# Biophysical ecosystem variation shapes oceanic predator communication

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# Abstract

Social information is predicted to be most valuable to consumers when they pursue patchy, ephemeral resources. Such resource dynamics emerge from coupling of physical and biological processes in the pelagic ocean. Integrating these paradigms from behavioral ecology and oceanography motivates the hypothesis that physical oceanographic forcing shapes resource distribution, which in turn alters oceanic consumers' production of social information. We tested these hypothesized physical-biological-social links using integrated observations of blue whale communication, the distribution of their krill prey, and physical oceanographic forcing in their foraging habitat. Physical forcing modulated both prey distribution and predator communication across nested temporal scales. Interannually, stronger upwelling led to greater krill abundance and more frequent detection of blue whales' foraging-associated type D calls. At finer temporal scale, stronger upwelling produced denser krill swarms and heightened production of blue whale D calls. Blue whales' widely propagating D calls correlate with high-quality foraging conditions and thus represent valuable social information for predators searching for patchy, ephemeral krill swarms in this vast, dynamic oceanic habitat. More broadly, these findings demonstrate that physical oceanographic forcing shapes predator communication by modulating the distribution of prey, providing insight into the biophysical drivers of social information use in Earth's largest living space.



**Keywords:** behavioral ecology, pelagic, predator-prey interactions, social foraging, collective behavior, social information, blue whale, krill, upwelling, biophysical interactions

# 1. Background

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[4-7]. 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[8-13]. 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[4–6,14,15].

Largely separately, advances in behavioral ecology theory have generated predictions about how spatiotemporal resource variation drives the use of social information[16,17] and the emergence of collective sensing (i.e., expanded, socially facilitated sensing beyond any individual's capacity alone)[18,19] 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[19–22]. Integrating these theoretical predictions with long-recognized coupling of physical and biological processes in pelagic ecosystems suggests fundamental links from physical forcing to prey distribution to predator communication in the ocean. For example, one might predict that physical oceanographic conditions which generate ephemeral, high-quality prey patches would promote predators' production of social foraging information[23]. Yet empirical tests of such predictions 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[24].

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 is the dominant physical process driving biological dynamics across temporal scales in the California Current ecosystem[25–27]. At seasonal scale, cumulative upwelling of nutrient-rich waters into the sunlit surface layer 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[26–28]. 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[29,30].

Eastern North Pacific blue whales (*Balaenoptera musculus*) obligately forage on dense aggregations of krill (primarily *Euphausia pacific* and *Thysanoessa spinifera*[26]) 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 an intensive foraging season[31–33]. 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[34–36] and facilitates blue whales' collective migratory departure from foraging grounds toward lower-latitude breeding grounds[37–39]. D calls have been associated with foraging[35,36,40,41], particularly in groups[23,34], though their specific function in social foraging remains unknown.

Here, we integrate detailed, concurrent, and persistent measurements of ocean physics and life to bridge understanding of pelagic ecology from physical forcing to prey distribution to predator communication. We implemented an autonomous, integrated observing system (Figure 1) which provided detailed measurements of physical forcing (upwelling), prey distribution (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.

# 2. Methods

## 2.1 Study design and instrumentation

We conducted this study using a network of seafloor and sea surface sampling platforms in outer Monterey Bay, California, 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 to provide local passive acoustic detection of blue whales and other species. 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 continuous 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[42,43], and in this study enabled quantification of blue whale song presence in the regional soundscape (see section 2.4 for details).

