Biophysical ecosystem variation shapes oceanic predator communication

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Abstract

Social information is predicted to be most valuable when pursuing patchy, ephemeral resources. Such resource dynamics emerge from biophysical coupling in the pelagic ocean, suggesting links from physical forcing to resource distribution to consumers' production of social information. We tested these hypothesized links using integrated observations of blue whale communication, distribution of their krill prey, and physical oceanographic forcing in their foraging habitat. Physical forcing modulated both prey availability and predator communication across nested temporal scales. Interannually, stronger upwelling led to greater krill abundance and elevated production of blue whales' foraging-associated calls. At finer scale, episodic upwelling produced denser krill swarms and heightened production of foraging-associated calls. Blue whales' widely propagating calls thus function as reliable social indicators of patch quality in their vast, dynamic pelagic habitat. These findings demonstrate that biophysical coupling in the ocean shapes predator communication and provide insight into the ecological drivers of social information use.

Introduction

The pelagic ocean comprises the vast majority of Earth's habitable volume[1] and is characterized by physical dynamism and biological patchiness across spatiotemporal scales[2,3]. Resources are extremely non-uniformly distributed in oceanic ecosystems, aggregating in ephemeral hotspots of biological activity[4–6]. In contrast to terrestrial ecosystems, pelagic primary producers drift with the physical medium in which they live, clustering in space and time as a result of interactions between dynamic physical forcing and biological processes[7–12]. This coupling of physical forcing and resource distribution has become a central paradigm in pelagic ecology and is foundational to understanding the distribution of oceanic organisms across trophic levels[4–6,13,14].

Largely separately, advances in behavioral ecology theory have generated predictions about how spatiotemporal resource variation drives the use of social information[15,16] and the emergence collective sensing[17] in resource pursuit. Theoretical models indicate that the value and evolutionary stability of producing and using social information is highest when pursuing resources which are particularly non-uniform in space and ephemeral through time[18–20]. Integrating these theoretical predictions with long-recognized coupling of physical and ecological processes in pelagic ecosystems suggests fundamental links from physical forcing to prey distribution to predator communication in the ocean. For example, one might predict[21] that physical oceanographic conditions which generate ephemeral, high-quality prey patches would promote predators' production of social foraging information. Yet empirical tests of such hypotheses are challenged by limited capacity to make concurrent measurements of physical forcing, prey distribution, and predator communication at appropriate resolution and scale. This empirical challenge is magnified in pelagic ecosystems, which are fluid, vast in three dimensions, and largely opaque to direct human observation[22].

The California Current, a dynamic, highly productive Eastern boundary upwelling ecosystem, provides an ideal venue to fill this empirical gap and test these theoretical physical-biological-social links. Wind-driven upwelling of nutrient-rich waters into the sunlit surface layer is the dominant physical process driving biological dynamics across temporal scales in the California Current ecosystem[23–25]. At seasonal scale, cumulative upwelling drives a spring-summer peak in primary production, setting the biological stage for abundant and diverse consumers including krill and blue whales throughout summer and fall[24–26]. On the scale of days to weeks, upwelling can also drive episodic changes in the aggregative behavior of krill and other mid trophic species, leading to denser swarms during upwelling conditions[27,28].

Eastern North Pacific blue whales (*Balaenoptera musculus*) obligately forage on dense aggregations of krill (primarily *Euphausia pacific* and *Thysanoessa spinifera*[24]) in the California Current ecosystem during summer and fall. Blue whales' extreme size, lunge-filter feeding mechanism, and migratory, capital breeding life history strategy require exploiting ephemeral, dense krill swarms during a limited foraging season[29–31]. How they efficiently find high-quality (dense) prey patches in their vast, fluid foraging habitat remains unknown. Throughout their foraging season, blue whales produce abundant and widely propagating social information in the form of their high-amplitude, low-frequency calls. Two distinct social signals are produced: "song" and "D calls". Song is associated with reproduction[32–34] and facilitates blue whales' collective migratory departure from foraging grounds toward lower-latitude breeding grounds[35–37]. D calls have been associated with foraging[33,34,38,39], particularly in groups[21,32], though their specific function in social foraging remains unknown.

Here, we integrated detailed, concurrent, and persistent measurements of ocean physics and life to bridge understanding of pelagic ecology from physical forcing to predator communication. We implemented an autonomous, integrated observing system (Figure 1) which provided detailed measurements of physical forcing (upwelling), prey availability (krill swarm local density and total biomass), and predator communication (blue whales' production of foraging-associated D calls and reproduction-associated song). Persistent sampling across two foraging seasons (2022-2023) enabled testing of predictions across nested temporal scales under the hypothesis that physical forcing shapes both resource distribution and consumers' production of social information. Specifically, we tested the predictions that stronger upwelling conditions correlate with greater krill prey availability and higher rates of foraging-associated call production by blue whale predators at both seasonal scale and the episodic scale (days-weeks) of upwelling events.

