NOVEL APPROACH REVEALS SPATIAL AND TEMPORAL CHARACTERISTICS IN SOUNDERS GRAY WHALE FORAGING IN NORTHERN PUGET SOUND, WA

by

Amanda Ellen Nehring Rueda

A Thesis
Submitted in partial fulfillment
Of the requirements for the degree
Master of Environmental Studies
The Evergreen State College
June 2025

This Thesis for the Master of Environmental Studies Degree

by

Amanda Ellen Nehring Rueda

has been approved for

The Evergreen State College

by

Sarah O’Neal

Member of Faculty

June 6, 2025
Date

Abstract

Novel Approach Reveals Spatial Characteristics of Sounders Gray Whale Foraging in Northern Puget Sound, WA

Amanda Rueda

Anthropogenically driven climate warming and sea ice reduction exerts major negative impacts on benthic invertebrate abundance and distribution in the Arctic. Foraging Eastern North Pacific (ENP) gray whales (*Eschrichtius robustus*) derive enormous amounts of energy from Arctic benthic prey to fuel one of the longest annual migrations of any mammal. Consequently, gray whale feeding ranges are increasingly diverging from typical migratory routes along the U.S West Coast, particularly following two unusual mortality events linked to altered prey dynamics in the Arctic. Understanding gray whale foraging habitat requirements will be crucial for the conservation and management of this species under increasing anthropogenic threats. This study focused on a unique group of ENP gray whales (the Sounders) that engage in ~100 mi stopover foraging periods within northern Puget Sound (NPS), WA along their northern migration. We quantified feeding area using aerial imagery taken from a fixed-wing plane between 2017-2024. About 14 km^2 of maximum gray whale feeding extent was identified within NPS intertidal regions throughout the study. Highest feeding area was consistently observed near the Snohomish River Delta in Possession Sound. Generalized linear mixed model results indicated whale presence and mean tidal height had a significant effect on total feeding area ($p = 0.0267$, $p < 0.0001$, $R^2=0.59$). Our model also indicated an increase in 2.28 km^2 of feeding area was associated with each additional Sounders gray whale present in NPS. Overlapping feeding area observations highlight consistent gray whale foraging habitat utilization in NPS over an 8-year period. These results can be broadly applied to understand ENP gray whale foraging habitat requirements as elevated variability in historical feeding grounds persist.

Table of Contents

List of Figures

List of Tables

Dedication

My grandfather was a fisherman who worked as a vessel mechanic at a salt mining company in Guerrero Negro, Mexico. He told a story about working on a ship that had been destroyed by a gray whale mother after striking her calf. So moved by this act of love, he dedicated a great portion of his life to conserving Ojo de Liebre Lagoon (also known as Scammon’s lagoon) without any degree, pay, or government recognition (Ellis, 1977). My dad also grew up with a love for the ocean which he passed to me. This is for both of my parents who I love dearly.

Acknowledgements

I am incredibly grateful for the many people who have supported me throughout my academic journey to this point. Words can’t express how thankful I am to have worked with Cascadia Research Collective on this study. Hannah Clayton, John Calambokidis, and Alex Vanderzee provided an incredible amount of technical and moral support. I am honored to learn from and call them and others from CRC my friends.

Thank you to Fred Lundahl and Julia Erickson for conducting the aerial surveys used in this study and for their continuous work and dedication towards studying this magnificent group of whales.

Thank you to my thesis reader, Sarah O’Neal for her guidance and feedback.

Literature Review

Background

Cetaceans possess evolutionary adaptations that have enabled highly advanced foraging capacities and gigantism (Goldbogen & Madsen, 2018). Order Cetacea broadly encompasses all species of whale, dolphin, and porpoise. Whales are further classified by two suborders, Odontoceti and Mysticeti (Chivers, 2009). Odontocetes, or toothed whales, evolved to use echolocation, the emission and transmission of high-frequency underwater sounds, to hunt prey, navigate, and communicate (Coombs et al., 2024). Mysticetes, or baleen whales, utilize keratinized tooth structures from the roof of their mouth to filter small sized prey aggregations in enormous amounts through a variety of strategies. Rorquals, including blue and humpback whales, have grooves from the throat to the belly button that expand to great magnitudes whilst lunging to engulf immense amounts of krill (Goldbogen et al., 2019). Right and bowhead whales skim at the sea surface to collect prey. Gray whales (*Eschrichtius robustus*), on the other hand, are most known for their benthic feeding strategy, utilizing suction along the sea floor to excavate hidden invertebrates (Nerini, 1984). Many cetacean and other marine mammal species provide valuable insight into a variety of ongoing changes occurring within marine ecosystems as ecosystem sentinels (Moore, 2008). The health and diet of these large animals brings awareness to the effects of increasing anthropogenic impacts on lower trophic levels. Historical fossil records along with modern technological advances such as biologging tag devices and drones have propelled the study of cetacean feeding and behaviors, but additional research is needed to fully understand foraging energetics at the species level (Goldbogen & Madsen, 2018).

Gray whales are the only extant species in the Eschrichtiidae family of suborder Mysticeti (Barnes & McLeod, 1984). Ranging from 36-50 ft long, gray whales are a mottled gray color and possess a dorsal ridge with 10-12 knobs trailing towards the peduncle rather than a dorsal fin (Rice et al., 1984). Gray whales were referred to as “devil fish” in the time of intense commercial whaling based on their determination and resistance against hunters. Gray whales are known to migrate and feed within 1km of the coast, which increases their likelihood of encountering anthropogenic threats such as ship strikes. This migratory behavior also provides a unique opportunity to study large whale foraging tactics. As anthropogenic impacts on global marine ecosystems increase and alter food webs, information regarding gray whale behavior will be crucial in addressing their conservation needs.

Overview

Eastern North Pacific (ENP) gray whales have experienced intense fluctuations in population abundance related to anthropogenic causes over several centuries. Commercial whaling along the Pacific Coast of North America depleted the population in the 1800s. Several unusual mortality events have since occurred following the ENP gray whale population recovery and federal delisting from the Endangered Species Act in 1994. Climate change has now been linked to decreased gray whale prey availability in Arctic feeding grounds due to sea ice reduction. Subsequently, some ENP gray whales have been observed feeding in abnormal areas and altering their migratory patterns. Gray whale habitat, feeding behavior, and prey choices influence their foraging efficiency and overall health. A small group of ENP gray whales diverge from their northern migratory route to forage on intertidal ghost shrimp in northern Puget Sound (NPS), Washington each year. This study will focus on visible gray whale feeding excavations, or “feeding pits”, within the sandy intertidal region to analyze gray whale feeding and habitat requirements which can be applied to understand the greater health of the ENP population in a time of high environmental variability.

Population Trends and Anthropogenic Threats

Whaling

Eastern North Pacific (ENP) and Western North Pacific (WNP) gray whales are two genetically and geographically distinct populations found in the northern Pacific Ocean (LeDuc et al., 2002). ENP gray whales are found along the western coast of North America and WNP gray whales along the eastern coast of Asia (Weller, 2002; Weller et al., 2012). Commercial whaling practices significantly reduced both extant populations beginning in the 1800s. Whaling peaked along the Coast of California from 1854-1865 and then began to decrease after 1874 due to a sharp decline in population abundance (Henderson, 1984). Significant female and calf mortalities greatly contributed to the decline in gray whale abundance and reproductive capacity (Henderson, 1972, 1984). The ENP population was reduced from ~ 15,000-30,000 individuals to less than 5,000 and the WNP population from ~ 1,500-10,000 individuals to near extinction (Stewart et al., 2023; Weller, 2002).

The International Whaling Commission (IWC) enacted a global moratorium that ended commercial whaling practices in 1986 (IWC, 2024b). Legislation including the Endangered Species Act (ESA, 1973) and Marine Mammal Protection Act (1972) also protected ENP gray whales in U.S waters. Eastern North Pacific gray whales were delisted from the ESA in 1994 by the National Oceanic and Atmospheric Administration (NOAA) when their population abundance estimation returned to just over 20,000 (Rugh et al., 1999). The WNP population remains endangered with an estimated population of less than 200 individuals (Bradford et al., 2008).

Several indigenous groups historically practiced subsistence hunting on gray whales including the Chukchi from the Chukotka Peninsula, Russia and the Makah Tribe from the northwest Olympic Peninsula, Washington state (IWC, 2024a; Krupnick, 1984; O'Leary, 1984).

Subsistence whaling is a traditional form of whale hunting that prioritizes community nutrition and culture rather than large catch numbers or profit (IWC, 2024a). The Makah Tribe received a Marine Mammal Protection Act waiver in June 2024, after years of judicial challenges, with a subsistence quota for 25 ENP gray whales over 10 years (NOAA Fisheries, 2024a).

Unusual Mortality Events

The ENP gray whale population has experienced several Unusual Mortality Events (UMEs), now being linked to altered feeding ground conditions due to anthropogenically driven climate change (Stewart et al., 2023). An unusual mortality event is declared in response to significant and unexpected marine mammal mortalities (NOAA Fisheries, 2024c). The first official gray whale UME occurred from 1999-2001 with about 651 strandings, followed by 2019-2023 with 690 (NOAA Fisheries, 2025). Population abundance was almost halved during the most recent UME from an estimated 26,960 (2015-2016) to 14,526 (2022-2023) whales (Eguchi et al., 2024). An unofficial gray whale UME also occurred from 1987-1989 with a similar decline in population abundance, though stranding extent may not have been detected due to reduced survey effort (Stewart et al., 2023). Several factors possibly contributed to the drastic strandings in 1999-2001 including starvation, contaminants, disease, parasites, fisheries interactions, and ship strikes (Gulland et al., 2005). The 2019-2023 UME was more specifically linked to ecological factors influencing prey and phenological shifts in the Arctic (Moore et al., 2022; NOAA Fisheries, 2025; Stewart et al., 2023).

