Acoustic signature reveals blue whales tune life history transitions to oceanographic conditions

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Acknowledgments: Thank you to M. Chapman, J. Fahlbusch, and M. Savoca for comments and helpful discussion on this manuscript. Thank you to C. Dawe, D. French, K. Heller, P. McGill, and the crew of the R/V Rachel Carson for design, deployment, and maintenance of the MARS hydrophone hardware system. Production of the decimated data used in this study was supported by B. Jones, D. Cline, P. McGill, and Y. Zhang. Sound propagation loss model results from Oestreich et al., 2020b were provided by J. Joseph and T. Margolina. WKO is supported by the National Science Foundation Graduate Research Fellowship Program (NSFGRFP) and as a David and Lucile Packard Foundation Stanford Graduate Fellow. The NSF funded installation and maintenance of the MARS cabled observatory through awards 0739828 and 1114794. Hydrophone recording through MARS was supported by the Monterey Bay Aquarium Research Institute, through a grant from the David and Lucile Packard Foundation.

Conflict of Interest Statement: We declare we have no competing interests.

Author Contributions: WKO and JPR conceived the study; JPR collected and contributed data; all authors designed the research; WKO and JPR performed analyses; WKO led the writing of the manuscript; all authors contributed to manuscript drafts and gave final approval for publication.

Data availability: Data and code used to conduct the analyses described here are available at: https://github.com/woestreich/blue-whale-phenology. For reproducibility and extensibility of results, original audio recordings for the entire study period, decimated to a sample rate of 2kHz, are accessible through the AWS Open Data registry: arn:aws:s3:::pacific-sound-2khz.

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Abstract

1. Matching the timing of life history transitions with ecosystem phenology is critical for the survival of many species, especially those undertaking long-distance migrations. As a result, whether and how migratory populations adjust timing of life history transitions in response to environmental variability are important questions in ecology and conservation. Yet the flexibility and drivers of life history transitions remain largely untested for migratory marine populations, which contend with the unique spatiotemporal dynamics and sensory conditions found in marine ecosystems.
2. Here, using an acoustic signature of blue whales' regional population-level transition from foraging to breeding migration, we document significant interannual flexibility in the timing of this life history transition (spanning roughly four months) over a continuous six-year study period.
3. We further show that timing of this transition follows the oceanographic phenology of blue whales' foraging habitat, with a later transition from foraging to breeding migration occurring in years with an earlier onset, later peak, and greater accumulation of biological productivity.
4. These results indicate that blue whales use flexible cues, likely including individual sensing of foraging conditions and long-distance vocal signals from conspecifics, to match timing of this population-level life history transition with interannual oceanographic variability in their vast and dynamic foraging habitat. The use of flexible cues in timing a major life history transition may be key to the persistence of this endangered population facing the pressures of rapid environmental change.
5. Further, these findings extend theoretical understanding of the flexibility and drivers of population-level migration beyond insights derived primarily from group-living and terrestrial migrants, illuminating the drivers and flexibility of a life history transition in a relatively solitary marine migrant.

Keywords: bioacoustics, blue whale, flexibility, life history, marine megafauna, migration, phenology, upwelling

1 Introduction

Many species depend on matching the timing of life history transitions with ecosystem phenology for survival (Visser & Gienapp, 2019; Walther et al., 2002). Matching of behavior with ecosystem phenology drives the life history of many migratory populations (Alerstam et al., 2003), including those that rely on migration driven by the seasonal availability of forage throughout their range (Abrahms et al., 2020; Aikens et al., 2020). In extreme cases, high-quality foraging conditions for a migratory population are seasonal and occur in habitat geographically distant from habitat preferable for reproduction and rearing of young (Dingle & Drake, 2007). In such seasonal environments and long-distance migrations, matching the timing of the life history transition between foraging and migration to breeding grounds with ecosystem phenology is critical for population health (Both et al., 2006; Winkler et al., 2014). Reliance on optimization of this life history transition is amplified for capital breeding organisms, given that foraging must fuel the extreme energetic demands of long-distance movement (Alerstam et al., 2003), reproduction (Braithwaite et al., 2015), and rearing of young (Costa et al., 1986). As anthropogenic climate change leads to increased variability and directional change in phenology at lower trophic levels (Edwards & Richardson, 2004; Thackeray et al., 2016), there is increasing interest in understanding the cues for life history transitions, and whether these cues allow flexibility in timing of migratory populations' life history transitions in order to maintain phenological synchrony with lower trophic levels (Cotton, 2003; Stenseth & Mysterud, 2002; Winkler et al., 2002, 2014; Xu et al., 2021).

These topics have received substantial research attention in recent years, yielding insights into the drivers and relative flexibility of life history transitions in primarily group-living and often terrestrial migratory populations. Relatively fixed endogenous factors such as photoperiod are known to play a role in the timing of life history transitions (Gwinner, 1996) and can lead to trophic mismatch as a result of changes in habitat phenology (Post & Forchhammer, 2008), but environmental (Marra et al., 2005; Shipley et al., 2020), physiological (Deppe et al., 2015), and social (Guttal & Couzin, 2010; Jesmer et al., 2018; Mueller et al., 2013) cues can enhance the flexibility of migratory populations' life history transitions in response to environmental variability. However, environmental variability and gradients are often noisy, meaning that individual-level sensing and response to such variability can lead to non-optimal timing of life history transitions (Couzin, 2018). Studies on mobile animal groups comprised of proximate individuals have established theoretical understanding of how migratory populations overcome this problem, with individual and emergent collective sensing of environmental variability (Torney et al., 2018) allowing for optimal timing of life history transitions (Guttal & Couzin, 2010) and collective long-distance migrations (Couzin, 2018). This body of work has established the importance of group or population size and density in optimizing collective sensing and the timing of life history transitions under environmental variability (Berdahl et al., 2013). Yet it remains unclear whether this theoretical understanding of cues for and flexibility in the life history transitions of migratory populations extends to long-distance marine migrants. The marine environment poses unique challenges and opportunities to migratory populations as compared to terrestrial systems. For one, the spatiotemporal dynamics of forage availability differ, with marine systems (especially pelagic systems) noted for extreme spatial patchiness and temporal ephemerality of prey resources relative to terrestrial systems (Benoit-Bird & McManus, 2012; Hazen et al., 2013; Kavanaugh et al., 2016; Marquet, 1993; Steele, 1985, 1991). Additionally, marine habitats differ in their sensory environment, with the liquid medium limiting the range of visual sensing but greatly enhancing the possibility of long-distance acoustic sensing and vocal communication (Au & Hastings, 2008; Payne & Webb, 1971). As a result, the evolution of cues for and flexibility in life history transitions of long-distance marine migrants might differ substantially from theoretical understanding derived from terrestrial systems.

The Northeast Pacific blue whale (*Balaenoptera musculus*) population provides an ideal study system for interrogating population-level flexibility of life history transitions in the marine environment. This endangered population migrates seasonally between higher-latitude foraging grounds off California and the northern reaches of the California Current Large Marine Ecosystem (CCLME) in summer and fall, and lower-latitude breeding grounds near Baja California and the Costa Rica Dome in the winter and spring (Bailey et al., 2010; Stafford et al., 1999, 2001). These migrations are tightly linked with the seasonal and episodic formation of dense aggregations of blue whales' obligate prey, krill (specifically *Thysanoessa spinifera* and *Euphausia pacifica*; (Benoit-Bird et al., 2019; Cade et al., 2021; Croll et al., 2005)) resulting from wind-driven upwelling (Figure 1A). Upwelling ecosystems display temporal lags between upwelling, increases in primary productivity, and subsequent increases in the abundance of zooplankton (including krill) and higher trophic level predators such as blue whales (Barlow et al., 2021; Croll et al., 2005). In the CCLME, increasing krill abundance and the arrival of blue whales at foraging hotspots lags the upwelling-driven increase in primary productivity by 3-4 months (Croll et al., 2005), meaning that ideal foraging conditions for blue whales begin months after the onset of upwelling and persist for months following the annual peak in upwelling. While blue whales are not strict capital breeders and are known to forage at least in a limited capacity at lower latitudes typically associated with breeding (Busquets-Vass et al., 2021), summer and fall feeding in key foraging areas along the coast of California provides the primary source of sustenance for this population (Busquets-Vass et al., 2021; Pirotta et al., 2018). As a result, matching of foraging effort with the timing of peak prey abundance and density in these foraging habitats is critical to fueling subsequent southward migration from foraging grounds to breeding grounds and successful reproduction and rearing of young (Pirotta et al., 2018). Previous work has shown that blue whales' northward progression during the foraging season is driven by spatial memory that enables tracking of long-term average foraging conditions (Abrahms et al., 2019). Yet how blue whales respond to interannual variability in wind-driven upwelling and krill availability to time their transition to breeding migration following residence on foraging grounds remains unknown.

