Title

Oceanographic influence on Cuvier's beaked whales (Ziphius cavirostris) occurrence in the Southern California Bight

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Publication Date

2022

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA SAN DIEGO

Oceanographic influence on Cuvier's beaked whales (*Ziphius cavirostris)* occurrence in the Southern California Bight

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Catalina Aguilar

Committee in charge:

Professor Simone Baumann-Pickering, Chair
Professor Peter Franks
Professor John Hildebrand

2022

The Thesis of Catalina Aguilar is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2022

DEDICATION

This thesis is dedicated to my parents, Julio and Holly Aguilar, who have sacrificed so much for me to be here and provided me with their unconditional love, support, advice, and encouragement throughout my journey.

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ACKNOWLEDGEMENTS

I would first like to thank Professor Simone Baumann-Pickering for taking me into the Scripps Acoustic Ecology Lab as a master's student and giving me the opportunity to conduct research under her mentorship. Additionally, I would like to thank my committee members Peter Franks and John Hildebrand for taking on the role as my advisors and providing their guidance. I'm particularly grateful to Peter Franks for the oceanography advice and hours spent helping me analyze and interpret mesoscale activity data on MATLAB.

I cannot begin to thank Dr. Alba Solsona-Berga enough for taking on the role of my research mentor and sharing her time, knowledge, programming skills and scripts, support, and advice through every step of this project. Without her, none of this could have been possible. Thank you so much for everything.

I would like to acknowledge several researchers and graduate students in the lab for always being so welcoming and lending a helping hand along the way: Shelby Bloom, Michaela Alksne, Natalie Posdaljian, Vanessa Zobell, Rebecca Cohen, Ashlyn Giddings, Eva Hidalgo-Pla, and Morgan Ziegenhorn. I would also like to acknowledge anyone who has built and fixed equipment, coordinated instrument deployment and recovery, and processed data.

Finally, I would like to thank my family and friends for their unconditional love, support, encouragement, and advice. They are truly the best support system anyone can have. I am so incredibly appreciative of my parents who have sacrificed so much for me to be here today.

This thesis, in full, is currently being prepared for submission for publication of the material. Aguilar, Catalina; Baumann-Pickering, Simone; Solsona-Berga, Alba. The thesis author was the primary investigator and author of this material.

ABSTRACT OF THE THESIS

Oceanographic influence on Cuvier's beaked whale (*Ziphius cavirostris)* occurrence in the Southern California Bight

by

Catalina Aguilar

Master of Science in Marine Biology

University of California San Diego, 2022

Professor Simone Baumann-Pickering, Chair

The distribution of highly mobile, top marine predators such as cetaceans is largely driven by oceanographic conditions that shape foraging grounds and modulate the abundance and distribution of prey resources. However, due to their oceanic habitat and cryptic behavior, little is known on how deep-diving foragers respond to changes in the water column. This study used passive acoustic data collected at two sites in the Southern California Bight along with environmental data to examine spatial and temporal patterns of Cuvier's beaked whale (*Ziphius cavirostris)* occurrence in relation to oceanographic conditions over time. Here, I show that seasonal changes in oceanographic conditions and mesoscale dynamics influence seasonal patterns of Cuvier's beaked whale presence across the study region. Specifically, I found that

Cuvier's beaked whales were more likely encountered in winter and spring when water temperature, salinity, and relative vorticity at the surface were low while temperature at 200 m were high. Consequently, fluctuations in detection rates of Cuvier's beaked whales from year-to-year and between sites suggest that abrupt changes in these oceanographic variables seem to influence interannual variability in seasonal patterns of presence. These results provide baseline data on spatio-temporal distribution of Cuvier's beaked whales in the Southern California Bight and emphasize the value of coupling long-term acoustic monitoring with environmental data to better understand elusive cetacean species' habitat use and relationship to oceanographic changes, which may aid the development of management strategies related to global climate change and anthropogenic noise.

INTRODUCTION

Cetaceans are highly mobile, top marine predators that rely on sound production for spatial orientation, communication, and localization of prey (Au 1993) to obtain nutrients and meet energy demands. Some species have evolved remarkable adaptations that enable deep-diving behavior (Tyack et al. 2006) to exploit prey resources in deep pelagic habitats that house a high diversity, abundance, and biomass of marine organisms (Robinson 2004). However, investigations into food web relationships can be challenging in less accessible ecosystems such as the deep pelagic ocean where sampling capabilities are limited (Robinson 2004). As a result, there is little known on how deep-diving foragers respond to changes in the water column.

Beaked whales (family Ziphiidae) are a highly diverse family of deep-diving cetaceans with 22 described species, yet they are among the most poorly understood marine mammals on earth (Cox et al., 2006). There is little information regarding their abundance, distribution, or habitat preferences; they spend relatively little time at the surface and occur almost exclusively in deep (> 1,000 m), typically offshore waters near topographically complex areas such as seamounts, canyons, and steep continental shelves (Cox et al. 2006, Hooker et al. 2019). They have evolved remarkable physiological and behavioral characteristics to regularly conduct long, deep dives with short intervening surface bouts to forage on mesopelagic and benthopelagic fish, squid, and crustaceans (Tyack et al. 2006).

Cuvier's beaked whales (*Ziphius cavirostris*) are the most frequently encountered and widely distributed of all the beaked whale species, with sightings worldwide from all but high polar waters (Falcone et al. 2009). They are often found in the Southern California Bight (SCB), with regular appearances in habitats with steep slopes around San Clemente Island (Baumann-Pickering et al. 2014, Schorr et al. 2014). This suggests long-term site fidelity to the region and highlights the importance of conducting long-term monitoring to assess habitat use of beaked whales in the SCB region. Gathering baseline data on Cuvier's beaked whale spatio-temporal patterns in the SCB is important to better understand population status, and to devise strategies to manage areas impacted by global climate change and exposed to anthropogenic sound sources such as shipping, explosion, and mid-frequency active sonar.

The SCB supports a highly productive and diverse pelagic ecosystem. The region is characterized by complex topography, oceanography, and physical processes including the California Current (CC), California Undercurrent (CUC), California Countercurrent (CCC), and equatorward wind-driven upwelling, and mesoscale features such as eddies (Hickey 1998, Checkley & Barth 2009). The CC is an equatorward-flowing surface (upper 200 m) current that transports cold, fresh water from the north Pacific; the CUC and CCC are poleward-flowing currents that transport warm, salty water north from the Equatorial Pacific (Bray 1999, Hickey 1998, Checkley & Barth 2009). These currents show large seasonal variations that are related to local productivity. The CC is strongest in spring and contributes to predominantly upwelling-favorable equatorward flow over the SCB (Hickey 1993; Giddings et al., 2022). In contrast, the CCC dominates during the summer and fall, bringing warmer water in the SCB and pushing the CC further offshore (Hickey 1993). Eddies and other mesoscale features are also strongest in the summer and fall, with higher horizontal convergence and divergence (Checkley & Barth 2009, Giddings et al., 2022). In addition to these seasonal variations, the SCB experiences interannual variability through climate forcing such as the El Niño Southern Oscillation (ENSO) (Wang & Fiedler 2006). El Niño events produce anomalously weak upwelling of shallow, warm, and fresh source waters, while La Niña conditions produce the contrary with anomalously strong upwelling of deep, cold source waters (Jacox et al. 2015). These circulation patterns, along with complex topography that create areas of entrainment for phytoplankton and zooplankton (Checkley & Barth 2009), make the SCB a highly biologically productive region and offers species-rich feeding opportunities for beaked whales.

Due to their habitat preferences and deep-diving behavior, beaked whales are challenging to visually observe at sea in anything less than ideal conditions (Tyack et al. 2016). Since beaked whales are acoustically active during their foraging dives, this makes them prime candidates for passive acoustic monitoring (PAM) (Mellinger et al. 2007). Long-term PAM is a useful, noninvasive approach to collect information on relative abundance, distribution, and temporal patterns of species presence. Like other toothed whales, beaked whales produce echolocation clicks while foraging to detect, characterize, and localize prey (Au 1993). These echolocation clicks are typically species-specific and can be used for species identification based on their spectral and temporal features. Beaked whale signals have a polycyclic structure and species-specific frequency modulated (FM) pulse upsweep (Baumann-Pickering et al. 2013). Beaked whale species can be discriminated by their respective FM pulse sweep, peak frequency, spectral peaks, click duration, and inter-pulse intervals of the echolocation clicks (Johnson et al. 2004, Baumann-Pickering et al. 2013). Specifically, Cuvier's beaked whale acoustic signals can be identified based on a characteristic FM pulse upsweep, peak frequency of 40 kHz, spectral peaks of 17 and 23 kHz, and a dominant inter-click interval of 0.4-0.5 seconds (Baumann-Pickering et al. 2013).

Here, I combine long-term passive acoustic recordings and environmental data to examine the spatio-temporal patterns of Cuvier's beaked whale occurrence at two sites in the SCB in relation to oceanographic changes over time. I first use passive acoustic data to document spatial and temporal occurrence of Cuvier's beaked whales across sites between January 2007 to

September 2020. Then, I use passive acoustic data and environmental data to generate single-variable generalized additive models (GAMs) to examine the potential significance of various environmental variables in shaping temporal patterns of Cuvier's beaked whales in the SCB. I then examine relationships between seasonal presence of Cuvier's beaked whale detections with seasonal cycles in oceanographic conditions and mesoscale activity. Finally, I use annual anomalies to examine interannual variability in Cuvier's beaked whale occurrence in response to changes in oceanographic conditions over the recording period. The results highlight the importance of utilizing long-term monitoring to understand how species distributions may be impacted by changing oceanographic conditions. With a better understanding of temporal patterns and habitat preferences, it may be possible to more effectively manage and conserve beaked whale species in the SCB in terms of anthropogenic impacts and global climate change.