Materials and methods

Study design and instrumentation

We conducted this study using a network of seafloor and sea surface sampling platforms in outer Monterey Bay, CA, USA over August 16 – November 30 of both 2022 and 2023. This sensing network included four platforms (Figure 1). A mooring (platform 1 in Figure 1A) deployed at 122° W, 36.75° N provided hourly measurements of water column salinity using a string of Sea-Bird SBE 37 IM MicroCAT Conductivity, Temperature, Depth (CTD) sensors at 11 depths from 1-300 m. An autonomous surface vehicle (platform 2) equipped with a dual-frequency echosounder system sampled a circular transect centered on 122.0973° W, 36.8008° N with a radius of 1.5 km, providing measurements of prey distribution, abundance, and coarse taxonomic composition. A seafloor mooring (platform 3) deployed at 122.107° W, 36.794° N, bottom depth 300 m, was equipped with a SoundTrap ST600 underwater acoustic recorder, which sampled continuously at 48 kHz. This mooring also housed an upward-facing acoustic Doppler current profiler (ADCP) which sampled with an acoustic frequency of 150 kHz at 5 second intervals to provide a backscatter-based proxy for total forage community biomass. Finally, we leveraged the Monterey Accelerated Research System cabled seafloor observatory (platform 4), located at 122.186° W, 36.713° N, depth 891 m, which housed an icListen HF omnidirectional hydrophone sampling continuously at 256 kHz. This persistent, long-term passive acoustic monitoring dataset has previously provided a useful regional view on the acoustic behavior of various pelagic predators[40,41].

Physical oceanography

Coastal upwelling, the dominant physical oceanographic driver of biological productivity in this ecosystem, decreases temperature and increases salinity in surface waters[42]. Because salinity is the conservative tracer of upwelling, we calculated salinity based on hourly data from the CTD mooring. For each day of our summer-fall study periods, we calculated daily, depth-dependent salinity anomalies as standard deviations relative to the mean computed across the 2022 and 2023 study periods (Figure 1B). For each day, we also calculated a 10-day running mean of salinity anomalies centered on the focal day. We used this metric to identify the transition between upwelling and post-upwelling physical regimes in each study year, defining this transition as the first day of each study year with a negative smoothed salinity anomaly.

To quantify cumulative seasonal upwelling across the full upwelling season in which each of our summer-fall study periods were embedded (Figure 2A), we used the coastal upwelling transport index[25] (CUTI) at 37° N. CUTI is an estimate of vertical transport into the surface mixed layer, and is calculated from a data-assimilating regional ocean model[25]. We calculated the cumulative sum of CUTI at daily resolution for each year of our study (2022-2023) in comparison to the long-term (1988-present) climatological mean, 5th percentile, and 95th percentile for each day of the year (Figure 2A).

To make statistical comparisons of upwelling between years (Figure 2B; CUTI) and between physical oceanographic regimes within years (Figure 4A; *in situ* salinity anomaly), we conducted Wilcoxon rank sum tests using daily values.

Prey dynamics

Acoustic backscatter data from prey were measured from two platforms: continuous measurements from the moored ADCP and multiple, multi-week circular-transect surveys in each sampling year using a multi-frequency scientific echosounder carried by an autonomous surface vessel. The autonomous vehicle, a Wave Glider, is a small wave-propelled platform consisting of two parts – a surface float and a submerged glider that are attached by a flexible tether[43]. The vehicle exploits wave energy to provide forward propulsion, typically at a speed of ~0.5 m/s during these deployments. The Wave Glider carried a Simrad EK80 Wideband Autonomous Transceiver and two 7˚ single beam transducers mounted to the bottom of the surface float, one at 70 kHz and one at 120 kHz. Echosounder data were collected at a ping rate of 0.5 Hz to a maximum depth of 800 m using a 1.024 ms long, narrowband pulse. Prior to sampling, each was calibrated using a 38.1 mm tungsten carbide standard reference sphere.

Echosounder data were cleaned and motion corrected using Echoview v14.1 software. The average area scattering at 120 kHz ($m^2 nmi^{-2}$), a linear proxy of total mid-trophic biomass, was calculated each day over all daylight hours (one hour after sunrise to one hour before sunset, as defined by the US Naval Observatory). The combination of frequencies allows coarse taxonomic classification of acoustic scatterers over the upper 200 m of the water column, with scattering at least 3 dB higher at 120 kHz relative to 70 kHz indicating zooplankton and a flatter frequency response indicating fish[44]. To further isolate krill based on their grouping behavior, scattering data at 120 kHz that was consistent with zooplankton was filtered, retaining only aggregations, defined as contiguous areas of scattering at least 5 pings long by 5 bins (50 cm) high. We calculated the daily mean backscatter (dB re $1m^{-1}$) within these features, providing a proxy of local krill density within aggregations on a logarithmic scale.

To make statistical comparisons of these metrics between years (Figure 2C) and between physical oceanographic regimes within our summer-fall study periods (Figure 4B), we conducted Wilcoxon rank sum tests using daily values.

Predator communication

We quantified blue whales' production of social information via analysis of continuous passive acoustic monitoring (PAM) data. Individual D calls were identified in PAM data via manual inspection using RavenPro v1.6.4 software. We implemented a widely used and well-validated "call index" method[28,35,36,45-47] to quantify blue whale song intensity in the regional soundscape. This acoustic energy-based metric reliably quantifies both individual and overlapping song calls produced by many "chorusing" individuals[35,47].

These methods enabled calculation of a daily, normalized ratio of D calls relative to song production (Figure S2). This metric accounts for the potential confounding effect of shifts in blue whale density alone driving changes in D call production, by instead quantifying the relative production of each social information type regardless of regional density (see Supporting Information for details). We used daily values of this metric in Wilcoxon rank sum tests for comparisons between years (Figure 2D) and physical oceanographic regimes (Figure 4C).

Finally, from platform 4 (Figure 1A) we calculated the night:day ratio of song production across each year of our study at daily resolution to estimate timing of blue whales' population-wide behavioral transition from foraging to southward breeding migration as in[36]. This shift in the diel patterning of song coincides with the cessation of foraging and onset of breeding migration, as previously validated via on-whale bio-logging measurements[35].