Threats

Gray whales are directly vulnerable to entanglement, pollution (physical, chemical, and auditory), and ship strikes (Sato & Wiles, 2021). Entanglement is when animals become caught in human gear, line, or debris and either become trapped or tangled for long periods. Large whale entanglement often leads to death due to breathing and feeding restriction (NOAA Fisheries, 2024b). Chemical and physical pollution can disturb whales and be consumed by lower prey species, negatively impacting marine food webs. Pollution can also be through ship noise which has been shown to increase stress hormones of gray whales along the coast of Oregon (Lemos et al., 2022). Lastly, ship collision is especially dangerous for gray whale populations that forage in nearshore environments and can cause life threatening blunt force trauma or open wound injuries (Douglas et al., 2008).

Migratory Behavior and Subgroups

Migration

Eastern North Pacific gray whales migrate more than 15,000 km annually from breeding grounds in Baja California Sur, Mexico to feeding grounds in the Bering and Chukchi Seas (Stewart et al., 2023). Breeding and birthing of calves occurs between December and April in the warm lagoons of Laguna Ojo de Liebre (Scammon’s Lagoon) and Laguna San Ignacio (Jones et al., 1984). Gray whales begin their nearshore northern migration during late March and typically reach Arctic feeding grounds by June (Urbán R et al., 2021). ENP whales feed in northern waters until late fall, then return south to Mexico for mating and reproducing.

Pacific Coast Feeding Group

Pacific Coast Feeding Group (PCFG) whales are an ENP gray whale subpopulation that remain feeding between northern California and northern Vancouver Island from approximately June to November during northward annual migration (Calambokidis, 2015). This group consists of about 200-250 individuals that often feed throughout the summer along the U.S West Coast rather than completing migration to the Arctic. Genetic evidence and sighting observations show PCFG whales exhibit site fidelity, returning to the same location over time (Frasier et al., 2011).

Recognizing PCFG whales as a separate “seasonal subpopulation” or “management unit” strengthens management efficiency, specifically for the resumption of Makah subsistence whaling. Several PCFG whale foraging grounds are identified as Feeding- Biologically Important Areas (F-BIAs), which are designated to better inform spatial management and conservation decisions in areas that are utilized by cetacean populations (Calambokidis et al., 2024).

Northern Puget Sound Gray Whales

A group of ENP gray whales were first identified foraging in NPS in the 1990s (Calambokidis, 2016). These NPS gray whales, the “Sounders”, annually return to feed near Whidbey and Camano Islands (Calambokidis et al., 2024). Sounders forage during the spring, typically from March-June, then continue migrating north with the greater ENP population. Some individuals arrive in Puget Sound earlier than March, including CRC-53 (Little Patch) who was sighted in either December or January for the past 5 seasons (2020-2025) and likely did not return to Mexico to breed during these years (CRC unpublished data, 2025). Individual gray whales must be documented returning to NPS for multiple years to be characterized as a “Sounder” rather than a visiting migratory whale. Less than 12 Sounders were identified in 2018, which increased to 18 individuals by 2022. This increase in Sounders identifications often coincided with UME periods linked to altered prey dynamics in the Arctic (CRC unpublished data, 2025). Sounders gray whales are not a recognized subgroup of the ENP population and do not forage for extended periods in the same range as PCFG whales. However, their NPS foraging range is a designated F-BIA which is important for informing regional resource managers (Calambokidis et al., 2024).

Gray Whale Feeding

Background

Gray whale feeding mechanisms include suction, skimming, and engulfing (Nerini, 1984). Gray whales are equipped with baleen plates that are fewer, thicker, and sturdier than the baleen of other Mysticetes. This baleen formation allows gray whales to sift prey from mouthfuls of sediment and water during benthic feeding. Gray whales are opportunistic and generalist feeders which allows for consuming a wide selection of prey throughout their range. Wintering and migrating gray whale stomach contents have included sardines, larvae, and smelt (Nerini et al., 1980). However, gray whales in northern feeding grounds primarily suction feed on benthic organisms such as amphipods.

Northern Puget Sound

Gray whales foraging in NPS engage in a high-risk version of benthic suction feeding within intertidal areas (Calambokidis et al., 2017). These gray whales access the intertidal region during high tide in water depths from 2-3 m, then laterally suction feed on ghost shrimp (*Neotrypaea californiensis*) (Weitkamp et al., 1992). Ghost shrimp are burrowing crustaceans that live within the top 70 cm of sandy substrate in the mid-low intertidal zone (Pruitt & Donoghue, 2016). Ghost shrimp are commercially harvested for fishing bait in Whidbey Basin and Willapa Bay, Washington. They are also harvested by the Tulalip Tribe in Port Susan. Concern regarding ghost shrimp harvest and Sounders foraging led to a commercial ghost shrimp harvest moratorium on state owned aquatic lands by the Washington Department of Natural Resources (DNR) in 2014 (Pruitt & Donoghue, 2016).

Feeding Pits

Gray whales use suction to displace sediment, water, and prey into their mouth during benthic feeding (Nerini, 1984). Feeding pits are the remaining impressions in sediment following gray whale foraging events, ranging from 1-3 m long and 0.5-1.5 m wide (Johnson et al., 1984). Feeding pits are a key indication of gray whale feeding location in both subtidal and intertidal habitats, as seen in Arctic sonar scans and NPS intertidal aerial surveys (Nerini et al., 1980; Weitkamp et al., 1992). Precise feeding tracks are valuable in understanding gray whale habitat use and prey consumption. Approximately 2,700-3,200 feeding pits were observed in 1990 from fixed-wing aerial surveys in NPS and appeared most concentrated in Saratoga Passage (Weitkamp et al., 1992). In 1991, feeding pit observations increased to 19,000 but were most concentrated in Port Susan. Feeding pits were also commonly observed in linear or rosette arrangements, which further provoked curiosity regarding Sounders foraging behavior and efficiency.

Conclusion

Previous Literature

Although there is extensive research on the migratory patterns of Eastern North Pacific gray whales and their feeding ecology in northern foraging grounds, there is limited published literature on Sounders gray whales and even less on their long-term foraging behaviors in NPS. Weitkamp et al. (1992) were the first to visualize and quantify densities of feeding pit aggregations within Puget Sound in the early 1990s. Cascadia Research Collective has developed a long-term photo-identification catalog on the Sounders and implemented suction-cup video tags to understand feeding behavior and movements since 2016. Acoustic behavior of foraging Sounders was examined using suction cup tags from 2016, 2019, and 2021 (Clayton et al., 2023).

These studies provide strong arguments for continued research on Sounders gray whales based on their unique migratory divergence, overlapping foraging grounds with ghost shrimp fisheries, and complex feeding and social behaviors.

Significance and Implications

Multiple entities may be interested in understanding the complexities of gray whale foraging within NPS, including NOAA Fisheries, the Washington Department of Natural Resources, and the Makah Tribe. As climate change continues to negatively impact northern feeding ground productivity, mitigating anthropogenic impacts on contemporary feeding grounds will ensure the health of stopover migratory ENP gray whales.

Introduction

Arctic benthic communities are severely impacted by climate change in response to rapid sea ice reduction (Stewart et al., 2023). Sea ice cover provides protective barriers between oceanic currents and the sea floor, maintaining fine sediment composition that supports benthic invertebrate habitat (Moore et al., 2003; Stewart et al., 2023). Additionally, ice-associated algae aid benthic dispersal of particulate organic carbon, essential to bottom dwelling crustaceans and amphipods. Benthic invertebrates are crucial prey sources for marine megafauna, including the gray whale (*Eschrichtius robustus*). Ampeliscid (tube building) amphipods dominated the migratory Eastern North Pacific (ENP) gray whale diet within the Bering Sea and Chirikov Basin prior to the 1980s (Moore et al., 2003). However, recent ENP gray whale mortality events and poor body conditions are now linked to shifting prey dynamics in Arctic feeding areas (Stewart et al., 2023). The recurrent nature of these unusually high mortality events, each resulting in 15-25% reduction in population abundance, further supports the urgency to monitor gray whale health and further understand their foraging requirements.

Gray whales are generalist feeders, and forage opportunistically throughout their 15,000-20,000 km migration from Baja California Sur, Mexico to the northern Bering, Chukchi, and Beaufort Seas (Christiansen et al., 2021; Moore et al., 2003; Nerini, 1984; Stewart et al., 2023). Stomach content analysis indicates gray whales may consume more than 19 genera of invertebrates including amphipods, polychaetes, and decapods (Gelippi et al., 2022; Moore et al., 2003; Nerini, 1984). Swarming pelagic mysids, sardines, and zooplankton may also be consumed along their typical migratory route using an alternative surface skimming technique. Most commonly however, prey are engulfed using suction sieving along the sea floor while swimming laterally (Cacchione et al., 1987; Nerini, 1984). Massive sediment disturbance from gray whale benthic feeding results in a series of depressions, or "feeding pits", visible in side-scan sonar records along their migration route and foraging grounds (Cacchione et al., 1987; Johnson et al., 1984). Long furrow depressions have also been reported and associated with gray whale presence in the Chirikov basin, though their relation to benthic feeding is not yet understood (Nerini et al., 1980).

Gray whale feeding excavations, or feeding pits, were first observed in northern Puget Sound (NPS) Washington intertidal regions in the 1990s (Weitkamp et al., 1992). Sediment core samples from intertidal pit depressions and whale necropsy investigations identified ghost shrimp (*Neotrypaea californiensis)* as the target prey for NPS gray whales, known as the "Sounders". Burrowing ghost shrimp exist in large densities within sandy, estuarine, intertidal zones along the Pacific coast (Griffis & Chavez, 1988). To access abundant intertidal dwelling ghost shrimp, Sounders exhibit a high-risk lateral feeding strategy during high tide in depths of 2-3 m (Calambokidis et al., 2017).

Recurrent springtime sightings of gray whales within NPS followed the first "unofficial" unusual gray whale mortality event which began in 1988 (Calambokidis et al., 2002). In 1996 and 1997, a small group of ENP gray whales were documented feeding around Whidbey Island and the Snohomish River Delta, but their duration in NPS was variable and limited (Calambokidis et al., 1998; Calambokidis & Quan, 1997). By 2016, almost a dozen gray whales were annually diverging 100-miles from their typical migratory route to forage in NPS from March-May before continuing to the Arctic (Calambokidis, 2016). Presently, there are ~ 22 identified Sounders, and annual sightings now extend from December through June (CRC unpublished data, 2025). Earlier and prolonged gray whale presence within NPS suggests some individuals are not completing the southerly phase of migration to Mexico after feeding in the summer. Foraging Sounders exhibit immense growth in body conditions after few months of feeding, which greatly contrasts whales that are hindered by prey dynamics in the Arctic and along the Pacific coast during periods of unusual mortality (Durban & Fearnbach, in prep; Stewart et al., 2023).