METHODS

i. Acoustic Data Collection

Acoustic data were collected using high-frequency acoustic recording packages (HARPs) (Wiggins & Hildebrand 2007) deployed at two sites (Figure 1) in the Southern California Bight: one west of San Clemente Island (H) and one southwest of San Clemente Island (N). HARPs (Figure S1) are autonomous, battery-operated instruments that are equipped with a calibrated hydrophone suspended 10-30 m above the seafloor mounted instrument frames, data loggers, and a releasable ballast-weight anchor (Wiggins and Hildebrand, 2007). All HARPs were programmed to record continuously at a sampling rate of 200 kHz with a 16-bit quantization, which provided an effective bandwidth from 10 Hz to 100 kHz that captures detection of high frequency odontocete echolocation clicks. Sequential deployments at each site over multiple years enabled nearly continuous monitoring between August 2007 or January 2009 to September 2020 at sites H and N, respectively. Temporal coverage between deployments varied due to battery life, data storage capacity, and servicing efforts (Table 1, Figure S2).

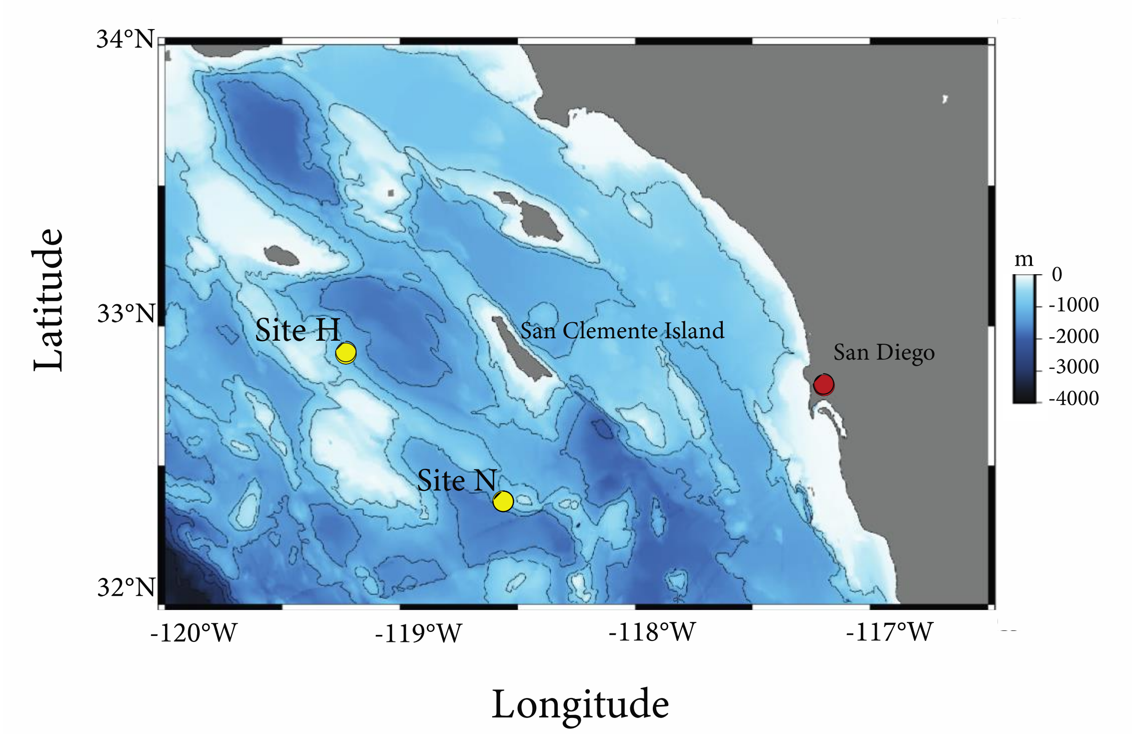

Figure 1: Map of the study area in the Southern California Bight. Map showing the latitude-longitude location of study sites (site H and N) denoted as yellow dots. Location of the site was averaged among deployments. Blue color bar represents water depths. Black lines indicated 500 m contours. Grey denotes land masses.

Table 1: Summary of HARP locations/depths and recording period.

Site	Location	Depth (m)	HARP Recording Dates	Recording Effort (days)	Total Number of Days with Detections	Average Number of Detections (hours/day)
H	32° 50.76’N, 119° 10.57’ W	1,000	7/24/2007 – 9/30/2020	3,586	2,761	1 ± 1.2
N	32° 22.21’ N, 118° 33.85’ W	1,300	1/14/2009 – 9/30/2020	3,621	1,501	0.32 ± 0.59

ii. Echolocation Click Detection

Echolocation clicks attributable to Cuvier's beaked whales were identified using a combination of automated detection and manual verification methods. All echolocation signals were initially identified with an automated Teager Kaiser energy detector (Soldevilla et al. 2008; Rochet al., 2011). The individual click detections were digitally filtered with a 10-pole Butterworth band-pass filter with a pass-band between 5 kHz and 95 kHz. Filtering was done on 800 sample points centered on the echolocation signal. Spectra of each detected signal were calculated using 2.56 ms (512 samples) of Hann-windowed data centered on the signal. Click parameters including peak frequency, center frequency, and bandwidth were calculated according to definitions from Au (1993). A decision of presence or absence of beaked whale signals was based on detections in a 75 s segment containing at least seven detections. Segments of data were classified as containing beaked whale echolocation clicks if more than 13% of all initially detected signals over 75 s contained peak and center frequencies above 32 and 25 kHz respectively, a duration of more than 355 μs, and a sweep rate of more than 23 kHz/ms (Baumann-Pickering et al. 2014). The start and end of each segment containing beaked whale signals were logged and their durations were added to estimate presence.

The automatically detected echolocation signals were verified using the open-source software DetEdit (Solsona-Berga et al. 2020) to manually remove any false-positive clicks that were not attributable to Cuvier's beaked whales. This allowed users to visualize inter-click intervals (ICIs), long-term spectral averages (LTSAs), received levels, and spectra of clicks classified by the algorithm. LTSAs were created using a 5 s time average and a 100 Hz frequency resolution. To account for the frequency-dependent instrument response of each deployment, spectra were corrected for the hydrophone transfer function. Only clicks exceeding a peak-to-peak received level of 121 dB re 1 μPa were included to provide a consistent detection threshold.

iii. Acoustic Data Analysis

Manually validated detections were divided into 1 min time-bins over periods with recording effort at each site. Cuvier's beaked whale presence was determined based on the number of 1 min time bins in which echolocation clicks were positively detected at each site. Because beaked whales perform long silent periods of shallow diving between deep foraging dives (Warren et al. 2017), temporal autocorrelation was accounted for by creating auto-correlation function (ACF) plots of detections using the *autocorr* function (Box, Jenkins, & Reinsel 1994) in MATLAB. The number of 1-min bins with manually validated detections were summed per hour and then averaged per day to match the daily resolution of the oceanographic data.

Relative occurrence of Cuvier's beaked whale echolocation signals was analyzed with respect to distribution across sites. To compare spatial variations in Cuvier's beaked whale presence, the number of hours with manually validated detections were summed for each site. Because recording effort varied across years and sites, daily detections were normalized by recording effort by dividing the number of hours with presence by the percentage of effort within a given day. Daily detections were averaged by week of year to examine seasonal patterns. To examine interannual patterns, the number of hours with detections were averaged by month and subtracted from the overall average across the timeseries to produce a presence anomaly. Diel patterns were not explored in this analysis as oceanographic data were not available at that resolution.

iv. Environmental Data Analysis

Environmental data were obtained from the California State Estimation - Short-term State Estimation (CASE-STSE) product (http://ecco.ucsd.edu/case.html) for the time period of January 2007 to September 2020. The CASE-STSE product assimilates all available ocean observations in the time period and region of the California Current System using a general circulation model (MITgcm) (Hoteit et al., 2013). CASE-STSE utilizes least squares fits to merge a series of 3-month estimates initialized from HYCOM/NCODA global analysis data to produce 30-day model hindcasts of the ocean state. The model domain extends from 28°N to 40°N and 130°W to 114°W with a 1/16° horizontal resolution (~ 7 km) and 72 vertical (depth) levels. The vertical resolution varies from 5 m at the surface to 500 m at depth, with spacing gradually increasing until the maximum depth. The environmental variables extracted include temperature (°C), salinity (PSU), and meridional (U) and zonal (V) current velocity vectors (m/s). Daily values were averaged across a 5 km x 5 km square centered around each site location and extracted at three depth levels of 5 m, 200 m, and 500 m to characterize the local physical oceanography. Environmental variables exceeding 500 m were not accounted for due to the lack of measurements below 500 m depth within the broader vicinity of our sites.

Analysis of the local physical environment was computed using similar conventions to those used to analyze passive acoustic data. Environmental data were averaged by week of year to examine seasonal patterns in oceanographic conditions. Anomalies were used to compare interannual variability of presence with environmental variables, with daily values extracted at each depth level averaged by month and subtracted from the climatological mean to produce an anomaly.

V. Characterization of Local Ocean Circulation

Current direction, current speed, and relative vorticity were calculated from the modeled U and V to quantify horizontal stirring and mesoscale activity. Current direction was calculated in MATLAB using the following convention:

$$direction = 180 * \text{atan2}\ (u, v)$$

where direction is noted in degrees. As this generates an output of +/- 180°, 360 was added to negative degree values to convert it into a 0-360° range. Direction is interpreted as flow originating from the east (0/360°), north (90°), west (180°), and south (270°). Current speed was calculated using the following convection:

$$speed = \sqrt{u^2 + v^2}$$

where $speed = m/s$. Relative vorticity is a measure of fluid rotation relative to the Earth's surface (Stevens and Crum 2003). It can be related to the amount of "circulation" or "rotation" in a fluid and accounts for external forces such as wind that contributes to ocean flow (Talley et al. 2011). The vertical component of relative vorticity is calculated with the following convention:

$$\zeta = (\frac{\partial V}{\partial X} - \frac{\partial U}{\partial Y})$$

where $\zeta = sec^{-1}$. Vorticity values show areas characteristic of mesoscale features such as fronts, eddies, and filaments. Thus, higher positive/negative values of relative vorticity coincide with the presence of stronger mesoscale features. In the Northern Hemisphere, positive relative vorticity corresponds to cyclonic (counterclockwise) flow and negative relative vorticity corresponds to anticyclonic (clockwise) flow. Cyclonic eddies are cold-core eddies with upward bending of the pycnocline bringing deep waters to shallower depths (upwelling) while anticyclonic eddies have warm cores where the pycnocline bends downward (downwelling).