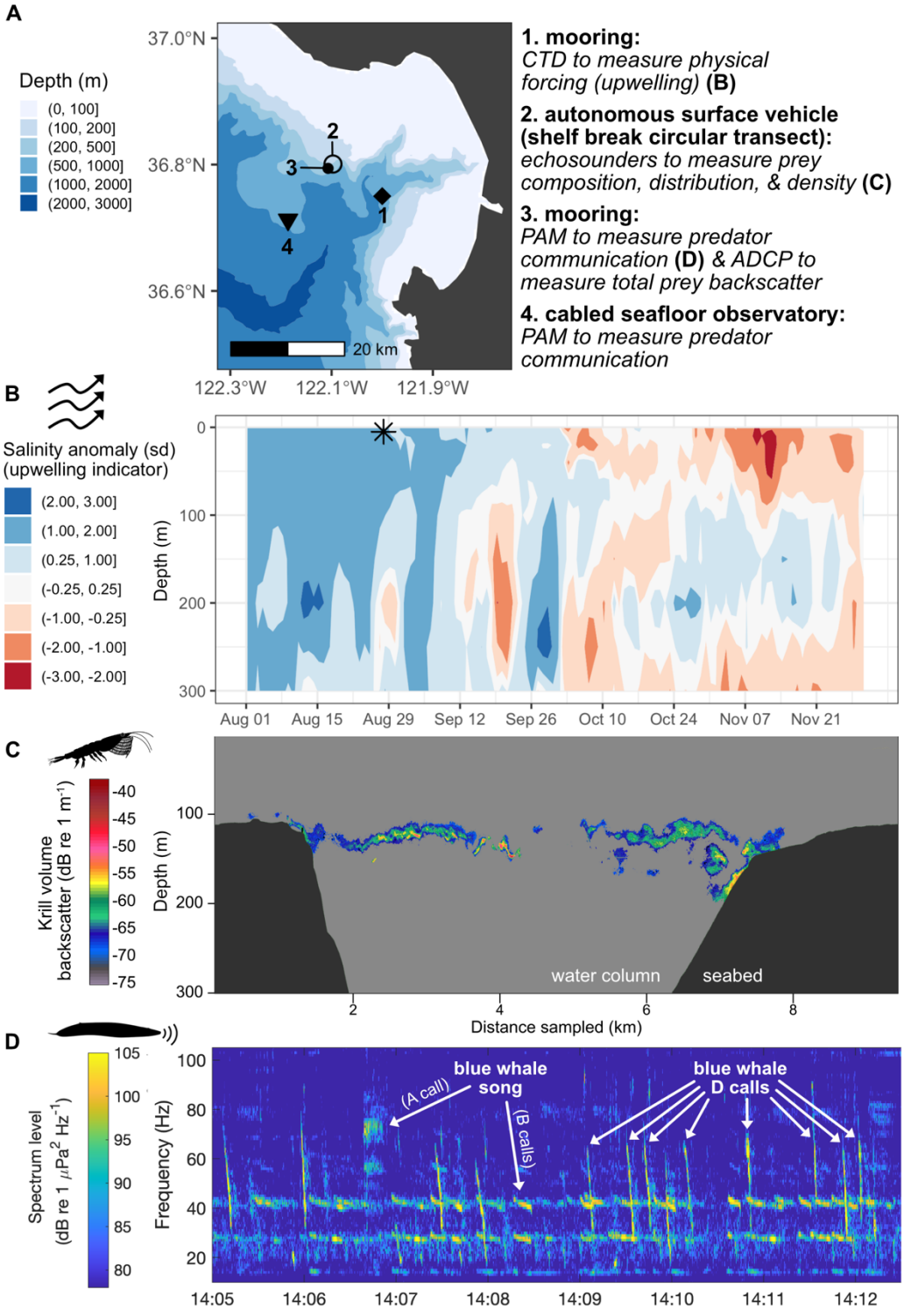


**Figure 1. Persistent, concurrent observations of physical forcing, prey dynamics, and predator communication. (A)** Study region and observing system. CTD = conductivity, temperature, depth; ADCP = acoustic Doppler current profiler; PAM = passive acoustic monitoring. **(B)** Time series (2022) of salinity anomaly measured at mooring 1 (positive anomaly indicates stronger 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 song and D calls detected in passive acoustic data from platform 3.

