



Intermittent upwelling impacts zooplankton and their gray whale predators at multiple scales

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ABSTRACT: Coastal upwelling dynamics influence the abundance and distribution of marine zooplankton; however, knowledge of how intermittent upwelling patterns impact nearshore prey retention and predator foraging is limited. The Pacific Coast Feeding Group (PCFG) of gray whales forage between northern California and southern British Columbia from early June through the end of November. In Port Orford, Oregon, a subregion of the PCFG foraging range, gray whales demonstrate selection preference for prey patches consisting of elevated zooplankton abundance. Using a 6 yr data set, we characterized the influence of oceanographic conditions on zooplankton relative abundance and gray whale foraging effort in this subregion. Here, we tracked gray whale movements using a theodolite (263 tracklines) and simultaneously quantified prey availability through GoPro camera drops ($n = 520$) off a research kayak between July and August from 2016–2021. Boosted regression tree models assessed the influence of broad (seasonal) and fine (days to weeks) temporal scale upwelling metrics, sea surface temperature, and kelp condition on daily zooplankton abundance and gray whale foraging effort. Results show that at both temporal scales, environmental factors impact ecological response, with zooplankton abundance and gray whale foraging effort maximal at moderate values of upwelling and relaxation, highlighting the importance of intermittent upwelling. These findings document the role of intermittent upwelling on zooplankton availability and whale foraging effort in a nearshore system, which can improve conservation management of this region.

KEY WORDS: Upwelling–relaxation dynamics · Pacific Coast Feeding Group · PCFG gray whale · Predator–prey relationships · Nearshore ecosystem · Kelp · Temporal lags · Boosted regression trees

1. INTRODUCTION

Physical and biological factors are known to influence the abundance and distribution of marine zooplankton and their predators. However, the explanatory power of these factors differs across spatio-temporal scales (Hunt et al. 1999). As zooplankton are important prey for many marine predators, understanding the magnitude and scales of environmental drivers of zooplankton availability to predators is crit-

ical because these factors regulate potential energetic gain, with direct implications for predator population ecology and health. In marine environments, where prey is known to be patchy (Hyrenbach et al. 2000) and zooplankton swarms are prone to predator evasion (Kaltenberg & Benoit-Bird 2013), extended searching for prey patches can be energetically costly for predators. Hence, understanding resource availability as it varies in time and space is crucial for conservation management, especially as ocean con-

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ditions are impacted by climate change (Joh & Di Lorenzo 2017), which may increase environmental stochasticity.

Eastern boundary upwelling systems are known to have a disproportionately high contribution to biological productivity that propagates to higher trophic levels (Chelton et al. 1982, Bograd et al. 2023). As in all eastern boundary upwelling systems, spring and summer conditions in the California Current System (CCS) along the west coast of North America are characterized by wind-driven upwelling where surface waters are advected offshore via Ekman transport, bringing cold, nutrient-dense waters to the surface. This biophysical process is known to increase primary productivity, influence phyto- and zooplankton retention and aggregation, and provide foraging opportunities for marine predators.

While strong northerly winds dominate during the upwelling season in Oregon, USA, nutrient retention that leads to productivity occurs when these winds relax (Barth et al. 2007). The intermittent upwelling hypothesis (IUH) posits that the balance between upwelling and relaxation periods (i.e. intermittent upwelling) during spring and summer seasons determines the input of biological availability and retention of key nutrients, enhances prey availability, and influences species interactions (Menge & Menge 2013). Intermittent upwelling occurs when there is alternation between upwelling and relaxation, typically occurring at a scale of 1–2 wk. Menge & Menge (2013) theorized the impact of this variation in intermittent upwelling with studies along coastal areas of Oregon, California, and New Zealand. They found that intermittency between upwelling and relaxation explained ~37% of the variance among ecological interactions. More theoretical models of the IUH established a baseline of 3 d for the duration of relaxation days needed for nutrient uptake and confirmed that optimal wind patterns for phytoplankton growth are periodic (Zimmerman et al. 1987, Dugdale et al. 1990, Yokomizo et al. 2010). Through a long-term field study, Wilkerson et al. (2006) established that an upwelling pulse followed by a relaxation event lasting 3–7 d led to increased phytoplankton availability and zooplankton biomass.

Applied investigations of ecological responses to intermittent upwelling have centered mainly around pelagic euphausiids and anchovies (Benoit-Bird et al. 2019) or larval recruitment, retention, and settlement in nearshore regions (Wing et al. 1995, Roegner et al. 2003, 2007, Dorman et al. 2005, Narváez et al. 2006, Morgan et al. 2009, Shanks & Morgan 2018). While links between the biophysical processes of wind-

driven upwelling systems and marine predator foraging have been documented (Croll et al. 2005, Keiper et al. 2005, Kono-Martínez et al. 2017, Sato et al. 2018, Barlow et al. 2021, Ryan et al. 2022), the impact of intermittent upwelling and wind relaxation days on predator–prey interactions remains largely understudied, particularly in nearshore areas of the CCS, where zooplankton are critical prey items for important commercial and recreational fisheries (Bosley et al. 2014) and protected marine megafauna, including gray whales *Eschrichtius robustus* (Newell & Cowles 2006, Hildebrand et al. 2021, 2022).

