dominated by cool temperate waters (ranging from 4°C to 19°C) of the northward-flowing Alaska Current anad the southwrd-flowing California Current, with areas of coastal upwelling in the spring and summer providing a nutrient-rich environment and high densities of forage for marine species (Whitney and Freeland 1999, Whitney et al. 2005, Checkley and Barth 2009). The fall is a transition into the downwelling season that lasts through the winter (Checkley and Barth 2009). The nearshore region is home to large numbers of subpolar and temperate marine species including marine mammals (e.g., gray [*Eschrichtius robustus*], humpback [*Megaptera novaeangliae*], and killer whales [*Orcinus orca*], harbor porpoise [*Phocoena phocoena*], Steller's [*Eumetopias jubatus*] and California [*Zalophus californianus*] sea lions, Pacific harbor seals [*Phoca vitulina*], sea otters [*Enhydra lutris*]), coastal fish (e.g., salmon, herring, rockfish, flatfish, sharks, and skates), coastal seabirds (e.g., common murres [*Uria aalge*], cormorants [*Phalacrocorax* spp.], gulls, and alcids), and marine invertebrates (e.g., crustaceans, jellyfish, anemones, echinoderms, mollusks).

METHODS

Tagging

This research was conducted under a National Marine Fisheries Service Marine Mammal Protection Act and Endangered Species Act scientific research permit (number 369-1757) authorizing the close approach and deployment of implantable satellite tags on large whales. All tagging procedures authorized by the permit, and used in this manuscript, were subjected to an internal National Marine Fisheries Service review. We carried out this study in strict accordance with the policies and guidelines of the Oregon State University Institutional Animal Care and Use Committee (permits 3657 and 4118).

We applied satellite-monitored radio-tags to gray whales off the coast of Oregon and northern California in 2009, 2012, and 2013 (Fig. 1). Tagging expeditions consisted of a series of short (1–3-day) shore-based trips; we determined the timing and location of such trips by local whale abundance and weather conditions. We deployed tags along the central Oregon coast near Seal Rock ($n = 4$), Cape Foulweather ($n = 6$), and Nelscott Reef ($n = 2$) from September to mid-October, and in northern California near Point St. George ($n = 23$) from late October to December.

Tags consisted of SPOT5 (Wildlife Computers, Redmond, WA, USA) or ST-15 Argos (Telonics, Mesa, AZ, USA)

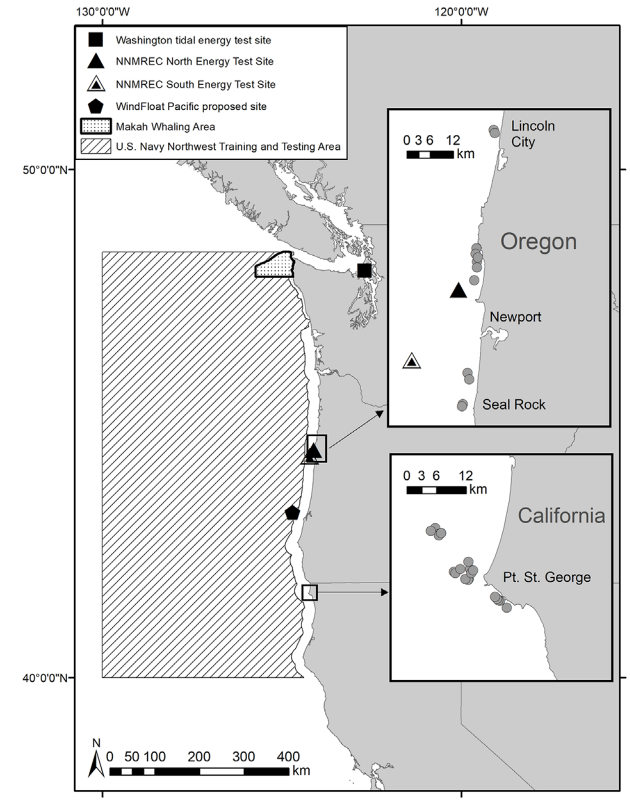

Figure 1. Deployment locations (gray circles) of 35 satellite-monitored radio-tags applied to gray whales in the Pacific Coast Feeding Group off Oregon and California, USA, in 2009, 2012, and 2013. We also present the locations of proposed and existing marine renewable energy sites, including the Northwest National Marine Renewable Energy Center (NNMREC) test sites, the Makah Whaling Area, and the United States Navy's Northwest Training and Testing Offshore Area (NWTT).

transmitters housed in stainless steel cylinders (SPOT5: 2.0-cm diameter, 16.3- or 21.3-cm length; ST-15: 1.9-cm diameter, 19-cm length) with a whip antenna on 1 end and a penetrating tip and anchoring structures on the other (similar to the tag design described in Mate et al. 2007). We used 2 battery configurations in the SPOT5 tags: a short tag with 2 Saft A cells (172 g), and a longer tag with 3 Saft A cells (210 g). The ST-15 tags weighed 204 g. Tags were designed for nearly complete implantation beneath the whale's skin and were partially coated with a long-dispersant antibiotic in a methacrylate matrix to reduce the risk of infection (Mate et al. 2007). Tags were programmed to transmit for 4 1-hour periods each day that optimized the number of satellite orbits passing overhead.

We deployed tags from a 6.7-m rigid-hulled inflatable boat, using the Air Rocket Transmitter System (ARTS; Heide-Jørgensen et al. 2001) at ranges of 0.5–4.5 m from the whale. Tags were implanted into whales' backs, 0.2–3 m forward of the first dorsal knuckle and 5–30 cm down from the whale's dorsal midline. We tagged only adult-sized gray whales that appeared to be in good health (i.e., not emaciated or heavily infested with external parasites). We collected biopsy samples (skin and blubber) to determine sex using a Barnett crossbow and a sterilized coring tip attached to an arrow (Palsbøll et al. 1991). We also obtained identification photographs (Darling 1984) during and after tagging and shared these with collaborators to enhance the study of tag effects and healing (Norman et al. 2018).

Argos Location Calculation and Analysis

Tag locations were calculated by Service Argos using the process described in Mate et al. (2011). Argos locations are classified into 6 categories (location classes [LC] 3, 2, 1, 0, A, and B) depending on their estimated error and the number of messages received during a satellite pass, ranging from the most accurate LC 3, with an estimated error radius of <200 m, to the least accurate LC B, with an estimated error radius of >5 km (Vincent et al. 2002). We filtered whale tracks to remove LC B locations derived from only 1 message, locations on land farther than their Argos error radius, and locations resulting in travel speeds >15 km/hour. Travel speeds in excess of 15 km/hour are rare for gray whales (Mate et al. 2003, Lagerquist et al. 2012). We then computed great-circle distances to the closest point on the mainland for each high-quality whale location (Argos LC 1, 2, and 3), using the NEAR toolbox function in ArcMap version 10.0 (Environmental Systems Research Institute, Redlands, CA, USA). We used Vancouver Island and Haida Gwaii, Canada, as the land references for whale locations west of these islands. We downloaded bathymetry data (ETOPO1) from the National Geophysical Data Center (Boulder, CO, USA) to provide a 1 arc-minute global relief model of the sea floor (Amante and Eakins 2009). We extracted depth values for high-quality Argos locations from this product using the extract values to points toolbox function in ArcMap version 10.0. We used only high-quality filtered locations for distance to shore and depth determinations to avoid erroneous distance and depth values that could arise from the use of poor-quality locations with large error radii.