## 2.2 Physical oceanography

Coastal upwelling, the dominant physical oceanographic driver of biological productivity in this ecosystem, decreases temperature and increases salinity in surface waters[44]. Because salinity is the conservative tracer of upwelling, we calculated salinity based on hourly data from the CTD mooring (Platform 1; Figure 1). 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. This approach provided a local, *in situ* indicator of the physical oceanographic regime. We used this metric to identify the transition between *strong upwelling* and *weak upwelling* physical oceanographic 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[27] (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[27]. 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, 5$^{th}$ percentile, and 95$^{th}$ percentile for each day of the year (Figure 2A).

## 2.3 Prey dynamics

Acoustic backscatter data from prey were measured from two platforms, providing continuous total estimates of prey abundance and periodic assessments of prey composition and density. Continuous measurements of total backscatter were made from a moored ADCP (on Platform 3; Figure 1). ADCP backscatter was averaged over the typical depth range of blue whale foraging in the region (75 – 250 m[45]) for each day. Because the ADCP does not provide calibrated estimates of backscatter, we used log-transformed daily values to calculate daily total backscatter anomalies at daily resolution (Figure 3C) as the number of standard deviations relative to the mean for each sampling year.

A multi-frequency scientific echosounder carried by an autonomous surface vehicle (Platform 2; Figure 1) provided estimates of the abundance and local density of krill during multiple, multi-week circular-transect surveys in each sampling year. 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[46]. 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. The echosounder-bearing Wave Glider completed approximately 5 laps of the sampling circle (Figure 1A) per day, providing robust daily-resolution metrics representative of shelf break prey conditions in outer Monterey Bay[29,30].

Echosounder data (Figure 1C) were cleaned and motion corrected using Echoview v14.1 software. The average area scattering at 120 kHz ($m^2nmi^{-2}$), 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[47]. 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 2B) and between physical oceanographic regimes within our summer-fall study periods (Figure 4A), we used generalized least-squares regression models with a first-order continuous autoregressive correlation structure to account for temporal autocorrelation in daily observations.

### 2.4 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 from platform 3 (Figure 1) via manual inspection using RavenPro v1.6.4 software. We implemented a widely used and well-validated "call index" method[30,37,38,48–50] to quantify blue whale song intensity in the regional soundscape as recorded from platform 4 (Figure 1). This acoustic energy-based metric reliably quantifies both individual and overlapping song calls produced by many "chorusing" individuals[37,50].

These methods enabled calculation of a daily, normalized ratio of D calls relative to song production. 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 blue whale density (see Supporting Information for additional details). We used daily values of this metric in generalized least-squares regression models with a first-order continuous autoregressive correlation structure, enabling comparisons between years (Figure 2C) and physical oceanographic regimes (Figure 4B) while accounting for temporal autocorrelation in daily observations.

## 3. Results

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

Our study captured interannual variation in physical forcing, prey abundance, and predator communication (Figure 2). Cumulative upwelling transport in 2022 exceeded the 95$^{th}$ percentile of historical annual records (1988-2023), whereas cumulative upwelling in 2023 fell below the long-term annual mean (Figure 2A). We observed similar differences in prey abundance between years, with significantly higher values of a proxy for krill biomass (see Methods section 2.3) in 2022 compared to 2023 (Figure 2B). The metric of blue whale foraging call (D call) production relative to song production was only moderately higher during 2022 relative to 2023 (Figure 2C). However, D calls were much more frequently detected in 2022 relative to 2023 in terms of both

total D call count (1244 in 2022 vs. 359 in 2023) and the percentage of days with at least one D call detected (54.2% of sampling days in 2022 vs. 24.3% of sampling days in 2023). In summary, compared to 2023, blue whales produced foraging-associated calls (D calls) in the study region more frequently in 2022—a year characterized by greater seasonal cumulative upwelling and higher krill prey abundance (Figure 2).