Current direction, current speed, and vorticity were averaged over a 5 km x 5 km square centered around each site location to characterize the local physical processes at each site. Additionally, daily spatial maps of current direction, current speed, and relative vorticity were plotted over a 90 km x 90 km area around the study area to spatially examine mesoscale features throughout the period of observation.

vi. Statistical Analysis

Generalized additive models (GAMs) were developed using the *mgcv* (Wood 2011) package in R (R Core Team 2021) to examine temporal patterns of echolocation clicks at each site with total presence in hours per day as the response variable and month and year as the predictor variables. Year and month were modeled as a factor. A Tweedie distribution with a logistic function was used to account for the detection data being zero-inflated. Additionally, GAMs were used to examine each local physical oceanographic variable at each site as a single-predictor variable in relationship to beaked whale presence. Each physical oceanographic predictor variable was examined at three depth levels (5 m, 200 m, and 500 m). Smoothing parameters were optimized using the restricted maximum likelihood (REML) criterion with a four-knot basis to reduce overfitting (Marra and Wood 2011). Current direction was modeled with a smooth function that was estimated by a cyclic cubic regression spline to better interpret transitions in water flow between the four directions (north, south, east, and west). All other physical oceanographic predictor variables were modeled with a smooth function that was estimated by a cubic spline.

RESULTS

i. Spatio-Temporal Variability of Acoustic Presence

A cumulative 4,714 hours with Cuvier's beaked whale presence were collected between January 2007 to September 2020 (Table 1, Figure S2) across two sites in the Southern California Bight: one located to the west of San Clemente Island (H) and one to the southwest of San Clemente Island (N). Cuvier's beaked whale signals were regularly detected across the two acoustic recording sites but exhibited variations in their spatial distributions (Figure 2). Higher relative acoustic presence occurred at site H (77% recording days) with an average of one hour per day with echolocation signals. Conversely, less presence occurred at site N (41% recording days) with an average of 19 minutes per day with echolocation signals (Figure 2, Figure S2).

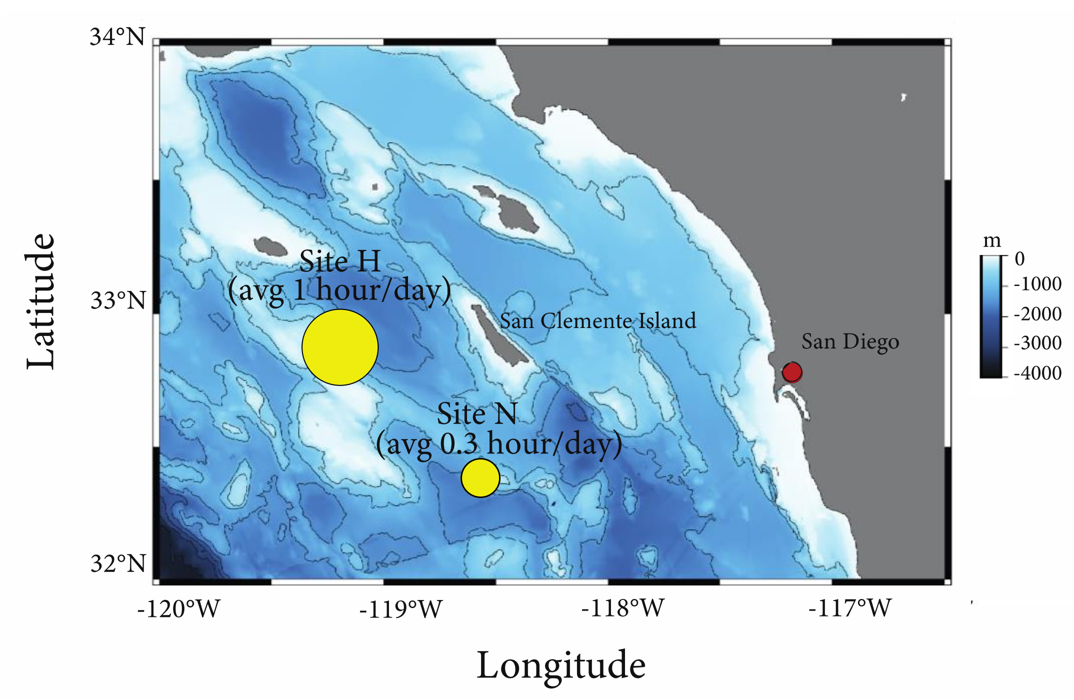

Figure 2: Map showing relative acoustic presence at each site. Map showing the relative occurrence of Cuvier's beaked whales across study sites (site H and N) denoted as a yellow circle. Circle size is scaled to percentage of effort at each site. Blue color bar represents water depths. Black lines indicated 500 m contours. Grey denotes land masses.

Similar seasonal patterns in detections were observed at both sites H and N (Figure 3a). Echolocation clicks were most common during spring and winter at both sites, with this seasonal pattern being most pronounced at site H (Figure 3a). Both sites demonstrated intermittent peaks throughout the year; at site H there were peaks during April and November, and at site N there were peaks during January, April, and December (Figure 3b). Fewer clicks were observed between August and September, followed by an increase occurring after September and October at site H and site N, respectively (Figure 3b). At site H, spring months (March, April, May) were significantly different from the reference month (January) with higher acoustic presence, and lower presence during summer and fall months (July, August, September) (Figure 3b, Table S1). Conversely, at site N, spring (April and May) and winter (December) months were statistically similar to the reference month (January), with higher levels of observed presence in the winter months compared to the spring (Figure 3b, Table S1).

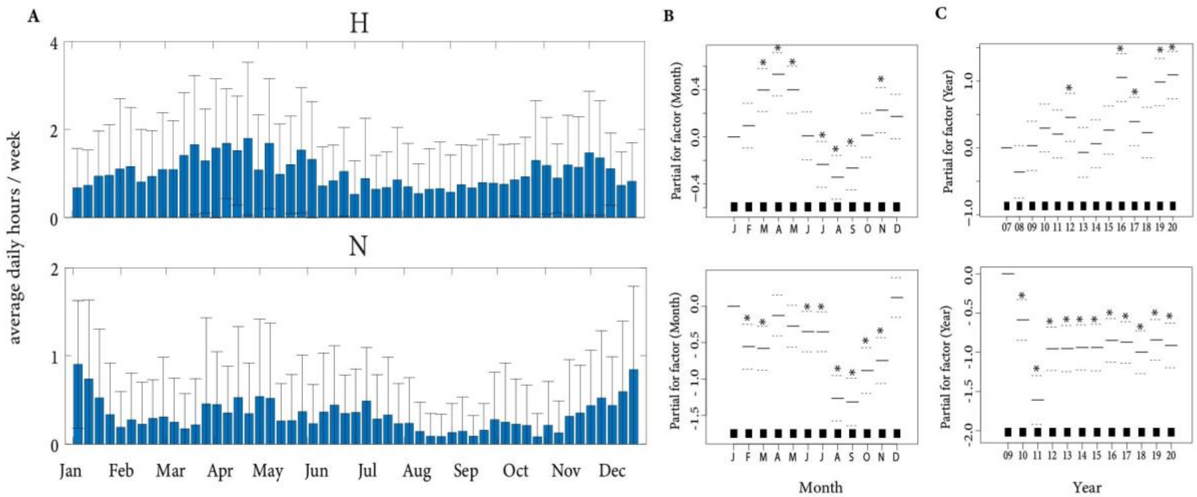

Figure 3: Relative seasonality and annual patterns of Cuvier's beaked whales. Mean weekly presence of Cuvier's beaked whale clicks (A). Data was averaged across July 2007 to September 2020 and January 2009 to September 2020 at sites H and N, respectively. Black error bars represent standard error. Corresponding generalized additive models (GAMs) with total daily hours of click presence modeled as a function of month (B) and year (C). Horizontal bars represent two standard error bounds. Asterisks represents months and years that are statistically significant from each other. Y-axis scales vary to show model fit.

Cuvier's beaked whale occurrence varied across years at site H, with a positive trend of increasing presence, with some variability every two to three years (Figure 3c). Years that were significantly different relative to the initial year (2007) at site H were 2012, 2016, 2017, 2019, and 2020 (Figure 3c, Table S1). Higher detection rates at site H were observed in these years, while lower detections not statistically different from the reference year (2007) were observed in 2008, 2011, 2013, 2017, and 2018 (Figure 3c). There was no clear interannual trend observed at site N; however, all years at site N were significantly different from the reference year (2009) (Figure 3c, Table S1). Acoustic presence was significantly higher during the initial year (2009), followed by a decrease in detections during 2010 and 2011 (Figure 3c). Detections then increased again in 2012 and remained relatively stable throughout the subsequent years of the time series (Figure 3c). Higher detection rates were observed at site N in 2009, 2012, 2016, and

2019 while lower detections were observed in 2011 and 2018 (Figure 3c). Similar patterns in acoustic presence were observed during 2012 to 2015 as well as 2016 and 2017 (Figure 3c).

ii. Seasonality of Oceanography and Cuvier's Beaked Whales

GAM models were applied to evaluate the daily presence of Cuvier's beaked whale in relation to singular environmental variables (Table 2). Physical oceanographic variables in the 5 m and 200 m depth bin were more significant at predicting the variability of Cuvier's beaked whale acoustic presence at both sites H and N compared to variables at 500 m depth (Table 2). Significant predictors at both sites included sea surface temperature (SST), sea surface salinity (SSS), sea surface current direction, sea surface relative vorticity, temperature at 200 m, current direction at 200 m, and salinity at 500 m (Table 2).