Several factors remain unclear regarding Sounders migratory and foraging behaviors. This study analyzed spatial and temporal variation in Sounders feeding area using aerial imagery of intertidal feeding pits. We used these data along with spatial analyses to quantify gray whale feeding area in 8 identified regions. The results provide insight into the habitat and feeding requirements of a relatively healthy group of gray whales which can be broadly applied across the greater ENP population to understand the impact of altered prey dynamics due to climate change.

Methods

Data Collection

Aerial Surveys

Gray whale intertidal feeding was observed by 19 aerial surveys conducted from 2017-2024 in NPS (Table 1). Surveys were conducted monthly between March-July during low tidal windows. March, April, and May were most consistently surveyed while June and July were surveyed 1-2 times each. The most surveyed years were 2022, 2024, and 2023, respectively. Survey flights began from Langley, Whidbey Island and maintained an altitude between 1000-1200 ft with similar trajectories, as weather conditions and aerial regulations allowed. Survey visibility was occasionally limited by water coverage and solar glare. On one occasion, the survey flight was completed in the reverse direction to reduce glare. Additionally, Whidbey Island Naval Airspace restricted survey capacity near Oak Harbor. Aerial images were captured through the right window of the aircraft, using a using a Canon 7D Mark II camera with a 70-200 mm lens from 2017-2023 and wide-angle 17-40 mm lens in 2024. Photographs of the exposed intertidal region were taken approximately every 3 seconds at a 90-degree angle.

Whale Presence

Sounders gray whale presence in NPS was quantified using sightings data from Cascadia Research Collective (Olympia, WA). We used the number of Sounders sighted in NPS up to 3 weeks prior to each aerial survey, based estimated feeding pit longevity (2-3 weeks). This ensured whale presence data was associated with fresh feeding observed in each survey.

Table 1. Summary of aerial survey data. Total feeding area was calculated using the sum of observed feeding polygon measurements. Whale presence based on Cascadia Research Collective sightings data within 3 weeks of survey date. Observed regions represents the quantity of regions (1-8) captured in each survey.

Survey Date	Flight Duration (min)	Days Since Prev. Survey	Mean Tidal Height (ft)	Whales Present NPS	Observed Regions	Total Feeding Area (km^2)
5/26/2017	69		-2.86	5	8	2.77
4/21/2018	55	330	-0.27	10	8	2.87
4/22/2018	63	1	5.23	11	8	1.72
4/28/2019	33	372	5.69	13	4	0.30
5/10/2019	94	12	-0.05	14	6	4.24
5/11/2020	51	367	5.59	15	6	2.47
5/31/2021	27	385	2.92	10	5	0.77
3/21/2022	57	294	0.46	13	6	2.31
4/20/2022	64	30	-1.82	12	6	4.25
5/17/2022	77	27	-2.98	17	8	5.98
6/15/2022	63	29	0.52	6	8	4.99
7/12/2022	68	27	-0.92	2	6	2.56
3/25/2023	60	256	0.29	12	6	4.47
4/22/2023	68	28	-1.41	15	7	5.38
5/7/2023	60	15	-2.06	13	8	4.41
3/15/2024	53	313	-0.18	9	7	1.11
4/10/2024	44	26	-1.67	10	7	4.35
5/10/2024	45	30	0.55	13	6	3.03
6/5/2024	49	26	-2.69	4	6	3.69

Mean Tidal Height

Tidal data was derived from NOAA Tide Predictions, Station 9447659, Everett WA (NOAA Tides & Currents, 2025). Average tidal height was calculated based on aerial survey flight time and date.

Observed Regions

We identified 8 regions within the NPS survey area to understand spatial feeding dynamics (Table 2). Regions were delineated based on historical feeding observations and geographic boundaries. The number of observed regions within each aerial survey (value 1-8) was quantified to account for variation in survey coverage.

Table 2. Summary of northern Puget Sound regions. Maximum gray whale feeding area was calculated by merging all feeding polygons within each region and summing their total area from 2017 to 2024.

Region	Name	Boundaries	Maximum Feeding Area (km^2)
1	Delta	Snohomish River Delta – S Tulalip Bay, NE Hat Island	5.31
2	N Tulalip	N Tulalip Bay – Port Susan Bay	4.26
3	E Camano	Lona Beach – Camano Head	1.09
4	SW Camano	Camano Head – Elger Bay	0.96
5	NW Camano	Lowell Point – Skagit Bay	0.34
6	NE Whidbey	Mariner's Cove – Hidden Beach	0.84
7	Holmes Harbor	Pratts Bluff – Rocky Point	0.28
8	SE Whidbey	Baby Island – Clinton	0.76

Quantification of Foraging Area

Polygons (n= 1089) were created outlining gray whale feeding areas visually identified by feeding pits present in aerial survey images using Google Earth Pro version 7.3.6.10201 (2025). Polygon location and shape were verified by georeferencing sediment patterns and landmarks between survey images and satellite imagery. The “Time Slider” feature on Google Earth Pro allowed for comparison between aerial survey imagery and historical satellite imagery with different tidal heights. Gray whale feeding pits that were visible from satellite imagery provided additional reference for historical feeding pit locations within NPS (Harrison & Calambokidis, 2017).

Weathered (approximately 2-3 week old) feeding pits were outlined by polygons (n= 83) but removed from statistical analysis. Non-weathered feeding pits resemble an ellipse shape, with defined or moderately defined borders, sometimes with seabirds present. If both weathered and non-weathered feeding pits were present, polygons were created in relation to the non-weathered pits.

Gray whale feeding polygons were downloaded from Google Earth Pro as a KML (Keyhole Markup Language) and converted into an ESRI Shapefile format using MyGeodata Converter (2025). Polygon data was transformed to EPSG Coordinate Reference System (CRS) 32610 for Universal Transverse Mercator (UTM) Zone 10N. Total feeding area was quantified by summing the areas of polygons identified in each survey (Table 1). The maximum feeding area by region represents the largest extent of observed feeding from 2017-2024, determined by merging polygons and calculating their total area (Table 2). Area calculations and statistical analysis were performed in R version 4.5.0 (R Core Team, 2025).

Data Analysis

We tested a series of Generalized Linear Mixed Models (GLMM) to explain the variation in total gray whale feeding area across surveys. Prior to model fitting, we used a Shapiro-Wilk's test and determined feeding area data to be normally distributed ($p = 0.704$). We also determined predictor variables were not collinear using Pearson's correlation coefficients ($r < \pm 0.5$). Total feeding area (m^2) was scaled by 10^6, converting units to km^2 for model convergence and comparability of effects. One survey (July 12, 2022) was removed from the dataset as it was the only sample from July and could not be meaningfully compared with other months.

We constructed a set of 13 candidate models, each using a Gaussian distribution. Predictor variables considered were whale presence, mean tidal height, number of observed regions, month, and year. Models were ranked using the Akaike Information Criterion corrected for small sample sizes (AICc).

Results

Intertidal Foraging Characteristics

Gray whale feeding pits were observed throughout the intertidal zone in every aerial survey and extended to the high tide line in many circumstances. Feeding pit arrangements ranged from small clusters or linear groupings of approximately 5-10 depressions to dense aggregations containing up to several hundreds (Fig. 1). Spiraled patterns of feeding pits were common, especially near the Snohomish River Delta and Warm Beach. Feeding pits were not observed within seagrass or algal beds, though they were occasionally found adjacent to them. Drift algae appeared to settle and remain within feeding pits, particularly in the months of June and July.

Figure 1. Intertidal feeding pits in northern Puget Sound photographed during aerial surveys. (Left) North of Tulalip Bay. (Right) North of Jetty Island. Photographs by Julia Erickson.

Regional and Temporal Feeding

Total gray whale feeding area was about 61.67 km^2 across all aerial surveys from 2017-2024. Feeding area ranged from 0.30-5.98 km^2 by survey, with an average of 3.25 ± 1.59 km^2.

Greatest gray whale feeding was documented in May 2022 (5.98 km^2) followed by April 2023 (5.38 km^2; Table 1). Overall, no linear trends were apparent by year (Fig. 2). However, data suggested an association between month, whale presence, and feeding area (Fig. 3). Whale presence appeared to increase from March-May and then decrease drastically in June (Fig. 3a). Accordingly, feeding area increased steadily from March then decreased in July (Fig. 3b).

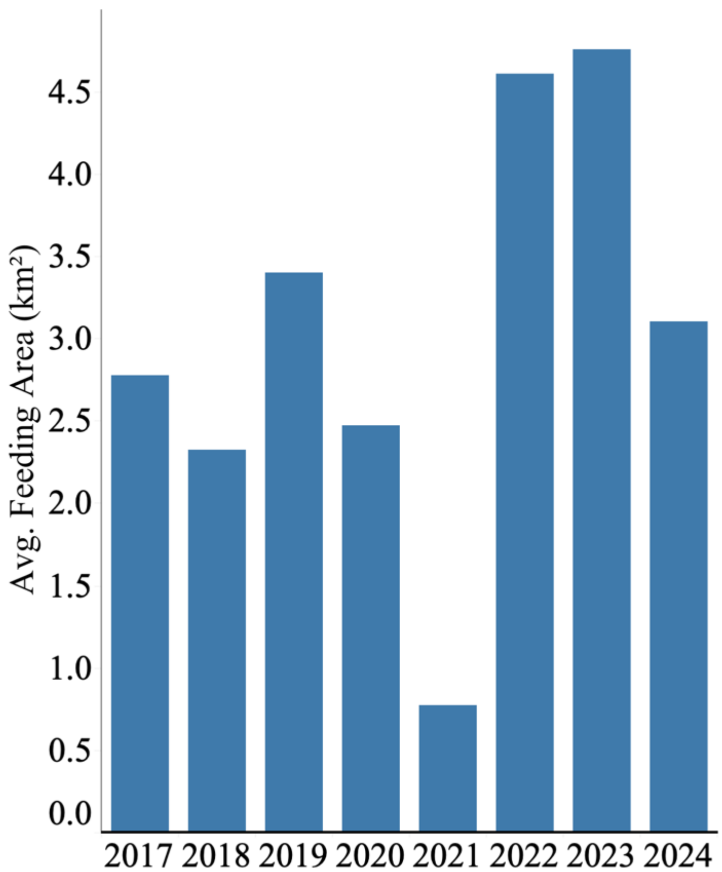

Figure 2. Average gray whale feeding area (km^2) in northern Puget Sound by year. Feeding area measured using polygons surrounding areas of observable feeding pits.

