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

William K. Oestreich[a,1], Briana Abrahms[b], Megan F. McKenna[a], Jeremy A. Goldbogen[a], Larry B. Crowder[a], and John P. Ryan[c]

[a]Hopkins Marine Station, Department of Biology, Stanford University, Pacific Grove, CA, USA

[b]Center for Ecosystem Sentinels, Department of Biology, University of Washington, Seattle, WA, USA

[c]Monterey Bay Aquarium Research Institute, Moss Landing, CA, USA

[1]To whom correspondence should be addressed. **Email**: woestreich@stanford.edu

Acknowledgments: Thank you to M. Chapman, J. Fahlbusch, and two anonymous reviewers 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. 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 (Oestreich, 2022). For reproducibility and extensibility of results, original audio recordings for the entire study period are available through the AWS Open Data registry at: https://registry.opendata.aws/pacific-sound/.

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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 variability in the 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 findings suggest that blue whales delay the transition from foraging to southward migration in years of the highest and most persistent biological productivity, a finding consistent with the hypothesis that this population maximizes energy intake on foraging grounds rather than departing toward breeding grounds as soon as sufficient energy reserves are accumulated.
5. The use of flexible cues (e.g., foraging conditions and long-distance acoustic signals) in timing a major life history transition may be key to the persistence of this endangered population facing the pressures of rapid environmental change. Further, these results extend theoretical understanding of the flexibility and drivers of population-level migration to 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 found only on seasonally-productive foraging grounds which are 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 intensive feeding on seasonal foraging grounds and subsequent migration to lower-forage-quality 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 energy intake on seasonal high-quality foraging grounds must fuel the extreme energetic demands of long-distance migration to and from breeding grounds with limited forage availability (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).

In recent years, significant research effort has yielded insights into the drivers and relative flexibility of life history transitions in primarily group-living and often terrestrial migratory populations. Relatively fixed exogenous factors such as photoperiod are known to play a role in the timing of life history transitions (Gwinner, 1996). Under changes in ecosystem phenology, reliance on such fixed cues can lead to trophic mismatch (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, broader-scale environmental gradients and changes are often obscured by fine-scale environmental variability or occur at spatial or temporal scales exceeding the sensory capabilities of individuals, meaning that sensing and response to individually-sensed 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 might overcome this problem via individual and emergent collective sensing of environmental variability (Berdahl et al., 2013). Collective sensing refers to the use of both individual sensory information and the behavior of conspecifics in behavioral decision making, effectively pooling information (Berdahl et al., 2013) and allowing for more optimal timing of life history transitions and collective long-distance migrations (Couzin, 2018; Guttal & Couzin, 2010). This body of work has established the importance of group or population size and density in optimizing collective sensing and behavior (including migration) under environmental variability (Couzin, 2018; 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 from terrestrial habitats 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, both the relative flexibility in life history transitions and the evolution of cue types used to time these life history transitions in long-distance marine migrants might differ substantially from theoretical understanding derived from terrestrial systems.

The Eastern North 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, Seakamela, et al., 2021; Croll et al., 2005)) resulting from wind-driven upwelling (Fig. 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. Although 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 for 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) from even a single monitoring location (as in the present study; Fig. 1B; (Oestreich, Fahlbusch, et al., 2020)). The Eastern North Pacific blue whale 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 (Fig. 1C). Although song is thought to be produced exclusively by male blue whales (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 Eastern North 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, Fahlbusch, et al., 2020). Previous work has shown that acoustic presence alone can be a poor proxy for behavior—for example, within a given period of acoustic presence, population-level behavior can vary widely and include distinct behavioral periods (e.g., foraging, migration) which are not resolved using acoustic presence alone (Oestreich, Fahlbusch, et al., 2020). 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 analyzed six years (summer 2015 to spring 2021) of nearly-continuous (95% coverage) passive acoustic monitoring data from a key foraging area for the Eastern North Pacific blue whale population (Monterey Bay, CA, USA), acoustically identifying timing of the transition from foraging to breeding migration in each year. We then compared 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 may allow for collective flexibility in an annual 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 (Fig. 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 (Fig. 1B). The hydrophones have a bandwidth of 10 Hz to 200 kHz and sampled at 256 kHz with a bit depth of 24. Calibration of the sequentially-deployed hydrophones is described in Oestreich, Fahlbusch, et al. (2020). 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 (Fig. 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, Fahlbusch, et al., 2020). The B call was chosen as the target acoustic signal for this study for several reasons: 1) it has the highest received-level and is the most common blue whale song unit in the Eastern North Pacific; 2) it has predictable spectral characteristics that allow for efficient and effective quantification (see Section 2.2); and 3) it can be used to determine population-level behavioral state (foraging vs. southward migration; described in detail in Section 2.2).