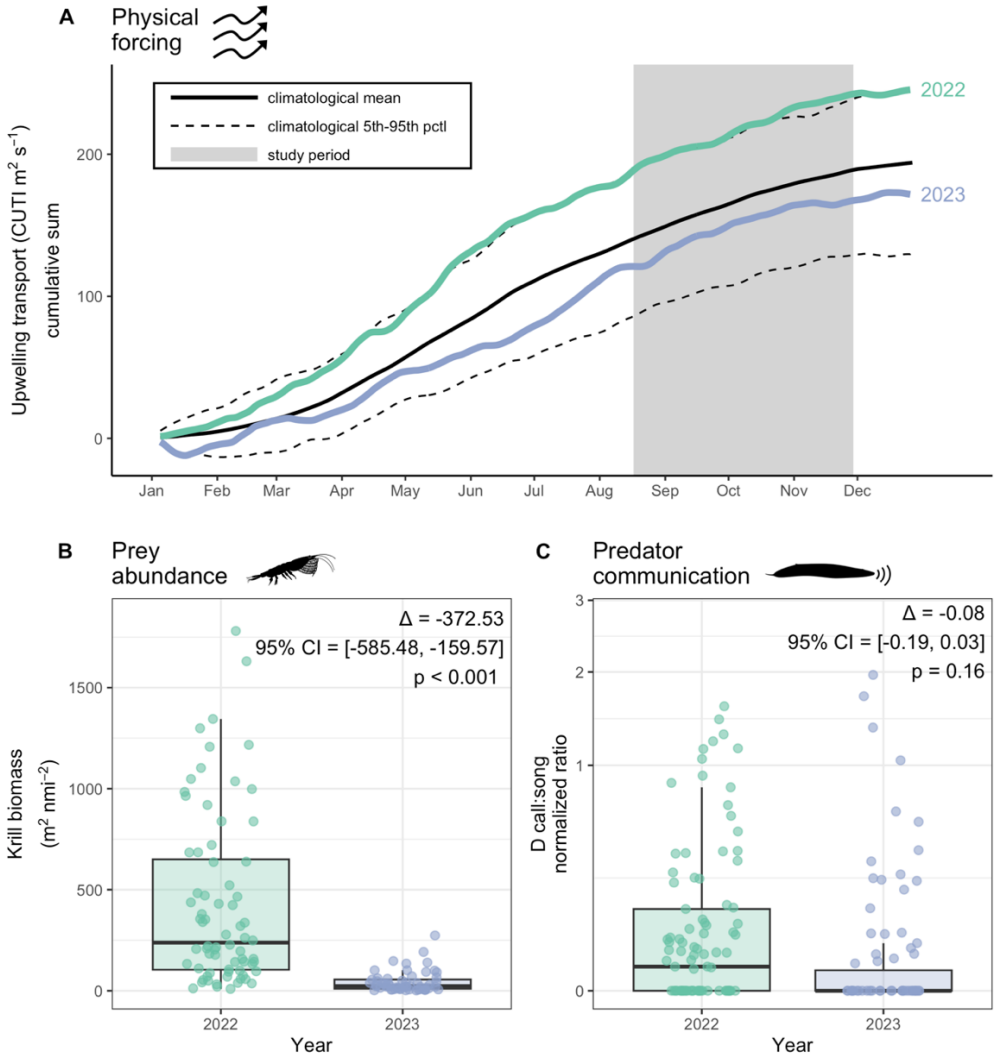


**Figure 2. Interannual variation in seasonal physical forcing, prey dynamics, and predator communication.** **(A)** Colored lines indicate cumulative upwelling during each year of the study. Solid and dashed black lines indicate the climatological mean and 5$^{th}$-95$^{th}$ percentile of cumulative upwelling over 1988-2023. 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 zooplankton biomass values during the study period. **(C)** Interannual comparison of daily blue whale call production, calculated as the normalized ratio of D calls relative to song. D calls were detected on 54.2% of sampling days in 2022 vs. 24.3% of sampling days in 2023. In (B-C), we report the estimated change (2023 relative to 2022), 95% confidence interval, and p-value from generalized least-squares regression models with a first-order continuous autoregressive correlation structure. Boxplots indicate the median (center line), 25$^{th}$-75$^{th}$ percentile (box), and 1.5 times the interquartile range (whiskers), with daily data plotted as points.

