Beaked whales and El Niño: evidence for ENSO effects on Blainville's beaked and goose-beaked whale space use in Hawaiian waters

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ABSTRACT: Large-scale climatic phenomena, like the El Niño—Southern Oscillation (ENSO) cycle, influence marine systems across the Pacific and beyond. The effects of these cycles on Hawaiian marine communities, particularly their impact on cetaceans, remains understudied. Using location data obtained from satellite tags deployed on Blainville's beaked whales *Mesoplodon densirostris* and goose-beaked whales *Ziphius cavirostris*, and sightings data from 2 decades of surveys off the west coast of Hawai'i Island, we examined the effects of ENSO, season, and 2 other climatic cycles on the space use and sighting rates of these species. Beaked whale sighting rates during El Niño phases were more than double those during La Niña periods, and every period of effort during Central Pacific-'flavored' El Niño conditions yielded sightings of both species. Seasonal variation in goose-beaked whale sighting rates was also found. Moreover, both species exhibited variation in space use between climatic phases, with goose-beaked whales displaying a higher propensity to use the windward side of the island after extended La Niña conditions. Shifts in prey availability or predation avoidance in relation to seasons or ENSO events may be the primary drivers behind these findings. More tagging and sighting effort will be necessary to confirm the level of cycle intensity at which these species respond to ENSO cycles, as well as which combinations of climatic phenomena most intensely influence their environment. Our results provide valuable insights for the potential of climate change to influence space use by beaked whales and other odontocetes.

KEY WORDS: El Niño—Southern Oscillation · *Mesoplodon densirostris* · *Ziphius cavirostris* · Pacific Decadal Oscillation · North Pacific Gyre Oscillation · Long-term data sets · Killer whale · Interannual variability

HŌ'ULU'ULU MANA'O: Pā nā mea aniau nui, e like ho'i me ke au o ka Unena Hema o El Niño (ENSO), i nā kaiaola kai ma ka Pākīpika a ma 'ō aku paha. 'A'ole nō nānā a kālailai 'ia nā hopena o ia mau aniau nui ma nā kaiaola kai Hawai'i, keu ho'i ka pā 'ana o nā māmela noho kai. Ho'ohana 'ia ka 'ikepili kahua i loa'a mai nā lepili ho'oka'a'ike lewa i kau 'ia ma nā koholā nuku pa'apū (*Mesoplodon densirostris*) a me nā koholā nuku nēnē (*Ziphius cavirostris*), a ho'ohana pū 'ia ka 'ikepili 'ikena o nā ana'ikena o 'elua kekeke i mālama 'ia ma kapakai komohana o Hawai'i mokupuni no ka nānā 'ana i nā hopena o kahi a me ka helu 'ikena o ia mau lāhui ma muli ho'i o ENSO, ke kau, a me 'elua hou aku au aniau. Pālua ka helu 'ikena o nā koholā nuku pa'apū ma ke au El Niño ma ka ho'ohālikelike 'ana me nā au La Niña, a 'ike 'ia nā lāhui 'elua ma ke au o El Niño ma ka Pākīpika Kūwaena. Ua 'ike pū 'ia ka 'aui 'ana o ke kau ma ka helu 'ikena o nā koholā nuku nēnē. Eia kekahi, hō'ike nā lāhui 'elua i ka 'aui 'ana o ko lākou wahi ma waena o nā 'epaki aniau, 'oi aku ka nui o ka papaha, 'o ka wahi o nā koholā nuku nēnē ka 'ao'ao ko'olau o ka mokupuni ma hope o ka wā lō'ihi o ka La Niña. 'O nā kumu nui paha o ia mau hopena, 'o ia ho'i ka loli o ka hiki ke loa'a i ka 'ai, a i 'ole ho'i ka hō'alo 'ana i ke 'ano luapo'i i loko o nā kau a hana ENSO paha. Pono e ho'onui i ka ho'olepili a 'ike 'ana i mea e hō'oia aku ai i ka ikaika o ke au ma ka wā e pā ai kēia mau lāhui i nā au ENSO, a i mea e hō'oia pū aku ai i nā huihuina aniau e pā nui ana i ko lāua kaiapuni. Hō'ike kā mākou mau hua i ka 'ike waiwai no ka hiki i ka lolina aniau ke pā i nā wahi o nā koholā nuku a pēlā pū i nā koholā niho 'ē a'e.

1. INTRODUCTION

The Pacific marine environment is influenced by large-scale climatic phenomena such as the El Niño–Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO) cycles. ENSO cycles, characterized in the Pacific basin by alternating warm (El Niño) and cold (La Niña) phases, are driven by changes in the trade winds and oscillate at time scales between 4 and 7 yr (Di Lorenzo & Schneider 2010). During El Niño, the trade winds weaken, resulting in warm surface waters in the eastern Pacific, while La Niña brings colder than average sea surface temperatures (SSTs) due to stronger trade winds to the same area (Philander 1983), with the effects of this cycle varying based on region. ENSO has an opposite effect in the western Pacific, where cold, nutrient-rich water arrives at coasts during El Niño periods (Philander 1983). Both of these phases can have profound impacts on marine ecosystems, disrupting atmospheric circulation patterns and causing changes in rainfall and nutrient dispersion worldwide (Wooster & Fluharty 1985). Within El Niño phases, 2 distinctive classifications are used to indicate the center of SST anomalies: the Central Pacific 'flavor,' denoting periods with larger SST anomalies in the central Pacific, and the Eastern Pacific flavor, for periods with larger SST anomalies in the eastern Pacific (Kao & Yu 2009).

The PDO, meanwhile, is a longer-term (15 to 25 yr cycle) climatic pattern in the North Pacific Ocean made up of multiple physical processes, with similar warm and cold phases (positive and negative; Newman et al. 2016). Since a PDO phase can last up to 30 yr, it can have severe impacts on the intensity of El Niño and La Niña events, depending on the location and phase. For example, during positive PDO phases, the warm SST anomalies associated with El Niño are often intensified, resulting in mostly milder subsequent La Niña events (Newman et al. 2016).

The NPGO describes changes in the North Pacific Subtropical Gyre at similar time scales as the PDO, and is highly correlated with fluctuations in productivity, including variation in salinity, nutrients, and chlorophyll concentration (Di Lorenzo et al. 2008). During periods of positive NPGO values, the North Pacific Current is strengthened and leads to an increase in Alaskan Coastal and California current transports.

Previous studies have documented the effects of large-scale climatic cycles around the Hawaiian Islands. The Hawaiian Archipelago lies in a unique position in the central North Pacific, where the islands disrupt the continuous movement of the trade winds (Smolarkiewicz et al. 1988). The tall volcanoes of Hawai'i Island particularly limit trade winds from reaching the leeward (west) side of the island (Leopold 1949, Huang & Chen 2019). Positive PDO and El Niño events generally result in altered precipitation patterns, coral bleaching, and abnormally warm SSTs (Rooney & Fletcher 2005), although in the main Hawaiian Islands, these direct results could be dependent on the flavor of the El Niño event. This is evidenced by the wider breadth of warmer SST anomalies in Central Pacific El Niño events (McCoy et al. 2017), which more significantly impact the regions between 20° S and 30° N that include the Hawaiian Islands (Lu et al. 2020). During Eastern Pacific-flavored El Niño events, the Hawaiian Archipelago does not experience the same level of warm SST anomalies (Di Lorenzo et al. 2010, McCoy et al. 2017). Periods of El Niño conditions can lead to elevated sea levels and winter swells in the main Hawaiian Islands, although this phenomenon is not consistently observed and may lag behind particularly strong El Niño events (Long et al. 2020).

Seasonal variation plays an important role in localized climatic changes. Although the Hawaiian Islands are not exposed to the seasonal sweeping shifts in temperature noted in temperate regions, the area is generally split into 2 seasons: a wet winter (Kau Ho'oilo) and a drier summer (Kau wela or just Kau). The area along the west coast of the island of Hawai'i has a distinct maximum rainfall in the summer, unlike much of the rest of the region (Meisner 1976, Giambelluca et al. 1986), including the windward side, which reaches maximum rainfall conditions during the winter (Huang & Chen 2019). Oceanographic seasons in the Hawaiian Islands, as defined by Flament et al. (1996), are characterized by features such as changing water temperature and increased swell height during the winter. Interactions may occur between seasonal and ENSO processes. During positive PDO and ENSO periods, particularly in the wet season from November to May, rainfall patterns influence freshwater runoff into nearshore waters (NOAA 2015a) and lead to reduced rainfall during El Niño winters and warmer temperatures in El Niño summers, with La Niña forcing wetter winters and cooler summers. Additionally, El Niño periods are associated with an increased likelihood of tropical cyclones impacting the Hawaiian Islands during hurricane season (NOAA 2015b), which can have implications for coastal erosion and sediment transport (Rooney & Fletcher 2005), and lower net primary productivity (Kavanaugh et al. 2018).

The effects of these climatic cycles on marine life in the Pacific have been documented through intensive research and long-term study. Though limited research exists on the impact of ENSO on the Hawaiian marine ecosystems specifically, weakened trade winds during El Niño reduce upwelling of nutrient-rich waters in other areas (Chavez et al. 1999, Friederich et al. 2002). If a similar effect occurs in the Hawaiian Archipelago, the entire food chain could be affected (Benson et al. 2002). Looking at the effects of these cycles on primary production in the region, Pang (2011) found no discernible ENSO-related differences in phytoplankton productivity, whereas Lim et al. (2022) observed phytoplankton decline and a series of chlorophyll anomalies through El Niño conditions, with a post-El Niño rebound rejuvenating the ecosystem thereafter. Off O'ahu, Karl et al. (1995) noted increased nitrogen-fixing cyanobacteria activity during El Niño, likely due to increased upper water column stratification. Other studies suggest ENSO- or PDO-induced prey changes affecting marine predators (McCoy et al. 2017, Wren et al. 2019; Table S1 in the Supplement at www.int-res.com/articles/suppl/m751p189_supp.pdf).

Research exploring the effects of large-scale climatic cycles on difficult-to-study species at high trophic levels, like marine mammals, remains relatively deficient both inside and outside the Hawaiian Archipelago. However, in order to better manage these species in the face of climate change and other longer-term climatic fluctuations, it is essential to uncover patterns or trends in relative abundance and spatial distributions between different phases of these cycles (Gulland et al. 2022). Perhaps best documented are the impacts of these climatic phenomena on pinnipeds and odontocetes, although trends have been noted in baleen whales as well (Table S1). Around the Hawaiian Islands, pelagic false killer whale *Pseudorca crassidens* depredation rates in Hawaiian longline fisheries were lower during La Niña events, although the statistical relationship was weak (Fader et al. 2021). The variation in marine predator—fisheries interaction rates across oceanographic conditions could indicate that this species relies more on depredation to meet energy requirements as a result of lower availability of natural prey.