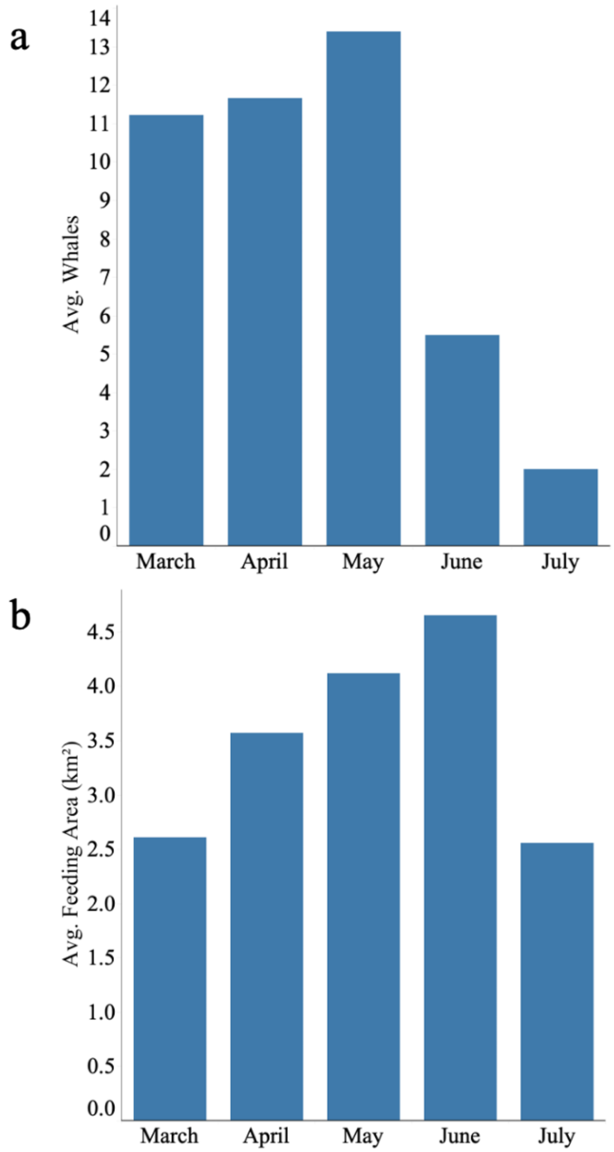

Figure 3. Average number of gray whales observed in northern Puget Sound within 3 weeks of aerial surveys by month (a), and average feeding area (km^2) in northern Puget Sound across all surveys by month (b). Both graphs represent data from 2017-2024.

Although no linear trends were apparent by year, average feeding area varied by region (Fig. 4). The Snohomish River Delta exhibited the largest average feeding area compared to all other regions by year, except for in 2021, which was likely due to missing data.

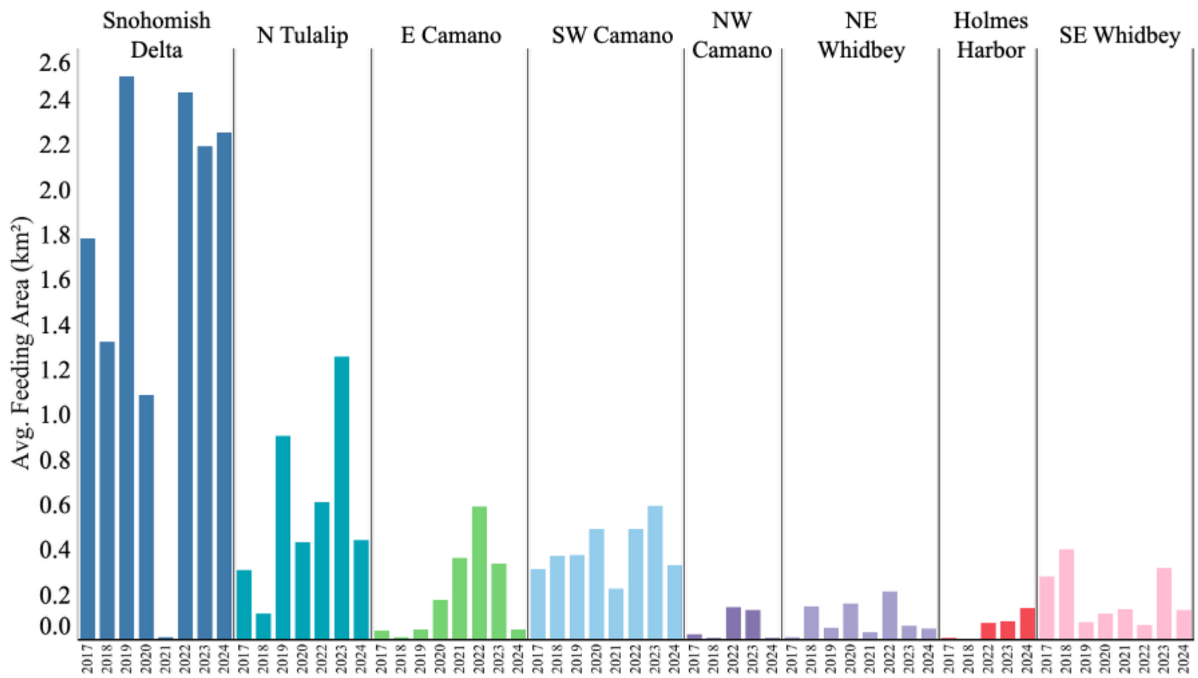

Figure 4. Average feeding area (km^2) by region and year in northern Puget Sound**.** Regions are colored and grouped along the x-axis and ordered from 1-8 (left-right).

Overall, regions 1-4 had the largest average feeding areas from 2017-2024 (Fig. 5a). The Snohomish River Delta (region 1) had the greatest average feeding area across seven out of eight years, with the greatest feeding in 2019 with 2.5 km^2. North Tulalip (region 2) had the second highest feeding average in 2023 with 1.3 km^2. Regions 5-8 maintained average feeding areas below 0.5 km^2 throughout the study period, with Southeast Whidbey Island ranking the highest among these regions over five years (Fig. 5b).

Feeding area peaked in April, May, or June. March and July often ranked smallest in regional feeding area compared to other months (Fig. 3b). The Snohomish River Delta had the highest monthly feeding area, averaging over 1.5 km^2 across all 5 months and exceeding 2.5 km^2 in June (Fig. 6a). In contrast, E Camano had the second highest monthly feeding in June, with approximately one-third of the feeding observed in the Snohomish River Delta during the same month (~ 0.8 km^2).

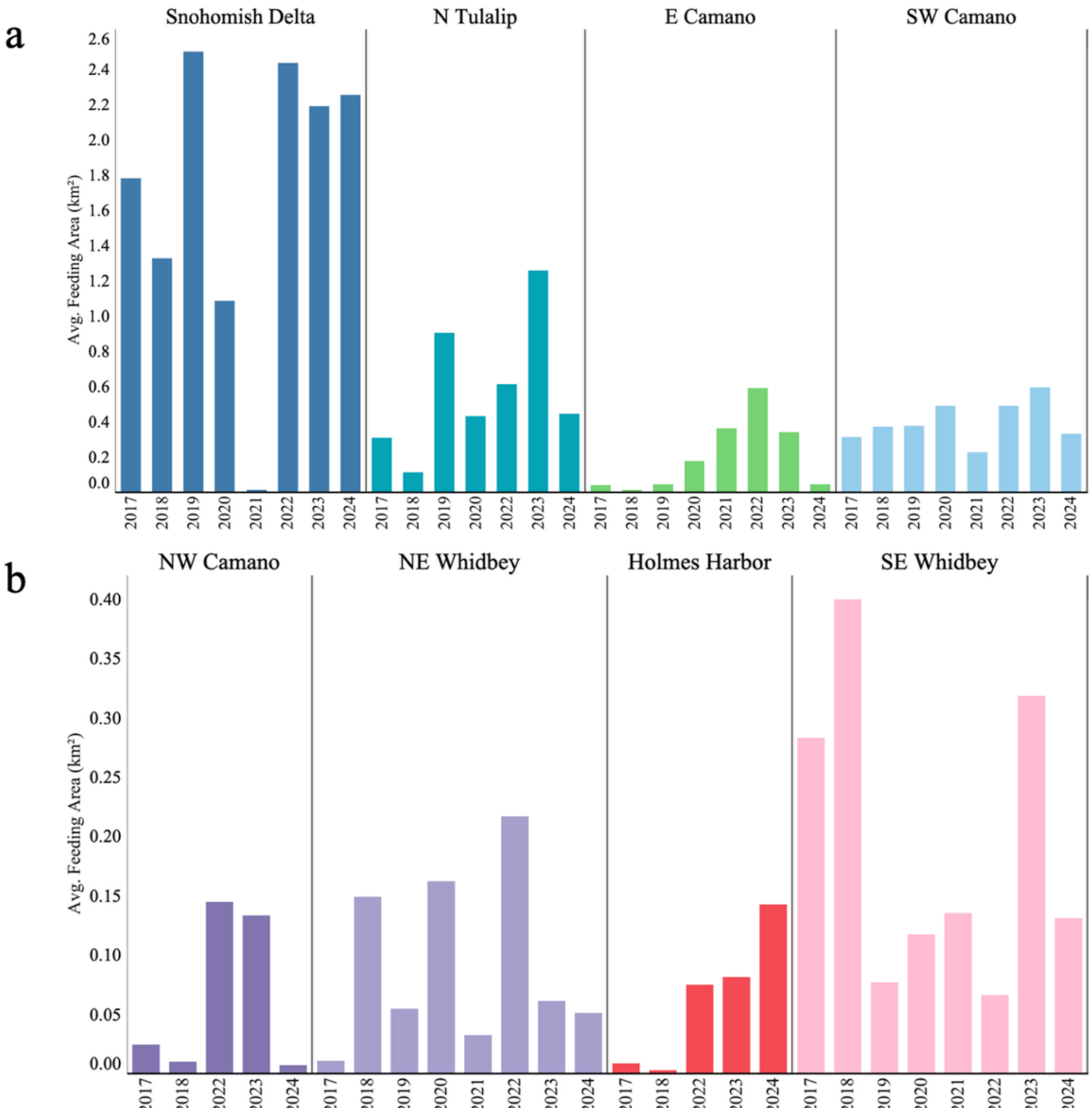

Figure 5. Average gray whale feeding area (km^2) in northern Puget Sound by region and year. Y-axis scales differ to show variation across years for regions with smaller feeding areas. Regions are organized in ascending order from 1-4 (a) and 5-8 (b). Values missing on the x-axis indicate a region was not surveyed in that year.