**Physical oceanographic regimes mediate variation in prey density and predator communication**

We also observed concurrent shifts in physical forcing, prey density, and predator communication within each year of the study (Figure 3). In 2022, the strong upwelling physical regime persisted until October 4 (Figure 3A-B). This early October transition to weak 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 D calls (Figure 3F). Although the multi-frequency echosounder system (Figure 3D-E) 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 metrics of prey dynamics and predator communication increased again briefly in mid-November 2022 (Figure 3C-F).

In 2023, the strong upwelling physical regime persisted only until September 11 (Figure 3A-B). The 2023 transition from strong to weak 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 2B) 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 strong upwelling physical regime (Figure 3E). Blue whales' relative production of foraging-associated calls also dropped following the transition to weak 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 strong upwelling physical regime in 2023.

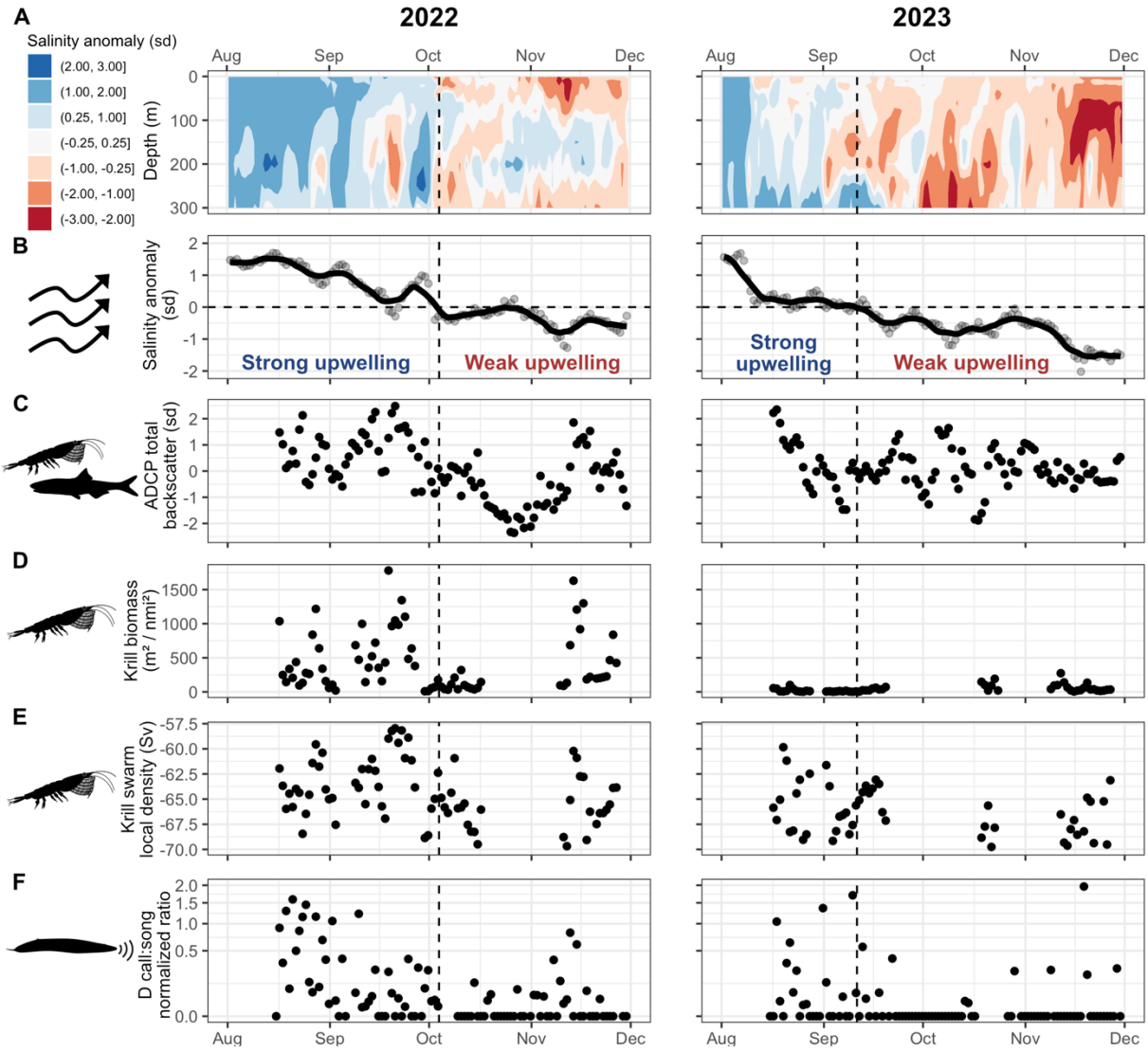


**Figure 3. Time series of physical forcing, prey dynamics, and predator communication. (A)** Salinity anomaly, the conservative physical tracer of upwelling, shown over depth and time. **(B)** Depth-averaged salinity anomaly, including both daily mean (points) and 10-day running mean (line). **(C)** 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 (volume backscattering strength (Sv) in dB re 1 $m^{-1}$). **(F)** Daily blue whale call production, calculated as the normalized ratio of D calls relative to song. The physical regime shift from strong to weak upwelling in each year is indicated by the vertical dashed line across all panels (see Methods).

Examining the physical oceanographic regimes pooled across both years, we found differences in both krill swarm local density and blue whales' production of foraging-associated calls depending on the physical oceanographic regime (Figure 4). Krill swarm local densities were higher during periods of strong upwelling compared to the weak upwelling physical regime (Figure 4A). Similarly, blue whales' production of foraging-associated D calls relative to reproduction-associated song was significantly higher during periods of strong upwelling compared to weak upwelling (Figure 4B). 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 S1). There were also more days with at least one D call detected during the strong upwelling regime (68.0% of sampling days) than during weak upwelling conditions (23.7% of sampling days).