Given the potential influence of these cycles on the distribution and behavior of various odontocetes, it is clear that understanding the responses of less abundant or more elusive species is of paramount importance. Among these species, deep-diving beaked whales (members of the family Ziphiidae) stand out, as they are highly susceptible to human disturbances and anthropogenic noise (Cox et al. 2005, Bernaldo de Quirós et al. 2019). Several ziphiid species (e.g. Longman's beaked whale *Indopacetus pacificus*; Table S1) exhibit some differences in habitat use between ENSO cycle periods. In passive acoustic monitoring studies at fixed locations in Hawai'i, Ziegenhorn et al. (2023a,b) found that detections of Blainville's beaked whales *Mesoplodon densirostris* were significantly higher during La Niña periods at both sites studied (Manawai, Hawai'i Island), while goose-beaked whales *Ziphius cavirostris* had a similar relationship off Hawai'i Island and a weaker one at Manawai. An increase in detections for both species off of Hawai'i Island was documented during the 2010—2011 La Niña event, which corresponded with negative PDO and positive NPGO values (Ziegenhorn et al. 2023b). Therefore, the study hypothesized that a combination of the 3 events could lead to the most productive combination of these cycles for odontocetes in the main Hawaiian Islands.

In the main Hawaiian Islands, resident populations of Blainville's beaked and goose-beaked whales have been studied extensively for more than 2 decades (Baird et al. 2006, 2008, 2011, McSweeney et al. 2007, Schorr et al. 2009, Abecassis et al. 2015, Baird 2019). Resident Blainville's beaked whales are generally encountered in slope waters on the leeward side of Hawai'i Island and also occur in deep water off Maui, Moloka'i, and O'ahu (Baird 2019). Goose-beaked whales typically use comparatively deeper waters on both sides of Hawai'i Island and north of Maui (Baird 2019). While there is limited knowledge regarding the prey preferences of the 2 beaked whale populations resident to Hawai'i, MacLeod et al. (2003) noted niche specialization in diet between *Mesoplodon* species and goose-beaked whales around the world, with *Mesoplodon* species generally feeding on medium-sized cephalopods and goose-beaked whales feeding on larger cephalopods. A study analyzing the stomach contents of goose-beaked whales in the North Pacific also demonstrated that their diet predominantly consisted of cephalopods, including those belonging to the family Ommastrephidae (West et al. 2017). Analyzed alongside movement patterns, the stomach contents of a single stranded Blainville's beaked whale off Hawai'i Island indicated that it likely foraged on micronekton-associated squids and fishes in similar proportions (Abecassis et al. 2015). Since both of these populations are generally resident to the islands, any noticeable shifts in their relative abundance or space use over a longer period of time may be a consequence of broad-scale climactic vari-

ability, such as ENSO cycles, on their prey (or their prey's prey) as opposed to direct impacts on the whales themselves. Species following prey movements during shifts in ENSO periods have been documented before, such as Indo-Pacific bottlenose dolphins *Tursiops aduncus* exhibiting an unprecedented decline in abundance and peak in emigration after a strong El Niño event in 2009 that lessened rock lobster settlement (Sprogis et al. 2018). Effects on habitat use may also be heightened or directly impacted by season, although both species of beaked whale have been sighted in all oceanographic seasons around the islands (Baird et al. 2013). Detections of Blainville's beaked whales using data from a high-frequency acoustic recording package (HARP) were documented to increase at least marginally in the summer at Hawai'i Island (Baumann-Pickering et al. 2014, Ziegenhorn et al. 2023a), possibly driven by shifts in foraging hotspots (Abecassis et al. 2015). A fall–winter peak in acoustic detections at Hawai'i Island has been noted for goose-beaked whales (Baumann-Pickering et al. 2014, Ziegenhorn et al. 2023a).

In this study, we investigated the potential effects of ENSO cycles, in combination with PDO and NPGO cycles and oceanographic season, on the sighting rates and space use of Blainville's beaked and goose-beaked whales around Hawai'i Island. We used a combination of longitudinal sighting and effort data off the leeward (west) side of Hawai'i Island, as well as satellite tag data, to assess habitat use among ENSO phases. We also explored the potential effect of ENSO and PDO phases on killer whale *Orcinus orca* sightings off Hawai'i Island. While this species is not resident to the islands (Baird et al. 2003, Baird 2016), it is a known predator of beaked whales (Jefferson et al. 1991, Wellard et al. 2016, Gualtieri & Pitman 2019), and its occasional presence around the islands thus may have an influence on beaked whale space use. This work has implications both for the potential responses of beaked whales to climate variability, and for studies estimating abundance of beaked whales or the effects of human activities on their space use.

2. MATERIALS AND METHODS

2.1. Sighting and encounter rates

Sightings and effort data off Hawai'i Island were collected from 2002 through 2022 using small to medium-sized vessels, with GPS locations collected every 5 min (see Baird et al. 2013, 2024 for details) and Beaufort sea state recorded as it changed. Odontocete groups were approached, photographed, and identified to species, and group sizes were estimated. Other data recorded included sighting start and end time and location, and sighting cue (e.g. splash/blow/fin, radio call, re-locating tagged individuals using VHF or satellite signals). Survey effort was quantified by the number of hours on-effort and kilometers covered per day. For analyses of group size, habitat use, and sighting rates, we only used sightings cued by 'splash/blow/fin' to exclude sightings initiated by re-locating tagged individuals or those reported by other boats. Time spent during encounters with other species was not considered 'on-effort' and was excluded from the effort data set. Sightings and effort data were aggregated and analyzed with periods of contiguous effort within or spanning multiple months aligned with ENSO, PDO, and NPGO index values (see Table 1). Months with less than 30 h of effort (with the exception of the first month of effort) were also combined with neighboring months even if effort was not contiguous. All periods were defined by the month with the greatest amount of effort. To assess variability, sightings per unit effort (SPUE: sightings per 100 h of effort) and sea state were analyzed for each phase of the ENSO cycle (La Niña, Neutral, and El Niño) for which survey effort was available. Data were restricted to depths of over 375 m, to remove areas in which beaked whales are not likely to be sighted (Baird 2019). Sea state was compared across phases using a Kruskal-Wallis test with the 'Kruskal.test()' function in the 'stats' package in R (R Core Team 2024); sea state of all 5 min effort locations for each month or contiguous period of effort were averaged for this test. Group size was also compared across phases and seasons using a Kruskal-Wallis test. Kruskal-Wallis tests were supplemented by pairwise Wilcoxon rank sum tests in the 'stats' package (R Core Team 2024) to identify pairs of phases/seasons with significant differences when applicable.

Killer whale sightings around the eastern main Hawaiian Islands were also compiled to assess the possibility that the effects of ENSO cycles on this beaked whale predator may impact beaked whale space use. Since sightings of killer whales in the Hawaiian Islands are rare, other sources in addition to our dedicated survey efforts were incorporated to look at their potential usage of the region during different ENSO phases, including sightings by other researchers and community members (e.g. Mobley et al. 2001, Baird et al. 2006).

2.2. Satellite telemetry

During a subset of beaked whale encounters from 2007 through 2015, efforts were made to satellite-tag some individuals. Location-only (SPOT5) and location and dive depth transmitting (SPLASH10) tags manufactured by Wildlife Computers were deployed on the whales in the LIMPET configuration (Andrews et al. 2019) using a pneumatic projector. Detailed information on tag deployment methods and programming can be found in Schorr et al. (2009). Tagged individuals were photographed to confirm sex and compared to a photo-identification catalog (McSweeney et al. 2007) to confirm whether they were part of the island-associated or open-ocean population (see e.g. Baird et al. 2011) and that no individuals were tagged more than once. Sex was determined based on the presence or absence of erupted teeth and the extent of linear scarring, since only adult males have extensive linear scarring caused by fighting with other males (McSweeney et al. 2007).

Tag location data were first processed by CLS Woods Hole Group through the Kalman location algorithm (Lopez et al. 2014). Prior to analysis, processed tag location data were filtered using the Douglas Argos filter (Douglas et al. 2012; accessed through Movebank, Kranstauber et al. 2011) in order to remove unrealistic or low-quality locations, which were identified based on the algorithm's assessment of the animals' travel speed, distance between points, angles, and location quality. The filtered locations were then fit to a continuous-time correlated random walk model using the 'crawl' package in R (Johnson et al. 2008, Johnson & London 2018) and predicted at 4 h intervals. Predicted locations were rerouted around land using a 300 m isobath for both species, using the 'pathroutr' package (London 2021). Any predicted locations that were interpolated between gaps of original (Argos) locations spanning ≥1 d were excluded prior to analyses, as such locations were characterized by large degrees of uncertainty. To account for pseudoreplication, if 2 or more tagged individuals remained closely spatially associated, then the individual with the shorter track of the 2 was removed prior to analyses (Schorr et al. 2009).

2.3. Climatic index processing

To evaluate the strength of ENSO events and variation, we used monthly Multivariate ENSO Index (MEI) values from the Physical Sciences Division of NOAA (https://psl.noaa.gov/enso/mei/) for our ana-

lyses, as in Gladics et al. (2014). The MEI uses a threshold of 0.5 to identify ENSO events, with a value ≤ −0.5 indicating La Niña and ≥0.5 indicating El Niño. Values in between −0.5 and 0.5 describe neutral phases, defined as periods without La Niña or El Niño conditions. Event magnitudes were classified as 'weak' (|0.5−0.8|), 'moderate' (|0.9−1.8|), or 'strong' (|≥1.9|). In addition, El Niño events were categorized as 1 of the 2 flavors (Central Pacific or Eastern Pacific) using the classification consensus table from Capotondi et al. (2021). Our decision to utilize the MEI, as opposed to alternatives such as the Oceanic Niño Index (ONI), was driven by the aim to gain a comprehensive and holistic understanding of the diverse fluctuations in species distribution associated with ENSO cycles. MEI values incorporate several atmospheric and oceanic variables, including sea level pressure, SST, cloudiness, and both zonal and meridional wind components (Wolter & Timlin 1993), in contrast to other indices, like the ONI, which only rely on SST anomalies.

PDO index values, which measure variance in PDO SST anomalies, were obtained on a monthly basis from the National Centers for Environmental Information (NCEI) website (https://www.ncei.noaa.gov/access/monitoring/pdo/) to assess the combined effects of large-scale climatic processes. A neutral PDO period, much like for ENSO, was defined using a threshold of |0.5|. NPGO index values were also obtained on a monthly basis from the National Science Foundation and the National Aeronautics and Space Administration (https://www.o3d.org/npgo/), where they are calculated using sea surface height anomalies. Oceanographic seasons, defined as fall (November to January), winter (February to April), spring (May to July), and summer (August to October), were adapted from Flament et al. (1996) based on variations in sea level, temperature, and wind speed. Fall and winter correspond to the traditionally wetter and cooler Hawaiian winter, while spring and summer belong to the drier Hawaiian summer. Sighting rates during oceanographic seasons were also compared alongside associated ENSO events for both species.