Table 2: Summary of statistical outputs of generalized additive models (GAMs) explaining daily Cuvier's beaked whale presence and singular environmental predictor variables at three depths (5 m, 200 m, 500 m). Current direction was modeled as a smooth additive term using cyclic cubic regression (bs = "cc"). All other predictor variables were modeled as smooth additive terms using shrinkage version of cubic regression (bs = "cs"). Smoothing parameters were selected using the restricted maximum likelihood (REML) method. Models were fit using a Tweedie distribution with a log link function. The categorical P-value significance for each predictor variable is given as *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Gray shading represents predictor variables that were not statistically significant (p-value < 0.05).

Site	H								N							
Response Variable	**Est**	**Std. Error**	**t value**	**P-value**	df	F	Dev. exp. (%)	R^2 adj.	**Est**	**Std. Error**	**t value**	**P-value**	df	F	Dev. exp. (%)	R^2 adj.
Temperature																
5m	-0.03	0.02	-1.5	≤ 0.01 ***	2.9	43.8	3.0	0.04	-1.2	0.03	-38	≤ 0.01 ***	2.5	21.4	2.0	0.02
200m	-0.03	0.02	-1.6	≤ 0.01 ***	2.5	51.4	3.4	0.06	-1.2	0.03	-37	≤ 0.01 **	2.9	4.9	0.5	≤ 0.01
500m	< -0.01	0.02	-0.25	0.148	0.4	0.28	0.03	≤ 0.01	-1.2	0.03	-37	0.22	2.6	1.3	0.1	≤ 0.01
Salinity																
5m	-0.02	0.02	-1.0	≤ 0.01 ***	2.9	26.9	1.7	≤ 0.01	1.2	0.03	-37	≤ 0.01 ***	1.0	5.6	0.6	≤ 0.01
200m	-0.01	0.02	-0.65	≤ 0.01 ***	2.9	14.6	1.0	≤ 0.01	1.2	0.03	-37	0.092	1.3	1.0	0.1	≤ 0.01
500m	-0.03	0.02	-1.7	≤ 0.01 ***	2.7	53.5	3.8	0.06	-1.2	0.03	-37	0.049 *	2.3	2.0	0.2	≤ 0.01
Current Direction																
5m	-0.02	0.02	-0.85	≤ 0.01 ***	1.9	32.1	1.5	0.02	-1.2	0.03	-37	0.015 *	1.6	3.3	0.3	≤ 0.01
200m	-0.01	0.02	-0.48	≤ 0.01 ***	1.7	13.7	0.6	≤ 0.01	-1.2	0.03	-37	≤ 0.01 **	1.6	4.9	0.4	≤ 0.01
500m	-0.01	0.02	-0.27	0.104	1.6	1.7	0.1	≤ 0.01	-1.2	0.03	-37	≤ 0.01 ***	1.6	6.6	0.5	≤ 0.01
Current Speed																
5m	-0.01	0.02	-0.49	≤ 0.01 ***	2.6	7.6	0.6	≤ 0.01	-1.2	0.03	-37	0.16	2.4	1.4	0.2	≤ 0.01
200m	-0.01	0.02	-0.61	≤ 0.01 ***	2.9	10.1	0.8	≤ 0.01	-1.2	0.03	-37	0.462	≤	≤	≤	≤ 0.01
500m	< -0.01	0.02	-0.36	≤ 0.01 **	2.6	4.3	0.3	≤ 0.01	-1.2	0.03	-37	0.267	0.25	0.1	0.02	≤ 0.01
Relative Vorticity																
5m	-0.02	0.02	-0.92	≤ 0.01 ***	2.9	20.8	1.5	≤ 0.01	-1.2	0.03	-37	≤ 0.01 ***	2.6	9.2	1.0	≤ 0.01
200m	-0.01	0.02	-0.37	≤ 0.01 **	2.9	4.7	0.3	≤ 0.01	-1.2	0.03	-37	≤ 0.01 **	1.6	2.9	0.3	≤ 0.01
500m	< -0.01	0.02	-0.25	0.083	0.6	0.58	0.06	≤ 0.01	-1.2	0.03	-37	0.174	0.5	0.3	0.04	≤ 0.01

Modeled predictions of weekly presence showed an optimum SST and SSS range at site H and a negative relationship at site N (Figure 4). At site H, detections had a peak at SST ~ 16°C and SSS ~ 33.6 PSU (Figure 4). Both sites demonstrated an optimum range of Cuvier's beaked whale acoustic presence for relative vorticity with higher presence during low vorticity (Figure 4). Beaked whale acoustic presence at H demonstrated a positive relationship with currents at the surface and 200 m originating from between northeast to northwest directions, whereas N demonstrated a positive relationship with currents at the surface and 200 m originating from between northwest to southwest direction (Figure 4). A positive relationship of beaked whale detections and temperature at 200 m was observed at site H. At site N, the relationship was more defined by a minimum around 8.5°C to 9°C and unclear relationship above 9.5°C due to low sample size (Figure 4). Finally, there was a minimum of Cuvier's beaked whale detections with salinity at 500 m at around 34.3 PSU at both sites and higher detections at both lower and higher salinity values at this depth (Figure 4).

Seasonal cycles in the local physical oceanography coincided with seasonal patterns in Cuvier's beaked whale occurrence (Figure 4). During spring, a peak in echolocation clicks occurred with low SST, low SSS, lower variability in current direction and low relative vorticity at the sea surface, and temperature at 200 m falling in a range between 8.5°C to 9°C (Figure 4). Currents at the sea surface and 200 m during this period on average originated from the west direction at both sites H and N (Figure 4). During September, a minimum in detections occurred with a peak in SST, high SSS, higher variability in current direction and relative vorticity at the sea surface, low temperature at 200 m, and higher variability in current direction at 200 m and salinity at 500 m (Figure 4). Currents at the sea surface and 200 m during this period on average originated from the west and southwest directions at sites H and N, respectively (Figure 4).

However, given the higher fluctuations in standard deviation, it is important to note that a decrease in acoustic presence with currents at the surface and 200 m along with salinity at 500 m appears to be related to mesoscale changes in these oceanographic variables rather than seasonal patterns during this period. Detections increased following September and October at sites H and N, respectively, as SST and SSS decreased and oceanographic conditions closely mirrored those observed in spring (Figure 4).

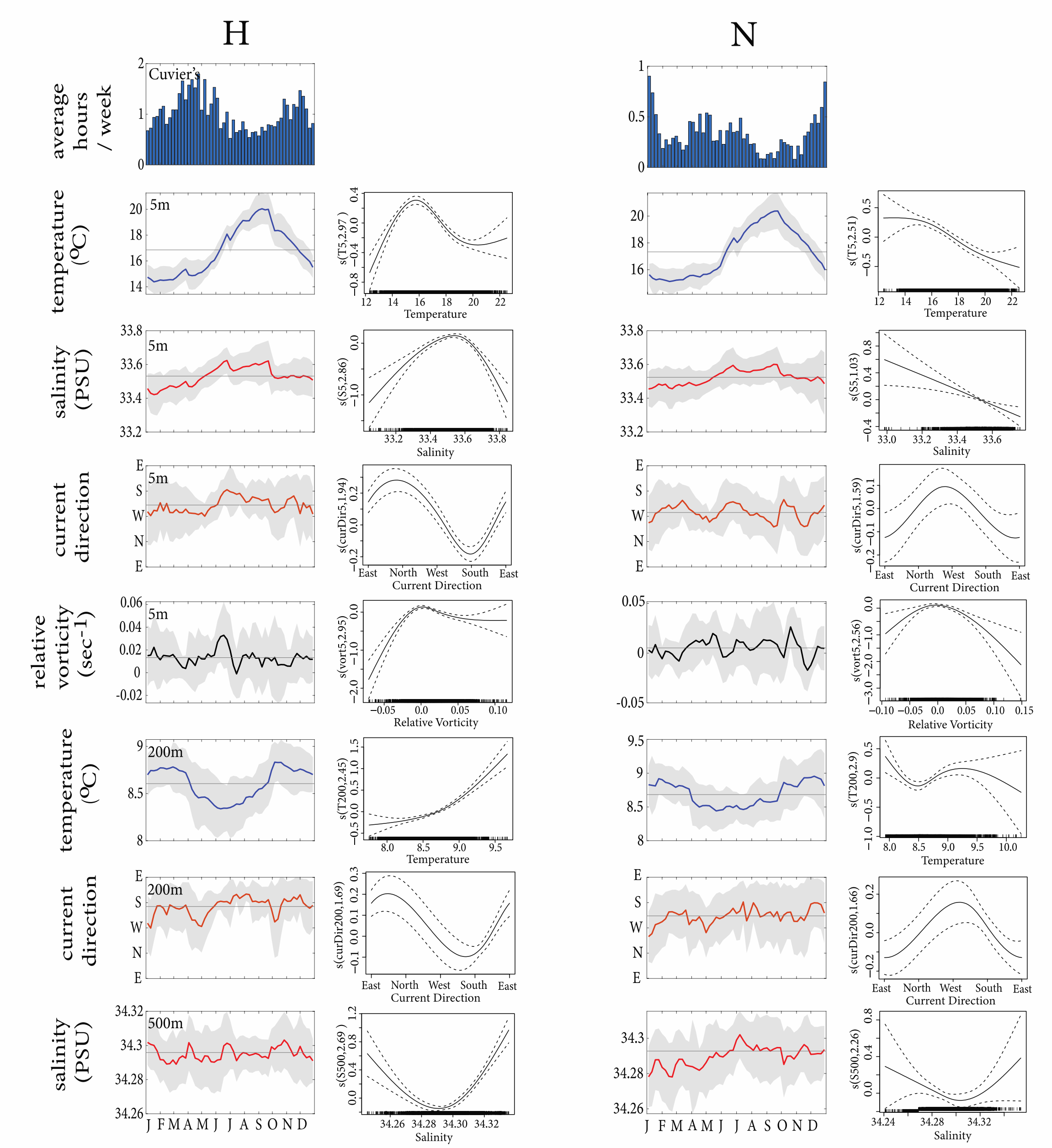

Figure 4: Seasonality of Cuvier's beaked whales as it relates to environmental variables. Left column: Observations of average hours of detections per week as well as average temperature (color line) and standard deviation (grey shade) at 5 m, salinity at 5 m, current direction at 5 m, vorticity at 5 m, temperature at 200 m, current direction at 200 m, and salinity at 500 m over time. Right column: Modeled relationships (GAM) of probability of beaked whale detection given singular environmental variables (spline as black line with dashed line showing 95% confidence interval).

iii. Interannual Variability of Oceanography and Occurrence

As previously noted, the number of detections at sites H and N appeared to fluctuate from year-to-year, with some years demonstrating more deviation from the reference year than others (Figure 3c). Monthly anomalies of acoustic presence and relevant environmental variables were compared through the entire study period and across sites to better understand how changes in the physical environment influenced interannual variability in Cuvier's beaked whale spatio-temporal occurrence (Figure 5). Oceanographic conditions and physical processes exhibited differences in their interannual fluctuations (Figure 5). Current direction and relative vorticity exhibited short-term changes indicative of mesoscale activity, with changes occurring on a time scale of one to several months (Figure 5). In contrast, trends in SST, SSS, temperature at 200 m, and salinity at 500 m demonstrated changes occurring over a couple of months up to a couple of years (Figure 5).