Switching State Space Model Analysis

We applied a Bayesian switching state-space model (SSSM) developed by Jonsen et al. (2005) to all filtered locations for each whale track, using the software R version 2.12.1 (R Core Team 2018) and WinBUGS version 1.4.3 (Spiegelhalter et al. 2003). The model provided a regularized track with 2 estimated locations/day, after accounting for Argos satellite location errors and movement dynamics of the animals. The SSSM model ran 2 Markov chain Monte Carlo (MCMC) chains each for 30,000 iterations, with the first 10,000 iterations being discarded as a burn-in, and the remaining iterations being thinned, removing every fifth one to reduce autocorrelation. Two behavioral modes were modeled by the SSSM, based on mean turning angles and autocorrelation in speed and direction, with the means of the MCMC samples providing a continuous value from 1 to 2 (Jonsen et al. 2005). As in Bailey et al. (2009), we chose values ≥1.75 to represent locations with area restricted searching (ARS) behavior and values <1.25 to represent locations with transiting behavior. We classified the behavior at locations with values in between these cutoffs as uncertain.

We isolated the portion of the SSSM track in the PNW feeding area for each whale by removing all southward and northward migration locations. We identified the start date of southward migration as the first transiting location of directed southward travel that continued beyond (south of) Cape Mendocino, California. We identified the end of northward migration as the last transiting location of directed northward travel after passing Cape Mendocino. These feeding-area tracks were the primary focus of this study. One exception to these migration endpoints was tag 5700834, which appeared to begin its southward migration on 3 December 2012 but after reaching Point Sur, California, on 11 December, turned around and traveled north to an area off La Push, Washington, on the west coast of the Olympic Peninsula (arriving on 31 Dec) before heading south (to Mexico) on 1 January 2013. Because this animal clearly re-entered the PNW feeding area, we included this portion of its track (3 Dec–1 Jan) in feeding area movements.

Home Range Analysis

We derived individual feeding-area home range (90% isopleth) and core areas (50% isopleth) for whales with >50 feeding-area SSSM locations (including all behavioral modes) using the local convex hull utilization distribution generator α-LoCoH (Getz et al. 2007) in ArcMap version 10.0. This method (i.e., LoCoH) provided a conservative estimate of the area encompassing a proportion of the number of locations (contained by the above-referred isopleths) and has an advantage over parametric kernel methods because it directly draws upon the spatial structure of the data, allowing for hard boundaries and irregular exclusionary areas in the environment (Getz et al. 2007). This method is particularly useful when dealing with gray whales that are found extremely close to shore. We removed portions of home ranges and core areas that extended onto land. We chose a minimum value of 50 SSSM locations following the recommendation of Seaman et al. (1999) for fixed-kernel estimation using least squares cross-validation for bandwidth selection, which worked well here because all but 1 of the tracks with ≥50 locations resolved the 50% isolpleth (or core areas). We used linear regression to explore the relationship between log-transformed number of SSSM locations and log-transformed home range and core areas sizes to see whether tracking duration influenced the size of these areas. We used a significance threshold of 0.05 for this and all other statistical tests.

We calculated great circle distances and speeds between SSSM locations for tracks with >50 locations. We calculated overall range as the great circle distance between the southernmost and northernmost feeding-area SSSM locations for each of these whales. For comparison with Calambokidis' et al. (2012) analysis of regional sighting patterns of gray whales in the PCFG, we calculated the length of the 75% inner quantile of location latitudes. We defined the 75% inner quantile as the middle 75% of the range of latitudes. We then calculated great circle distances between the farthest south and north location in this 75% inner quantile and reported in km and nautical miles for direct comparison with Calambokidis et al. (2012).

Residence Time

We determined the residence time, or the time a whale spent in each area, for all tagged whales in areas where ≥3 successive ARS locations occurred (ARS patch; Bailey et al. 2009). The ARS patches ended when ≥2 consecutive locations had behavioral mode values <1.75. We calculated residence time as the difference in time between the last and first ARS locations in the patch. To compare with previous PNW feeding area descriptions (Calambokidis et al. 2012), we assigned ARS patches to one of the following regions of the coast: northern California (NCA, from Cape Mendocino to the OR-CA border), southern Oregon (SOR, from the OR-CA border to Coos Bay), central Oregon (COR, from Coos Bay to Tillamook), northern Oregon (NOR, from Tillamook to the Columbia River), Grays Harbor Plus (GH+, southern WA coast from the Columbia River to Taholah, but primarily Grays Harbor), northern Washington (NWA, from Taholah to Cape Flattery), south Vancouver Island (SVI, from Victoria to Barkley Sound), west Vancouver Island (WVI, from Barkley Sound to northwest tip of Vancouver Island), northern British Columbia (NBC, British Columbia waters north of Vancouver Island), and southeast Alaska (SEAK, including Yakutat and Icy Bays).

To compute estimates of time spent inside the Makah Whaling Area (MWA; Fig. 1), we derived interpolated locations at 10-minute intervals between filtered Argos locations, assuming a linear track and a constant speed. These interpolated locations provided evenly spaced time segments from which reasonable estimates of time spent could be generated and were especially useful when tracklines crossed the MWA boundary. We calculated time spent within the MWA as the sum of all 10-minute segments from the interpolated tracks that were completely within these areas. We expressed percentage of time spent in these areas as a proportion of the track duration. We calculated the amount of overlap between whale home range and core area and the MWA using the intersect toolbox function in ArcMap version 10.0. We used a similar procedure for home range and core area overlap for the United States Navy's Northwest Training and Testing Offshore Area (NWTT; Fig. 1). We obtained the MWA boundary from the Draft Environmental Impact Statement on the Makah Tribe Request to Hunt Gray Whales (National Oceanic and Atmospheric Administration 2015). The NWTT boundary was provided by the United States Navy and we modified its eastern boundary north of Pacific Beach, Washington, to represent only the portion where in-water activities occur (≥3 nautical miles from shore).

RESULTS

We applied 35 tags to gray whales in 2009, 2012, and 2013 (Table 1). We received no transmissions from 2 of these tags. Total tracking periods for the remaining 33 tags ranged from 3 days to 383 days ($\bar{x} = 119.4 \pm 98.1$ [SD] days). The biopsies collected from 23 of the tagged whales indicated there were 12 males and 11 females (Table 1). Identification photographs taken during or after the tagging approach

Table 1. Tracking summary for satellite tags deployed on gray whales in the Pacific Coast Feeding Group off Oregon and California, USA, in 2009, 2012, and 2013 (excluding 2 tags deployed in 2012 that did not transmit).