2.4. Statistical modeling

Univariate comparisons of sighting rates across ENSO phases, season, NPGO cycles, and PDO cycles were conducted with Kruskal-Wallis tests, with pairwise Wilcoxon tests applied to identify statistically significant pairs when applicable. We then examined

the collective influence of these variables on sighting rates through generalized additive models (GAMs). Pearson correlation coefficients were calculated for pairs of indices prior to model fitting, and 0.7 was considered the threshold for exclusion. For both species, we modeled the number of sightings per contiguous period of effort with a Poisson distribution and a log-link function, and an offset of the log of effort hours to effectively model sighting rates. Predictor variables included smoothed MEI, PDO, and NPGO terms to account for any non-linear relationship that may exist in the data. Oceanographic season was included in the model as a categorical parametric term. MEI, PDO, and NPGO terms were fit with penalized thin-plate regression splines with the basis dimension size restricted to 5 to prevent overfitting (Wood 2017). GAMs were fit using the 'mgcv' package (Wood 2006) with restricted maximum likelihood (REML) optimization. Variable selection was conducted using a shrinkage approach in the 'mgcv' package, which penalizes non-significant variables to zero (Marra & Wood 2011). Models were validated using the 'gam.check()' function within the 'mgcv' package and through visual assessments of residuals. Model performance was assessed through the percent of the deviance explained as computed by the 'gam()' model function. Partial effects plots were made using the 'gratia' package (Simpson 2024). A descriptive comparison of sighting rates by season within ENSO phases (e.g. summer El Niño versus summer La Niña) was also conducted. Due to limited and unequal sample sizes across groups caused by this interaction, these comparisons were not included in the quantitative models.

To investigate variation in the space use and ranging behavior of satellite-tagged goose-beaked whales in relation to ENSO phases and season, range-use ratios were calculated for each individual throughout their deployment. Range-use ratios (Webber et al. 2020) define the proportion of an individual's overall range that the individual uses over a specified time period (e.g. daily, weekly, monthly). Lower range-use ratio values (closer to 0) indicate more confined movements, and higher values (closer to 1) represent more wide-ranging movements (Webber et al. 2020). Here we would expect that lower range-use ratios would be indicative of beaked whales inhabiting areas with more abundant prey, and higher range-use ratios suggestive of beaked whales searching more widely for prey if it was less abundant. We used 7 d range use ratios for satellite-tagged beaked whales given the temporal scale of the tag data available (i.e. frequency of locations, deployment duration) and

what would remain ecologically relevant. For each tagged whale's 7 d segments, we calculated range-use ratios by dividing the core range of the 7 d period by the overall home range of the entire deployment (Webber et al. 2020). We used minimum convex polygons to estimate the core (50% isopleth) and overall (95% isopleth) home ranges ('adehabitatHR,' Calenge 2023). From there, ratios were compared among ENSO phases and season by calculating the grand mean and median (mean and median of all of each individual's mean and median values). To assess this relationship while accounting for individual variation, we used generalized additive mixed effects models (GAMMs) in the R package 'mgcv' (Wood 2006). Weekly range-use ratio was modeled as the response variable using a beta distribution with a logit link function. As in the sighting rate models, MEI was modeled as a smooth term with a penalized thin-plate regression spline (basis dimension size = 5) and season as a categorical parametric term. Because of limited data across all seasons, we grouped seasons into 2 categories: winter/spring and summer/fall. Individual ID was included as a random effect. Models were optimized using REML and variable selection was conducted with the same shrinkage approach described for analysis of sighting rates. Blainville's beaked whale tags were not included in this analysis due to insufficient data from the El Niño period. No tag or range-use ratio analyses were conducted in relation to PDO or NPGO cycles as the temporal span of the tag data set, and tag duration in general, is limited relative to the effects of these 2 phenomena on the environment.

3. RESULTS

3.1. Sighting and effort analyses

Between 2002 and 2022, survey efforts were made in 23 different periods during La Niña conditions (2105 h, 52.6% of total time), in 15 different periods during the neutral phase (1287 h, 32.1% of total time), and in 7 different periods during El Niño conditions (613 h, 15.3% of total time) off the leeward side of Hawai'i Island (Table 1). Coverage of survey effort and ENSO periods was roughly similar to but slightly biased towards La Niña periods based on the occurrence of those ENSO periods over the 21 yr span of the study (Fig. 1), during which 46.0% of months were those of La Niña conditions (n = 127), 37.7% were in the neutral phase (n = 104), and 16.3% were months of El Niño conditions (n = 45). Average Beaufort sea

Table 1. Summary of survey efforts and beaked whale sightings off Hawai'i Island for all months of effort, with months combined if consecutive or near consecutive and Multivariate ENSO Index (MEI) values taken from the month with the most effort. ENSO: El Niño—Southern Oscillation

Year	Season	Month	Effort (h)	ENSO period	MEI	Sightings per 100 h effort Blainville's	Goose-beaked
2002	Winter	April	28.7	Neutral	−0.4	3.5	0.0
2002	Summer	September	47.5	El Niño	0.7	2.1	8.4
2003	Spring	May	51.5	La Niña	−0.5	1.9	0.0
2003	Summer	October	127.6	Neutral	0.3	0.8	3.9
2004	Summer	September—October	105.1	El Niño	0.5	1.9	1.9
2004	Fall	November—December	91.0	Neutral	0.4	0.0	0.0
2005	Fall—Winter	January—February	88.8	Neutral	0.1	2.3	4.5
2006	Winter	March—April	177.1	La Niña	−0.8	2.3	1.1
2006	Spring	July	50.2	Neutral	0.2	0.0	0.0
2006	Fall	November—December	136.3	El Niño	0.8	2.2	5.9
2007	Summer	August	95.7	La Niña	−0.9	1.0	0.0
2008	Winter—Spring	April—May	168.9	La Niña	−1	0.0	1.2
2008	Spring	July	114.7	La Niña	−0.9	0.9	1.7
2008	Fall	December	65.2	La Niña	−1.1	0.0	3.1
2009	Winter—Spring	April—May	100.5	La Niña	−0.7	2.0	4.0
2009	Summer	October	68.8	El Niño	0.6	1.5	4.4
2009	Fall	December	71.1	El Niño	1.1	2.8	7.0
2010	Winter	April	81.3	Neutral	0.4	0.0	2.5
2010	Spring—Summer	July—August	116.8	La Niña	−2.5	1.7	1.7
2010	Fall	December	78.1	La Niña	−1.9	0.0	1.3
2011	Spring	May	58.3	La Niña	−1.3	1.7	0.0
2011	Summer	August—September	96.3	La Niña	−0.9	1.0	2.1
2011	Summer—Fall	October—November	192.7	La Niña	−1.4	0.5	3.1
2012	Summer	August	105.5	Neutral	−0.4	5.7	3.8
2012	Spring	May	218.7	Neutral	0	0.0	0.5
2013	Spring	May	110.9	La Niña	−0.9	0.0	1.8
2013	Summer—Fall	October—November	86.3	Neutral	−0.2	1.2	4.6
2014	Spring	July	78.2	Neutral	0.4	2.6	1.3
2014	Fall	November—December	136.6	Neutral	0.3	0.0	2.9
2015	Winter—Spring	April—June	93.0	El Niño	0.5	3.2	0.0
2015	Fall	November	90.4	El Niño	1.9	1.1	2.2
2016	Spring	July	59.2	Neutral	−0.5	1.7	1.7
2016	Summer	September	38.0	Neutral	−0.3	0.0	0.0
2017	Spring	June	81.1	La Niña	−0.6	0.0	0.0
2017	Summer	October	48.5	La Niña	−0.6	0.0	0.0
2018	Winter	April	45.0	La Niña	−1.3	0.0	0.0
2018	Summer—Fall	October—November	54.4	Neutral	0.2	1.8	0.0
2019	Winter	April	34.6	Neutral	0.3	2.9	5.8
2019	Summer—Fall	October—November	66.8	Neutral	0.4	3.0	6.0
2020	Spring	May—July	60.3	La Niña	−0.9	0.0	3.3
2020	Summer—Fall	August—November	62.0	La Niña	−1.2	1.6	3.2
2021	Winter—Spring	March—May	147.4	La Niña	−1	2.7	0.0
2021	Fall	November	74.1	La Niña	−1.4	0.0	5.4
2022	Spring	June	47.1	La Niña	−2.1	0.0	0.0
2022	Summer	October	54.1	La Niña	−1.7	1.8	5.5