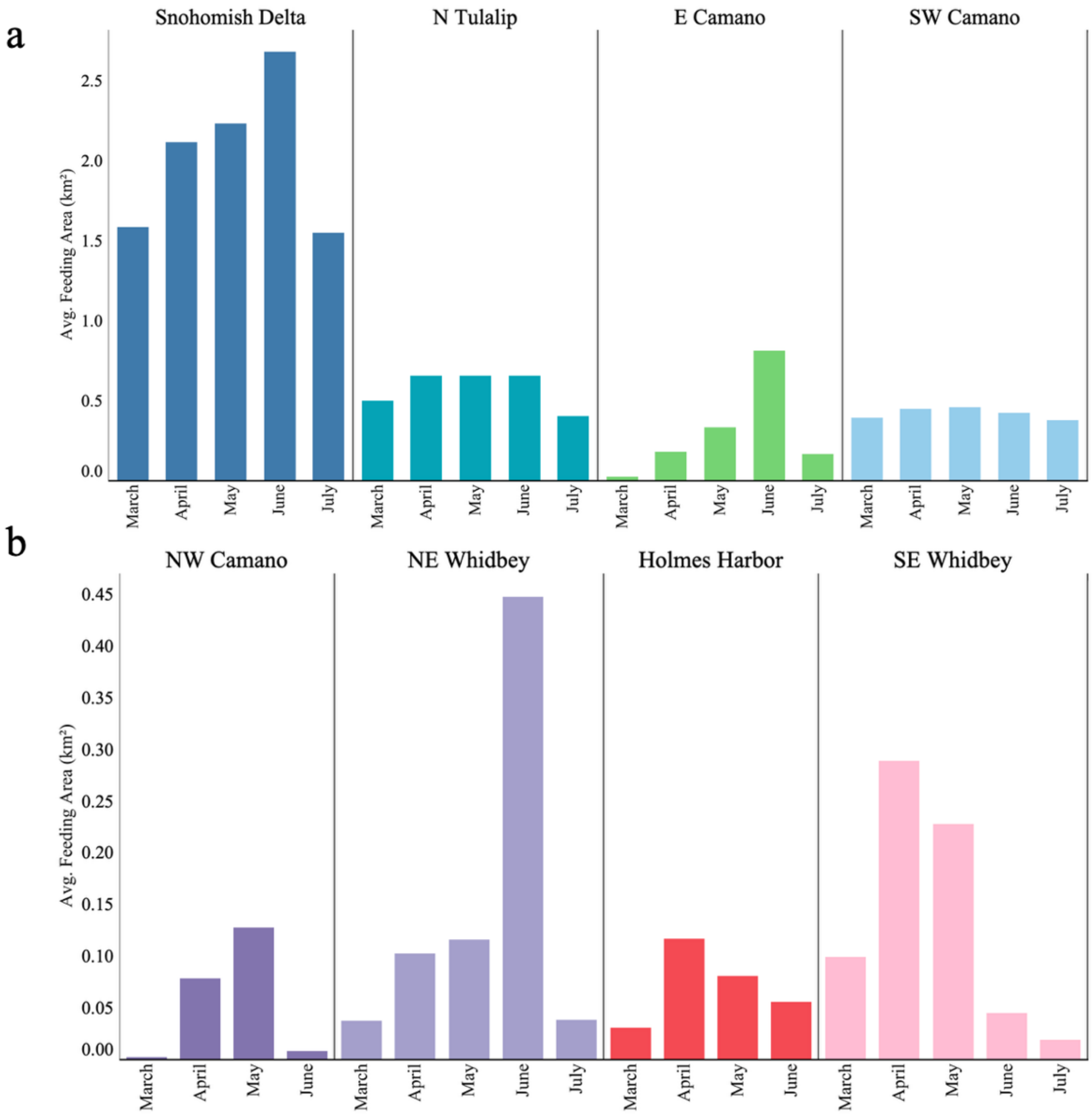

Figure 6. Average gray whale feeding area (km^2) in northern Puget Sound by region and month. Y-axis scales differ to show variation across months for regions with smaller feeding areas. Regions are organized in ascending order from 1-4 (a) and 5-8 (b). Values missing on the x-axis indicate a region was not surveyed in that month.

We found a total maximum foraging area of 13.84 km^2 in NPS (Table 2). Region 1, including NE Hat Island and the Snohomish River Delta, encompassed 38% of maximum NPS foraging area (5.31 km^2). Region 2, from N Tulalip Bay to Port Susan Bay, encompassed 31% of maximum NPS foraging area (4.26 km^2). Holmes Harbor had the lowest maximum foraging area (0.28 km^2).

Feeding Area Model

Model Selection

We compared 13 candidate models using AICc values (Table 3). Model 8 was ranked as best fit, including whale presence and tidal height as fixed effects (AICc = 63.23, R^2 = 0.59). Model 5 was also well supported but not selected due to the principle of parsimony (AICc = 63.44).

Fixed Effect Estimates

Model 8 indicated whale presence had a significant, positive effect on feeding area (β = 0.567, $p = 0.0267$; Table 4). Based on this coefficient estimate, and holding all other variables constant, each additional whale was associated with an increase in 2.28 km^2 of feeding area in NPS. Conversely, mean tidal height had a significant, negative effect on feeding area (β = -1.222, $p < 0.0001$). Accordingly, tidal height had the most drastic influence on total feeding area (Fig. 7).

Table 3. Generalized linear mixed model (GLMM) selection with AICc values ranked from most to least fit. Response variable across all models was total gray whale feeding area, scaled to km^2 prior to analysis.

Model	Model Terms	df	logLik	AICc	ΔAICc	AIC Weight
8	whales + tide	4	-26.08	63.23	0.00	0.32
5	whales + month + tide	5	-24.22	63.44	0.21	0.29
6	whales + regions + tide	5	-24.96	64.92	1.69	0.14
3	whales + month + regions + tide	6	-23.06	65.75	2.52	0.09
13	regions + tide	4	-27.63	66.33	3.10	0.07
12	month + tide	4	-27.73	66.54	3.31	0.06
7	month + regions + tide	5	-27.17	69.34	6.11	0.01
2	whales + year + month + regions + tide	7	-22.26	69.73	6.50	0.01
10	whales + regions	4	-30.55	72.18	8.95	0.00
11	month + regions	4	-30.97	73.02	9.79	0.00
4	whales + month + regions	5	-29.36	73.71	10.48	0.00
9	whales + month	4	-32.27	75.62	12.39	0.00
1	whales + (1|year) + (1|month) + (1|regions) + (1|tide)	7	-33.39	91.97	28.74	0.00

Table 4. Generalized linear mixed model (GLMM) output. Total gray whale feeding area was used as the response variable ($R^2 = 0.59$).

Term	Estimate	SE	z	p
Intercept	3.284	0.243	13.522	< 0.001
Whales	0.567	0.256	2.216	0.0267
Tidal Height	-1.222	0.256	-4.773	< 0.001

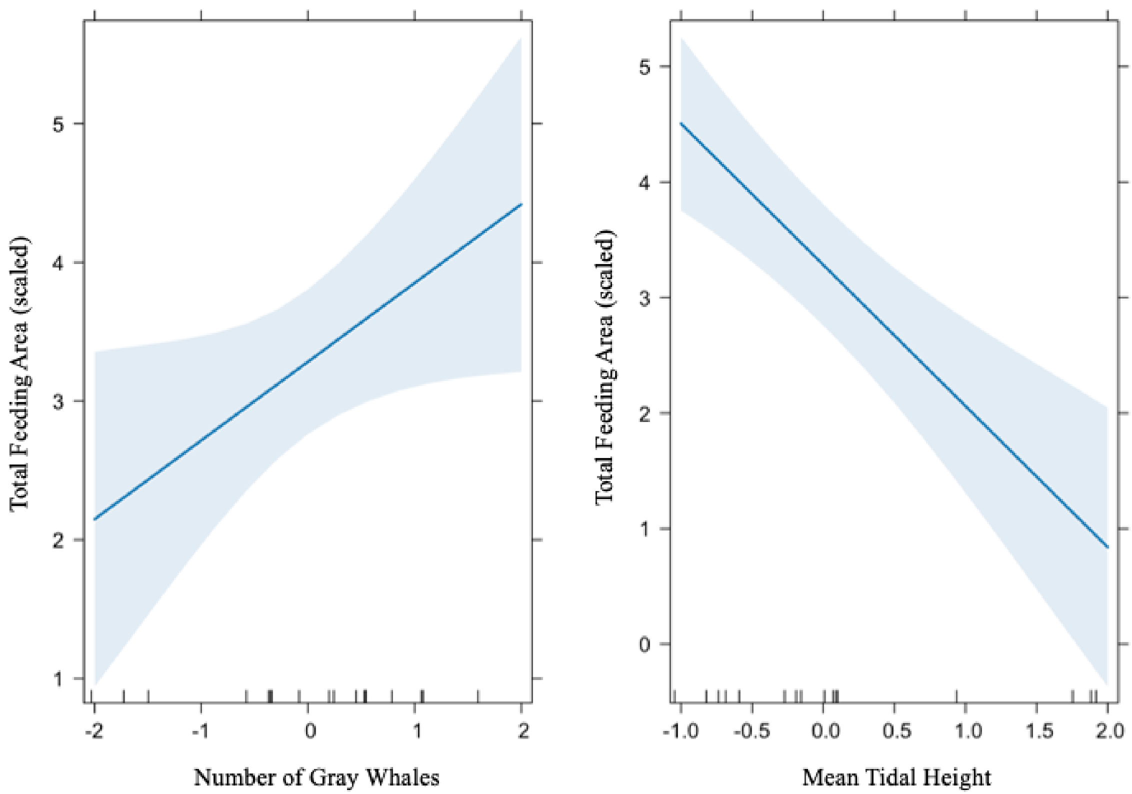

Figure 7. Effects plots of whale presence and mean tidal height on total feeding area. Blue shaded areas represent 95% confidence intervals.

