A comparative spatial analysis of location data from satellite-tagged Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales off Hawai'i Island

Seasonal analyses of Odontocete spatial distribution off the island of Hawai'i

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A comparative spatial analysis of location data from satellite-tagged Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) Beaked Whales Near Hawaiʻi

Abstract of a master's degree internship report at the University of Miami, Rosenstiel School of Marine, Atmospheric, and Earth Science. Supervised by: *Holli Eskelinen, Ph.D. and Robin W. Baird, Ph.D.*

Globally, there are few long-term studies of multiple species of beaked whales inhabiting the same area. The main Hawaiian Islands are an exception, where resident populations of Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales have been studied concurrently for twenty years. The mechanisms facilitating their coexistence are poorly understood but could include partitioning in their diet and space use. There is evidence for vertical partitioning from dive behavior, but how they partition resources and habitats is an important aspect of their co-occurrence. Using location data obtained from satellite-linked tags (*n* = 10 for each species; 2006-2015), I examined differences in habitat use and home ranges over periods of 7-158 days (median duration = 28.9 days). Cuvier's spent much of their time in deep waters (grand median = 2,260 m), closer to canyons (median distance= 5.6 km), and farther from the 200 m isobath (median distance = 20.6 km). Blainville's used shallower waters (grand median = 1,195 m), were farther from canyons (median distance = 11.0 km) and were closer to the 200 m isobath (median distance = 13.1 km). Both species used waters of similar distance offshore (Cuvier's grand median = 18.3 km, range: 0.3-93.6 km), although Blainville's occasionally traveled farther offshore (grand median = 17.7 km, range: 0.1-189.4 km). Blainville's, unlike Cuvier's, did not utilize the windward side of Hawaiʻi Island, where slopes extend farther offshore. Still, both species were mostly concentrated on the leeward side of Hawaiʻi, with the exception of some use of the area north of Maui and Molokaʻi. While Cuvier's beaked whales were demonstrated to have larger home ranges (95% population kernel density estimate = 62,511 km^2) than Blainville's beaked whales (95% population kernel density estimate = 44,945 km^2), there was individual variation in home range sizes for both species. These results provide additional insight into the mechanisms that allow two resident populations of different beaked whale species to co-exist.

Keywords: beaked whales, spatial analyses, Hawaiian odontocetes, Blainville's beaked whale, Cuvier's beaked whale, *Mesoplodon densirostris*, *Ziphius cavirostris***,** home range analyses, kernel density estimates, spatial comparison, habitat partitioning, lunar phases, seasonal distribution, ENSO cycles, species co-occurrence

Seasonal analyses of Odontocete spatial distribution off the island of Hawaiʻi: Examining the Seasonal Environmental Preferences of Odontocetes around Hawaiʻi

Abstract of a master's degree internship report at the University of Miami, Rosenstiel School of Marine, Atmospheric, and Earth Science. Supervised by: *Holli Eskelinen, Ph.D. and Robin W. Baird, Ph.D.*

Throughout the year, resident Hawaiian odontocetes navigate their home ranges as the cyclic nature of the year morphs around them. While seasonal changes are slight throughout the waters surrounding the islands, variations in sea surface variables and prey availability may lead to differences in spatial usage amongst marine mammals. Incorporating sightings data collected by Cascadia Research Collective from select years of similar effort between 2002 and 2021, habitat characteristics and variables were compared between two sets of months of similar amounts of effort (spring and fall) for the 13 most frequently encountered species of odontocetes off the west side of Hawai‘i Island. Sightings were further subset by controlling for effort, restricting data by sea state, and sighting cue. To test statistical significance and covariate variation between seasons, Generalized Estimating Equations (GEEs) were performed on data from pantropical spotted dolphins (*Stenella attenuata*), a species sighted at similar frequencies between both seasons. For analyses involving all species, sperm whales (*Physeter microcephalus)* were sighted in larger group sizes (M_{Fall}=9.9, M_{Spring}=5.1), farther from shore (M_{Fall}=24.5 km, M_{Spring}=10.3 km), and deeper depths (M_{Fall}=3,498 m, M_{Spring}=2,051 m) during the fall**,** while many other species had less notable differences between the two seasons**.** Variation in slope and sea state best explained general spotted dolphin presence throughout the study area, with differences in sea state, latitude, and distance from shore especially describing seasonal habitat usage. In the spring, spotted dolphins were generally sighted in waters of more southern latitudes, lower sea states (M_{Fall}=1.9, M_{Spring}=1.5), and farther from shore (M_{Fall}=10.5 km, M_{Spring}=13.9 km). These results describe the seasonal occurrence of this species, laying the groundwork for similar analyses with other Hawaiian odontocetes in the near future.

Keywords: Hawaiian odontocetes, seasonal variation, habitat usage, habitat modeling, resident species, Hawai’i Island, pantropical spotted dolphins, sperm whales, *Stenella attenuata*

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1.0 Introduction

Variation in habitat usage plays a considerable part in the lives of many cetaceans. For example, blue whales (*Balaenoptera musculus*) follow a strong seasonal signal in terms of krill, targeting their prey's peaks in abundance near California (Fossette et al., 2017). These peaks correlated strongly with indices of upwelling. Meanwhile, the more generalist humpbacks (*Megaptera novaeangliae)* were similarly documented following patterns of krill density and upwelling occurrence. How does competition impact the overlap between these species? Humpbacks generally arrive earlier in the year to feast on krill, and as blue whale density increases, they switch prey to fish, depending on the relative abundance (Fossette et al., 2017). This change in diet also forced humpbacks nearer to the shelf to find fish, while blue whales stayed offshore near the krill. Competition for resources in such a way has been documented before: a phenomenon labeled "seasonal sympatry." Seasonal sympatry leads to increased energy gain across species and reduced interspecific competition.

When looking at spatial usage between different species, the "character displacement hypothesis" can be an essential aspect of how they interact. This hypothesis suggests that competition drives the evolution of morphological differences between species in areas where they overlap (Brown & Wilson, 1956). For example, the aforementioned humpback whales, which are smaller and more maneuverable than blue whales, can more easily switch to fish when the two species are in close proximity to each other. Fin whales have similarly demonstrated horizontal niche separation with humpbacks (Herr et al., 2016). Character displacement can even come into play with echolocation click sound level frequency and adaptations in competing odontocetes due to selection pressure (Kyhn et al., 2010).

In the Hawaiian archipelago specifically, numerous resident species of odontocetes have come to call the area their home. Off the island of Hawaiʻi, many species exhibit site fidelity around areas of slightly higher productivity, while other more offshore species are likely influenced by large cyclonic eddies and the island mass effect **(**Baird et al., 2008c**;** Doty & Oguri, 1956). Hawaiʻi, which is a tropical island with rapid shelf breaks coming from shore, has allowed for an oasis of productivity, leading to many nearshore resident odontocetes with large ranges around the island and a distribution that includes deeper waters as foraging habitat. Other topographic features on the seafloor cause more upwelling, including canyons (Vetter et al., 2009) and slopes in general.

Several dynamic oceanographic variables can affect habitat usage, as well as prey productivity or occurrence. These factors have long been essential in the field of habitat modeling, especially for marine mammals. Chlorophyll-a concentrations, detected by satellite ocean-color sensors detecting a small chlorophyll fluorescence signal, have been used to describe areas of high primary productivity/ photosynthesis and, therefore, potential predator occurrence (Letelier & Abbott, 1996; Vachon et al., 2022). Fluctuations in drivers such as sea surface temperature, height, and general sea state have also been demonstrated to affect species' habitat usage (Abecassis et al., 2015; Forney et al., 2015), as well as their distance to oceanographic topographic features such as seamounts **(Roberts, 2016)**, canyons (Vetter et al., 2009), shore (Ferguson et al., 2006), island or continental slopes, as well as depth utilization. All of these elements, which can affect primary productivity or just general animal occurrence due to factors like reproduction and socialization, play an important part in habitat specialization and usage.

A. A comparative spatial analysis of location data from satellite-tagged Blainville's (Mesoplodon densirostris) and Cuvier's (Ziphius cavirostris) beaked whales off Hawai'i Island

Throughout the history of cetology, beaked whales (family Ziphiidae) have remained one of the most challenging groupings of marine mammals to study. Despite making up around a fourth of all extant whale species, their tendency to dive to great depths for extended periods and their relatively low abundance have limited the ability to study them (Baumann-Pickering et al., 2013). However, studying these organisms is of the utmost importance, as they are quite susceptible to anthropogenic noise, such as high intensity naval sonar. Interactions with anthropogenic noise has led to strandings and mortalities, demonstrating how important their diet, spatial usage, niche partitioning, and acoustics are to be understood (Simmonds & Lopez-Jurado, 1991). While there have only been a handful of documented strandings in Hawaiʻi (Faerber & Baird, 2010**)**, several populations of Cuvier's and Blainville's beaked whales use these waters to feed (Baird, 2019).

Off the Main Hawaiian Islands (MHI), both Cuvier's and Blainville's beaked whales are managed as individual single stocks (Baird, 2019), despite the presence of both island-resident and offshore populations (Baird et al., 2011; Baird, 2016). The open ocean and resident island populations can be distinguished using their sighting histories, depth at the encounter, known association with members of a population, and spatial usage for tagged individuals (Baird, 2019). Few areas in the world feature multiple long-term studies on co-occurring species of beaked whales within a limited range, let alone studies with satellite tags which have been incredibly beneficial in providing insight into these species' dynamic lives.

Beaked whales exhibit some complexity in their sociality and acquisition of resources. Specifically, Blainville's beaked whales seem to utilize the Hawaiian Islands' slopes and ridges to find resources (Baird, 2019). Cuvier's beaked whales are often solitary but may form groups of several adult males, females, and calves- possibly related to predator avoidance. Adult male individuals have been observed in synchrony while engaging in long foraging dives (Cioffi et al., 2021), although it is not certain how long these associations last. At least one male-male pair associated with each other over a period of nine years or more, much like associations formed by pairs of bottlenose dolphins (*Tursiops truncatas*, Baird, 2019). Blainville's beaked whales, which exhibit larger social groups than Cuvier's, demonstrate little adult male- adult male association, with most groups formed by females, their juvenile offspring, and occasionally a single adult male. Groups often seem to form to aid individuals in avoiding predators, especially among females with small calves (Baird, 2019).

Social network data paired with satellite tag data have demonstrated clear preferences regarding niche partitioning between both species. In general, it appears that Cuvier's dive deeper than Blainville's, although there is evidence that Blainville's occasionally feed near the sea floor (Baird, 2019). Interestingly, Cuvier's appear to remain closer to shore than Blainville's, diving in the nearshore deep water areas on Hawaiʻi's windward side, which has not been documented for the comparatively shallow water Blainville's beaked whales (Baird, 2019).

Off the Canary Islands, Arranz et al. (2011) similarly demonstrated how Blainville's beaked whales are often found in relatively shallow waters, deep-diving to rich bentho-pelagic areas around oceanic islands when prey cannot be found in the shallower meso-depths around 200-500 m. A preference towards island slopes is apparent for studied resident populations of Blainville's beaked whales, who likely follow similar foraging styles near these areas (Arranz et al., 2011). Diving in search of prey, Blainville's beaked whales were also found to have differences in diel migration, with the whales beginning foraging at shallower depths during the nighttime (Arranz et al., 2011). Nonforaging intermediate dives, which differ from shallow water inter-breath intervals, have also demonstrated diel differences. These dives seem to be completely absent during nighttime hours, indicating that they are somehow tied to light levels (Baird et al., 2008b).

Hawaiian beaked whales have evidenced somewhat strong site fidelity, with some populations remaining island-associated (McSweeney et al., 2007; Schorr et al., 2009; Baird et al., 2019). Many foraging marine organisms follow food resources as they change in density and composition throughout three dimensions, and beaked whales are no different. Abecassis et al. (2015) demonstrated how the distribution of Blainville's beaked whales could be explained by bathymetry, water temperatures, and micronekton distribution as they follow their prey into shallower waters during the nighttime. Micronekton abundance has previously been linked to eddies, as offshore foraging grounds for melon-headed whales (*Peponocephala electra*; Woodworth et al., 2011), lunar cycles (specifically the new moon), and cyclonic upwelling eddies (Drazen et al., 2011). Some individuals and groups have demonstrated an association with the ʻAlenuihāhā channel (Schorr et al., 2009), an area known for its frequent sonar activity.

Using passive acoustic monitoring to document broad-scale spatial differences between species, Ziegenhorn et al. (2023) demonstrated how Blainville's and Cuvier's beaked whales use different parts of the Hawaiian archipelago based on several environmental variables (including surface conditions and climate indices). Incorporating data captured from the west sides of Hawaiʻi and Kauaʻi, as well as Manawai (Pearl and Hermes Atoll) in the northwestern Hawaiian Islands, it was determined that Blainville's could be found year-round at all 3 of the sites, while Cuvier's were only reliably found at Hawaiʻi and Manawai. This difference in the usage of the main Hawaiian islands is also demonstrated in the biologically important areas developed by Kratofil et al. (2023).

Blainville's beaked whales generally had higher detections with negative Multivariate ENSO Index (MEI) values, lower salinities near Hawaiʻi, and a positive relationship with sea surface height near Kauaʻi (Ziegenhorn et al., 2023). Off Manawai, Blainville's were found more often when negative ENSO values occurred (El Niño conditions), as well as higher temperatures and PDO. Cuvier's beaked whales similarly had a negative relationship with MEI, with detections increasing in cold water and higher sea surface height near Hawaiʻi. Near Manawai, Cuvier's again demonstrated higher detections with higher sea surface height and PDO values but did not seem to have as strong of a relationship with MEI values (Ziegenhorn et al., 2023). This study also demonstrated a negative relationship with salinity for Blainville's beaked whales, as well as temperature for both species. These factors appear to influence their spatial distribution around the archipelago.

Outside of tropical oceanic waters, such as the Alboran Island near Spain, Cuvier's beaked whales demonstrate small spatial overlap with other cetacean species, most frequently encountered near Risso's dolphins (*Grampus griseus;* Gimenez et al., 2018). Cuvier's beaked whales here seem to typically increase in abundance towards deeper waters as well.

In general, there is a dearth of information about the habitat usage or movements of Blainville's beaked whales, especially in the open ocean. Baird et al. (2011) tracked a single individual likely from an offshore population, which moved over 900 km in just 20 days. These open-ocean populations are rarely sighted but remain in potential danger due to their continued potential exposure to anthropogenic sound (e.g., Navy sonars). Photo identification data has also helped recognize species, location, individuals, and even sex during long-term studies.

Based on data collected from other marine mammals, it is clear that habitat availability and use is an essential aspect of understanding their behavior and distribution, as well as potential competition between individuals (Claridge, 2006). However, with two species co-occurring in the Hawaiian waters, how do they partition the habitat between them? How does each species use different bathymetric, oceanographic, and geomorphic features? Does either species prefer areas of higher nutrients, temperatures, or sea conditions? Using satellite tag data from both species, this project aims to conduct analyses to bring us closer to answering these questions. As mentioned above, sightings data also exists for these species, but the difficulties in ascertaining the habitat use of deep-diving mammals based on surface encounters limit analyses. Therefore, this study aims to use tag data to analyze and look for spatial segregation and habitat partitioning between the two species on a temporal and horizontal scale, with the goal of revealing potential differences. Findings will be essential to furthering our understanding of their habitat, spatial usage, and interactions as these species continue to be impacted by anthropogenic noise and activities (Hooker et al., 2019).

B. Seasonal analyses of Odontocete spatial distribution off the island of Hawaiʻi

Based on NOAA line transect surveys, there is a noted higher abundance of sperm whales (*Physeter macrocephalus*) in the winter and fall off the Hawaiian islands, specifically off the west side of Hawaiʻi Island (Bradford et al., 2022). Seasonal shifts can be a significant aspect of odontocete spatial usage. However, seasonal variation can be challenging to define in areas like the Hawaiian archipelago, where seasonal oceanographic differences are marked by fluctuations in variables such as wave height and wind speed, rather than the larger shifts in weather and temperature seen in more temperate localities. Based on these factors, Flament et al. (1996) defined Hawaiʻi's oceanographic seasons as fall (November to January), winter (February to April), spring (May to July) and summer (August to October). With at least 18 species of odontocetes detected by Cascadia Research Collective, their allocation of resources throughout the year, as well as habitat usage and partitioning, paint a picture of shared habitat over a large region of oceanic topography shifts. Fluctuations in sympatry and species distribution may occur due to variables such as prey habits and migration, so it is essential to understand the processes behind seasonal variation in cetaceans worldwide.

For example, in the waters off of British Columbia and Washington, the three pods within the southern resident killer whale (*Orcinus orca)* population spend the summers using the region very differently from one another. While all groups utilized their own core areas, foraging variations have segregated the three pods over time (Hauser et al., 2007). Despite this, they sometimes intermingle, with each pod taking a different leading role during these congregation times, depending on the pairing. Sperm whales (*Physeter macrocephalus*) utilize fine-scale habitat partitioning between vocal clans based on local conditions (Vachon et al., 2022). Little overlap occurs between these clans, with evidence of cultural differentiation, not foraging specialization, being the main driver behind any preference.

Hauser et al. (2014) demonstrated the differences between two populations of beluga whales (*Delphinapterus leucas*). Both populations used shallow shelves in the fall, while remaining near the ocean's slope/basin in the spring and summer. The two populations briefly overlap in September and at least one utilized canyons as prime foraging spots when currents and winds formed a stratified front there. While not an odontocete, bowhead whales (*Balaena mysticetus)* in the Bering Sea were documented remaining near areas with 90-100% sea ice concentration during the winters, using the waters much differently than in the summer while sea ice levels are lowest (Citta et al., 2011).

Using their echolocation signals, beaked whale species can be identified using frequency modulated upsweep pulses (Baumann-Pickering et al., 2014), which can help determine patterns of foraging and seasonality by looking at daily presence and diel patterns. While species like Cuvier's beaked whales are distributed worldwide, specific populations appear to have strong site fidelity year-round (Kowarski et al., 2018). In the Ligurian Sea, recorders detected beaked whales year-round without much change by season (Giorli et al., 2016). Cuvier's beaked whales appear to lack significant seasonal changes around the Hawaiian Islands, with individuals reliably detected throughout numerous identification studies

(McSweeney et al., 2007). However, they were indicated to have a slight fall/winter peak within a 5 km radius of acoustic detections by Ziegenhorn et al. (2023).

Site fidelity based around seasonal feeding grounds has been demonstrated in sperm and minke whales (Calambokidis et al., 2001; Dorsey et al., 1990). With so many Hawaiian species being resident to the island's slopes, this phenomenon will be necessary to consider, as it is an incredibly essential aspect of animals' ranges and habitat usage. Reproduction could also potentially be an aspect governed by the region's seasons. While more research is necessary to determine seasonal shifts in reproduction for many species, several species have been sighted with calves on a seasonal basis. Bottlenose dolphin neonates have been documented in Hawaiʻi from fall through spring, indicating a potentially seasonal reproduction pattern despite small temperature fluctuations (Baird et al., 2009), although calves have been observed throughout the year since then (Baird, 2016). Baird (2016) noted several more potentially seasonal reproductive patterns for several species, including pilot whales, rough-toothed dolphins, and pantropical spotted dolphins.

Due to the high number of resident populations, odontocetes located near Hawaiʻi generally appear to be more tied to the region than many other areas with abundant marine mammals. A 2013 study by Baird et al. showed that 14 of 18 species surveyed were documented in all oceanographic seasons, with seven species found in every month (Table A, updated). While the study only focused on strong seasonal signals, it was assumed that any fluctuations amongst species were small. Ziegenhorn et al. (2023) further demonstrated seasonality around the Hawaiian islands by incorporating passive acoustic monitoring, with the goal of looking at broad-scale long-term trends for several potentially resident species. Three sites were analyzed: one off the west side of Hawaiʻi, one west of Kauaʻi, and one near Manawai. In general, this study showcases how seasonal patterns are wholly dependent not just on species, but on area as well.

In the study, Cuvier's beaked whales were detected on 57 percent of the days in Manawai and had fall/winter peaks in detections at Manawai and Hawaiʻi, indicating a possible seasonal pattern. Blainville's beaked whales were often heard at both Hawaiʻi and Manawai: 38 and 91 percent of days, respectively. They had a slight seasonal pattern in Manawai, with a minor increase in detections from July to August. Stenellid dolphins were found in high numbers at all three sites, with detections highest in winter at Hawaiʻi. False killer whales (*Pseudorca crassidens*) were commonly detected in the fall at Hawaiʻi, while they had an early summer peak near Kauaʻi. Rough-toothed dolphins (*Steno bredanensis*) had more frequent spring detections at Kauaʻi, winter detections in Hawaiʻi, and summer at Manawai. Short-finned pilot whales (*Globicephala macrorhynchus*) only exhibited a pattern at Kauaʻi, where winter detections were highest.

This study predicts that odontocetes will generally follow the slight seasonal shifts in oceanographic factors but may exhibit some changes in environmental usage as prey shifts according to seasonal effects. Are there certain habitat or topographic features that draw species to specific areas at different times of the year? Or could other, shorter scale cycles be more responsible for the species' movement, as in Owen et al. (2019)? This research will be essential in understanding odontocete movements and spatial usage throughout the year, as well as being beneficial towards future field studies.

Table A.

List of all species identified during Hawaiian field effort by Cascadia Research Collective. Based on a subset described in Baird et al. (2013) and the methods section. Organized in decreasing order of sample size after the number of months and seasons documented in. Wi = Winter, Sp = Spring, Su = Summer, and Fa = Fall.

	Group Size					
Species	Mean	SD	Min	Max	Median	# Months/Seasons Documented
Short-finned pilot whale	19.1	14.1	1	240	17	12/All
Pantropical spotted dolphin	71.6	59.2	1	500	60	12/All
Rough-toothed dolphin	9.6	12.5	0	190	6	12/All
Common Bottlenose dolphin	8.7	9.1	1	90	5	12/All
Spinner dolphin	47.2	41.5	0	220	35	12/All
Dwarf sperm whale	2.8	1.8	1	10	2	11/All
Cuvier's beaked whale	2.2	1.2	1	7	2	10/All
Melon headed whale	203.9	157.3	1	1100	175	12/All
False killer whale	14.3	9.8	1	62	13	11/All
Blainville's beaked whale	3.9	2.4	1	13	3	12/All
Pygmy killer whale	11.9	8.1	2	45	12	11/All
Sperm whale	9.1	11.9	1	100	5	10/All
Striped dolphin	31.2	23.2	1	130	30	9/All
Unidentified odontocete	1.5	0.8	1	5	1	9/All
Unidentified dolphin	4.8	11.3	1	70	1	9/All
Unidentified beaked whale	1.8	0.8	1	5	2	4/Wi, Su, Fa
Pygmy sperm whale	1.4	0.5	1	4	1	4/ Sp, Su, Fa
***Kogia* sp.**	1.8	0.8	1	4	2	7/All
Killer whale	5.0	1.7	4	9	4	4/Sp, Su, Fa
Fraser's dolphin	64.1	34.0	15	150	75	4/Wi, Sp, Su
Risso's dolphin	11.9	10.9	1	45	8	7/All

2.0 Materials & Methods

A. A comparative spatial analysis of location data from satellite-tagged Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales off Hawai'i Island

Archived telemetry datasets were used to assess and compare the spatial distribution of Blainville's (Figure A) and Cuvier's (Figure B) beaked whales. Specific details on deployment methods and tag programming are provided in Baird et al. (2010) and Schorr et al. (2009). Briefly, location-only (SPOT5) and location and dive depth transmitting (SPLASH10) tags manufactured by Wildlife Computers (Redmond, Washington) were deployed on the whales in the LIMPET configuration (Figure C, Andrews et al., 2019), communicating with the Argos satellite system. The tags were deployed with pneumatic projectors and attached with titanium darts. Between 2006 and 2013, Cascadia Research Collective (CRC) satellite tagged 12 Blainville's beaked whales off of the leeward side of Hawai'i Island, as well as a single tag off of O'ahu in 2017 (Abecassis et al., 2015; Baird et al., 2010; Baird, 2016, 2019; Schorr et al., 2009). Ten Cuvier's beaked whales were also satellite tagged between 2008 and 2015 on the leeward side of Hawai'i Island (Baird et al., 2010; Baird, 2010, 2019). The whales tagged included individuals of both sexes, as well as both previously sighted and unknown animals. Summary information on these tag deployments is shown in Tables B and C, as well as Figure S3.

Data obtained using tag transmissions included the date, time, latitude, longitude, and measures of positional uncertainty. Prior to analyses, location data were filtered through the Douglas Argos filter (Douglas et al., 2012; accessed through MoveBank) to remove low quality and unrealistic locations. Low quality locations were those marked unlikely by the algorithm based on the animals' average speed, the distance between points, angles, and the quality of the point (i.e., Argos location quality class, from LC3-LCZ). Filtered locations were fit to a 4-hour continuous time correlated random walk model using the *crawl* package (Johnson et al., 2008; Johnson & London, 2018). For *ctmm* analyses, explained below, fitted models were also used to estimate locations at the original time point of the Argos location, such that the resulting track would be smoothed to account for location error.