state of effort (range = 0–6) was not significantly different between ENSO phases (Kruskal-Wallis test, p = 0.054). There was more effort in the summer (1357 h, 14 periods) than in the spring (986 h, 12 periods), fall (953 h, 11 periods), or winter (708 h, 8 periods). Survey effort for ENSO periods was also markedly biased towards the summer and fall, with only 1 effort period during winter El Niño conditions and none during spring El Niño conditions. There were 54 total sightings of Blainville's beaked whales (21 during La Niña, 18 during neutral periods, and 15 during El Niño) and 96 sightings of goose-beaked whales (38 during La Niña, 31 during neutral periods, and 27 during El Niño) over the course of the study period (Table 1, Fig. 2). Based on sighting values during contiguous periods of effort, median sighting rates were higher for both species during El Niño periods (Fig. 3). Blainville's were sighted more than twice as often during El Niño (SPUE median = 2.1) than La Niña (SPUE median = 0.9; Kruskal-Wallis test, p = 0.042; post hoc Wilcoxon test for pair, p = 0.021). Goose-beaked whales were also sighted more than twice as often during El Niño (SPUE median = 4.4) compared to La Niña (SPUE median = 1.7), although this difference was not significant (Kruskal-Wallis test, p = 0.090). They were both sighted at comparatively moderate rates during the neutral phase (Blainville's SPUE median = 1.2, goose-beaked whale SPUE median = 2.5); no statistical differences in sighting rates between neutral and other phases were found. Goose-beaked whale sighting rates typically increased with MEI strength, with 3 of the 4 highest sighting rates (SPUE = 5.8–8.4) occurring during higher weak (MEI = 0.7, 0.8) and moderate (MEI = 1.1) Central Pacific El Niño periods. Lower sighting rates occurred during weaker El Niño periods, as well as the only period of effort during an Eastern Pacific El Niño event (MEI = 1.9, SPUE = 2.2). The
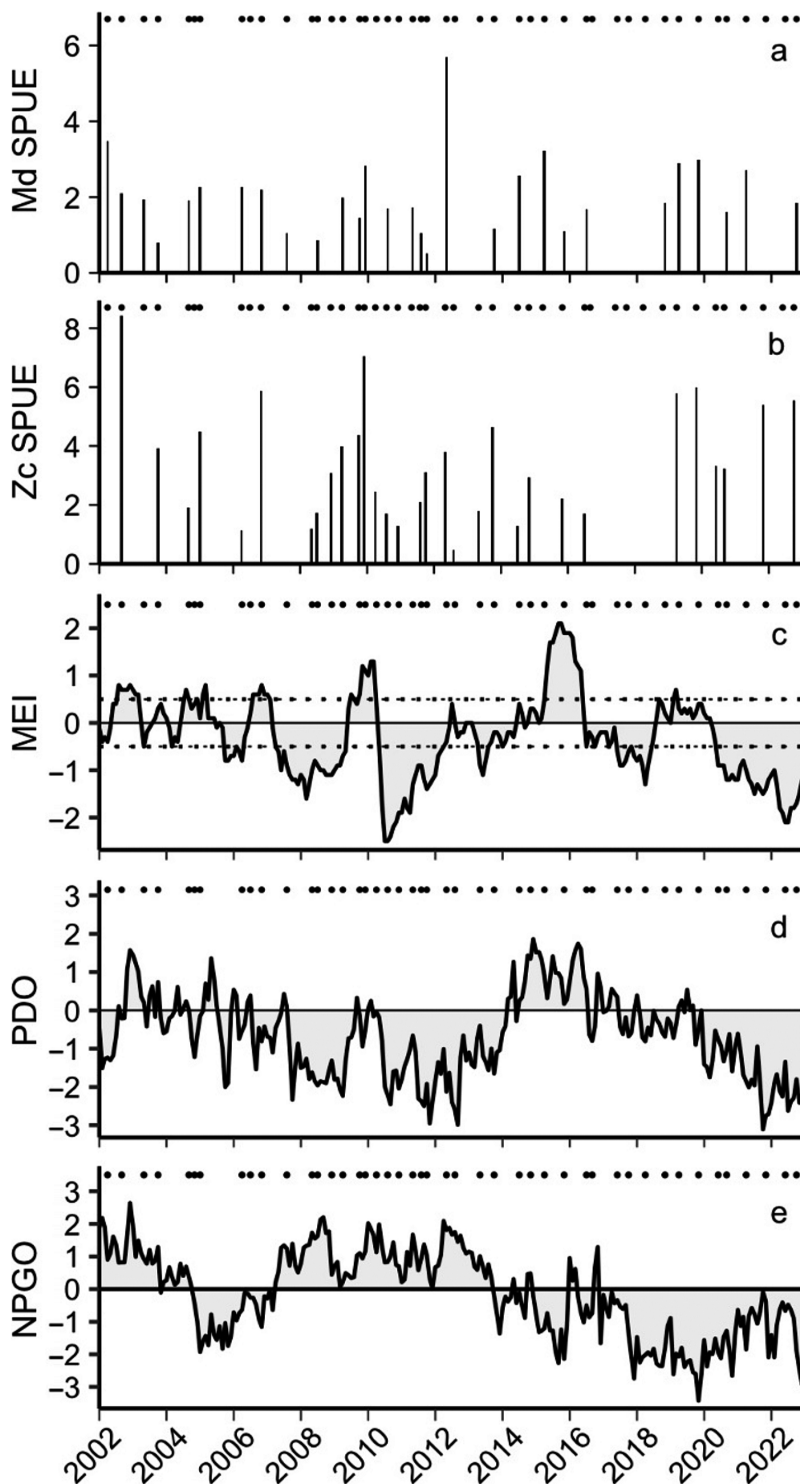
Fig. 1. Timeseries of sighting rates (sightings per unit effort, SPUE) for (a) Blainville's beaked whales *Mesoplodon densirostris* (Md) and (b) goose-beaked whales *Ziphius cavirostris* (Zc). Also shown are (c) Multivariate ENSO Index (MEI; proxy for El Niño–Southern Oscillation phase), (d) Pacific Decadal Oscillation (PDO), and (e) North Pacific Gyre Oscillation (NPGO) values throughout the course of this study. The dotted lines in the MEI plot represent the transition points at 0.5 and −0.5, which delimit the neutral phase between El Niño and La Niña conditions. The black dots at the top of each plot indicate months of effort

same pattern was not noted for Blainville's beaked whales, although the month of effort off Hawai'i Island during that strong Eastern Pacific El Niño event featured the lowest sighting rate of that species overall during El Niño periods (SPUE = 1.1). Killer whales, a potential predator of both species, were not sighted off Hawai'i Island during El Niño conditions during our study period, although there were sightings during El Niño conditions in the decade prior (Table S2). They were observed in the waters off of the leeward side of Hawai'i in all seasons through the study period, although they were sighted more often during the spring (n = 10) than fall (n = 6), summer (n = 5), or winter (n = 1).

Blainville's beaked whales were encountered in slightly larger groups during La Niña phases (mean = 4.1 ± 2.6, median = 4, range 1–11) than during El Niño (mean = 3.8 ± 2.4, median = 3, range 1–9) or the neutral phase (mean = 3.5 ± 2.2, median = 3, range = 1–9), although these differences were not statistically significant (Kruskal-Wallis test, p = 0.388; Fig. S1a). In contrast, goose-beaked whales had larger group sizes during El Niño phases (mean = 2.6 ± 1.3, median = 3, range = 1–5), with smaller average group sizes during La Niña and the neutral phase (means = 2.1 ± 1.1, medians = 2, range = 1–5 for both), but these differences were also not statistically significant (Kruskal-Wallis test, p = 0.209; Fig. S1b). Group sizes for Blainville's beaked whales across season were larger in the spring (mean = 4.8 ± 2.5, median = 4) and fall (mean = 4.4 ± 2.4, median = 4) than in the summer (mean = 3.3 ± 2.9, median = 2) or winter (mean = 2.8 ± 1.5, median = 3), but again, these differences were not statistically significant (Kruskal-Wallis test, p = 0.165; Fig. S2a). Goose-beaked whale group sizes across seasons were similar during summer (mean = 2.4 ± 1.2, median = 2), fall (mean = 2.3 ± 1.1, median = 2), and spring (mean = 2.1 ±
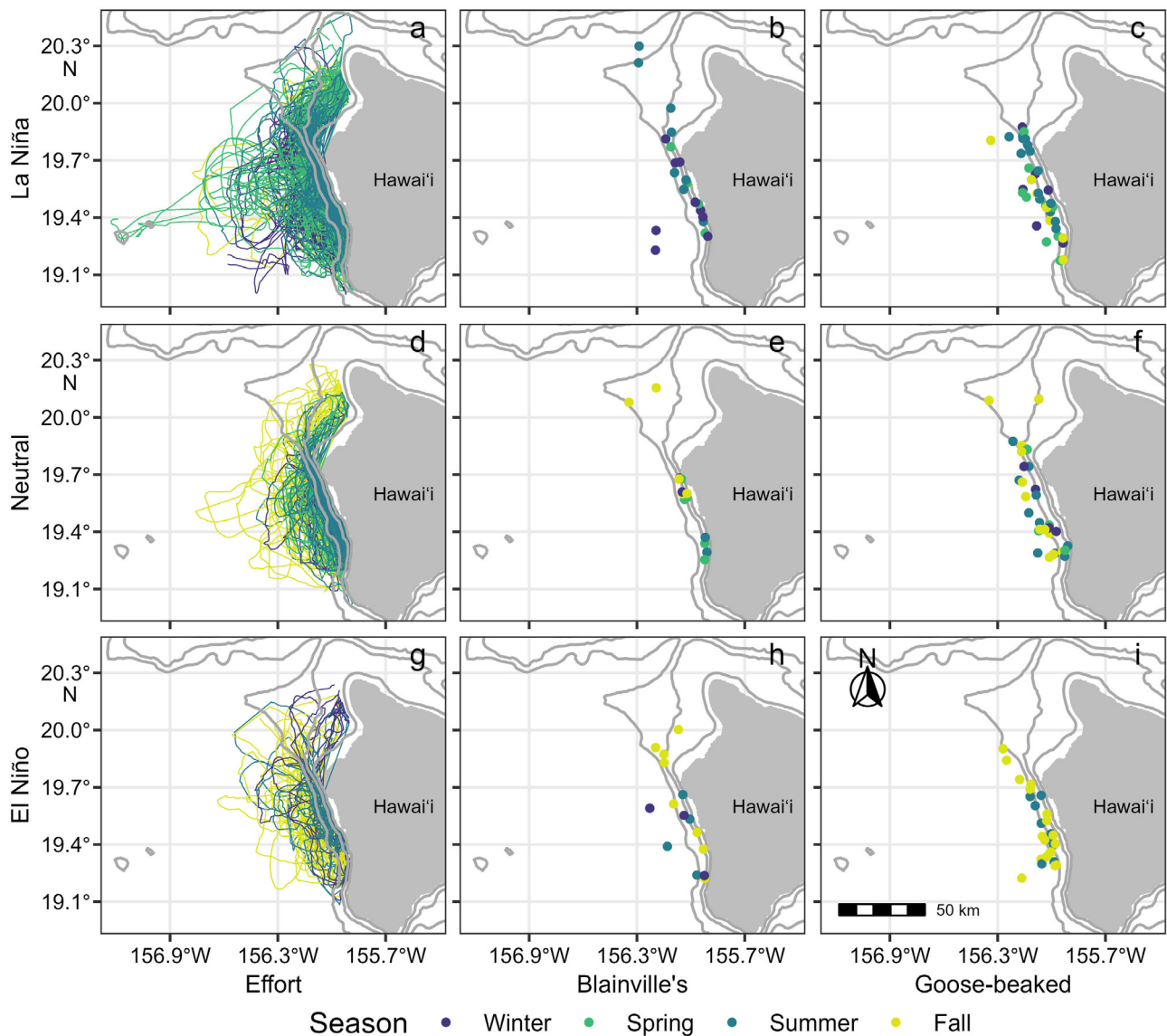
Fig. 2. (a,d,g) Effort tracklines along with sightings of (b,e,h) Blainville's beaked whales and (c,f,i) goose-beaked whales off the leeward coast of Hawai'i during La Niña periods (a–c), neutral periods (d–f), and El Niño periods (g–i). The gray lines indicate the 200, 1000, and 2000 m isobaths, and different colors indicate the oceanographic season of majority effort or sighting period

1.3, median = 2) but slightly lower during winter (mean = 1.6 ± 1.3, median = 1; Kruskal-Wallis test, p = 0.102; Fig. S2b).