Results

Physical forcing mediates inter-annual variation in seasonal prey abundance and predator communication

Our 2-year study period captured strong interannual variation in physical forcing, prey abundance, and predator communication (Figure 2). Cumulative upwelling transport in 2022 exceeded the 95th percentile of historical annual records (1988-2023), whereas cumulative upwelling in 2023 fell below the long-term annual mean (Figure 2A). This interannual difference in physical forcing was reflected at daily scale, with 2022 characterized by significantly higher daily upwelling transport values relative to 2023 (Figure 2B). We observed similar differences in prey abundance between years, with significantly higher values of scattering strength from fluid-like acoustic scatterers (a proxy for krill biomass; see Materials and methods) in 2022 compared to 2023 (Figure 2C). We also found significant interannual differences in predator social behavior, with blue whales producing more foraging-associated D calls in 2022 relative to 2023 in terms of both total D call count (1244 in 2022 vs. 359 in 2023) and D calls relative to reproduction-associated song (D call:song normalized ratio; Figure 2D). Even when restricting the interannual comparison only to the upwelling period in each year, blue whales produced significantly more D calls relative to song in 2022 than in 2023 (Figure S1). The onset of southward breeding migration in this blue whale population (inferred from shifting diel song patterns previously attributed to the shift from foraging to migration[35,36]) also occurred later in 2022 (Figure 2A), indicating an extended foraging season relative to 2023. In summary, compared to 2023, blue whales produced more foraging-associated calls in 2022—a year characterized by greater seasonal cumulative upwelling, higher krill prey abundance, and an extended foraging season (Figure 2).

Physical forcing mediates intra-annual variation in episodic prey density and predator communication

We also observed strong, concurrent shifts in physical forcing, prey density, and predator communication within each year of the study (Figure 3). In 2022, the upwelling physical regime persisted until October 4 (Figure 3A-B). This early October transition to post-upwelling physical conditions coincided with decreases in total forage species backscatter (including krill, other zooplankton, and fish; Figure 3C), krill biomass (Figure 3D), local density of krill within aggregations (Figure 3E), and blue whales' relative production of foraging-associated social signals (Figure 3F). Although the multi-frequency echosounder system (Figure 1C) did not sample for the second half of October 2022, the continuous total forage backscatter metric (Figure 3C; representative of the broader forage assemblage, including krill, other zooplankton, and fish) remained low during this period, indicating that krill biomass remained low throughout October. Each of these prey and predator social behavior metrics increased again briefly in mid-November 2022 (Figure 3C-F).

In 2023, the upwelling physical regime persisted only until September 11 (Figure 3A-B). The 2023 transition between upwelling and post-upwelling physical regimes was not clearly associated with changes in krill biomass (Figure 3D), as this metric was low throughout the 2023 study period (Figure 2C) in correspondence with weaker seasonal cumulative upwelling (Figure 2A). Even with low total krill abundance, however, the highest densities of krill within aggregations in 2023 were observed during the upwelling physical regime (Figure 3E). Blue whales' relative production of foraging-associated social signals also dropped following the cessation of upwelling, with many days of zero D calls occurring after September 11 (Figure 3F). However, similar to 2022, some days of elevated D call activity and high densities of krill within small patches occurred after the end of the upwelling physical regime in 2023.

Examining the physical oceanographic regimes pooled across both years, we found significant differences in both krill swarm local density and blue whales' relative production of foraging-associated social signals depending on the physical oceanographic regime (Figure 4). Krill swarm local densities were significantly higher during periods of upwelling relative to the post-upwelling physical regime (Figure 4B). Similarly, blue whales' production of foraging-associated D calls relative to reproduction-associated song was significantly higher during periods of upwelling relative to the post-upwelling physical regime (Figure 4C). In both years, the drop in D call:song ratio following the shift in physical regime was attributable to a decrease in D call production rather than an increase in song production (Figure S2).

Discussion

Social information plays a keystone role in behavioral ecology and evolution[48-50], enabling groups to collectively sense and track resources in biophysically dynamic ecosystems[51,52]. Connecting the links between physical forcing, resource distribution, and social communication can therefore advance understanding of when, why, and how social information use and emergent collective behaviors evolve in such environments[20]. Social foraging theory predicts that the value and production of social information depend on spatiotemporal resource dynamics[15,16], conferring particular advantage in pursuit of patchy, ephemeral resources[18,19]. These resource dynamics are characteristic of pelagic ecosystems[4–6], where physical oceanographic forcing strongly influences ecological patterns and interactions[7–11]. Integrating these theoretical concepts implies historically underexplored connections between physical forcing and the social information produced by pelagic predators. Our results provide strong empirical evidence for these hypothesized links, showing that physical forcing shapes prey distribution and, in turn, predator communication.

Across temporal scales, variation in physical oceanographic forcing mediated blue whales' social signaling behavior via corresponding changes in the abundance and density of their obligate krill prey. Interannually, blue whales produced more foraging-associated calls relative to other social signals when greater seasonal upwelling of nutrients facilitated higher prey abundance (Figure 2). Within years, blue whales produced more foraging-associated calls relative to other social signals during upwelling periods characterized by locally higher prey patch density (Figures 3-4). These findings indicate that blue whales' widely propagating, foraging-associated D calls serve as reliable social indicators of high-density krill swarms in their vast and dynamic foraging habitat. More broadly, these results demonstrate that long-recognized connections between physical and ecological processes in pelagic ecosystems extend even to shaping predator communication.