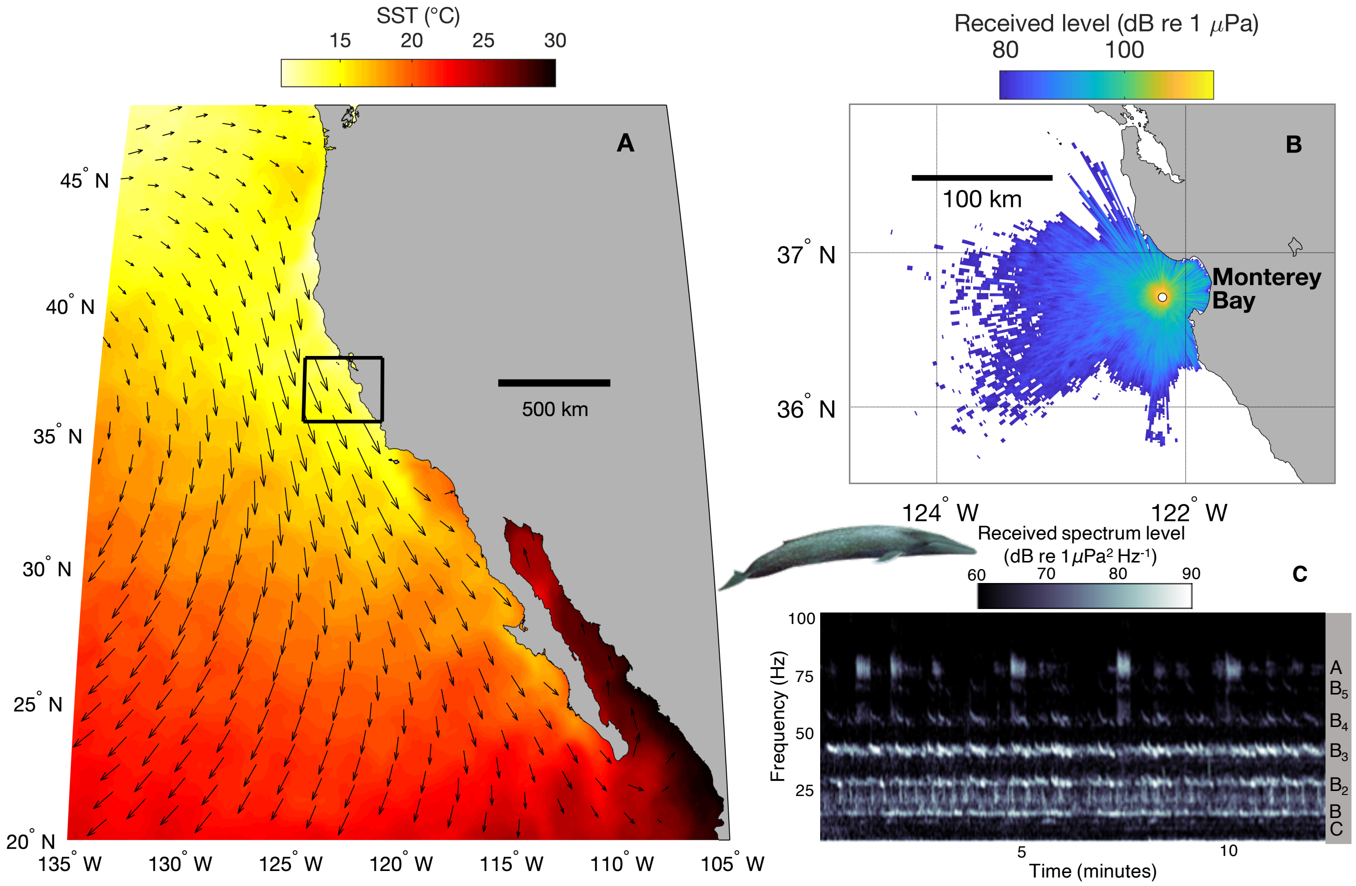

Figure 1. Study system. (A) Eastern North Pacific sea surface temperature (SST, shown in color, from Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, 0.01°) and winds (shown in vectors, monthly means ranging from 0.17 – 10.49 m s^{-1}, from All Metop ASCAT, 0.25°) for June 2018; box inset in panel (B). **(B)** (Adapted from Oestreich, Fahlbusch, et al., 2020) 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 (labeled as "B") and second through fifth harmonics, e.g., "B_2" for second harmonic), and C calls are labeled. Spectrogram generated from data with 2 kHz 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, metrics derived from previously published methods (Oestreich, Fahlbusch, et al., 2020) 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 singular and overlapping ("chorusing") blue whale songs (Oestreich, Fahlbusch, et al., 2020). CI was calculated using long-term spectral averages (LTSAs) with frequency and time resolution of 1 Hz and 5 seconds, respectively. For each day and for solar elevation categories within each day (< -12° for night; > 0° for day), spectrum levels were averaged and CI was calculated as the ratio of these mean spectrum levels at signal peak (mean across 43-44 Hz) and background (mean at 37 and 50 Hz) frequencies. To describe the phenology of blue whale song presence each year, we identified the first and final dates of song presence (CI 15-day running mean ≥ 1.01), as well as the peak of song signal received at MARS (maximum of the CI 15-day running mean). The 15-day running mean was used to smooth daily values and avoid mischaracterization of the first, final, and peak dates of song production due to transient acoustic signals from other sources (e.g., vessels) in the frequency range of blue whale song.

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 (Fig. 1B; (Oestreich, Fahlbusch, et al., 2020)). This previous work combined acoustic analysis of five years of population-level blue whale song data with individual-level bio-logging analyses to attribute the significant drop in CI_{night}:CI_{day} values to the population-level transition from foraging to southward migration. 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 weeks (Oestreich, Fahlbusch, et al., 2020). To identify behavioral transitions in each year of this study (2015-2020), we used one-sided t-tests for each day of the time-series, comparing samples comprised of the 30-day period immediately preceding and following a given day (total n = 60 days). Each day with p-value < 0.05 for this t-test was considered part of the behavioral transition from foraging to migration. Following this procedure, we identified the first, middle, and final dates of the behavioral transition in each year. Although additional sample window sizes were considered for this statistical definition of the behavioral transition (see Fig. S1), the 30-day sample period was chosen because (1) it matches that used by Oestreich, Fahlbusch, et al. (2020) 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 (Fig. S1), consistent with the population-level acoustic signature described by Oestreich, Fahlbusch, et al. (2020). 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 (Fig. 2; see Fig. S2 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}. 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.

2.3 Ecosystem phenology

Previous studies have demonstrated a strong relationship between Eastern North 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 calculated the annual accumulation of BEUTI at 37° N (Fig. 3).

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 ($BEUTI_{STI}$), the peak of BEUTI ($BEUTI_{MAX}$), the end of positive upwelling accumulation ($BEUTI_{END}$), the total upwelling accumulation during the full upwelling season from $BEUTI_{STI}$ to $BEUTI_{END}$ ($BEUTI_{TUMI}$), and late-season upwelling accumulation from $BEUTI_{MAX}$ to $BEUTI_{END}$ ($BEUTI_{LUMI}$). 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 was 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).