Regarding the PDO index, effort was conducted during 27 periods of cold conditions, 14 periods of neutral conditions, and 4 periods of warm conditions. Sighting rates were highest for Blainville's during neutral PDO periods (SPUE mean = 1.5 ± 1.1, median = 1.7), followed by warm (SPUE mean = 1.4 ± 1.4, median = 1.2) and cold PDO conditions (SPUE mean = 1.2 ± 1.4, median = 1.0), although this relationship was not statistically significant (Kruskal-Wallis test, p = 0.674). Goose-beaked whales were

sighted at slightly higher rates during periods of neutral conditions (SPUE mean = 2.8 ± 2.7, median = 2.1) than cold (SPUE mean = 2.2 ± 2.2, median = 1.7) or warm conditions (SPUE mean = 2.1 ± 1.7, median = 2.3), but this relationship was also not statistically significant (Kruskal-Wallis test, p = 0.784). For NPGO index values, which were split mostly evenly into 23 and 22 periods of negative and positive conditions, respectively, Blainville's were sighted at similar rates during negative (SPUE mean = 1.3 ± 1.2, median = 1.6) and positive NPGO periods (SPUE mean = 1.3 ± 1.4, median = 1.0). Goose-beaked whales were sighted at higher rates during periods of positive
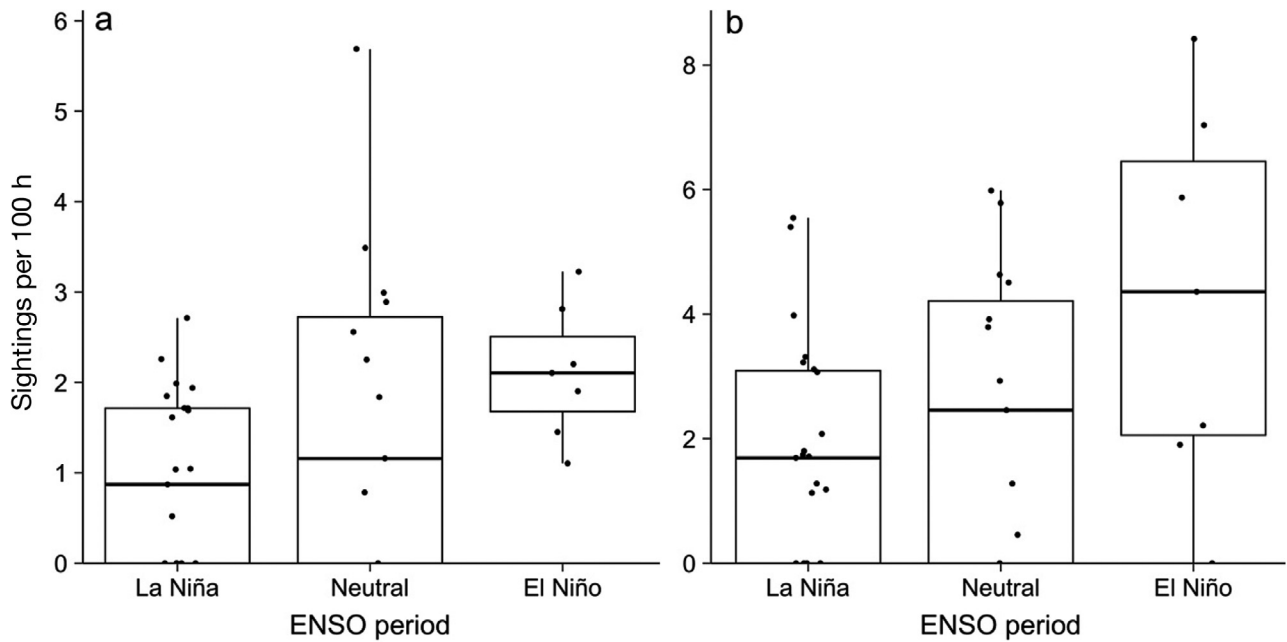
Fig. 3. (a) Blainville's beaked whale and (b) goose-beaked whale monthly sighting rates (sightings per 100 h of effort) by ENSO phase, with months combined into continuous periods as in Table 1 and monthly sighting rate values jittered to avoid visual overlap. The horizontal line within each box represents median values, with lower and upper box lines representing the 25th and 75th quartiles, respectively. Vertical lines emerging from boxes showcase 1.5 times the interquartile range. Note that the y-axis scales differ for each graph

NPGO values (SPUE mean = 2.5 ± 2.2, median = 2.0) than negative (SPUE mean = 2.2 ± 2.4, median = 1.3). Neither relationship was statistically significant (Kruskal-Wallis test, Blainville's, p = 0.754; goose-beaked, p = 0.475).

Seasonal analyses indicated that Blainville's beaked whale sighting rates were highest in winter (SPUE mean = 2.1 ± 1.3, median = 2.5) but similar between fall (SPUE mean = 1.2 ± 1.3, median = 1.1), spring (SPUE mean = 1.2 ± 1.7, median = 0.4), and summer (SPUE mean = 1.1 ± 0.7, median = 1.1). Goose-beaked whales were sighted at higher rates during fall (SPUE mean = 3.5 ± 2.5, median = 3.1) and summer (SPUE mean = 2.8 ± 2.5, median = 2.6) than winter (SPUE mean = 1.7 ± 2.2, median = 0.6) or spring (SPUE mean = 1.2 ± 1.3, median = 1.2). No significant relationship between sighting rate and season was found for either Blainville's beaked whales (Kruskal-Wallis test, p = 0.192) or goose-beaked whales (Kruskal-Wallis test, p = 0.077).

Considering all variables collectively, the fitted GAMs generally supported the same trends observed in univariate comparisons, with some slight differences. The goose-beaked whale model (16.0% deviance explained; Fig. 4; Table S3) indicated a statistically significant effect of season, with sighting rates being highest in fall compared to spring (p = 0.005) and winter (p = 0.012). MEI had a slight, non-significant linear effect on goose-beaked whale sighting rates, with sightings increasing with increasing MEI value (edf = 0.2; p = 0.254), while there was no evidence for an effect of NPGO and PDO on sighting rates (edf < 0.0001 for both; p = 0.797, p = 0.668, respectively). The Blainville's beaked whale model (11.7% deviance explained; Fig. 5; Table S4) indicated a slightly stronger linear effect of MEI on sighting rates compared to goose-beaked whales, although this did not have a statistically significant effect (edf = 0.6; p = 0.127). There was no statistically significant relationship with season (Table S4), although rates were slightly higher in the winter compared to fall (p = 0.079; Fig. 5). There was a weak, decreasing linear effect of NPGO (edf = 0.1; p = 0.288) and no effect of PDO (edf < 0.0001; p = 0.638) on Blainville's beaked whale sighting rates.

Looking at a potential link between oceanographic seasons and ENSO events, visual inspections indicate that Blainville's beaked whale sighting rates were less variable within seasons during El Niño phases (at least for summer and fall with sufficient sample sizes), and more variable among seasons during neutral and La Niña phases (Fig. 6a).
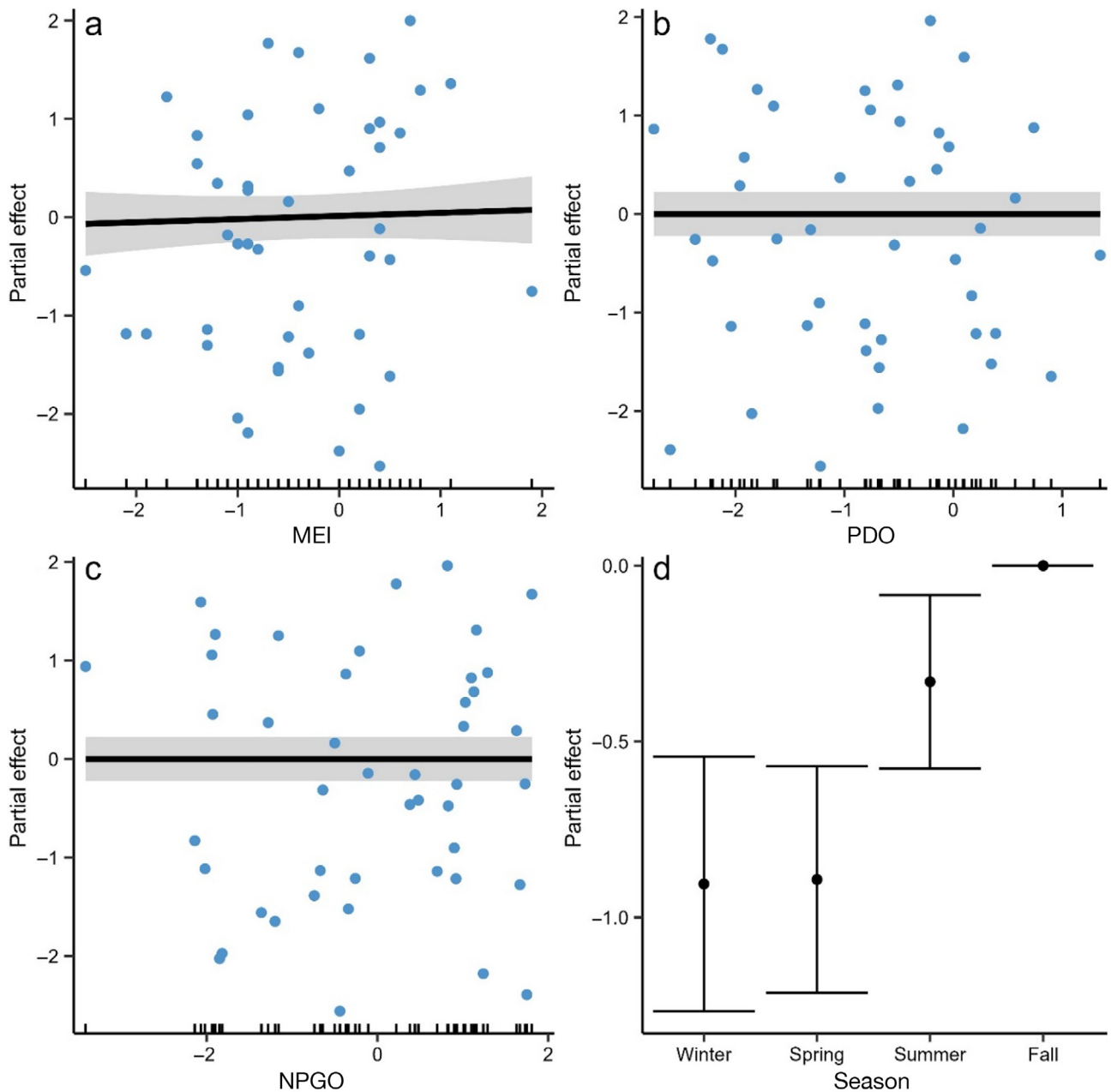
Fig. 4. Generalized additive model partial effects plots of (a) MEI, (b) PDO, (c) NPGO, and (d) season on sighting rates for goose-beaked whales. Fitted lines are black, and the gray shaded ribbons represent the 95% confidence intervals. Partial residuals are plotted as blue points, and the distributions of the data points are shown as vertical lines on the *x*-axis. For season, the partial residuals are represented by points for each season and vertical lines above and below represent 95% confidence intervals

Sighting rates for goose-beaked whales were highest during El Niño events for summer and fall (Fig. 6b), while seasons in periods of neutral values appeared similar throughout the year. During La Niña events, goose-beaked whale sighting rates throughout the year appeared to gradually increase from the winter to a peak in the fall.

