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LETTER

Oceanic giants dance to atmospheric rhythms: Ephemeral wind-driven resource tracking by blue whales

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Abstract

Trophic transfer of energy through marine food webs is strongly influenced by prey aggregation and its exploitation by predators. Rapid aggregation of some marine fish and crustacean forage species during wind-driven coastal upwelling has recently been discovered, motivating the hypothesis that predators of these forage species track the upwelling circulation in which prey aggregation occurs. We examine this hypothesis in the central California Current Ecosystem using integrative observations of upwelling dynamics, forage species' aggregation, and blue whale movement. Directional origins of blue whale calls repeatedly tracked upwelling plume circulation when wind-driven upwelling intensified and aggregation of forage species was heightened. Our findings illustrate a resource tracking strategy by which blue whales may maximize energy gain amid ephemeral foraging opportunities. These findings have implications for the ecology and conservation of diverse predators that are sustained by forage populations whose behaviour is responsive to episodic environmental dynamics.

KEYWORDS
blue whales, coastal upwelling, dynamic management, foraging ecology, marine ecosystems, movement ecology, predator–prey dynamics, resource tracking

INTRODUCTION

Understanding how animals track resources in space and time is increasingly recognized as central to advancing the fields of movement ecology, foraging ecology and conservation (Abrahms et al., 2021; Barlow & Torres, 2021; Nathan et al., 2008). For pelagic animals in upwelling ecosystems, the boom and bust of biogenic productivity plays a fundamental role in the transfer of energy from small plankton to larger marine vertebrates including fish, seabirds and marine mammals (Ainley et al., 1995; Szoboszlai et al., 2015). During highly productive seasons, oscillations in the physical environment caused by wind-driven upwelling can rapidly cause forage species like krill and schooling fish to aggregate (Benoit-Bird et al., 2019). These aggregations of prey

are important to large predator foraging success by increasing prey capture rate and energy intake (Goldbogen et al., 2011, 2019; Hazen et al., 2015). However, the patterns and processes underlying how these top predators predict, detect and exploit patchy and ephemeral prey swarms remain poorly understood.

This dearth in our understanding of how animals find food in patchy oceanic habitat is particularly evident at the largest scale, where blue whales (*Balaenoptera musculus*) feed on groups of small-bodied crustaceans, krill (Croll et al., 2005; Fiedler et al., 1998; Schoenherr, 1991). With a body length that can exceed 30 m and a body mass that can exceed 150 tonnes, the blue whale is the largest animal ever to have evolved (Goldbogen et al., 2019; Goldbogen & Madsen, 2021). Meeting the high energetic demands of their massive bodies has required evolution of morphology and behaviours that enable efficient foraging (Goldbogen et al., 2011, 2019; Hazen et al., 2015). An individual blue whale can consume more than 20 tonnes of krill in a day (Savoca et al., 2021), and they preferentially consume food patches comprising krill that are larger and more energy-dense than average within a local foraging habitat (Croll et al., 2005). Beyond highly efficient and effective foraging at the individual level, social foraging mediated by long-distance vocal signalling may enable blue whale populations to collectively locate exceptional but ephemeral foraging opportunities (Cade, Fahlbusch, et al., 2021; Cade, Seakamela, et al., 2021).

The blue whale population inhabiting the eastern North Pacific, estimated to be between 1500 and 2000 individuals (Calambokidis & Barlow, 2020; Carretta et al., 2021), migrates annually between foraging habitat spanning California to the Gulf of Alaska and breeding habitat off Mexico and Central America (Bailey et al., 2009; Calambokidis et al., 2009, 2015). Biologically important areas for this population have been identified from long-term observations of where blue whales aggregate to forage (Calambokidis et al., 2015). One of these areas is in Monterey Bay National Marine Sanctuary (MBNMS; Figure 1a). MBNMS resides within the central California Current Ecosystem, an eastern boundary current system in which wind-driven coastal upwelling transports cold