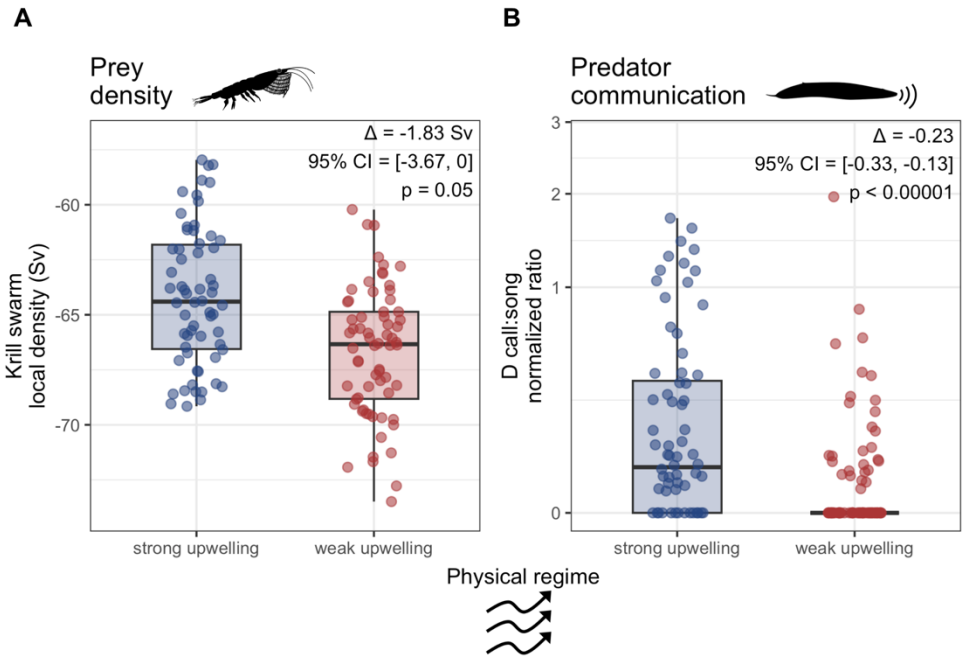


**Figure 4. Physical oceanographic regimes mediate prey density and predator communication. (A)** Distribution of the logarithm of daily krill swarm local densities (volume backscattering strength (Sv) in dB re 1 $m^{-1}$) binned by physical oceanographic regime. Because Sv is measured in dB, the Δ of -1.83 Sv represents a 34.4% decrease in swarm density between strong and weak upwelling (95% CI = -57.1 – 0% density difference). **(B)** Distribution of daily blue whale D call:song normalized ratio values binned by physical oceanographic regime. D calls were detected during 68.0% of sampling days during the strong upwelling regime vs. 23.7% of sampling days during the weak upwelling regime. In each panel, daily data are aggregated across both study years. We report the estimated change (strong upwelling relative to weak upwelling), 95% confidence interval, and p-value from generalized least-squares regression models with a first-order continuous autoregressive correlation structure. Boxplots indicate the median (center line), $25^{th}$-$75^{th}$ percentile (box), and 1.5 times the interquartile range (whiskers), with individual daily data plotted as points.

# Discussion

Social information plays a keystone role in behavioral ecology and evolution[51–53]. Among other functions, communication of information between individuals enables groups to collectively sense and track resources[54,55]. 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 biophysically dynamic ecosystems[19,22,56]. Social foraging theory predicts that the value and production of social information depend on spatiotemporal resource dynamics[16,17], conferring particular advantage in pursuit of patchy, ephemeral resources[20,21]. These resource dynamics are characteristic of pelagic ecosystems[4–6], where physical oceanographic forcing strongly influences ecological patterns and interactions[8–12]. Integrating these theoretical concepts implies historically underexplored connections between physical forcing and the social information produced by pelagic predators, mediated by shifts in prey distribution. Our results provide 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' production of social information via corresponding changes in the abundance and density of their obligate krill prey. Interannually, blue whales produced foraging-associated D calls more frequently in the year (2022) when greater seasonal upwelling of nutrients facilitated higher prey abundance (Figure 2). Within years, when controlling for their overall acoustic presence in the region, blue whales produced more foraging-associated D calls during strong upwelling periods characterized by locally higher prey patch density (Figures 3-4). These findings indicate that blue whales' foraging-associated D calls are consistently correlated with high-density krill swarms which form during upwelling conditions. These widely propagating calls