Discussion

This study presents the first quantification of Sounders gray whale foraging area in NPS while examining spatial feeding characteristics from 2017-2024. We utilized a free and easily accessible program and georeferencing to create polygon shapes around gray whale feeding areas in the intertidal region using aerial survey imagery. These methods could be applicable for studying foraging behavior and extent across a variety of species and habitats, especially across large scales.

Sounders Foraging Area

Sounders gray whale presence in NPS significantly increases observable intertidal feeding area. Our model indicated an increase in 2.28 km^2 of feeding area was associated with each additional gray whale observed in NPS. Additionally, the greatest combined extent of feeding area reached 13.84 km^2 within NPS across all surveys. These data suggest a capacity of 6 gray whales utilizing NPS intertidal habitat at a time. The median number of Sounders observed in NPS by month during the peak foraging months (March to May) in 2017-2024 ranged from 11-14 (CRC unpublished data, 2025). Therefore, there may be additional foraging area not observed in this study that supports gray whale feeding. Although, considering the high abundance of ghost shrimp and variability in feeding pit abundance by location in NPS, it is also likely that multiple whales can utilize the same feeding areas throughout the season. Therefore, more research is needed to further specify Sounders gray whale capacity in NPS.

Long-term NPS Habitat Utilization

Tremendous consistency in gray whale foraging habitat utilization was observed across the 8-year timespan (Fig. 8). Evidence from previous research indicates that this habitat utilization may have persisted over 34 years (Weitkamp et al., 1992). Foraging locations throughout Port Susan and Saratoga Passage from 2017-2024 align with locations documented from 1990-1991 (Fig. 9). However, in our study we also observed gray whale feeding in Holmes Harbor, Skagit Bay, and the northeast inlet of Hat Island. In contrast, we did not observe feeding along the west side of Hat Island or to the same extent between Snatelum Point and Hidden Beach or between Tillicum Beach and Camano Head.

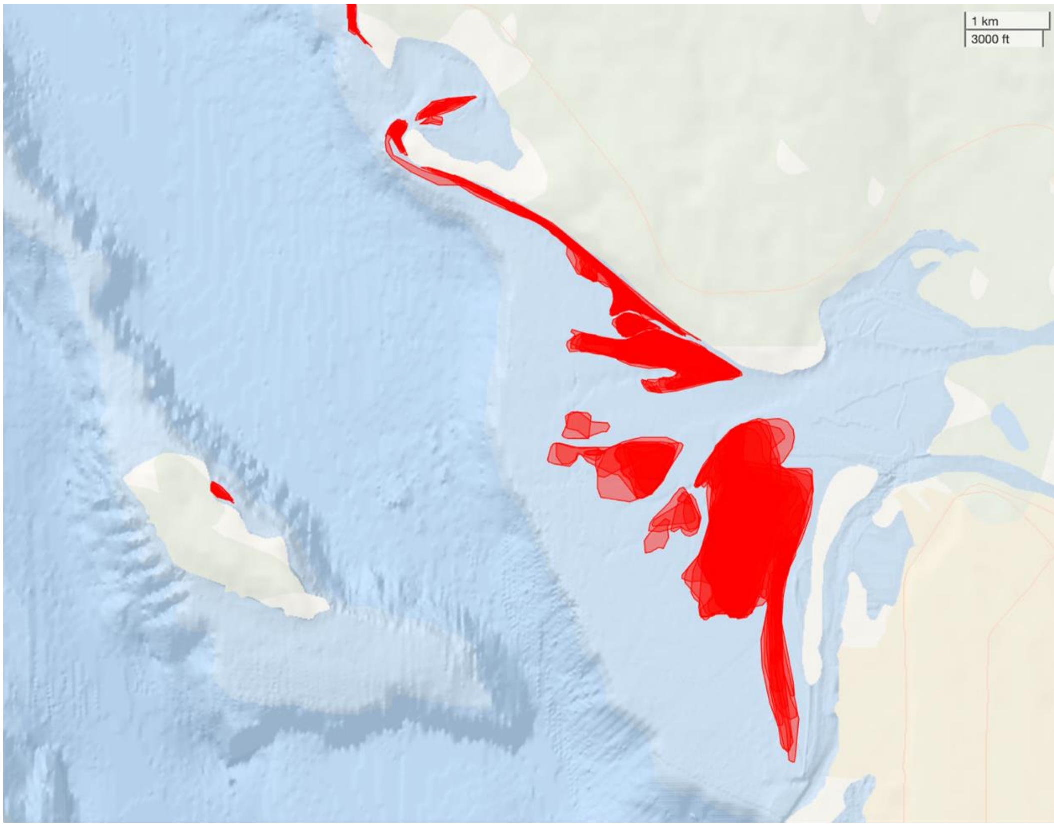

Figure 8. Map of overlapping gray whale feeding areas observed near the Snohomish River Delta, Tulalip Bay, and NE Hat Island from 2017-2024.

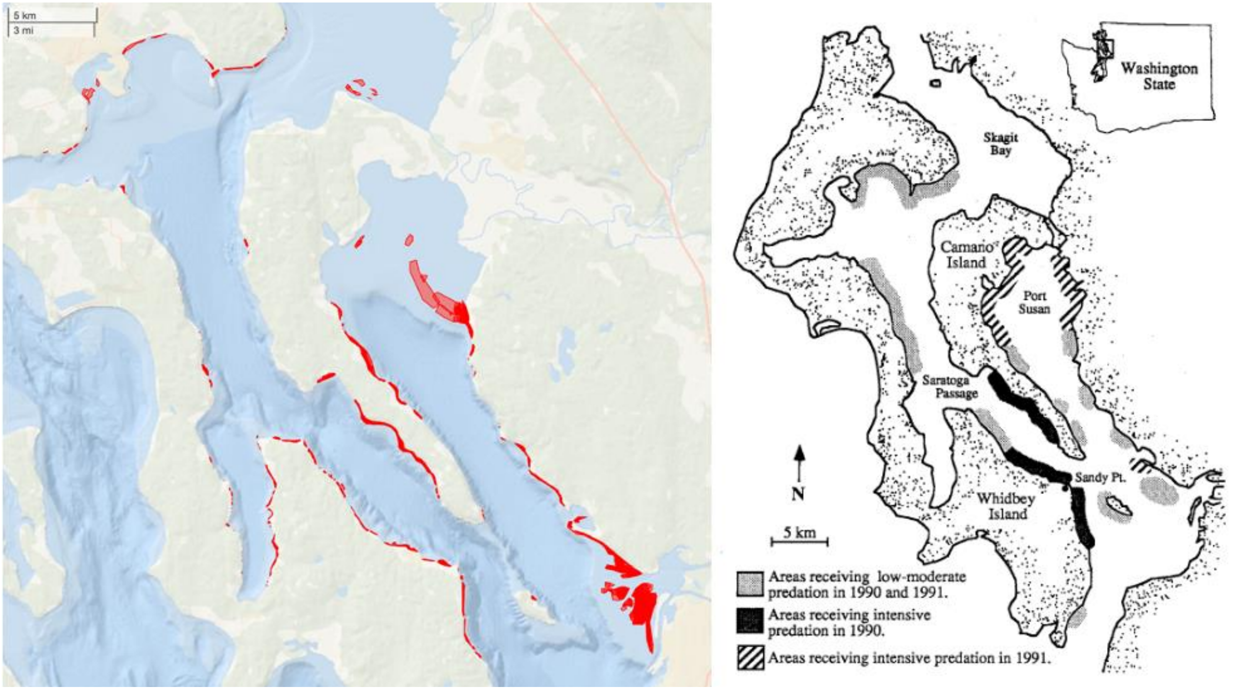

Figure 9. (Left) Map of gray whale feeding in northern Puget Sound (2017-2024) using polygons drawn around areas of intertidal feeding pits observed in aerial survey imagery. (Right) Estimated feeding locations (1990-1991) observed in aerial surveys (Weitkamp et al., 1992).

Management Implications

These results should be used to inform NPS entities such as the Washington Department of Natural Resources (DNR), the U.S Coast Guard, and the Washington State Department of Transportation (WSDOT). Ghost shrimp are commercially harvested for fishing bait in the same areas that gray whales forage in NPS, specifically along SE Whidbey Island and SW Camano Island (Pruitt & Donoghue, 2016). Additionally, the degree and consistency of Sounders foraging near the Snohomish River Delta presents potential concern regarding vessel traffic from the nearby Everett marina and the Mukilteo-Clinton Washington State Ferry route. Gray whales are particularly vulnerable to large vessel collisions as coastal foragers, which can lead to injury and fatalities (Douglas et al., 2008). Thus, Sounders gray whales require particular consideration in NPS vessel traffic regulations due to their small group size, which has already experienced 2 documented incidents of vessel disturbance. The first documented case occurred in April 2017, when CRC-22 (Earhartt) was cut after a boat collision off Whidbey Island in NPS (Lewis, 2017). Most recently, a ship collision lead to the death of CRC-2259 near San Francisco Bay in April 2025 (Cascadia Research Collective, 2025).