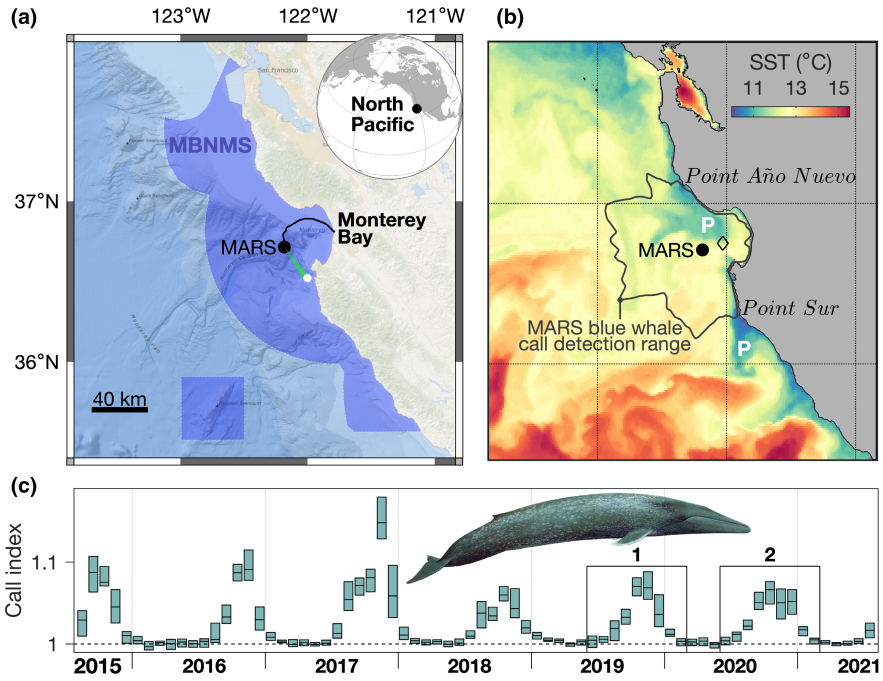

FIGURE 1 Ecological setting. (a) The study region is in Monterey Bay National Marine Sanctuary (MBNMS) along the eastern margin of the North Pacific. Hydrophones are operated through the Monterey Accelerated Research System (MARS) cabled observatory (black line and circle; main node at 36.713°N, 122.186°W, 891 m depth). The white circle marks the GPS location of a tagged blue whale, acquired 10 min after a series of blue whale calls recorded on the tag were matched to calls received at MARS, and the green-shaded sector defines the span of MARS acoustically estimated bearings to calls originating from that tagged whale (see Results). (b) An infrared sea surface temperature (SST) image from 10 November 2020 14:44 UTC represents synoptic patterns of coastal upwelling plumes (cool SST labelled P) at a time when blue whale behavioural response to upwelling was observed. Point Año Nuevo and Point Sur are the primary locations in the Monterey Bay region where coastal upwelling plumes originate (Rosenfeld et al., 1994). The black contour defines the approximate domain within which bearings to calling blue whales can be reliably estimated (see 'Materials and methods'). The diamond marks the location of a mooring where temperature and salinity were monitored. (c) This 6-year time-series from MARS passive acoustic monitoring represents seasonal and interannual variation in blue whale call activity. Shown are the monthly interquartile range and median values of the daily blue whale B-call index (see 'Materials and methods'). The two periods of blue whale call activity for which we examine directional acoustic vector sensor data are indicated by the numbered boxes. Whale artist: Larry Foster.

(Figure 1b; upwelling plumes labelled P), nutrient-rich subsurface water into the sunlit surface layer, thereby fuelling abundant photosynthetic primary production (Barber & Smith, 1981; Huyer, 1983; Pennington & Chavez, 2000; Ryther, 1969). Enrichment of primary production, in turn, supports the populations of forage species upon which many other species depend (Cimino et al., 2020; Santora et al., 2017).

Resource tracking by blue whales in the California Current Ecosystem has previously been explored, primarily at the scale of seasonal migratory movements. Following the breeding season, the timing of blue whale migration into foraging habitat consistently occurs during spring, when krill populations develop after the seasonal rise of primary productivity (Abrahms et al., 2021; Croll et al., 2005). Resource tracking during this annual migration is thought to be enhanced by long-term memory of relatively stable and productive foraging habitat (Abrahms et al., 2019). Blue whales vary the timing of their departure from foraging habitat by up to 4 months from year to year, potentially as a strategy to maximize energy gain before the breeding season (Oestreich et al., 2022; Oestreich, Fahlbusch, et al., 2020). During annual periods of residence within foraging habitat, blue whales must frequently find dense prey aggregations. While it is known that blue whale foraging occurs primarily at the edge of the continental shelf and in submarine canyon habitat, where dense krill swarms develop (Cade, Fahlbusch, et al., 2021; Cade, Seakamela, et al., 2021; Croll et al., 2005; Fiedler et al., 1998; Santora et al., 2018; Schoenherr, 1991), little is known about the hydrodynamic, behavioural, and sensory influences that underlie successful resource tracking by blue whales in highly dynamic habitat. Studies off New Zealand have examined temporal lags between wind, ocean temperature and indicators of blue whale presence, toward forecasting whale distribution patterns for dynamic management (Barlow et al., 2021; Barlow & Torres, 2021), however no studies have yet tracked blue whale movement in relation to dynamic upwelling circulation.

It has recently been discovered that krill and other forage species aggregate during upwelling (Benoit-Bird et al., 2019), and opportunistic encounters with exceptionally dense aggregations of foraging blue whales in the Monterey Bay region coincided with upwelling plume boundaries at the shelfbreak where exceptional krill foraging conditions existed (Cade, Fahlbusch, et al., 2021; Cade, Seakamela, et al., 2021). These recent insights motivate the hypothesis that blue whales track the coastal upwelling features in which krill aggregation occurs. Here, we use observations of predator, prey and environmental dynamics to examine this hypothesis and reveal resource tracking by blue whales at previously inaccessible spatiotemporal scales, with meaningful implications for conservation.

MATERIALS AND METHODS

Directional acoustic vector sensing of blue whale calls

Passive acoustic monitoring (PAM) of blue whale calls used the Monterey Accelerated Research System (MARS) cabled observatory, located in the centre of MBNMS (Ryan et al., 2016; Figure 1a). Omnidirectional PAM through MARS has been applied to study baleen whale ecology (Oestreich et al., 2022; Oestreich, Fahlbusch, et al., 2020; Ryan et al., 2019), predator–prey dynamics (Urmy & Benoit-Bird, 2021) and anthropogenic noise (Krumpel et al., 2021; Ryan et al., 2021; Simonis et al., 2020). Directional PAM through MARS was enabled by an acoustic vector sensor, a GeoSpectrum Technologies M20, deployed in January 2019 (Smith et al., 2022). This type of sensor has been applied to demonstrate tracking of humpback whales off Hawaii (Tenorio-Hallé et al., 2022). Although blue whale D calls have been associated with foraging (Oleson et al., 2007), B calls are the most powerful and prevalent of the four call types made by blue whales in our study region (Oestreich et al., 2022; Oestreich, Fahlbusch, et al., 2020; Širović et al., 2015) and comprise the focal signal used here to detect and track blue whales. Because the recording environment is foraging habitat, the directional patterns of all blue whale calls are relevant to understanding spatiotemporal attributes of their foraging behaviour and ecology.

Beyond core PAM data acquisition and processing methods (Smith et al., 2022), we developed methods to extract bearings from the MARS observatory to blue whale B-call origins. June through February of two sequential years (numbered boxes in Figure 1c) were examined. Each annual detection period begins in late summer with the rise of song behaviour and ends in winter when the whales migrate to lower latitudes for the breeding season (Oestreich et al., 2022; Oestreich, Fahlbusch, et al., 2020). The third harmonic of the B-call (Figure 2a,b) typically has the highest ratio of peak to background energy (Oestreich, Fahlbusch, et al., 2020; Oleson et al., 2007; Wiggins et al., 2005) and is targeted in this analysis. The basis for analysis is the call index (Figure 1c), which quantifies the ratio of maximum power spectral density (psd) within the frequency band of call energy to average psd in two adjacent background frequency bands that do not contain energy from low frequency baleen whale calls (Oestreich, Fahlbusch, et al., 2020; Širović et al., 2009). Using power and directional spectra at 1-s by 0.5 Hz resolution, the analysis tracks the frequency downsweep within the call to extract the direction of call origin at the frequency of peak energy (Figure 2b). Automated results for each second include the call index and the bearing of maximum psd within the peak band of the call.