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

Abbreviation	Meaning
CI	Call index (used to detect blue whale song presence) [1]
CI_{night}:CI_{day}	Night-to-day ratio of call index (used to determine blue whale regional population-level behavioral state)[1]
BEUTI	Biologically effective upwelling transport index [2]
$BEUTI_{STI}$	Spring transition index (date on which cumulative BEUTI reaches its minimum value) [3]
$BEUTI_{MAX}$	Peak of seasonal upwelling (date of greatest rate of change in cumulative BEUTI) [3]
$BEUTI_{END}$	End of seasonal upwelling (date on which cumulative BEUTI reaches its maximum value) [3]
$BEUTI_{TUMI}$	Total upwelling magnitude index (total BEUTI accumulated from STI to END) [3]
$BEUTI_{LUMI}$	Late upwelling magnitude index (total BEUTI accumulated from MAX to END) [4]

2.4 Statistical analyses

We used linear regression to evaluate the relationships between the annual timing of blue whales' population-level behavioral transition and annual metrics of oceanographic phenology. For each metric of oceanographic phenology (Table 1, Fig. 3), linear regressions were calculated separately using the first, center, and final dates of the population-level behavioral transition (Figs 4, S4) and song presence (Figs S3-S4) from each year of the study period as the dependent variable. Because blue whale song was present at the start date of recording in 2015, the first date of song presence in this year could not be determined, and this year was excluded from statistical analyses involving the onset of song presence. Using the F-statistic for each linear regression, we tested for significance using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995) with a false discovery rate of 0.1. We implemented the Benjamini-Hochberg procedure to correct for multiple testing (15 hypothesis tests each for blue whale song presence and blue whale behavioral transition) and provide a more conservative threshold for identifying significant results. Both p-values before multiple testing correction and results from the Benjamini-Hochberg procedure are available via the code and data repository for this manuscript (Oestreich, 2022). 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 (elevated CI) was relatively consistent over the six-year study period (Fig. 2A; Table S1). 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 (Fig. 2B). The yearday spans of this behavioral transition (Table S1; Fig. 2B) also emphasize the high degree of interannual variability, with behavioral transitions ranging from as short as 27 days in duration (2018) to as long as 126 days (2017).

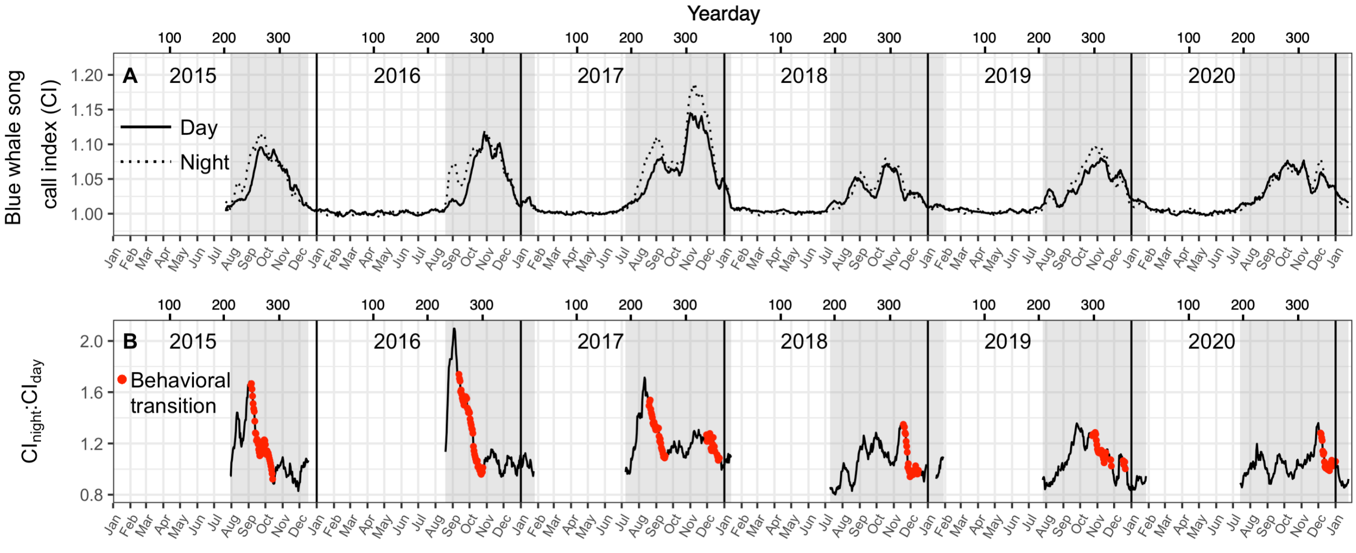

Figure 2. Time series of blue whale population-level song production. (A) Daily, filtered (15-day running mean) blue whale song call index (CI), a metric of blue whale song intensity, during night and day. **(B)** Daily, filtered (15-day running mean) CI_{night}:CI_{day}. Dates of statistically significant decrease in CI_{night}:CI_{day}, indicative of the population-level behavioral transition from foraging to migration, are represented by red dots. In both panels, gray shading indicates the period of blue whale song presence (CI 15-day running mean $\geq$ 1.01) in each year of the study period.

3.2 Oceanographic phenology of foraging habitat

Phenological metrics of biologically effective upwelling (Table 1) varied over the six-year study period (Fig. 3; Table S2). The spring transition index of BEUTI ($\text{BEUTI}_{\text{STI}}$) ranged from yearday 5 to 43. The peak of BEUTI ($\text{BEUTI}_{\text{MAX}}$) ranged from yearday 118 (2016) to 185 (2020). The end date of BEUTI accumulation ($\text{BEUTI}_{\text{END}}$) ranged from yearday 329 (2019) to 361 (2016; 2020). The total upwelling magnitude index of BEUTI ($\text{BEUTI}_{\text{TUMI}}$) 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 ($\text{BEUTI}_{\text{LUMI}}$) ranged from 600.0 (2015) to 1485.8 (2017) mmol m^{-1} s^{-1}.