Lack of understanding of population-level life history transitions persists for blue whales and many other migratory populations largely due to the difficulty of simultaneously observing many individuals' behavior over immense spatial and temporal scales, especially in marine systems (Dingle & Drake, 2007). But blue whales provide a unique opportunity for long-range observation of population-level behavior due to their powerful low-frequency vocalizations, which are detectable over tens of thousands of square kilometers off the coast of California via passive acoustic monitoring (PAM) (Figure 1B; (Oestreich et al., 2020b)). The Northeast Pacific population produces at least four call types (A, B, C, and D), with sequenced patterns of A, B, and C calls collectively referred to as blue whale song (Figure 1C). While song is thought to be produced exclusively by males in this population (McDonald et al., 2001), this vocal signal is often considered representative of population-level presence of both sexes, given known seasonal synchrony in population-wide departure from foraging grounds (Bailey et al., 2010) and increased observation of male-female pairs immediately preceding southward migration from foraging habitat (Sears & Perrin, 2009). Beyond population-level presence, blue whale song can provide insight into the behavioral state of this population based on diel patterns in song. Individuals in the Northeast Pacific population are known to produce songs primarily at different times of day during foraging versus migratory behavior. This diel patterning provides an acoustic signature of the population-level transition from foraging to southward migration, defined by the significant seasonal decrease in the night-to-day ratio of regional song production

(Oestreich et al., 2020b). Previous studies have shown that acoustic presence alone can mask patterns in population-level behavior occurring within a time period of acoustic detection (Oestreich et al., 2020b), but the known acoustic signature of blue whales' transition to migration alleviates this problem by revealing distinct behavioral modes within the time period when blue whales are acoustically present on their summer-fall foraging grounds.

Here, we use this acoustic signature of blue whales' population-level transition from foraging to migration to test for flexibility in this critical life history transition under interannual oceanographic variability in blue whales' foraging habitat. We first analyze six years (2015 through early 2021) of nearly-continuous (95% coverage) passive acoustic monitoring data from a key foraging area for the Northeast Pacific blue whale population (Monterey Bay, CA, USA), acoustically identifying timing of the transition from foraging to breeding migration. We then compare the timing of this life history transition to metrics of oceanographic phenology to address two questions: 1) Is there interannual variation in population-level timing of transition to migration from a key foraging hotspot? And 2) if so, are the observed variations in the timing of this life history transition related to variations of ocean productivity phenology in their foraging habitat? The findings presented here shed light on the adaptability of a long-distance marine migrant to climate-driven phenological variability and change, and yield insight into the sensory cues that allow for a collective life history transition in a vast and dynamic oceanic habitat.

2 Materials and Methods

2.1 Study area and acoustic recordings

This study focused on a key foraging area for blue whales within the broader California Current Large Marine Ecosystem (CCLME), the Monterey Bay region off central California (Figure 1A). Acoustic recordings were taken via two Ocean Sonics icListen HF omnidirectional hydrophones (Ryan et al., 2016) deployed sequentially at the Monterey Accelerated Research System (MARS) cabled observatory. MARS is located on Smooth Ridge (36° 42.75' N, 122° 11.21' W; depth 891 m) outside of Monterey Bay (Figure 1B). The hydrophones have a bandwidth of 10 Hz to 200 kHz and sampled at 256 kHz. Calibration of the sequentially-deployed hydrophones is described in (Oestreich et al., 2020b). Over the ~5.5-year study period (July 2015 – Jan 2021; covering six complete blue whale song seasons), these hydrophones provided nearly-continuous sampling (~95% coverage). The spatial range of acoustic detection of blue whale song covered a large area of blue whale habitat in and around Monterey Bay (Figure 1B), as determined via an acoustic transmission loss model for a sound source with characteristics of the third harmonic of a blue whale B call (the target signal for acoustic metrics calculated in this study; Section 2.2) under median noise conditions (Oestreich et al., 2020b).

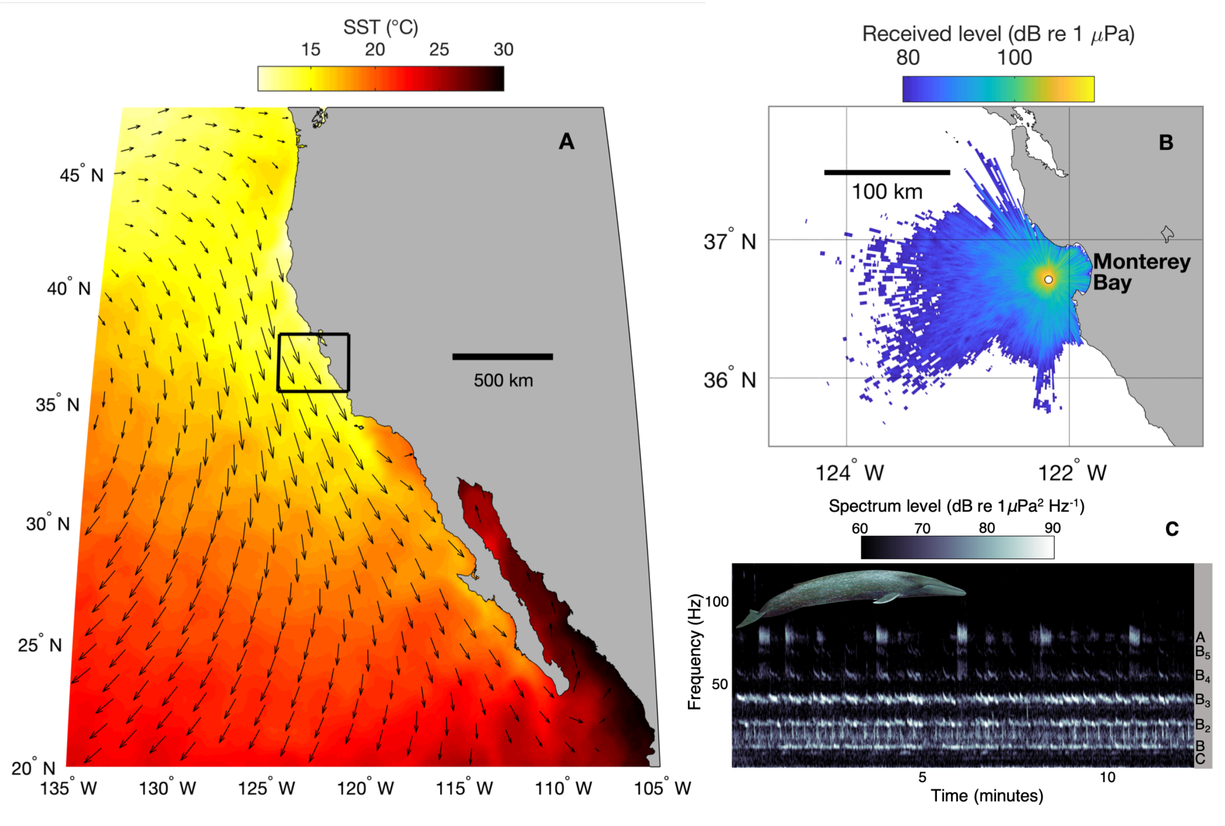

Figure 1. Study system. (A) Northeastern Pacific June SST and winds (2018); box inset in panel (B). **(B)** (Adapted from (Oestreich et al., 2020b)) Study area and modeled received level of blue whale B calls at the MARS hydrophone (circle); colored area displays received levels above typical background noise conditions, indicating the approximate sampling range of the MARS hydrophone for blue whale song. **(C)** Example ~12.5-minute period of recording from the MARS hydrophone on Nov 11, 2017, displaying blue whale song chorus. Frequencies associated with each unit of blue whale song, including A calls, B calls (fundamental frequency and second through fifth harmonics, e.g. B_2 for second harmonic), and C calls are labeled. Spectrogram generated from data with 2kHz sampling frequency via FFT with 2048 samples, 95 % overlap, and Hann window.