At the scale of the largest predator on Earth, the challenges of foraging are magnified by extraordinary ecological and physiological constraints. To survive, reproduce, and undertake long-distance migrations, blue whales must find and consume enormous quantities of their obligate krill prey during a several-month foraging season in their vast, dynamic foraging habitat. Their lunge-filter-feeding mechanism and immense body size require targeting dense krill swarms[29], which are both spatially patchy and temporally ephemeral in the eastern North Pacific[27,53,54]. We found that both seasonal krill abundance and episodic swarm density are tightly linked to physical oceanographic forcing. At seasonal scale, stronger cumulative upwelling led to greater krill biomass (Figure 2), likely due to enhanced primary production from nutrient enrichment and subsequent trophic transfer to primary consumers such as krill[24]. At finer temporal scale, local krill swarm density increased during upwelling conditions (Figure 3D; Figure 4B), likely arising from an combination of physical aggregation at oceanographic fronts[54] and behavioral responses such as swarming to avoid predation by more common raptorial predators[27,55] or offshore advection[56]. Yet this same swarming behavior increases susceptibility to predation by lunge-feeding blue whales, meaning that these massive predators exploit a “rare enemy effect”[57] to efficiently forage on dense krill swarms.

Blue whales co-occur with[28,58] and feed most frequently within[31] the physical oceanographic features in which krill most densely aggregate, but it remains unclear how they effectively locate and track these dense, ephemeral prey patches. Theoretical models predict that nonlocal information (such as widely propagating acoustic signals) should be particularly valuable for highly mobile consumers (such as blue whales) pursuing patchy, ephemeral resources (such as krill swarms in this upwelling ecosystem)[59]. Blue whales produce abundant nonlocal social information in their foraging habitat: their calls travel over tens to hundreds of kilometers[35] and dominate the low-frequency soundscape throughout their summer-fall foraging season[35,45,46,60]. We find that D calls in particular, which have been associated with foraging in groups[21,32], are most prevalent during periods of high-density krill patches arising from upwelling (Figures 3-4) and thus convey valuable nonlocal social information for locating ephemeral patches of plenty in a dynamic preyscape.

Why do blue whales produce this valuable social information? Whereas the value of this information to the receiver is clear, the incentives for producing such information are not as readily apparent: signaling to indicate high quality prey patches invites competition from conspecifics. This competition cost might be mitigated by the ephemeral nature of high-density krill swarms[21], which are unlikely to be depleted by predators before the swarm disperses[21,27,61]. Even in the absence of competition costs, some benefit to the signaler—either direct or indirect—must exist for this behavior to evolve. Kin selection[62] appears unlikely, as the D call signal is indiscriminate as to who specifically receives this information. Apparent cooperation between non-kin resulting from benefits to both signaler and receiver[63,64] provides a more likely explanation. Attracting conspecifics to areas of high krill swarm density could be beneficial to both signalers and receivers, increasing individual efficiency via collective sensing and tracking of transient prey patches across a vast and variable foraging habitat. This explanation is consistent with theoretical predictions in fluid ecosystems[20] and empirical evidence from cliff swallows, in which social signaling to collectively track wind-advected insect swarms enhances foraging efficiency[65] and predictability[66]. Blue whale D calls may function similarly, facilitating collective sensing and tracking of the dense krill swarms that arise during upwelling conditions.

Alternative hypotheses for the function of these signals also remain possible. D calls could act as competitive signals within foraging aggregations or perhaps even influence krill swarming behavior directly (D calls are within the typical hearing range of crustaceans[67]). Testing these functional hypotheses will require further integration of individual- and group-level behavioral observations[68] in future work, as in previous studies which revealed the role of song in blue whales' collective migration[35–37]. Regardless of their precise function, D calls consistently coincide with dense krill aggregations, indicating that they provide reliable, widely propagating social information about high-density prey patches in blue whales' dynamic foraging habitat.

Taken together, these findings reveal a cascade linking physical oceanographic processes, prey dynamics, and predator communication across temporal scales. By showing that physical forcing shapes both resource distribution and consumers' production of social information, this study extends established concepts of physical–ecological coupling in pelagic ecosystems to include predator communication. This empirical discovery integrates theoretical concepts from oceanography, social foraging, and behavioral ecology, providing evidence that physical variability can structure not only the resource landscape but also the social information landscape. Such understanding of how biophysical variation mediates social information use is critical for elucidating the eco-evolutionary processes which give rise to collective sensing and behavior in dynamic ecosystems.