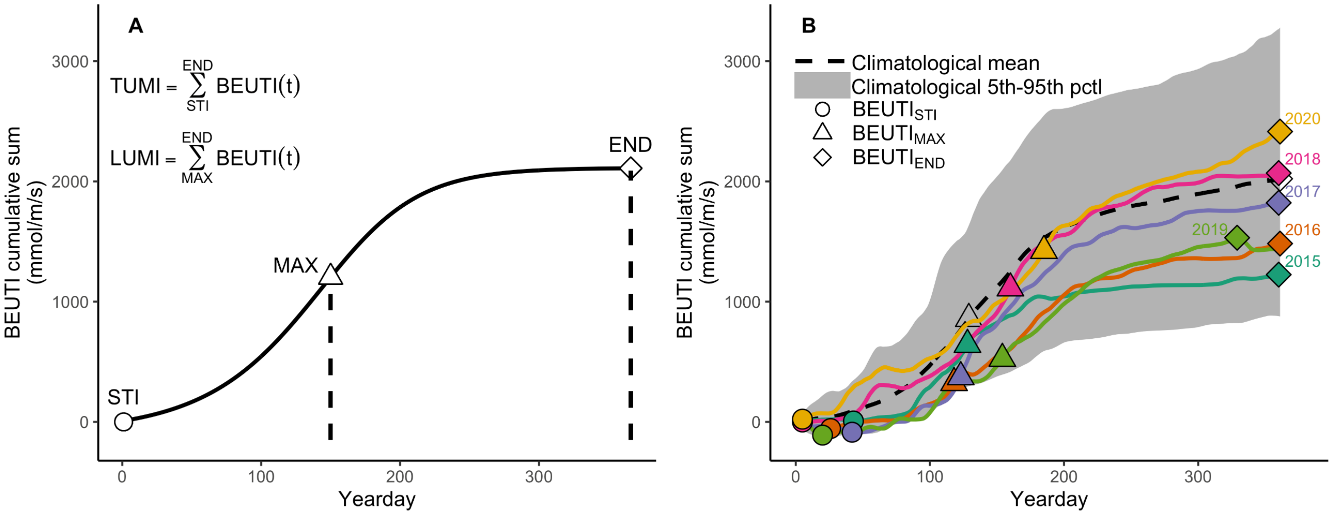

Figure 3. Phenology of biologically effective upwelling. (A) (Modified from (Bograd et al., 2009)) Idealized curve representing seasonal accumulation of BEUTI, with metrics of BEUTI phenology labeled and defined (see Table 1 for full definitions). **(B)** Daily, filtered (10-day running mean) values 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.

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 (specifically the start and center date) was negatively correlated with the spring transition index ($\text{BEUTI}_{\text{STI}}$; Fig. 4A). Timing of the behavioral transition to migration was positively correlated with both the peak in BEUTI ($\text{BEUTI}_{\text{MAX}}$; Fig. 4B) and total upwelling magnitude ($\text{BEUTI}_{\text{TUMI}}$; Fig. 4C). In particular, both the onset and center date of behavioral transition correlated positively with $\text{BEUTI}_{\text{MAX}}$, and both the center and final date of behavioral transition correlated positively with $\text{BEUTI}_{\text{TUMI}}$ (Fig. 4). There was no clear relationship between behavioral transition timing and the end of upwelling accumulation ($\text{BEUTI}_{\text{END}}$; Fig. S4C) 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 ($\text{BEUTI}_{\text{LUMI}}$; Fig. S4D), 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 (Figs 2B, S4D). 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 (Figs S3-S4).

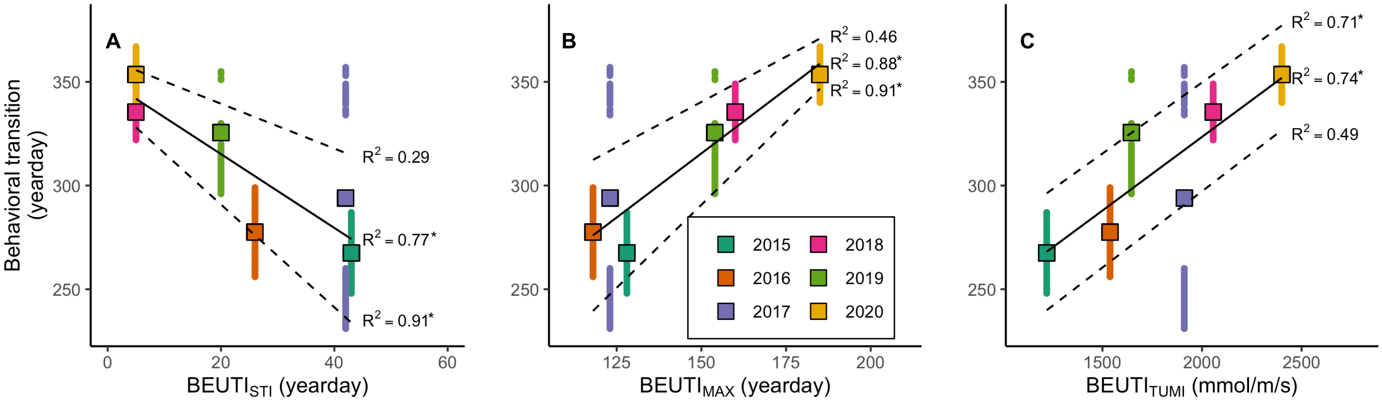

Figure 4. Relationships between blue whale life history transition and oceanographic phenology of foraging habitat. Upwelling phenology metrics are summarized for 37° N. Timing of the behavioral transition from foraging to migration compared to **(A)** the date of upwelling onset; **(B)** the date of peak upwelling; and **(C)** total upwelling accumulated from the spring transition to the end of the upwelling season. In all panels, squares indicate the middle date between first and final dates of behavioral transition, and points (which appear as continuous lines when no daily gaps are present) show the temporal extent of the behavioral transition as determined via t-tests (described in Section 2.2 and indicated by red dots in Fig. 2B). Solid black lines show linear regression comparing the middle date of each year's behavioral transition to upwelling metrics; dashed black 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 regressions with a significant F-statistic following multiple testing correction via the Benjamini-Hochberg procedure (see Methods Section 2.4 for more detail).

4 Discussion

Across marine and terrestrial systems, migratory populations rely on matching life history transitions with ecosystem phenology for population health, yet they 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 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 cues that may 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; and 3) the implications of this flexible life history transition for blue whale conservation and management of the productive upwelling system they inhabit.