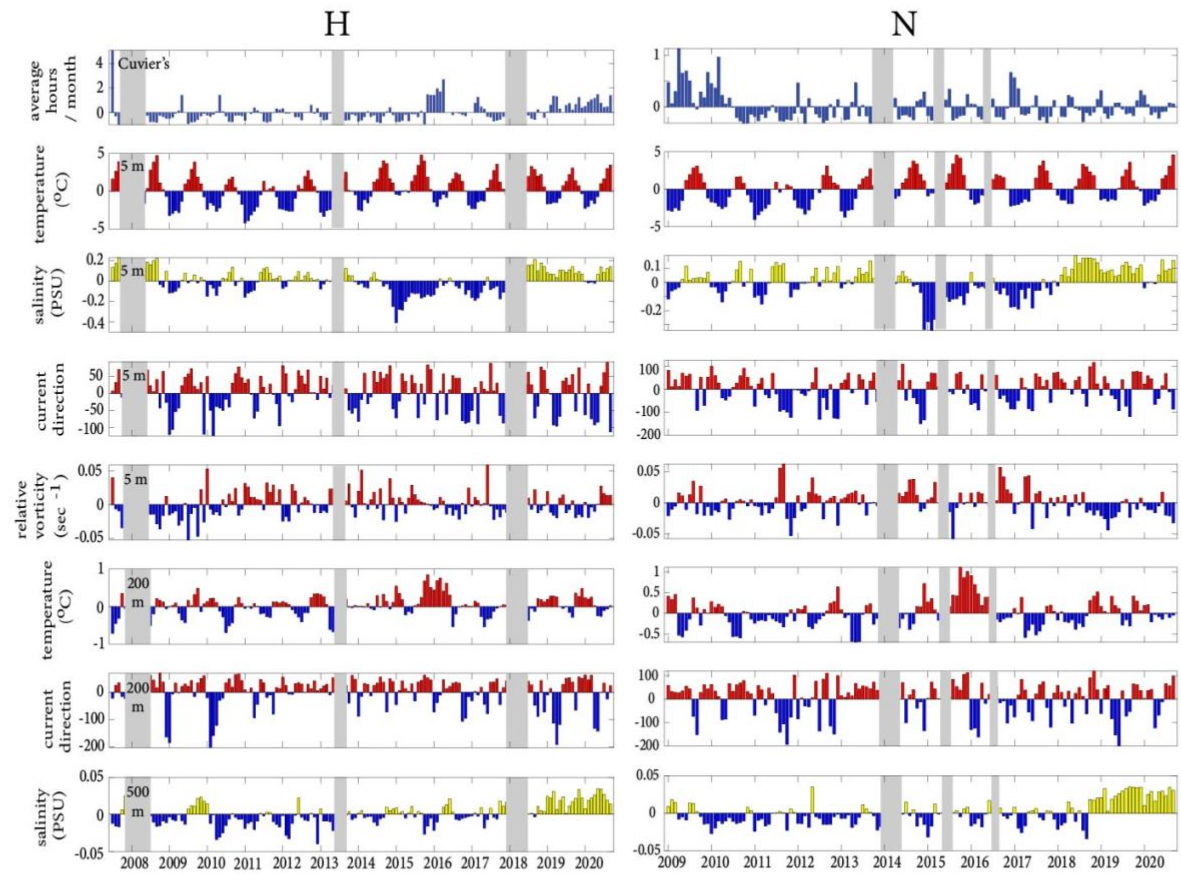

Figure 5: Interannual variability of Cuvier's beaked whales as it relates to environmental variables. Monthly anomalies of Cuvier's beaked whale detections, sea surface temperature, sea surface salinity, sea surface current direction, sea surface relative vorticity, temperature at 200 m, current direction at 200 m, and salinity at 500m are showed interannual variability.

Noticeable differences in the local physical environment and beaked whale acoustic presence occurred during 2009-2011 at site N, 2015-2016 at H and 2016-2017 at N, and 2019-2020 at site H (Figure 3c, Figure 5). The seasonal peak in SST in the June to September summer months was consistently observed at both sites across the timeseries, however, the magnitude of this peak fluctuated from year-to-year and between sites (Figure 5). This contributed to differences in the beaked whale acoustic presence recorded between sites H and N during the 2009-2011 and 2015-2016 time periods. A strong positive presence anomaly was observed at site

N in 2009 (Figure 5), this being the year with the highest number of hours recorded in the acoustic record (Figure 3c). Differences in detection rates are likely related to spatial variation in SST, with site H experiencing a higher and more definitive peak in the summer of 2019 compared to site N (Figure 5) which may have resulted in a spatial redistribution. In contrast, negative anomalies in SST and SSS were observed from mid-2010 to mid-2012. At the same time, negative anomalies in presence were observed at both sites, coinciding with little to no peak in SST during the summers of 2010 and 2011.

During the 2014 to 2016 period, strong positive anomalies in SST and temperature at 200 m along with negative anomalies in SSS were observed across the study region beginning in 2014 and persisted through 2015 (Figure 5). This contributed to a higher peak in SST during the summer months of both years (Figure 5). At the end of 2015, an increase in Cuvier's beaked whale presence was observed at both sites as SST decreased and SSS increased (Figure 6). This trend was most prominent at site H with 2016 being a year with one of the highest number of hours with presence recorded in the acoustic record, and a higher peak observed in late winter/early spring of 2015/2016 (Figure 3c, Figure 5). Additionally, there was a lower and less definitive SST peak in the summer of 2016 compared to those in previous years which was coincident with relatively low but consistent acoustic presence from July to November at both sites (Figure 5).

The 2016 period was followed by an increase in salinity at sites H and N (Figure 5). Positive anomalies of SSS and salinity at 500 m depth began in January and October 2018, respectively, and persisted through September 2020 (Figure 5). Higher and more consistent positive acoustic presence anomalies were observed during this period beginning in January 2019 and persisted through September 2020 (Figure 5). This trend was most prominent at site H due to spatial variation in the magnitude of SST and SSS, with site N experiencing a stronger positive anomaly in SSS and more definitive peaks in SST during the summer months of 2019 and 2020. However, as this period coincided with the COVID-19 pandemic, it is important to note that unprecedented change of anthropogenic activities in the area could have also contributed to the observed change in acoustic presence of Cuvier's beaked whales.

iv. Seasonal and Interannual Variability of Presence and Mesoscale Activity

Exemplary on-day spatial maps of the study region were used to visualize seasonal and interannual variability of mesoscale activity at the sea surface (Figure 6). Years 2014 and 2020 were highlighted based on a nearly complete acoustic record at both sites and as representatives to highly different oceanographic conditions (Figure 6). Previously noted, seasonal patterns in Cuvier's beaked whale acoustic presence, with detections occurring predominantly in the spring and fall or winter, were observed at both sites during 2014 (Figure 6). A peak in detections was observed in the spring with lower current speeds, more horizontal stirring, and weaker mesoscale features present at the sea surface across the region (Figure 6). This also coincided with current directions predominantly originating from the southeast and southwest directions at sites H and N, respectively (Figure 6). Mesoscale activity intensified at the sea surface during the summer with higher current speeds, stronger mesoscale features, and shifts in current direction beginning around June at both sites and persisting through September and October at H and N, respectively (Figure 6). This coincided with months of lower beaked whale acoustic presence (Figure 6). Presence increased again after September and October at sites H and N, respectively, as mesoscale activity at the sea surface calmed, reflecting similar patterns in mesoscale activity as those observed in the spring (Figure 6).

In contrast, a different seasonal pattern of acoustic presence and mesoscale activity were observed during 2020 (Figure 6). Cuvier's beaked whales demonstrated higher and more consistent presence at both sites as lower mesoscale activity persisted through much of the year, with some fluctuation in acoustic presence occurring on a time scale of one to several weeks (Figure 6). A slight dip in presence was observed at H from mid-June to mid-August when higher areas of convergence were present while intermittent dips in acoustic presence at N were observed from February-April and May-July when currents shifted to a northwest and southeast direction (Figure 6).