Future Research

Mean tidal height had a significant negative effect on gray whale feeding area, which is likely from water levels restricting intertidal region visibility. This could indicate an amount of gray whale feeding may be unobservable by aerial surveys even during low tide. Specifically, this may occur near the Snohomish River Delta and Port Susan Bay, where there is additional 0 m elevation habitat below observed feeding areas (Fig. 10). Therefore, tidal window availability presents challenges in quantifying the entirety of gray whale feeding area in NPS. Tidal windows in NPS vary by month, with lower and longer tides during daylight hours generally beginning after March (NOAA Tides & Currents, 2025). This limited aerial survey capacity during preliminary months of the gray whale foraging season (December-March). Additionally, the quantity and extent of surveys conducted in this study varied by year, which influenced our ability to analyze seasonal and regional variability.

In the future, measurement of feeding pit aging and densities by region will strengthen the resolution of spatial analyses. Sounders gray whales are sometimes observed foraging in a particular region for consecutive days before being sighted in other regions (CRC unpublished data, 2025). By integrating the additional feeding pit metrics above, these regional feeding observations can be analyzed on a seasonal and yearly scale.

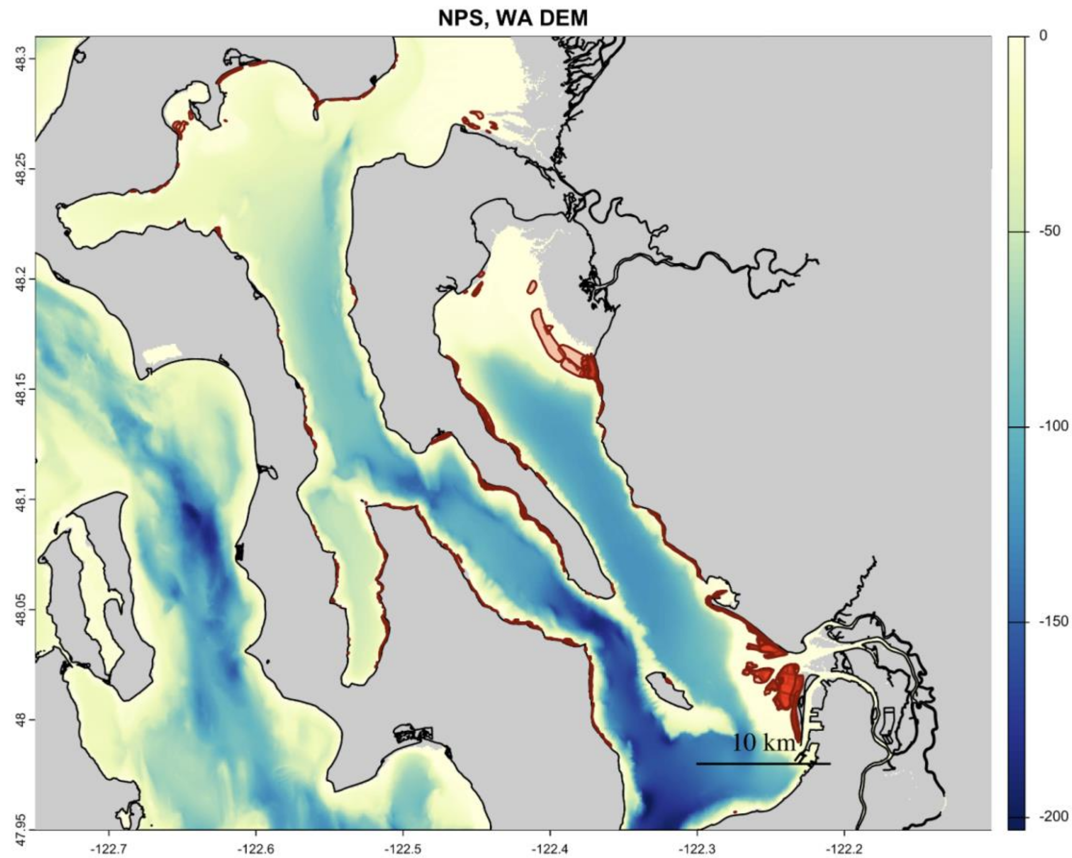

Figure 10. Gray whale intertidal feeding area in northern Puget Sound (2017-2024) plotted in red on a digital elevation model by Hannah Clayton (National Centers for Environmental Information, 2025). Light yellow-dark blue color scale indicates elevation/depth from 0-200 m.

Conclusion

Sounders gray whales exhibit stopover foraging along their northern migratory route to feed on an abundant supply of ghost shrimp in NPS intertidal regions. These ~ 22 whales represent a unique group from the ENP population, as their body conditions greatly improve after foraging in NPS for a limited time, while other individuals along the coast have been documented in poor body condition during periods of unusual mortality (Durban & Fearnbach, in prep; Stewart et al., 2023).

This study quantified Sounders gray whale foraging area and described spatial feeding characteristics over time using aerial survey imagery. Our findings show consistent gray whale foraging habitat utilization in NPS across 8 years. Observed feeding locations also support previous research indicating the employment of a high-risk intertidal feeding strategy by Sounders gray whales (Calambokidis et al., 2017).

Interdisciplinary collaboration can benefit Sounders gray whale health by considering these findings in NPS spatial management decisions such as the ghost shrimp harvest in Whidbey Basin and vessel traffic regulations in Possession Sound. Additionally, these data are relevant to ongoing prey and foraging energetics research to further understand gray whale feeding requirements (Clayton et al., in prep).

References

Barnes, L. G., & McLeod, S. A. (1984). The Fossil Record and Phyletic Relationships of Gray Whales. In *The Gray Whale: Eschrichtius Robustus* (pp. 3–32). Elsevier. https://doi.org/10.1016/B978-0-08-092372-7.50007-8

Bradford, A., Weller, D., Wade, P., Burdin, A., & Brownell, R. (2008). Population abundance and growth rate of western gray whales Eschrichtius robustus. *Endangered Species Research*, *6*, 1–14. https://doi.org/10.3354/esr00106

Cacchione, D. A., Drake, D. E., Field, M. E., & Tate, G. B. (1987). Sea-floor gouges caused by migrating gray whales off northern California. *Continental Shelf Research*, *7*(6), 553–560. https://doi.org/10.1016/0278-4343(87)90021-5

Calambokidis, J. (2015). Biologically Important Areas for Selected Cetaceans Within U.S. Waters – West Coast Region. *Aquatic Mammals*, *41*(1), 39–53.

Calambokidis, J. (2016). Study of seasonal resident gray whales feeding strategy in N Puget Sound, Wa. In 2016. *Contract Report for Cooperative Agreement CA-16-320*. https://cascadiaresearch.org/publications/calambokidis_2016_ca-16-320/

Calambokidis, J., Cade, D., & Fahlbusch, J. (2017). A high risk intertidal feeding strategy for gray whales examined with new suction-cup attached multi-sensor video tags. *Abstract (Proceedings) 22nd Biennial on the Biology of Marine Mammals, Halifax, Nova Scotia*.

Calambokidis, J., Darling, J. D., Deecke, V., Gearin, P., Gosho, M., Megill, W., Tombach, C. T., Goley, D., Toropova, C., & Gisborne, B. (2002). Abundance, range and movements of a feeding aggregation of gray whales (Eschrichtius robustus) from California to southeastern Alaska in 1998. *J. Cetacean Res. Manage.*, *4*(3), 267–276. https://doi.org/10.47536/jcrm.v4i3.839

Calambokidis, J., Kratofil, M. A., Palacios, D. M., Lagerquist, B. A., Schorr, G. S., Hanson, M. B., Baird, R. W., Forney, K. A., Becker, E. A., Rockwood, R. C., & Hazen, E. L. (2024). Biologically Important Areas II for cetaceans within U.S. and adjacent waters—West Coast Region. *Frontiers in Marine Science*, *11:1283231*. https://doi.org/10.3389/fmars.2024.1283231

Calambokidis, J., & Quan, J. (1997). Gray whales in Washington State: Report on research in 1996. *Final Report to National Marine Mammal Laboratory, Seattle, Washington. 30pp*. https://cascadiaresearch.org/publications/gray-whales-washington-state-report-research-1996/

Calambokidis, J., Schlender, L., Gosho, P., & Gearin, P. (1998). Gray whale photographic identification in 1997. *Final Report to the National Marine Mammal Laboratory, Seattle, WA*. https://cascadiaresearch.org/publications/gray-whale-photographic-identification-1997/

Cascadia Research Collective. (2025). *We are sad to share that one of our beloved Sounders gray whales, 2259, was found deceased in San Francisco Bay* [Online post]. Facebook. https://www.facebook.com/CascadiaResearch/posts/we-are-sad-to-share-that-one-of-our-beloved-sounders-gray-whales-2259-was-found-/1005491155040969/

Chivers, S. J. (2009). Cetacean Life History. In *Encyclopedia of Marine Mammals* (pp. 215–220). Elsevier. https://doi.org/10.1016/B978-0-12-373553-9.00055-9

Christiansen, F., Rodríguez-González, F., Martínez-Aguilar, S., Urbán, J., Swartz, S., Warick, H., Vivier, F., & Bejder, L. (2021). Poor body condition associated with an unusual mortality event in gray whales. *Marine Ecology Progress Series*, *658*, 237–252. https://doi.org/10.3354/meps13585

Clayton, H., Cade, D. E., Burnham, J., Calambokidis, J., & Goldbogen, J. (2023). Acoustic Behavior of Gray Whales Tagged with Biologging Devices on Foraging Grounds. *Frontiers in Marine Science*, *10:1111666*. https://doi.org/doi: 10.3389/fmars.2023.1111666

Coombs, E. J., Knapp, A., Park, T., Bennion, R. F., McCurry, M. R., Lanzetti, A., Boessenecker, R. W., & McGowen, M. R. (2024). Drivers of morphological evolution in the toothed whale jaw. *Current Biology*, *34*(2), 273-285.e3. https://doi.org/10.1016/j.cub.2023.11.056

Douglas, A. B., Calambokidis, J., Raverty, S., Jeffries, S. J., Lambourn, D. M., & Norman, S. A. (2008). Incidence of ship strikes of large whales in Washington State. *Journal of the Marine Biological Association of the United Kingdom*, *88*(6), 1121–1132. https://doi.org/10.1017/S0025315408000295

Eguchi, T., Lang, A., & Weller, D. (2024). Abundance of eastern North Pacific gray whales 2023/2024. *NOAA Technical Memorandum NMFS-SWFSC-695*. https://doi.org/10.25923/n5qa-0y54

Ellis, R. (1977). Of men, whales, and Captain Scammon. *National Parks & Conservation Magazine*, 9–13.