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 (Figs 2B, 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 (Figs 2A, S3), 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 (Fig. 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 an earlier onset, later peak, and greater total accumulation of biologically effective upwelling in the study region are characterized by later transition to migration (Fig. 4). These results, alongside the lack of a relationship between timing of transition to migration and late-season upwelling magnitude ($\mathrm{BEUTI}_{\mathrm{LUMI}}$; Fig. S4D), indicate that upwelling characteristics both before and during blue whales' arrival on foraging grounds play a greater role in determining timing of foraging and migration than upwelling dynamics during the period of blue whale presence alone. Further, the lack of a relationship between timing of transition to migration and the end date of upwelling accumulation is unsurprising given that blue whales initiate the population-level transition to migration before the final date of seasonal upwelling accumulation ($\mathrm{BEUTI}_{\mathrm{END}}$; Fig. S4C). These trends hold for the range of upwelling scenarios observed during the study period, but it is worth noting that these results are derived from a relatively small sample size (six years), covering only a subset of historically-observed upwelling conditions in the CCLME (Fig. 3B). Whereas we observed substantial variability in upwelling magnitude during the study period (nearly a twofold difference in total upwelling magnitude between the weakest and strongest upwelling years), only weak to moderately-strong cumulative upwelling occurred in Monterey Bay over 2015-2020 (Fig. 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 lower zooplankton abundance (Harvey et al., 2021). This potential consequence of strong upwelling would be particularly important along the shelf break, 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, Seakamela, 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 (Fig. 2A) and two distinct transitions from foraging to migratory behavior (Fig. 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 (Table S2). 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-to-days) by driving the dense aggregations on which blue whales selectively forage (Benoit-Bird et al., 2019; Cade, Seakamela, et al., 2021).

4.2 Flexible cues in the marine environment

4.2.1 Internal vs. external cues

Both the intra-annual (2017) and inter-annual (2015-2020) flexibility in blue whales' transition from foraging to migration suggest the use of external cues (e.g., sensing of an individual's proximate surroundings, long-distance social cues from conspecifics) and/or variable internal cues (e.g., energetic stores, demographic factors) driving the onset of migration. We first consider the relative likelihood of internal or external cues in driving the observed population-level flexibility in transition to migration. Whereas the timing of individuals' accumulation of sufficient energetic stores could play a role in individuals' timing of transition to migration, the results presented here suggest that blue whales instead continue foraging for as long as sufficient prey resources persist. Specifically, the correlations of later transition to migration with an earlier onset of upwelling ($\mathrm{BEUTI}_{\mathrm{STI}}$), a later peak in upwelling ($\mathrm{BEUTI}_{\mathrm{MAX}}$), and greater total upwelling magnitude ($\mathrm{BEUTI}_{\mathrm{TUMI}}$) (Fig. 4) all suggest that blue whales delay the transition from foraging to southward migration in years of the highest and most persistent biological productivity. If migration timing was primarily determined by the timing of accumulation of sufficient energy reserves, one would expect earlier migration in years with an earlier onset of upwelling ($\mathrm{BEUTI}_{\mathrm{STI}}$). However, the opposite pattern is observed here (Fig. 4A), suggesting that blue whales will maximize their energy intake on foraging grounds before facing ~7 months of sparse foraging opportunities and a round-trip migration of thousands of kilometers. Other internal cues beyond energetic stores (e.g., pregnancy, life stage) might also play a role in individual-level timing of migration. But the clear population-level flexibility in timing of transition to migration following upwelling phenology of blue whale foraging habitat suggests a role of additional external cues.

4.2.2 External cues: Individual sensing of environment and social cues from conspecifics

This blue whale population's flexibility in timing of transition to southward migration 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, Fahlbusch, et al., 2020). Furthermore, given their ability to track long-term average conditions via spatial memory in their northward migrations toward foraging grounds (Abrahms et al., 2019), 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. Whereas 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 understand 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 (Berdahl et al., 2017). The role of social cues from conspecifics could 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, Seakamela, 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 at an enormous spatial scale 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 terrestrial migratory species' 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 population-level life history transition alongside their evolved use of long-distance vocalizations over hundreds of kilometers in their aquatic habitat brings into question the appropriate spatial scales for consideration of "social groups" in marine migratory species.

4.3 Ecosystem sentinels and adaptability to global change

Whereas 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 (Fig. 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, Chapman, et al., 2020; Van 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 (Fig. 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 Eastern North 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 possible role of long-distance vocal communication in driving this flexibility in the transition to migration (see Section 4.2.2) as well as the documented role of vocal communication in other aspects of blue whales' life history and behavior (Cade, Fahlbusch, et al., 2021; Oleson et al., 2007; Schall et al., 2020), increasing anthropogenic noise in the oceans (Duarte et al., 2021) could pose a threat to this behavioral adaptability.

4.4 Conclusions and future investigation

Blue whales in the Eastern North Pacific display significant flexibility in the timing of their population-level life history transition from foraging to southward migration toward breeding grounds. Variability in the timing of this life history transition from a foraging hotspot follows annual metrics of oceanographic phenology in this foraging habitat, with later transitions to migration occurring in years with an earlier onset, later peak, and greater accumulation of biologically effective upwelling. Such flexibility to track interannual variability in oceanographic and foraging conditions may be critical to the survival of this endangered population in the face of global change. Further, the acoustic signature of this life history transition (Oestreich, Fahlbusch, et al., 2020) can act as an acoustic ecosystem indicator (Hazen et al., 2019), and might be applied in future work to additional foraging hotspots in this population's summer-fall foraging range. Although the precise interplay of cues allowing for flexibility in blue whales' life history transitions remains unclear, the potential contributions of long-distance social cues for effective emergent sensing in the unique conditions of oceanic ecosystems warrants further investigation, and could perhaps be further evaluated using an agent-based modeling approach (Dodson et al., 2020). The influence of internal cues such as energetic stores on migration timing might be further explored as well using recent methodological advances in assessing individual whales' body condition (Burnett et al., 2019). Our findings establish the basis for investigating the roles of such external and internal cues in blue whale migrations, and for extending 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. Timing of blue whale song presence and life history transition in each year of the study period. Song peak is defined as the date of the annual maximum call index (CI, 15-day running mean). Song presence is defined as the all dates with 15-day running mean CI ≥ 1.01. Transition to southward migration is defined by the significant drop in CI_{night}:CI_{day} (see Section 2.2 of the main text for more detail). Yearday values > 365 (or 366 in the 2016 leap year) indicate persistence of song or behavioral transition into the following calendar year. *Note: yearday 211 was the start of acoustic recordings in 2015.