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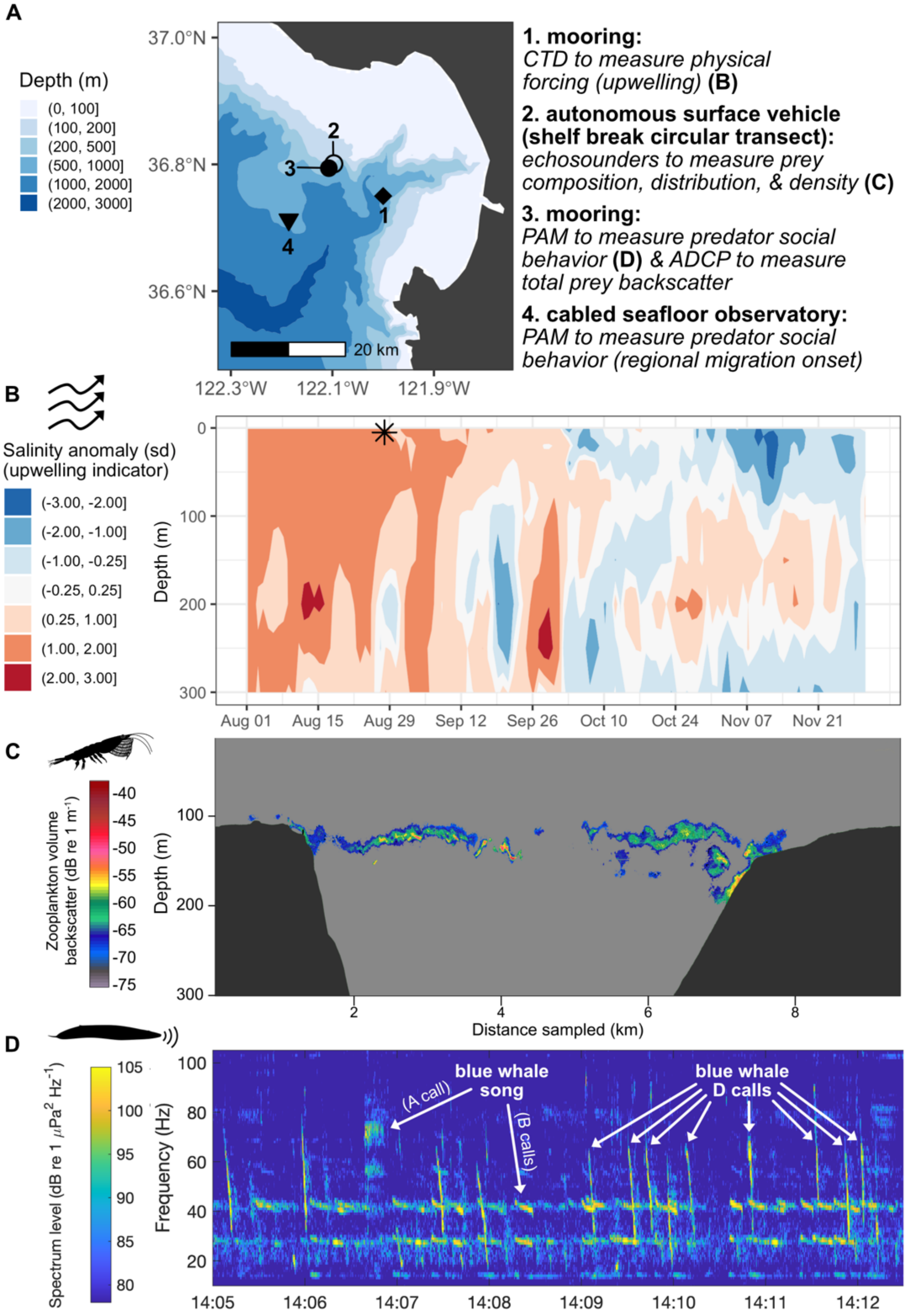

Figure 1. Persistent, concurrent observations of physical forcing, prey dynamics, and predator communication. **(A)** Study region and observing system. CTD = conductivity, temperature, depth; ADCP = acoustic Doppler current profiler; PAM = passive acoustic monitoring. **(B)** Time series (2022) of salinity anomaly measured at mooring 1 (positive anomaly indicates upwelling conditions). Asterisk indicates the day for which data are presented in panels C-D. **(C)** Krill patches measured along one circular transect of the autonomous surface vehicle carrying a downward-facing multi-frequency echosounder system (platform 2). **(D)** Blue whale social signals detected in passive acoustic data from platform 3.