While most gray whales in the Eastern North Pacific population (ENP; abundance ~14 526 individuals; Eguchi et al. 2022) migrate from wintering grounds in Baja California, Mexico, to foraging grounds in the Arctic and sub-Arctic region, a sub-group of the ENP known as the Pacific Coast Feeding Group (PCFG) use the very nearshore (<3 km) coastal environment between northern California and southern British Columbia (latitudes ranging from 41° to 52° N) as foraging grounds from early June through the end of November (Scordino et al. 2011). While PCFG gray whales (~212 individuals; Harris et al. 2022) demonstrate site fidelity to particular foraging sites within the PCFG range (Lagerquist et al. 2019), they also elicit flexibility in space use within the entire range as they move between foraging sites within a feeding season (Lagerquist et al. 2019) in search of prey. They forage benthically and throughout the water column (Darling et al. 1998) on a diversity of prey items including infaunal and epibenthic amphipods (Feyrer & Duffus 2011), mysids (Nelson et al. 2008), ghost shrimp (Dunham & Duffus 2001), and crab larvae (Jenkinson 2001, Nelson et al. 2008).

PCFG gray whales increase foraging effort when overall prey availability increases and display preferences for calorically rich species, such as *Holmesimysis sculpta* and *Neomysis rayii*, which are found in highest abundances near kelp and reef habitats (Newell & Cowles 2006, Hildebrand et al. 2022). Our study was conducted in Port Orford, Oregon, where there has been a documented decline in zooplankton abundance and gray whale foraging over an 8 yr period that occurred simultaneously with increasing purple sea urchin *Strongylocentrotus purpuratus* occurrence and declines in bull kelp *Nereocystis luetkeana* condition, providing evidence that a trophic cascade could extend to pelagic marine predators (Hildebrand et al. 2024). In their study, Hildebrand et al. (2024) demonstrated a strong positive relationship between zooplankton and kelp health, and weaker yet positive relationships between kelp and whales and

zooplankton and whales. Thus, while kelp provides important habitat for the zooplankton prey of PCFG gray whales at a fine scale, other environmental factors likely influence the availability of zooplankton and gray whale foraging in this nearshore ecosystem on both fine and broad temporal scales.

PCFG whales have high interannual variation in body condition that is potentially linked to shifts in environmental and oceanographic conditions (Lemos et al. 2020, Akmajian et al. 2021), and photogrammetric measurements have demonstrated that PCFG whales have lower body condition (a proxy for foraging success) overall than the ENP (Torres et al. 2022). As warm water temperatures and changing ocean conditions can alter zooplankton community structure (Brodeur et al. 2019) and reproductive rates (Shanks et al. 2020), an improved understanding of the links between environmental conditions and zooplankton abundance in the nearshore CCS will shed light on the potential impacts to the gray whales that rely on these nearshore prey resources. Thus, understanding the scales and patterns of environmental drivers of variation in zooplankton abundance available to PCFG whales is critical to anticipate individual health and population viability. Knowledge of the relationships between the environmental drivers of zooplankton abundance in very nearshore reef ecosystems across the northern CCS is limited (Baring et al. 2016, Walter et al. 2018, Elliott Smith & Fox 2022). Additionally, how intermittent upwelling influences the occurrence of cetaceans and their zooplankton prey in these same ecosystems remains to be fully understood. Proposed mechanisms underlying zooplankton response to intermittent upwelling can occur at both fine and broad scales, and can include nearshore retention during relaxation periods when upwelling-favorable winds are reduced or absent (Wroblewski 1980) as well as increased recruitment through pulses in primary productivity (Menge & Menge 2013). The impact of intermittent upwelling varies across species and life history (Roughgarden et al. 1988, Wing et al. 1995). In Monterey Bay, mysid abundance is influenced by upwelling processes, whereby high-frequency internal waves linked to upwelling processes are correlated with the presence of zooplankton aggregation layers (McManus et al. 2005); however, the response of mysid aggregations to upwelling in our study region remains to be investigated. Given that PCFG gray whales may face increasing nutritional stress due to environmental change (Lemos et al. 2020, Akmajian et al. 2021, Torres et al. 2022) alongside health threats caused by high microparticle ingestion (Torres et al. 2023) and

elevated physiological stress related to increased vessel traffic and ocean noise (Lemos et al. 2022b, Pirotta et al. 2023), these knowledge gaps are important to fill to support management efforts aimed at mitigating cumulative impacts on this small subgroup (Oldach et al. 2022). Thus, our study is motivated by 3 hypotheses: H_1 : fine-scale zooplankton abundance and gray whale occurrence are influenced by the same environmental factors with similar functional relationships; H_2 : increased alternations between upwelling and relaxation days (intermittent upwelling) will have a positive relationship with zooplankton abundance and gray whale occurrence; and H_3 : prey (zooplankton) and predator (gray whale) response depend on both broad (seasonal) and fine (days to weeks) temporal scales of intermittent upwelling dynamics. This study provides new findings on the relationships between environmental conditions, zooplankton abundance, and gray whale habitat utilization, including research on the IUH as it relates to marine predator and prey occurrence.