3.2. Satellite telemetry analyses

Between 2006 and 2013, 13 Blainville's beaked whales were tagged off Hawai'i Island, although 1 individual was believed to be from an open-ocean population (Baird et al. 2011) and is not considered further. After accounting for pseudoreplication, data
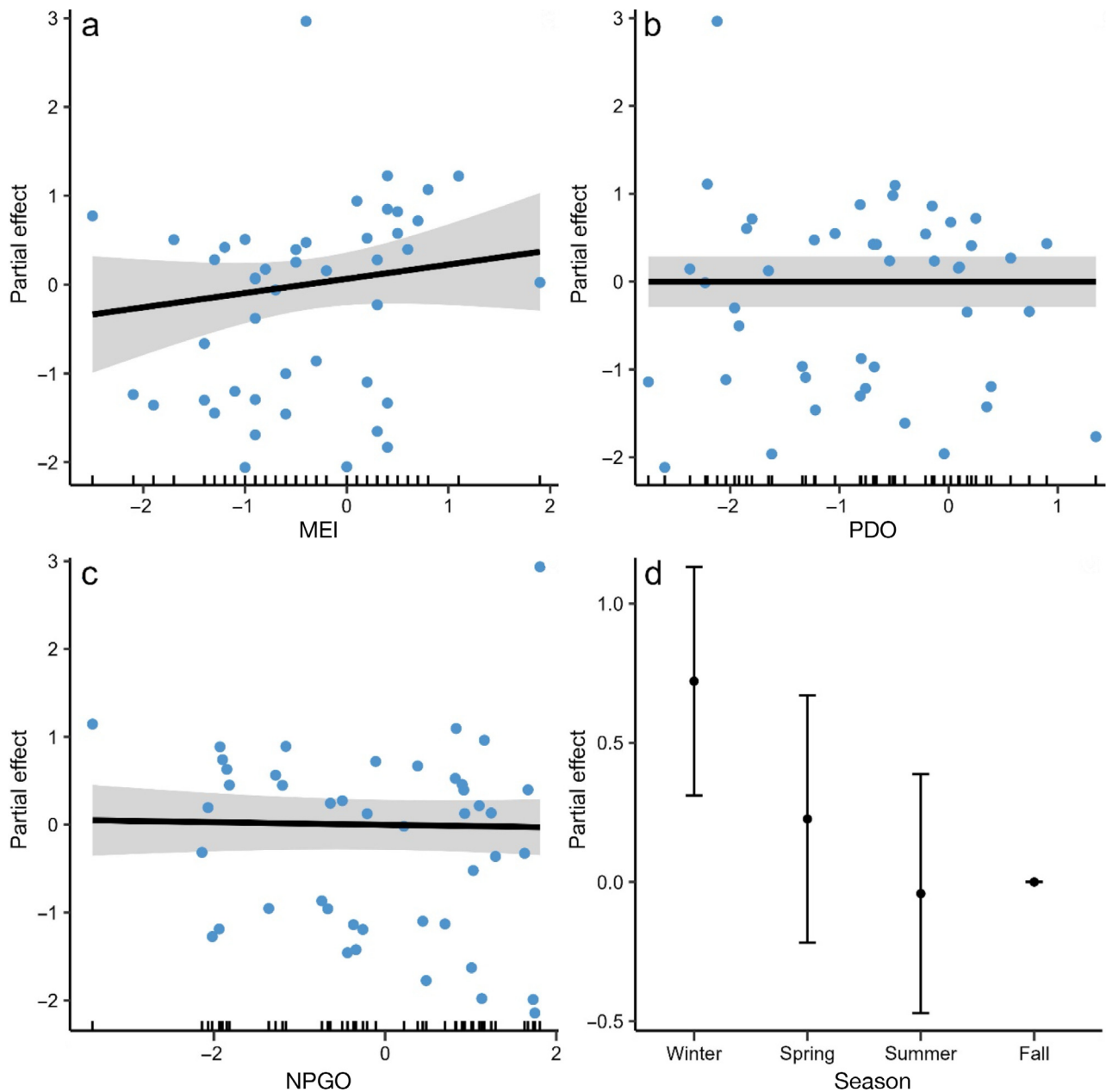
Fig. 5. As in Fig. 4, but for Blainville's beaked whales

from 10 tags deployed on Blainville's beaked whales were incorporated in analyses (Table 2). The tagged Blainville's beaked whales included individuals of both sexes, and based on photo-identification results, no individual was tagged more than once (Table 2). Blainville's beaked whale tag deployments covered El Niño phases (2 males and 1 female, 53 d of data; all during the weak Central Pacific El Niño event in the winter of late 2006), neutral phases (1 male, 1 female, and 1 unknown sex, 249 d of data; between 2 separate

events), and La Niña phases (3 females and 1 male, 240 d of data; between 2 separate events). Tagged Blainville's (Fig. 7) typically stayed on the leeward side of Hawai'i Island regardless of the ENSO phase, with the exception of 2 individuals (1 female and 1 male) that traveled north of Maui Nui during neutral and La Niña phases and 1 female that undertook a westward excursion during the neutral phase of mid-2012, after 24 mo of mostly moderate to strong La Niña conditions. During that same period, 1 of the
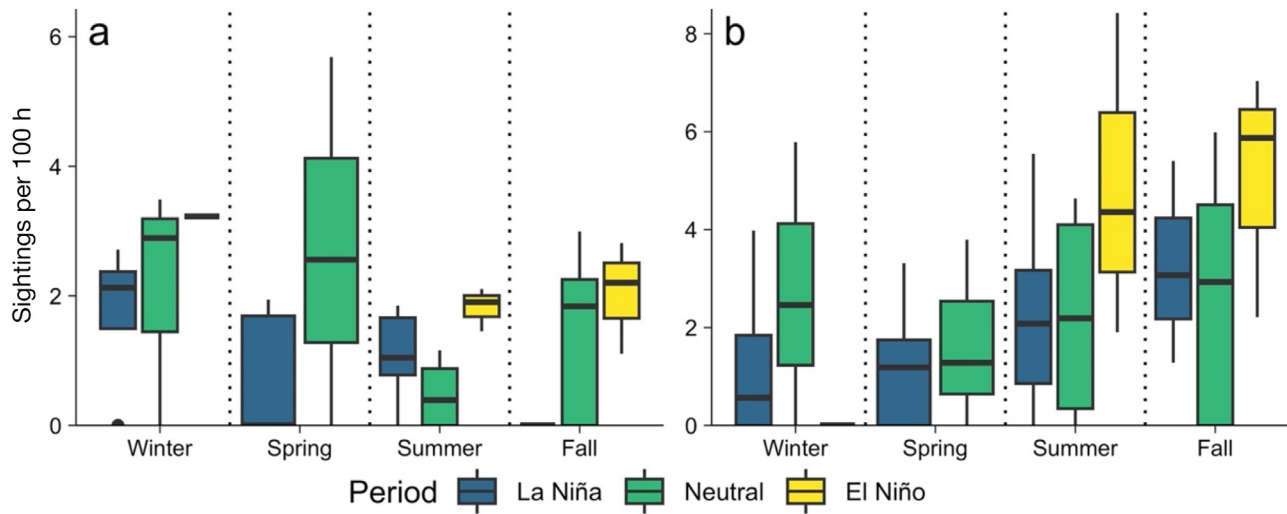
Fig. 6. (a) Blainville's beaked whale and (b) goose-beaked whale monthly sighting rates (sightings per 100 h of effort) by season and ENSO phase, with months combined into continuous periods as in Table 1. Box plot parameters as in Fig. 3

Table 2. Details on satellite tag deployments for Blainville's whales *Mesoplodon densirostris* (Md) and goose-beaked whales *Ziphius cavirostris* (Zc) used in this study. Season is based on oceanographic season in Hawai'i (Flament et al. 1996). CP: Central Pacific; EP: Eastern Pacific

Tag ID	Individual ID	Sex	Year	Season(s)	Month(s)	Duration (d)	ENSO phase ('flavor')
MdTag001	HIMd118	Male	2006	Fall	Nov−Dec	22.7	El Niño (CP)
MdTag002	HIMd120	Male	2006	Fall	Nov−Dec	15.1	El Niño (CP)
MdTag003	HIMd001	Female	2006	Fall	Dec	14.8	El Niño (CP)
MdTag004	HIMd025	Female	2008	Spring/Summer	Jul−Sep	62.6	La Niña
MdTag006	HIMd007	Female	2008	Spring/Summer	Jul−Sep	63.2	La Niña
MdTag007	HIMd148	Female	2008	Spring/Summer	Jul−Sep	71.2	La Niña
MdTag012	HIMd121	Male	2011	Summer/Fall	Oct−Dec	43.1	La Niña
MdTag013	HIMd206	Male	2012	Spring/Summer	May−Oct	158.8	Neutral
MdTag014	HIMd066	Female	2012	Spring	May−July	74.2	Neutral
MdTag015	HIMd198	Unknown	2013	Summer/Fall	Oct−Nov	16.2	Neutral
ZcTag002	HIZc027	Female	2008	Spring	May	12.4	La Niña
ZcTag003	HIZc008	Male	2008	Spring	May	22.8	La Niña
ZcTag006	HIZc041	Male	2009	Winter/Spring	Apr−Jun	36.2	La Niña[a]
ZcTag008	HIZc068	Female	2009	Summer/Fall	Oct−Nov	25.5	El Niño (CP)
ZcTag009	HIZc007	Female	2010	Winter/Spring	Apr−Jun	7.4	Neutral
ZcTag012	HIZc013	Female	2010	Fall	Dec	16	La Niña
ZcTag013	HIZc011	Female	2010/2011	Fall	Dec−Jan	43.8	La Niña
ZcTag018	HIZc076	Female	2011	Summer/Fall	Oct−Nov	32.4	La Niña
ZcTag033	HIZc101	Unknown	2014	Fall	Nov−Dec	13.2	Neutral
ZcTag044	HIZc102	Female	2015	Fall	Nov−Dec	49.5	El Niño (EP)

[a]ZcTag006 spent the last 4 d of its duration in a neutral Multivariate ENSO Index period

northbound individuals began its travels heading northwest off O'ahu. The other headed north 7 mo earlier after several months of moderate La Niña conditions, after which it turned around and remained in the escarpment/abyssal area to the northeast of the tip of Hawai'i Island (an area which no other tagged Blainville's used).