Tag number	Tag style[a]	Sex[b]	Tagging date	Tagging region[c]	Date of last message	Attachment duration (days)	Feeding area duration (days)	
							Pre-southbound migration	Post-northbound migration
5200827	SPOT5-long	F	2 Sep 2009	COR	16 Apr 2010	225.8	163.8	
5200831[d]	SPOT5-long	M	2 Sep 2009	COR	21 Sep 2010	383.0	383.0	
5200847	SPOT5-long	F	3 Sep 2009	COR	29 Sep 2009	26.1	26.1	
5201385	SPOT5-long	M	4 Sep 2009	COR	17 Sep 2009	13.1	13.1	
5204174	SPOT5-long	M	4 Sep 2009	COR	14 Sep 2009	9.2	9.2	
5205670	SPOT5-long	M	4 Sep 2009	COR	23 Sep 2009	18.1	18.1	
5205801	SPOT5-short	F	21 Sep 2009	COR	14 Dec 2009	83.2	72.2	
5205923	SPOT5-short	M	21 Sep 2009	COR	13 Nov 2009	52.2	52.2	
5205938	SPOT5-short	F	4 Dec 2009	NCA	26 Jun 2010	203.2		122.1
5210836	SPOT5-short	M	14 Nov 2009	NCA	18 Nov 2009	3.3	3.3	
5210838	SPOT5-short	F	6 Oct 2009	COR	27 Oct 2009	20.1	20.1	
5210842	SPOT5-short	F	15 Nov 2009	NCA	4 Jan 2010	49.2	49.2	
5223029	SPOT5-short	M	5 Oct 2009	COR	18 Nov 2009	43.9	43.9	
5223032	SPOT5-short	M	14 Nov 2009	NCA	2 Jan 2010	49.0	44.9	
5223033	SPOT5-short	M	15 Nov 2009	NCA	3 Feb 2010	79.1	26.2	
5223035	SPOT5-long	M	1 Dec 2009	NCA	13 Jan 2010	43.0	9.1	
5223038	SPOT5-long	F	3 Dec 2009	NCA	5 Feb 2010	64.2	41.3	
5223041	SPOT5-long	M	1 Dec 2009	NCA	19 Jul 2010	229.8	49.0	112.8
5700834	SPOT5-long	F	2 Nov 2012	NCA	15 Mar 2013	132.7	60.9	11.0
5700841	SPOT5-long	F	3 Nov 2012	NCA	20 Dec 2012	46.6	43.0	
5700848	SPOT5-long	F	2 Nov 2012	NCA	29 Apr 2013	177.1	73.0	25.0
5705726	ST-15	F	4 Oct 2012	COR	20 Jun 2013	257.6	60.3	115.7
5705736	ST-15	M	15 Nov 2012	NCA	23 Feb 2013	99.7	20.9	
5705746	ST-15	F	8 Oct 2012	COR	20 Oct 2012	11.6	11.6	
5705801	SPOT5-long	M	3 Nov 2012	NCA	20 Oct 2013	351.0	24.3	203.5
5723033	SPOT5-long	F	3 Nov 2012	NCA	17 Mar 2013	133.3	32.2	8.0
5723041	SPOT5-long	F	3 Nov 2012	NCA	23 May 2013	200.2		46.0
6000839	SPOT5-long	F	23 Oct 2013	NCA	13 Feb 2014	112.7	75.1	
6001385	SPOT5-long	F	19 Oct 2013	NCA	25 Mar 2014	156.6	72.8	22.0
6001387	SPOT5-long	F	20 Oct 2013	NCA	13 Mar 2014	144.0	100.0	
6001389	SPOT5-long	M	21 Oct 2013	NCA	2 May 2014	214.2	69.8	87.3
6005800	SPOT5-long	M	22 Oct 2013	NCA	10 Apr 2014	169.2	56.0	37.0
6005823	SPOT5-long	M	20 Oct 2013	NCA	9 Mar 2014	139.2	42.2	15.1
					$\bar{x}$	119.4	45.9	67.1
					SD	98.7	33.1	61.1

[a] SPOT5-long refers to SPOT5 tags with 3 batteries. SPOT5-short refers to SPOT5 tags with 2 batteries.
[b] F = female. M = male.
[c] Tagging region uses the same terminology described in the Methods section, after Calambokidis et al. (2012). COR refers to Central Oregon. NCA refers to Northern California.
[d] Whale with tag 5200831 did not migrate out of the Pacific Northwest feeding area. Its feeding-area duration was not divided into pre- and post-migration, and is not included in averages for those time segments.

enabled all whales to be identified as gray whales from the PCFG using a combination of photo-identification databases (administered by Cascadia Research Collective, Olympia, WA, USA). Resight information from Cascadia Research Collective provided sex information for the whales that were not biopsied, resulting in 18 females and 17 males for the 35 tagged whales.

Tagging dates ranged from 2 September to 3 December of each year, and most whales were tagged off northern California from October to December. As such, the results were weighted toward fall- and winter-feeding area movements. Spring and summer movements could only be described for whales whose tags lasted beyond their return migration into the study area. Fall and winter tracking periods (prior to southbound migration) ranged from 3 days to 163 days ($\bar{x} = 45.9 \pm 33.1$ days, $n = 30$; Table 1). We tracked 12 whales into the PNW following their northbound migration from wintering lagoons off Baja California, Mexico. Post-migration tracking periods within the feeding area for these whales ranged from 8 days to 203 days ($\bar{x} = 67.1 \pm 61.1$ days; Table 1).

We tracked the start of southbound migration out of the PNW feeding area for 18 of the tagged whales, with dates ranging from 3 December to 13 February. Sixteen of these whales departed from northern California (14 from Point St. George and 2 between Point St. George and Cape Mendocino). The remaining 2 whales departed from the Oregon-California border and near La Push, Washington, on the west side of the Olympic Peninsula, respectively. The endpoints of northbound migration also varied between whales, with the main stopping points being the areas off Point St. George (3 of 12 whales) and Grays Harbor, on the central Washington coast (6 of 12 whales). The remaining 3 northbound migrants ended their directed travel off the

Columbia River mouth (near Astoria, OR), the northwest Washington coast (near the tip of the Olympic Peninsula), and the central west coast of Vancouver Island (BC), respectively. The end dates for northbound migration ranged from 21 February to 18 April.

One gray whale (tag 5200831), a male, did not migrate south at all, remaining off the northern coast of California for the duration of the winter, with 2 extended periods off Point St. George (138 days from Sep to Feb, and 48 days from Mar to Apr). The animal moved north to the central Oregon coast for 24 days in late spring, traveled back and forth between the central and southern Oregon coast until mid-July, and then remained off Cape Blanco for 66 days until the end of its tracking period on 21 September 2010, 383 days after tagging.