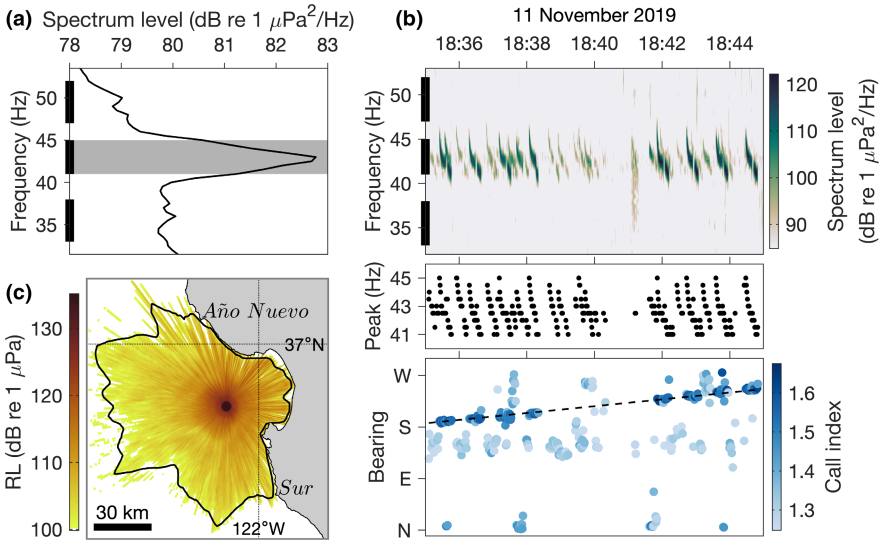

FIGURE 2 Directional acoustic vector sensor analysis methods. (a) Geometric mean spectrum levels for July 2019 through January 2020 illustrate a peak caused by the third harmonic of the blue whale B call. The frequency band for peak localization is shaded in grey; the frequency bands used for background are indicated by the thick black lines along the frequency axis, above and below the peak band. The call index is the ratio of maximum power spectral density (psd) within the frequency band of the call to average psd in the background bands (see 'Materials and methods'). (b) Example of data processing to obtain bearing estimates for blue whale B calls (direction of call origin relative to MARS). The top panel is a spectrogram representing the third harmonic of B calls (sample rate = 8 kHz, nfft = 16,000, hanning window, 50% overlap). For each second for which the call index exceeds 1.25, the middle panel shows the frequencies at which maximum energy was detected within the peak band (note the tracking of peak energy in the downswept B calls), and the bottom panel shows estimated bearings from MARS to the caller, extracted at the frequency of peak call energy. The dashed line indicates a steadily changing bearing presumed to be from a whale moving relative to the hydrophone. (c) The domain over which peak:background ratios are sufficient to reliably estimate the direction of call origin is approximated by modelling of acoustic transmission loss. This domain is defined by received level (RL) > 1.25 times mean spectrum levels within a frequency band below the peak band (panel a, 80 dB re 1 μPa²/Hz). The black contour is the outer limit of RL > 100, smoothed with a moving mean window of 7° bearing.

Automated analysis results were reviewed manually, first to identify the minimum index value for which B calls could be clearly and consistently distinguished, and their bearing relative to MARS could be reliably extracted. Representative of the full time series, the example in Figure 2b shows B calls received from multiple whales. All one-second intervals with a call index >1.25 clearly identify individual calls and allow tracking of their characteristic decrease in frequency. This segment shows calls originating from steady bearings as well as calls associated with a steadily changing bearing (dashed line in Figure 2b, lower panel), interpreted to be from an animal moving relative to the hydrophone. The second purpose of manual analysis was to exclude false positive detections caused by shipping noise. These periods were reliably distinguished from blue whale calling and removed. Manual review of the entire study period was conducted using custom software in MATLAB. The final analysis data set comprised the times and bearings of manually screened seconds having a call index >1.25.

Modelling of the B-call detection domain

To approximate the geographic region from which we can estimate the direction of call origin, we applied modelling of acoustic transmission loss, which is fully described in Oestreich, Fahlbusch, et al. (2020). Based on modelled transmission loss and a nominal B-call source level of 171 dB re 1 μPa-m (Thode et al., 2000), received levels (RL) were estimated for a region within 370 km of MARS. Although no directivity measurements of blue whale calls have been made, their low frequency calls are likely to be relatively omnidirectional. Considering a mean background of ~80 dB re 1 μPa²/Hz at MARS within the frequency band below the B-call peak band (Figure 2a), a minimum call index of 1.25 defines a minimum RL of ~100 dB re 1 μPa²/Hz for reliable estimation of call bearings. The domain that exceeds this minimum RL (Figure 2c) spans the coastal region between Point Año Nuevo and Point Sur, and it extends throughout most of Monterey Bay inshore of MARS and up to ~70 km offshore of MARS.