thus represent valuable information for predators about the presence of high-quality prey patches in this vast and dynamic foraging habitat. More broadly, these results demonstrate that long-recognized connections between physical and biological 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[31], which are both spatially patchy and temporally ephemeral in the eastern North Pacific[29,57,58]. We found that both seasonal krill abundance and episodic swarm density are tightly linked to physical oceanographic forcing. Comparing years, 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[26]. At finer temporal scale, local krill swarm density increased during upwelling conditions (Figure 3D; Figure 4A), likely arising from a combination of physical aggregation at oceanographic fronts[58] and behavioral responses such as swarming to avoid the risks of predation by more common raptorial predators[29,59] and offshore advection[60]. Yet this same swarming behavior increases susceptibility to predation by lunge-feeding blue whales, meaning that these massive predators exploit a "rare enemy effect"[61] to efficiently forage on dense krill swarms.

Blue whales co-occur with[30,62] and feed most frequently within[33,63] 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 which span only 100s-1000s of meters (Figure 1C) in a foraging habitat spanning much of the Pacific coast of North America. Theoretical models[64] 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). Blue whales produce abundant nonlocal social information in their foraging habitat: their calls travel over tens to hundreds of kilometers[37] and dominate the low-frequency soundscape throughout their summer-fall foraging season[37,48,49,65]. We find that D calls in particular, which have been associated with foraging in groups[23,34], 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 which may persist for only hours to days[23,29,30,63] in this 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[23], which are unlikely to be depleted by predators before the swarm disperses[23,29,66]. 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[67] 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[68,69] provides a more likely explanation. Attracting conspecifics to areas of high krill swarm density could be beneficial to both signalers and receivers, increasing individual foraging efficiency and consistency via collective sensing and tracking of transient prey patches[19] across a vast and variable foraging habitat. This explanation is consistent with theoretical predictions in fluid ecosystems[22] and empirical evidence from aerial foraging cliff swallows, in which social signaling to collectively track wind-advected insect swarms enhances foraging efficiency[70] and predictability[71]. Blue whale D calls may function similarly, facilitating collective sensing and tracking of the dense krill swarms that arise during stronger upwelling conditions.