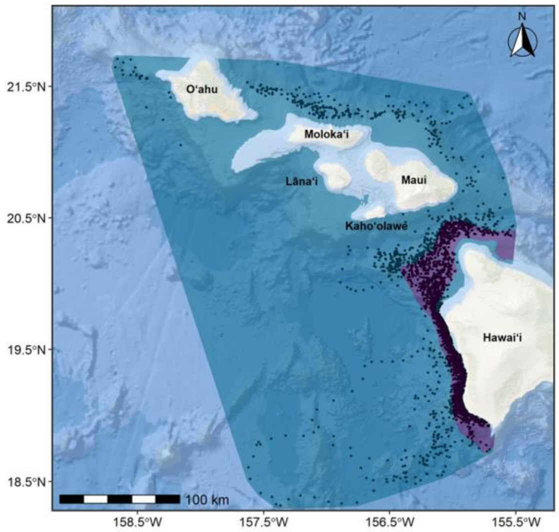

Figure A. Parent Biologically Important Area for Blainville’s beaked whales (blue polygon) between O’ahu and Hawai‘i Island, as well as child BIA representing the core area of use for the Hawai‘i Island community (purple polygon). Model-predicted locations of satellite-tagged Blainville’s beaked whales and sighting locations are shown as points under the polygons. (from Kratofil et al., 2023)

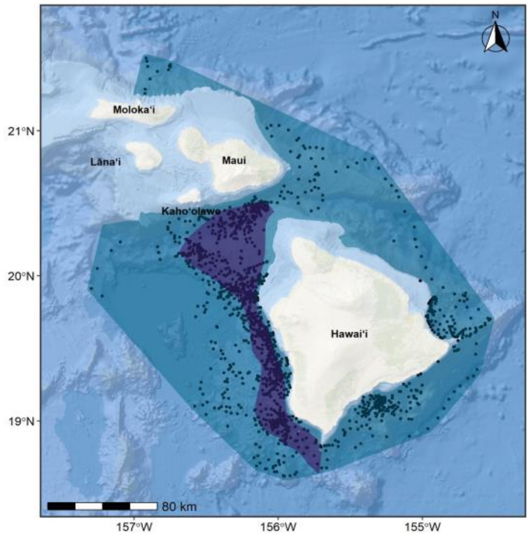

Figure B. Parent Biologically Important Area for Cuvier’s beaked whales (blue polygon) between Maui Nui and Hawai‘i Island, as well as child BIA representing the core area of use for the Hawai‘i Island community (purple polygon). Model-predicted locations of satellite-tagged Blainville’s beaked whales and sighting locations are shown as points under the polygons. (from Kratofil et al., 2023)

Using the *pathroutr* package (London, 2021), locations were rerouted around land using a polygon representing the 300-m isobath for both species. These re-routed locations were incorporated into two analyses investigating (1) differences in spatial distribution and overlap and (2) differences in habitat selection between Blainville's beaked whales and Cuvier's beaked whales, with the goal of assessing whether competitive exclusion may facilitate their co-occurrence in Hawaiʻi. When data were available for two individuals during the same period with the individuals remaining spatially associated, to account for pseudoreplicated pairs, the individual with the shorter track of the two was removed prior to analyses. This meant that two Blainville's beaked whale tags were excluded from most of this study, reducing the sample size from 12 to 10. Pseudoreplicated individuals were still included in some analyses for potential group comparison. The individual tagged near O'ahu was also excluded from the study, as it is likely from a different population and did not use the same area spatially as the rest of the tagged individuals. Analyses were conducted in the program R (R Core Team, 2022).

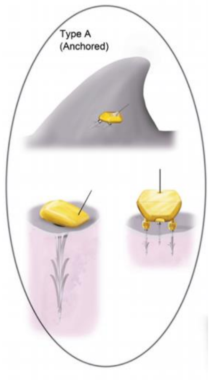

Figure C. Demonstration of Type A/LIMPET tag deployment configurations (Andrews et al., 2019).

Environmental Variable Analyses

Habitat variables considered included several temporal and spatial variables, such as distance from shore, seafloor depth, seafloor slope (calculated from a 50x50 bathymetry model by the University of Hawaiʻi at Manoa, 2016), salinity, water temperatures, current velocities, geomorphic feature usage, sea surface height, and light levels (Arranz et al., 2019). Oceanographic variables (sea surface temperature, sea surface height, sea surface salinity, current velocities) were obtained from the Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al., 2007) and the Regional Ocean Modeling System (ROMS; Partridge et al., 2019), depending on the time frame available. Each variable from the HYCOM and ROMS output were calculated at a 3-hour temporal resolution, with HYCOM utilizing an approximately 0.08 degree horizontal resolution and ROMS with a 4-km spatial resolution. Horizontal surface current magnitude ($|\overline{V}|$), while not directly obtained from the aforementioned sources, was defined as:

$$|\overline{V}|=\sqrt{|u^2+v^2|}$$

where u and v are the zonal and meridional components of the surface current, respectively (Woodworth et al., 2011). Minimum chlorophyll-a concentration information was obtained from the Moderate Resolution Imaging Spectrometer **(**MODIS; Letelier & Abott, 1996**)** at an 8-km spatial resolution on a monthly basis to account for cloud cover restricting satellite imagery and some potential lag between prey availability and primary production. Distances to several geomorphic features included in this portion of the study, listed in Table E**,** were defined via Blue Habitat (www.bluehabitat.org) and Harris et al. (2014). Distance to abyss was not included in analyses, as much of the seafloor surrounding this portion of the Hawaiian islands is classified as “abyss”. The non-normal distribution of variables led us to use the Wilcoxon rank sum test (also known as the Mann-Whitney U test) to compare variables between species and detect significant differences in habitat usage. We made the following assumptions: all tags between species were independent of each other, the sampling process was continuous (due to the *crawl* process), the samples were representative of the population, and the two samples had similar variances (tested using F-tests for homogeneity of variances). These assumptions indicated that the Mann-Whitney U test was a suitable pairwise comparison method between the species for most variables.

To analyze variation in long-term climatic processes, ENSO cycle periods (El Niño or La Niña) were determined through three-month averages of mean SST anomaly (Oceanic Niño Index; ONI) and historical records provided by NOAA (NOAA, 2023). Seasons were analyzed using the oceanographic seasons defined in Flament et al (1996). Finally, lunar phase and moon illuminated fraction, determined using the packages *lunar* (Lazaridus, 2015) and *oce* (Kelly et al., 2018) in r, were analyzed. Lunar phase was split into two groups: one with a 1st and 3rd quarter to portray waxing and waning, as well as one with gibbous and crescent phases in place of the quarters, separated by when moon illuminated faction was above or below 0.5.

Home range analysis

Overlap (or lack thereof) of the spatial distributions between the two beaked whale species was examined through the use of kernel density estimated home ranges. Due to the inconsistent sampling of tag data, an autocorrelated kernel density estimator was necessary. Using the R package *ctmm* (Calabrese et al., 2016), the re-routed estimated location data, at the original time points to account for a lower computational burden and more accurate weighting, were fit to a continuous-time stochastic process (CTSP) after selecting an appropriate model. Using this package, a proper movement model (e.g. Ornstein-Uhlenbeck) was fit using empirical variograms to visualize the autocorrelation structure of all data sets. The variograms, which demonstrate each individual’s average square distance traveled within given time lags, were then visually interpreted to look for potential range residency, indicated by a flattening or asymptotic appearance of the semi-variance values. Variograms were then compared to the individual model shape to confirm model selection and residency. For individuals with more variable range residency, some deployment durations were split according to shorter periods of flattening or asymptotic behavior (C. Fleming, U of Maryland, personal comm.).

Unlike normal kernel density estimates (here, IID models), which assume independence between data points, the CTSP process is robust to irregular sampling, separating the continuous-time movement process from the discrete-time sampling process. The fitted, selected process was then utilized to estimate each individual’s home range (UD) using autocorrelated kernel density estimation (AKDE), which, assuming that the documented movement behavior continues, can predict future spatial use. To reduce bias caused by uncertainty around home range crossing time and speed, individuals with especially brief tag deployment durations (<10 days) were not included in home range estimation, and individuals of substantial tag deployment duration but with limited numbers of range crossings (estimated effective-sample-size, $\tau_p < 5$) underwent the process resampling the sample distribution, or parametric bootstrapping (Fleming et al., 2019).

Using the UD estimates for each individual, a hierarchical population kernel density estimation function (PKDE), which involves placing kernels of density on every sampled time for the combined individuals’ AKDEs, was also utilized to determine a population-wide kernel density estimate for both species. This method accounts for irregular sampling and autocorrelation using a bandwidth optimized for population-range estimation.

Home range overlap (BA) between probability distributions, which can capture interaction potential, was also analyzed using the *ctmm* package. The Bhattacharyya coefficient was utilized to discover the interaction between each pair of individuals, as well as between both species. These overlap distributions may be helpful in providing further insight into spatial encounter usage, territoriality, behavior, and resource competition (Winner et al., 2018). The overlap measures and UDs were then incorporated to define the conditional distribution of encounters (CDE) between individuals, describing encounter probabilities and overlap for movement within each potential home range (Noonan et al., 2020). With encounters being keystone events essential in understanding ecological processes on a large scale, this function intends to describe potential areas where animals are most likely to encounter each other.

Table B.

Blainville's beaked whale satellite tag data summary (from Kratofil et al., 2023). UK=unknown

Island	# deployments	Study duration (first tag – last tag)	# unique years with deployments	# females/males/UK tagged	Median (range) deployment duration (days)	Total # Argos locations*	Total # 4-hourly *crawl* locations
O'ahu	1	2017	1	NA/1/NA	3	30	18
Hawai'i Island	13	2006-2013	6	6/5/2	45 (15-159)	4,939	3,030

Table C.

Cuvier's beaked whale satellite tag data summary (from Kratofil et al., 2023). UK=unknown

# deployments	Study duration (first tag – last tag)	# unique years with deployments	# females/males/UK tagged	Median (range) deployment duration (days)	Total # Argos locations*	Total # 4-hourly *crawl* locations
10	2008-2015	6	7/2/1	24 (7-49)	1,667	1,362

B. Seasonal analyses of Odontocete spatial distribution off the island of Hawai'i

Archived sightings data exist for 18 odontocete species and at least four unidentified odontocetes (three of which were confirmed to be an unknown species of dolphin, an unknown species of beaked whale, and an unknown *Kogiid*). Sightings data were collected by Cascadia Research Collective using small to medium sized vessels around the Hawaiian Islands with GPS logged locations collected for every 5 minutes of effort (Baird et al., 2013; Baird 2016). Odontocete groups were approached, photographed, identified to species, and group size estimated. Other data recorded and estimated included but was not limited to date, boat/vessel, species, island, time, latitude, longitude, sea condition (Beaufort scale), and sighting cue.

Using a 50x50 m bathymetry model (University of Hawaiʻi at Manoa, 2016) and the r package *sf* (Pebesma, 2018), all sighting and 5-minute effort locations were processed to determine slope (average in the 50x50 m cell), depth, distance from shore, and a host of other variables defined to best potentially describe odontocete distribution by season. Survey effort was quantified by the number of hours on effort each day and the number of kilometers covered per day.

For analyses of group size, distance seen, island, depth use, sighting rates, and sea state, bias was reduced using sighting cue data. Sightings removed included those initiated by satellite tag detections, radio calls, fishing vessel presence, and acoustic detections. To lessen bias in assessing relative abundance, certain sightings of spinner dolphins (*Stenella longirostris)* within 0.5 km of the mouth of Honokohau Harbor were excluded. This species has been noted to use specific bays like this one as resting areas during the day. A more detailed summary of these methods can be found in Baird et al. (2013).

Table D.

Sighting characteristics based on all on sightings for all islands from 2000 through 202#, as well as the subset described in Baird et al. (2013) and the methods section (i.e., removing those cued by radio calls, tracking tagged animals etc). Sightings per 100 hours of effort, distance first seen, and mean Beaufort scale by species is calculated for the subset of sightings.

Species	# all	# subset	% of subset	Sightings per 100 h	Distance first seen (m) mean	Beaufort scale mean
Short-finned pilot whale	860	758	25.69	8.35	772	1.84
Pantropical spotted dolphin	629	575	19.48	6.34	911	1.81
Rough-toothed dolphin	519	440	14.91	4.90	359	1.86
Bottlenose dolphin	380	318	10.78	3.46	407	2.00
Spinner dolphin	315	215	7.29	2.39	373	2.34
False killer whale	117	65	2.20	0.79	655	2.13
Melon headed whale	108	86	2.91	0.95	692	1.91
Dwarf sperm whale	99	97	3.29	1.07	349	1.45
Cuvier's beaked whale	97	97	3.29	1.04	1077	1.57
Blainville's beaked whale	75	66	2.24	0.71	416	1.42
Pygmy killer whale	64	53	1.80	0.58	342	1.79
Sperm whale	52	44	1.49	0.48	1351	1.93
Striped dolphin	44	41	1.39	0.46	1601	1.61
Unidentified odontocete	36	34	1.15	0.38	696	1.74
Unidentified dolphin	24	24	0.81	0.27	559	1.92
Risso's dolphin	18	17	0.58	0.19	407	1.94
Kogia sp.	15	15	0.51	0.13	308	1.27
Unidentified beaked whale	11	10	0.34	0.11	757	1.90
Pygmy sperm whale	8	8	0.27	0.09	595	0.63
Fraser’s dolphin	7	7	0.24	0.08	505	1.71
Killer whale	6	5	0.17	0.04	830	2.20

For seasonal analyses, data were standardized based on sightings per 100 hours of effort. To avoid differences in oceanographic factors and variable amounts of effort between islands, analyses were focused on effort just around the island of Hawaiʻi. While oceanographic seasons are typically determined by wind and surface temperature, such as in Baird et al. (2013), here, just two seasons were identified by comparing effort count, effort depth, and distance to shore in wide bins on both a monthly and yearly basis. Based on the compared data and similarities in amount of effort, "March through May" and "October through December" were labeled as "spring" and "fall," respectively. Years of sufficient and similar effort included in this study were 2002, 2006, 2009, 2011, 2013, 2018, 2019, and 2021. False killer whales were excluded from this study due to social cluster specific habitat use and group size being so heavily dependent on encounter duration (Baird et al., 2008a, 2012). Sea states above a three on the Beaufort scale were excluded from the statistical portion of this project, as sighting rates decrease significantly in rougher waters due to poor visibility of target animals.

Dynamic variables investigated in this portion of the project were attached to sighting and effort information using oceanographic variables obtained from the Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al., 2007) and the Regional Ocean Modeling System (ROMS; Partridge et al., 2019) as in project A. Potential seasonal indicators obtained from the aforementioned sources include sea surface temperature (SST), sea surface height (SSH), sea surface salinity (SALN), and current velocities (Ecurr and Ncurr. Horizontal current magnitude and chlorophyll-a concentrations were calculated and obtained using the above methods from Project A to examine primary productivity. Monthly chlorophyll-a concentrations were not available for the first season (spring, 2002). A lunar variable (moon_ill_fraction) was also included in this investigation due to its influence on the behavior of short-finned pilot whales (Owen et al., 2019) and pantropical spotted dolphins (*Stenella attenuata;* Shaff & Baird, 2021), and its interaction with other variables (moon_ill_fract*depth; moon_ill_fract*dist_shore) was considered in model development as well. Time of day variables were not included due to the overwhelming majority of sightings and field effort occurring during the day. All pairs of predictor variables were tested for collinearity using Pearson correlation coefficients, with covariates with coefficients above 0.7 considered correlated and not included in the same model (Dormann et al., 2012). For model convergence, variables were standardized by subtracting the mean and dividing by the standard deviation. After examining distributions, highly skewed variables were logged (Vachon et al., 2022).

Covariate combinations were included in final seasonal models using generalized estimating equations (GEEs; Liang & Zeger, 1986). GEEs, an extension of Generalized Linear Models, allow for correlated residuals and can account for spatio-temporal autocorrelation utilizing a correlation structure that does not require points to be independent. To build GEE-GAM models, covariates were inputted as predictors of seasonality by species using presence/absence models. Data were then clustered by a blocking variable created using the length of encounter, partially determined through autocorrelation among data points converging near 0 (as in Vachon et al., 2022). To build datasets for each species and to account for species presence during effort, all 5-minute effort points within the start and end times of an encounter were included in clusters with the original sighting point. Using this method, these grouped blocks with correlated data points are assumed independent, while residuals are allowed to be correlated. Due to GEE-specific specifications on blocking variable/cluster size, only species with appropriate numbers of blocks ($n > 40$) were included in models. Ultimately, a dataset was created for each species, with environmental variables, a timestamp, and information about specific species presence/absence.

Models were then fit individually for each species sightings dataset using the library *geepack* in R, with variable selection determined by relevance to seasonal analyses and model performance according to goodness-of fit analyses. Variables were inputted into the GEE-GAM models to describe differences in variables by species' seasonality. In total, four habitat model types were run for each species (Presence/Absence, Spring, Fall, and Season) with the same sets of covariates, similar to the process described in Vachon et al. (2022). Briefly, each model is described below.

1. Presence/Absence: a general model of the species' presence with a response variable of 0 for sighting absence and 1 for presence. This method showcases which covariates influence the species' presence in general, including both seasons. Season is included as a predictor here to test for differences in frequency of sightings compared to other variables.
2. Spring/Fall: two models to describe the habitat usage and distribution of sightings in their respective seasons, with a response variable of 0 indicating absence within that particular season and a 1 indicating presence.
1. Season: to demonstrate the effect of season on habitat usage, this model was fit to identify variables that best distinguish between Spring and Fall, with a response of 0 for Spring presence and a response of 1 for Fall presence. This model will not include absence data points.

Species with sufficient sample size for all three models included bottlenose dolphins, dwarf sperm whales (*Kogia sima)*, pantropical spotted dolphins, short-finned pilot whales, and rough-toothed dolphins. Cuvier's beaked whales, Blainville's beaked whales, pygmy killer whales, and melon headed whales had sufficient sample sizes to be included in the first and fourth model. However, they did not have large enough sample sizes in one or both seasons to be included in the Spring or Fall models. For the purposes of this report, statistical analyses focus on Pantropical spotted dolphins, who have similar numbers of sightings by effort in both seasons.

After these models were run, QIC, AUC, goodness of fit, and the predictive accuracy of each model was tested and compared to determine model performance, as in Pirotta et al. (2011) and Vachon et al. (2022). The receiving operating characteristic (ROC) curve was used with the R package *ROCR* (Sing et al., 2005) to calculate the area under the ROC curve (AUC). Goodness of fit, or the proportion of data points to be correctly assigned as presence/absence (or Spring/Fall in the season model), was calculated using confusion matrices and predicted data (Fielding & Bell, 1997). All of these elements were utilized to examine which models best predict seasonal usage of environmental and oceanographic covariates. To further assess model performance, precision and recall were also evaluated for each model. Sea surface temperature, sea surface height, and chlorophyll-a concentrations were not considered for the fourth model due to them being found at higher values in the Fall than in the Spring overall. Any inclusion of them in the fourth model would have biased results, leading to overconfidence in species' habitat usage. There was no indication of any of these variables affecting pantropical spotted dolphin presence other than them being significantly different between seasons for all effort.

3.0 Results

A. A comparative spatial analysis of location data from satellite-tagged Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales off Hawai'i Island

Environmental Variable Analyses

According to the results of the Mann-Whitney U test, most environmental or geomorphic features were found to be used differently between the species (Table E). In terms of depths utilized, Blainville's beaked whales used significantly shallower waters (grand median seafloor depths of 1,195 m), while Cuvier's beaked whales used deeper waters (grand median of 2,260 m). For distance to shore, the difference between the two species was not as great (Blainville's grand median = 17.7 km, range: 0.1-189.4 km); Cuvier's grand median = 18.31 km. 0.3-93.6 km), although the difference was still significant. In terms of geomorphic variables, Cuvier's beaked whales were a median distance of 5.6 km from canyons and 20.6 km from the continental shelf. Blainville's were found at much higher slopes and used waters farther from canyons, seamounts, and terraces, although the difference in terrace usage was not found to be statistically significant (Table E). Although all environmental variables were comparable, the Mann-Whitney U test revealed that the two species used waters of significantly different sea surface heights, salinities, and monthly chlorophyll-a concentrations (Table E). However, the supplementary F-tests conducted to compare variances showed that the salinity and chlorophyll-a concentration variables had unequal variances, which violated the assumptions of their final pairwise significance tests. No other variables violated this assumption.

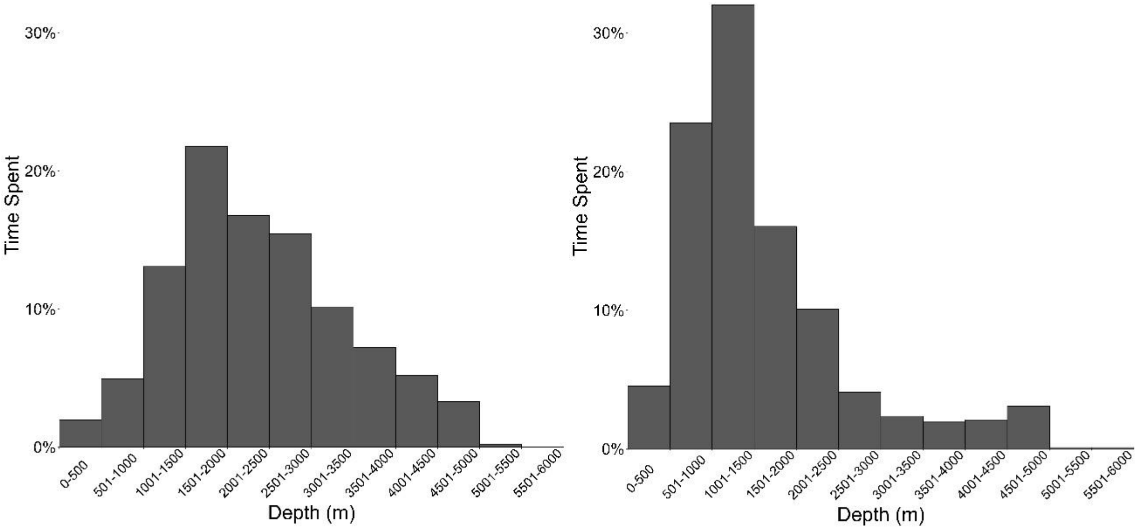

Figure D. Percentage of time spent in each 500 m depth bin by Cuvier's beaked whales (left) and Blainville's beaked whales (right) using estimated locations from satellite tags at 4 h time steps.

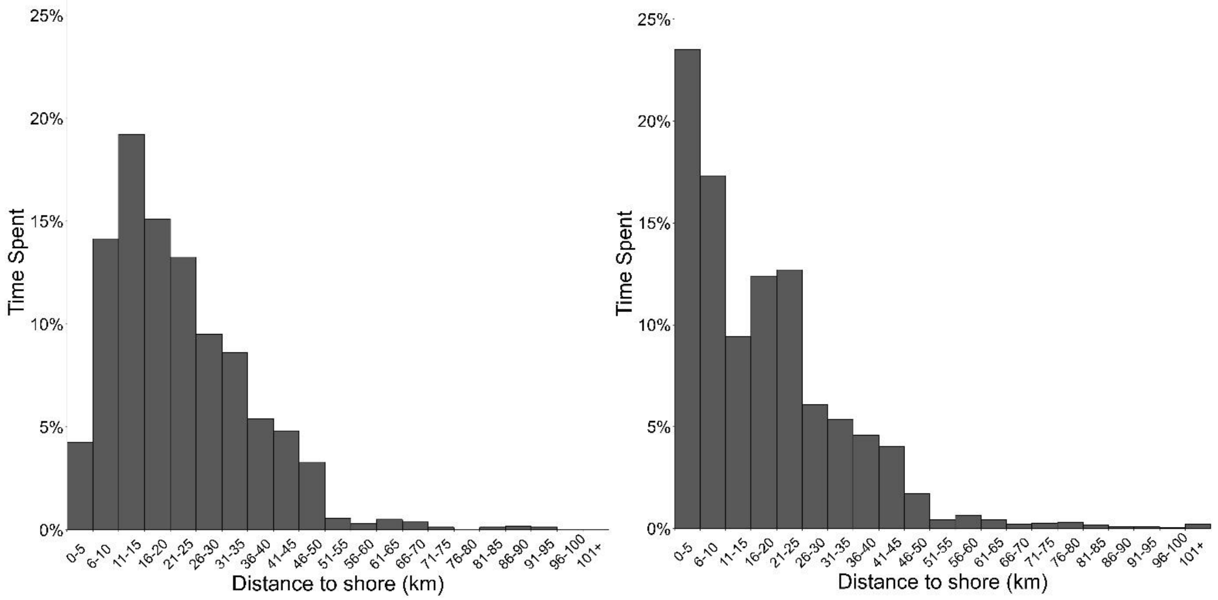

Figure E. Percentage of time spent in each 5 km distance to shore bin by Cuvier's beaked whale (left) and Blainville's beaked whale (right) using estimated locations from satellite tags at 4 h time steps.