Tagged-whale movements were variable, with whales being distributed from central California to Icy Bay, Alaska, throughout the feeding season (Fig. 2). Most whale locations were on the continental shelf, close to shore, with 90% of high-quality locations occurring <7.5 km from shore, and 75% of them occurring <4.7 km from shore (median = 2.5 km; Fig. S1, available online in Supporting Information). Only 4 high-quality locations occurred >20 km from shore; 2 off Point St. George (23 km and 31 km), one 27 km north of Vancouver Island, and one 51 km from shore in Queen Charlotte Sound between Haida Gwaii and mainland British Columbia. Ninety percent of high-quality locations were in water depths <37 m, and 75% of them were in depths <24 m (median = 12 m; Fig. S1). Three good-quality locations occurred in water depths >200 m; one in 268-m depth off Point St. George, one in 506-m depth at the south end of Chatham Strait in Southeast Alaska, and one in 711-m depth off Point St. George. Tagged whales occupied more northerly areas (AK, BC, WA) earlier in the feeding season, primarily in spring and summer, and then shifted to the south in fall and early winter (Fig. S2, available online in Supporting Information).

We examined diagnostic plots from the state-space model for all whales, all of which showed good convergence of the model parameters (example in Fig. S3, available online in Supporting Information). Posterior distributions of the behavioral mode parameters (turning angle and autocorrelation in speed and direction) were well differentiated between the 2 modes, indicating good classification (example in Fig. S4, available online in Supporting Information).

Home Range Analysis

We calculated home ranges for 23 whales whose tracks provided >50 SSSM locations in PNW feeding areas. These home ranges ranged in size from 81 km^2 to 13,634 km^2 ($\bar{x}$ = 3,107 ± 4,140 km^2; Table 2). We calculated core areas

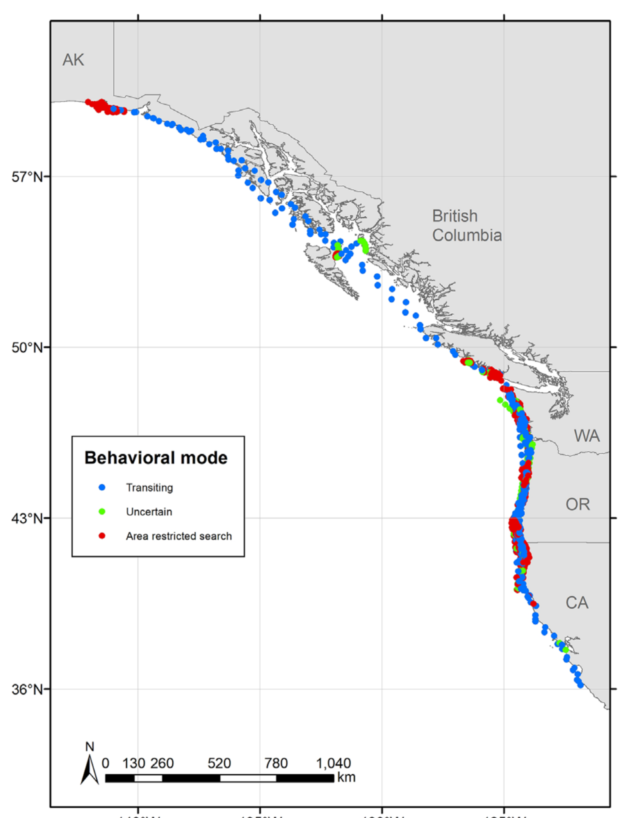

Figure 2. Switching state space model locations for satellite-monitored radio-tags deployed on 33 gray whales in the Pacific Coast Feeding Group off Oregon and California, USA, in 2009, 2012, and 2013. Only locations in the feeding area are shown.

Table 2. Feeding-area home range (90% isopleth) and core area (50% isopleth) sizes for 23 of the 35 gray whales in the Pacific Coast Feeding Group satellite-tagged off Oregon and northern California, USA, in 2009, 2012, and 2013. We calculated isopleths from switching state-space model (SSSM) locations derived from Argos tracks, using the local convex hull utilization distribution method. We used only those whales that provided >50 SSSM locations.

Tag number	Sex[a]	SSSM track duration (days)	Number of SSSM locations	Home range (km^2)	Core area (km^2)
5200827	F	164.5	329	1,251	206
5200831	M	382.5	765	1,874	250
5200847	F	26.0	52	11,797	2,260
5205801	F	73.0	146	979	380
5205923	M	52.0	104	1,372	634
5205938	F	122.0	244	5,034	2,788
5210842	F	49.0	98	110	11
5223029	M	43.5	87	1,069	754
5223032	M	44.5	89	389	57
5223038	F	41.5	83	473	82
5223041	M	160.5	321	7,227	1,986
5700834	F	61.0	122	13,634	3,976
5700841	F	43.0	86	330	
5700848	F	72.5	145	813	78
5705726	F	178.5	357	3,701	292
5705801	M	228.5	457	6,285	1,870
5723041	F	45.0	90	11,002	2,503
6000839	F	76.0	152	255	78
6001385	F	72.0	144	93	20
6001387	F	98.5	197	81	28
6001389	M	149.5	299	3,447	186
6005800	M	56.0	112	94	19
6005823	M	45.5	91	149	32
$\bar{x}$				3,107	840
SD				4,140	1,159

[a] F = female. M = male.

for 22 of these 23 whales, the sizes of which ranged from 11 km^2 to 3,976 km^2 ($\bar{x} = 840 \pm 1{,}159$ km^2). The LoCoH analysis for the whale with tag 5700841 could not resolve the core area using the recommended α-value (Getz et al. 2007). There was no linear relationship between log-transformed number of SSSM locations and log-transformed size of home ranges or core areas (linear regression $P = 0.23$ and $P = 0.51$, respectively). Home ranges and core areas did not differ in size between males and females (analysis of variance [ANOVA] $P = 0.54$ and $P = 0.52$, respectively).

Feeding-area home ranges covered most of the near-shore waters from northern California to Icy Bay, Alaska (Fig. 3). Core areas, illuminating regions of high use, showed a similar range and overlapped for multiple whales primarily off southern Washington, central Oregon, and southern Oregon-northern California (Fig. 4). The area of maximum overlap for home ranges (19 whales) and core areas (15 whales) occurred off Point St. George (Figs. 3 and 4).

For feeding-area tracks with >50 SSSM locations, overall ranges varied substantially, from 48 km to 2,398 km ($\bar{x} = 682 \pm 628$ km, $n = 23$; Table S1, available online in Supporting Information) and extended from 36°N to 60°N (Fig. S5, available online in Supporting Information). Mean distances and speeds between SSSM locations did not vary as much, however, with distances ranging from 4.5 km to 22.9 km ($\bar{x} = 14.6 \pm 7.4$ km) and speeds ranging from 0.4 km/hour to 2.8 km/hour ($\bar{x} = 1.2 \pm 0.6$ km/hr). Log-transformed overall range did not differ between males and females (ANOVA $P = 0.47$), nor did mean distances or speeds (ANOVA $P = 0.71$ and $P = 0.71$, respectively).

The length of the 75% inner quantile ranged from 4 nautical miles to 1,238 nautical miles (7–2,293 km), with a mean of 292 ± 329 nautical miles (541 ± 609 km; Table S1, available online in Supporting Information). Seventy percent of these lengths were >60 nautical miles (111 km), and 56% were >180 nautical miles (333 km).