Validation of directional acoustic vector sensing

To validate the novel in situ use of MARS directional acoustic vector sensing of blue whale B calls, we used animal-borne sensor data from a suction-cup attached tag (Figure 3). Tag data, including GPS locations and the whale's dive, foraging and calling behaviour, were processed as in Cade, Gough, et al. (2021). The tag's hydrophone was sampled at 24 kHz, the accelerometer

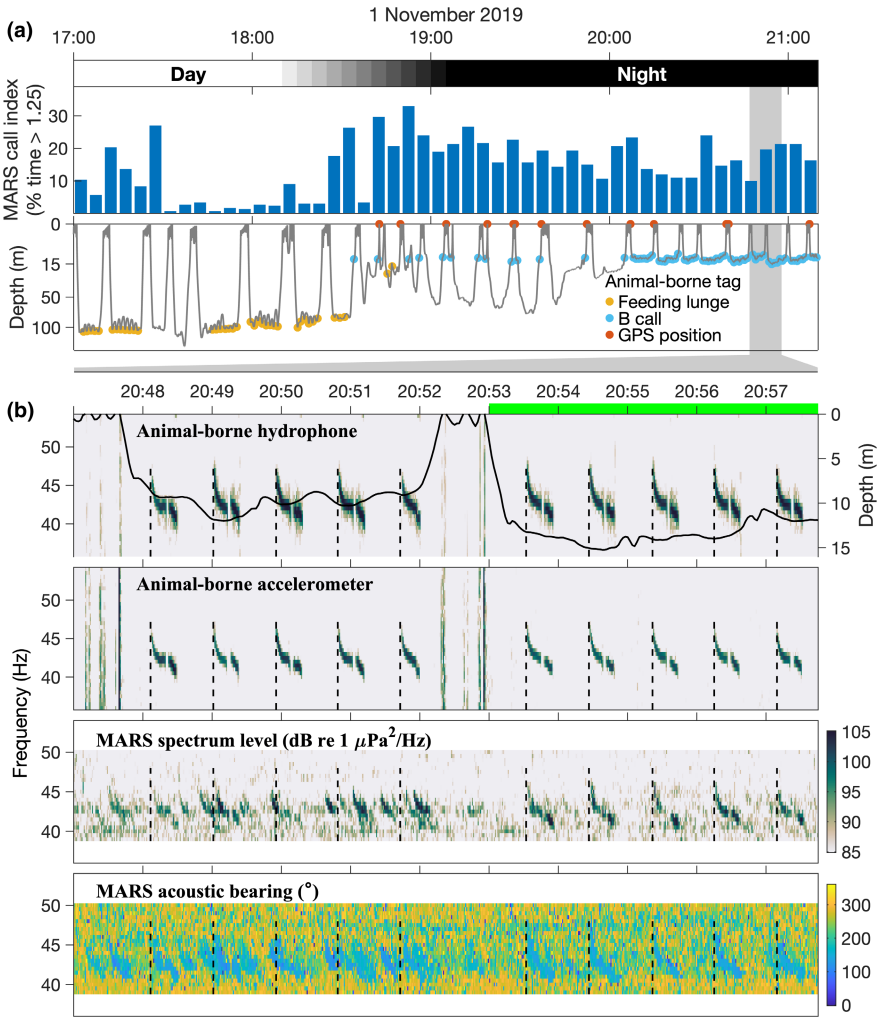

FIGURE 3 Validation of acoustic bearings from MARS to the origin of received blue whale calls. (a) Observations from MARS and an animal-borne tag characterize the period when sufficient tag GPS positions and call activity from the tagged whale enabled effective matchup with signals received at MARS. The percent of time for which the call index exceeded 1.25 at MARS is represented in 5-min bins. Behavioural events indicated in the animal depth profile were derived from multiple sensors on the tag (Cade, Gough, et al., 2021). (b) Detailed view of data from the animal-borne tag and MARS during the focal period of matchup (shaded in a), when calls made by the tagged whale were definitively matched to calls received at MARS. The depth profile overlaid on the spectrogram from the animal-borne hydrophone defines the whale's surfacing (breathing) intervals. The starts of calls from the tagged whale are indicated by vertical dashed lines in all panels. To align signals from the spatially offset platforms, the time axis of the MARS data was shifted by an appropriate acoustic propagation delay between source and receiver. The period highlighted in green along the top axis defines the period from which acoustically estimated call bearings, one average bearing per call, were compared with bearings based on GPS location (Figure 1a, the green sector spans the range of acoustically estimated bearings; the white circle is the GPS position).

at 400 Hz, the magnetometers and gyroscopes at 50 Hz and other sensors at 10 Hz. While the animal-borne hydrophone may record calls from both the tagged whale and nearby conspecifics, the animal-borne accelerometer can be used to validate which calls were from the tagged whale (Goldbogen et al., 2015; Oestreich, Fahlbusch, et al., 2020; Stimpert et al., 2015). In matching data from the animal-borne tag and the acoustic vector sensor at MARS, it was essential to identify periods when calling from the tagged whale could be accurately located by GPS data, and calls received at MARS could be attributed to the tagged whale. Within one of the tag deployment records was a period of calling by the tagged whale as well as multiple GPS locations when the whale surfaced. The cadence of singing and breathing from the tagged whale was compared to the MARS recordings to identify a period when calls from this whale could be isolated from other calls received at MARS, and the directions of these calls were compared across the two methods of bearing estimation: GPS versus acoustic.

Active acoustic sensing of forage species

Observations of forage species were made nearly continuously throughout the study period with a 38 kHz upward-looking scientific echosounder at MARS. The modified

Simrad EK60 echosounder transmitted a 2.048 ms ping upward in a 7-degree beam every 2.5 s using an output power of 400 W (Urmy & Benoit-Bird, 2021). This instrument could detect macrozooplankton, micronekton, and larger animals from its position at 890 m depth on the seafloor to the surface. Data were processed using Echoview software to remove ambient noise and spikes along with other invalid data including the ocean surface before additional analyses that used a combination of Echoview and custom scripts in LabVIEW. Aggregations, contiguous areas of scattering that were significantly higher in intensity than their surroundings in all directions, were detected following Benoit-Bird and Waluk (2021). The total area scattering and the area scattering within aggregations were calculated for each sampling day in the upper 200 m, spanning the dive depth range observed in foraging blue whales (Croll et al., 2005).