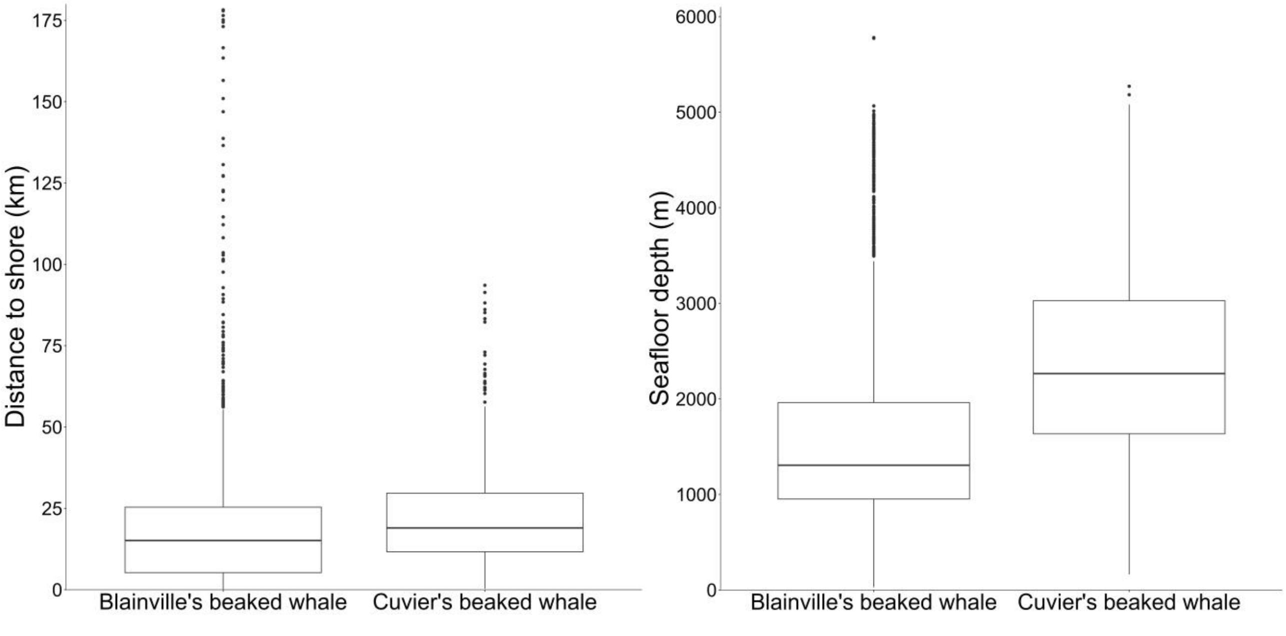

Figure F. Boxplots of distance to shore and depth for both species using estimated locations from satellite tags at 4-h time steps.

Table E.

Environmental, geomorphic, and topographic feature variable values for Cuvier's and Blainville's beaked whales. Pairwise significant differences calculated using p-values from the Wilcoxon rank sum (Mann-Whitney U) test. Depth (m) minimum values are below 300 m due to an error in polygon shaping that resulted in a handful of values for each species to be in waters shallower than 300 m.*

	Median		Range		Mean		St. Dev.		*p val.*
	Ziphius	*Mesop.*	*Ziphius*	*Mesop.*	*Ziphius*	*Mesop.*	*Ziphius*	*Mesop.*	
Depth (m)*	2,279	1,306	167-5,721	30-5,780	2,395	1,609	1,039	997	<0.001
Distance to shore (km)	19.5	15.2	0.3-93.6	0.1-189.4	22.0	19.2	13.2	20.9	<0.001
Distance to canyons (km)	6.1	10.3	0-59.5	0-156.1	9.5	14.1	10.4	15.8	<0.001
Distance to island shelf/200m	20.9	14.3	0.5-86.9	0.2-192.5	23.0	18.8	13.2	21.1	<0.001
Distance to seamounts (km)	50.4	58.1	0-175.5	0-153.7	52.7	57.4	27.6	29.2	<0.001
Distance to escarpments (km)	0.0	0.0	0-26.7	0-32.1	1.4	1.3	3.5	3.2	<0.001
Distance to ridges (km)	34.1	39.5	0-107.6	0-114.2	38.4	42.8	31.2	27.6	<0.001
Distance to terraces (km)	19.8	22	0-114.3	0-213.2	30.3	37.5	28.9	39.5	0.63
Slope (m)	7.3	9.8	0.1-54.4	0-82.7	9.6	11.8	7.8	9.6	<0.001
Chlorophyll-a concentrations (monthly, mg/m^3)	0.10	0.07	0-0.17	0.03-0.15	0.08	0.07	0.02	0.02	N/A
Sea surface temperature (C)	25.4	25.6	23.8-28.1	23.5-27.9	25.6	25.6	0.8	0.9	0.32
Sea surface height (m)	0.61	0.62	0.11-1.30	0.14-1.28	0.62	0.63	0.20	0.16	0.04
Horizontal current magnitude	0.22	0.27	0-1.50	0-1.20	0.29	0.31	0.30	0.20	<0.001
Sea surface salinity (psu)	35.0	34.9	34.4-35.7	34.3-35.4	35.0	35.0	0.20	0.20	N/A

Both Cuvier's that ventured to the windward side of Hawai‘i Island did so during weaker La Niña periods (Figure S4) coming out of stronger La Niña years. Specifically, individuals used this side of the island in mid-2009, at the end of an especially strong La Niña period that started in 2007, and late 2011, after another strong La Niña period that developed in the winter of 2010. Similarly, both Blainville's that used windward waters north of Maui were not documented there in El Niño periods (Figure S5). Both individuals, which were tagged during the 2010-2012 La Niña period, started heading north after months of moderately strong La Niña conditions. Several variables differed considerably between ENSO cycle periods (EN= El Niño, LN= La Niña). Cuvier's were seen at typically lower latitudes (Figure G) much farther from ridges (M_{EN}=63.0 km, M_{LN}=23.5 km) and terraces (M_{EN}=36.0 km, M_{LN}=21.0km) during EN periods, but closer to shore (M_{EN}=25.2 km, M_{LN}=19.7 km), at lower salinities (M_{EN}=35.1, M_{LN}=34.9), and at higher horizontal current magnitude (M_{EN}=0.38, M_{LN}=0.24) during the same period. Unlike Cuvier's, some tag location information on Blainville's were available during periods of neither high nor low ONI values in 2012 and 2013. However, in general, differences were smaller for this species between cycle periods (Figure H). Variable differences of note were distance to terrace (M_{EN}=35.3 km, M_{LN}=44.4 km, M_{Neither}=10.3 km), distance to shore (M_{EN}=18.4 km, M_{LN}=19.9 km, M_{Neither}=24.9 km), distance to the ridge (M_{EN}=42.2 km, M_{LN}=37.9 km, M_{Neither}=62.8 km), and slope (M_{EN}=9.5 m, M_{LN}=12.3 m, M_{Neither}=10.3 m). There were no large fluctuations between cycle periods for latitude, longitude, salinity, or horizontal current magnitude for this species. Sea surface temperature (Figure S6) and chlorophyll-a concentrations were found following the same patterns for both species: higher during EN periods and lower during LN periods. For Blainville's, chla_a concentrations during periods of neutral phases in late 2012 and 2013 were largely similar to concentrations during LN periods. To test if these results were meaningful, sightings of beaked whales, based on similar methods to those in project B (i.e., just off Hawaiʻi Island and at effort depths greater than 375 m), were examined for a possible decrease in frequency on the leeward side during LN phases, which was encountered (Table F).

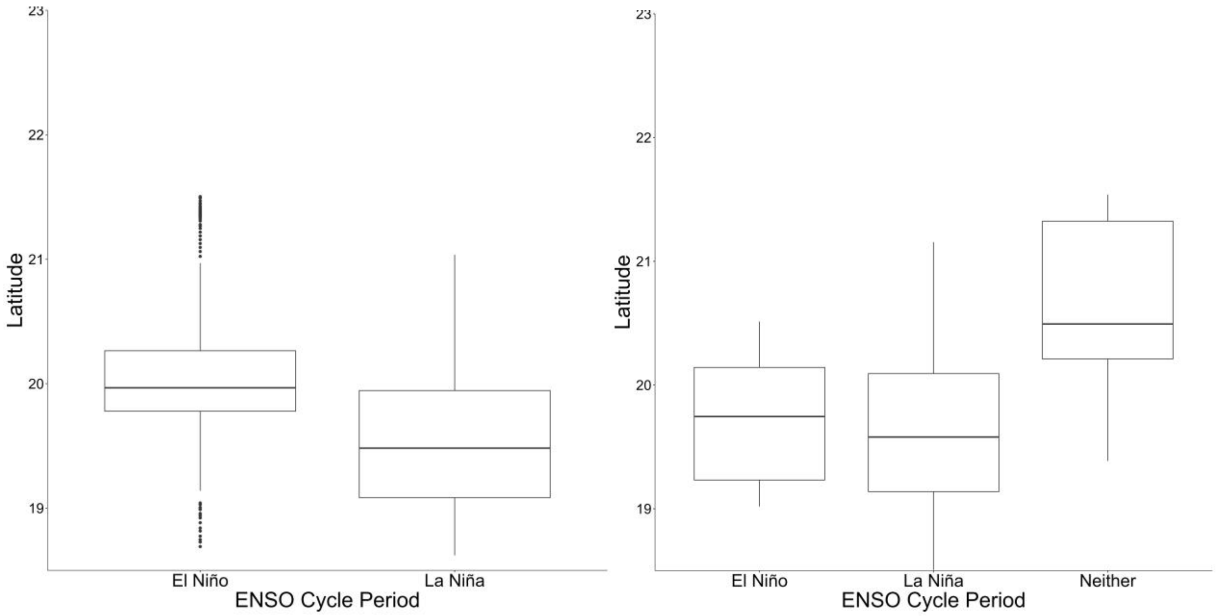

Figure G. Cuvier's (left) and Blainville's (right) differences in latitude during different ENSO cycle periods using estimated locations from satellite tags at 4-h time steps.

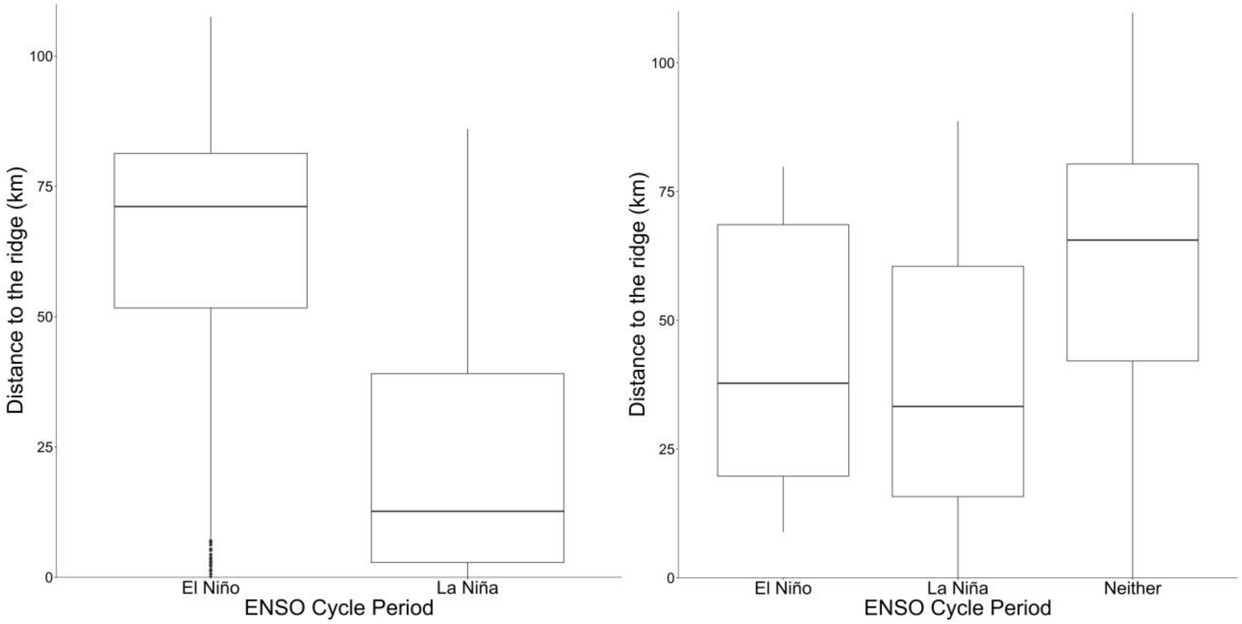

Figure H. Cuvier's (left) and Blainville's (right) differences in distance to ridges during different ENSO cycle periods using estimated locations from satellite tags at 4-h time steps. According to Harris et al. (2014), ridges are narrow elevations with features greater than 1000 m in relief.

Table F.

Differences in number of sightings (per 100 hours of effort) between both species during the three different phases of the ENSO cycle.

	Sightings per 100 hours of effort		
Species	El Niño	La Niño	Neutral phase
Blainville's beaked whale	1.41	1.00	0.56
Cuvier's beaked whale	2.69	1.48	1.67

The two species followed slightly different oceanographic seasonal patterns based on satellite tag locations. Cuvier's were found at their deepest depths in the summer (M_{SUMM}=2,794 m), while Blainville's were found most shallow at the same time (M_{SUMM}=1,161 m). Instead, Blainville's were found deepest in spring (M_{SPR}=1,894 m), which was the opposite for Cuvier's (M_{SPR}=2,135 m). While Blainville's used waters of a similar distance to shore in all seasons recorded, with a peak in the Fall, Cuvier's increased their distance from shore with each season from Winter to Fall (Figure I). Horizontal current magnitude peaked in the summer and fall for Cuvier's, while it remained somewhat consistent for Blainville's. Salinity also varied between seasons, being at its highest for Blainville's during spring (M_{SPR}=35.0 psu) and at lower values during summer and fall (M_{SUMM}=34.9 psu, M_{FALL}=34.9 psu), but peaking in summer and fall (M_{SUMM}=35.1psu, M_{FALL}=35.1 psu) for Cuvier's and with sharper decreases in spring and winter (M_{SPR}=34.8 psu, M_{WI}=34.9 psu). Sea surface temperature followed a similar pattern for both species throughout the seasons, with the highest values being seen in summer and the lowest in spring. Cuvier's were found on the eastern side of the island in all oceanographic seasons.

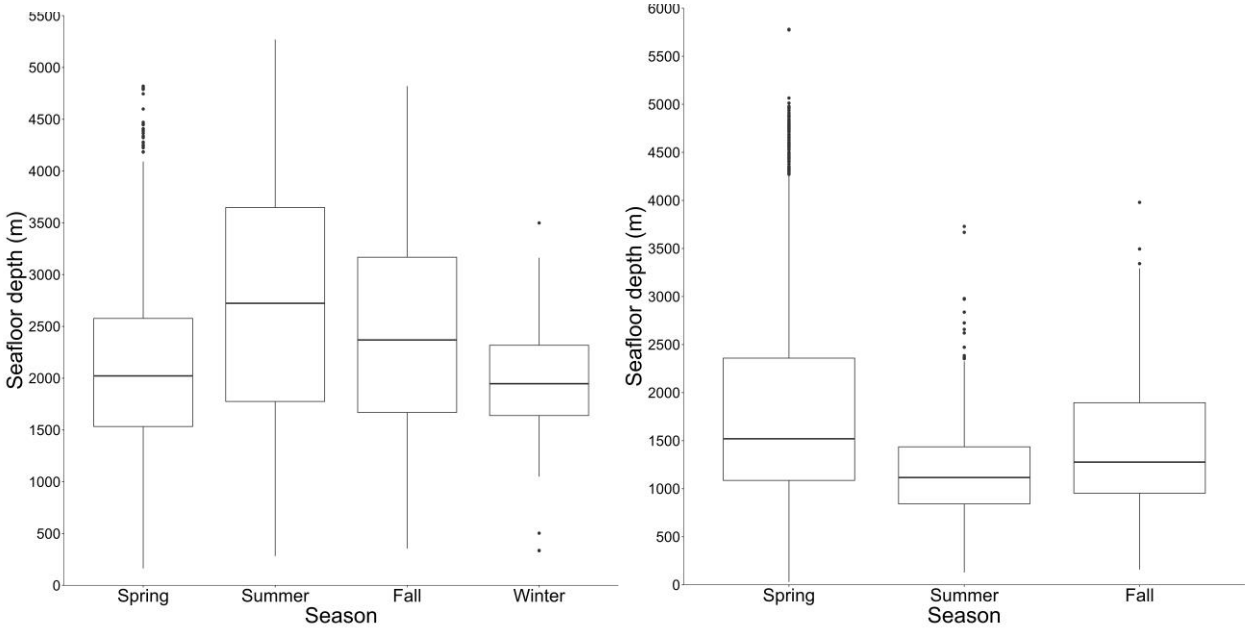

Figure I. Depth differences between season for Cuvier's beaked whale (left) and Blainville's beaked whale (right) using estimated locations from satellite tags at 4-h time steps.

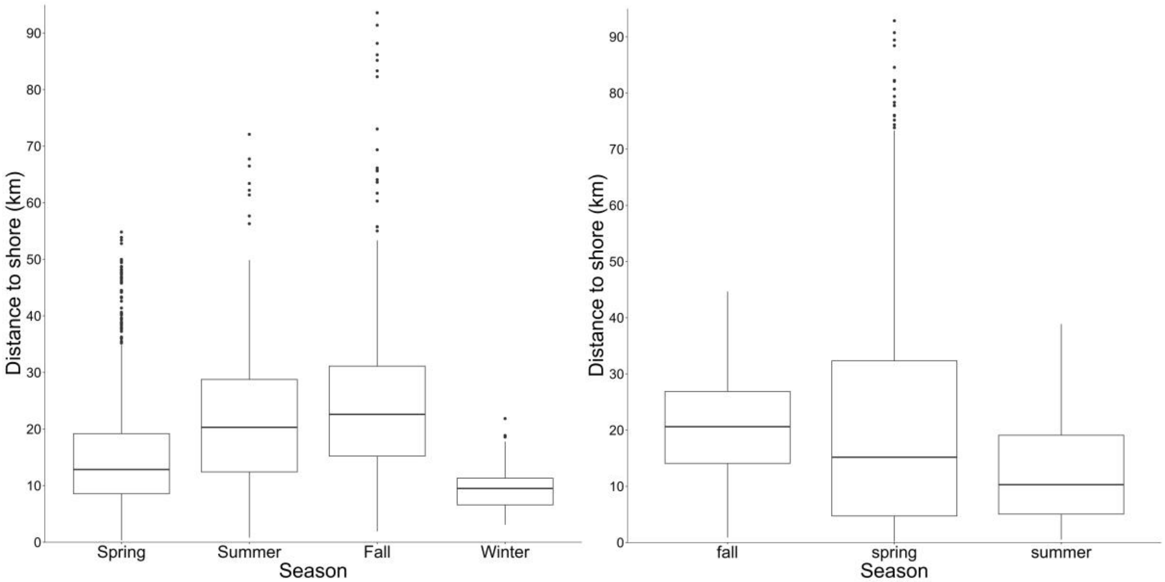

Figure J. Distance to shore differences between season for Cuvier's beaked whale (left) and Blainville's beaked whale (right) using estimated locations from satellite tags at 4-h time steps. The Y-axis is truncated for Blainville's beaked whales for comparison with Cuvier's beaked whales, despite several outliers above 100 km.

Cuvier's beaked whales were seen, on average, at 13% greater depths and 28% farther from shore between the full and new moon (during the 3rd quarter moon) than any other moon phase (depth mean: 2313 m, distance to shore mean: 20.3 km), but there was considerable overlap (Figure K). While there was no similar pattern for Blainville's beaked whale, they were found to be closer to shore during full and 3rd quarter moon phases on average, although there was considerable overlap (Figure K). However, one individual (MdTag014) used waters much farther from shore on occasion during those same periods (max 189.4 and 177.9 km, respectively). There was no notable pattern in depth for this species. When considering crescent and gibbous periods of the moon phase instead of quarter periods, differences were much smaller for both species.

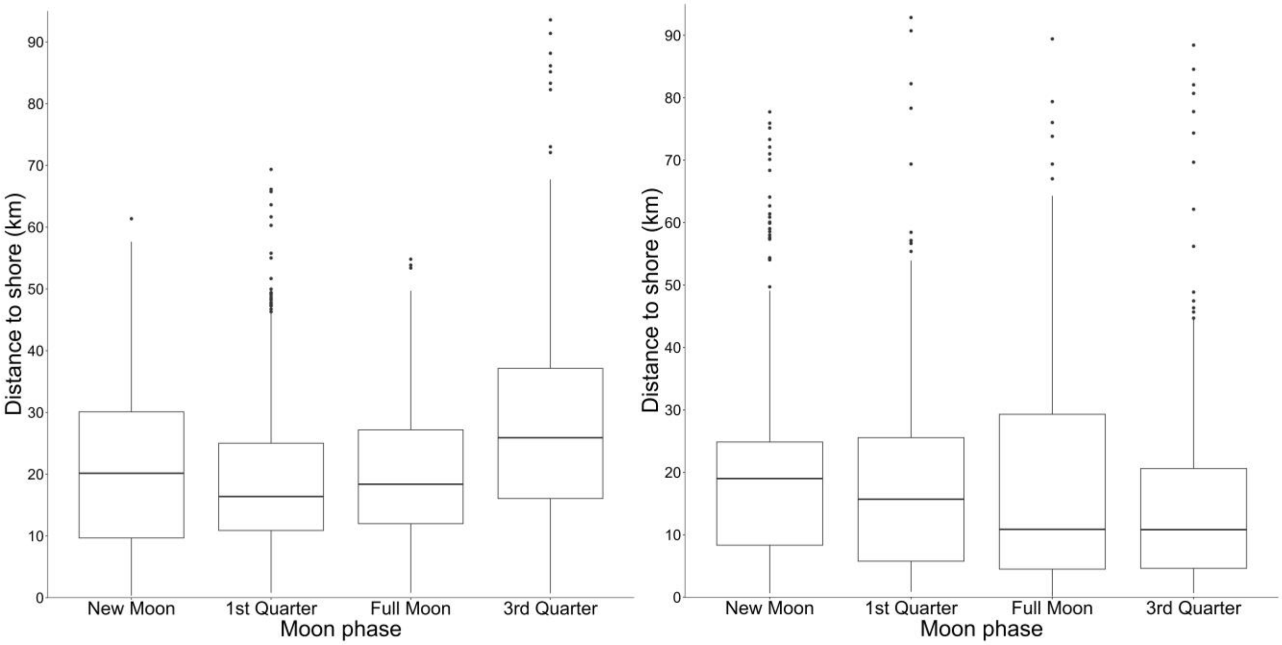

Figure K. Top: differences in distance to shore by moon phase for Cuvier's beaked whale (left) and Blainville's beaked whale (right). The Y-axis is truncated for Blainville's beaked whales for comparison with Cuvier's beaked whales, despite several outliers above 100 km.

Cuvier's were found at the higher horizontal current magnitude values during the 3rd quarter and full moon, but these values generally increased and decreased from new to 3rd quarter (means respectively: .27, .29, .31, .31). Meanwhile, Blainville's were found at similar $|\bar{V}|$ during the quarters and new moon (M = 0.33 for all three), but at the lowest by far during the full moon (M = 0.26). Results were similar when crescent/gibbous was considered instead of quarters. Both species also followed a similar pattern when monthly chlorophyll_a concentrations were compared to moon phase (Figure S7), with a peak during the new moon and a low during the full moon reported for Blainville's (M_{NEW} =0.071 mg/m^3, M_{FULL} = 0.065 mg/m^3) and Cuvier's (M_{NEW} =0.090 mg/m^3, M_{FULL} = 0.074 mg/m^3).

Neither species was found to have many noteworthy differences in horizontal spatial usage between day and night periods. Cuvier's were found using waters slightly closer to shore (M_{DAY}=21.2 km, M_{NIGHT}=22.5 km) and shallower (M_{DAY}=2,300 m, M_{NIGHT}=2,441 m) during the day, while Blainville's were found in waters of slightly higher sea surface height during the day (M_{DAY}=.64 m, M_{NIGHT}=.60 m), as well as similar differences in depth (M_{DAY}=1,544 m, M_{NIGHT}=1,631 m) and distance to shore (M_{DAY}=14.3 km, M_{NIGHT}=15.2 km) as Cuvier's. Both species used waters of similar temperatures, salinities, and monthly chlorophyll_a concentrations during both periods. Cuvier's used waters slightly closer to shore on average (M_{DUSK}=20.9 km) and of deeper depths (M_{DUSK}=2,489 m) at dusk.

Home range analysis

Home range calculation indicated that 95% autocorrected kernel density estimates for individual Cuvier's beaked whales ranged from 3,002 km^2 to 68,220 km^2 (median=5,560), while individual Blainville's home ranges ranged from 1,610 km^2 to 21,516 km^2 (median=3,525). A meta-analysis function (Figure S9) included in the *ctmm* package, indicated that Cuvier's beaked whale's home range sizes were, on average, 1.94 times larger than Blainville's beaked whale home range sizes (low: 0.13, high: 7.79), but the result was not statistically significant ($p = 0.13$). The conditional distribution of encounters (CDE), which estimates the 95% area where both species are most likely to encounter each other, provided an estimate of 5,728 km^2 (CI: 4,205-7,481 km^2; Figure F).