2.2 Acoustic analyses

To quantify presence of blue whale song and behavioral transition periods, previously published metrics (Oestreich et al., 2020b) were extracted for each year (2015-2020) of acoustic recordings. First, an index of blue whale calling (CI) was calculated as a signal to noise ratio from calibrated spectrum levels, providing a robust quantification of the presence of both individually-identifiable and overlapping (“chorusing”) blue whale songs (Oestreich et al., 2020b). To describe the phenology of blue whale song presence in the Monterey Bay region for each year, we identified the first and final dates of song presence (CI 15-day running mean $\geq$ 1.01), as well as the peak of song signal received at MARS (maximum of the CI 15-day running mean).

Previous work demonstrated that a significant decrease in the night-to-day ratio of CI (CI_{night}:CI_{day}) indicates a population-level behavioral transition from foraging to migration in the area effectively sampled by the MARS hydrophone (Figure 1B; (Oestreich et al., 2020b)). Because this acoustic feature emerges from many individuals’ transitions from foraging to migration (and associated change in vocal behavior), this behavioral transition occurs at the population-level over a period of days-to-weeks (Oestreich et al., 2020b). To identify behavioral transitions in each year (2015-2020), we use one-sided t-tests for each day of the time-series, comparing samples comprised of the 30-day windows immediately preceding and following a given day (total $n = 60$ days). While additional sample window sizes were considered for this statistical definition of the behavioral transition (see Figure S3), the 30-day sample window was chosen because (1) it matches that used by (Oestreich et al., 2020b) to originally identify and describe the seasonal decrease in CI_{night}:CI_{day} and its association with the population-level transition to southward migration; and (2) the 30-day sample window clearly identifies the most precipitous drops in CI_{night}:CI_{day} for each year (Figure S3), consistent with the population-level acoustic signature described by (Oestreich et al., 2020b). Due to day-to-day noise in both CI and CI_{night}:CI_{day}, time series of these metrics have been filtered (15-day running mean) for clearer visualization (Figure 2; see Figure S4 for visualization with alternative filter window sizes). However, statistical tests for significant changes in this time series consider only the unfiltered daily values for CI_{night}:CI_{day}. Using the statistical definition described above, we identified the first, middle, and final dates of the behavioral transition in each year.

2.3 Ecosystem phenology

Previous studies have demonstrated a strong relationship between Northeast Pacific blue whale presence and ecosystem productivity driven by upwelling (Abrahms et al., 2019; Burtenshaw et al., 2004; Croll et al., 2005). To describe the ecosystem phenology for the sampling area around the MARS hydrophone, we combined two approaches to quantifying the biological effects and phenology of upwelling in the Monterey Bay region. To quantify the seasonal accumulation of upwelling, we used the Biologically Effective Upwelling Transport Index (BEUTI) (Jacox et al., 2018). BEUTI builds upon physical estimates of vertical transport (such as the Bakun Index (Bakun, 1973); and the Coastal Upwelling Transport Index (Jacox et al., 2018)) by incorporating nitrate concentration with vertical transport at the base of the mixed layer to estimate vertical nitrate flux. For each year of the study period (2015-2020), we calculate the annual accumulation of BEUTI at 37° N (Figure 3).

Table 1. Abbreviations used throughout the text and figures. [1](Oestreich et al., 2020b); [2](Jacox et al., 2018); [3](Bograd et al., 2009); [4]Introduced in the present study.

Abbreviation	Meaning
CI[1]	Call index
$\mathrm{CI}_{\mathrm{night}}$:$\mathrm{CI}_{\mathrm{day}}$[1]	Night-to-day ratio of call index
BEUTI[2]	Biologically effective upwelling transport index
$\mathrm{BEUTI}_{\mathrm{STI}}$[3]	Spring transition index (date on which cumulative BEUTI reaches its minimum value)
$\mathrm{BEUTI}_{\mathrm{MAX}}$[3]	Peak of seasonal upwelling (date of greatest rate of change in cumulative BEUTI)
$\mathrm{BEUTI}_{\mathrm{END}}$[3]	End of seasonal upwelling (date on which cumulative BEUTI reaches its maximum value)
$\mathrm{BEUTI}_{\mathrm{TUMI}}$[3]	Total upwelling magnitude index (total BEUTI accumulated from STI to END)
$\mathrm{BEUTI}_{\mathrm{LUMI}}$[4]	Late upwelling magnitude index (total BEUTI accumulated from MAX to END)

To characterize the phenology of upwelling in the Monterey Bay region in each year of the study period, we implemented the approach pioneered by (Bograd et al., 2009) for quantification of key parameters in upwelling phenology. These parameters (Table 1) include the spring transition index of BEUTI ($\mathrm{BEUTI}_{\mathrm{STI}}$), the peak of BEUTI ($\mathrm{BEUTI}_{\mathrm{MAX}}$), the end of positive upwelling accumulation ($\mathrm{BEUTI}_{\mathrm{END}}$), the total upwelling accumulation during the full upwelling season from $\mathrm{BEUTI}_{\mathrm{STI}}$ to $\mathrm{BEUTI}_{\mathrm{END}}$ ($\mathrm{BEUTI}_{\mathrm{TUMI}}$), and late-season upwelling accumulation from $\mathrm{BEUTI}_{\mathrm{MAX}}$ to $\mathrm{BEUTI}_{\mathrm{END}}$ ($\mathrm{BEUTI}_{\mathrm{LUMI}}$). Each of these parameters was calculated for each year of the study period (2015-2020) as described by (Bograd et al., 2009) and in Table 1, using daily resolution cumulative BEUTI at 37° N (Jacox et al., 2018), filtered with a 10-day running mean. This smoothing is necessary for the present year-by-year analysis to accurately represent annual phenology rather than anomalous single-day spikes in upwelling (this running mean is not necessary in (Bograd et al., 2009), as they calculate these metrics for already-smoothed long-term climatological means of upwelling). Analyses were conducted in R version 4.0.2 (R Core Team, 2021) and MATLAB 2018b (The MathWorks Inc., 2018).

2.4 Statistical analyses

We used linear regression to evaluate the relationships between the annual timing of blue whales' population-level behavioral transition and metrics of oceanographic phenology. For each metric of oceanographic phenology (Table 1, Figure 3), linear regressions were calculated separately using the first, center, and final dates of the population-level behavioral transition (Figures 4, S2D-F) and song presence (Figures S1, S2A-C) from each year of the study period as the dependent variable. We tested for significance ($p < 0.05$, indicated by asterisks in Figures 4, S1, and S2) using the F-statistic for each linear regression. All statistical tests were conducted in R version 4.0.2 (R Core Team, 2021).