Residence Time

We calculated residence times in ARS patches for 26 tagged whales in the PCFG (Table 3), of which 9 had only 1 ARS patch in their track, whereas the remaining 17 whales had 2 to 13. Average residence times ranged from 1 day to 87 days (mean of means = 26.7 ± 20.5 days). Nineteen whales had individual residence times >30 days. One whale had 2 instances of these extended residencies and 2 whales had 3, which resulted in 24 extended residencies, ranging from 30.5 days to 142.5 days. These extended residence times occurred off Icy Bay, Alaska (55 days, $n = 1$), Barkley Sound, Vancouver Island (30.5 days, $n = 1$), Grays Harbor, Washington (54 days, $n = 1$), the central Oregon coast (32.5 and 41.5 days, $n = 2$), Cape Blanco, southern Oregon (65.5 days, $n = 1$), and Point St. George, northern California (31.5–142.5 days, $n = 18$).

The area near Point St. George, California, was the most heavily used area in all years. Although some whales spent time off Point St. George early in the feeding season, most of the extended stays in this area occurred in the mid- to late-fall (Oct, Nov, Dec). Tagging and re-sighting efforts in that area consistently observed relatively large numbers (≥15–20) of gray whales, often including whales that had shed their tags. In 2009, 9 of the 10 whales that had been tagged off Oregon were documented at Point St. George at the end of November. Ten of the 11 whales tagged in 2012 had locations at Point St. George; the exception was a whale (tag 5705746) that was tagged off central Oregon and remained there for the 11-day duration of its tracking period. All whales tagged in 2013 were tagged off Point St. George. The whales at Point St. George appeared to be feeding because we observed defecation and the whales would often surface from a deep dive and turn 180 degrees before diving again. We often observed groups of sea lions (*Zalophus californianus*) and sea birds in the immediate area, and there was often a dense scattering layer (made by acoustic returns from

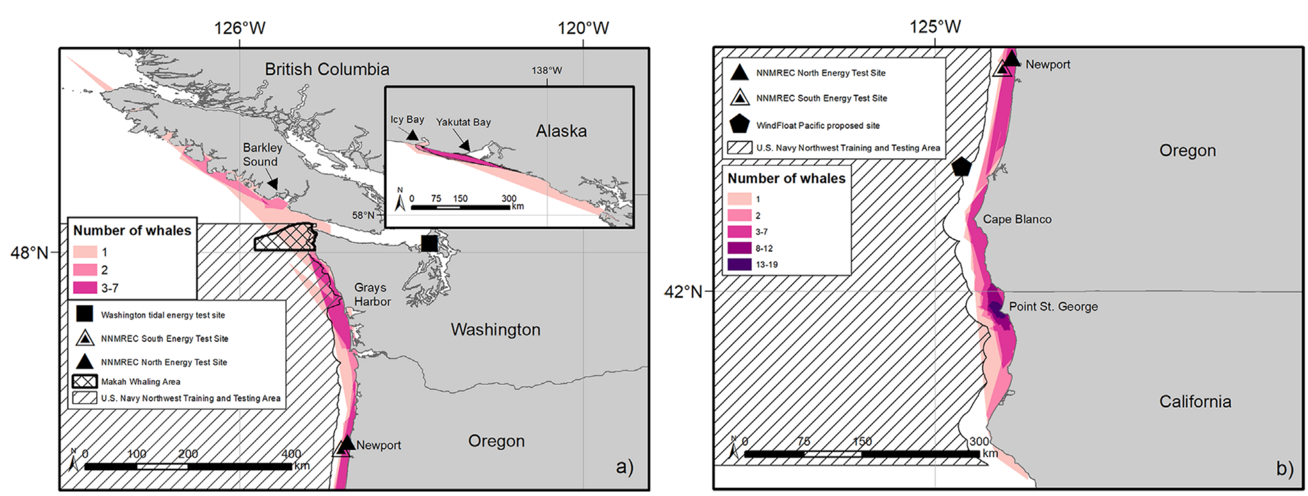

Figure 3. Feeding-area home ranges (90% isopleths) of satellite-tracked gray whales in the Pacific Coast Feeding Group tagged off Oregon and northern California, USA, in 2009, 2012, and 2013. Panel a shows a close-up view from British Columbia to central Oregon, with an Alaska inset and panel b shows a close-up view from central Oregon to northern California. We also present the locations of proposed and existing marine renewable energy sites, including the Northwest National Marine Renewable Energy Center (NNMREC) test sites, the Makah Whaling Area, and the United States Navy's Northwest Training and Testing Offshore Area (NWTT).

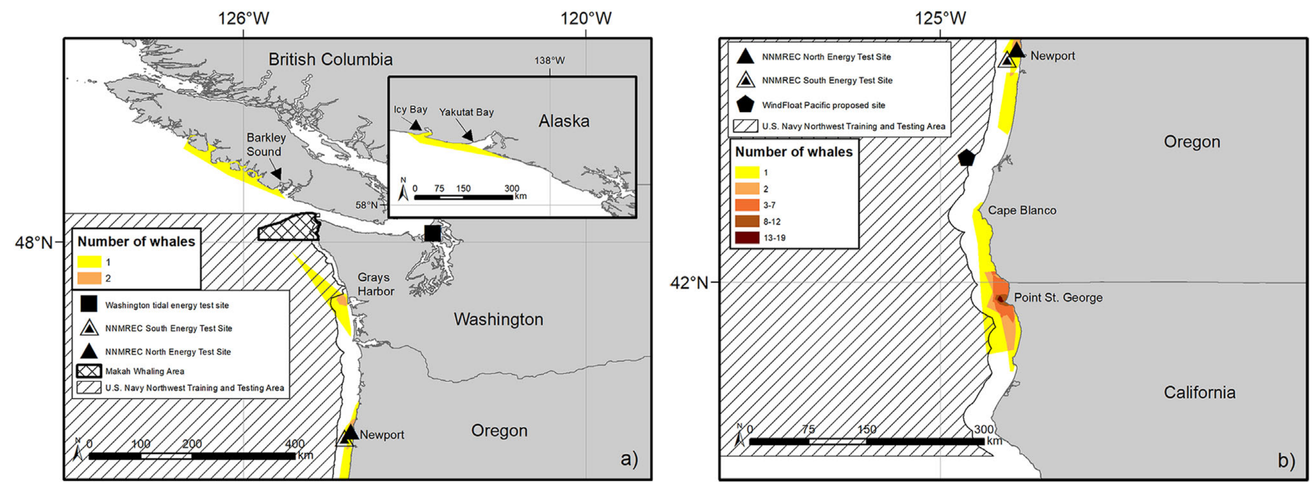

Figure 4. Feeding-area core areas (50% isopleths) of satellite-tracked gray whales in the Pacific Coast Feeding Group tagged off Oregon and northern California, USA, in 2009, 2012, and 2013. Panel a shows a close-up view from British Columbia to central Oregon, with an Alaska inset and panel b shows a close-up view from central Oregon to northern California. We also present the locations of proposed and existing marine renewable energy sites, including the Northwest National Marine Renewable Energy Center (NNMREC) test sites, the Makah Whaling Area, and the United States Navy's Northwest Training and Testing Offshore Area (NWTT).

presumed fish or zooplankton targets) measured by the tagging boat's echosounder.