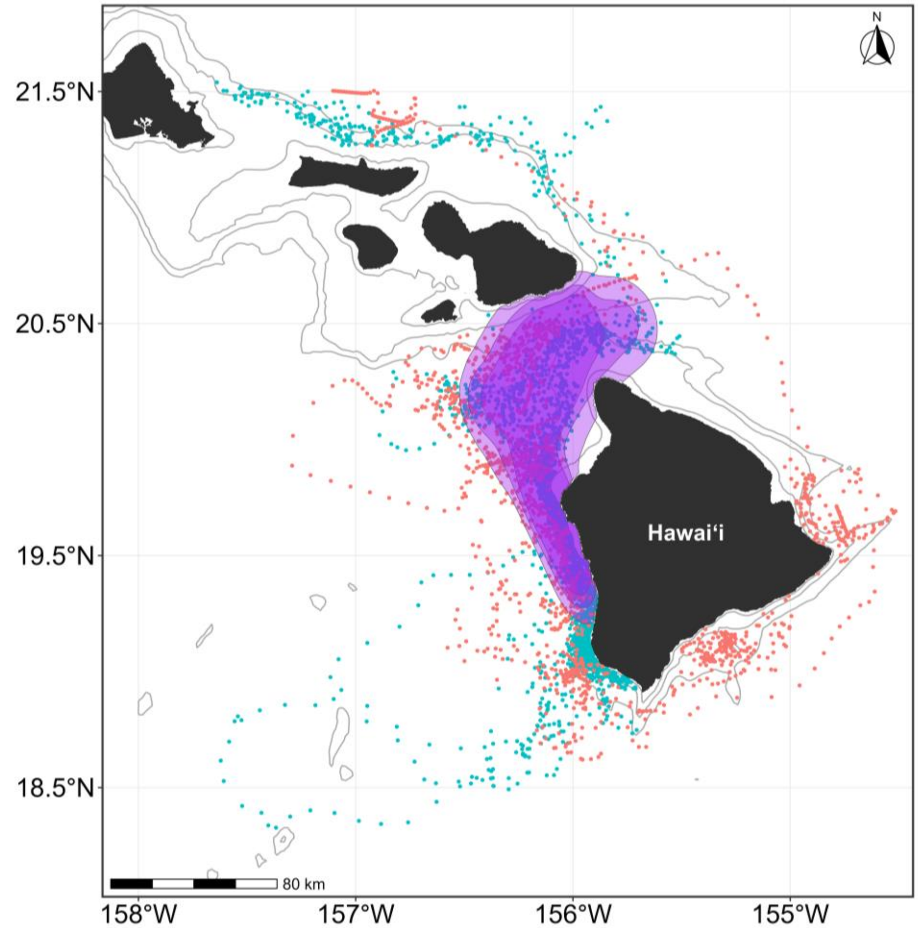

Figure L. Conditional distribution of encounters (CDE) for Blainville's (blue) and Cuvier's (red) beaked whales, excluding intraspecific encounters. Overlaid with tag locations fit to a 4-hour *crawl* model and re-routed around the 300-m isobath.

Area crossings, which describe the number of estimated home range crossings performed by the tagged individuals (i.e., number of times an individual traveled from one end of their home range to another), ranged from 3.95 - 14.65 days for Blainville's and 4.28 - 15.90 days for Cuvier's. Blainville's beaked whales were found to have an average home range crossing time of 3.38 days, ranging from 1.50 to 5.18 days. Cuvier's beaked whales had estimated home range crossing times of 3.51 days, ranging from 1.43 to 7.92 days. Speed was also estimated using the *ctmm* package, with Blainville's having a mean speed of 62.49 km/day (median = 48.83) and Cuvier's having a mean speed of 58.38 km/day (median = 53.60).

For Blainville's beaked whales, 95% population kernel density estimates were found to be 51,749 km^2 (CI: 33,221-74,318 km^2), while Cuvier's beaked whales had an estimate of 63,049 km^2 (CI: 35,889-97,735 km^2). Area crossings for both estimates were suitably high (24.19 and 15.79, respectively). Home range overlap between individuals of differing species, on a scale of 0 (no overlap) to 1 (identical), ranged from estimates of near 0 (MdTag012 and ZcTag006) to 0.96 (MdTag014 and ZcTag044). Population level overlap, calculated using population kernel density estimates (pKDEs), was very strong between the two species, with an estimated population-range overlap of 0.98 (low: 0.79, high: 1).

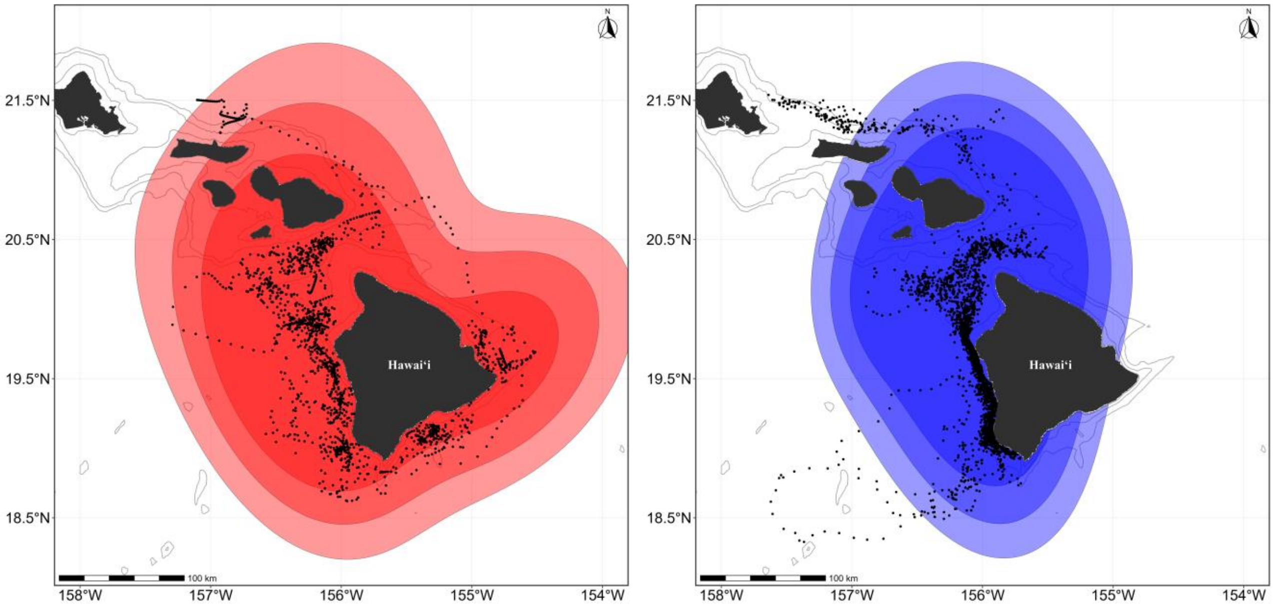

Figure M. Population kernel density estimates for Blainville's (blue) and Cuvier's (red) beaked whales. Overlaid with tag locations fit to 4-hour *crawl* and re-routed around the 300-m isobaths.

B. Seasonal analyses of Odontocete spatial distribution off the island of Hawaiʻi

After subsetting, the amount of effort between seasons was roughly comparable with slightly more effort in the fall (1,102 hours) than the spring (1,029 hours). While effort between seasons in terms of depth and distance to shore was similar in central tendency, they both exhibited some smaller scale differences (Figures N and O). Taking effort into account, sighting rates varied by season for most species (Figure P). Blainville's beaked whale, bottlenose dolphins, rough-toothed dolphins, short-finned pilot whales, sperm whales, and striped dolphins (*Stenella coeruleoalba)* were all sighted more frequently during the spring season. Cuvier's beaked whales, melon-headed whales, pygmy killer whales, and spinner dolphins had peaks in the fall. Sighting frequencies of both pantropical spotted dolphins and dwarf sperm whales were roughly comparable in both seasons.

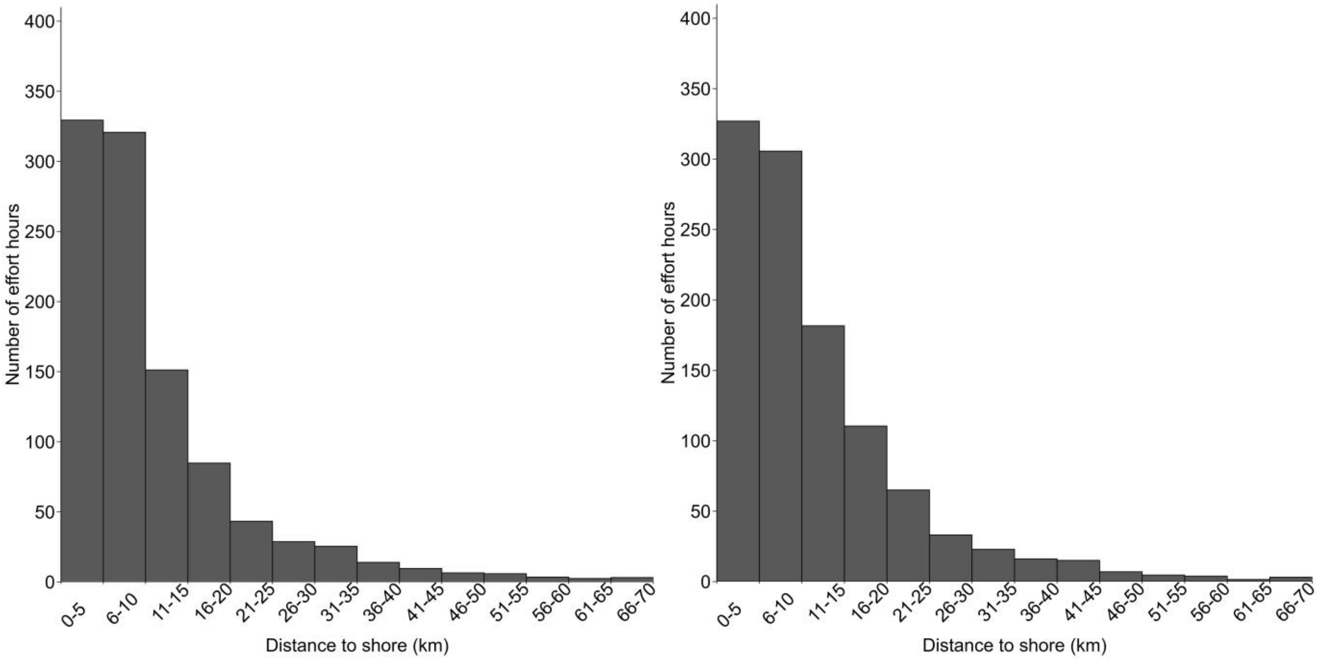

Figure N. Histograms of number of hours per 5-km distance to shore bins for spring effort (left) and fall effort (right) off Hawai‘i Island, truncated to only include values up until 70 km.

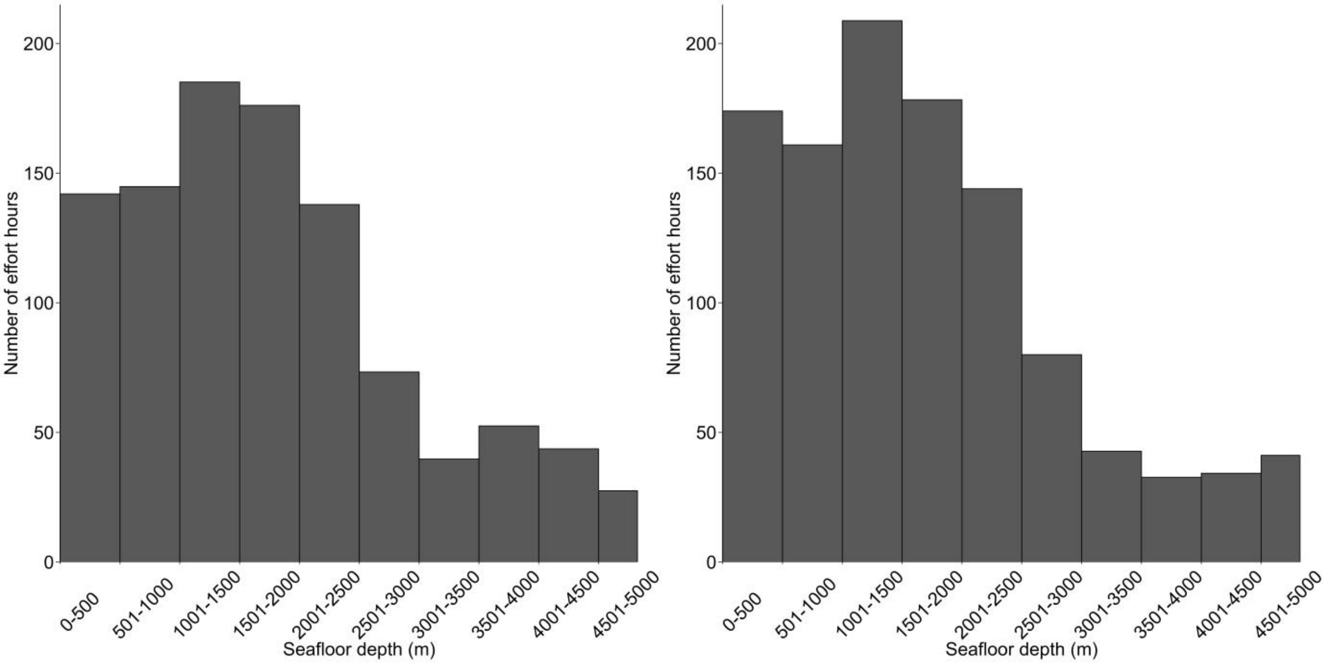

Figure O. Histograms of number of hours per 500 m depth bins for spring effort (left) and fall effort (right) off Hawai‘i Island.

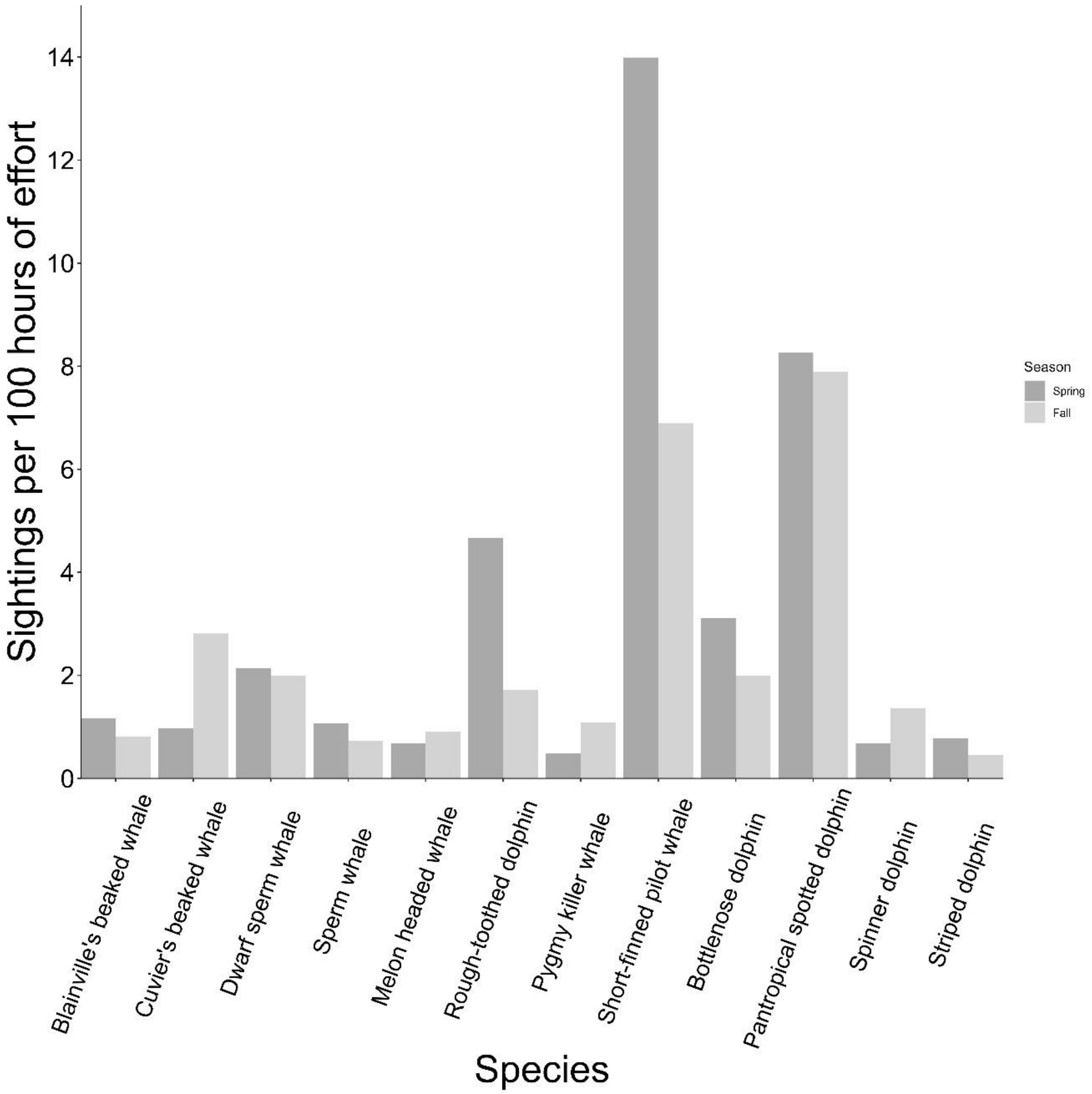

FIGURE P. Number of sightings per 100 hours of effort in each season by species.

Some species exhibited seasonal fluctuations in group size (FIGURE Q). Melon-headed whales, which generally had the largest group sizes overall, had group sizes four times larger in the fall than spring. Bottlenose dolphins, spinner dolphins, sperm whales, and Cuvier’s beaked whales, which have some of the smallest group sizes of any Hawaiian odontocete, were also encountered in noticeably larger groups in the fall than spring.

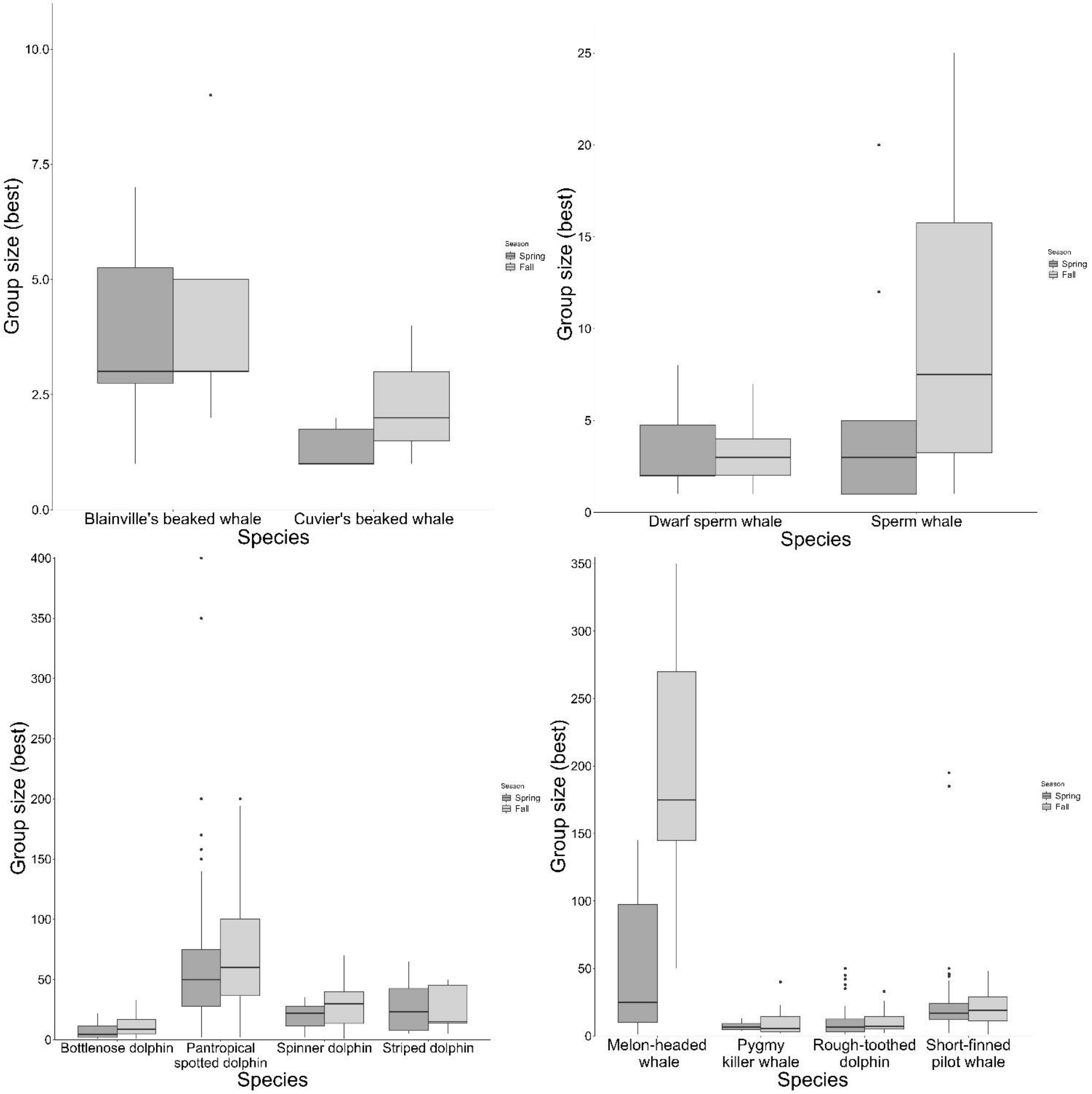

Figure Q. Box plots of group sizes in each season by species. Clockwise by group: Ziphiidae, Physeteroidea, Globicephalinae, and Delphininae.

Depths utilized also differed between seasons, depending on the species (Figure R). While most species used similar depths in both seasons, several were sighted in considerably deeper waters more often in the spring. These included pantropical spotted dolphins, pygmy killer whales, rough-toothed dolphins, and striped dolphins. Several other species featured slight shifts into deeper waters during the spring that corresponded with slightly deeper effort in spring. While only sperm whales were sighted using considerably deeper waters in the fall, Blainville’s beaked whales, Cuvier’s beaked whales, and spinner dolphins featured slightly deeper sightings in the fall than spring, unlike total effort.

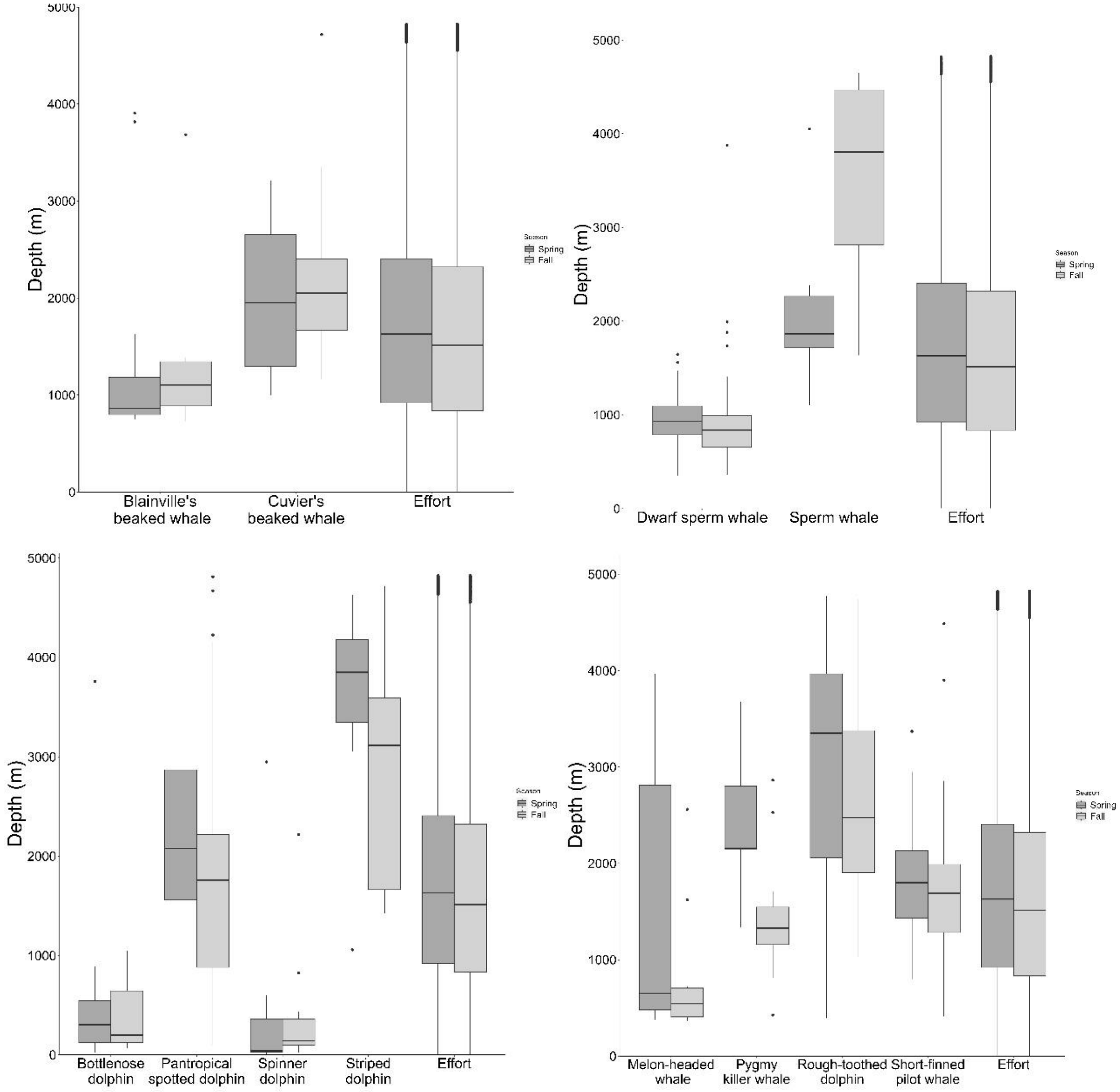

Figure R. Box plots of each species' depths in meters sighted in each season, alongside effort. Clockwise by group: Ziphiidae, Physeteroidea, Globicephalinae, and Delphininae.