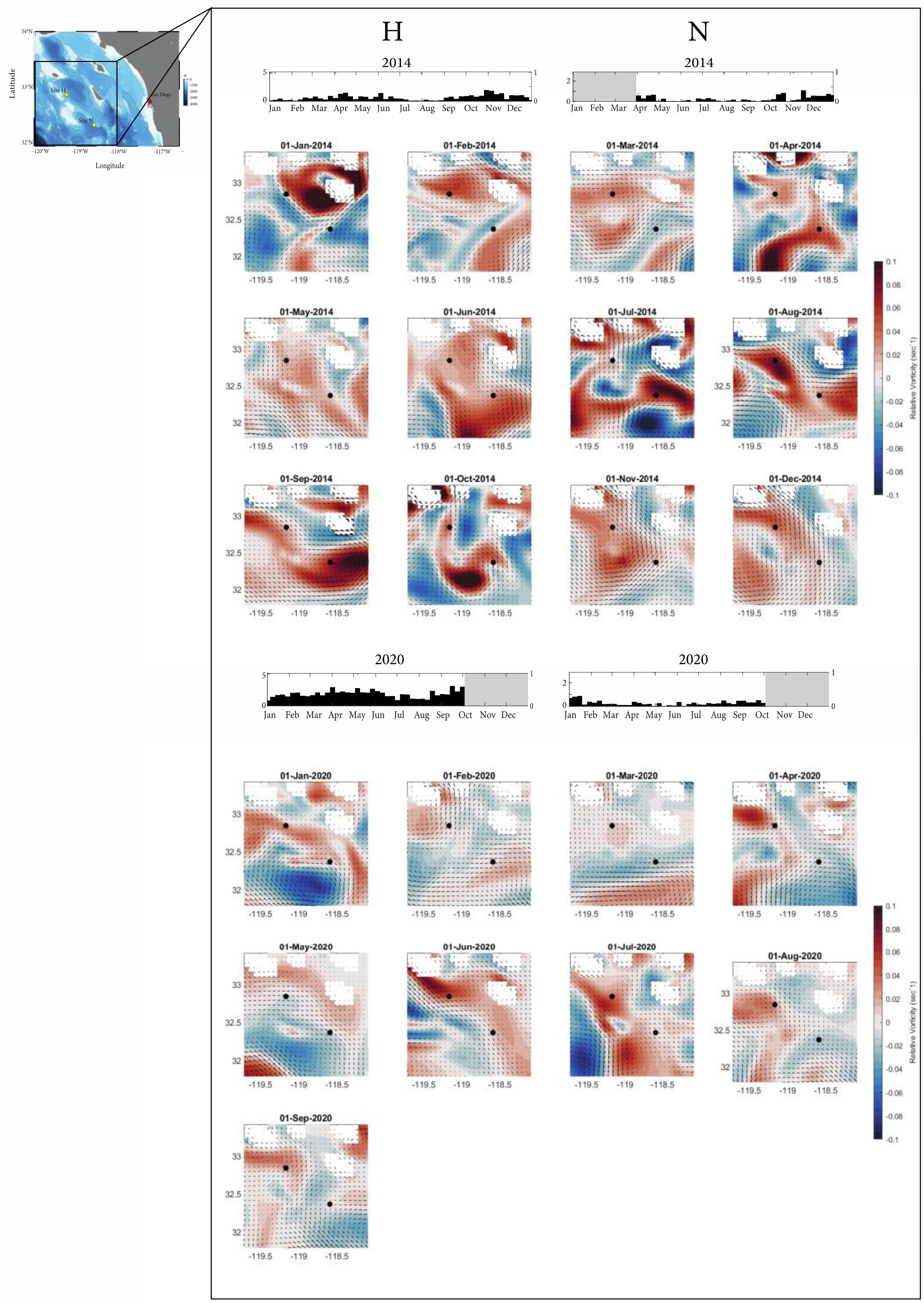

Figure 6: Acoustic presence and mesoscale activity around study sites in 2014 and 2020. Bar plots denote weekly acoustic presence at sites H and N during 2014 and 2019. Black box denotes 90 x 90 km radius around sites. Direction of arrows denote current direction and length of arrows denote current speed. Color denotes vorticity strength with red and blue corresponding to positive and negative vorticity, respectively.

DISCUSSION

This study provides further insight into the occurrence of Cuvier's beaked whales in the Southern California Bight and its relationship to oceanographic variables. Cuvier's beaked whale presence demonstrated distinct seasonal patterns at both sites, with a dip in presence occurring in summer. Single variable GAM models highlighted the importance of oceanographic conditions shaping Cuvier's beaked whale temporal patterns and habitat use. Seasonal cycles in oceanographic conditions and mesoscale activity are key drivers in modulating long- and short-term patterns in Cuvier's beaked whale presence at both sites H and N. Specifically, they are encountered most when sea surface temperature, sea surface salinity, and relative vorticity are low and temperature at 200 m is high at site H and falls in a range between 8.5°C to 9.0°C at site N. Consequently, changes in the intensity of oceanographic seasonal cycles as well as mesoscale activity are drivers of beaked whale acoustic presence and notable in inter-annual fluctuations of this presence.

i. Spatial Variability

Cuvier's beaked whales demonstrated spatial variation in their acoustic presence among recording sites, with generally higher acoustic presence occurring at site H. Reasons for this spatial separation may be complex but are likely attributable to differences in habitat and foraging conditions at each location. The study region is located within the United States Navy's Southern California Anti-Submarine Warfare Range (SOAR), which is a focal training area in the military's Southern California (SOCAL) range complex that extends to the west of San Clemente Island. Previous studies utilizing HARPs to investigate the impacts of naval operations on beaked whale occurrence in the SOCAL range complex have demonstrated that both sites are frequently exposed to mid-frequency active sonar (MFAS) events, with site N experiencing higher numbers of hours per week with sonar usage compared to site H (Rice et al. 2015, 2018, 2021). This suggests a potential reason for the lower numbers of Cuvier's beaked whale presence detected at site N: habitats near the recording location are exposed to consistently higher levels of anthropogenic disturbance from MFAS events. Additionally, previous studies combining squid metric data collected from an autonomous echosounder with beaked whale acouatic data collected from range hydrophones (Southall et al. 2019) documented heterogeneity in the distribution and quality of prey resources across the SCB region. Habitats located in the western portion of the SOAR range complex demonstrated more favorable foraging conditions with higher aggregations of prey, which allowed for beaked whales in habitats located near site H to meet and exceed energy demands with lower numbers of successful dives needed (Southall et al. 2019). These spatial patterns highlight the importance of conducting comparable studies over large spatial scales to better understand habitat use and inform conservation strategies.

ii. Seasonality

Cuvier's beaked whale echolocation clicks demonstrate strong seasonal patterns at both sites H and N. Cuvier's beaked whales were detected year-round, with a dip in acoustic presence during the summer. These seasonal patterns are consistent at both sites but most prominent at site H. Previous acoustic studies of Cuvier's beaked whales in the Southern California Bight (Baumann-Pickering et al. 2014, 2018) and offshore of Washington (Rice et al. 2021) have also noted similar seasonal patterns in occurrence (Baumann-Pickering et al. 2014, Baumann-Pickering et al. 2018) and therefore support earlier findings about the temporal patterns of these species in this area. The stability of these seasonal patterns over long periods of time highlights the importance of conducting passive acoustic monitoring in deep pelagic habitats that are relevant to these species.

iii. Oceanography and Mesoscale Features

The results of the GAM statistical analyses of environmental data highlighted many significant single-variable relationships with predictors at the sea surface and 200 m depth at both sites. Similar responses were found with Cuvier's beaked whales near canyons in the Bay of Biscay (Virgili et al. 2022), where surface and subsurface (≤ 200 m) dynamic variables, along with static variables that characterize seafloor topography, emerged as better predictor variables of habitat preferences than deep (600 m – 2000 m) ocean environmental variables. Virgili et al. (2022) hypothesized that the highly significant relationships observed with surface variables may indicate that beaked whale presence is related to mechanisms at the surface, or that these mechanisms may influence processes at depth.

The results of the GAM models demonstrated a negative relationship with SST and SSS at site N and a targeted optimum range at sit H, with a peak at in detections at SST ~ 16°C and SSS ~ 33.6 PSU. This narrow preference range is closely aligned to properties associated with the Pacific Subarctic Upper Waters (PSUW) described by Bograd et al. (2019) and provides evidence that Cuvier's beaked whales demonstrate a preference for the relatively low temperature and salinity content of the California Current. When looking at the seasonality of Cuvier's beaked whales as it relates to the local physical oceanography over time, acoustic presence decreased beginning in June and July at sites H and N, respectively, when SST and SSS surpassed their average ~ 17°C and ~ 33.5 PSU values. This suggests that a decrease in acoustic presence during the summer months may be related to a shift in water mass properties.

The relationships between daily acoustic presence and temperature at 200 m is likely related to general ecosystem seasonality, with site H demonstrating a positive relationship while site N demonstrated a more defined minimum around 8.5°C to 9°C. When looking at the local physical oceanography over time, temperature at 200 m had seasonal cycles during the late spring to summer months at both sites (Figure 4), which coincided with the onset seasonal upwelling in the CCS. Thus, the cause of a positive relationship between Cuvier's beaked whale acoustic presence and temperature at 200 m depth could be an indirect relationship caused by simultaneous increase in topographic forcing or cyclonic eddies that push the pycnocline and thermocline upward, moving cold water to shallower depths. In contrast, when looking at the local physical oceanography over time, the lack of a definitive seasonal cycle in salinity at 500 m suggests a more mesoscale relationship with Cuvier's beaked whale acoustic presence.

Daily acoustic presence had significant relationships with current direction and relative vorticity at the surface at both sites H and N, which suggest that Cuvier's beaked whale presence was in response to how these physical processes likely modulated prey resources. Beaked whales tend to occupy areas with steep bathyal features including basins, submarine canyons, and continental slopes (MacLeod and Zuur 2005), which are known to attract top predators by creating areas of entrainment of foraging resources (Hui 1979, Selzer & Payne 1988). Spatial variation in relationships with currents at the surface and 200 m depth may be the result of differences in the orientation of bathyal features at each site, meaning that currents would have to come from different directions at given the orientation of our two sites for the same effect of prey aggregation. Thus, I interpret that the basins act as a barrier and entrap micronekton communities (fish, squid, and crustaceans), leading to an increase in acoustic presence of Cuvier's beaked whales. Entrapment would vary within a basin depending on current conditions.

Alongside topographic steering, seafloor topography can influence ocean flow by inhibiting or enhancing the mixing of surface waters with deeper waters (Gille et al. 2004). The two banks closest to sites H and N have a minimum depth of 50 m and 100 m, respectively. Closely aligned directions of currents at the sea surface and 200 m depth at each respective site suggests an interaction between surface flow and deeper flow, with currents at 200 m depth being directly impacted by the topography of the banks whereas currents at the surface may be impacted by water moving up and down the canyon walls.