Upwelling dynamics and their spatial relationship to calling blue whales

Coastal upwelling was examined using multiple data sources. Satellite based infrared remote sensing of sea surface temperature (SST) describes regional patterns of upwelling. In the Monterey Bay region, coastal upwelling forms cold plumes (labelled P in Figure 1b) that originate in upwelling centres located at coastal land points—north of the Bay at Point Año Nuevo, and south of the bay at Point Sur. These plumes tend to flow equatorward, and the plume originating at Point Año Nuevo typically bifurcates, partly flowing into Monterey Bay (Ramp et al., 2005; Rosenfeld et al., 1994). Single scan Advanced Very High Resolution Radiometer SST images were acquired through the NOAA ERDDAP server. While clouds and fog often preclude remote sensing of SST, continuous moored observations of temperature and salinity at the mouth of Monterey Bay (located at the diamond in Figure 1b) enabled continuous detection of the presence of recently upwelled water in the bay. Wind-driven upwelling was examined using the daily coastal upwelling transport index (Jacox et al., 2018) from 37°N.

An essential consideration for interpreting directional relationships between coastal upwelling plumes and calling whales is the extent to which upwelling plumes flow within the domain of call detection at MARS. Because Point Sur is near the southern limit of the call detection range from MARS (Figure 1b), most of a plume originating at Point Sur (labelled P) flows outside the MARS detection domain, and only whales near the plume origin could be detected at MARS. In contrast, the Año Nuevo plume flows southward from its origin near the northern limit of the call detection range, placing the plume within the MARS detection domain (Figure 1b). This distinction between the two upwelling centers necessitates constraining examination of physical-biological relationships to the Point Año Nuevo plume.

RESULTS

Validation: Directional acoustic vector sensing of a tagged calling blue whale

Animal-borne tag data enabled validation of acoustic bearing estimates from MARS (Figure 3). The tag record shows that the whale transitioned from active foraging during the day, to mixed foraging and calling during dusk, to only calling during the night (Figure 3a). Within an approximately one-hour period during the night, the cadence of its calling and surface breathing intervals could be distinguished among the signals received at MARS. Within this hour, a series of two bouts of calls, each following a surface breathing interval, illustrate the criteria for reliable validation (Figure 3b). All calls registered on the tag hydrophone and tag accelerometer, strongly suggesting that they were from the tagged whale. While MARS reception of the first five calls coincided with the reception of calls from other whales, reception of the latter five calls did not (Figure 3b), thus supporting unambiguous comparison of acoustic and GPS bearings from MARS. The span of MARS-based acoustic bearings for the latter five calls (Figure 1a, green-shaded sector emanating from MARS to the southeast) aligned closely with GPS coordinates from the whale tag (Figure 1a, white circle). The GPS position shown nearly coincided with a GPS position acquired 25 min earlier, and examination of the whale's movements from a dead-reckoned track (using tag sensor data) indicated that the whale did not wander from the nearby GPS positions during this period. This accurate matchup between GPS and acoustic bearings supports MARS-based analysis of temporal variations in directional occupancy by calling blue whales.

Long-term patterns: Association of calling blue whales with upwelling plume areas

Approximately the same amount of total call time was analysed for each year: 405 and 449 h in 2019–2020 and 2020–2021, respectively. In both years, the bearings of maximum cumulative call detection aligned with bearings to the regions where plumes emanate from the coastal upwelling centres (Figure 4a,b). During 2019–2020, most of the calls comprising the strong local maximum around the bearing to Point Sur (Figure 4b) occurred during September–November 2019 (Figure 4c, upper panel). During 2020–2021, call activity peaks of approximately equal magnitude were aligned with each upwelling centre/plume region (Figure 4a,b). Call activity centred around the bearing to Point Sur was greatest during September–October, while that centred around the bearing to Point Año Nuevo peaked during November–December (Figure 4c, lower panel). Narrower maxima aligned with the Point Sur