2. MATERIALS AND METHODS

2.1. Study area

Data for this study were collected beginning in July through the end of August for 6 consecutive years (2016–2021) near Port Orford, Oregon, USA (42.750° N, 124.500° W) (Fig. 1). All fieldwork efforts began at sunrise (~06:30 h) and continued throughout daytime hours, provided that weather conditions were favorable (e.g. low fog, wind speed < 10 knots, swell 0.91 m, Beaufort sea state < 3). This study is part of a long-term effort to investigate the fine-scale foraging ecology of gray whales *Eschrichtius robustus* using theodolite tracking and kayak-based *in situ* sampling methods. The extent of the study area is approximately 12 km² and is within the PCFG summer foraging ground. This area is proximal to the port of Port Orford, where the commercial fishing industry comprises the majority of vessel traffic (Sullivan & Torres 2018).

2.2. Zooplankton and kelp data

A tandem kayak was used to sample zooplankton abundance at 2 sites within the study area where gray whales frequently forage: Mill Rocks and Tichenor Cove (Fig. 1). These sites are 1 km apart, with 6 kayak sampling stations in each site. The nearshore marine

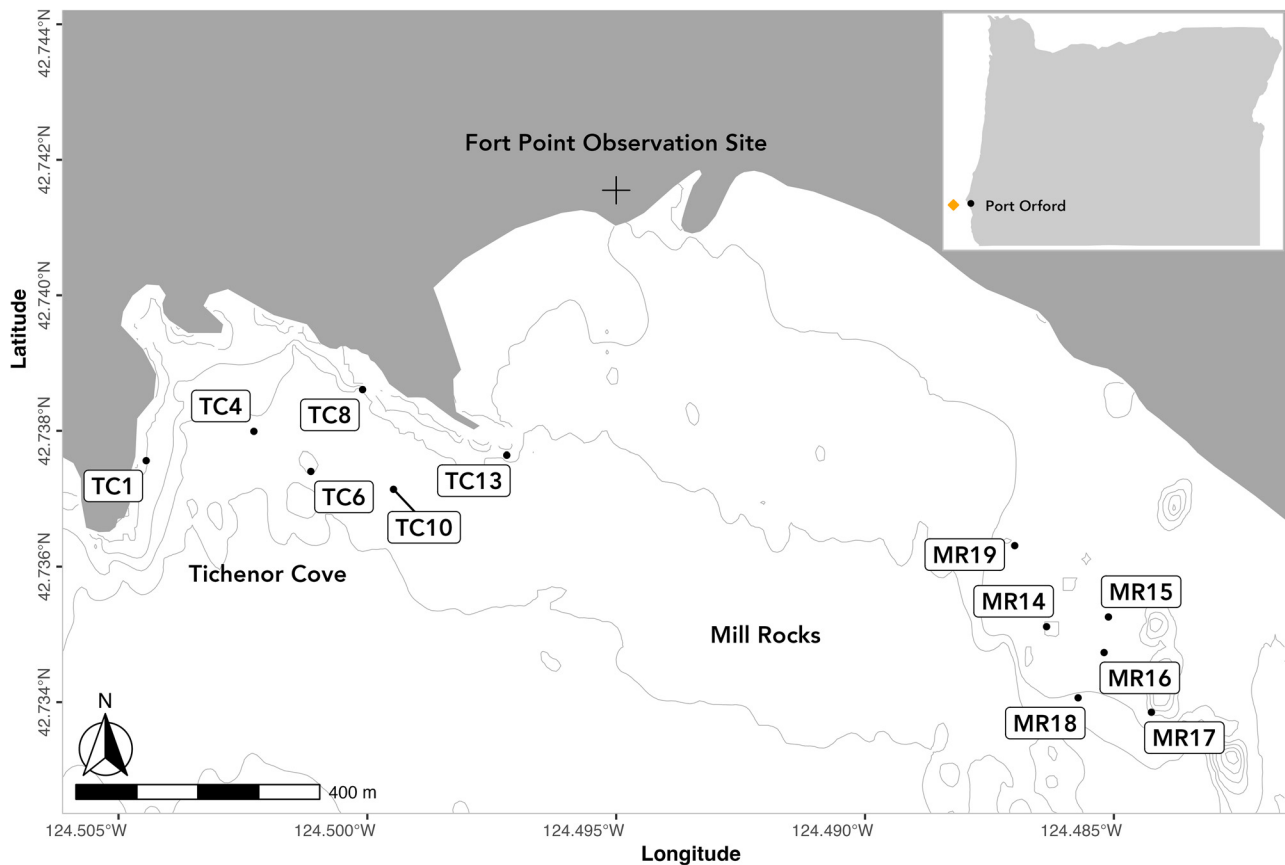


Fig. 1. Study area in Port Orford, Oregon, USA, with 12 kayak sampling stations (black circles) for GoPro camera deployments; bathymetric contour lines at 5 m depth bins from NOAA's 1/3 arc-second MHW Coastal Digital Elevation Model; and Fort Point Observation Site (black cross), a central cliff overlook used for whale surveys. Inset: state of Oregon showing Port Orford; orange diamond: NOAA Buoy 4601 location

environment at these stations is characterized by a mosaic of rocky reef, bull kelp beds, and sandy bottom habitat.