Year	**Song peak** (yearday)	**Song presence** (first-final; yearday)	**Transition to southward migration** (median; yearday)	**Transition to southward migration** (first-final; yearday)
2015	268	211*-351	268	248-287
2016	302	232-392	278	256-299
2017	307	189-378	294	231-357
2018	293	191-364	336	322-349
2019	315	207-392	326	296-355
2020	310	196-394	354	340-367

Table S2. 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	$\mathrm{BEUTI}_{\mathrm{STI}}$ (yearday)	$\mathrm{BEUTI}_{\mathrm{MAX}}$ (yearday)	$\mathrm{BEUTI}_{\mathrm{END}}$ (yearday)	$\mathrm{BEUTI}_{\mathrm{TUMI}}$ (mmol/m/s)	$\mathrm{BEUTI}_{\mathrm{LUMI}}$ (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

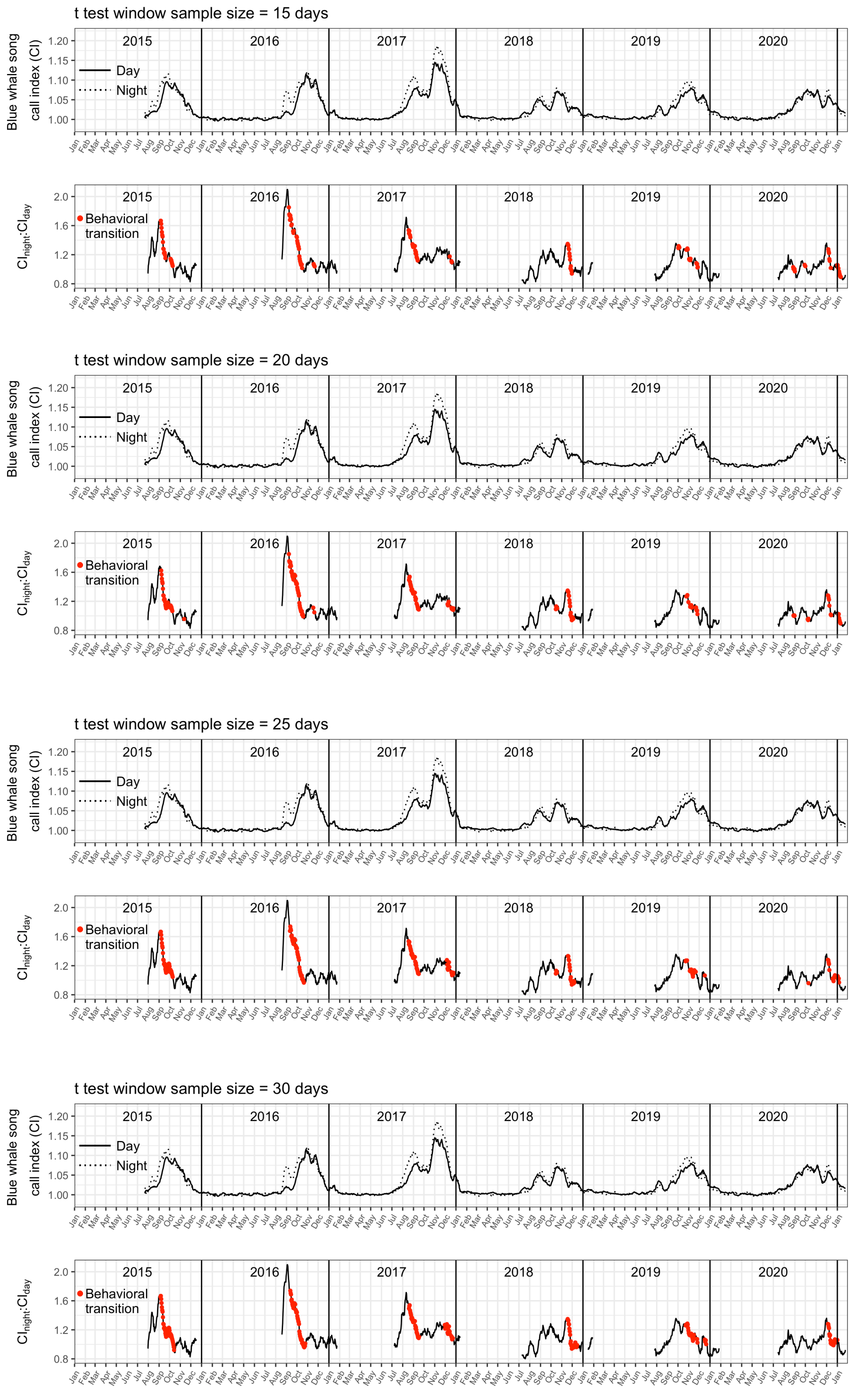

Figure S1. Statistical definition of behavioral transition, comparing a range of sample sizes. Dates of significant decrease in $\mathrm{CI_{night}:CI_{day}}$, indicative of the population-level behavioral transition from foraging to migration, are indicated by red dots. These periods of significant decrease in $\mathrm{CI_{night}:CI_{day}}$ were determined using one-sided t-tests for each day of the time-series, comparing samples comprised of the windows immediately preceding and following a given day.

A range of sample sizes for these t-tests were explored, as indicated above each panel. Subtle differences in the derived period of behavioral transition are apparent at different sample sizes—for example, smaller sample sizes (15-25 days) indicate very brief periods of behavioral transition in 2020 which precede the much more precipitous and persistent drop in $CI_{night}:CI_{day}$ apparent in December 2020. Sample size = 30 days (final panel of this figure) was chosen as the statistical definition of the behavioral transition for all subsequent comparisons of timing of behavioral transition and oceanographic phenology because (1) this definition identifies the most precipitous and persistent drops in $CI_{night}:CI_{day}$; and (2) this definition represents a more conservative estimate of which drops in $CI_{night}:CI_{day}$ indicate the annual population-level life history transition from foraging to migration.