The negative relationship observed with higher positive and negative values of relative vorticity at the surface suggest that Cuvier's beaked whale presence decreased during time periods with higher upwelling and downwelling intensities. Micronekton communities in deep-sea ecosystems are largely dependent on primary production in the epipelagic zone for food supply (Rogers et al. 2015). Mesoscale eddies can impact the distribution of mesopelagic micronekton through several mechanisms such as trapping micronekton inside eddy cores, creating thermal niches that sustain the growth of different species compared to the surrounding waters, and enhancing primary production (Penna & Gaube 2020). However, higher mesoscale intensities could potentially inhibit the presence of beaked whales by physically exporting nutrients essential to their prey out of the area too quickly for them to exploit (Ruzicka et al. 2016). Associated with the complex topography of the area, these physical processes are likely to determine prey availability and in turn, the distribution and abundance of Cuvier's beaked whales.

iv. Interannual Variability

The detection rates recorded at both sites throughout the acoustic record fluctuated from year-to year, with some years demonstrating higher variability compared to others. The observed relationships with presence anomalies and oceanographic anomalies illustrated that Cuvier's beaked whale seasonal patterns fluctuated with changes in oceanographic conditions and mesoscale activity. Noticeable differences in detection rates were observed during 2009-2011, 2015-2016, and 2019-2020 at both sites, which coincided with abrupt shifts in El-Niño southern oscillation (ENSO) that potentially impacted current strength, coastal upwelling, salinity, and SST (Mantua and Hare 2002) during these time periods (Mantua and Hare 2002).

An increase in Cuvier's beaked whale presence was observed at site N in 2009, with site N experiencing higher detection rates throughout this period compared to site H (Figure 5). Previous studies using climate indices to investigate that state of the California Current System (CCS) during this period revealed a relatively weak and short-lived El Niño event that contributed to weaker than normal upwelling and several extended relaxation events over time scales of several days to weeks in the southern region of the California Bight (Bjorkstedt et al. 2010). This demonstrates that fluctuations in acoustic presence during this period are likely related to weak upwelling events over the study region influenced by a shift to El Niño conditions. However, differences in acoustic presence between sites are likely attributable to spatial variations in the intensity of SST: site H experienced a higher and more definitive peak in SST during the summer compared to site N.

Detection rates at site N started to decrease in spring 2010, coinciding with a decreasing trend in SST and SSS at both sites, contributing to little-to-no peak in SST during the summer. Previous studies using climate indices to investigate the state of the CCS during this period revealed a transition to La Niña conditions that coincided with an unusually strong upwelling event following an El Niño beginning in early spring off the coast of Southern California (Bjorkstedt et al. 2010) which was followed by strong upwelling events in the SCB through 2011, leading to strong negative SST anomalies (Bjorkstedt et al. 2011) over the study region. Thus, fluctuations in detection rates at site N during the 2010 and 2011 period are likely related to an abrupt shift from El Niño to La Niña that contributed to stronger upwelling and colder, fresher surface waters.

Anomalously higher SST was observed from 2014 to 2016, with a higher-than-average peak in SST observed at both sites in the summers of 2014 and 2015. Additionally, anomalously lower SSS was observed beginning in January 2014 and persisting through January 2018 at both sites. This coincided with the onset of the 2014-2016 marine heat wave (MHW) that contributed to anomalously warmer waters at the surface (Weber et al. 2021). Detection rates at site H increased at the end of 2015 and beginning of 2016 following the MHW as SST decreased, leading to a lower and less definitive peak in SST during the summer compared to previous years.

Higher and more consistent detection rates were observed at both sites beginning in January 2019 and persisting through September 2020. This trend was most prominent at site H with anomalously higher detection rates compared to site N. Spatial maps of mesoscale activity during this period also demonstrated differences in their general seasonal cycles, with weaker eddies and more favorable current directions persisting throughout 2019. This coincided with relatively weak El Niño conditions that recurred in the winters of 2018/2019 and 2019/2020 (Thompson et al. 2019).

An increasing trend in SSS was observed at both sites beginning in January 2018 and persisted through September 2020. Additionally, an increasing trend in salinity at 500 m was observed beginning in mid-2018 and persisted through September 2020. Previous studies examining temperature and salinity extremes in the CCS and its source waters have also noted similar patterns in SST and SSS between 2014 to 2019 (Ren and Rudnick 2021, Weber et al. 2021). Their evidence suggested that high salinity values observed at the surface from 2017 to 2019 are a potentially new source water for the California Current (CC), with salinity values in the near-surface CC closely matching those of the California Under Current (CUC). Changes in water masses coming into the CCS may bring different biogeochemical signatures and nutrient properties to the region, potentially indirectly impacting species distributions by directly impacting prey resources (Ren and Rudnick 2021).

These findings further complement the anomaly trends observed for oceanographic conditions during this 2019-2020 period and suggest that fluctuations in detections are likely related to changes in the salinity of source waters and seasonal cycles of mesoscale activity that potentially impacted Cuvier’s beaked whales preferred prey. However, differences in detection rates observed between sites are likely attributable to differences in SST, with site N experiencing a higher and more definitive peak in SST during the summers of 2019 and 2020 compared to site H. Another potential reason for the higher and more consistent detection rates observed in 2020 is decreased marine vessel traffic due to the coronavirus SARS-CoV2 (COVID-19) global pandemic, which began in March 2020 and is still ongoing. Decreased underwater noise due to fewer ships may have allowed cetaceans to experience lower levels of anthropogenic disturbance. While research regarding the impacts of the COVID-19 pandemic on cetaceans is still in progress, I hypothesize that potential limitations in Naval operations and subsequent MFAS use could have minimized disturbance levels in SOAR habitats. However, further studies investigating the direct impacts of sonar use and beaked whale occurrence during 2020 would be needed to confirm this hypothesis.

These results illustrate that interannual variability in Cuvier's beaked whale occurrence and distribution are driven by changes in seasonal oceanographic conditions and mesoscale activity that were influenced by lower-frequency climate forcing such as ENSO and MHWs. They also highlight the need to couple long-term acoustic data with environmental data to understand impacts of global climate change on beaked whale habitat use.

CONCLUSIONS

This study uses passive acoustic monitoring and environmental data to examine spatial and temporal distributions of Cuvier's beaked whales off the coast of Southern California in relation to oceanographic changes over time. Regular detection of Cuvier's beaked whales across the acoustic record demonstrates that the basin located to the west of San Clemente may be an important foraging habitat for deep-diving cetaceans.

Seasonal patterns were evident for Cuvier's beaked whale detections at both sites, with an increase in detections during the spring and winter. This is largely attributable to seasonal cycles in SST, SSS, and temperature at 200 m and weaker mesoscale activity. They exhibited spatial separation in their relationships with current directions at the sea surface and 200 m. Cuvier's beaked whales at site H demonstrated a preference for currents originating from between northeast and northwest directions while site N demonstrated a preference for currents originating from between southwest and northwest directions, which is likely related to the topography associated with the habitats at each recording location and its influence on prey modulation. Consequently, changes in the seasonal cycles of oceanographic conditions and mesoscale activity from year-to-year create interannual variability in the seasonal patterns of Cuvier's beaked whale presence. This variability across years and between sites are likely attributed to differences in the intensity of these changes experienced.

These results highlight the importance of utilizing long-term acoustic monitoring to improve information on the ecology, distribution, and habitat preferences of cryptic and highly mobile species, such as beaked whales. Further investigations coupling acoustic and environmental data is needed to expand the relationship between habitat preferences, as more holistic habitat modeling is a valuable tool that can help identify factors structuring a species distribution, abundance, and behavior on a wide range of temporal and spatial scales. It also demonstrates the importance of understanding factors that may impact their abundance and distribution, such as changes in the local physical environment and subsequently water column. This information can be used for the development of effective conservation and management strategies, especially given that beaked whale habitats are impacted by global climate change and they regularly inhabit regions with high anthropogenic noise. While environmental variables represent factors that influence prey resources and subsequently marine mammal distribution, further investigations could benefit from the use of direct prey measurements to provide insight in habitat and foraging preferences.

Acknowledgements

This thesis, in full, is currently being prepared for submission for publication of the material. Aguilar, Catalina; Baumann-Pickering, Simone; Solsona-Berga, Alba. The thesis author was the primary investigator and author of this material.