Relative zooplankton abundance data were collected from the research kayak at every station using a GoPro camera and time–depth recorder (TDR) (Solinst Levellogger 3001 F100/30) array. The GoPro camera is programmed for continuous video recording, attached to a weighted pipe, and systematically submerged into the water via a downrigger. When the array reaches the bottom, it is retrieved at a downrigger speed of a half rotation per second (approximately 0.2 m s^{-1}). GoPro videos are synched with depth data from the attached TDR. Following the methods of Hildebrand et al. (2022), a single analyst processed the GoPro imagery to obtain a useful and accurate metric of relative zooplankton density at each sampling station per day. In brief, screenshots of the video were taken at 5 s intervals during the retrieval cast to obtain still imagery from the GoPro video. Images were then overlaid by a 3×3 cell grid

and each grid cell was scored on a scale of 0–5 (0: no zooplankton present; 5: highest zooplankton density; NA: indeterminable due to low light and/or other obstructions). The calculated mean of all grid cells provides the relative abundance for a single still image, and the mean values for all images in a cast are summed to obtain a metric of zooplankton relative abundance (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m752p001_supp.pdf). Then, the values obtained for each cast were averaged across all sampling stations for each day of sampling to obtain a daily relative zooplankton abundance metric in the study area.

Using the same GoPro videos, a ranked score of kelp condition based on the impact of sea urchin grazing on both fronds and stalks was calculated following Hildebrand et al. (2022) (see Text S1 for full details). Using reference videos, each station was assigned one of 5 categories: no kelp (NK), all damaged (AD), mostly damaged/some healthy (MD), mostly healthy/some damage (MH), and all healthy

(AH). For analysis, these kelp condition categories were converted to a numerical score (NK: 1; AD: 2; MD: 3; MH: 4; AH: 5) and the mean kelp condition across all sampling stations on each day was calculated.

2.3. Whale survey data

Fort Point observation site is an unobscured cliff location overlooking the study sites where whale surveys were conducted and sea state conditions monitored for kayak safety. Whale occurrence and movements were tracked using a Sokkia model DT210 theodolite connected to a laptop that runs the software Pythagoras (Gailey & Ortega-Ortiz 2000). We used a Canon EOS 70D camera to obtain high-quality photo-identification images of tracked whales. When it was not possible to obtain identification photographs (due to timing and/or distance), high-powered binoculars were used to spot, track, and identify the whale. To derive gray whale behavior states (travel, search, forage), whale surfacing locations obtained by the theodolite were analyzed via residence in space and time (RST; Torres et al. 2017) methodology, where distance traveled between surfacing and time between each surfacing are calculated. RST assigns a behavior state to each point within a whale trackline according to the space and time occupied by an individual within a given radius of 40.7 m, and classifies behavior into 3 states: time-intensive, time- and distance-intensive, and transit. This radius size was derived based on the mean travel speed of PCFG gray whales and the whale tracking sampling interval (Torres et al. 2017) and was deemed ecologically appropriate as it falls within the range of baleen whale visual acuity (Mass & Supin 1997, Torres 2017), and is slightly greater than 3 body lengths of an average adult gray whale (Agbayani et al. 2020, Bierlich et al. 2023). Based on observed behavioral patterns of gray whales at this fine scale and in alignment with Hildebrand et al. (2022), behavioral interpretation of these states is as follows: time-intensive constitutes foraging behavior, time- and distance-intensive is equivalent to searching behavior, and transit is considered traveling behavior.

2.4. Environmental data

Coastal wind speed and sea surface temperature (SST) data were acquired from *in situ* NOAA Buoy

Station 46015, 28 km west of Port Orford (42.753° N, 124.844° W; https://www.ndbc.noaa.gov/station_page.php?station=46015) (Fig. 1). The northward wind stress component (τ_y) was calculated from the wind speed and direction recorded at the buoy station following the methods of Large & Pond (1981) (described in Kochanski et al. 2006; see Text S2 for code). The northward wind stress component (hereafter referred to as wind stress) was selected, as it describes the magnitude of upwelling-favorable wind in the region (Barth et al. 2007). Hourly measurements of both SST and wind stress were averaged to obtain daily values for each metric, for all years in this study.

The magnitude and seasonal accumulation of coastal upwelling and relaxation were derived from the Coastal Upwelling Transport Index (CUTI; <https://oceanview.pfeg.noaa.gov/products/upwelling/cuti>) for latitude 42° N. CUTI estimates vertical transport using regional sea surface height, surface wind stress, and mixed layer depth via regional ocean reanalysis (Jacox et al. 2018). A 10 d smoothing filter was applied to daily CUTI values to smooth potentially anomalous daily values and reveal trends in annual phenology. Then, daily CUTI values were used to calculate the cumulative daily upwelling index value for each sampling day, and the cumulative upwelling information was used to determine the physical spring transition index (ST) and end of the upwelling season for each year following established upwelling phenological definitions (Bograd et al. 2009, Oestreich et al. 2022, Barlow et al. 2024). Then, mean CUTI during the upwelling season (all days between ST and the end of the upwelling season) was calculated across all study years (mean: 0.6) and used as a threshold to define periods of relaxation, whereby a day was considered a 'relaxation event' when the daily CUTI value fell below the mean CUTI during the upwelling season (see Table S1 for full phenological metrics). We decided that CUTI was the best variable to determine relaxation timing, as data gaps from the NOAA buoy would prohibit incorporating 2 yr of data. Relaxation was summarized through 2 different metrics: cumulative number of relaxation days and recent relaxation. The cumulative number of relaxation days is the summation of days below the mean CUTI value since ST, and recent relaxation is the sum of relaxation days within a 10 d moving average (i.e. within the 10 d prior to the day of interest) to account for the temporal scale at which relaxation can occur (Menge & Menge 2013) (see Fig. S2). These calculations resulted in 2 fine-scale (daily CUTI, recent relaxation) and 2 broad-scale (cumulative CUTI since ST, cumulative number of relaxation days since ST)

metrics of upwelling and relaxation that were incorporated into subsequent analyses. Cumulative CUTI since ST and cumulative number of relaxation days since ST were selected for this analysis over day of the year, though these metrics are related, as CUTI best captures biologically relevant variation in seasonal patterns.

