Acoustic Vector Sensing of Blue and Fin Whale Habitat Occupancy off Central California

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***Abstract*—Temporally varying geographic distributions of whale populations are difficult to visually monitor across large marine ecosystems. Acoustic vector sensing (AVS) of the powerful calls produced by baleen whales enables continuous monitoring over large areas with spatial information contained in the bearing estimates to whales. Using three years of AVS data in Monterey Bay National Marine Sanctuary, we examine the habitat occupancy of endangered blue and fin whale populations. The calls of fin whales persistently originated primarily in offshore deep-water (ODW) habitat, shifting into shelf / slope habitat only occasionally. The calls of blue whales originated primarily in shelf / slope habitat. However, detection of blue whales in ODW habitat increased significantly across the study period with stronger wind-driven upwelling that increased krill abundance and expanded foraging habitat. This expansion increased both the spatial overlap of blue and fin whales and the exposure of blue whales to ship strike risk. AVS is an effective method of passive acoustic monitoring for informing marine ecological research and conservation.**

***Index Terms*—acoustic vector sensing, marine ecosystems, blue whale, fin whale**

I. Introduction

The protected habitat of Monterey Bay National Marine Sanctuary (MBNMS) lies within the central latitude range of Biologically Important Areas (BIAs [1]) for endangered blue and fin whale populations in the eastern North Pacific (Fig. 1). Whale sighting data spanning decades indicate overlap in the foraging habitat of these gigantic species, yet their core BIAs (darker blue and green areas in Fig. 1a) diverge in the region of MBNMS, with that of fin whales much farther offshore.

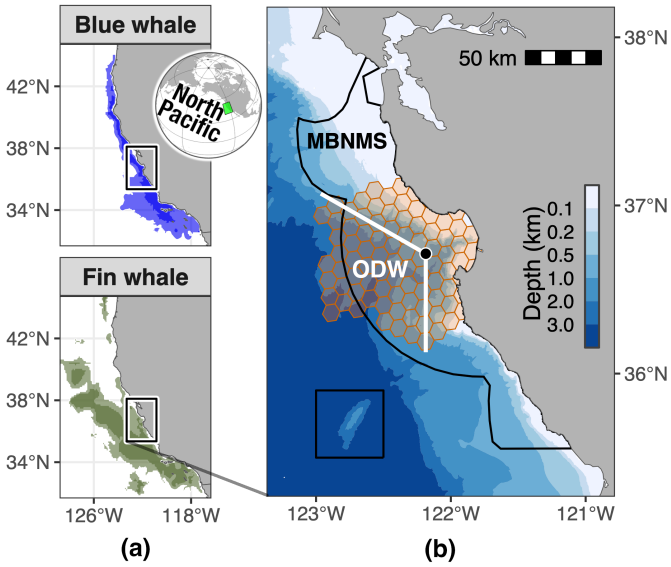

Fig. 1. (a) Biologically Important Areas (BIAs) for blue and fin whales in the eastern North Pacific; darker shading defines the core BIA of each species. (b) Bathymetry within and around Monterey Bay National Marine Sanctuary (MBNMS) relative to the location of passive acoustic monitoring at the Monterey Accelerated Research System (MARS) cabled observatory (black circle located at 36.713°N, 122.186°W, 890 m depth). White lines define a bearing range relative to MARS that approximately separates shelf and slope habitat from offshore deep-water (ODW) habitat, as well as crossover points in the distributions of bearing for blue and fin whale calls received at MARS (see Results). Orange shaded cells represent areas from which a calling blue whale would be detected at MARS at levels exceeding 1.25× median background ambient noise [2] (see methods). The full scale bar represents 50 km.

Passive acoustic monitoring (PAM) is a highly effective method of detecting soniferous species, particularly those that produce powerful low-frequency sounds that travel far. Since 2015, PAM has been supported by the MARS cabled observatory in MBNMS (Fig. 1b) [3]. PAM from omnidirectional hydrophones at MARS has advanced understanding of the presence and behavioral ecology of baleen whales [2], [4]–[10] and toothed whales [11], [12] in MBNMS. Beyond omnidirectional PAM, spatial information provided by acoustic vector sensing (AVS) can deepen ecological insight, and it has been applied to study both baleen and toothed whales [2], [13]–[15]. AVS observations in MBNMS enabled the discovery that foraging blue whales are highly attuned to episodic variations in coastal ocean circulation, tracking wind-driven upwelling plumes in which their prey form dense aggregations [2], [16]. Here we apply three years of AVS in the region of MBNMS, in the central California Current Ecosystem, to examine the habitat occupancy and ecology of endangered populations of the two largest animal species—blue and fin whales.