Frasier, T., Koroscil, S., White, B., & Darling, J. (2011). Assessment of population substructure in relation to summer feeding ground use in the eastern North Pacific gray whale. *Endangered Species Research*, *14*(1), 39–48. https://doi.org/10.3354/esr00340

Gelippi, M., Caraveo-Patiño, J., Gauger, M. F. W., Popp, B. N., Panigada, S., & Marcín-Medina, R. (2022). Isotopic composition of the eastern gray whale epidermis indicates contribution of prey outside Arctic feeding grounds. *Scientific Reports*, *12*(1), 7055. https://doi.org/10.1038/s41598-022-10780-1

Goldbogen, J. A., Cade, D. E., Wisniewska, D. M., Potvin, J., Segre, P. S., Savoca, M. S., Hazen, E. L., Czapanskiy, M. F., Kahane-Rapport, S. R., DeRuiter, S. L., Gero, S., Tønnesen, P., Gough, W. T., Hanson, M. B., Holt, M. M., Jensen, F. H., Simon, M., Stimpert, A. K., Arranz, P., … Pyenson, N. D. (2019). Why whales are big but not bigger: Physiological drivers and ecological limits in the age of ocean giants. *Science*, *366*(6471), 1367–1372. https://doi.org/10.1126/science.aax9044

Goldbogen, J. A., & Madsen, P. T. (2018). The evolution of foraging capacity and gigantism in cetaceans. *Journal of Experimental Biology*, *221*(11), jeb166033. https://doi.org/10.1242/jeb.166033

Griffis, R. B., & Chavez, F. L. (1988). Effects of sediment type on burrows of Callianassa californiensis Dana and C. gigas Dana. *Journal of Experimental Marine Biology and Ecology*, *117*(3), 239–253. https://doi.org/10.1016/0022-0981(88)90060-3

Gulland, F. M. D., Pérez-Cortés, H. M., Urbán, J. R., Rojas-Bracho, L., Ylitalo, G., Weir, J., Norman, A., Muto, M. M., Rugh, D. J., Kreuder, C., & Rowles, T. (2005). Eastern North Pacific Gray Whale (Eschrichtius robustus) Unusual Mortality Event, 1999-2000. *NOAA Technical Memorandum NMFS-AFSC-150*.

Harrison, N., & Calambokidis, J. (2017). Google Earth satellite images provide novel method for examining feeding areas of gray whales in Puget Sound, Washington. *22nd Biennial on the Biology of Marine Mammals, Halifax, Nova Scotia, October 22-27, 2017*. https://cascadiaresearch.org/publications/google-earth-satellite-images-provide-novel-method-examining-feeding-areas-gray-whales/

Henderson, D. A. (1972). *Men & whales at Scammon’s Lagoon*. Dawson’s Book Shop.

Henderson, D. A. (1984). *Nineteenth Century Gray Whaling: Grounds, Catches and Kills, Practices and Depletion of the Whale Population*. Acad. Pr.

IWC. (2024a). *Aboriginal Subsistence Whaling in the Arctic*. https://iwc.int/management-and-conservation/whaling/aboriginal

IWC. (2024b). *Commercial Whaling*. https://iwc.int/management-and-conservation/conservation/whaling/commercial

Johnson, K. R. & Nelson, C. H. (1984). Side-Scan Sonar Assessment of Gray Whale Feeding in the Bering Sea. *Science,* 225(4667), 1150-1152.DOI:10.1126/science.225.4667.1150

Jones, M. L., Swartz, S. L., & Leatherwood, S. (Eds.). (1984). *The Gray whale: Eschrichtius robustus*. Academic Press.

Krupnick, I. (1984). Gray Whales and the Aborigines of the Pacific Northwest: The History of Aboriginal Whaling. In *The Gray Whale: Eschrichtius Robustus* (pp. 103–118). Academic Press Inc.

LeDuc, R. G., Weller, D. W., Hyde, J., Burdin, A. M., Rosel, P. E., Brownell, Jr., R. L., Würsig, B., & Dizon, A. E. (2002). *Genetic differences between western and eastern gray whales (Eschrichtius robustus)*. *4*(1), 1–5.

Lemos, L. S., Haxel, J. H., Olsen, A., Burnett, J. D., Smith, A., Chandler, T. E., Nieukirk, S. L., Larson, S. E., Hunt, K. E., & Torres, L. G. (2022). Effects of vessel traffic and ocean noise on gray whale stress hormones. *Scientific Reports*, *12*(1), 18580. https://doi.org/10.1038/s41598-022-14510-5

Lewis, M. (2017, April 26). *Whale in vessel collision on 23 April 2017 identified* [Cascadia Research Collective]. https://cascadiaresearch.org/project_article/whale-vessel-collision/

Moore, S. E. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, *89*(3), 534–540. https://doi.org/10.1644/07-MAMM-S-312R1.1

Moore, S. E., Clarke, J. T., Okkonen, S. R., Grebmeier, J. M., Berchok, C. L., & Stafford, K. M. (2022). Changes in gray whale phenology and distribution related to prey variability and ocean biophysics in the northern Bering and eastern Chukchi seas. *PLOS ONE*, *17*(4), e0265934. https://doi.org/10.1371/journal.pone.0265934

Moore, S. E., Grebmeier, J. M., & Davies, J. R. (2003). Gray whale distribution relative to forage habitat in the northern Bering Sea: Current conditions and retrospective summary. *Canadian Journal of Zoology*, *81*(4), 734–742. https://doi.org/10.1139/z03-043

MyGeodata. (2025). *MyGeodata*. https://mygeodata.cloud/

National Centers for Environmental Information. (2025). *Bathymetric Data Viewer*. NOAA. https://www.ncei.noaa.gov/

Nerini, M. (1984). A Review of Gray Whale Feeding Ecology. In *The Gray Whale: Eschrichtius Robustus* (pp. 423–450). Elsevier. https://doi.org/10.1016/B978-0-08-092372-7.50024-8

Nerini, M., Jones, L., & Braham, H. W. (1980). *GRAY WHALE FEEDING ECOLOGY*.

NOAA Fisheries. (2024a, June 25). *Makah Tribal Whale Hunt | NOAA Fisheries* (West Coast). https://www.fisheries.noaa.gov/west-coast/marine-mammal-protection/makah-tribal-whale-hunt

NOAA Fisheries. (2024b, November 6). *Large Whale Entanglement Response | NOAA Fisheries*. https://www.fisheries.noaa.gov/national/marine-life-distress/large-whale-entanglement-response

NOAA Fisheries. (2024c, November 8). *Marine Mammal Unusual Mortality Events | NOAA Fisheries*. https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-unusual-mortality-events

NOAA Fisheries. (2025). *Active and Closed Unusual Mortality Events*. https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events

NOAA Tides & Currents. (2025). *Tide Predictions*. https://tidesandcurrents.noaa.gov/noaatidepredictions.html?id=9447659&legacy=1

O'Leary, B. (1984). Aboriginal Whaling from the Aleutian Islands to Washington State. In *The Gray Whale: Eschrichtius Robustus* (pp. 79–100). Academic Press Inc.

Pruitt, C., & Donoghue, C. (2016). *Technical Report: Ghost shrimp and gray whale feeding: North Puget Sound, Washington*. Washington State Department of Natural Resources.

R Core Team. (2025). [Computer software] (Version 4.5.0).

Rice, D. W., Wolman, A. A., & Braham, H. W. (1984). The Gray Whale, Eschrichtius robustus. *Marine Fisheries Review*, *46*(4), 7–14.

Rugh, D. J., Muto, M. M., Moore, S. E., & DeMaster, D. P. (1999). Status Review of the Eastern North Pacific Stock of Gray Whales. *NOAA Technical Memorandum NMFS-AFSC-103*.

Sato, C., & Wiles, J. G. (2021). Periodic status review for the gray whale in Washington. *Washington Department of Fish and Wildlife, Olympia, Washington*.

Stewart, J. D., Joyce, T. W., Durban, J. W., Calambokidis, J., Fauquier, D., Fearnbach, H., Grebmeier, J. M., Lynn, M., Manizza, M., Perryman, W. L., Tinker, M. T., & Weller, D. W. (2023). Boom-bust cycles in gray whales associated with dynamic and changing Arctic conditions. *Science*, *382*(6667), 207–211. https://doi.org/10.1126/science.adi1847

Urbán R, J., Jiménez-López, E., Guzmán, H. M., & Viloria-Gómora, L. (2021). Migratory Behavior of an Eastern North Pacific Gray Whale from Baja California Sur to Chirikov Basin, Alaska. *Frontiers in Marine Science*, *8*, 619290. https://doi.org/10.3389/fmars.2021.619290

Weitkamp, L., Wissmar, R., Simenstad, C., Fresh, K., & Odell, J. (1992). Gray whale foraging on ghost shrimp (Callianassa californiensis) in littoral sand flats of Puget Sound, USA. *Canadian Journal of Zoology*, *70*, 2275–2280. https://doi.org/10.1139/z92-304

Weller, D. (2002). The Western gray whale a review of past exploitation. *Journal of Cetacean Research and Management*, *1*(1), 7–12.

Weller, D., Klimek, A., Bradford, A., Calambokidis, J., Lang, A., Gisborne, B., Burdin, A., Szaniszlo, W., Urbán, J., Gomez-Gallardo Unzueta, A., Swartz, S., & Brownell, R. (2012). Movements of gray whales between the western and eastern North Pacific. *Endangered Species Research*, *18*(3), 193–199. https://doi.org/10.3354/esr00447