2.5. Time series cross-correlation analysis

As we would not expect zooplankton abundance to have an immediate response to environmental variability given that a response cannot be instantaneous due to the several physical and biological intermediate steps (Largier et al. 2006, Barlow et al. 2021), a time-series analysis was conducted to quantify lags between different oceanographic variables and zooplankton abundance, and thereby identify more appropriate temporal scales of environmental mechanisms. The cross-correlation function (CCF) in the 'astsa' (applied statistical time series analysis; Stoffer 2014) package in R measures the correlation between 2 time series at different lagged time steps. We used the CCF to assess the lag at which the correlation between selected fine-scale oceanographic variables (daily CUTI, daily wind stress, and daily SST) and zooplankton abundance was the highest. Unfortunately, the Port Orford NOAA buoy did not record data for 2018 and 2019 and for 3 d during our sampling period in 2017, so cross-correlations including wind stress and SST were only conducted on available data.

The CCF analysis was run separately for each sampling year to assess the lagged cross-correlations (time step measured in days). Given the short time window of sampling (6 wk in each year), data did not require time-series decomposition to remove seasonal variation prior to analysis. Then, the mean and median autocorrelation function (ACF) values per lag step (0–10 d) were compiled to identify the strongest relationship between a given environmental variable and relative zooplankton abundance across the data set. Results were then cross-verified with available literature to determine the most appropriate temporal lags to include in multivariate modeling. To address the hypothesis that whales respond to the same environmental conditions as zooplankton and within the same temporal phase at a site scale (H_1 and H_3), we applied the same lags determined for each environmental variable in the zooplankton cross-correlation analyses to the subsequent whale response model.

2.6. Multivariate analysis using boosted regression tree models

We implemented boosted regression trees (BRTs), which are tree-based machine learning models, to infer functional relationships between both zooplankton relative abundance (BRT_{zoop}) and whale presence or absence (BRT_{whale}) and environmental metrics. BRTs are complex additive regression models that are capable of fitting non-linear relationships, allow for and describe interactions between predictors, and are flexible to missing data (Elith et al. 2008). For both the BRT_{zoop} and the BRT_{whale} , BRT models were created using the 'dismo' and 'gbm' packages (Greenwell et al. 2019, Hijmans et al. 2024), and final functional response plots were created using the 'pdp' package (Greenwell 2017) in R. Prior to BRT model fitting, we conducted a Pearson's correlation analysis to test for correlation among the oceanographic predictor variables, and any pair of predictor variables with a correlation coefficient of >0.7 or <-0.7 were not included simultaneously in the same model (see Fig. S3). This correlation analysis included day-of-year as a predictor variable to assess whether seasonal phenology was driving overall patterns.

Theodolite tracking data of whales was converted into a binomial metric of behavior state based on the RST behavioral classifications of each track location. Gray whale locations classified as either forage or search behaviors were considered presence data (1), and both will hereafter be referred to as gray whale foraging effort. For a given observation day, travel behavior and absence of a whale observation during the cliffside observation effort were considered absence data (0). To normalize the distribution of binomial data that was skewed toward zeros (absence or traveling), the total number of presences was divided by the total number of absences and added as a weight in the final BRT analysis, as this has been shown to increase the accuracy of BRT models (Barbet-Massin et al. 2012).

The BRT_{zoop} model assessed the relationships between selected oceanographic variables and prey using a Poisson distribution, while the weighted BRT_{whale} model used a binomial distribution to examine relationships between the oceanographic predictor variables and whale behavior. Both BRT_{zoop} and BRT_{whale} were iteratively tested to assess the optimal combination of tree complexity (1–3), learning rate (0.05, 0.001, 0.005, 0.01), and number of starting trees (50, 100). Tree complexity represents the number of interactions allowed in the model, and low values were chosen because increasing eco-

logical interactions decreases ecological interpretability. If the model had not converged when 1000 trees were reached, the learning rate was reduced (Elith et al. 2008). Bag fraction was fixed at 0.75. Candidate models were generated from these parameters, and optimal model parameters were then selected based on model performance metrics (final learning rate, number of trees, cross-fold correlation coefficient, and cross-validated [CrV] deviance explained). CrV deviance explained describes how well the candidate models fit a subset of withheld data (Buston & Elith 2011), and higher values of CrV deviance indicate a balance between complexity and fit (Torres et al. 2013). Area under the receiver operating characteristic curve (AUC) was also used to assess overall performance for the binomial BRT_{whale} model. The AUC assesses the measure of separability between true positive and true negative values between 0 and 1; an AUC > 0.7 is considered reliable (Swets 1988).