II. Methods

A. Acoustic Vector Sensor Data Acquisition and Processing

Acoustic vector sensing (directional passive acoustic monitoring) for this study utilized a GeoSpectrum Technologies M20 sensor deployed on the MARS cabled observatory (Fig. 1b). The sensor, its configuration for this deployment, and its calibration and data processing have been published [17]. Further, the methods for processing AVS data for blue whale calls have been published, together with ground truth demonstrated using whale biologging [2]. Here we provide a summary of the analysis methods consistently applied for both whale species.

Processing of AVS data was constrained to the months during which the predominant acoustic behavior of both blue and fin whales, singing, occurs within the study region each year: July through February [10]. For each of three annual periods of whale song detection, all AVS data were processed to paired daily spectrogram (power spectral density) and azigram (bearing) arrays at resolutions of 1 second and 0.5 Hz. Call presence was detected using established energy detection methods [5], [10], [18] applied to the dominant call types of each species—blue whale B calls and fin whale 20 Hz pulses. The empirically determined threshold for call detection was a power spectral density (PSD) signal level $1.25\times$ background noise measured in dB [2]. Above this threshold, blue and fin whale calls consistently showed sharp distinction in both spectrograms and azigrams. Within each 1 second window of call detection and within the narrow frequency band of peak energy in the focal calls (40–45 Hz for blue whales and 19–23 Hz for fin whales), bearing estimates were extracted from the single 0.5 Hz frequency band at which PSD was greatest [2]. This automated processing was followed by manual review of all detection results, removing any periods during which low-frequency vessel noise contaminated the frequency bands of the whale calls. Quality controlled results comprised 2,508 hours of bearing estimates from MARS to calling whales, 46% of which were from blue whales and 54% of which were from fin whales. This time-series (Fig. 2) is the basis for all AVS analyses presented.

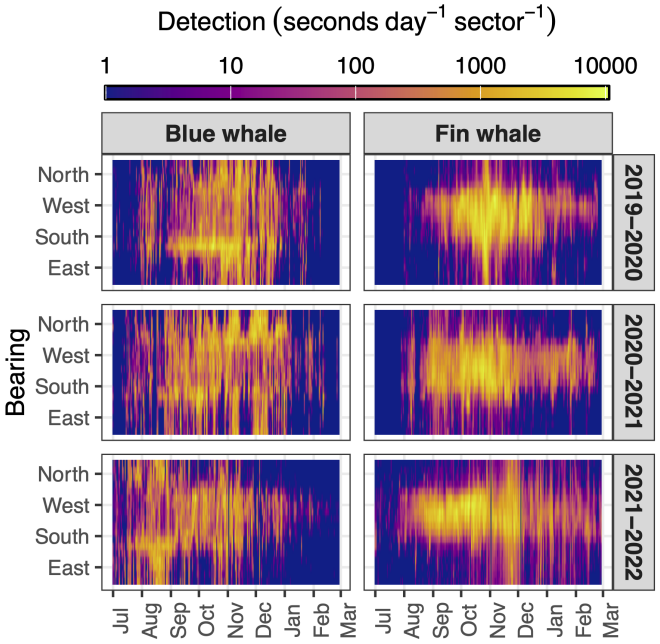

Fig. 2. Daily detection levels of blue and fin whale song calls originating within 20º bearing sectors relative to MARS (location in Fig. 1b)