In terms of distance to shore (Figure S), effort was largely the same between both periods. Species that similarly showed no obvious differences by season included bottlenose dolphins, rough-toothed dolphins, and short-finned pilot whales. Blainville's beaked whales and sperm whales were seen using waters considerably farther from shore in the fall. Animals that were seen in waters slightly farther from shore in the spring than the fall were Cuvier's beaked whales, pantropical spotted dolphins, striped dolphins and melon-headed whales, with only pygmy killer whales and melon-headed whales being seen notably farther from shore in the spring.

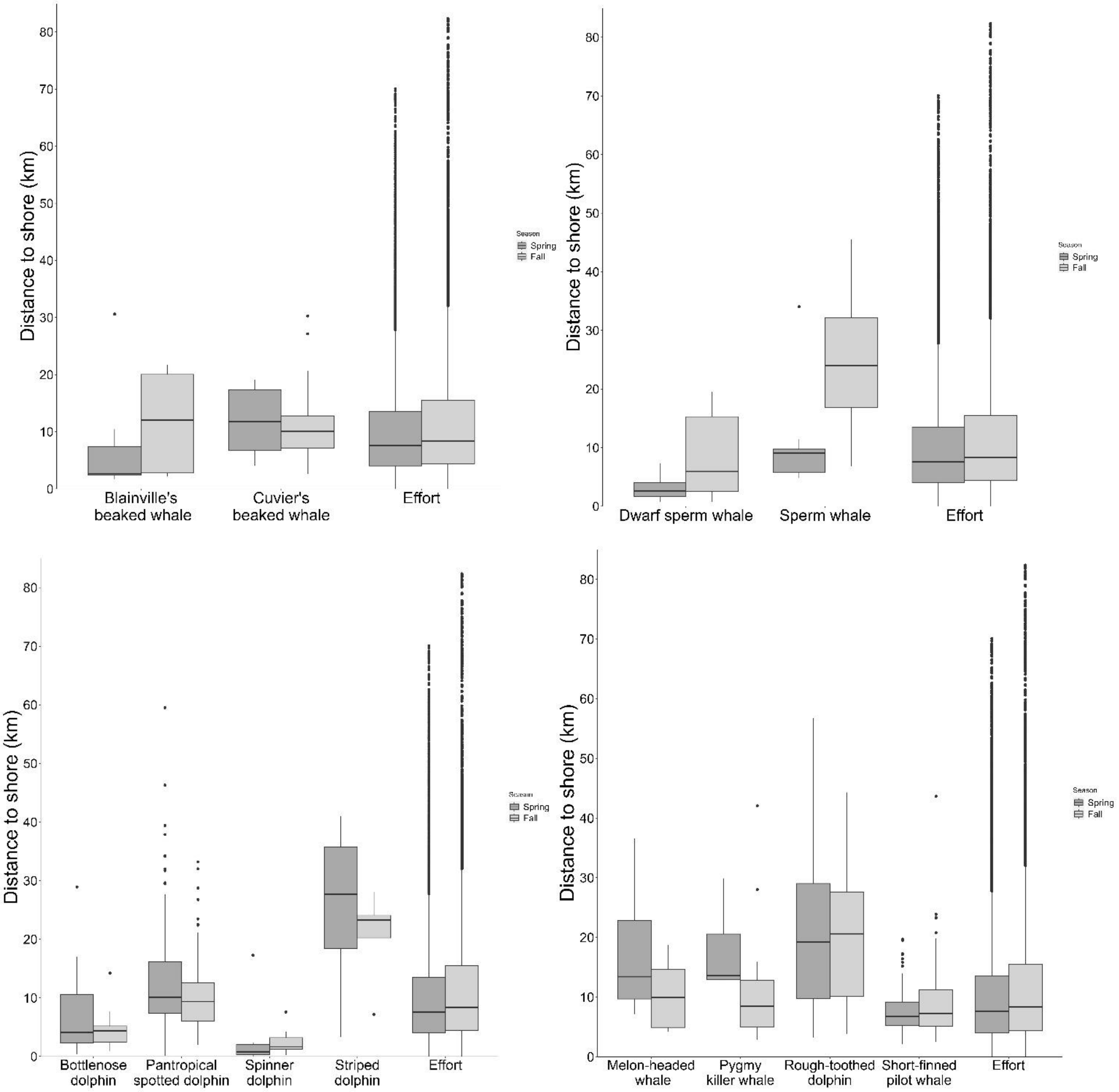

Figure S. Box plots of each species' distance to shore in kilometers sighted in each season, alongside effort. Clockwise by group: Ziphiidae, Physeteroidea, Globicephalinae, and Delphininae.

Habitat Modeling

Covariate results (Figures S12-S15)

While neither was significant by the 0.05 threshold, both slope and sea state were found to impact some presence. Spotted dolphins were found at lower sea states, which indicated that increasing sea state decreased the odds of encountering the species ($p = 0.056$) year-round. Lower slope also led to more encounters with spotted dolphins ($p = 0.086$) year-round. They were found at somewhat lower overall levels of slope ($M = 8.8$, range = 0.1-47.0) than effort was ($M = 11.3$, range = 0-77.2). Sea states below a Beaufort scale of three were also lower for points with spotted dolphin presence ($M = 1.70$, range = 0-3) than all effort ($M = 1.77$, range = 0-3). No other covariates significantly affected spotted dolphin presence in the final Presence/Absence model.

In the fall, pantropical spotted dolphin preferred waters of generally lower slopes and of slightly more northern latitudes. Slope indicated a significant negative association between it and presence ($p = 0.001$). Latitude was significant as well ($p = 0.05$), indicating that they could reliably be found at higher latitudes. The intercept was also significant here ($p = 0.03$). The spring season found them in waters of slightly lower chlorophyll-a concentrations, at more southern latitudes (potentially closer to ridges), and at higher slopes. However, none of these were found to be significant relationships for predicting presence. Sea-state, meanwhile, was statistically significant ($p < 0.001$), indicating that for every one-unit increase in sea state, the log-odds of spotted dolphins being present decreased by 0.824. There was no significant relationship between species presence and sea state in the fall ($p = 0.89$). Logdist_shore was almost significant ($p = 0.06$), with the species being found closer to shore during the fall.

In the final Season model, sea state was again found to be significant, with the species utilizing waters with higher values in the Fall ($p = 0.02$). There was no large difference in sea state throughout effort for either season ($M_{\text{Fall}} = 1.81$, $M_{\text{Spring}} = 1.96$), but values were slightly higher in the spring, unlike the final spotted dolphin results ($M_{\text{Fall}} = 1.93$, $M_{\text{Spring}} = 1.46$). In the model, sea states above a three were excluded, due to sea states were still higher in the fall for this species ($M_{\text{Fall}} = 1.73$, $M_{\text{Spring}} = 1.60$), while effort followed the opposite trend ($M_{\text{Fall}} = 1.71$, $M_{\text{Spring}} = 1.83$). This model also found latitude to be extremely statistically significant ($p = 0.001$), with spotted dolphins being found at more northern latitudes in the fall and farther south in the spring, whereas for effort there was no real difference. This is reflected in each season’s distance to ridges and terraces, which were (positively and negatively, respectively) highly correlated with latitude and not included in any models. While no effort approached ridges, pantropical spotted dolphins were much closer to ridges in the spring than fall ($M_{\text{Fall}} = 70.3$ km, $M_{\text{Spring}} = 48.3$ km). While effort followed the same pattern, the difference was not nearly as striking ($M_{\text{Fall}} = 55.4$ km, $M_{\text{Spring}} = 49.9$ km). Spotted dolphins were sighted farther from shore in the spring ($M_{\text{Fall}} = 10.5$ km, $M_{\text{Spring}} = 13.9$ km), which was significant ($p < 0.05$). While not tested, distance to shore was highly negatively correlated with distance to seamounts, which they were sighted closer to in the spring ($M_{\text{Fall}} = 65.6$ km, $M_{\text{Spring}} = 56.3$ km). The intercept was also found to be significant in this mode ($p = 0.005$).

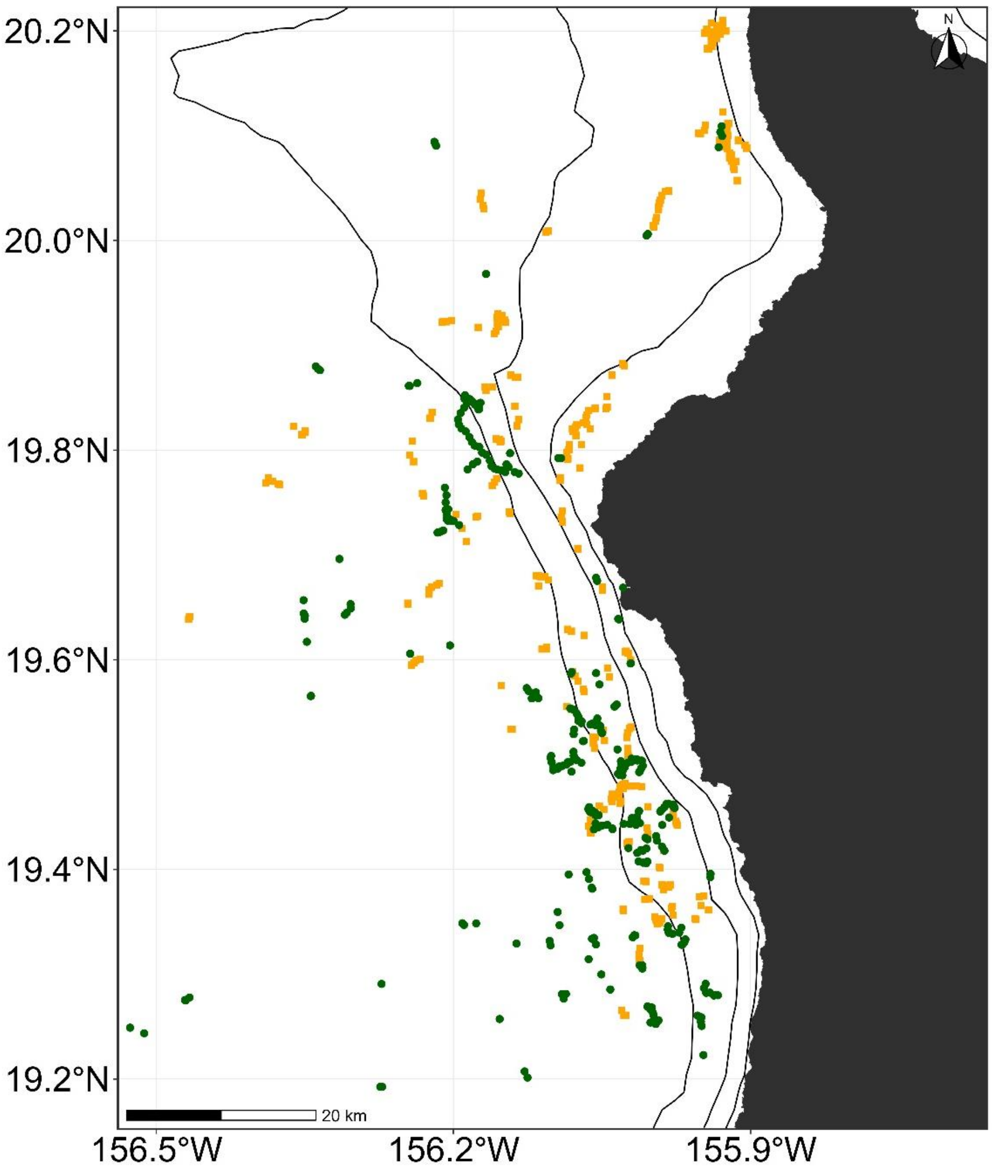

Figure T. Map of Pantropical spotted dolphin sightings, including the 5-minute effort points during which sightings occurred. Orange squares indicate fall sightings and green dots indicate sightings in the spring.

Model performance

All autocorrelation plots converged to 0, indicating that encounter was an appropriate blocking variable (Figure S11). The QIC values for the last three models, especially season, were relatively low, indicating a good fit of the models to the data. Presence/Absence was higher, which may have been the result of its larger sample size. The AUC values ranged from 0.65 to 0.80, with the Season model having the highest AUC, followed by the Spring model, Fall model, and lastly, the P/A model. The AUC value, which measures the ability of the model to distinguish between positive and negative cases, indicated that the Fall and Presence/Absence models are worst at distinguishing between presence and absence of sightings compared to the other models, although all other models correctly distinguished over 2/3rds of the sightings.

The Season model had the highest overall predictive accuracy of 75.8%, while the Spring model had the lowest predictive accuracy of 60.4%. However, it is worth noting that the Spring model has the highest precision value of 0.81, which suggests that the model is better at identifying true positives, or correctly identified sightings, but not very good at predicting the actual number of sightings, as indicated by a low recall value of 0.07. This signifies an overestimation in the number of sightings compared to effort. The Season and P/A models have the highest predictive accuracy values of 75.8% and 66.6%, respectively, but their recall values differ significantly. While their precision values were the same, the spring model had the highest overall despite its low recall, indicating that this model is good at identifying sightings but overestimates their frequency.

Table G.

Variable combinations for all model types.

Model	Variables	QIC	AUC	Predictive accuracy (%)	Precision/Recall
Presence/ Absence	Season + Year+ Slope+ Latitude+ Longitude + Sea_State + Moon_ill_fract	6067	0.65	66.6	.57/0.05
Fall	Slope + Latitude + logdist_shore + Sea_State + chla_monthly + hor_curr_mag	2849	0.67	61.9	.63/.04
Spring	Slope + Latitude + logdist_shore + Sea_State + chla_monthly + hor_curr_mag	2984	0.72	60.4	.81/.07
Season	Slope + Latitude + logdist_shore + Sea_State + hor_curr_mag	785	0.80	75.8	.57/.86

1. Discussion

A. A comparative spatial analysis of location data from satellite-tagged Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales off Hawai'i Island

Habitat and environmental variable usage

Both species were shown to use similar areas, and, as expected based on previous observations (Baird, 2019), only Cuvier's were documented off the windward side of the island. Both species exhibited forays into the more open ocean and excursions to the windward areas north of Maui and Moloka'i on occasion. However, most of the area used for both species occurred in the hotspot on the leeward, or western, side of Hawai'i Island. This is an area of noteworthy productivity, especially above 19.7°N. There, Blainville's utilize especially nearshore waters, typically staying close to the island shelf (Figure S2). These observations closely align with previous studies (Baird 2019, Abecassis et al. 2015), which used most of the same tags in their studies.

Cuvier's beaked whales were found to utilize waters with seafloor depths twice that of Blainville's. Most of their time was spent in areas between 1,000 and 3,500 m, while Blainville's spent the most time in waters with a seafloor depth between 500 and 2,500 meters. In terms of distance to shore, the above results differ slightly from Baird (2019), where, while not statistically significant, Cuvier's were found closer to shore than Blainville's (Grand median of 15.0 and 21.2 km, respectively). The differences in the results here may at least partly stem from the differences in time step associated with the *crawl* package: in that study, a 12-hour step was used, while here, a 4-hour step was used. It is worth noting that the differences between distance to shore here are small and do indicate Blainville's as traveling farther from shore on occasion. MdTag014, which traveled the farthest offshore of any individual in this study (Max= 189.4 km), headed southwest from Hawai‘i Island in two large loops, interacting with ridges, seamounts, and escarpments before heading north to an area of terrace and slopes just south of Maui. A review of geomorphic variables by Harris (2012) concluded that ridges are notable areas for their geothermal water venting activity, which house numerous potential prey species endemic to them, while escarpments and terraces have been known to support thriving coral communities.

Cuvier’s beaked whale usage of waters closer to canyons appears to be due to their occurrence on the island's windward side, specifically in the south and southwest where canyons form (see Figure S1), as well as their usage of the waters near canyons off Hawai‘i’s southernmost tip, which Blainville’s appear to avoid (Figure S2). Likewise, this difference in usage can also potentially explain their median farther distance from the island shelf (which is associated with the shore and the 200m isobaths). Canyons are excellent keystone areas of biomass productivity, especially for more scavenging mobile or bottom fish, invertebrates, and crustaceans like lutjanid snappers and synaphobranchid eels (Vetter et al., 2009). While not statistically significant, on average Blainville’s were found slightly farther from terraces. However, a single terrace northwest of the tip of Hawai‘i Island was a hotspot for their occurrence and was not used by Cuvier’s nearly as often (Figures S1, S2). Instead, Cuvier’s were found to frequently use the sloped, likely hilly abyssal area just north of that terrace in the ‘Alenuihāhā channel. It is possible that this boundary is due to either habitat or diet preferences, with Cuvier’s foraging on more deep-dwelling species than Blainville’s, but further research on diet, habitat usage and behavior of both species will be necessary to understand these differences. Marine terraces are typically areas of raised seafloor, and throughout the area around the MHI, they appear to form at the edges of sloped areas just off the coast of the islands (Figures S1, S2). Terraces often form as raised reef systems (Faichney, 2010), which indicates that Blainville’s could potentially use this area to prey on reef or terrace-attracted deepwater prey that Cuvier’s does not. This may support MdTag014’s usage of far offshore areas as well if it had been using the similarly presumed coral-clad escarpments and seamounts to the southwest of the study area. Although they do feature some large crustacean species, prey aggregations are typically rarer in abyssal areas than other seafloor features (Harris, 2012), although further information is needed about how prey in higher water columns aggregate around these features to determine what could be drawing beaked whales there. These could also be areas of socialization or breeding for the populations, but more research is needed to look at trends in these behaviors. Both species generally avoided the large expanse of abyssal plain surrounding the islands, minus occasional consistent travel.

There were no noticeably large differences between the two species in terms of environmental variables, such as temperature, sea surface height, and chlorophyll-a concentrations, which was similar to the findings from Ferguson et al. (2006) throughout the Pacific. However, sea surface height and horizontal current magnitude were found to be significantly different than each other through statistical pairwise comparison, despite seemingly small differences in spread and central tendency. While chlorophyll-a concentrations and salinity differences between species were statistically significant, both values violated the assumption of homogenous variances. Previously, Blainville’s beaked whales had been tied to waters of lower salinities off of Hawai‘i Island (Ziegenhorn, 2022). While this study did not conclusively find any large differences in salinity between these two species, Cuvier’s used waters of a range of slightly higher salinities (range= 34.4-35.6 psu) than Blainville’s (range= 34.3-35.4 psu). However, without many pairwise comparisons between species, it is difficult to compare salinity values in a meaningful way.

Temporal spatial usage

ENSO phase variations are arguably some of the most important large-scale cycles to affect the Hawaiian islands, as well as much of the globe. In general, Cuvier's were found to be more affected by variability in ONI values, although more tag data will be needed during all periods of the cycle to describe further differences, especially when comparing small-scale habitat usage to large climate variabilities. Cuvier's only used the windward side of the island during La Niña periods, when water temperatures around the islands were colder. They were also found to use waters closer to shore, at more shallow depths, and of lower horizontal current magnitudes and salinities during that part of the cycle, while these variables did not appear to affect Blainville's in the same way. As expected, sea surface temperatures were much higher during the El Niño period for both species, but Cuvier's were found in waters of higher SST during El Niño and lower waters of SST during La Niña than Blainville's. Interestingly, during periods of little positive or negative ONI values (2013), Blainville's were found at the lowest temperatures overall, likely due to one tag being deployed towards the end of the year.

While there was little temporal overlap between tags of different species, one Blainville's (MdTag012) was tagged during the same La Niña period that featured Cuvier's ZcTag018 on the windward side of Hawaiʻi at the end of 2010. During this same period, MdTag012 traveled north to the windward side of Maui. The only other tagged whale to utilize the waters north of Maui (and farther northwest near Molokaʻi), was MdTag013 which was deployed towards the tail end of the same La Niña period in 2012. It began heading north just as ONI values started approaching zero and entered a fall/winter in a neutral phase. While no Blainville's tags were tracked utilizing this same area during El Niño, only three tags were deployed during those years, and all were of shorter durations (<23 days). Unlike Blainville's, tagged Cuvier's used more the northern waters on the windward side of Maui Nui during both periods.

With tagged Cuvier's only using waters off the windward side of Hawaiʻi during La Niña years, and tagged Blainville's only heading to waters north of Maui during the same La Niña periods, it is essential to understand the effects of these cycles on the Hawaiian waters. The leeward side of the island, where both species spend most of their time, lies in a "rain shadow" due to the mountain slopes blocking moisture and forming clouds on the windward slopes. However, during the colder LN periods, the islands are deluged with heavier rainfall during the wet season. EN periods, meanwhile, feature warmer waters and larger potential prey spawning which lead to more catch per unit effort (CPUE) by fisheries on certain species, like bigeye tuna (Chan, 2023). CPUE was typically lower for these species during LN periods. While the preferred prey differences between the two species in this region are currently unknown, beaked whales around the world generally prey on cephalopods and open ocean fishes. Cuvier's in the North Pacific have specifically been found to forage on mostly cephalopods, with smaller amounts of fishes and crustaceans also found to make up part of their diet (West et al., 2017). In the northwestern Pacific, neon flying squid (*Ommastrephes bartramii*), an oceanic squid in the family *Omnastrephidae*, was noted to decrease in recruitment during La Niña periods (Chen et al., 2007). While there have been no documentation of either beaked whale species preying on neon flying squid, other species in *Omnastrephidae* have been documented to make up a part of Cuvier's beaked whale (West et al., 2017). With many species of fishes at potential lower aggregation sizes or farther from shore during La Niña, longer events may force some individuals of both species to travel to other areas, like the windward side of the islands for Cuvier's and Maui Nui for Blainville's, in search of prey or in relation to other oceanographic or environmental variables.

These findings are further supported by the sightings data. Cuvier's beaked whales were sighted over 1.5 times more frequently during El Niño (EN) periods than during La Niña (LN) and neutral periods. Although no tag locations were recorded during the neutral phase, sighting rates from those periods were largely comparable to sighting rates during the LN phase. In contrast, Blainville's beaked whales were sighted at different rates between the three periods, with the highest number of sightings occurring during EN phases and the lowest during the neutral phase. Further analysis of these factors, such as incorporating a lag between periods to investigate potential delayed effects, will be necessary for a comprehensive comparison of these periods. Nonetheless, the higher frequency of sightings and the preference for the leeward side of Hawaiʻi Island by both species suggest that EN years may provide a more nutrient-rich habitat there.

The large differences in distance to shore and depth during the 3rd quarter moon phase in between full and new moon, which were still slightly present when split into gibbous and crescent phases (when they were farther from shore), indicates a potential relationship between Cuvier's beaked whale movements and shifting moon phase. Previously, Cuvier's beaked whales near southern California have been documented to avoid near-surface depths in brighter moonlight (Barlow et al., 2020) as a potential means of predator avoidance by species like killer whales and sharks (McSweeney et al., 2007; Baird, 2016). Manzano-Roth (2021) found unidentified beaked whales near Kauaʻi foraging more during lower lunar illumination (around the new moon phase). Barlow et al. (2020) also showcased how Cuvier's in the eastern Pacific Ocean forage at more shallow depths when in waters with deeper seafloor, while foraging closer to the bottom in more shallow waters. While our study did not take vertical movements into account, Cuvier's avoidance of areas of deeper waters during the 1st quarter, as illumination is increasing, and the full moon, when the moon is at its brightest, indicates that they could be using these deeper waters to forage at more shallow depths more often during periods of lower illumination, perhaps due to more competition from other species at nearshore depths. In terms of Blainville's, Baird (2019) and Henderson et al. (2016) found some individuals to forage at shallower depths during the new moon. If Blainville's follow a similar pattern to Cuvier's, foraging at more shallow depths in deeper waters, then that trend may be represented here by Blainville's farther distance to shore during the new moon, although there were no large differences in depth among moon phases for this species.

Abecassis et al. (2015) noted some association between Blainville's beaked whales and micronekton. Micronekton density near Cross Seamount, which lies southwest of the study area, has previously been associated with the new moon, during which these organisms have been seen at greater numbers and more shallow depths (Drazen et al., 2011). Similarly, the monthly chlorophyll-a concentrations for both species here were highest during the new moon and lowest during the full moon (Figure S7). Trophic lag between chlorophyll-a production, micronekton presence, and predators should be on a short enough scale that they are not affected by variation or shifts. The differences in spatial usage between lunar phases may at least partially be explained by moon-affiliated primary production or prey preferences. Based on stomach content analyses of Blainville's beaked whale, as well as depth foraging habitats, Abecassis et al. (2015) showcased how they likely forage on micronekton-associated squids and fishes just below high densities of micronekton. Given the likelihood that Cuvier's have a similar general diet, and with them being farther from shore and at deeper depths during the 3rd quarter into the new moon, they may be taking advantage of a window when more visual predators, like tuna, could be less successful.