3 Results

3.1 Timing of blue whale song presence and life history transition

The annual timing of blue whale song presence was relatively consistent over the six-year study period (Figure 2A; Figure S1). In 2015, song presence ranged from yearday 211-351 (yearday 211 was the start date of acoustic recordings); in 2016 from yearday 232-392 (ending Jan 26th of the following year); in 2017 from yearday 189-378; in 2018 from yearday 191-364; in 2019 from yearday 207-392; and in 2020 from yearday 196-394. The peak in blue whale song call index (CI; 15-day running mean) during 2015-2020 occurred on yearday 268, 302, 307, 293, 315, and 310, respectively. In all figures and reported results, yearday values > 365 (or 366 in the 2016 leap year) indicate persistence of song or behavioral transition into the following calendar year.

The annual timing of the behavioral transition from foraging to migration (measured as significant decrease in CI_{night}:CI_{day}) was more variable, ranging from as early as yearday 231 (Aug 19th) in 2017 to as late as yearday 367 (Jan 1st of the following year) in 2020 (Figure 2B). The yearday spans of this behavioral transition emphasize the high degree of variability: 248-287 (40 days), 256-299 (44 days), 231-357 (126 days), 322-349 (27 days), 296-355 (59 days), and 340 to 367 (28 days), from 2015-2020, respectively (Figure 2B). The corresponding middle dates of the behavioral transitions occurred on yeardays 268, 278, 294, 336, 326, and 354, respectively.

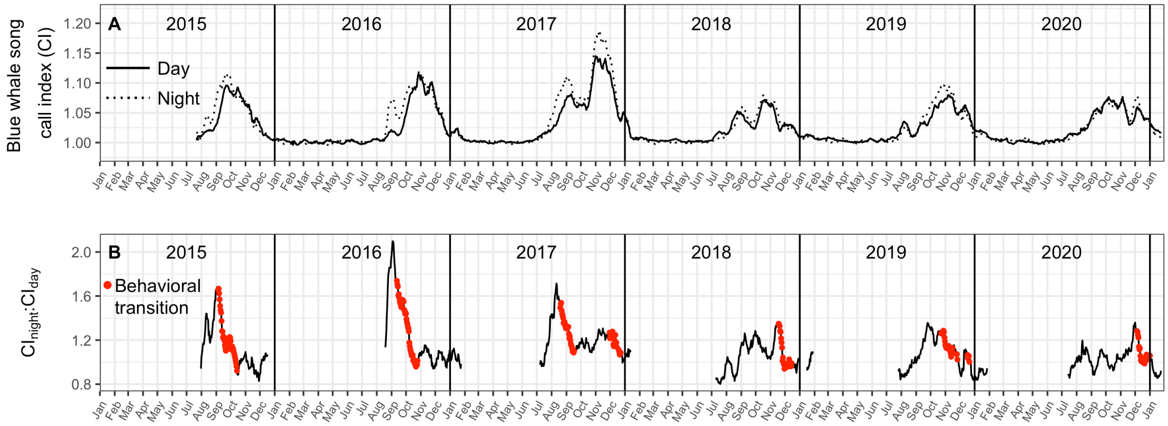

Figure 2. Time series of blue whale population-level song production. (A) Daily, filtered (15-day running mean) blue whale song call index (CI), a metric of blue whale song intensity, during night and day. **(B)** Daily, filtered (15-day running mean) CI_{night}:CI_{day}. Dates of significant decrease in CI_{night}:CI_{day}, indicative of the population-level behavioral transition from foraging to migration, are represented by red dots.

3.2 Oceanographic phenology of foraging habitat

Phenological metrics of biologically effective upwelling (Table 1) varied over the six-year study period (Figure 3; Table S1). The spring transition index of BEUTI ($BEUTI_{STI}$) ranged from yearday 5 to 43. The peak of BEUTI ($BEUTI_{MAX}$) ranged from yearday 118 (2016) to 185 (2020). The end date of BEUTI accumulation ($BEUTI_{END}$) ranged from yearday 329 (2019) to 361 (2016; 2020). The total upwelling magnitude index of BEUTI ($BEUTI_{TUMI}$) varied by nearly a factor of 2, ranging from 1220.2 (2015) to 2400.4 (2020) mmol m^{-1} s^{-1}. The late season upwelling magnitude index of BEUTI ($BEUTI_{LUMI}$) ranged from 600.0 (2015) to 1485.8 (2017) mmol m^{-1} s^{-1}.

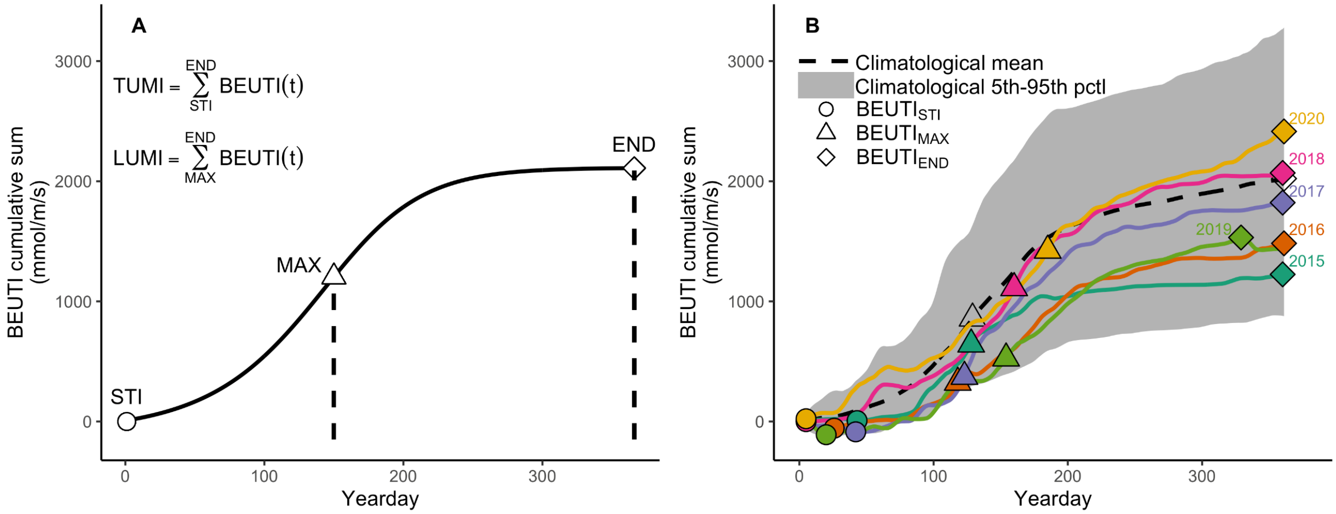

Figure 3. Phenology of biologically effective upwelling. (A) (Modified from (Bograd et al., 2009)) Idealized curve representing seasonal accumulation of BEUTI, with metrics of BEUTI phenology labeled and defined. **(B)** Daily, filtered (10-day running mean) values of the cumulative sum of BEUTI at 37° N for each year of the study period (2015-2020), relative to the long-term (1988-2020) climatological mean (dashed line), and envelope of the 5th to 95th percentiles (shaded). Dates of the spring transition (circles), peak upwelling (triangles), and end of upwelling season (diamonds) are overlaid. See Table 1 for definitions.