B. Analyses of Whale Call Bearings

Bearing distributions were characterized in total relative to the species distinctions indicated by the core BIAs (Fig. 1a). To examine variations in habitat occupancy, bearings were divided into sectors that distinguish shelf / slope habitat and offshore deep-water (ODW) habitat. This division was approximated by vectors from MARS to the South (180º) and Northwest (300º), with shelf / slope habitat inshore of the vectors and ODW habitat offshore of the vectors (Fig. 1b). The percent of call origination in ODW habitat was a key metric, quantified at daily and hourly resolution. To base results only on days and hours with substantial levels of detection, the minimum threshold for inclusion in analyses was 5 minutes of detection. This threshold exceeded the 25^{th} percentile of daily detection levels and the 70^{th} percentile of hourly detection levels (including zero values). Daily %ODW was compared across years graphically using violin and box plots and statistically using Wilcoxon rank sum tests [19]. To examine simultaneous occupancy of both species, probability density distributions of hourly %ODW were computed overall and for each year individually. Because blue whale detections uniquely showed significant interannual changes in %ODW, variations in their exposure to ship strike risk were further examined using a bearing range encompassing the offshore shipping fairways: 180º to 322º.

C. Ecosystem Data and Analyses

Analyses of ecosystem data focused on the upwelling of nutrients that fuel primary productivity and thus support the

food web, measured abundances of krill—essential prey of both whale species, and the spatial scales of whale foraging habitat. Upwelling nutrient supply was examined using the biologically effective upwelling transport index (BEUTI [20]) computed for 37°N, at the northern end of Monterey Bay (Fig 1b). Krill abundances were examined using standardized data for forage species sampled by midwater trawl surveys conducted annually between late April and mid June, acquired by the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS [21]–[23]). Krill catch-per-unit-effort (CPUE) data were compared across years graphically using violin and box plots and statistically using Wilcoxon rank sum tests [19]. The spatial scale of cool thermal habitat (indicative of upwelled water in the surface mixed-layer) was examined using the Habitat Compression Index (HCI [24]–[26]) for 35º to 40ºN.

III. Results

A. Habitat Occupancy Patterns

Considering the entire time series (Fig. 2), call origin distributions differed markedly between whale species (Fig. 3a). Fin whale calls originated predominantly in ODW habitat (Figs. 1b,3a). This spatial peak in fin whale call origin coincided with a trough in blue whale call origin (Fig. 3a). Blue whale call detections exhibited a bimodal distribution, with peaks along the flanks of the single fin whale peak.

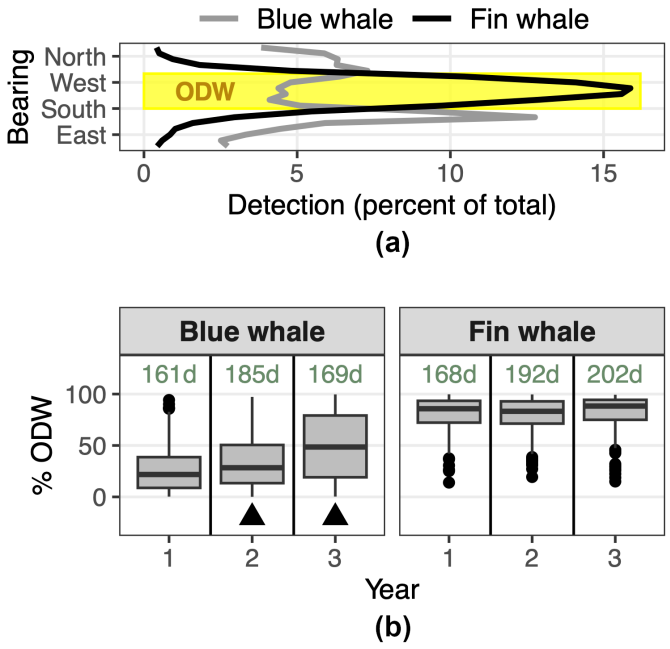

Fig. 3. (a) Normalized bearing distributions (relative to MARS, Fig. 1b) of total call detection throughout the study period (1151 hours for blue whales, 1357 hours for fin whales). The highlighted bearing range corresponds to that defined west of the white bearing lines in Fig. 1b, i.e. offshore deep-water (ODW) habitat. (b) Boxplots of the daily percent of call detection that originated in ODW habitat (%ODW). Black circles are outliers. The number of days represented each year for each species is noted at the top. Black triangles indicate a significant ($p < 0.01$) shift in the population of values in one year relative to the prior year.