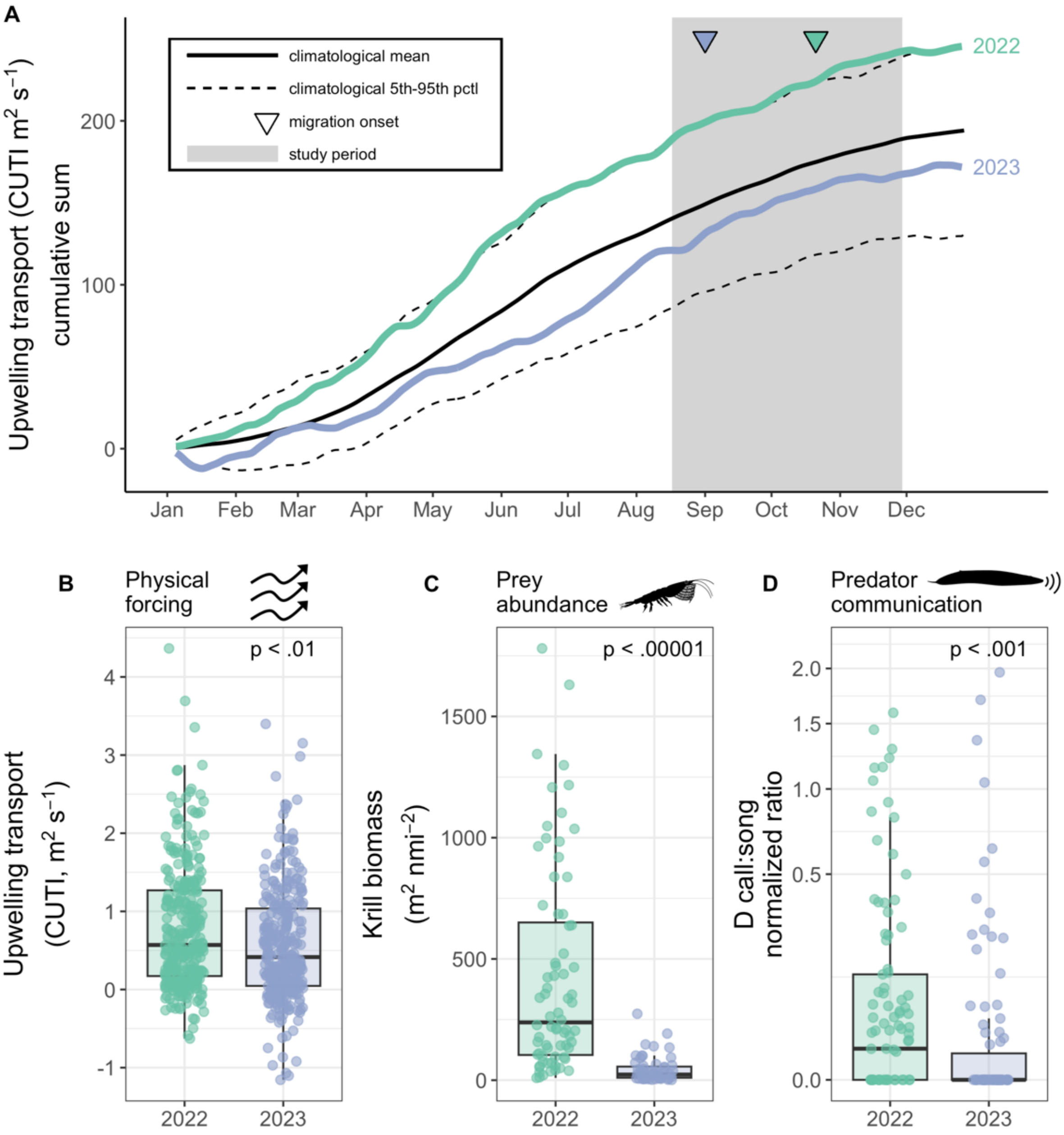

Figure 2. Interannual variation in seasonal physical forcing, prey dynamics, and predator communication. (A) Colored lines indicate the cumulative sum of physical upwelling transport (10-day running mean) during each year of the study. Solid and dashed black lines indicate the climatological mean and 5th-95th percentile of cumulative upwelling over 1988-2023. Colored triangles indicate the onset of southward breeding migration[36]. Gray shading indicates the time period in both study years over which the network of observing platforms (Figure 1) sampled. **(B)** Interannual comparison of daily upwelling transport values during the upwelling season. **(C)** Interannual comparison of daily zooplankton biomass values during the study period. **(D)** Interannual comparison of daily blue whale social signal production, calculated as the normalized ratio of D calls relative to song. In (B-D), the p-value is shown for a Wilcoxon rank sum test for significant differences between the distributions from each year. Boxplots indicate the median (center line), 25th-75th percentile (box), and 1.5 times the interquartile range (whiskers), with daily data plotted as points.