3.3 Timing of life history transition follows oceanographic phenology

The annual timing of the population-level behavioral transition from foraging to migration showed clear relationships with phenological metrics of biologically effective upwelling, the primary driver of biological productivity in this eastern boundary upwelling system (Jacox et al., 2018). Timing of the behavioral transition to migration was positively correlated with both the peak in BEUTI (BEUTI$_{MAX}$; Figure 4A) and total upwelling magnitude (BEUTI$_{TUMI}$; Figure 4B). In particular, both the onset and center date of behavioral transition correlated positively with BEUTI$_{MAX}$, and both the center and final date of behavioral transition correlated positively with BEUTI$_{TUMI}$ (Figure 4). Timing of the behavioral transition (specifically the start and center date) was negatively correlated with the spring transition index (BEUTI$_{STI}$; Figure S2). There was no clear relationship between behavioral transition timing and the end of upwelling accumulation (BEUTI$_{END}$; Figure S2) due to little interannual variability in the timing of the end of upwelling accumulation. There was also no clear relationship between behavioral transition timing and late season upwelling magnitude of BEUTI (BEUTI$_{LUMI}$; Figure S2), though notably, 2017 was both the year of greatest $\text{BEUTI}_{\text{LUMI}}$ and also the year in the study period with two clearly separated and sustained periods of behavioral transition (Figure 2B, Figure S2). The annual timing of blue whale song presence and peak showed no relationship with phenological metrics of BEUTI due to little interannual variability in the timing of population-level song presence and peak and the lack of behavioral context when using song presence alone (Figure S1, Figure S2).

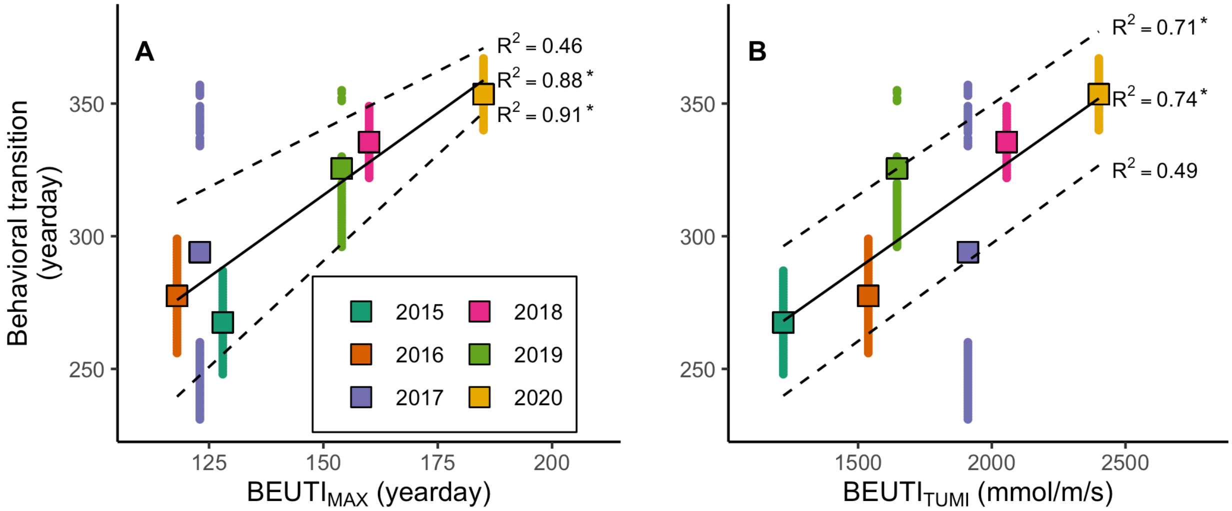

Figure 4. Relationships between blue whale life history transition and oceanographic phenology of foraging habitat. Upwelling phenology metrics are summarized for 37° N. **(A)** Timing of the behavioral transition from foraging to migration compared to the date of peak upwelling. **(B)** Timing of the behavioral transition from foraging to migration compared to total upwelling accumulated from the spring transition to the end of the upwelling season. In both panels, squares indicate the middle date between first and final dates of behavioral transition, and points show the temporal extent of the behavioral transition. Solid lines show linear regression comparing the middle date of each year's behavioral transition to upwelling metrics; dashed lines show linear regression comparing the first and last days of behavioral transition to the same upwelling metrics. R^2 values are reported for each regression, with asterisks indicating linear regression with a significant F-statistic ($p < 0.05$).

4 Discussion

Across marine and terrestrial systems, migratory populations rely on matching life history transitions with ecosystem phenology for population health, yet must contend with the challenges of interannual variability and climate-driven directional change in phenology (Both et al., 2006; Winkler et al., 2014). Theoretical understanding of whether and how migratory populations navigate this challenge has recently emerged, primarily from terrestrial and often group-living species (Deppe et al., 2015; Marra et al., 2005; Mueller et al., 2013; Post & Forchhammer, 2008; Shipley et al., 2020). Here, we present the evidence of population-level flexibility in a key life history transition of a long-distance marine migrant, finding that blue whales are able to match the timing of the population-level transition from foraging to breeding migration with ecosystem phenology despite very low population density in a vast and dynamic pelagic habitat. Below, we discuss 1) the dynamics and drivers of this flexible life history transition; 2) the implications of this flexible life history transition for blue whale conservation and management of the productive upwelling system they inhabit; and 3) the cues that allow for such flexibility in a vast and dynamic marine habitat, thus extending theoretical understanding of migratory species' life histories and behavior to relatively solitary migrants contending with the unique dynamics of marine ecosystems.

4.1 Flexibility in a life history transition

In this study, we find that delineating between foraging and migratory acoustic features of blue whale song reveals interannual flexibility in the timing of transition to migration from an important foraging area, spanning as much as 4 months (Figure 2B; Figure 4). This flexibility would not have been evident without considering the behavioral context of vocalizations. Specifically, we find little interannual variability in the presence of blue whale song in the Monterey Bay region (Figure 2, Figure S1), consistent with previous findings from another key foraging area for this population in the Southern California Bight (Szesciorka et al., 2020). Our findings indicate that species presence alone may not always be a good indicator of behavioral responses to environmental variability. Both acoustic (Burtenshaw et al., 2004; Haver et al., 2020) and visual (Calambokidis et al., 2015) survey methods indicate that at latitudes higher than that of the present study (i.e., the Gulf of the Farallones (~38° N) and poleward), blue whales tend to persist in foraging-associated shelf break habitat later into the annual cycle. This persistence is thought to be associated with foraging effort (Bailey et al., 2010; Calambokidis et al., 2015) and likely follows the later peak and persistent elevated levels of both upwelling (Jacox et al., 2018) and biomass at lower trophic levels (Burtenshaw et al., 2004; Mackas et al., 2006) at these higher latitudes. Vocalizing individuals migrating southward through the Monterey Bay region from these later-season foraging areas to the north are the likely source of elevated song levels around Monterey Bay for weeks (e.g., 2020) to months (e.g., 2016) after the local transition from foraging to southward migration (Figure 2B), underscoring the importance of behavioral context in acoustic detection.

The observed flexibility in timing of population-level transition from foraging to migration is related to phenology of the primary driver of ocean productivity in this ecosystem, biologically effective upwelling. Specifically, years with a later peak in and greater total accumulation of biologically effective upwelling in the study region are characterized by later transition to migration (Figure 4). While these trends hold for the range of upwelling scenarios observed during the study period, only weak to moderately-strong cumulative upwelling occurred in Monterey Bay over 2015-2020 (Figure 3B). Extremely strong upwelling can lead to offshore advection, causing offshore transport of planktonic organisms (Bakun et al., 2015; García-Reyes & Largier, 2012), and leading to less krill available along the shelf break (Harvey et al., 2021), where the combination of bathymetric and oceanographic features are amenable to the dense krill aggregations on which blue whales depend during their intensive summer foraging (Benoit-Bird et al., 2019; Cade et al., 2021). Continued monitoring of this population’s behavioral phenology during years of strong to extreme upwelling will provide greater insight into whether or not the relationships between ecosystem phenology and blue whale behavior extend to years characterized by stronger upwelling conditions and associated offshore advection of krill prey.