Interannual variation also differed between species (Fig. 3b). The predominance of fin whale call origination in ODW habitat persisted across years with no significant changes. Relatively few outliers with fin whale %ODW below 50% (Fig. 3b) represent short-term shifts in call origination outside of the persistent ODW range (Fig. 2). In contrast, the initial predominance of blue whale call origination in shelf / slope habitat (low %ODW) shifted toward a more even distribution across habitat types over the study period, with significant ($p < 0.01$) shifts toward greater ODW occupancy in each successive year (Fig. 3b).

Beyond overall patterns derived from all detection results (Fig. 3a) and days with substantial levels of detection (above the 25^{th} percentile, Fig. 3b), assessing the degree to which blue and fin whales simultaneously shared habitat domains requires a more instantaneous characterization. Based on 2,764 hours during which both species were detected at substantial levels (above the 70^{th} percentile; Fig. 4a), probability density distributions of %ODW represent simultaneous occupancy overall and annually (Fig. 4b).

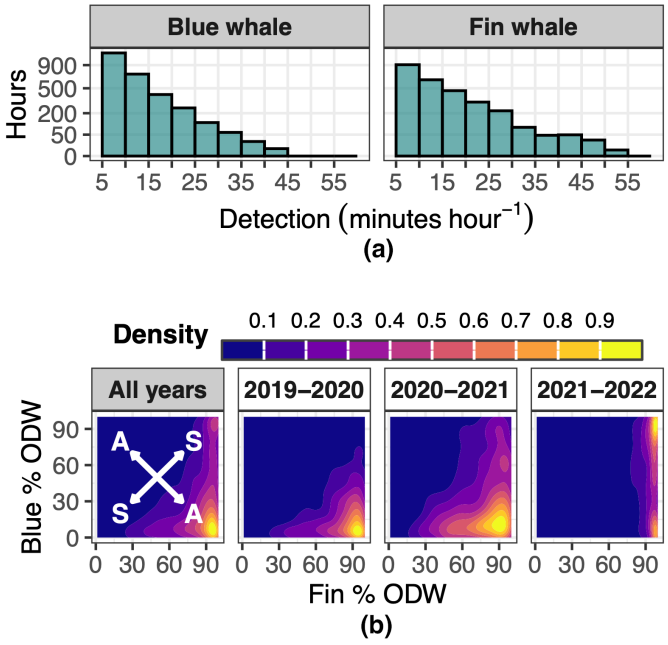

Fig. 4. (a) Histograms of detection levels for 2,764 hours during which both blue and fin whale call detection simultaneously exceeded 5 minutes hour^{-1}. (b) Simultaneity of ODW habitat occupancy for both whale species, quantified as normalized probability density distributions. S = sympatry; A = allopatry.

Sympatry (habitat overlap) is indicated if densities are maximum at either high or low %ODW for both species (S labels in Fig. 4b). Allopatry (habitat separation) is indicated if densities are maximum at high %ODW for one species and low %ODW for the other species (A labels in Fig. 4b). Across all years, blue and fin whales tended toward allopatry, with maximum normalized density at high %ODW occupancy for fin whales and low %ODW occupancy for blue whales (Fig. 4b). Allopatry was most pronounced during the first

year (2019-2020 in Fig. 4b). Allopatry was also dominant in the second year (2020-2021 in Fig. 4b), however densities increased in both sympatric quadrants of the distribution relative to the previous year. The third year showed a shift to dominance of sympatry, with maximum density in the high %ODW corner of the distribution (2021-2022 in Fig. 4b).

B. Blue Whale Habitat Shifts in Relation to Ship Strike Risk

Shifts in blue whale habitat occupancy into ODW habitat (Figs. 3, 4) imply consequences for the exposure of an endangered species to a key anthropogenic threat. Examining 515 days of substantial daily detection (Fig. 5a), we consider interannual variation in blue whale exposure to ship strike risk [27]. Shipping fairways (black lines in Fig. 5b) run through ODW habitat within the area over which MARS AVS detects whales (highlighted in orange in Fig. 5b). The offshore bearing range between 180º and 322º (white lines in Fig. 5b) spans the large-vessel fairways over the region of whale acoustic detection. Quantified using daily values of the percent of call origination in the area transected by large-vessel fairways, ship strike risk exposure increased each year (Fig. 5c).