Ten goose-beaked whales were satellite tagged between 2008 and 2015, and data from all individuals were used in the analyses. The tagged goose-beaked whales included individuals of both sexes, and based on photo-identification results, no individual was tagged more than once (Table 2). Goose-beaked whale tag deployments covered El Niño phases (2
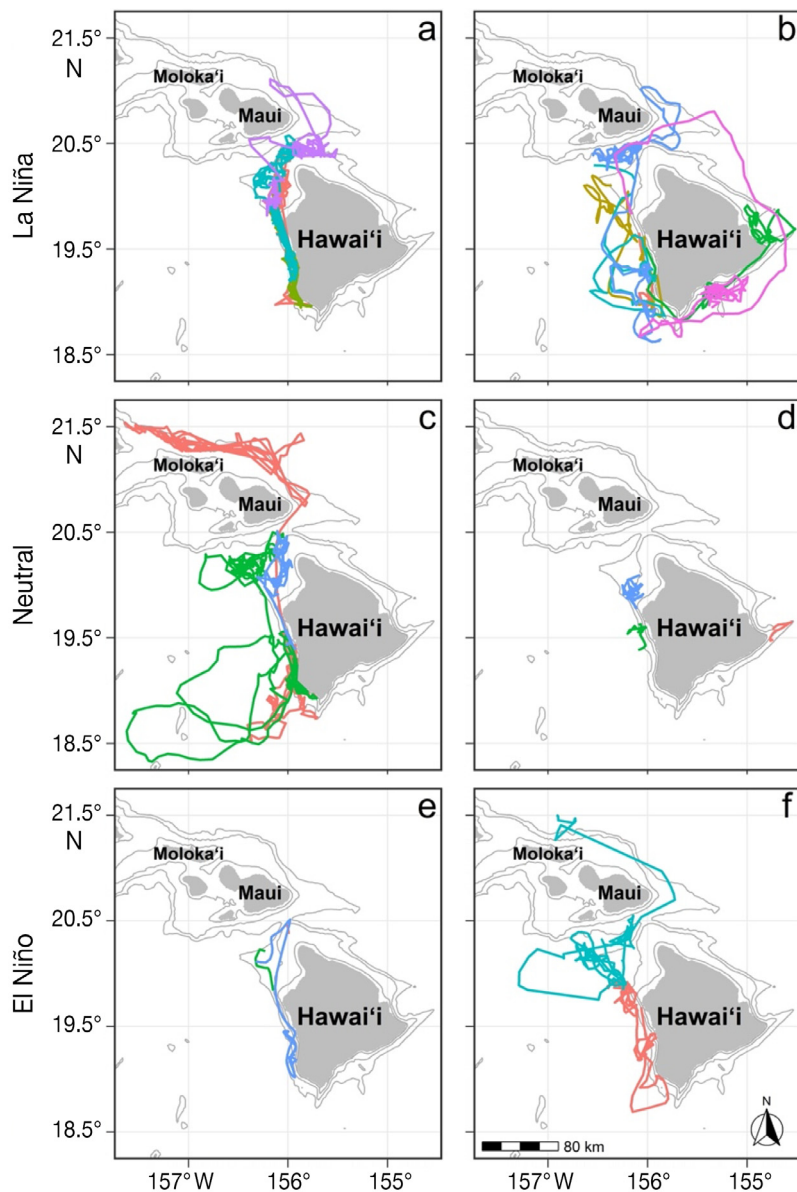
Fig. 7. (a,c,e) Blainville's beaked whale and (b,d,f) goose-beaked whale movement model estimated positions at a 4 h time step and rerouted around land using a 300 m isobath, by ENSO cycle period (a,b: La Niña; c,d: neutral; e,f: El Niño). Track colors represent each deployment and the gray lines indicate the 200, 1000, and 2000 m isobaths Note: the tags in Panel (f) each represent a 'flavor' of El Niño, with the top (teal) tag during the 2015 Eastern Pacific ENSO event and the bottom (red) tag during the 2009 Central Pacific ENSO event

sitioned towards a neutral phase. Both tagged whales that used the east side of the island (1 male and 1 female) did so after extended periods of La Niña (26 mo for the spring/summer 2009 individual and 19 mo for the fall/winter 2011 individual). Two individuals (both females) traveled north of Maui, 1 during the winter of 2010 (after several months of strong La Niña, MEI between −1.7 and −2.5), and 1 during the fall/winter of 2015 after several months of strong Eastern Pacific El Niño (MEI between 1.2 and 2.1). Transmissions from the female tagged in 2015 were last received with it heading west, north of Moloka'i, in the winter of 2015. Another female, tagged during the Central Pacific El Niño event in 2009, stayed on the leeward side of the island for the entire 25 d of its tagging duration.

Among ENSO phases, average range use weekly ratio values (Table 3) were lower for goose-beaked whales during El Niño periods (grand mean = 0.065, grand median = 0.045; n = 2 individual tags across 12 wk) and La Niña periods (grand mean = 0.103, grand median = 0.055; n = 6 individual tags across 26 wk) than neutral phases (grand mean = 0.130, grand median = 0.130; n = 2 individual tags across 4 wk). Considerable variability between range-use ratios was noted as well; only 2 of the 12 weeks of data during El Niño periods were above a range-use value of 0.10, with 1 week belonging to each individual, respectively. Only 1 tag had any weeks of range-use values close to 0.5: ZcTag002 (0.48, week 1 of 2), during a La Niña period. One individual, ZcTag006, had a very short weekly range-use period at the end of its duration that was just 2 d into a period of neutral conditions. Similarly, the final 2 d of the previous week also fell under neutral conditions, so all 4 d of neutral MEI values for this individual were removed from this analysis. Weekly range-use ratio values for goose-beaked whales were higher in winter/spring (grand mean = 0.122, grand median = 0.114, n = 4 individual tags across 13 wk) than summer/fall (grand mean = 0.086, grand median =

females, 75 d of data; during 1 Central Pacific and 1 Eastern Pacific event), neutral phases (1 female, 1 male, 1 unknown sex, 25 d of data; between 2 separate events), and La Niña phases (4 females, 2 males, 160 d of data; between 2 separate events). Tagged goose-beaked whales (Fig. 7) only traveled to the windward (east) side of Hawai'i Island during La Niña periods, although 1 tagged male ended there as the cycle tran-

Table 3. Summaries of weekly range-use ratio values for tagged goose-beaked whales in each phase of the ENSO cycle. 'Season' is based on oceanographic season in Hawai'i (Flament et al. 1996). CP: Central Pacific; EP: Eastern Pacific

Tag	ENSO phase ('flavor')	Season(s)	Weekly periods (n)	Mean	Median	Range	SD
ZcTag002	La Niña	Spring	2	0.27	0.27	0.06−0.48	0.29
ZcTag003	La Niña	Spring	4	0.09	0.07	0.02−0.19	0.08
ZcTag006	La Niña[a]	Winter−Spring	6	0.04	0.02	0.01−0.09	0.04
ZcTag008	El Niño (CP)	Summer−Fall	4	0.10	0.08	0.01−0.22	0.09
ZcTag009	Neutral	Winter	1	0.09	0.09	0.02−0.15	0.09
ZcTag012	La Niña	Fall	3	0.12	0.13	0.07−0.15	0.04
ZcTag013	La Niña	Fall	7	0.04	0.04	0−0.11	0.04
ZcTag018	La Niña	Summer−Fall	5	0.06	0.02	0−0.20	0.09
ZcTag033	Neutral	Fall	2	0.17	0.17	0.13−0.21	0.05
ZcTag044	El Niño (EP)	Fall	8	0.03	0.01	0−0.12	0.04

[a]ZcTag006 spent the final weekly period of its duration in a neutral Multivariate ENSO Index period, which is reflected in the summary statistics provided in Section 3.2

0.075, n = 6 individual tags across 29 wk). While accounting for individual variability, analyses indicated that weekly range-use ratios were not significantly affected by ENSO (GAMM; edf < 0.0001, p = 0.666) nor season (p = 0.415; Table S5). While not statistically significant, there was some evidence for individual variation (p = 0.083).

4. DISCUSSION

Based on sighting rates and satellite tag data, goose-beaked whales exhibit a potential preference for the nearshore waters off the leeward side of Hawai'i Island during periods of El Niño conditions, which is especially apparent when just looking at the Central Pacific flavor of El Niño. The only period without sightings of one species during El Niño conditions was during the very weak beginning of the Eastern Pacific El Niño event of April 2015, which came after over a year of neutral conditions. Oceanographic season also appears to influence sighting rates of goose-beaked whales, with higher rates during the summer and fall. Furthermore, the windward side of the island, which has more direct exposure to trade winds and the wet season, was only used by tagged individuals of this species after many months of La Niña periods. One tagged goose-beaked whale moved to the waters north of Moloka'i during the winter Eastern Pacific El Niño event of 2015−16, suggesting the possibility that there may be different responses in relation to the 2 flavors (Eastern Pacific or Central Pacific) of El Niño events. While not statistically significant, this positive effect of El Niño conditions on sighting rates was preserved (albeit

weakly) after considering other variables (season, NPGO, PDO) in a comprehensive model. Given our small sample sizes, this suggests some biological significance of these findings, and additional research on goose-beaked whales and climate is clearly warranted.

Similarly, although the results do not indicate strong evidence for an effect of interannual climatic phenomena on Blainville's beaked whales, the differences in sighting rate for this species between different phases of the ENSO cycle are still striking, with individuals on the leeward slopes of Hawai'i Island sighted at more than twice the rates during El Niño periods than during La Niña periods (Fig. 3). Sighting rates for this species stayed very consistent during El Niño events, with each contiguous period having between 1.0 and 2.6 sightings per 100 h of effort off Hawai'i Island. This is in contrast to the results of Ziegenhorn et al. (2023b), in which acoustic detections of both species increased off Hawai'i Island during La Niña conditions. A possible explanation for this difference is that the acoustic recorder from that study was in about 650 m depth, with a limited detection range (~2 km), and was thus only capturing beaked whale acoustic presence over a relatively small and comparatively shallow (particularly for goose-beaked whales) part of their range. Similarly, there are slight differences between our findings on seasonal variation and those reported by Baumann-Pickering et al. (2014) and Ziegenhorn et al. (2023a). For example, goose-beaked whale acoustic detection rates were lower during the summer months in Ziegenhorn et al. (2023a), while sighting rates were relatively high during this season in our study. These discrepancies could be due to the same reasons described above,

but also a result of our use of oceanographic seasons (Flament et al. 1996), which are defined by slightly different month-breaks than traditional seasons (offset by a single month), or by the addition of nighttime and near-continuous acoustic monitoring. It is also possible that the water depths beaked whales use may shift seasonally or in response to ENSO cycles (e.g. moving slightly shallower or slightly deeper), but our sample size of sightings and effort in specific depth ranges is insufficient to address this question. Similarly, it is possible that beaked whale movements may vary on smaller spatial scales in different ENSO phases, e.g. moving inshore and offshore more regularly during one phase or another, which would influence acoustic detections at a fixed site. This highlights the importance of assessing the influence of large-scale climatic phenomena on species' distributions using a variety of methods that capture different spatial and temporal scales. Also notable is the complete lack of sightings of either species after the 2015—16 El Niño period, from September 2016 until November 2018. Sighting rates appeared to drop off during that Eastern Pacific El Niño event (the only flavor of its kind noted here), and 1 individual (ZcTag044) was tracked north of Maui in December 2015 after being tagged off Hawai'i Island in November of that year. Hasson et al. (2018) noted a persisting basin-wide sea surface salinity anomaly around 20° N starting in October 2015, which had not previously been observed in this region. Through shifts in ocean dynamics (e.g. shifts in currents and evaporation), this El Niño-driven anomaly of high salinity levels could have influenced the beaked whale prey base in a manner that subsequently altered the space use by both species off of Hawai'i Island. Ziegenhorn et al. (2023b) also noted a similar drop in acoustic detections for goose-beaked whales around this time. Clearly, the uniqueness of each ENSO event highlights the need for further research on the influence of dynamic environmental variables in association with the distribution of these species.