Portions of the Argos tracks of 8 whales crossed the proposed MWA and 4 of these animals had locations inside the MWA (Fig. S6, available online in Supporting Information). The amount of time spent in the MWA for these whales ranged from 2 hour to 27 hour ($\bar{x} = 17.1 \pm 11.5$ hr). Six of these whales had SSSM locations inside the

Table 3. Residence times (number and duration of area restricted search [ARS] patches) and locations in the Pacific Northwest feeding area for 26 of the 35 gray whales in the Pacific Coast Feeding Group satellite-tagged off Oregon and northern California, USA, in 2009, 2012, and 2013. The ARS information was provided by a Bayesian switching state-space model (SSSM) analysis of the Argos tracks.

Tag number	Sex[a]	Tagging location[b]	Number of SSSM locations	% locations in ARS	Number of ARS patches	$\bar{x}$/max. duration of ARS patch (days)	ARS patch locations
5200827	F	COR	329	93.6	4	38.2/142.5	COR, SOR, NCA
5200831	M	COR	765	83.7	13	24.0/137.5	COR, SOR, NCA
5204174	M	COR	18	16.7	1	–/1.0	COR
5205670	M	COR	36	97.2	1	–/17.0	COR
5205801	F	COR	146	84.9	3	20.2/41.5	COR, NCA
5205923	M	COR	104	61.5	4	8.0/15.5	COR, SOR, NCA
5205938	F	NCA	244	71.3	5	16.7/55.0	SEAK, NBC, WVI
5210842	F	NCA	98	98.0	1	–/48.0	NCA
5223029	M	COR	87	91.9	2	19.5/31.5	SOR, NCA
5223032	M	NCA	89	93.3	2	20.5/36.5	NCA
5223035	M	NCA	17	76.5	1	–/6.5	NCA
5223038	F	NCA	83	95.2	1	–/39.5	NCA
5223041	M	NCA	321	61.7	6	15.7/48.0	NWA, COR, NCA
5700834	F	NCA	143	36.4	5	4.9/8.0	NWA, GH+, SOR, NCA
5700841	F	NCA	86	75.6	1	–/32.0	NCA
5700848	F	NCA	195	82.1	4	19.6/43.5	GH+, SOR, NCA
5705726	F	COR	354	91.2	8	19.9/54.0	WVI, NWA, GH+, COR, SOR, NCA
5705746	F	COR	23	95.6	1	–/10.5	COR
5705801	M	NCA	453	68.0	12	12.4/32.5	NWA, NOR, COR, SOR, NCA
5723041	F	NCA	74	63.5	2	11.7/13.5	SEAK, GH+
6000839	F	NCA	151	100	1	–/75.5	NCA
6001385	F	NCA	184	99.5	2	45.7/71.5	GH+, NCA
6001387	F	NCA	196	89.3	1	–/87.0	NCA
6001389	M	NCA	309	82.5	3	42.3/67.5	SEAK, SOR, NCA
6005800	M	NCA	185	59.5	2	27.7/53.5	SOR, NCA
6005823	M	NCA	120	99.2	2	29.5/44.5	NWA[c], GH+, NCA
$\bar{x}$ (SD)				79.5 (20.5)		26.7 (20.5)/46.7 (35.4)	

[a] F = female. M = male.
[b] Tagging location uses the same region terminology described in the Methods section, after Calambokidis et al. (2012). COR = Central Oregon. GH+ = Grays Harbor Plus. NBC = Northern British Columbia. NCA = Northern California. NWA = Northern Washington. SEAK = Southeast Alaska. SOR = Southern Oregon. WVI = Western Vancouver Island.
[c] The ARS patch for tag 605823 includes the Makah Whaling Area.

MWA, representing 15 locations (5 ARS, 8 transiting, 2 uncertain). Locations of tagged whales in the MWA occurred during 6 months (Feb, Mar, Apr, May, Sep, Dec), and of these, ARS locations occurred in 3 (Feb, Apr, May). Home ranges for 2 gray whales overlapped with the MWA, representing 20% of the home range for tag 5200847 and <1% of the home range for tag 5223041 (Table S2, available online in Supporting Information; Fig. 3). These overlapping portions of home ranges covered 67% (2,324 km^2) and <1% (8 km^2) of the 3,461-km^2 MWA, extending 54 km and 7 km offshore for tag 5200847 and tag 5223041, respectively. There was no overlap between gray whale core areas and the MWA.

Portions of the Argos tracks of 10 whales crossed into the NWTT, 9 of which had 135 locations. Nine whales had SSSM locations in the NWTT, representing 84 locations (44 ARS, 30 transiting, 10 uncertain). Locations of tagged whales occurred in the NWTT during 8 months (Jan, Feb, Mar, Apr, May, Aug, Nov, Dec), and ARS locations occurred in 6 months (Jan, Mar, Apr, May, Aug, Dec). Home ranges for 6 gray whales overlapped with the NWTT, representing between 2% and 28% of their home ranges (Table S2, Fig. 3). Core areas for 2 gray whales overlapped with the NWTT, representing 8% of the core area for tag 5700834 and 53% of the core area for tag 5723041 (Fig. 4). These overlapping home ranges and core areas covered <1% of the NWTT, with the westward extent of the overlapping portions ranging from 10 to 60 km from shore.

DISCUSSION

The detailed feeding area movements of gray whales presented here provide valuable information about habitat use and residency in the PNW. Although home ranges extended throughout the entire PNW, from northern California to southeast Alaska, areas of high use (i.e., regions with overlapping core areas for multiple gray whales) were centered off southern Oregon-northern California, central Oregon and southern Washington, with the area off Point St. George being the most heavily used. The absence in this study of overlapping core areas in other places in the PNW where gray whales congregate, such as the west coast of Vancouver Island (Darling 1984, Calambokidis et al. 2012), does not suggest these areas are unimportant. Rather, these absences are most likely the result of when and where whales were tagged (the majority were tagged off northern CA in fall) and the small sample of tagged whales that were tracked into the following spring and summer. Tagging of gray whales earlier in the feeding season and in more areas would provide a more complete picture of gray whale use of the PNW. Even with this caveat, the tracking information gained in this study confirms some of the findings of previous photo-identification studies, but also fills some data gaps inherent in those studies, all of which is useful in evaluating gray whales' exposure to risk from anthropogenic activities in the marine environment.