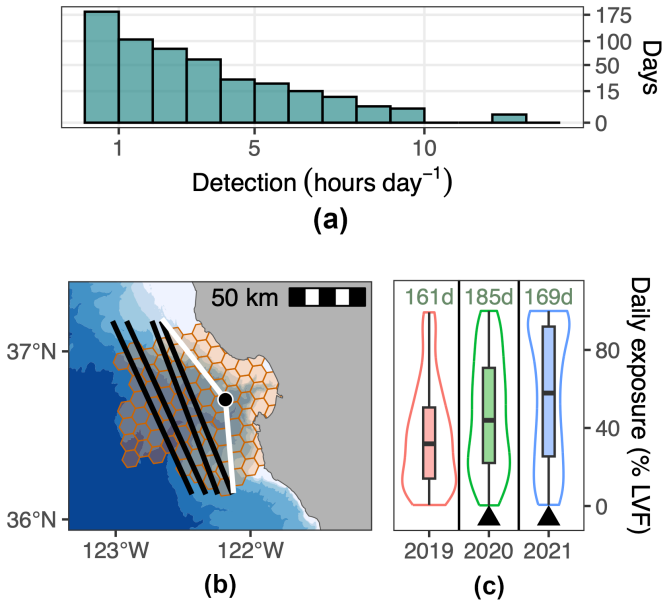

Fig. 5. (a) Histogram of detection levels for 515 days during which blue whale call detection exceeded 5 minutes. (b) Bathymetry relative to the location of passive acoustic monitoring at MARS (black circle), the detection domain (orange), large vessel fairways (recommended tracks, black lines), and the bearing range (white lines) in which vessel fairways transect the detection domain. Bathymetry contour levels are the same as those in Fig. 1b. (c) Violin and box plots represent the distributions of daily values of the percent of blue whale call origination in the area transected by large vessel fairways (%LVF). The number of days represented in each year is noted at the top. Black triangles indicate significant ($p < 0.01$) shifts in the population of values in one year relative to the prior year. Years are labeled by the first calendar year of each annual period of blue whale song detection (Fig. 2).

C. Ecological Underpinnings of Habitat Shifts

The increasing occupancy of ODW habitat by blue whales over the three-year study period (Figs. 3–5) paralleled an increasing trend in wind-driven upwelling (Fig. 6). Stronger upwelling of nutrients into ocean-margin habitat can influence whale foraging ecology by increasing the primary productivity that ultimately supports the growth and distribution of prey populations [28], and by expanding available foraging habitat [25]. The Biologically Effective Upwelling Transport Index (BEUTI) for the study region shows that nutrient supply for primary productivity increased each year. This trend was pronounced during the upwelling season (identified by U in Fig. 6), February through July [29], during which BEUTI doubled over the study period. This period of the year is also the most formative for the trophic transfer that supports the growth of prey populations [30]. The Habitat Compression Index (HCI) during the upwelling season also increased over the three-year period (U in Fig. 6b), indicating increased area of upwelling influence within the foraging habitat.