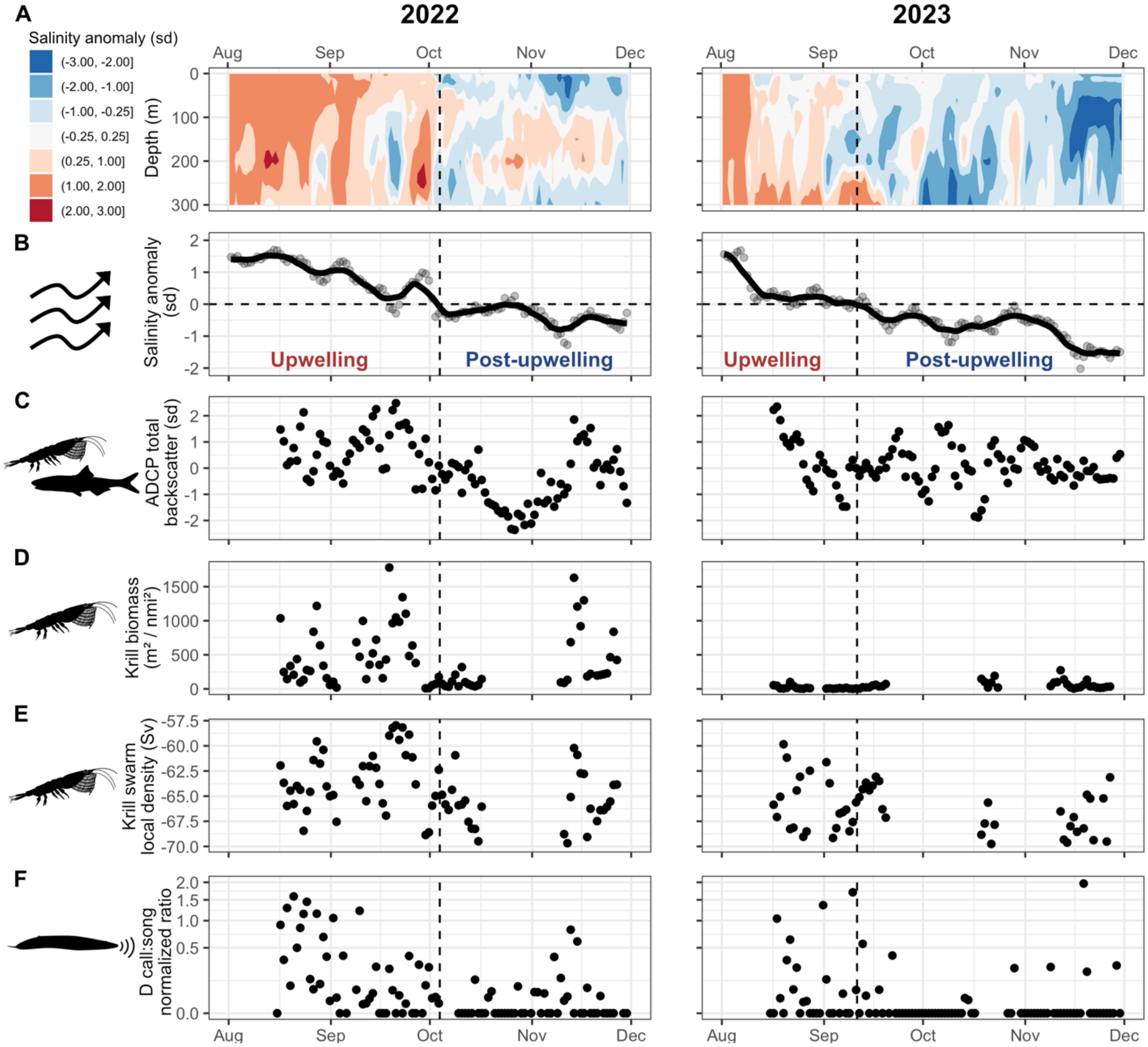

Figure 3. Time series of physical forcing, prey dynamics, and predator communication. (A) Salinity anomaly, the conservative physical tracer of upwelling, shown over depth and time. **(B)** Depth-averaged salinity anomaly, including both daily mean (points) and 10-day running mean (line). **(C)** Daily total backscatter anomaly measurements made via acoustic Doppler current profiler (ADCP), which does not discriminate between fish and zooplankton biomass. **(D)** Daily echosounder-measured krill biomass. **(E)** Daily echosounder-measured krill local density (Sv in dB re 1 m^{-1}). **(F)** Daily blue whale social signal production, calculated as the normalized ratio of D calls relative to song. The physical regime shift from upwelling to post-upwelling in each year is indicated by the vertical dashed line across all panels (see Methods).

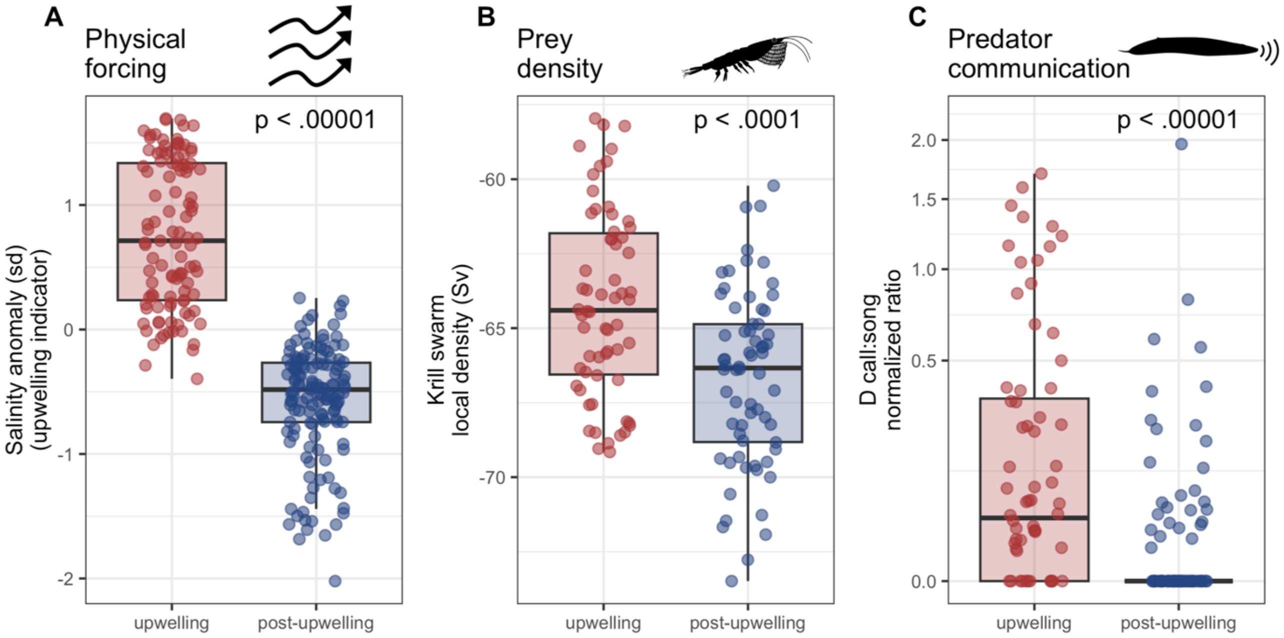

Figure 4. Physical regimes mediate prey density and predator communication. (A) Distribution of daily depth-averaged salinity anomaly values (standard deviations from the mean) binned by physical regime. **(B)** Distribution of daily krill swarm local densities binned by physical regime. **(C)** Distribution of daily blue whale D call:song normalized ratio values binned by physical regime. In each panel, daily data are aggregated across both study years, and the p-value is shown for a Wilcoxon rank sum test for significant differences between the distributions from each physical regime. Boxplots indicate the median (center line), 25th-75th percentile (box), and 1.5 times the interquartile range (whiskers), with individual daily data plotted as points.

Supporting Information

Biophysical ecosystem variation shapes oceanic predator communication

Additional information on calculation of the normalized D call:song ratio.

The normalized D call:song ratio was calculated for each day (*t*) of the study period by first normalizing each component (D calls per day and daily song call index) to the interval [0, 1] using their respectively observed minimum and maximum values, then dividing these normalized values, as in equations 1-3:

$$(1)\quad Dcall_{norm}(t) = \frac{Dcall(t) - Dcall_{min}}{Dcall_{max} - Dcall_{min}}$$

$$(2)\quad Song_{norm}(t) = \frac{Song(t) - Song_{min}}{Song_{max} - Song_{min}}$$