In addition to inter-annual flexibility, 2017 provides evidence of intra-annual flexibility in this migration from foraging habitat, with two distinct peaks in song presence (Figure 2A) and two distinct transitions from foraging to migratory behavior (Figure 2B). This pattern in 2017 suggests that whales migrating southward through the Monterey Bay region were able to initiate a second “wave” of foraging behavior in this region along their southward migration, perhaps taking advantage of food resources resulting from anomalously strong late-season biologically effective upwelling (Figure 3B; Figure S2; Table S1). One of the two key krill species on which blue whales prey on these foraging grounds (*E. pacifica*) is known to have pulsed, year-round recruitment with spawning peaks coincident with periods of upwelling (Brinton, 1976; Siegel, 2000). The most intensive spawning occurs in spring, leading to peak larval concentrations during May-August. This spring cohort is marked by rapid maturation leading to spawning capability after ~4 months (fall) (Siegel, 2000). The late-season foraging in 2017 suggests that blue whales may be able to take advantage of enhanced fall spawning by *E. pacifica*, particularly in years with strong late-season upwelling conditions which can support the growth and survival of this fall cohort. Additionally, pulsed upwelling events in the late season, like those driving the late-season accumulation of upwelling in 2017, also make krill more available to blue whale predators on shorter time scales (hours-days) by driving the dense aggregations on which blue whales selectively forage (Benoit-Bird et al., 2019; Cade et al., 2021).

4.2 Ecosystem sentinels and adaptability to global change

While diel patterns in song and associated behavioral states might play an important role in signaling among blue whales and coordinating migration at mesoscales, these acoustic signals can also be useful to resource managers as a real-time indicator of krill availability and ecosystem state. In this way, patterns of song and associated timing of migration from foraging habitat make blue whales an acoustic ecosystem sentinel (Hazen et al., 2019). Given the long-distance propagation of blue whale vocalizations (Figure 1B), patterns of blue whale song provide information on blue whale behavior and associated forage availability for near-real-time research and natural resource management uses (Oestreich et al., 2020a; Parijs et al., 2009). For example, 2015 and 2016 were the years with earliest mean date of behavioral transition in the present study, coincident with a prolonged marine heatwave that both reduced upwelling (Figure 3B) and impacted the abundance, distribution, and community structure of both lower trophic levels and predators in the CCLME (Brodeur et al., 2019; Ryan et al., 2019). The acoustically-inferred timing of blue whales' transition to migration reveals the response of a krill-specialist predator to this marine heatwave, providing information on the availability of forage for a range of krill-dependent predators.

Beyond providing information on ecosystem state, monitoring of blue whales' behavioral response to oceanographic variability sheds light on the adaptability of this endangered population to environmental variability and change. Migratory species with little life history flexibility are considered to be least equipped to respond to variability and long-term changes in the ecosystems they inhabit, making them most vulnerable to the effects of global climate change (Winkler et al., 2014). The considerable flexibility in timing of transition to migration shown here suggests adaptability of the Northeast Pacific blue whale population to changes in the CCLME, including marine heatwaves (Brodeur et al., 2019) and altered timing, spatial structure, and intensity of upwelling (García-Reyes et al., 2015; Wang et al., 2015). However, given the likely role of long-distance vocal communication in driving this flexibility in the transition to migration, increasing anthropogenic noise in the oceans (Duarte et al., 2021) could pose a threat to this behavioral adaptability.

4.3 Flexible cues in the marine environment

Both the intra-annual (2017) and inter-annual (2015-2020) flexibility in blue whales' transition from foraging to migration suggest the use of proximate environmental and/or social cues driving the onset of migration. This flexibility stands in contrast to long-term stability in the timing of arrival at key stopover sites during northward migration toward foraging grounds (Abrahms et al., 2019; Fossette et al., 2017). With little proximate sensory information on forage availability during the northward migration to foraging grounds, reliance on spatial memory is valuable for tracking long-term mean conditions (Abrahms et al., 2019). In initiating migration from foraging habitat, however, this population has multiple sources of real-time information on forage availability across spatial scales, including: 1) proximate sensory information on biotic and abiotic conditions (Dodson et al., 2020); 2) recent information on foraging conditions in areas previously visited; and 3) long-distance acoustic information on the behavioral state (foraging or migrating) of conspecifics, perhaps providing information on prey availability over hundreds-to-thousands of square kilometers of potential foraging area (Oestreich et al., 2020b). Furthermore, blue whales likely integrate information over broader spatial and temporal scales, considering forage conditions across a range of foraging sites visited in a given year. While the present study only considers flexibility in transition to migration from a specific foraging site, future work might apply this acoustic signature of blue whale migration across a range of key foraging locations to more fully understanding how this population responds to ecosystem variability across a range of scales.

Use of multiple sensory cues for initiating flexible life history transitions can be useful to migratory individuals inhabiting dynamic habitats (Couzin, 2018; Peters et al., 2018). For example, collective life history transitions in migratory populations can be driven by many individuals sensing both an environmental gradient or change and also one another's behavioral responses (Torney et al., 2018). The role of social cues from conspecifics can be particularly significant in dynamic environments marked by ephemeral aggregation of forage species, where any individual's limited sensing of their proximate environment may not be representative of broader forage availability (Couzin, 2018). Pelagic habitats present an extreme case of ephemerality and dynamism in forage availability (Benoit-Bird & McManus, 2012; Marquet, 1993; Steele, 1991), particularly at the scales most relevant to blue whale foraging (Benoit-Bird et al., 2019; Cade et al., 2021), exacerbating the potential for discrepancies between an individual's immediate surroundings and wider-ranging availability of foraging opportunities. Theoretical understanding from study of terrestrial and group-living migrants suggests that social cues from conspecifics provide particularly useful information in this scenario (Berdahl et al., 2013; Couzin, 2018). Further, theory indicates that increasing group size and density can improve accuracy in emergent sensing of such noisy environmental signals (Berdahl et al., 2013), as individual-to-individual information transfer via visual (Strandburg-Peshkin et al., 2013) or vocal (Dunlop et al., 2008) signaling typically requires relative proximity. In some cases of high group density with correlated individual sensing of a complex broader environment, however, decision making in smaller proximate groups can be beneficial (Kao & Couzin, 2014). Yet as shown here, blue whales match timing of a population-level life history transition with interannual variability in ecosystem phenology despite a relatively solitary life history and low population density in their vast and dynamic foraging habitat. Blue whales might both circumvent the need for proximity in collective sensing and avoid the pitfalls of highly-correlated individual-level sensing (Kao & Couzin, 2014) via their evolved use of high source-level, low frequency vocalizations that propagate over great distances in the marine environment (Goldbogen & Madsen, 2021; Payne & Webb, 1971; Torres, 2017). Of course, vocal signaling plays a significant role in many terrestrial migratory species' life history transitions, collective migration (Larkin & Szafoni, 2008), and social interactions, at times over surprisingly large spatial scales (e.g., several km, as in the low frequency communication of African elephants (McComb et al., 2003)). But the clear flexibility in blue whales' timing of a collective life history transition alongside their evolved use of long-distance vocalizations over hundreds of km in their aquatic habitat brings into question the appropriate spatial scales for consideration of "social groups" in migratory species. These findings build upon understanding of the cues which enable flexible life history transitions, and extend theoretical understanding of the grouping and social dynamics conducive to effective emergent sensing in the unique conditions of oceanic ecosystems.

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Supporting Information for "Acoustic signature reveals blue whales tune life history transitions to oceanographic conditions"

Table S1. Phenological metrics of biologically-effective upwelling in Monterey Bay, CA. Spring transition index, maximum index, end index, total upwelling magnitude index, and late upwelling magnitude index of BEUTI at 37° N for each year of the study period (2015-2020).