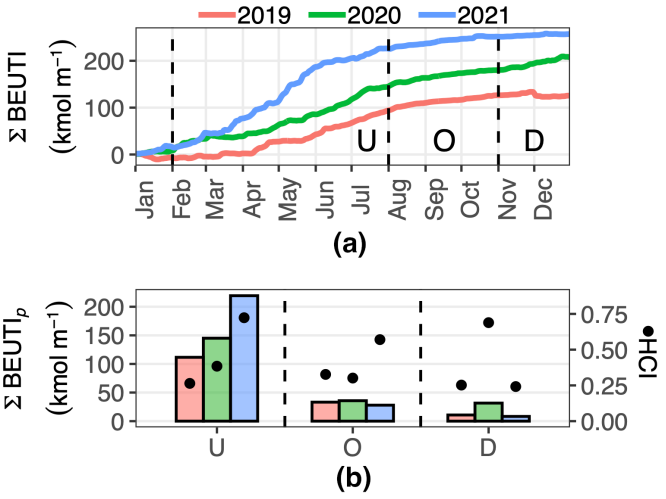

Fig. 6. (a) Cumulative Biologically Effective Upwelling Transport Index (BEUTI) at 37ºN. Oceanographic seasons are labeled: Upwelling (U), Oceanic (O) and Davidson Current (D). The annual period shown, until the end of each calendar year, covers 98% of all blue whale call detection (Fig. 2). (b) Total upwelling by year and season, and the Habitat Compression Index (HCI [25]) for 35º to 40ºN. Higher HCI values indicate expansion of foraging habitat.

Based on a thirty year record, a previous study showed that krill abundances off central California were exceptionally low in 2019 [31], the first year of the present study. Trawl sampling was strongly curtailed in 2020 due to impacts of the COVID-19 pandemic, however sampling effectively spanned the immediate study region and the greater central California coast in both 2019 and 2021 (Fig. 7a). Significantly higher abundances of krill in 2021 (Fig. 7b) paralleled the increases in upwelling and HCI (Fig. 6).

IV. Discussion

Biologically Important Areas (BIAs) for blue and fin whales in the eastern North Pacific, based on decades of observations [1], provide a valuable empirical basis for understanding the biogeography of these endangered populations. The spatial detail of these BIAs informs not only resource management

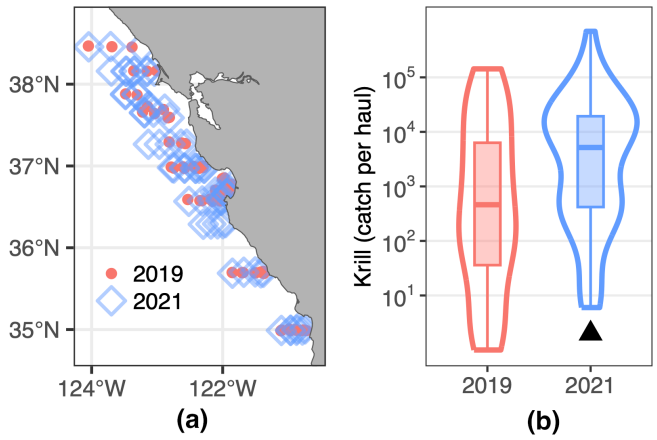

Fig. 7. (a) Locations of RREAS mid-water trawl sampling (catch-per-unit-effort; CPUE) of total krill for two of the three study years. (b) Combined violin and boxplot representations of the krill data from the sampling stations shown in panel a. The black triangle indicates a significant ($p < 0.01$) shift in the population of values between 2019 and 2021.

and conservation, but also key questions for continuing research. One question that arises from examination of blue and fin whale BIAs in the region of MBNMS concerns habitat overlap. How much do these two largest animal species that rely on the same prey share habitat? What ecological drivers influence their overlap and at what time scales? By providing continuous monitoring of both species' habitat occupancy over a large area of essential foraging habitat, AVS allows new insights into these questions, reaching beyond the long-term, time-integrated views provided by the BIAs.

Considering the study period overall, blue and fin whales tended to be allopatric. This tendency is consistent with divergence of their core BIAs moving from south to north across the study region. However, the degree of allopatry or sympatry changed significantly across years. The habitat occupancy of blue whales exhibited greater responsiveness to interannual variations in upwelling and HCI, and this responsiveness shifted the balance of allopatry / sympatry. This ecological pattern likely reflects the fact that the core blue whale BIA resides over shelf and slope habitat in the study region. This relatively near-coastal habitat is where upwelling originates and where upwelling plumes structure pelagic habitat during much of the year. Prior research using AVS has shown how blue whales track episodic upwelling plume flows and how their bimodal peak in bearing distribution relative to MARS aligns with bearings to the two primary coastal upwelling centers in this region [2]. Further, integration of animal– and satellite–borne sensing has revealed how a foraging blue whale can precisely locate thermal fronts of an upwelling plume through systematic search behaviors that are highly responsive to near-surface thermal gradients, thereby enabling successful feeding on dense krill swarms within the fronts [32]. In contrast, the core fin whale BIA resides more than 100 km offshore of the coastal upwelling centers in this region. While upwelling supports growth of the prey populations that feed both whale species, the movement ecology of blue whales is evidently more responsive to variations in upwelling and thus the stronger determinant of interannual variations in habitat overlap between species. The AVS data of this study period also indicate that fin whale occupancy of shelf and slope habitat occurs episodically and can increase sympatry over shorter time scales. Understanding the oceanographic processes that may drive such shifts in fin whale habitat occupancy is a topic of future research.