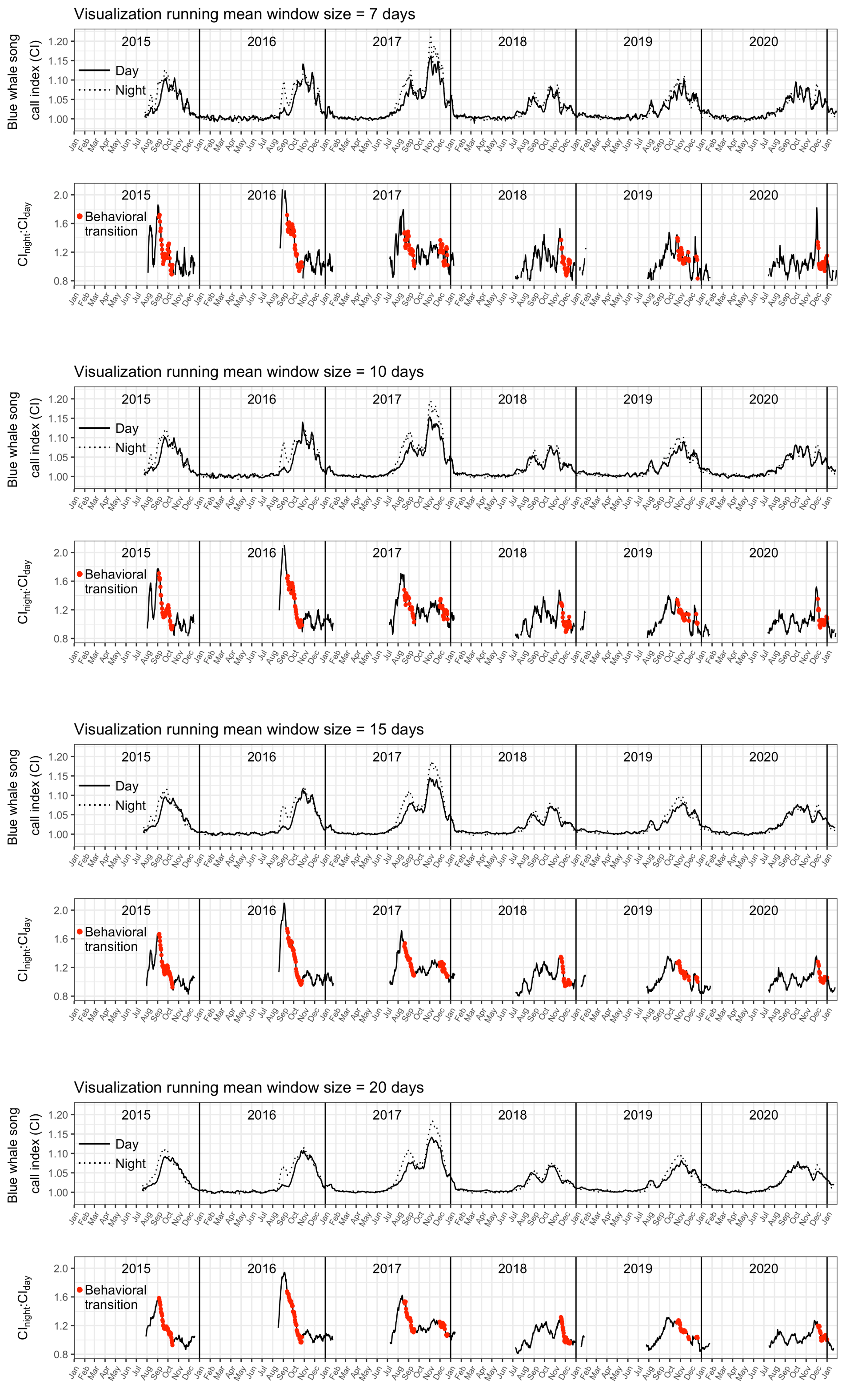

Figure S2. Visualization of CI and CI$_{night}$:CI$_{day}$ using a range of running mean window sizes. T-test window size = 30 days (see Figure S1; used for defining behavioral transition) for all panels. Dates of significant decrease in CI_{night}:CI_{day}, indicative of the population-level behavioral transition from foraging to migration, are indicated by red dots. Main text Figure 2 uses the 15-day running mean window size for visualization of CI and CI_{night}:CI_{day} to provide a detailed view of the significant intra-seasonal variability in these acoustic metrics without obscuring the clearest drops in CI_{night}:CI_{day} due to fine-temporal-scale (i.e. on the scale of days) noise in CI. While the 15-day window was chosen for visualization in Figure 2, this choice has no impact on the statistical definition of the significant drop in CI_{night}:CI_{day} (indicative of the population-level transition from foraging to migration), as unfiltered daily CI_{night}:CI_{day} values are used in this statistical determination of the behavioral transition.

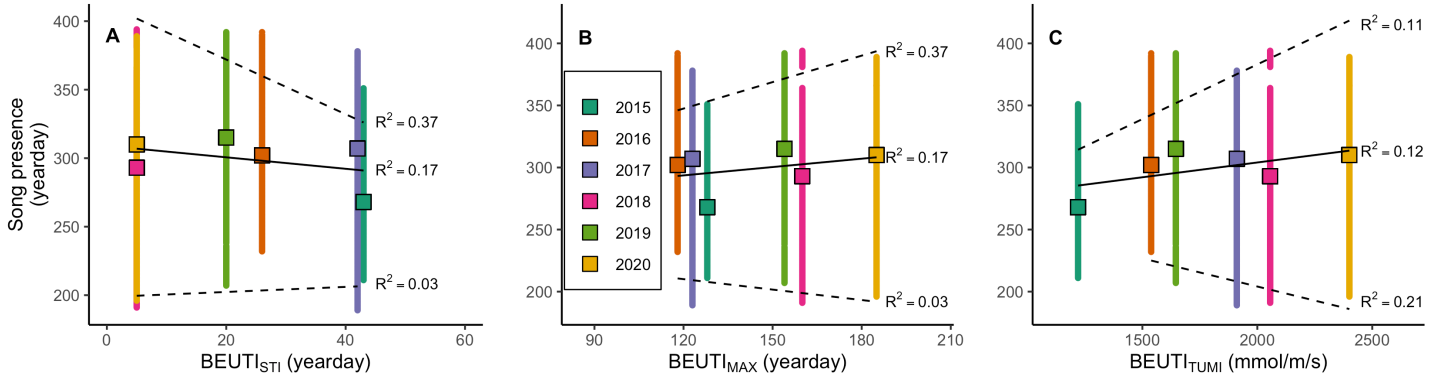

Figure S3. Relationship between blue whale song presence and metrics of biologically effective upwelling phenology (see also Figure 4, main text). Upwelling phenology metrics are summarized for 37° N. Blue whale song presence compared to **(A)** the date of seasonal upwelling onset; **(B)** the date of peak upwelling; and **(C)** total upwelling accumulated from the spring transition to the end of the upwelling season. In all 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 black lines show linear regression comparing the date of peak song to upwelling metrics; dashed black 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. Note: yearday 211 (the extent of the points displayed here for 2015) was the start of acoustic recordings in 2015. For this reason, the start date of song presence in 2015 is excluded from the linear regressions.