Photo-identification studies of gray whales in the PNW have yielded considerable information about whales in the PCFG, including distribution, seasonal occurrence, site fidelity, and abundance (Darling 1984, Calambokidis et al. 2002, 2009, 2012, Scordino et al. 2014*b*). They have also provided insight into overall range, individual residency, and movement between regions in the PNW, but because sightings are static and influenced by the timing and location of effort, they do not provide a complete picture. The tagging results gained in this study complement photo-identification efforts by filling in temporal gaps with continual location tracking over weeks to months. Calambokidis et al. (2002) reported a progression from north to south in the movement of gray whales in the PCFG throughout the summer and fall feeding season, a finding that is borne out by our tracking results. Despite only a few tracks lasting into the following summer feeding season, we did see a predominance of locations in more northerly areas (WA, northern BC, and southeast AK) in early spring and summer with locations in Oregon and northern California occurring in mid-late summer and fall. Also, like photo-identification studies, this study shows that some whales exhibit clustered locations within a small range and others are highly dispersed throughout several regions. Overall, however, ranges of tagged gray whales were considerably longer than those from photo-identification studies, with 70% of tagged whales having 75% inner quantiles greater than 60 nautical miles (111 km), and 56% having inner quantiles greater than 180 nautical miles (333 km), compared to 41% and 18%, respectively, for whales from photo-identification studies (Calambokidis et al. 2012). Tracking data also showed that interchange between areas is more extensive than reported from photo-identification studies, with tagged whales visiting multiple (and often, non-neighboring) areas in a single feeding season. In addition to the obvious differences in data collection, mentioned above, differences noted here may also be due, in part, to the different sampling periods, with information from photo-identification studies being described primarily for the period of June through November (and in some years, from very few days of effort in some regions), compared to all months for information from this study.

Gray whales use the northern California area late in the summer feeding season (Calambokidis et al. 2002). However, surveys there did not typically take place in November and December, when most tagged whales from this study were occupying the Point St. George area, so its importance may have been under-represented. The predominance of overlapping core areas off Point St. George and the long residencies there (16 whales with maximum residence times of 31.5–142.5 days for this area, including 4 whales tagged in OR) highlights the importance of this area as a late-season feeding site, and perhaps a staging area for gray whales in the PCFG prior to southbound migration. All but 2 of the 33 tracked whales spent time in the Point St. George area, and 18 of these whales spent time in this region just before migrating south. Some of the predominance in locations in the area off Point St. George reflects the large number of tag deployments there (23 out of 35 whales). Whales tagged in Oregon, however, also used the area; we tracked 7 of 12 whales tagged off central Oregon to Point St.

George before they migrated south. All but 1 of the remaining 5 whales tagged in Oregon were photographed at Point St. George after losing their tags, suggesting that many whales from more northern regions in the PNW also congregate there late in the feeding season. The observed feeding behavior exhibited by the relatively large number of whales in this area suggests it may provide an important final source of food before winter migration. On 2 days in November 2012, we also observed social behavior, with 2–3 whales milling very close to each other, swimming belly-to-belly at the surface and rubbing pectoral fins on each other. We also observed a penis extrusion during one of these encounters. These observations suggest Point St. George may also provide breeding opportunities for gray whales. Apparent mating activity of gray whales in northern areas has also been observed off Vancouver Island (Hatler and Darling 1974), northern California, Washington, and northern Alaska (Rice and Wolman 1971).

One male gray whale (tag 5200831) remained off Point St. George throughout the winter and did not migrate, providing evidence of a gray whale not participating in the winter migration to Mexico. It has been hypothesized that female gray whales may not complete the migration to Mexico if their calves are born farther north (Shelden et al. 2004). Gray whale calls have also been recorded throughout the winter in the Beaufort Sea (Stafford et al. 2007), suggesting either that some whales do not migrate, or that there is sufficient variation in the timing of migration in and out of the region that whales are collectively present throughout the year. Resight photographs of milling whales taken at the Point St. George area in mid-winter (27 Jan 2010) provided identification of 5 tagged whales from this study. The tags on these whales had all been shed by early January 2010 so we did not obtain migration information. The resights indicate either late migration departures for these whales, or the possibility that they too may have overwintered in northern California.

The other 2 areas of high use identified in this study were the central Oregon coast and the southern Washington coast, specifically the area off Grays Harbor. Core areas overlapped for 2 whales in both of these areas, and home ranges overlapped for up to 7 whales off central Oregon and up to 5 whales off southern Washington. Residence times ranged from 1 day to 41.5 days for central Oregon and 3.5 days to 54 days for southern Washington, highlighting these areas as important feeding habitat for gray whales in the PCFG. The central Oregon coast is experiencing increased interest in the development of marine renewal energy, with Northwest National Marine Renewable Energy Center test site facilities off Newport (Northwest National Marine Renewable Energy Center 2016) and proposed wind energy development off Coos Bay (Bureau of Ocean Energy Management 2016). These developments have the potential to cause behavioral disturbance to whales or even injury from collision with cables, structures, and vessels, or entanglement in cables and lines (Henkel et al. 2014). One of the test sites off Newport (South Energy Test Site, 11 km from shore) and the wind energy development off Coos Bay (~24–30 km from shore) are farther from shore than most gray whale locations in these areas (90% of high-quality locations for tagged gray whales in this study were <8 km from shore), and as such may have minimal influence on feeding gray whales. The Northwest National Marine Renewable Energy Center's North Energy Test Site is located between 4 km and 6 km from shore off Yaquina Head, Oregon, but this is still outside the majority of tagged gray whale locations (67% of which are closer than 4 km to shore, 50% of which are closer than 2.4 km to shore).

The area of high use off southern Washington (principally Grays Harbor) came within 3 km of the boundary of the NWTT, which extends all the way to shore at Pacific Beach, Washington (~30 km north of Grays Harbor). The core area for 1 of these whales extended into the NWTT north of Grays Harbor, with its westernmost edge extending out to 42 km offshore. The NWTT extends along the coasts of northern California (just south of Cape Mendocino), Oregon, and Washington, out to approximately 460 km from shore. The eastern boundary for in-water activities of the NWTT is 5.5 km from shore north of Pacific Beach, and 22 km from shore south of Pacific Beach. The home ranges of 4 other gray whales also extended into the NWTT off Washington, with home range western edges ranging 10–60 km offshore. The core area for yet another gray whale in this study included part of the NWTT south of Point St. George, California, with its western boundary extending 33 km offshore. None of the overlapping areas accounted for >1% of the area of the NWTT, however. Gray whale locations occurred in the NWTT during January, February, March, April, May, August, November, and December, with whales exhibiting ARS behavior in all but February and November. In November 2016, the Navy announced its decision to implement adjustments to types and levels of activities in the NWTT, as necessary to support current and planned training and testing requirements (U.S. Department of the Navy 2016). Such activities have the potential to disturb or injure whales; however, the National Marine Fisheries Service has determined the level of effect to be negligible, with the implementation of protective measures (lookouts, activity-specific mitigation zones, time-area limitations; U.S. Department of the Navy 2016). Most high-quality locations for tagged whales in this study were <9 km from shore; therefore, the potential exposure of gray whales to Navy activities is small. The one exception to this would be in the area of Pacific Beach, Washington, where the boundary of the training range extends to shore.