A relative lack of data for tagged goose-beaked whales during periods of neutral conditions, with 2 comparatively short tag deployments and one 4 d period when a longer deployment transitioned into a neutral period, was likely unable to capture the full range of movements for this species. Weekly neutral range-use especially was grossly underestimated in proportion to the amount of time spent in neutral phases, leading to potentially overinflated range-use values due to short tag durations. While the results suggest that tagged goose-beaked whales exhibited more extensive use patterns on a weekly basis during La Niña periods than El Niño, the GAMM indicated that individual variability likely explains a more meaningful amount of this variation. This is not unexpected, as localized environmental conditions, varying over shorter time scales than season and ENSO, may better influence beaked whale space use decisions within a given deployment period. Given the small amount of data going into this model (42 observations), and variation in tag attachment duration (Table 2), more tag data will be useful in characterizing variation in ranging behavior between season and ENSO phases.

Overall, our effort and tag data were biased towards La Niña conditions. In particular, tag data from Blainville's beaked whales were limited during El Niño periods and on goose-beaked whales during both El Niño and neutral periods. La Niña has been the most common period of the ENSO cycle since 2000, and thus it is slightly overrepresented in all aspects of this study. Future efforts should focus on obtaining more sightings and tag deployments during these data-limited periods (neutral conditions and El Niño). Survey efforts are also seasonally biased towards summer, so increasing coverage during other seasons could aid in our understanding of seasonal variation in occurrence and space use of these species. Broader spatial coverage in effort, including effort on the windward side of Hawai'i Island, would be greatly beneficial for uncovering the relationships of these species with climatic variables. Unfortunately, poor weather conditions that typify windward environments are generally unsuitable for small-boat field work. To our knowledge, Blainville's beaked whales have never been documented on the windward side of Hawai'i Island (Mobley et al. 2000, Baird 2016, Kratofil et al. 2023). The use of passive acoustic monitoring methods (e.g. Ziegenhorn et al. 2023b) could be a valuable alternative for obtaining species occurrence data in such windward environments.

Any positive effects of El Niño or season on the presence of both species, as well as the more localized spatial usage during El Niño periods for goose-beaked whales, could be a result of shifts in prey distribution, as observed with other species of odontocetes (Simmonds & Isaac 2007, Sprogis et al. 2018). While there has been very little research on the specific diets of these populations, several Pacific squids and fishes have been noted to shift their distribution or increase recruitment during periods of El Niño conditions. These include ommastrephids (Chen et al. 2007, Keyl et al. 2008), which at least partially make up the diet of other Pacific populations of goose-beaked whale (West et al. 2017), and several

species of mesopelagic planktivore and piscivore fishes in the California Current (Koslow et al. 2014). At a seasonal scale, variations in nutrient abundance driven by higher rainfall on the windward side of the island during wet months and increased rainfall on the leeward side during the islands' dry season (Huang & Chen 2019) could result in shifts in prey dynamics. Little to no research has been done on the effects of different ENSO phases or season on known Blainville's beaked whale prey species (Abecassis et al. 2015, K. West pers. comm.), or on the populations of mesopelagic micronekton that form the basis of this food web.

Predation risk is thought to be a motivator for much of beaked whale behavior (Aguilar de Soto et al. 2012, 2020, Baird 2019). It is possible that the presence of killer whales, a comparatively rare but potential predator of both species in Hawaiian waters (Baird et al. 2006, McSweeney et al. 2007, Baird 2016), could influence beaked whale space use. Unlike either goose-beaked or Blainville's beaked whales, killer whales are not resident to the Hawaiian Islands, so these oceanic groups may be influenced by the effects of ENSO cycles in different areas that could theoretically draw them to or away from the central Pacific. Beaked whales in other regions have been documented to reduce their vocalizations in shallow depths (Aguilar de Soto et al. 2012; during ascents from vocal dives or above 170 m in the water column), and this is suspected to be a predator-avoidance strategy (Tyack et al. 2006). Off Hawai'i Island, no killer whale sightings occurred in the El Niño periods during the time frame of this study (Table S2), although some occurred shortly after El Niño winters (including the highest number of sightings in the summer of 2016, when both beaked whale species were completely absent from our sighting efforts). Shifts in the distribution of central Pacific killer whales during different phases of the ENSO cycle have not been previously noted, and predation risk may be a strong enough motivator to deter beaked whales from the area during certain La Niña and neutral conditions. Where beaked whales may move to, to avoid overlap with killer whales, is unclear. The slightly larger group sizes noted for Blainville's beaked whales during La Niña periods could be a result of increased predation pressure, although this trend is not significant and does not carry over to goose-beaked whales, for which the differences in group size are less apparent between phases (Fig. S2).

Both goose-beaked and Blainville's beaked whales are also at least occasionally attacked by large sharks in Hawai'i, likely tiger *Galeocerdo cuvier* and white

sharks *Carcharodon carcharias* (McSweeney et al. 2007, Baird 2016). White sharks specifically have been observed attacking juvenile goose-beaked whales off California (Long & Jones 1996). Tiger sharks have been noted to undertake large annual migrations in association with SST, although a connection with ENSO cycles has not yet been observed (Holland et al. 2019) outside of the East Australian Current (Niella et al. 2022). While no discernible relationship with El Niño events has been found for Pacific white sharks, a complete absence of records for this species at boreal latitudes was noted during (typically colder) La Niña years from 1950 to 2004 (Martin 2004). This could indicate higher white shark presence at lower latitudes during La Niña periods. Eastern Australian white sharks have been noted to occur more heavily in waters with SSTs between 17 and 23°C, but changing temperature was not hypothesized to directly influence their habitat selection beyond affecting productivity (Lee et al. 2021). White sharks have previously been caught at higher rates during cooler temperatures off Western Australia and South Africa (Lee et al. 2018, Wintner & Kerwath 2018), which could potentially indicate higher presence during La Niña years, when SSTs are lower. Furthermore, future emphasis should be placed on the lagged effects of ENSO cycles on predators, considering the prolonged impact on trophic changes observed over extended periods in terrestrial ecosystems (Jaksic 2001).

Through climate change, it has been suggested that the frequency of certain flavors of ENSO events will be impacted more than variability or overall amplitude (Yeh et al. 2009), with Central Pacific El Niño events occurring more frequently going into the future. It is possible that we have already seen this shift in flavor frequency when looking at the classifications given by Capotondi et al. (2021), with the majority of El Niño events classified in the last 2 decades being of the Central Pacific flavor. Therefore, the behaviors and space use noted here during mostly Central Pacific events could be increasingly representative of the majority of El Niño periods ahead. With the more direct effects on the region during these periods (McCoy et al. 2017), more regular beaked whale presence may continue to be observed. Still, no 2 ENSO periods are the same (Mason & Goddard 2001), so variability is continued to be expected. Importantly, phase strength will have to be considered with greater weight going forward. As more field data are collected, a clearer picture of species interactions with different types and strengths of ENSO events should emerge.

Extended periods of negative PDO values, particularly since 1998, have generally coincided with more prominent La Niña phases and subdued El Niño events. Particularly, the most robust El Niño conditions in this data set occurred during the comparatively brief period of positive PDO values from 2014 to 2016, which also marked the sole instance of an Eastern Pacific event demonstrated here. This observation aligns with the findings of Ziegenhorn et al. (2023b), who noted the in-tandem trends of the ENSO and PDO cycle. The pronounced correspondence between the 2 climatic phenomena ensures the difficulties in disentangling the singular effects of either, without considering both. Although our study period is likely not long enough for definitive conclusions of this long-term climatic process, the lagged effects of PDO phases have been noted to cause changes in odontocete population dynamics (Lusseau et al. 2004), so it is still worthwhile to examine PDO independently and in combination with other processes, such as ENSO cycles. This is evident in our assessment of sighting rates: while Blainville's beaked whales show similar patterns to ENSO results, goose-beaked whales differ.

While not as striking as the differences between sighting rates during different periods of the ENSO cycle, future insight into the effects of NPGO cycles on both species should also be considered. A positive effect on the number of detections during periods of a combination of positive NPGO and negative ENSO/PDO states, as in Ziegenhorn et al. (2023b), was not necessarily noted for the same La Niña period of 2010–2011. During that period, sighting rates for Blainville's remained under 2 sightings per 100 h of effort and goose-beaked whales barely reached 3 sightings per 100 h of effort (Table 1). The Blainville's beaked whale sighting rate also indicated a weak, albeit not statistically significant, negative trend with NPGO. The differences between the results of this study and those of Ziegenhorn et al. (2023b) likely also stem from the small acoustic detection radius utilized by the recorders, highlighting general differences in insights gained between these methods. The effects of this cycle should still be considered in the future, especially for tagged individuals, with only 1 goose-beaked whale tagged during a negative NPGO period (November 2015) during our study period.

These results provide insights into the potential responses of Blainville's and goose-beaked whales to seasonal shifts and different large-scale climate cycles, especially phases of ENSO. Further research and field efforts are clearly needed to elucidate the effects of these phases on their movements, behaviors, diets, and predators. Future studies should also consider the localized effects of season on these factors in conjunction with ENSO, as well as the further effects of individual variation on habitat use. These findings highlight the importance of considering both large- and finer-scale climatic variability for the conservation and management of these species, as a number of climatic processes, along with their impacts on oceanographic conditions, could have some implications on population dynamics, short-term habitat use, and spatial movement.

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