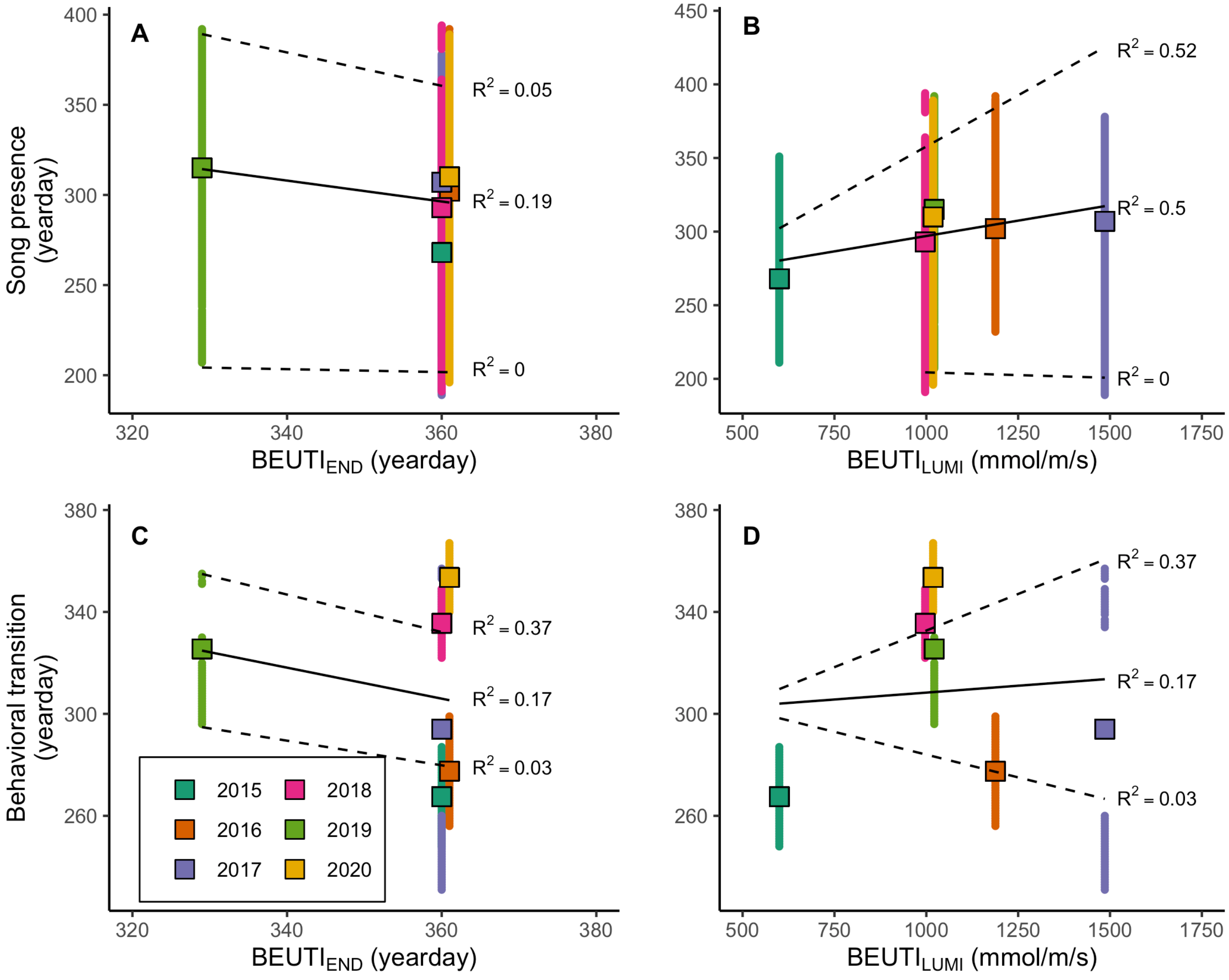

Figure S4. Relationship between blue whale vocal behavior and additional metrics of biologically effective upwelling phenology (see also Figure 4, main text). Upwelling phenology metrics are summarized for 37° N. (A-B) Song presence compared to upwelling phenology metrics including: **(A)** date of end of upwelling accumulation (BEUTI$_{\mathrm{END}}$); and **(B)** late season upwelling accumulation (BEUTI$_{\mathrm{LUMI}}$) from the peak to the end of the upwelling season. In panels (A-B), 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 ≥ 1.01). **(C-D)** Behavioral transition from foraging to migration compared to upwelling metrics including: **(C)** date of end of upwelling accumulation (BEUTI$_{\mathrm{END}}$); and **(D)** late season upwelling accumulation (BEUTI$_{\mathrm{LUMI}}$) from the peak to the end of the upwelling season. In panels (C-D), squares indicate the mean date between first and final dates of behavioral transition and points (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 black lines show linear regression comparing the peak of song presence (panels A-B) or the middle date of each year's behavioral transition (panels C-D) to upwelling metrics; dashed black lines show linear regression comparing the first and last days of song presence (panels A-B) or behavioral transition (panels C-D) to the same upwelling metrics. R^2 values are reported for each regression; none of the regressions displayed here had a significant F-statistic following the methods described in Section 2.4 of the main text. Note: yearday 211 (the extent of the points displayed here for 2015) was the start of acoustic recordings in 2015. For this reason, the start date of song presence in 2015 is excluded from the linear regressions.