Alternative hypotheses for the function of these signals also remain possible. D calls could instead 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[72]). Testing these functional hypotheses will require further integration of individual- and group-level behavioral observations[73] in future work, as in previous studies which revealed the role of song in blue whales' collective migration[37–39]. Regardless of their precise function, D calls consistently coincide with dense krill aggregations (Figures 3-4), indicating that they provide reliable, widely propagating social information about high-density prey patches which arise primarily during stronger upwelling conditions in blue whales' dynamic foraging habitat.

# Conclusions

This study reveals 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–biological coupling in pelagic ecosystems to include predator communication. This empirical discovery integrates theoretical concepts from biological and physical oceanography, social foraging, and collective behavior, 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 production is critical for elucidating the eco-evolutionary processes which give rise to collective sensing and behavior in physically and biologically dynamic ecosystems.

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# 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**

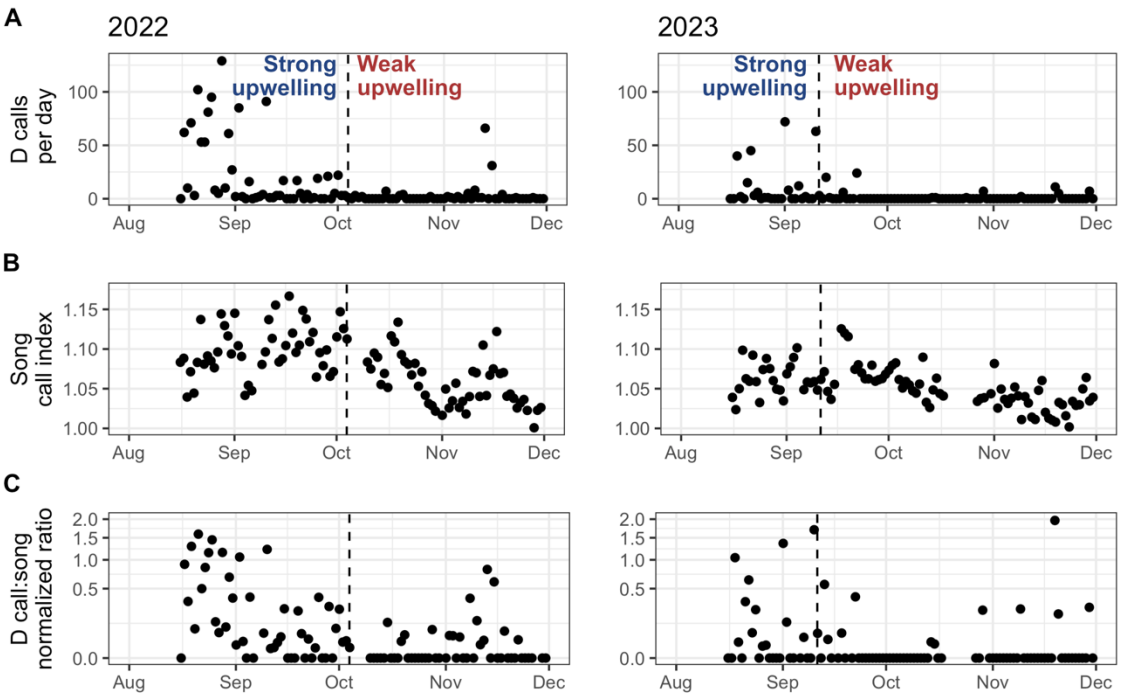


**Figure S1. Time series of component metrics comprising the D call:song normalized ratio over the study period in each year. (A)** D calls per day. **(B)** Song call index. **(C)** Normalized ratio of D calls relative to song, as presented in Figure 3 of the main text and described in Equations 1-3 of the Supplementary Information.