$$(3)\quad Dcall : song\ (t) = \frac{Dcall_{norm}(t)}{Song_{norm}(t)}$$

Supporting Information Figures

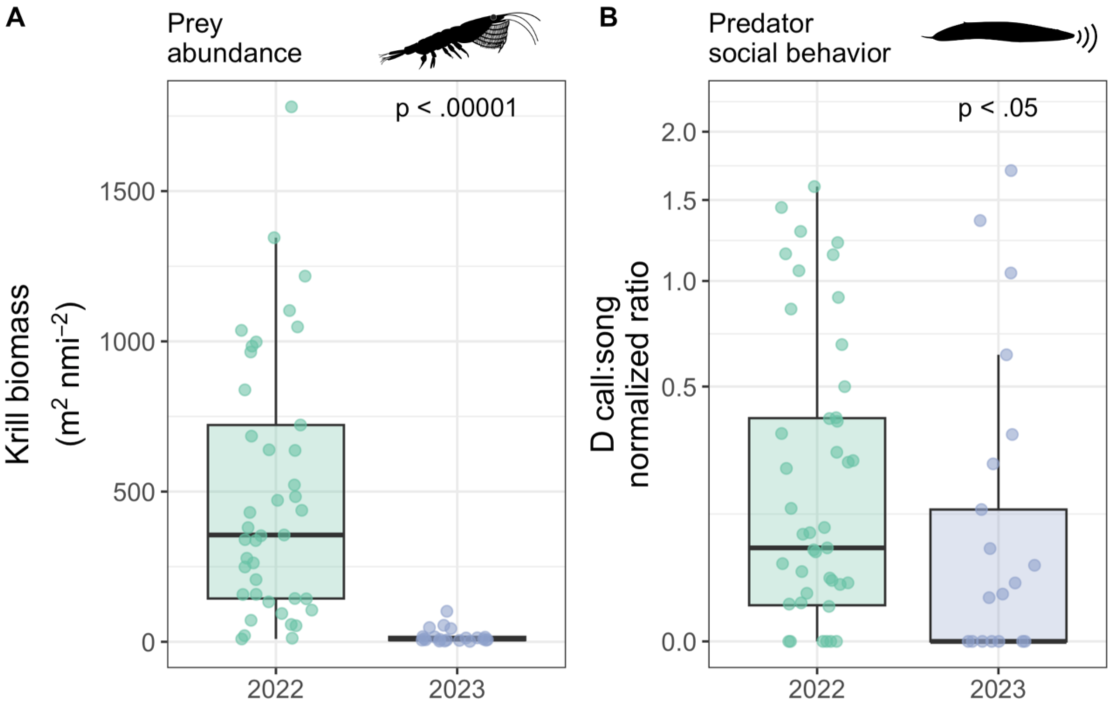

Figure S1. Interannual comparisons of prey abundance and predator social behavior restricted to each year's upwelling period. As in Figure 2 of the main text, but including only days from the upwelling physical regime from each year (defined in Figure 3 of the main text). **(A)** Interannual comparison of daily zooplankton biomass values. **(B)** Interannual comparison of daily blue whale social signal production, calculated as the normalized ratio of D calls relative to song. In (A-B), the p-value is shown for a Wilcoxon rank sum test for significant differences between the distributions from each year. Boxplots indicate the median (center line), 25th-75th percentile (box), and 1.5 times the interquartile range (whiskers), with daily data plotted as points.

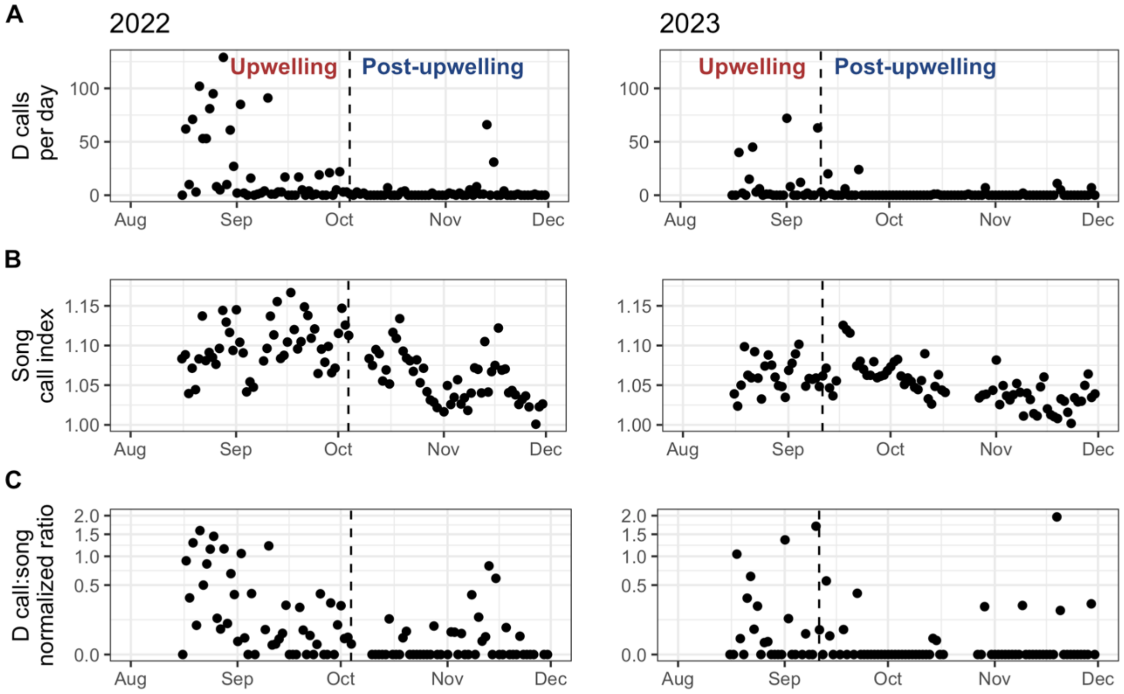

Figure S2. Time series of component metrics comprising the D call:song normalized ratio over the study period in each year. (A) D calls per day. **(B)** Song call index. **(C)** Normalized ratio of D calls relative to song, as presented in Figure 3 of the main text and described in Equations 1-3 of the Supplementary Information.