3. RESULTS

3.1. Data collection summary

Over the 6 yr period, field teams successfully collected 520 GoPro videos and conducted 761.9 h of whale survey effort (Table 1). All videos were used for image scoring, resulting in 20377 still images that were scored, of which 2239 were obscured and scored as NA. Kayak-based sampling of relative zooplankton abundance resulted in 99 sampling days included in the BRT_{zoop} model. Gray whale *Eschrichtius robustus* survey effort resulted in 62 individual whales observed, with 263 individual theodolite tracks recorded, including 11299 combined foraging and searching points (see Fig. S4). Overall, 165 d of whale survey effort were included in the BRT_{whale} model, with 63 presence days (days with forage or search behavior observed) and 102 absence days (no whales observed or only transit behavior observed; Table 1).

Fine-scale oceanographic variables displayed fluctuations both within and between sampling periods (Fig. 2). Wind stress across all years showed alternations between upwelling-favorable winds and relaxation days, illustrating intermittent upwelling conditions. The number of recent relaxed days showed variability across years, but with a distinct increase toward the end of the sampling period each year; SST similarly often increased towards the end of the sampling periods. Zooplankton abundance dropped precipitously from 2016 to 2021 (Fig. 2).

While the fine-scale oceanographic variables demonstrated variability among years, patterns in broad-scale oceanographic variables revealed distinct annual shifts. There was a steady increase in cumulative CUTI from 2016 to 2021 (Fig. 3). Notably, while 2021 showed the greatest total cumulative CUTI, it was also the year with the lowest zooplankton abundance. However, 2018 had the third-highest cumulative CUTI and a very early ST and also had the greatest zooplankton abundance (Table 1). The number of relaxation days since the ST (Fig. 3) across all years showed variation in magnitude and, while cumulative CUTI was high in 2021. The lowest zooplankton abundance, as seen in 2021, occurred when cumulative CUTI since ST was highest and the number of relaxed days since ST was third lowest across all years (Fig. 3).

3.2. Time series cross-correlation analysis

Among the potential lag days assessed (0–5 d), wind stress and zooplankton abundance showed the highest mean positive correlations at a 1 d and second highest at a 4 d lag (Fig. 4). All potential lags were considered in candidate models for multivariate BRT analysis (see Section 2.5), but wind stress at a 4 d lag was ultimately chosen for this study due to the statistical mean ACF values from cross-correlation analysis, available literature that supported the biological plausibility of this lag (Roegner

Table 1. Sampling summary table showing total number of *in situ* GoPro Casts, mean zooplankton relative abundance, cliff site whale survey effort, ratio of whale presence and absences days, and number of whale tracks by field season years (2016–2021)

	2016	2017	2018	2019	2020	2021
<i>In situ</i> GoPro videos	n = 47	n = 56	n = 154	n = 53	n = 64	n = 146
Relative zooplankton abundance	279.16	313.38	1245.23	238.79	121.69	15
Total whale survey effort (min)	7743.91	7036.90	8958.30	7318.92	7072.63	7583.65
Total whale presences:absences (d)	17:12	6:21	11:19	21:7	6:20	2:23
Total whale tracks	77	21	59	58	40	8