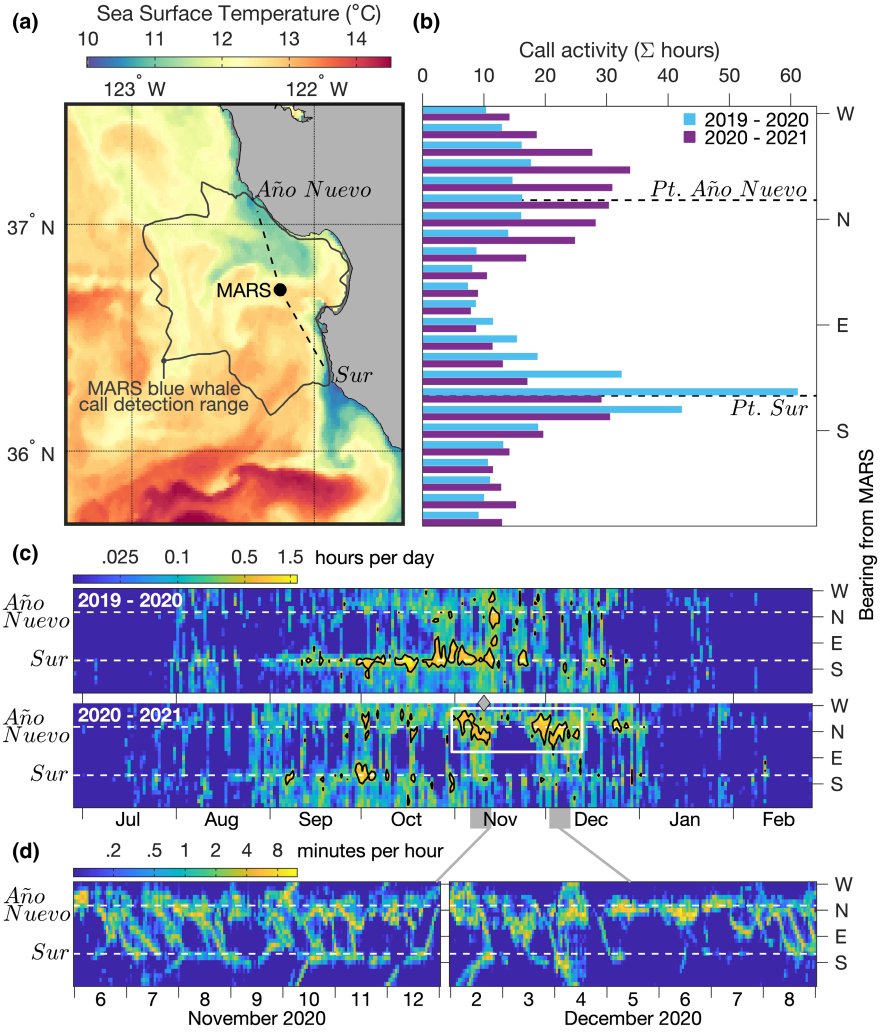

FIGURE 4 Overview of whale-call bearings relative to coastal upwelling centres. (a) Upwelling centres are associated with coastal land points north and south of Monterey Bay, as illustrated by plumes of cold water originating at Point Año Nuevo and Point Sur in this sea surface temperature (SST) image from 10 November 2020 14:44 UTC. The dashed lines mark the bearings from MARS to the coastal origins of the upwelling plumes. (b) Total hours of call index values exceeding 1.25 during annual periods of song presence (numbered in Figure 1c) within 15° directional bins. Dashed lines indicate bearings from MARS to the coastal upwelling centres (as in (a)). (c) Daily representation of (b) for each annual period. For 2020–2021 (lower panel), the grey diamond indicates the time of the SST image in panel (a), and the white box defines the focal period examined in Figure 5. (d) Hourly representation of directional call activity during periods when a consistent pattern of blue whale behavioural response to upwelling was observed (grey shaded periods below panel (c)).

upwelling centre are consistent with the condition that only the northernmost portion of this plume would reside within the MARS call detection domain during upwelling conditions (Figure 4a,b). The broader peak aligned with the Point Año Nuevo plume in each year is consistent with the condition that this entire plume, spanning a broader directional range, would reside within the call detection domain during upwelling conditions (Figure 4a,b).

Episodic patterns: Blue whales track wind-driven upwelling plumes

Consideration of blue whale resource tracking is methodologically constrained to the Point Año Nuevo upwelling plume (Figure 4a, see 'Materials and methods'). The strongest call activity from a directional sector spanning this plume origin occurred during two periods in 2020: early-mid November and late November through mid-December (Figure 4c, white box in lower panel). Both periods showed (1) movement from west of the bearing to Point Año Nuevo to east of this bearing, and (2) persistence of elevated call activity east of the bearing to Point Año Nuevo for at least a week (periods shaded grey below Figure 4c). Movement patterns were resolved at the level of individual whales (Figure 4d; tilted maxima in the time/direction plane) and included oscillatory westward and eastward movement immediately east of the bearing to Point Año Nuevo (Figure 4d, sawtooth-shaped maximum with apices at the bearing to Point Año Nuevo during 10–11 November).

The patterns of whale movement corresponded to patterns in atmospheric, oceanic and prey conditions (Figure 5). The two periods of eastward movement across the northern hemisphere of the call detection domain (Figure 4c, white box in lower panel) are evident as increases in the percentage of calling that originated from the NE quadrant (Figure 5a–c). Both periods coincided with the presence of an upwelling plume in the bay (periods labelled U1 and U2 in Figure 5b–d); plume presence is indicated by surface outcropping of water density contours at M1 (Figure 5a,d). Each period of upwelling plume presence in the bay followed strong peaks in the coastal upwelling transport index (Figure 5e), showing that wind forcing caused the oceanic circulation with which movement of calling blue whales was associated. Biomass of prey species within aggregations closely followed the upwelling index (Figure 5e), which explained 49% of the variability in area scattering found within aggregations in the upper 200 m during this period, but only 10% of the variability in total area scattering. During upwelling events (U1 and U2 in Figure 5b–e) more than 80% of scatterers were within aggregations, but during wind relaxation periods (R1 and R2 in Figure 5b–e) less than 20% of scatterers were found in aggregations.

Attributes of variation were similar across physical, biological and behavioural changes through upwelling cycles. The first upwelling response period (U1 in Figure 5b–e) was marked by a single large peak in upwelling strength, followed by a steep outcropping of isopycnals to the surface that lasted a week, high biomass of prey species within aggregations, and persistently high percentages of call activity originating from the NE quadrant. The second event (U2 in Figure 5b–e) was marked by three peaks in upwelling strength, followed by more variable shoaling of isopycnals to the surface over 3 weeks, high and more variable biomass of prey within aggregations, and more variably elevated percentages of call activity originating from the NE quadrant.

The directional occupancy of blue whales was consistent through multiple cycles in wind state (Figure 5f). During wind relaxation, blue whale calling originated primarily from the northwestern quadrant of the call reception domain: 82% during R1 and 96% during R2. This quadrant spans offshore habitat (beyond the continental shelf), the Point Año Nuevo upwelling plume origin