Year	$\mathbf{BEUTI_{STI}}$ (day of year)	$\mathbf{BEUTI_{MAX}}$ (day of year)	$\mathbf{BEUTI_{END}}$ (day of year)	$\mathbf{BEUTI_{TUMI}}$ (mmol/m/s)	$\mathbf{BEUTI_{LUMI}}$ (mmol/m/s)
2015	43	128	360	1220.2	600.0
2016	26	118	361	1538.2	1188.1
2017	42	123	360	1910.8	1485.8
2018	5	160	360	2055.8	996.8
2019	20	154	329	1645.5	1021.6
2020	5	185	361	2400.4	1018.5

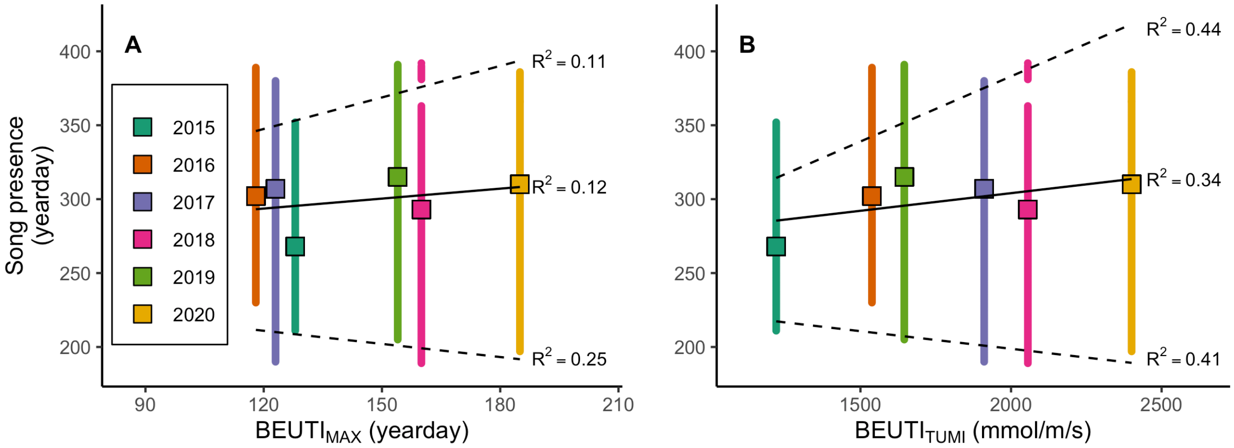


Figure S1. Relationship between blue whale song presence and metrics of biologically effective upwelling phenology (see also Figure 4, main text). Upwelling phenology metrics are summarized for 37° N. (A) Blue whale song presence compared to date of peak upwelling. **(B)** Blue whale song presence compared to total upwelling accumulated from the spring transition to the end of the upwelling season. In both panels, squares indicate the annual peak in CI and points (which appear as continuous lines when no daily gaps are present) show the temporal extent of song presence (CI 15-day running mean ≥ 1.01). Solid lines show linear regression comparing the date of peak song to upwelling metrics; dashed lines show linear regression comparing the first and last days of song presence to the same upwelling metrics. R^2 values are reported for each regression; note the lack of significant F-statistic values for all regressions in contrast to Figure 4 of the main text. In all panels, yearday values > 365 (or 366 in the 2016 leap year) indicate persistence of song or behavioral transition into the following calendar year.

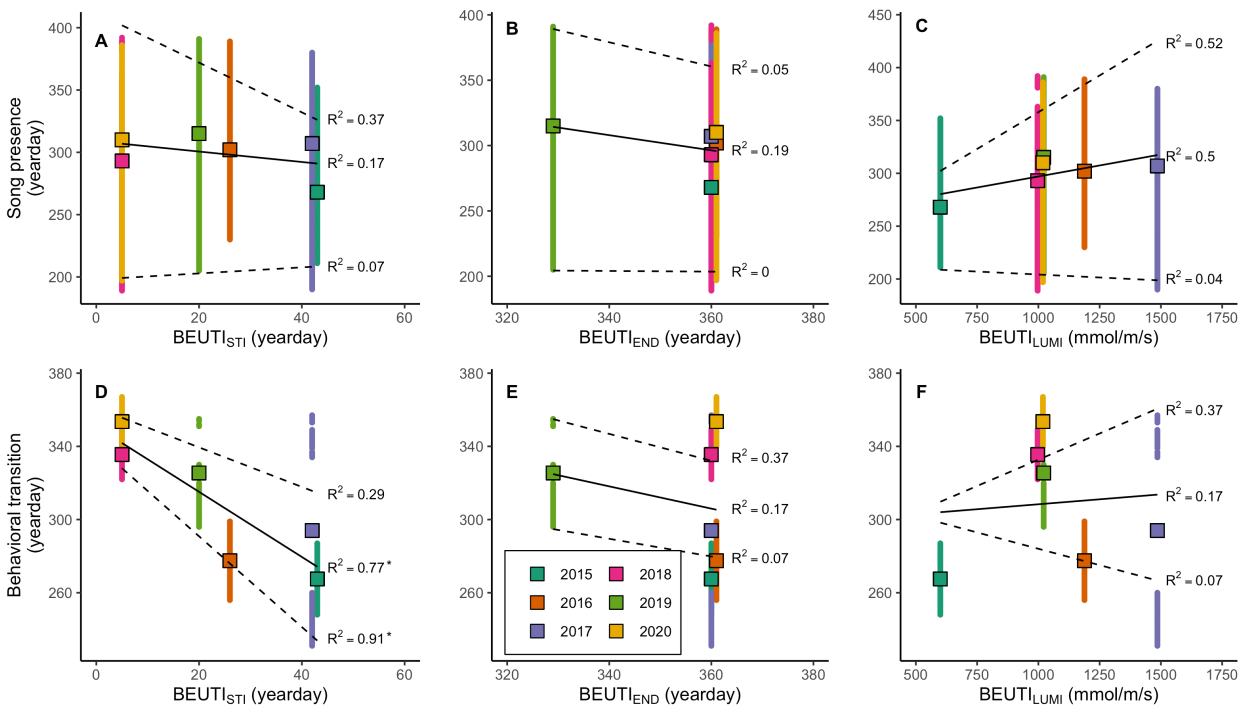
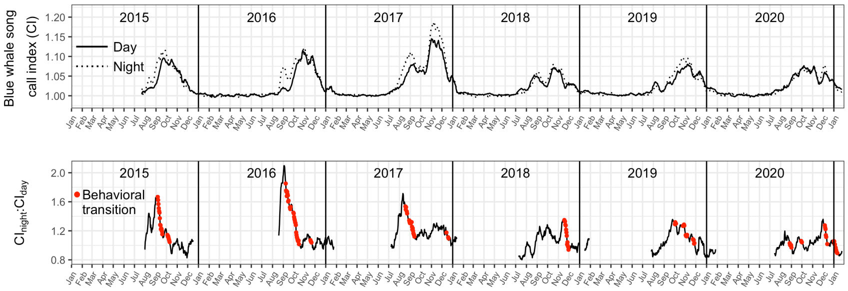
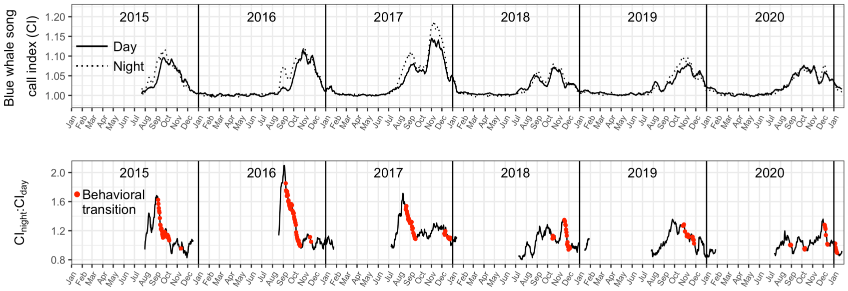