While there weren't large differences between time-of-day for either species, both species were found about a kilometer closer to shore and using waters of 1000 meters more shallow during daylight hours. Diel variation for both species has been noted before in terms of dive depth, with Barlow et al. (2020) finding Cuvier's to spend more than double the amount of time at near-surface depths during nighttime. Baird et al. (2008b) also showcased this, with both Cuvier's and Blainville's beaked whales undertaking intermediate dives of 100-600 m and 30-300 m that are completely absent at night, likely to again minimize higher predation risk during the day. In terms of horizontal spatial usage, however, it appears that both species generally stick to waters of shallower depths and closer to shore during the day. When examining pseudoreplicates, of which Blainville's had three (MdTag005, MdTag006, MdTag008) that remained associated with each other over much of their tag duration, individuals were seen at slightly higher differences in latitude and longitude during the day than at night. While diel differences in grouping behavior have not been documented for this species, this could imply that groups may remain more closely associated during the night than daytime, which could potentially explain some of the differences in habitat usage. While the typical prey of both species, deepwater squid and fishes, have not been known to undertake any sort of diel migration, Abecassis et al. (2015) demonstrated how Blainville's beaked whales may follow micronekton inshore during the nighttime. These results were not necessarily reflected here, although analyses on an individual basis may be helpful in determining area usage.

Home range analysis

The *ctmm* package has proven to be an important aspect of terrestrial home range estimation and examining overlap. However, the method may be overly restrictive for these marine species with hard boundaries (i.e., land or shallow water), short tag durations, habitat usage that may change throughout the year, lower *n*, and poor location error. The autocorrelated destiny estimation method makes several important assumptions, such as tagged animals being assumed to be representative of the rest of their population. Secondly, many of the variograms made with the *ctmm* package do not indicate range residency (Figure S8) and have been modified using data thinning. Data thinning, as performed above, is not an ideal method for resource selection functions, as it involves discarding potentially important information about environmental usage and can lead to biased coefficient estimates and narrow confidence intervals (Alston et al., 2022). On top of this, autocorrelated kernel densities lead to equal inflation of kernel density estimates in all areas, providing an overprediction of usage in areas where no animals were seen in. This is evidenced in the above population kernel density estimates, where the resident populations of Blainville's and Cuvier's beaked whales are presumed to use waters they've never been known to utilize. Land barriers, such as the islands themselves, can be removed using the shapefile function in the package, but only for the final autocorrelated estimate and not for the initial gaussian home range estimate. The methods outlined here likely give an inflated image of how these two species use the area that is not at the moment beneficial in predicting usage.

Two individuals had aKDE sizes much larger than any other individual within their specific species (ZcTag018 and MdTag014). Both of these animals featured large movements to the west and east, respectively, during and towards the end of the 2010-2012 La Niña event. While these individuals were still considered range resident through variogram analysis, including these areas in the population kernel density estimate may be problematic, as their frequency of use by either species has yet to be determined. If beaked whales affected by ENSO events, then these areas may not be an important portion of their home range. Further studies and tagging of both species during and outside of La Niña periods should shed more light on their usage of these areas.

While the CDE captured the bulk of the area where Cuvier's and Blainville's interact, it underestimated many locations due to the low sample size of tags included in the final model. Many individuals not included in population kernel density estimates (either because of pseudoreplication or no range residency) had spatial overlap outside of the CDE (Figure L). It also likely overestimated the area to the northwest of the island, where, as mentioned above, there appears to be some segregation between species along terrace and abyssal/slope features.

Of course**,** field studies with additional tag deployments will also be essential to developing further understanding of how these species partition the environment between them, as well as methods to learn more about each species' diet (e.g., stomach content or fecal analysis of stranded animals, genetic analyses of fecal samples collected at the surface, or analysis of compound-specific fatty acids of biopsy samples). To properly calculate home range and showcase habitat usage, future studies should incorporate other methods of kernel density or home range estimates. On top of this, they should consider more environmental and topographic features, such as water density, as well as other cycles of climatic changes. As discussed in Ferguson et al. (2006), slopes should also be calculated on a larger scale. For some tag points, the individual may be at the edge of a steep dropoff that would indicate high slope despite the animal only momentarily passing over it. On a larger scale, this same location's slope would be greatly changed if analyses were conducted to take this into account. Scale in general can be quite problematic in relation to spatial analyses and predictive models, with processes occurring at different levels. So while factors like ENSO cycles may be incredibly important, it is just as necessary to understand shorter-term cycles, such as seasons, lunar phase, time of day, etc. A hierarchical scale framework, as described in Redfern et al. (2006), could be greatly beneficial to analyses of these species.

B. Seasonal analyses of Odontocete spatial distribution off the island of Hawaiʻi

Bradford et al. (2022) noted a clear increase in the abundance of sperm whales off of Hawaiʻi Island when comparing summer/fall to winter. In that study, winter line-transect surveys occurred from January through March, with the summer/fall surveys occurring through early fall. Here, fall was represented as October through December, a period which was partially included but combined with summer in studies like Bradford et al. (2017). While sighting rate (FIGURE P) did not indicate large differences in sperm whale sightings between seasons, the fall season found them in considerably larger group sizes, at much deeper depths, and noticeably farther from shore. These results did not coincide with slight shifts in effort depths and distance to shore. It appears likely that this species could be affected by the seasons in Hawaiʻi, and further research will be essential in understanding the mechanisms behind this shift. Barlow et al. (2022) hypothesized that the species' difference in abundance between seasons could be correlated with seasonal migration patterns, demonstrated by Whitehead (2003) for some heavily male populations of sperm whales. Our results suggest sperm whales in Hawaiian waters, which appear to roam broadly offshore (Rone et al., 2015), are being significantly impacted by seasonal variation, using much different areas in larger aggregations during the late fall than the spring. Dwarf sperm whales, of which there are resident populations (Baird et al., 2021), had considerably less variation between the two seasons, although group sizes were slightly bigger and depths deeper in the fall.

Pantropical spotted dolphins were found in slightly larger group sizes in the fall than in the spring, but the two seasons were similar overall. This species' group size has previously been linked to proximity to yellowfin tuna (*Thunnus albacares)* through documentation by fishing vessels (Baird & Webster, 2020), although this could be an artifact of the ease of sighting larger group sizes. The fishing industry reaches its seasonal peak in July through August (Itano, 2000), which is not represented here, so one may expect to find larger group sizes in the summer months between these two seasons, which is also peak calving season (Baird, 2016). Calving season, which extends from April to December but peaks in July through October for the species, could explain the slightly larger group sizes in the fall.

Most species that featured notably larger group sizes in one season than the other were at their largest in the fall, with striped dolphins being the only exception. This could indicate that larger aggregations are not generally tied to food abundance, as many fishes enter their mating/reproductive periods during the spring. This could be further exemplified by higher levels of chlorophyll_a concentrations in the fall than spring (Figure S16). Social factors could also impact odontocete spatial usage with many species having been found following a seasonal reproductive pattern as implied by Baird et al. (2009). Previously, bottlenose dolphin calving has been noted to occur in lower temperatures during winter (Fearnback et al., 2011), although Baird (2016) demonstrated how calving occurred year-round for the species in the MHI. Similarly, spinner dolphins and dwarf sperm whales (*n*=4*)* were also noted to have been sighted with newborn calves in different seasons, so none of the shifts in sighting frequency or group size for these species are a likely result of seasonal reproduction. Despite this, dwarf sperm whales have been sighted in smaller group sizes and at more shallow depths when neonates were present, so the slight differences in these values, as outlined above, could indicate that calving is higher during the spring than the fall. Not enough is known about the life history of beaked whales to draw any conclusions about seasonal differences in reproduction.

While melon-headed whales were not sighted often overall, they congregated in the largest groups by far, with group sizes being notably larger in the fall than the spring despite similar sighting frequencies between seasons. Baird (2016) noted that their calving period peaked from March to June, indicating that group sizes are potentially smaller during reproductive, or at least major calving, periods. Unlike melon-headed whales, pygmy killer whale offspring have only been seen in August and October, which could at least partially be the cause of their increase in sightings, closer distance to shore, and use of waters much more shallow in the fall. Again, both of these species had low sighting rates, so future field effort will be helpful to determine more about seasonal variations in these factors.

Rough-toothed dolphins and short-finned pilot whales, which did not have large differences in group size between seasons, were sighted at much higher rates in the spring than fall. Both species have summer calving season peaks (Baird, 2016). Interestingly, while rough-toothed dolphins did not have a large difference in distance to shore between seasons, they were sighted in waters nearly 1,000 m deeper in the spring than the fall. Further studies should find a way to incorporate at least summer effort for more extensive coverage.

GEEs

Ultimately, the full statistical seasonal analysis included only one species (pantropical spotted dolphin). Despite being one of the most frequently encountered species off Hawaiʻi island, pantropical spotted dolphins remain one of the lesser-studied species in the area. The presence/absence model indicated that, in general, spotted dolphin presence is associated with lower slope levels and sea state. Other populations of spotted dolphins, such as those found in Costa Rica, have also been linked to less steep marine slopes (Acevedo & Burkhart, 1998). Since all sightings were during the day, when pantropical spotted dolphins have been known to feed (Silva et al., 2016), these associations could be related to feeding. The species generally consume smaller fish and crustaceans. The Hawai'i population of spotted dolphins has a notable relationship with yellowfin tuna fisheries, with an association rate of 29.7% between the fishery and spotted dolphins specifically (Baird & Webster, 2020). Yellowfin tuna, with whom they have historically been associated with in large aggregations (Perrin & Hohn, 1981), have a spawning season in Hawai'i that takes place primarily from April through September/October (Itano, 2000). This spawning period is only represented by the end of this spring season and the beginning of this fall. With more equal amounts of effort in all months, it will be beneficial for future analyses to consider these spotted dolphin presence in relation to these summertime months. While yellowfin tuna has been linked to seamounts, there is no evidence from satellite tags ($n = 1$) that this resident population of spotted dolphins has traveled far enough to any of the offshore seamounts. However, seamounts were loosely correlated with distance from shore (cc = 0.65), so it’s possible that some presence could be explained by proximity to yellowfin tuna aggregations at offshore seamounts.

It is likely that specific slope usage is an aspect of habitat partitioning. Many other populations of different species, including bottlenose dolphins (who have lower slope levels overall due to them inhabiting nearshore areas before the shelf break), use different levels of slope near Hawaiʻi Island, with pantropical spotted dolphins having previously been documented partitioning the environment by using different slopes than bottlenose dolphins in Costa Rica (Acevedo & Burkhart, 1998). Pantropical spotted dolphins were found in areas of lower slope than effort, such as areas where there is more gradual change in depth. Despite this, it may be beneficial to include slope on a larger scale, as the 50x50 model included here is likely too small to indicate realistic usage of these waters.

Of all covariates, slopes utilized (Figure S10) was best found to describe spotted dolphin presence in the fall. Latitude and the intercept followed slightly behind, indicating that the species used lower latitudes than effort during this period. The intercept being significant in both the Fall and Season Models indicate that there is a statistically significant difference between sightings and effort in the Fall, as well as sightings between seasons.

While there were no major differences in effort sea state between the seasons overall, pantropical spotted dolphins were sighted using areas of significantly lower sea state in the spring, as indicated by the last three models. Sea state, which is a categorical variable (Beaufort scale range 0-3 here) estimated using visual cues, is typically a combination of wind, currents, depth, and the area. It was not found to be correlated with zonal or meridional current velocities, as well as the horizontal current magnitude, which was never found to be significant in predicting spotted dolphin habitat usage. Sea state by effort was generally higher in the spring (M_{Fall}=1.71, M_{Spring}=1.83), which aligns with the higher values of SSH and reports by Flament et al. (1996).

They also were found at generally higher slopes in the spring than fall, although this was not significant in the season model. This exclusion from the season model could be an artifact of model performance and which other covariates were included/excluded, but it is likely that slope usage does not significantly change throughout the year. Instead, the species prefers waters of lower slope no matter the time of year.

Latitude also differed between seasons, with the species being found using more northern waters, closer to terraces, during the fall. Terraces, which are subsided erosional landforms (Moore et al., 2010) or submerged reefs growing horizontally at sea level (Faichney, 2010), are some of the lesser studied ocean floor features (Harris, 2012). Given that terraces are often areas of high coral cover, and that most Hawaiian reef fishes reach a spawning maximum during the spring (Lobel, 1989), it would be intuitive to think that the dolphins use this area to feed on higher concentrations of fishes in the spring. However, their closer proximity to these areas during the fall, as well as their more near distance to shore in the spring, indicates that the species may not be affected by seasonal reproductive patterns in those species of fish. In the spring, sightings approached ridges, which are part of the planet’s volcanic system and support exotic and unique benthic communities of invertebrates due to the venting of hot seawater (Harris, 2012). It is unknown if spotted dolphins feed on these organisms, but if their target prey aggregations congregate near these areas during the fall and winter, then the dolphins may be attracted to those locales. Nevertheless, there could be a multitude of other reasons for the seasonal differences in areas utilized, many of which are aspects of behavior and sociality. Further research on spotted dolphin aggregations and breeding/calving periods will be greatly beneficial in documenting these changes.

While most sightings here are likely from the resident population of spotted dolphins off of Hawaiʻi, it cannot be discounted that other individuals from other populations may have traveled to the area. There are at least two other populations of spotted dolphins native to the MHI and infrequent visits by open-ocean/pelagic populations. At least one individual from the Lānaʻi population has been demonstrated to move into waters used by the Hawaiʻi Island stock (Baird & Webster, 2019). It is unknown at this time if there are any large differences in habitat use between populations or any predictable seasonal "migrations" between islands. Still, it is worth noting that some individuals included here may be from other populations, potentially variables close to being statistically significant here.

Model Performance

Modeling spotted dolphins in both seasons greatly reduced QIC and improved AUC. However, it reduced predictive accuracy, which measures the accuracy of the predicted values compared to the observed values. In terms of predictive accuracy, the Season model was best able to predict seasonality of spotted dolphins. It also had the highest QIC and AUC, which indicates that the model is stronger and best at differentiating differences. However, it was the only model that did not account for effort, which is an incredibly essential aspect in analyzing habitat usage. For the most meaningful analysis, the results indicated by this model need to be interpreted alongside the results of the other three models.

We suggest that the low recall in the first three models is likely due to an overestimation of sightings by the predictive model. This is clearly shown in the fourth model, where presence/absence is not applicable. Effort by CRC featured numerous interactions with nearly two dozen species that were not taken into account for this model, which does not take into account the possibility of sightings of other species. The lower predictive accuracy of the earlier models further exemplifies this. Despite this, model performance overall led to more accuracy and goodness of fit than not, indicating that these variables likely have some effect on this population of resident spotted dolphins between the seasons.

2. Conclusion

The implications of both projects on odontocete spatial usage provide an essential outlook into the mechanisms that drive habitat selection. Marine mammals all around the world have been greatly impacted by anthropogenic noise, disturbance, and expansion. Understanding the habitat, spatial, and temporal usage of areas by different species will be essential in combatting these disturbances' effects on marine species. With odontocetes especially so at risk due to their reliance on auditory cues, it is of paramount importance to describe how their lifestyles are being impacted by and changing due to anthropogenic sources.

For beaked whales, there were differences in spatial usage and habitat patterns, potentially facilitating their co-occurrence. However, the complexity of the drivers behind spatial segregation limit projects like these, and although there were inklings of several trends related to season, time of day, lunar phase, and ENSO cycle variabilities, further research will be required to understand how these mechanisms drive habitat selection. Still, Cuvier's were usage of canyons, the northwest abyssal area, and deeper waters farther from shore indicates a species with potential diet and habitat differences than the closely related Blainville's, who prefer more shallow waters closer to shore, as well as the northwest terrace area (possibly related to reefs).

Seasonal analyses did indicate some differences between species, with pantropical spotted dolphins being seen at higher sea states and latitudes in the spring, as well as using waters farther from shore in the fall. Previously, there had been little indication of seasonal patterns for this species, and this project aims to open a discussion about their habitat usage throughout the year. For other species, this project lays the groundwork for further analyses.

Near-future analyses associated with project A will involve incorporating predictor variables on top of 95% kernel density estimates to compare the spatial and behavioral differences between the two species. Several topographic variables and general variables will be tested for collinearity as described above. The tag data will then be modeled in relation to environmental variables in a use versus available framework (Manly et al., 2002) to investigate differences in habitat selection between the two species. Recorded tag positions represent locations (and thus habitat variables) used by the animal, and random locations, sampled from the estimated home ranges, will represent the available habitat. Based on the use vs. availability framework described above, logistic regressions, with a response variable indicating whether the animal used a habitat covariate (1) or not (0), will be fit as a generalized additive model (GAM). "Use" locations will be the tag locations, while "available" locations were represented by randomly sampled points from each animal's home range.

For Project B, further analyses on the other species will be run in the same fashion presented here for spotted dolphins. Past that, as more species are sighted and more years of comparable effort have gone underway, other species, such as Cuvier's beaked whale, may be included in analyses like these.

Personally, these ongoing projects have been an incredible experience and process. The methods and results thus far were presented at the MPS Internship Symposium, as well as the 2023 Northwest Chapter of the Student Society for Marine Mammalogy conference. Data obtained from this project will be used in future projects and research by Cascadia Research Collective. We are also hoping to move forward with both of these projects for publication in some form. At the moment, I look forward to seeing these projects' final form, and remain grateful for the opportunity to have worked with such incredible organizations.

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Appendices

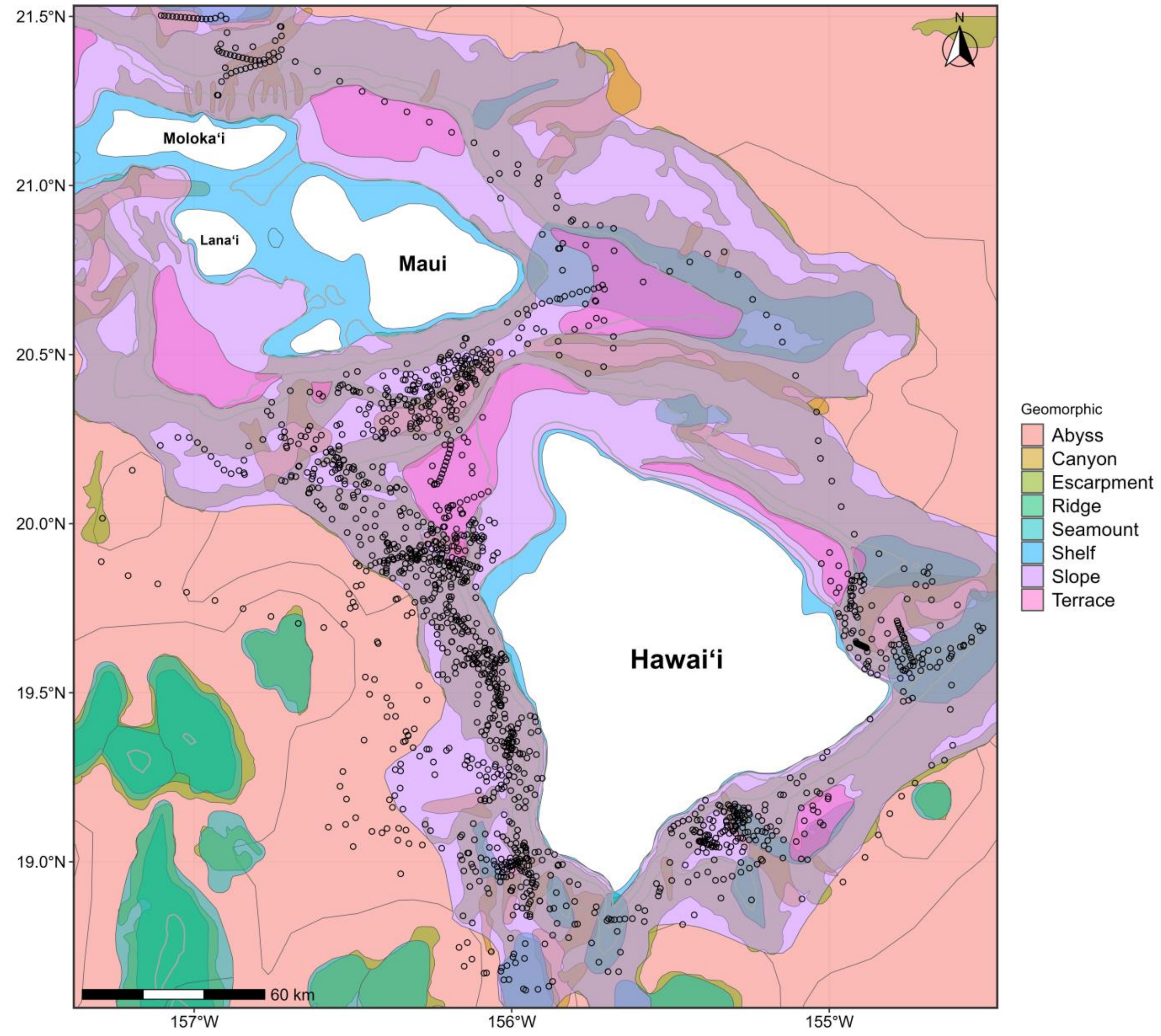

Figure S1. Geomorphic features included in analyses with Cuvier's beaked whale tags overlaid on top.

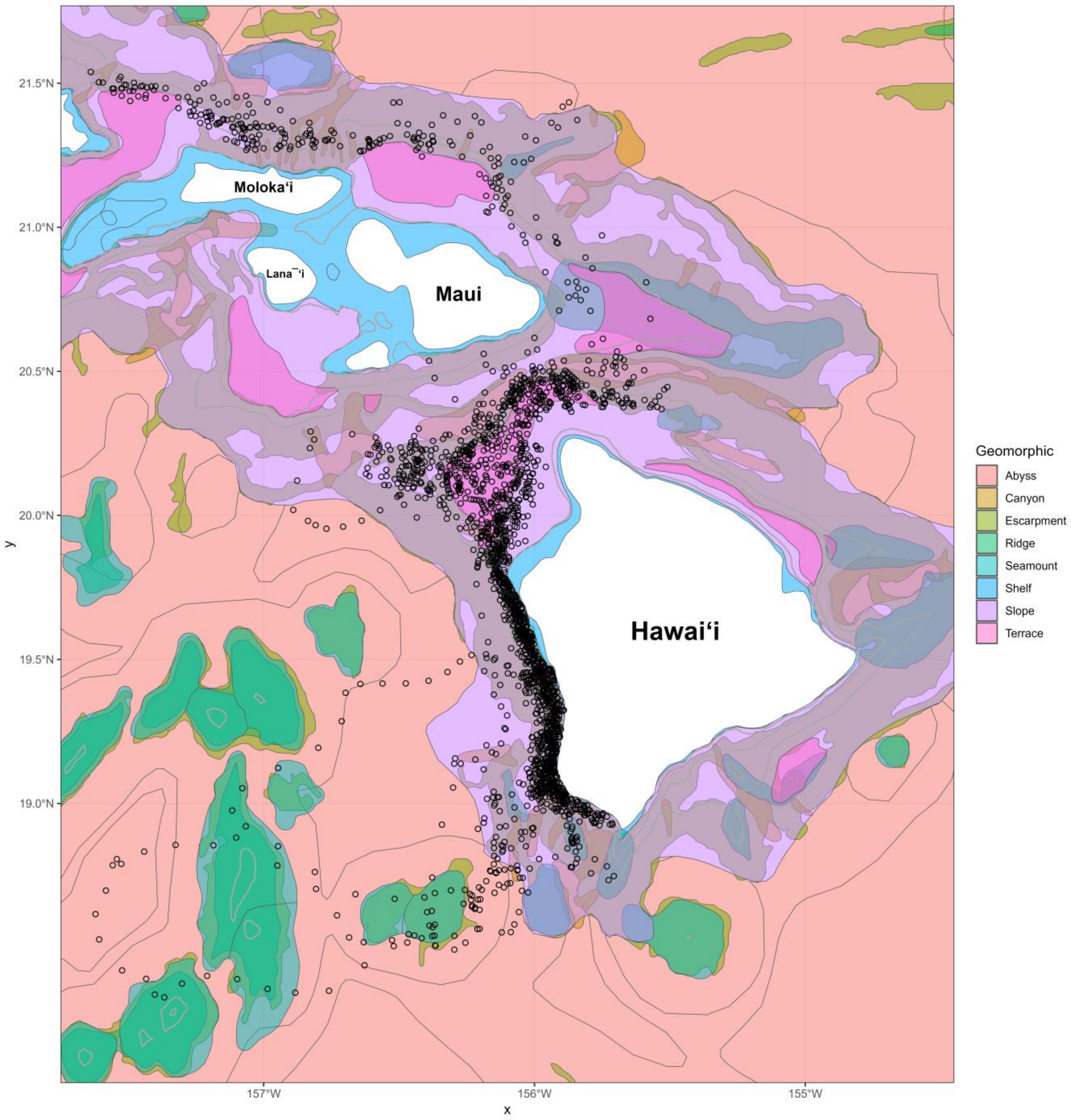

Figure S2. Geomorphic features included in analyses with Blainville’s beaked whale tags overlaid on top.