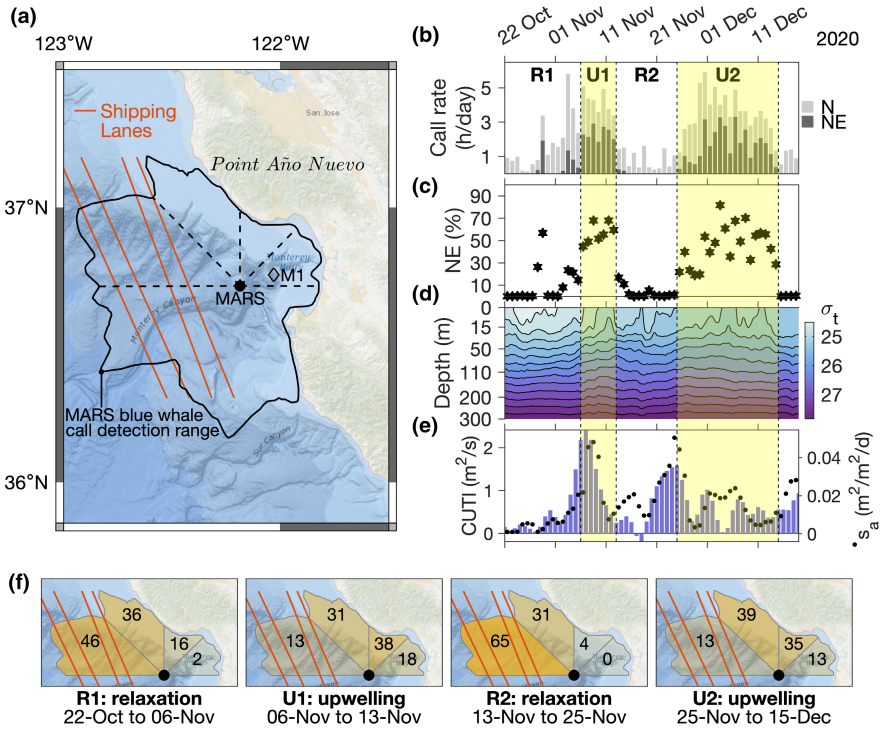

FIGURE 5 Ephemeral wind-driven resource tracking by blue whales. (a) Reference map. Octant radials (dashed black lines) within the northern hemisphere of the call detection domain define ecologically significant features for interpreting blue whale movement (see the text). Red lines define recommended tracks for vessels 300 gross tons and heavier. (b) MARS call detection rate summed for the northern hemisphere (N) around MARS and the northeast quadrant (NE, the two octants northeast of MARS in panel (a)). (c) Percentage of call detection time from the northeast quadrant (NE/N). (d) Water column density measured at mooring M1 (location in panel (a)). (e) The coastal upwelling transport index (CUTI) for 37°N, at the north end of Monterey Bay (bars) and area scattering (s_a) within patches in the upper 200 m above MARS (points), representing aggregation of forage species. Daily CUTI values were smoothed with a 3-day running mean. Periods highlighted in yellow across panels ((b)–(e)) indicate persistently elevated percentages of calling from the NE quadrant (panel (c)), coincident with the presence of recently upwelled water in Monterey Bay (outcropping of isopycnals to the surface in panel (d)). (f) Percentages of call time originating from each octant of the northern hemisphere of the call reception domain are labelled and coloured according to magnitude during alternating periods of wind relaxation and upwelling (as identified in panels (b)–(e)).

and foraging habitat along the shelfbreak (Figure 5a,f). During both wind relaxation periods, calling whales predominantly occupied the WNW octant that is transected by four shipping lanes (Figure 5f). During upwelling, the percentage of calling that originated from the northeastern quadrant greatly increased: by factors of 3.1 and 12 during U1 and U2, respectively. This quadrant spans foraging habitat where upwelling plumes flow into Monterey Bay and over Monterey Canyon (Figures 4a and 5a,f). These behavioural patterns involved not only occupancy of habitat through which shipping lanes transect, but also movement across shipping lanes between alternate states of wind forcing (Figure 5a,f).

DISCUSSION

Applying integrative observations of predator, prey and environment, we examined a hypothesis based on the recent discovery that forage species form dense aggregations during wind-driven coastal upwelling—a phenomenon that can greatly enhance foraging efficiency and trophic transfer of energy (Benoit-Bird et al., 2013, 2019). Our hypothesis is that blue whales track the coastal upwelling circulation in which their most essential resource, aggregated krill, occurs. After validating the effectiveness of passive acoustic methods to monitor directional patterns of calling blue whales and applying these methods to 2 years of data, we find support for this hypothesis. This window into dynamic and ephemeral resource tracking was enabled by novel passive acoustic sensing technology, the application of which can advance not only ecological knowledge, but also prediction toward informed dynamic management and protection of an endangered species (e.g., avoiding the collocation of whales with shipping lanes and fishing gear).

Continuous active acoustic sensing over MARS allowed local observation of the response of forage species to upwelling. As in work focused on the earlier part of the upwelling season (Benoit-Bird et al., 2019), large increases in area scattering within patches in the upper 200 m occurred during the upwelling periods even as the total scattering over this depth range remained relatively consistent. While the majority of scattering at the acoustic frequency utilized is likely caused by swimbladder-bearing fish rather than the krill that are direct prey of blue whales, krill and forage fish show similar aggregation during upwelling (Benoit-Bird et al., 2019), and the observation of forage species response connects upwelling dynamics to the prey field and predator responses during our study. In this critical foraging habitat for blue whales, influences of upwelling on the prey field are key, and metrics showed major increases in potential foraging efficiency. Scattering strength differences indicate that the aggregations found during upwelling had at least a tenfold higher density of animals and often a hundredfold higher density than found during wind relaxation.

Detection of blue whale behavioural responses to upwelling was possible for the plume that develops within the acoustic detection domain of the MARS observatory. When blue whale calling was active in the region where this plume develops, thus providing the signal required for directional monitoring, calling whales consistently tracked the movement of upwelling plumes clockwise around the northern hemisphere of the call detection domain. Projected onto a map, this change in the direction of blue whale call origin translates into alongcoast movement into Monterey Bay, the path followed by coastal upwelling plumes. Upwelling plume presence in Monterey Bay, monitored using in situ data, repeatedly coincided with a shift in the occupancy of calling blue whales from an offshore region into the upwelling plume domain overlying shelfbreak and canyon habitat that is known to be essential to blue whale foraging (Cade, Fahlbusch, et al., 2021; Cade, Seakamela, et al., 2021; Croll et al., 2005; Schoenherr, 1991). Consistent with the pattern of movement in response to episodic upwelling plumes, the long-term directional statistics show maxima in blue whale call activity aligned with the bearings to the upwelling centers at coastal headlands and the plumes that episodically emanate from them.