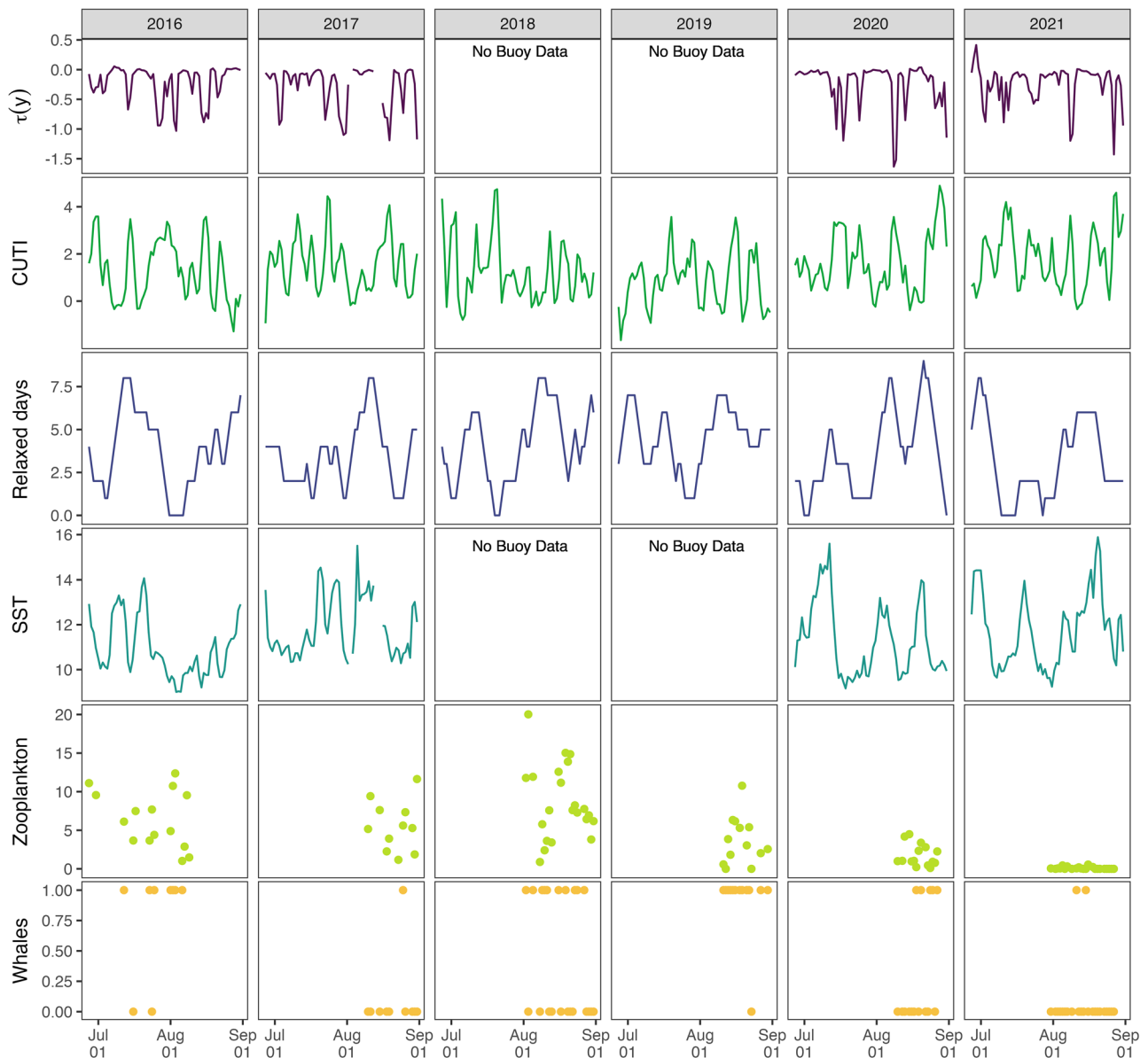


Fig. 2. Time-series plots showing patterns of fine-scale (daily) oceanographic variables: wind stress [$\tau(y)$], daily cumulative upwelling transport index (CUTI), number of recent relaxed days in 10 d window (relaxed days), and sea surface temperature (SST); and the biological response of both relative zooplankton abundance (Zooplankton) and whale foraging effort (Whales; 0: absent or transit; 1: forage) for all years within our sampling window (2016–2021) where data were available (data from NOAA buoy not available in 2018 and 2019)

et al. 2003, 2007, Mace & Morgan 2006), and impact on preliminary BRT model performance. CUTI and zooplankton abundance correlation was strongest at a 3 d lag (Fig. 4). This lag selection was supported by the literature, as upwelling has been shown to correlate with wind stress at a 1 d lag (Narváez et al. 2006). Thus, since wind stress at a 4 d lag was chosen for the final model (as described above), it also follows that using CUTI at a 3 d lag was appropriate for our final analysis.

SST and zooplankton abundance showed the strongest positive correlation between a 0 and 1 d lag (Fig. 4). These lag values align with the ranges given in the available literature, where SST changes due to shifts in wind stress were observed at a lag of 0–4 d (Narváez et al. 2006). All potential lags for SST (0–5 d) were considered in preliminary multivariate BRT analysis, but SST at a 0 d lag was chosen as it reflected the strongest value in our data-driven correlation assessment. Day of the year was also included in the