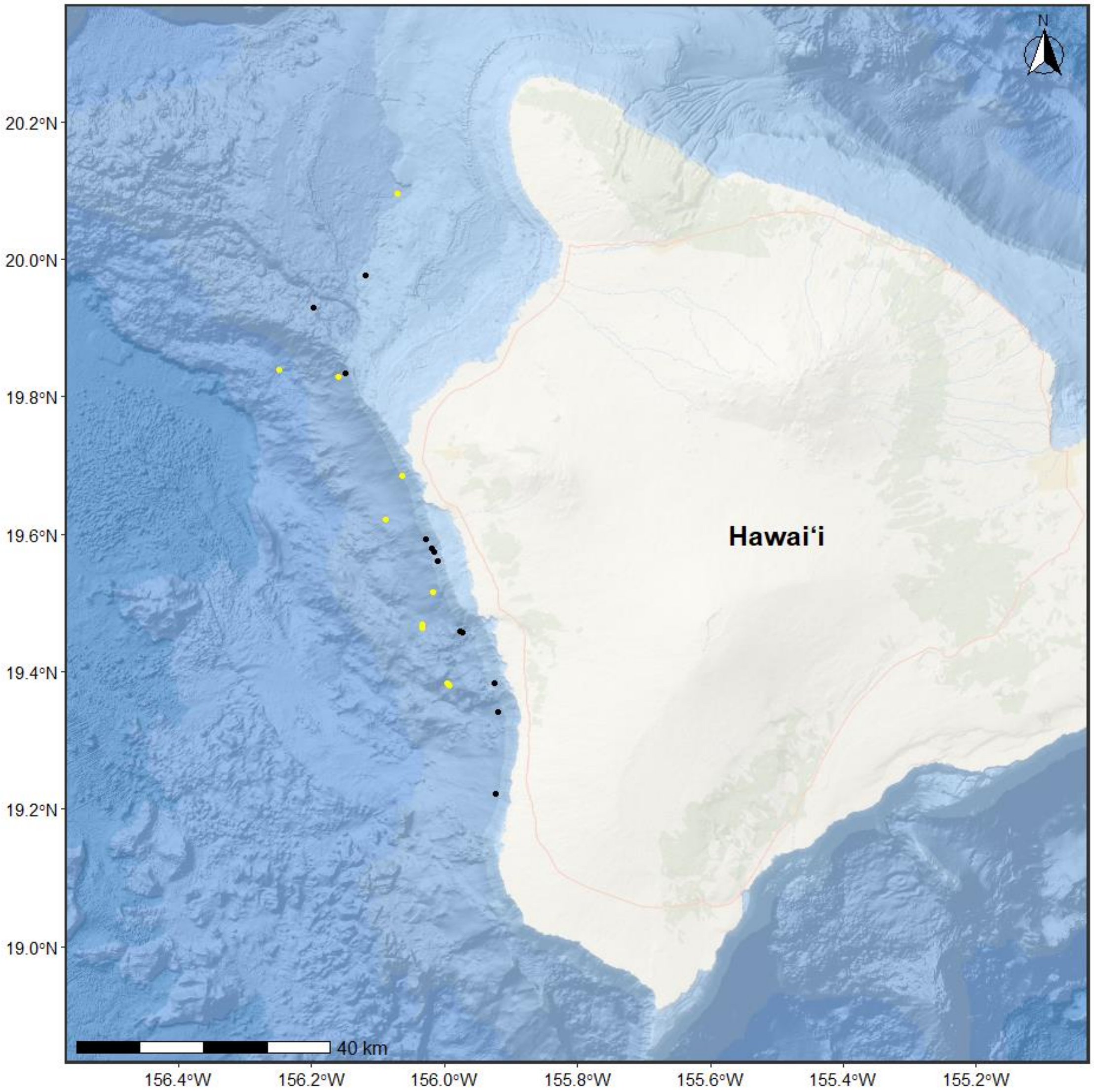

Figure S3. Beaked whale tag deployment locations. Blainville’s beaked whale deployments are in black and Cuvier’s beaked whale tag deployments are in yellow.

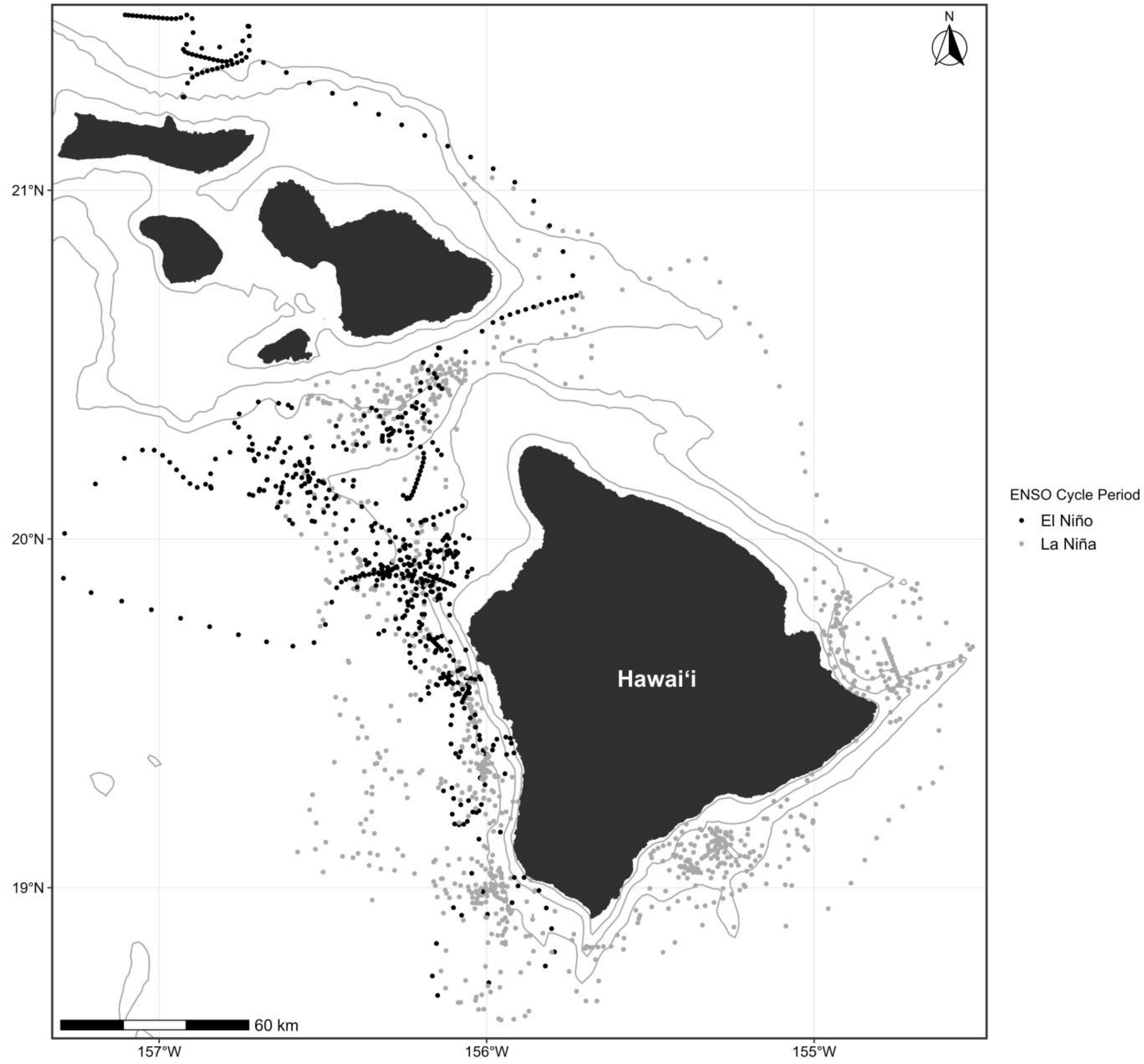

Figure S4. Cuvier's beaked whale 4-hr *crawl* tag locations by ENSO cycle period.

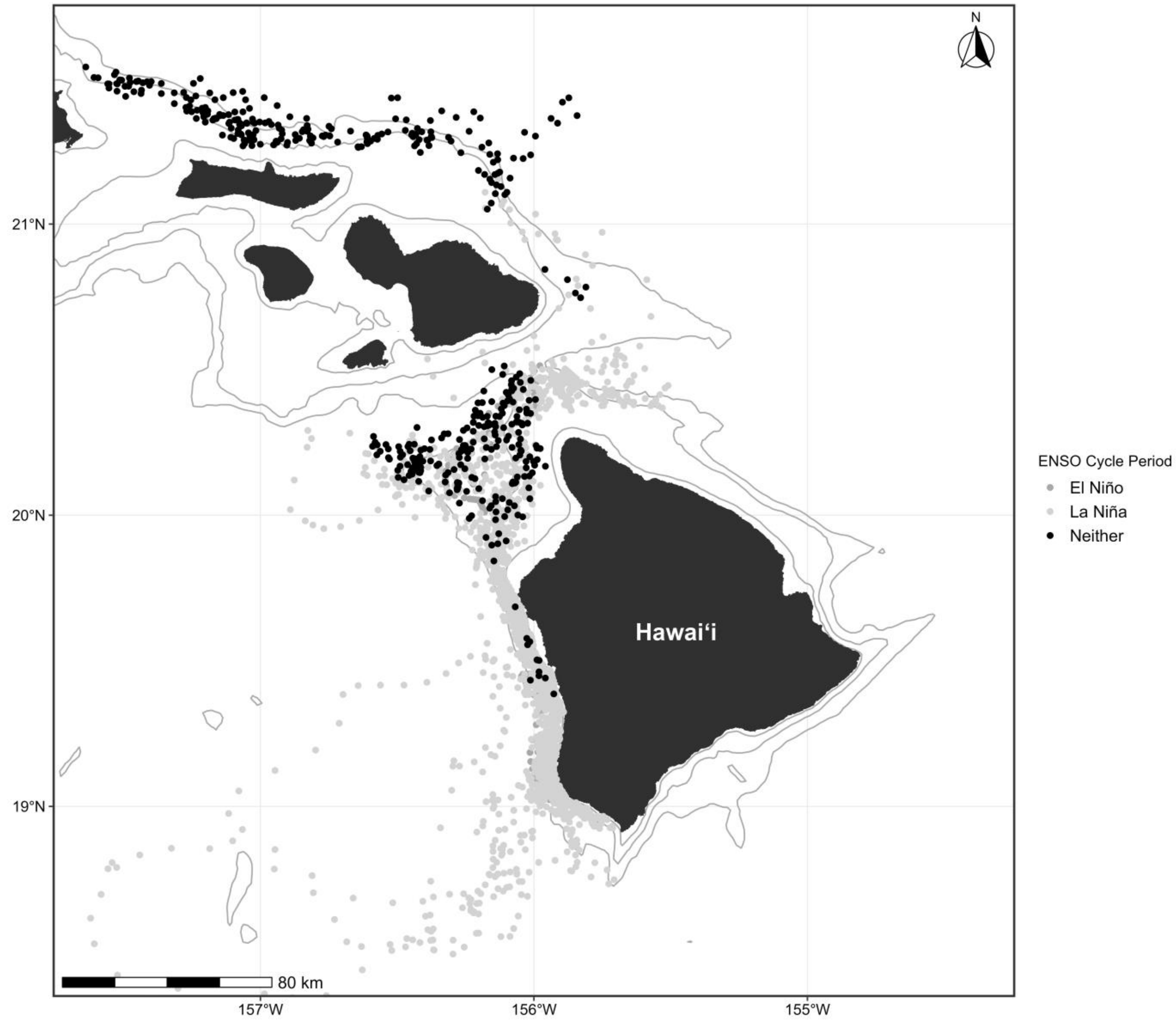

Figure S5**.** Blainville's beaked whale 4-hr *crawl* tag locations by ENSO cycle period.

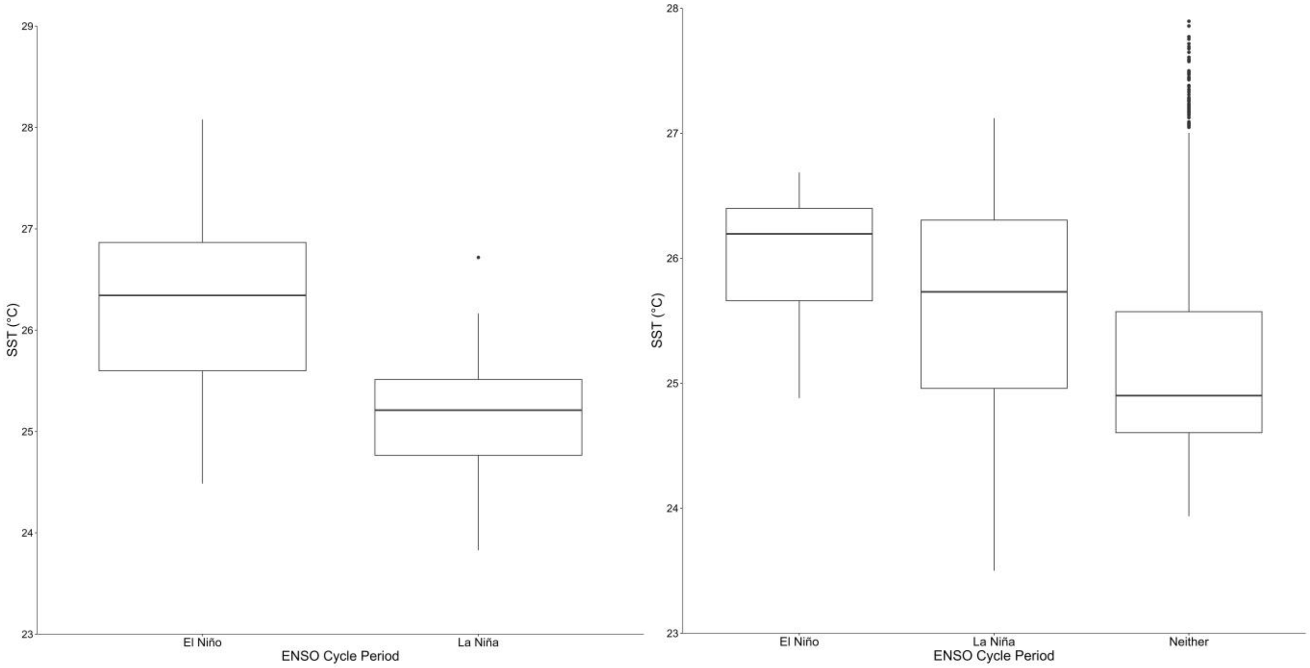

Figure S6. Differences in SST during different ENSO cycles between Cuvier’s (left) and Blainville’s (right) beaked whales.

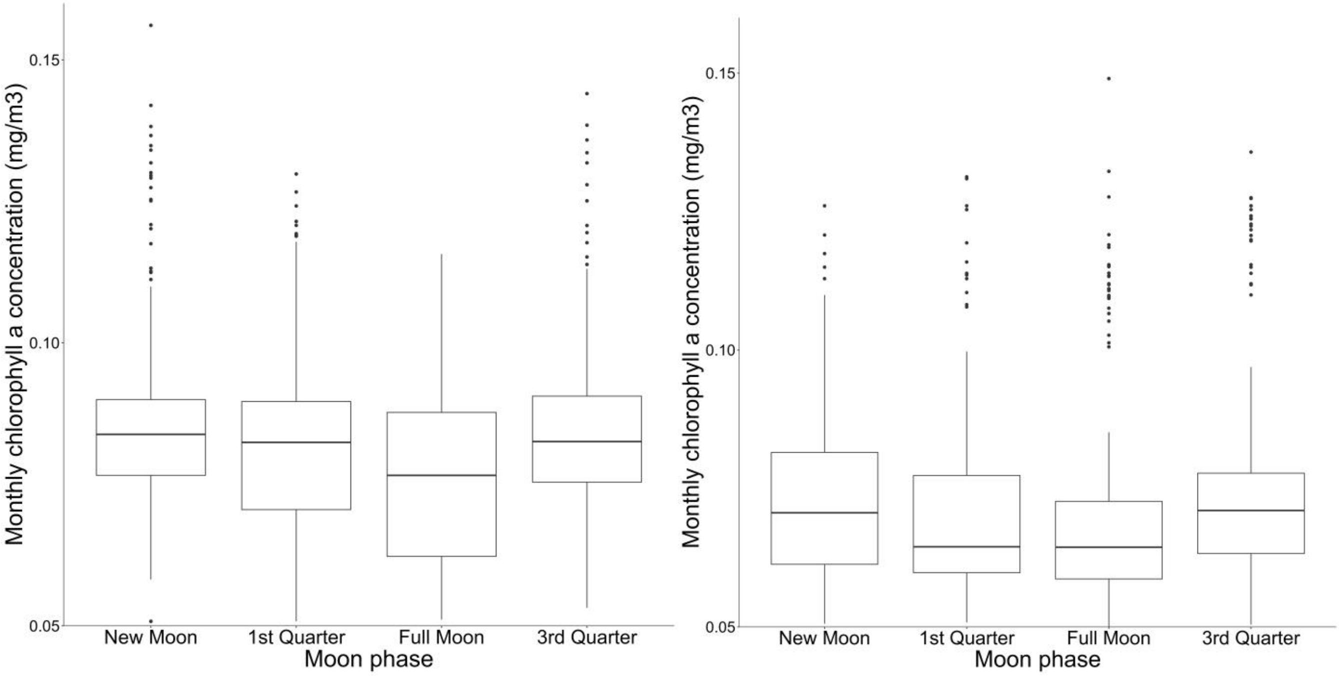

Figure S7. Differences in monthly chlorophyll-a concentrations during different lunar phases between Cuvier’s (left) and Blainville’s (right) beaked whales.

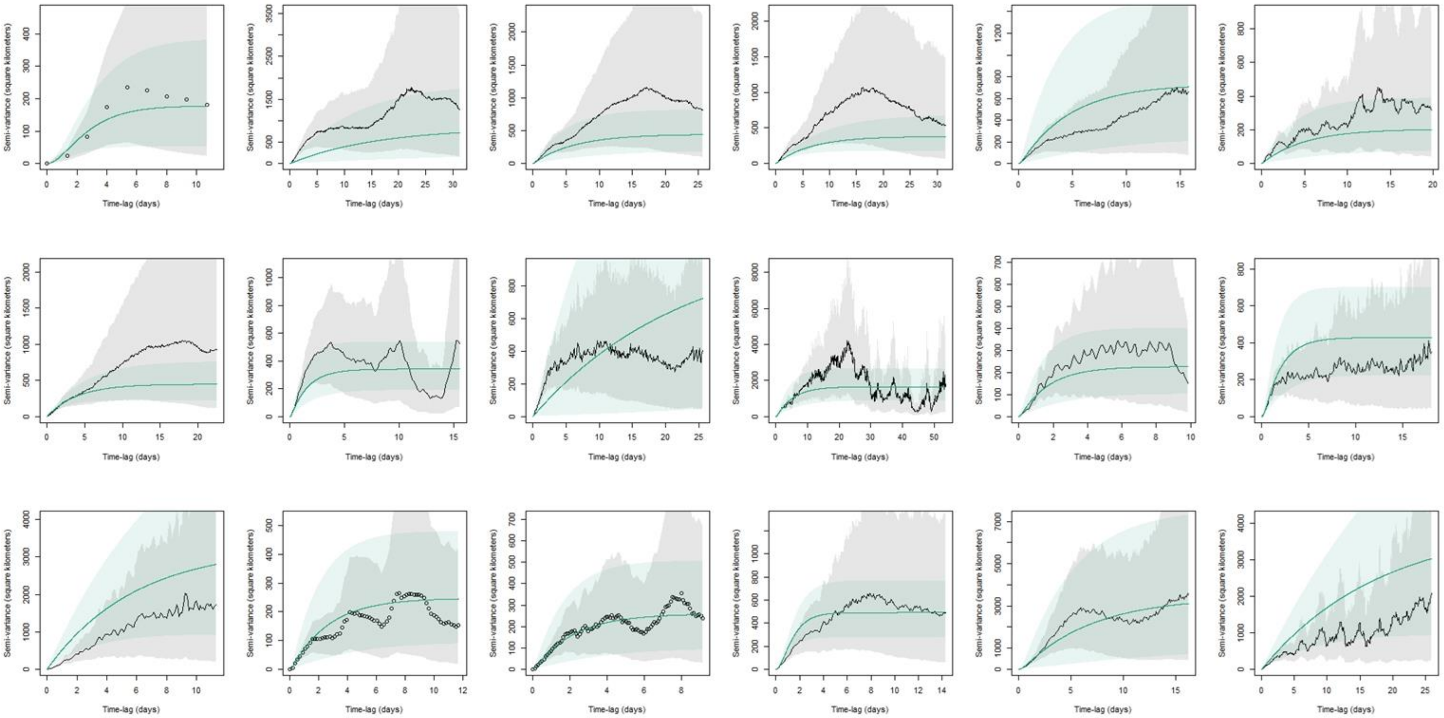

Figure S8. Variograms analyzed for range residency through the *ctmm* package in R, where a flattening of the values indicating range residency.

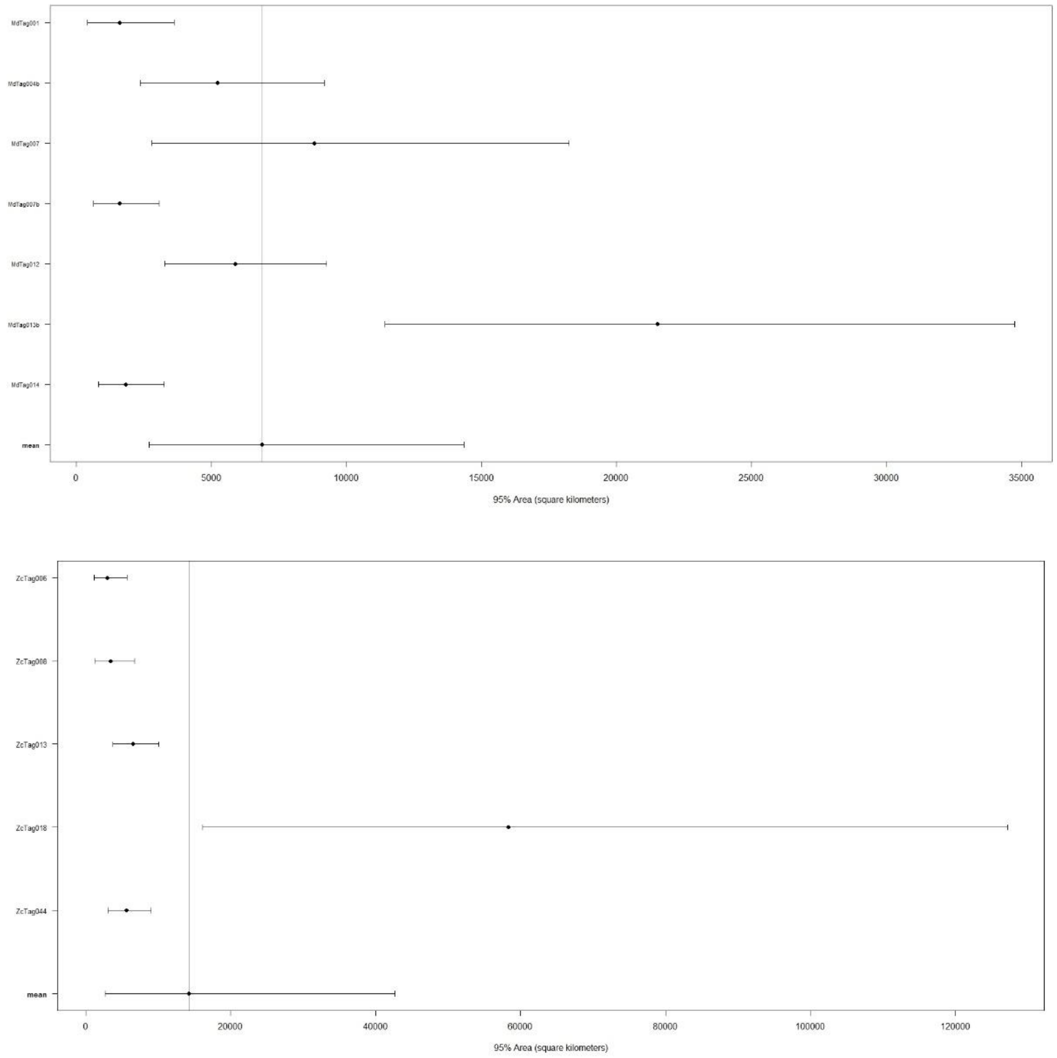

Figure S9. Meta analyses for Blainville’s beaked whale and Cuvier’s beaked whale, indicating the extreme outliers in kernel density home range size for two individuals.