Upwelling plumes can cover a large expanse of coastal ocean habitat. For example, the Point Año Nuevo plume that coincided with the first period of blue whale behavioural response covered approximately 1000 km^2. However, it is probable that certain plume areas and conditions are particularly important for blue whale foraging ecology. Monitoring of krill populations off central California during spring and summer indicates a strong maximum along the shelfbreak between Monterey Bay and Cordell Bank to the north (Santora et al., 2011). In the Monterey Bay region, opportunistic encounters with dense aggregations of foraging blue whales, comprising up to 40 individuals within an area of 1-km radius, coincided with locations where the boundaries of coastal upwelling plumes intersected the shelfbreak (Cade, Fahlbusch, et al., 2021). Two such events were interpreted to result from hydrodynamics and krill behaviour that create favourable foraging conditions for blue whales: dense, thick, and evenly distributed krill swarms that are accessible to depth oscillations of lunge-feeding dive behaviour.

Understanding the strategies and sensory cues that animals use to track resource availability in space and time is increasingly recognized as central to advancing the fields of movement and foraging ecology (Abrahms et al., 2021; Nathan et al., 2008). A number of recent studies have shown that migratory animals track latitudinal (e.g., Aikens et al., 2017; Boustany et al., 2010) and elevational (e.g., Bastille-Rousseau et al., 2019) gradients in the phenology of primary productivity. Yet in marine ecosystems, significant finer-scale patchiness and ephemerality of high-density forage availability remains even within the broad-scale latitudinal and

seasonal progression of phytoplankton blooms and energy transfer to higher trophic levels (Kotliar & Wiens, 1990; Steele, 1978). The strategies and cues marine predators use to track these finer-scale variations in forage quality largely remain unclear, yet are critical to predators' survival in marine habitats displaying extreme heterogeneity in forage availability (Benoit-Bird et al., 2013; Benoit-Bird & Au, 2003; Fauchald et al., 2000; Rose & Leggett, 1990). While previous work has shown the strategies driving broader-scale arrival at (Abrahms et al., 2019) and departure from (Oestreich et al., 2022) key foraging locations for migratory blue whales, the results presented here reveal a strategy by which this krill-obligate predator tracks resource availability at finer spatiotemporal scales. This fine-scale movement strategy likely enables efficient foraging on exceptionally dense but ephemeral krill swarms (Cade, Seakamela, et al., 2021), in turn allowing for blue whales' long-distance migrations and remarkable body size (Goldbogen et al., 2019; Goldbogen & Madsen, 2021).

Fine-scale resource tracking of prey-aggregating upwelling plumes may be enabled by memory as well as individual and collective sensory cues, including both environmental cues and potentially those from conspecifics. As interpreted from tracking of blue whale migration in relation to ecosystem conditions on contemporary and climatological time scales, blue whales may apply long-term memory to return annually to foraging habitat that is relatively stable and productive (Abrahms et al., 2019). The upwelling that causes prey aggregation consistently originates at coastal topographic features, which may enable long-term memory to play a role in blue whale habitat occupancy and foraging success. In the upwelling plumes themselves, thermal anomalies and gradients as well as prey patchiness itself may provide proximate environmental sensory cues. Further, the potential role of collective sensing within this blue whale population has been interpreted from studies of both foraging (Cade, Fahlbusch, et al., 2021) and migration (Oestreich et al., 2022). To the extent that behavioural responsiveness in the present study depends upon collective sensing, the powerful calls of blue whales may provide long-distance acoustic sensory cues. Likely beyond our best technology, highly evolved use of sound by blue whales may enable detection, localization and tracking of conspecifics. Through individual and collective sensing, a regional blue whale population may share information to assess and track dynamic and patchy ecosystem variations that are key to success in the most essential life activity in this habitat—foraging (Pirotta et al., 2018).

Across terrestrial and marine habitats, knowledge of landscape/seascape ecology, movement ecology, and resource tracking is essential to informing effective conservation measures (Abrahms et al., 2021; Fryxell et al., 2004, 2005; Tischendorf & Fahrig, 2000; Wiens, 2009). A primary concern for the conservation of blue whales is mortality from ship strikes because shipping corridors intersect essential habitat, and blue whale response to oncoming large ships is ineffective in avoiding collision (McKenna et al., 2015). The present study reveals that during periods of wind relaxation blue whales in the Monterey Bay region occupy habitat transected by shipping lanes, and they move across lanes in response to the most fundamental process that shapes their foraging habitat, episodic wind-driven upwelling. This discovery motivates consideration of how research and monitoring can enhance conservation. Dynamic management strategies (Barlow & Torres, 2021; Hazen et al., 2017; Lewison et al., 2015; Oestreich, Chapman, & Crowder, 2020) include real-time alerts of animal presence to inform reduction of vessel speeds and collision risk (Baumgartner et al., 2019). Long- and short-term descriptions of shipping traffic and whale presence (Blondin et al., 2020) and of ecosystem features that shape habitat occupancy—such as upwelling plumes—may also inform mitigation of collision risk, potentially through adjustment of shipping lanes and speeds during periods of the year when risk is greatest. While substantial additional data and validation of models are required to contemplate using environmental cues in a predictive capacity to forecast whale foraging aggregations, this study suggests not only that it may eventually be possible but also how it might eventually be done. Improved understanding of the spatiotemporal relationships between upwelling dynamics and blue whale foraging ecology in this region will emerge from ongoing and future research programs, toward advancing the forecasting skill that is essential to dynamic management (Barlow & Torres, 2021). Considering similar behavioural ecology of other soniferous rorqual whale species, including endangered fin whales, the ecological understanding that emerges is relevant to a greater framework for the conservation of protected species and biodiversity.

AUTHORSHIP

JPR designed the study with co-authors, developed analysis methods for the directional acoustic data, and led the synthesis of results with KBB and WKO. KBB and CMW collected and analysed acoustic prey data. PL and KBS collected passive directional acoustic data; PL performed initial processing. JAG, DEC, JAF and JC deployed whale tags; DEC, JAF and WKO performed initial processing and analysis of tag data. BLS guided analysis and integration of tag acoustic and accelerometry data. BLS and AD guided consideration of dynamic management applications. JEJ and TM modelled acoustic transmission loss for blue whale calls. JPR wrote the first draft of the manuscript, and all authors contributed to editing.

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