APPENDIX

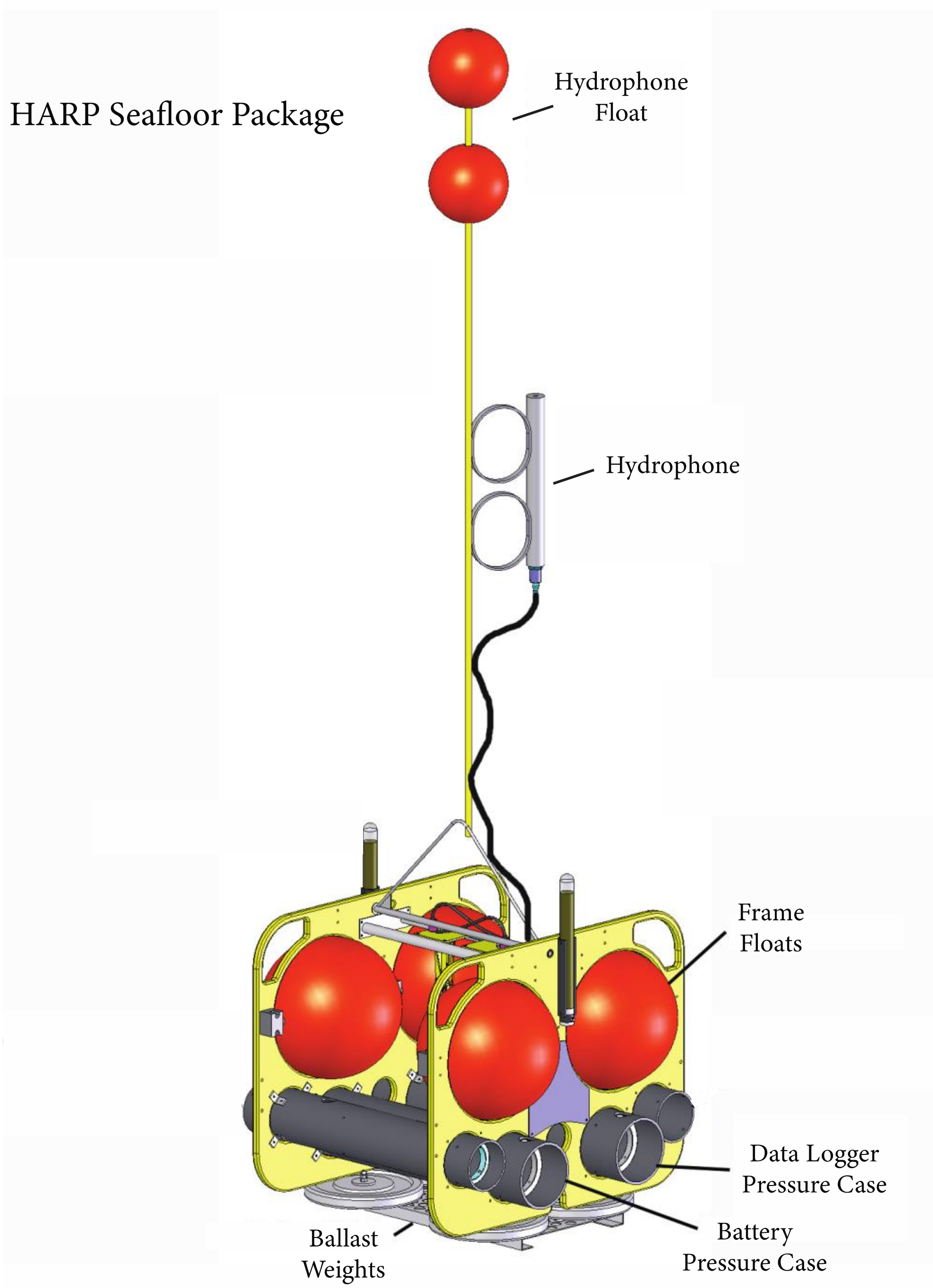

Figure S1: High-frequency Acoustic Recording Package (HARP) design. Passive acoustic recordings were collected using a HARP Seafloor package equipped with a hydrophone suspended 10 m above the seafloor, data logger, battery, acoustic release electronic pressure cases, ballast weights, and 4-channe

Table S1: Summary of statistical outputs of generalized additive models (GAMs) explaining daily Cuvier's beaked whale presence and temporal predictor variables. Month and year were modeled as a factor. Smoothing parameters were selected using the restricted maximum likelihood (REML) method. Models were fit using a Tweedie distribution with a log link function. The categorical P-value significance for each predictor variable is given as *** p < 0.001; ** p < 0.01; * p < 0.05. Gray shading represents predictor variables that were not statistically significant (p-value < 0.05).

Explanatory Variables	H				N			
Temporal Factor	Est	Std. Error	t value	P-value	Est	Std. Error	t value	P-value
January	-0.09	0.07	-1.4	0.172	-0.69	0.09	-7.2	≤ 0.01 ***
February	0.09	0.1	0.99	0.321	-0.55	0.15	-3.7	≤ 0.01 ***
March	0.4	0.09	4.4	≤ 0.01 ***	-0.58	0.15	-3.8	≤ 0.01 ***
April	0.53	0.09	5.8	≤ 0.01 ***	-0.13	0.14	-0.9	0.366
May	0.4	0.1	4.0	≤ 0.01 ***	-0.27	0.14	-1.9	0.056
June	0.01	0.1	0.08	0.937	-0.35	0.14	-2.5	≤ 0.01 *
July	-0.23	0.1	-2.4	0.016 *	-0.35	0.14	-2.6	≤ 0.01 *
August	-0.34	0.09	-3.7	≤ 0.01 ***	-1.27	0.16	-8.1	≤ 0.01 ***
September	-0.26	0.09	-2.9	≤ 0.01 **	-1.31	0.16	-8.1	≤ 0.01 ***
October	0.01	0.09	0.14	0.888	-0.88	0.16	-5.7	≤ 0.01 ***
November	0.23	0.1	2.3	0.019 *	-0.75	0.16	-4.7	≤ 0.01 ***
December	0.17	0.09	1.8	0.066	0.12	0.14	0.89	0.376
2007	-0.46	0.17	-2.8	≤ 0.01 **	—			
2008	-0.36	0.2	-1.8	0.068	—			
2009	0.034	0.18	0.19	0.854	-0.35	0.09	-4.1	≤ 0.01 ***
2010	0.29	0.18	1.7	0.098	-0.59	0.13	-4.5	≤ 0.01 ***
2011	0.21	0.18	1.2	0.247	-1.61	0.16	-10.3	≤ 0.01 ***
2012	0.46	0.18	2.6	≤ 0.01 *	-0.96	0.14	-6.9	≤ 0.01 ***
2013	-0.07	0.19	-0.36	0.722	-0.95	0.15	-6.5	≤ 0.01 ***
2014	0.06	0.18	0.35	0.726	-0.94	0.14	-6.5	≤ 0.01 ***
2015	0.23	0.18	1.5	0.137	-0.94	0.15	-6.3	≤ 0.01 ***

Table S1: Summary of statistical outputs of generalized additive models (GAMs) explaining daily Cuvier's beaked whale presence and temporal predictor variables, Continued

2016	1.05	0.18	5.9	≤ 0.01 ***	-0.85	0.14	-6.1	≤ 0.01 ***
2017	0.39	0.18	2.2	0.028 *	-0.87	0.13	-6.6	≤ 0.01 ***
2018	0.23	0.19	1.2	0.223	-1.0	0.14	-7.3	≤ 0.01 ***
2019	0.99	0.18	5.6	≤ 0.01 ***	-0.84	0.13	-6.5	≤ 0.01 ***
2020	1.09	0.18	6.2	≤ 0.01 ***	-0.91	0.14	-6.4	≤ 0.01 ***

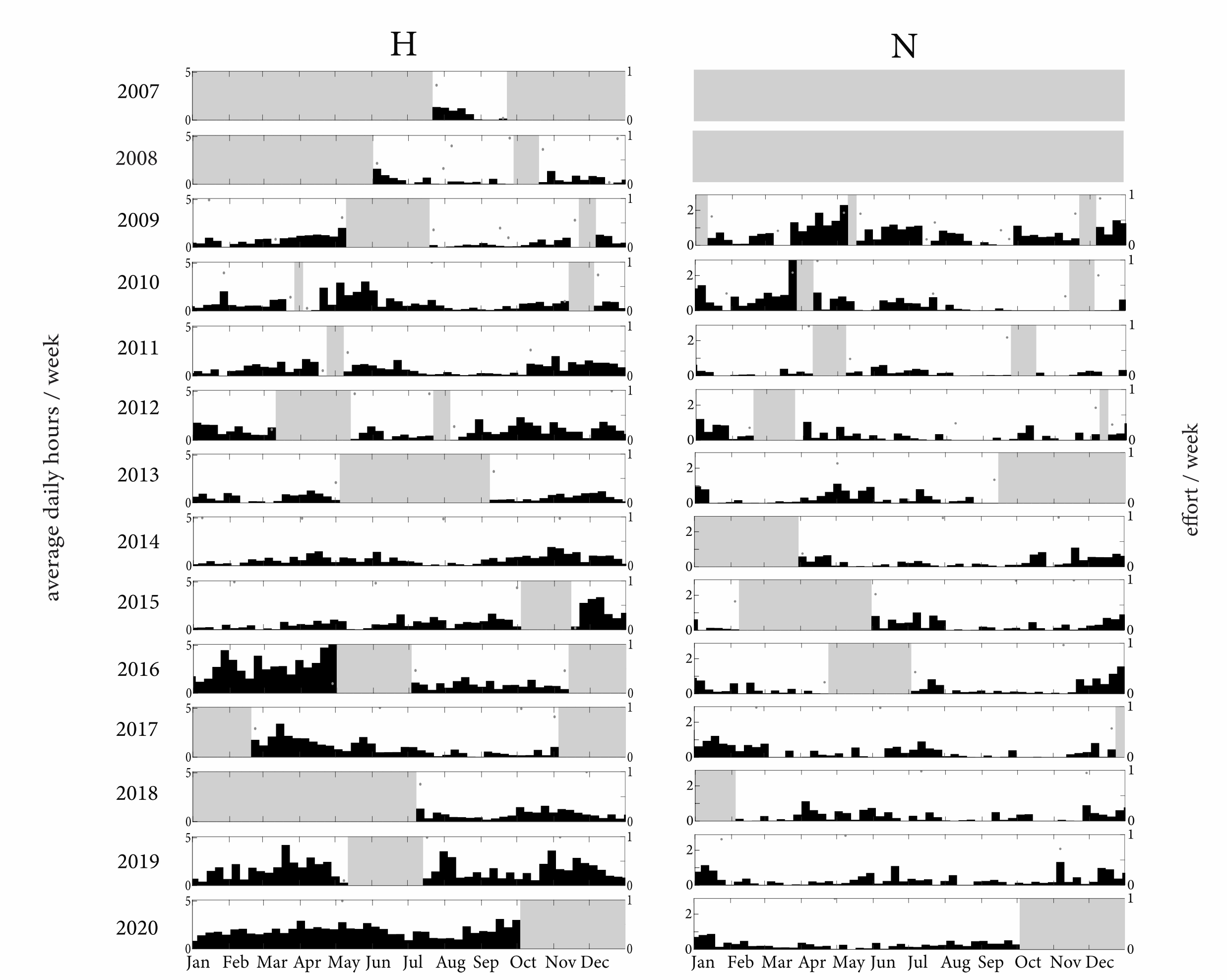

Figure S2: Weekly average of daily acoustic presence in hours of Cuvier's beaked whale between January 2007 to September 2020 at sites H and N. Gray dots represent percent of effort each week in weeks with less than 100% recording effort. Gray shading represents periods with no effort. Absence of gray dots or shading absent represents weeks with full recording effort.

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