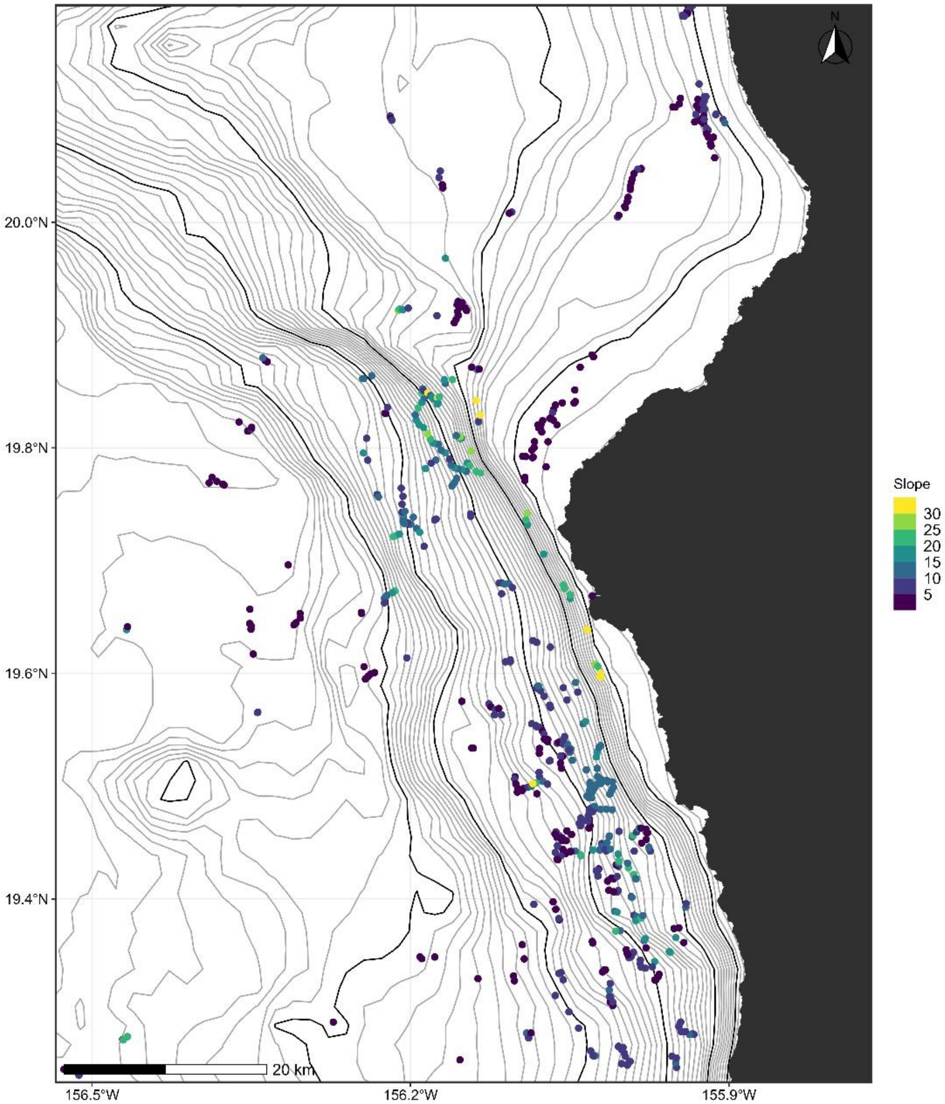

Figure S10**.** Map of Pantropical spotted dolphin sightings, with gray lines indicating each 100m depth contour, black lines indicating the 200, 1000, 2000, 3000, and 4000 m depth contours, and color indicating slope in meters.

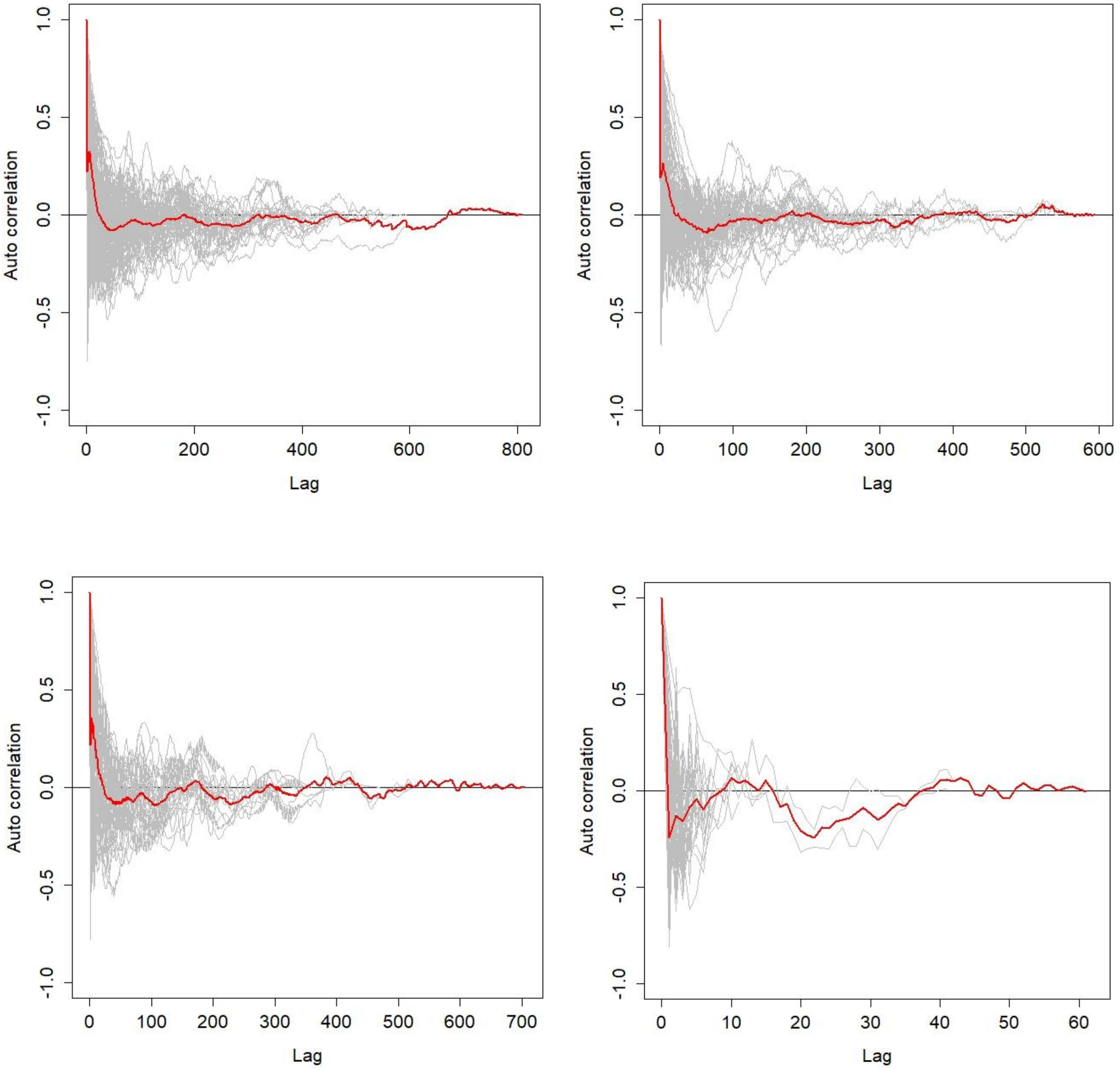

Figure S11**.** Autocorrelation function residual plots of the final models (in order of model number). All plots converge to zero, which suggests that the blocking variable of encounter is appropriate for GEEs. Created using the *acf* function in R.

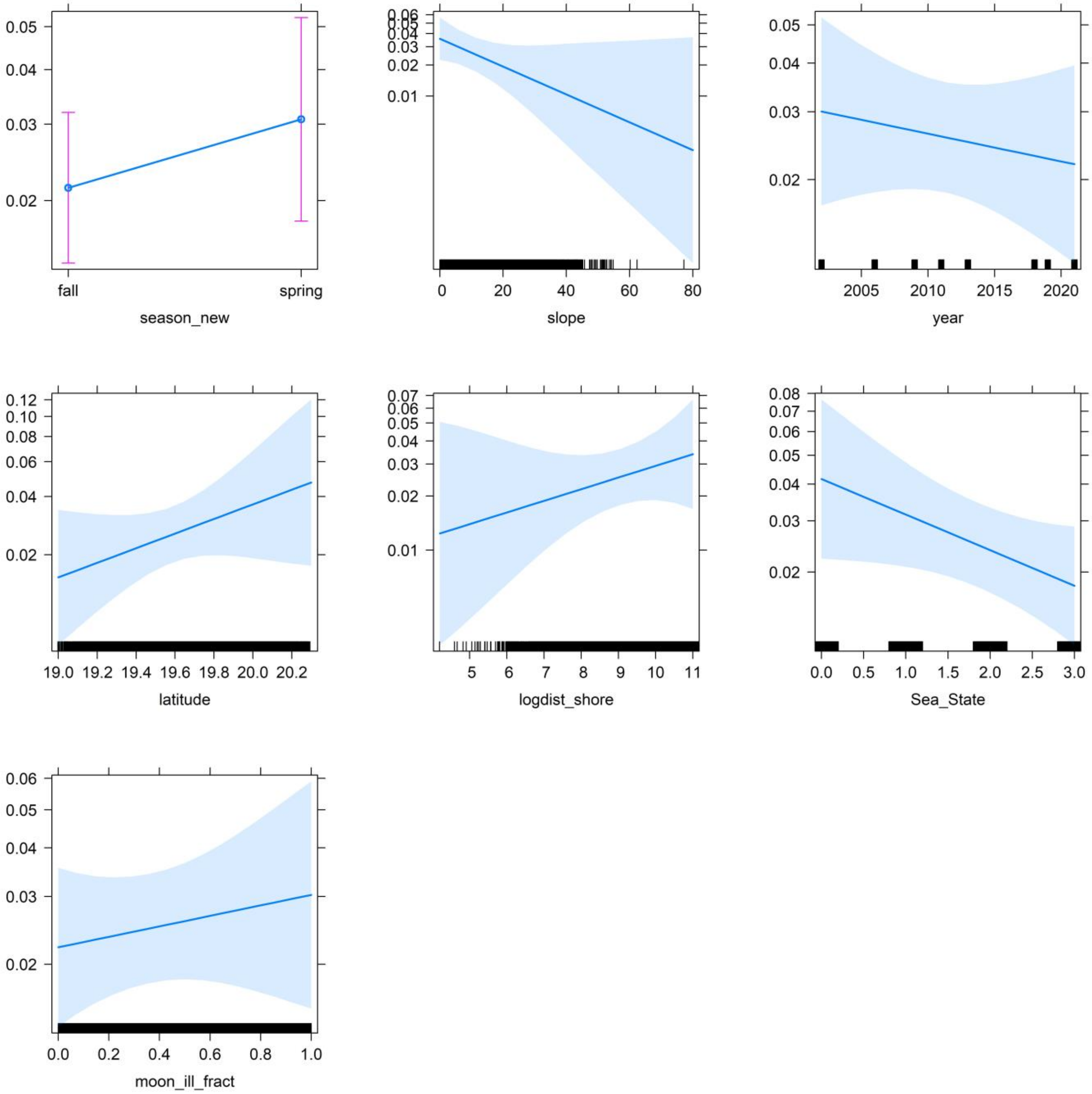

Figure S12. Effect plot for Presence/Absence model.

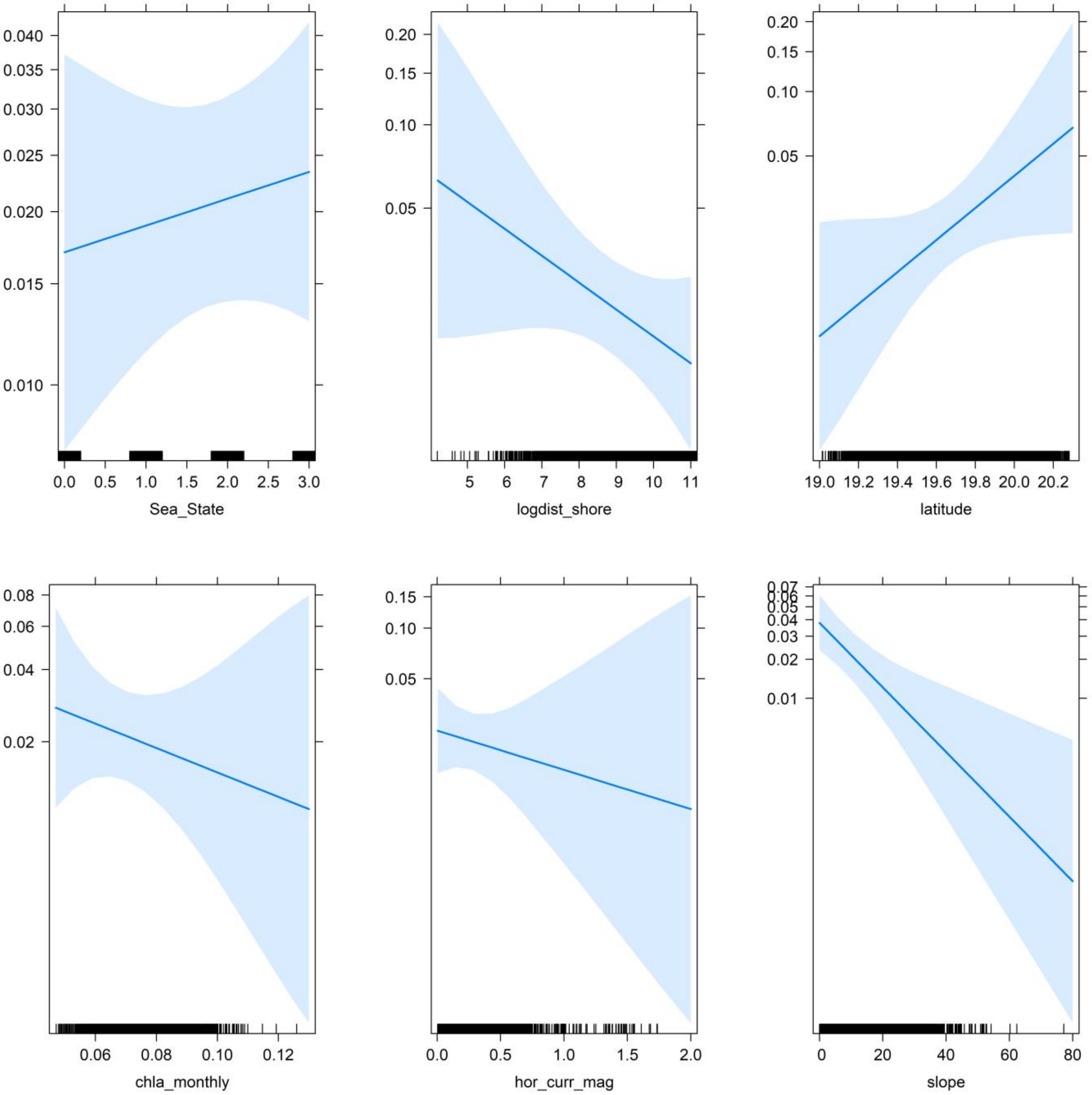

Figure S13. Effect plot for Fall season model.

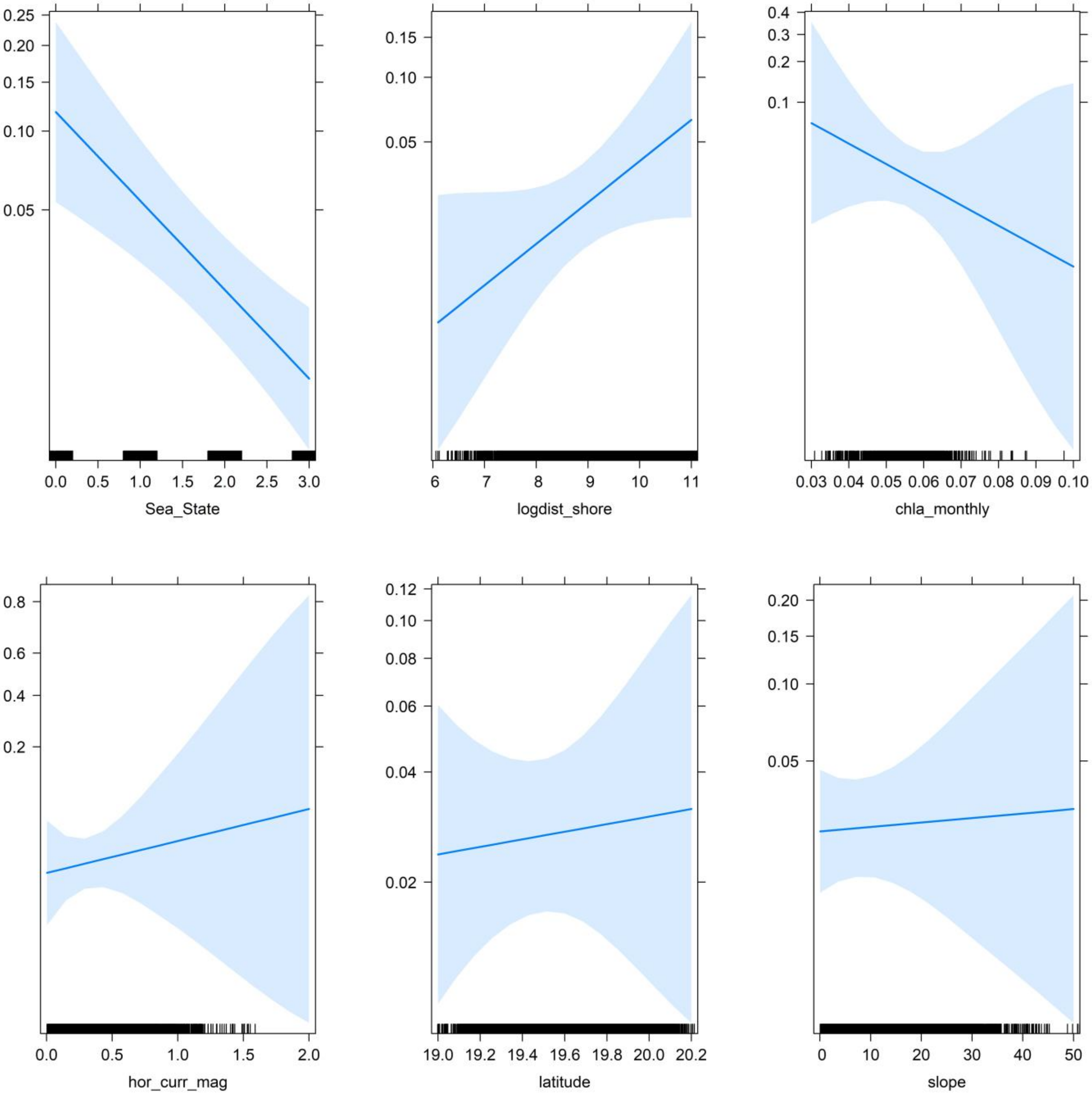

Figure S14**.** Effect plot for Spring season model. For example, slope at the bottom right showcases how sightings decrease with an increase in slope.

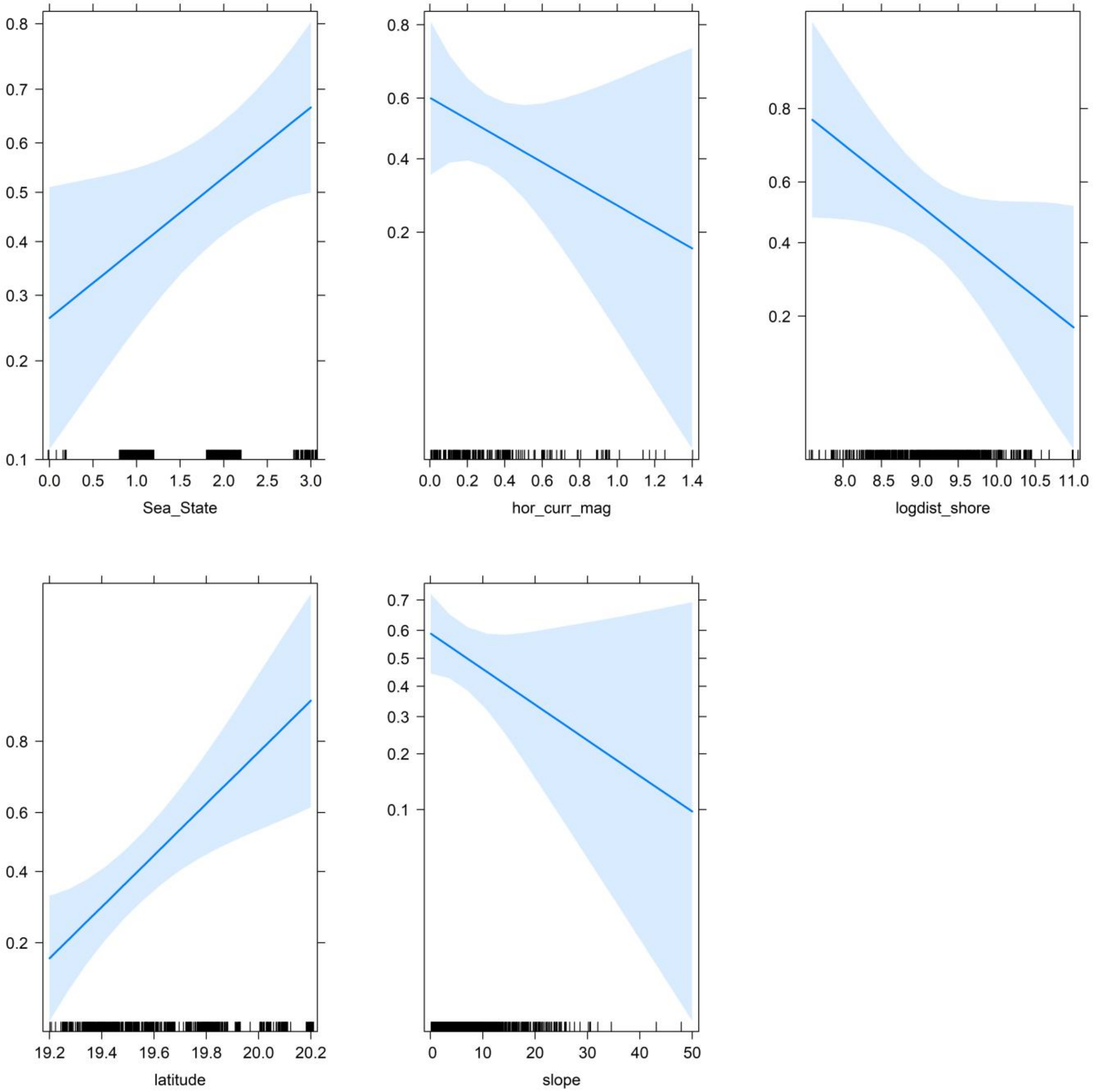

Figure S15**.** Effect plot for season model.

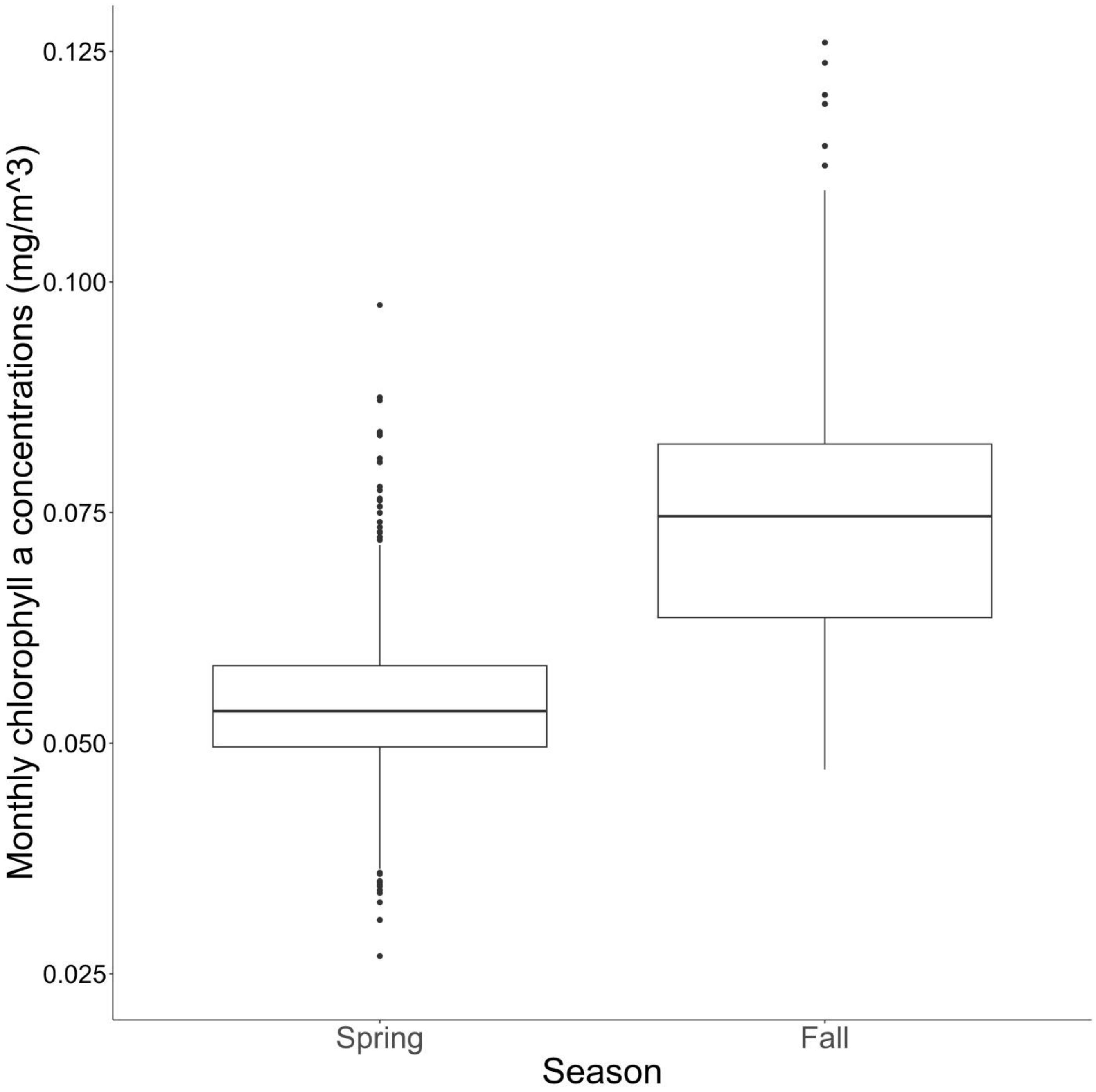

Figure S16. Chlorophyll-a concentrations between seasons for all effort.