Both the central Oregon coast and the southern coast of Washington contain large commercial fishing ports, and the Columbia River at the Oregon-Washington border represents the busiest river mouth along the west coast for commercial shipping, with barges, container ships, and tankers all traveling to and from Portland, Oregon and beyond. The Oregon commercial crab fishery is one of the largest producers of Dungeness crab (*Metacarcinus magister*) on the United States West Coast (Oregon Department of Fish and Wildlife 2017*a*). Washington, California, and British Columbia also have large commercial crab fisheries (Department of Fisheries and Oceans Canada 2017, Washington Department of Fish and Wildlife 2017, California Department of Fish and Wildlife 2017*a*). Such traffic and fishing activity present the possibility of increased risk of ship strikes and entanglement in fishing gear for gray whales. Scordino and Mate (2012) estimated a minimum annual mortality from fisheries bycatch and ship strike of 1.83 gray whales in the PCFG per year between 1990 and 2010, and Scordino et al. (2014*a*) reported minimum annual rates of serious injury and mortality in United States and Canadian waters ranging from 1.4 to 2.6 gray whales in the PCFG between 2008 and 2012. A more recent study compiling data from 1924 through 2015 documented a minimum of 397 reports of non-hunting, human-caused injuries and mortalities of gray whales in the North Pacific, of which an estimated 299.8 resulted in mortality (Scordino et al. 2017). The most common reported cause of injury and mortality was from net fisheries, followed by unknown entanglements, ship strikes, and pot fisheries. Ship strikes were the most common reported cause of injury and mortality in the 1970s, whereas net fishery entanglements were the most common cause in the 1980s and 1990s, and pot fisheries and unknown entanglements were the most common in the 2000s and 2010s (Scordino et al. 2017). A decline in gillnet fishing effort off the West Coast of the United States and Canada from the 1980s (Barlow et al. 1994) and a shift of set-net fisheries to ocean waters deeper than 60 fathoms in parts of California may have contributed to a decrease in net fishery entanglements after the 1990s (Scordino et al. 2017). To address the problem of entanglements, the California Dungeness Crab Fishing Gear Working Group developed a Best Practices Guide to minimize whale entanglement risk (California Department of Fish and Wildlife 2017*b*) in their fishery. Mitigation efforts are also underway in Oregon, where the Oregon Department of Fish and Wildlife, Oregon Sea Grant, and the Oregon Dungeness Crab Commission are partnering to engage stakeholders and develop options for short- and long-term modifications to gear and fishery practices (including possible seasonal closures) to reduce the risk of whale entanglements (Oregon Department of Fish and Wildlife 2017*b*). The detailed information regarding gray whale high use areas and residency provided in this study can help inform these efforts by highlighting the most persistent areas of gray whale use and facilitating management approaches that seek to reduce spatio-temporal overlap with fisheries.

In addition to high-use areas described above, areas north of Vancouver Island may also represent important feeding areas for some gray whales in the PCFG. Three of the 12 tagged whales that were tracked into spring spent time in southeast Alaska; a 2009-tagged whale spent 56 days (in Apr and May) near Icy Bay before heading south to the east side of Haida Gwaii, a 2012-tagged whale spent 10 days in May near Icy Bay before its tag stopped transmitting, and a 2013-tagged whale spent 20 days in May between Icy Bay and Yakutat Bay before its tag stopped transmitting. Despite small sample sizes, 3 gray whales in 3 separate years spent extended periods of time near Icy Bay, Alaska, suggesting this area may represent important early-season feeding habitat for some whales in the PCFG.

Information regarding seasonality and distribution of whales in the PCFG, in relation to the rest of the gray whale population in the ENP, is critical for the Makah Tribe, who want to resume their gray whale hunt as part of their Neah Bay Treaty rights (National Oceanic and Atmospheric Administration 2017). To minimize the influence of such a hunt on gray whales in the PCFG, the Makah Tribe has proposed spatial closures, limiting hunting to the Pacific Ocean portion of their usual and accustomed fishing grounds, and a closure during the feeding season, between 1 June and 30 November (Scordino et al. 2013). Because 31% of gray whales along the outer coast of northwest Washington during the migratory season (Dec through May) have been found to be gray whales in the PCFG (Scordino et al. 2013), the Makah Tribe also proposed an allowable PCFG limit during the hunt to ensure that accidental takes of whales in the PCFG do not deplete that segment of the population (International Whaling Commission [IWC] 2013, Scordino et al. 2013). To determine whether gray whales in the PCFG are taken during the hunt, all landed whales will be photographed and compared with the PCFG identification catalog and any matches will be counted against the allowable PCFG limit (Scordino et al. 2013). The IWC evaluated the effects of the Makah Tribe's proposed hunt management plan and reported that the hunt met their objectives of conservation while allowing limited hunting provided that all whales struck and lost in May would be counted against the allowable PCFG limit or that a December to April hunt be accompanied by a photo-identification program each year to monitor the relative probability of harvesting individuals from the PCFG in the MWA (IWC 2013, Scordino et al. 2013). The locations of tagged whales in this study confirm that time of year may be a poor indicator of subpopulation identity for whales passing through the MWA. Tagged gray whales were in or near the MWA during 6 different months, including those that overlap with migratory timing of gray whales from the ENP (Dec, Feb, Apr, May). Tagged whales exhibited ARS behavior in the MWA during these winter and spring months, highlighting the possibility that gray whales in the PCFG may be feeding there outside of the usual feeding season, in addition to transiting through the area. This information lends further support to the cautionary measures proposed by the Makah Tribe to ensure the allowable PCFG limit is not exceeded during their gray whale hunt.

All 12 of the tagged whales in this study that were tracked beyond their northbound migration from Mexico arrived in the feeding area in late winter or early spring (Feb, Mar, or Apr), well before the cutoff used in abundance estimations of gray whales in the PCFG by Calambokidis et al. (2012). Calambokidis et al. (2012) used 1 June as the seasonal start date for their abundance estimates based on 13 years of photo-identification data because they showed that whales seen prior to that date were more likely to be gray whales from the ENP migrating through the region on their way to Arctic feeding grounds. The tagged whales in this study have all been photographed multiple times in the PNW during the feeding season (J. Calambokidis, Cascadia Research Collective, personal communication), confirming they are individuals from the PCFG. Early arrival of gray whales in the PCFG to the feeding area is unlikely to affect abundance estimates because these whales are very likely to remain in the feeding area after the 1 June start date and would therefore be available for photographic recapture. The early arrival does have relevance, however, with respect to management efforts and evaluation of risk for gray whales from human activities in the ocean. Gray whales in the PCFG are feeding in the PNW well before summer and this information should be taken into account when considering marine spatial planning or coastal development in these areas.

MANAGEMENT IMPLICATIONS

The results of this tagging study fill important information gaps regarding distribution and residence times of gray whales in the PNW, especially in areas or times without much survey effort. The information is useful with respect to the proposed Makah whale hunt and in the planning and mitigation of United States Navy activities in the NWTT, especially in the nearshore waters off the Washington coast. Knowledge about areas of high use for gray whales is also helpful in the appropriate siting of coastal development, such as marine renewable energy facilities (wave and offshore wind) and in efforts to reduce the risk of ship strikes and entanglements in fishing gear.

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