Figure S2. Relationship between blue whale vocal behavior and additional metrics of biologically effective upwelling phenology (see also Figure 4, main text). Upwelling phenology metrics are summarized for 37° N. (A-C) Song presence compared to upwelling phenology metrics including: **(A)** date of spring transition ($\text{BEUTI}_{\text{STI}}$); **(B)** date of end of upwelling accumulation ($\text{BEUTI}_{\text{END}}$); and **(C)** late season upwelling accumulation ($\text{BEUTI}_{\text{LUMI}}$) from the peak to the end of the upwelling season. In panels (A-C), squares indicate the annual peak in CI and points (which appear as continuous lines when no daily gaps are present) show the temporal extent of song presence ($\text{CI} \geq 1.01$). **(D-F)** Behavioral transition from foraging to migration compared to upwelling metrics including: **(D)** date of spring transition ($\text{BEUTI}_{\text{STI}}$); **(E)** date of end of upwelling accumulation ($\text{BEUTI}_{\text{END}}$); and **(F)** late season upwelling accumulation ($\text{BEUTI}_{\text{LUMI}}$) from the peak to the end of the upwelling season. In panels (D-F), squares indicate the mean date between first and final dates of behavioral transition and points (again appearing as continuous lines when no daily gaps are present) show the temporal extent of the behavioral transition. In all panels, yearday values > 365 (or 366 in the 2016 leap year) indicate persistence of song or behavioral transition into the following calendar year. Solid lines show linear regression comparing the middle date of each year's behavioral transition to upwelling metrics; dashed lines show linear regression comparing the first and last days of behavioral transition to the same upwelling metrics. R^2 values are reported for each regression, with asterisks indicating linear regression with a significant F-statistic ($p < 0.05$).

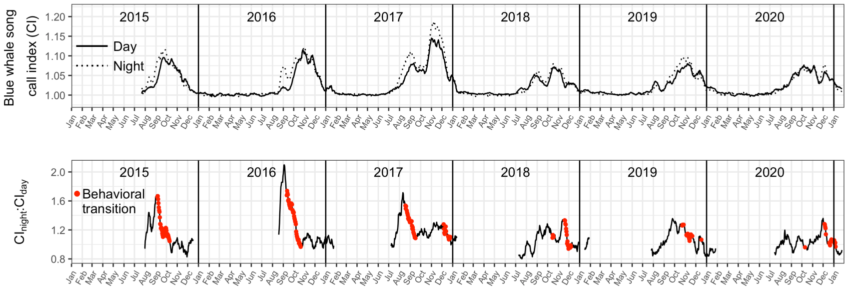
t test window sample size = 15 days



t test window sample size = 20 days



t test window sample size = 25 days



t test window sample size = 30 days

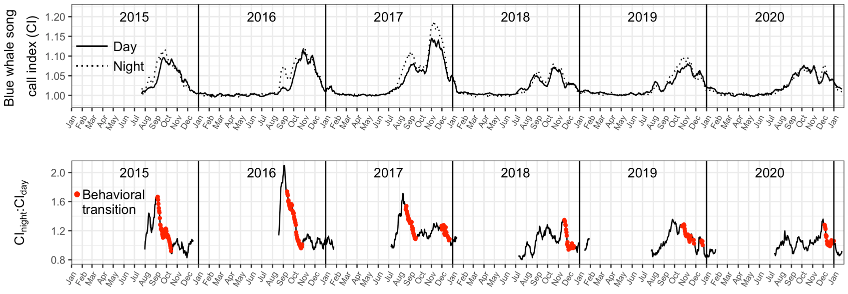
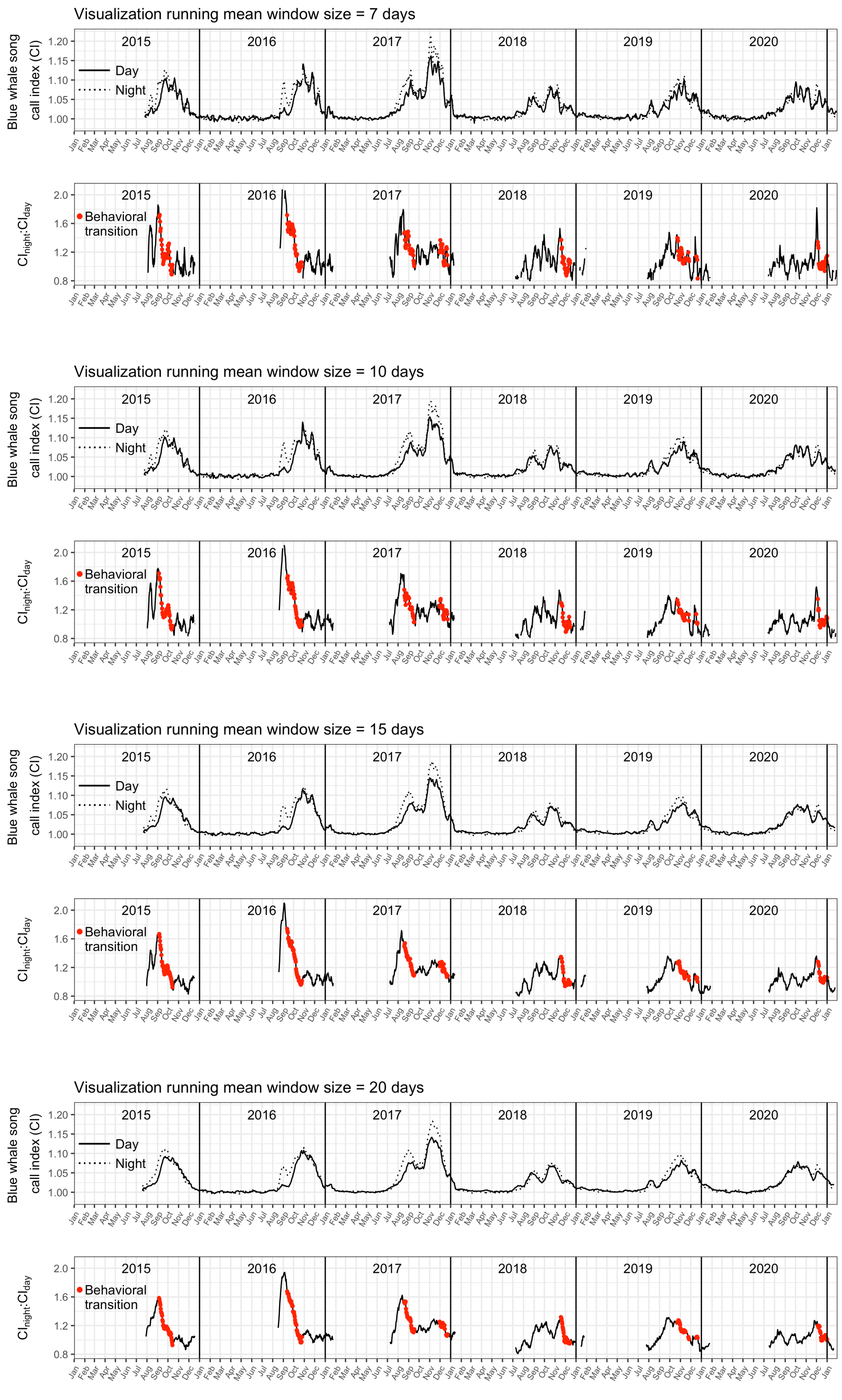


Figure S3. Statistical definition of behavioral transition, comparing a range of sample sizes. Sample size = 30 days (final panel of this figure) was chosen as the statistical definition of the behavioral transition for the reasons articulated in the Methods and Materials section of the main text.



Visualization running mean window size = 7 days

Visualization running mean window size = 10 days

Visualization running mean window size = 15 days

Visualization running mean window size = 20 days

Figure S4. Visualization of CI and $CI_{night}:CI_{day}$ using a range of running mean window sizes. T test window size = 30 days (Figure S1; for defining behavioral transition) for all panels.