Most of the acoustic detection of whale habitat occupancy occurred during fall and winter, when the acoustic behavior of singing by these whale species is prevalent in the study region [10]. Although significant levels of blue whale acoustic detection occur during winter (the Davidson Current period beginning in November), the interannual patterns in blue whale habitat occupancy found in this study were not consistent with the patterns of upwelling that occurred during the winter season itself. Instead, habitat occupancy tracked variations in upwelling that occurred earlier in the year. The primary productivity that is most formative for the growth of prey populations occurs annually during spring and summer [29]. Prey populations thus represent *oceanic memory* of upwelling, stored in the biomass of forage species that change greatly in relative abundance and spatial distribution on interannual and longer time scales [21]–[23].

Resource abundance and distribution can influence the spatial overlap of predators with shared prey preferences [33]. In general, theory predicts that greater forage availability can reduce interspecific competition, permitting sympatry between predators [34]. However, if reduced resource abundance also constrains the distribution of profitable foraging patches (i.e., resources concentrated in few locations and times), one might instead predict greater spatial overlap under resource scarcity despite the costs of competition [35]. In the ecological context of this study we find evidence for the former hypothesis, showing that interannual increases in the abundance of krill prey that are central to the diet of both whale species coincided with increases in spatial overlap between the whale species. The geographic separation of core BIAs for these whale species across the study region may partly explain this ecological pattern, as blue whales responded to increased prey abundance and offshore extension of favorable foraging habitat. Further, differences in the diets and foraging strategies of blue and fin whales may contribute to an allopatric tendency suggested by the divergence of core BIAs and the overall AVS results. Blue whales consume krill almost exclusively, and much of their foraging occurs along the continental shelf break and within aggregative surface circulation features off central California [6], [36]–[38]. Fin whales may specialize in feeding on offshore krill populations that have different behavioral relationships to circulation phenomena, and they may have a more flexible diet, e.g. also consuming fish. These whale species may have evolved to specialize in slightly different prey environments, for example fin whales using their speed and smaller size to exploit smaller offshore patches while blue whales exploit larger, denser prey patches along the shelf

and shelf edge. Such distinctions in foraging strategies may contribute to niche separation between these whale species in this study region, while allowing for greater habitat overlap when they respond to changes in the ecosystem.

Sound is a powerful carrier of information in the sea, particularly for low-frequency sounds such as the song calls of blue and fin whales. Omnidirectional passive acoustic monitoring effectively detects the presence of these gigantic mammal species over large areas, and this alone is valuable to scientific research and its role in informing protection of these endangered whale populations. Yet beyond detecting presence, spatial information is essential to advancing conservation. Potentially harmful anthropogenic factors have geographic footprints, and the most impactful intersections between anthropogenic factors and whale populations may differ not only between species, but also for the same species in different regions. For example, compression of cool thermal habitat by marine heatwaves and other phenomena can cause humpback whales to forage more in nearshore habitat where entanglement in fishing gear is exacerbated [24], [26]. In contrast, blue whale exposure to ship strike risk in this study region may be exacerbated under conditions of habitat expansion, to which the whales respond by foraging more in offshore habitat that is transected by shipping fairways. North of the study region, where shipping lanes aggregate vessel traffic approaching and leaving ports in San Francisco Bay, habitat compression may instead exacerbate the near-coastal intersection of ships and multiple whale species. Spatial-temporal risk assessment methods are needed to address such complex conservation and management priorities, and they require data-based understanding [27], [39], [40]. The unique data provided by acoustic vector sensing represents an effective and valuable resource for understanding the ecology of these protected giants, and in applying better understanding to support recovery of their populations.

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