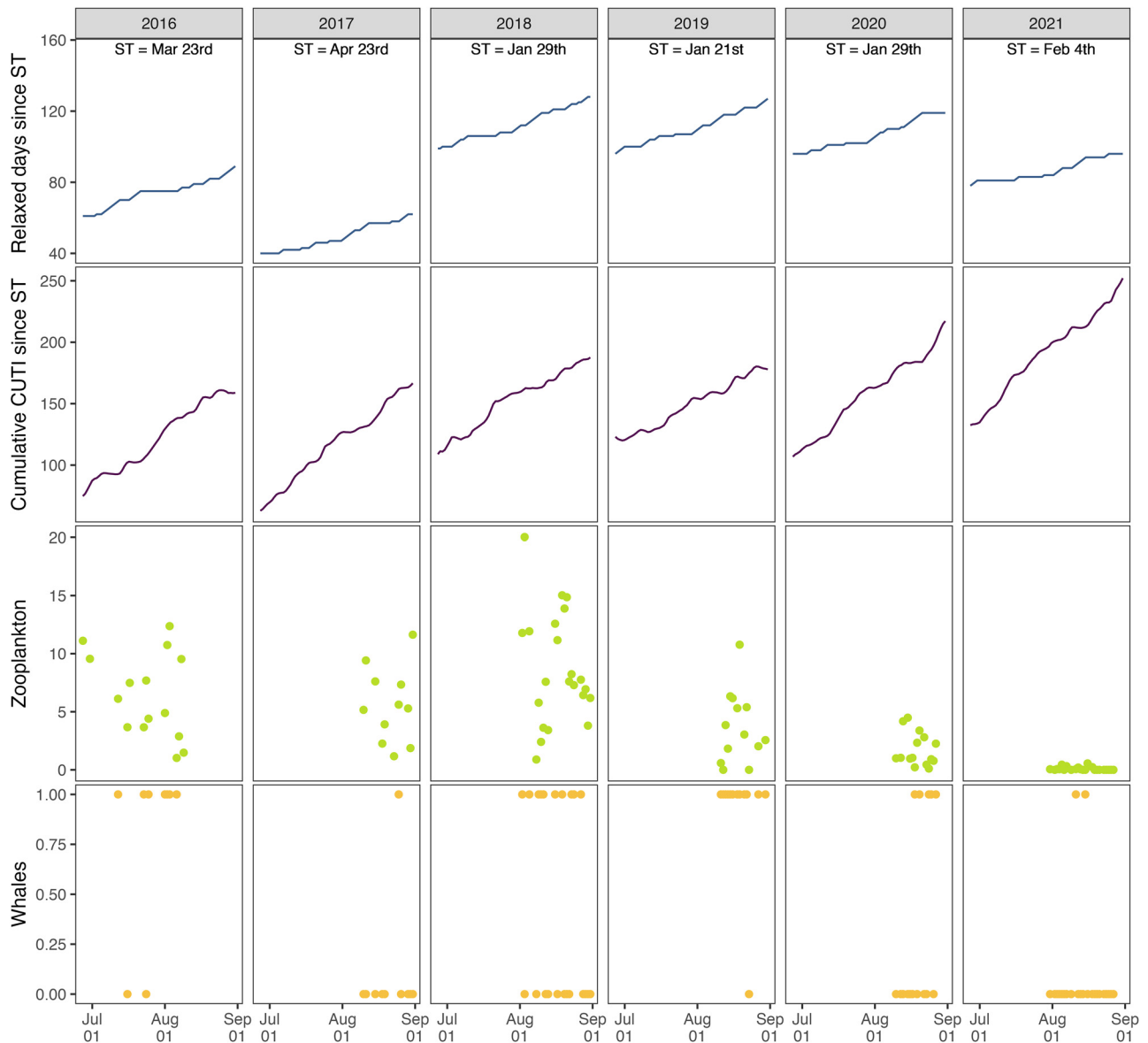


Fig. 3. Time-series plots showing the patterns of broad-scale oceanographic variables (relaxation days since the physical spring transition [ST]) and cumulative coastal upwelling transport index [CUTI] since the ST), relative zooplankton abundance, and whale foraging effort, for all years within our sampling window (2016–2021). The date of ST in each year is given at the top of each column

preliminary BRT analysis but was found to have a negligible impact on model performance (Figs. S5 & S6).

3.3. Zooplankton response to environmental variables

Pearson's correlation analysis revealed no significant correlations between oceanographic predictor variables ($r > -0.7$ and < 0.7) (see Fig. S2), so all predictors were initially included in the final BRT

models. However, only predictor variables that contributed more than 5% to the model were ultimately retained (Elith et al. 2008).

BRT_{zoop} had 52.6% of the CrV deviance explained by the selected environmental variables and cross-fold correlation of 75% with a learning rate of 0.0025, total trees of 1950, and tree complexity of 2 (Fig. 5). Kelp condition was the top contributor to the model (32%; Fig. 5a), with a functional relationship in which zooplankton abundance sharply increases as kelp condition improves. Cumulative CUTI since the spring

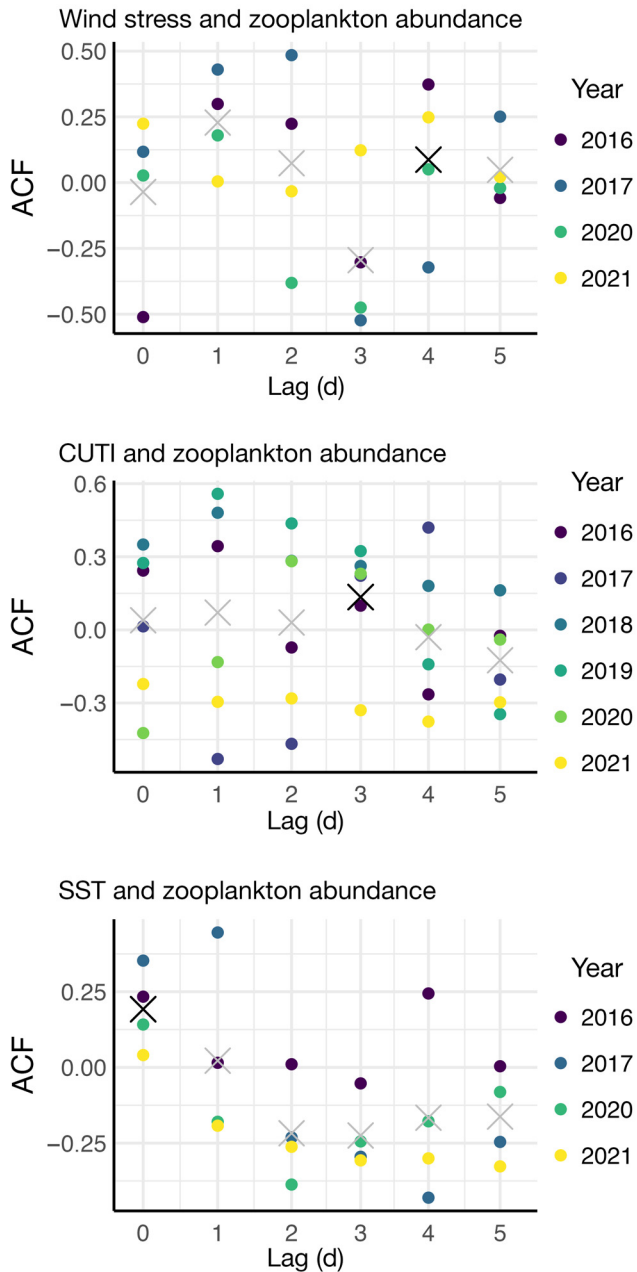


Fig. 4. Cross-correlation plots showing the mean correlation auto-correlation factor (ACF) values across 0–5 d lags between selected oceanographic variables (wind stress, cumulative coastal upwelling transport index [CUTI], and sea surface temperature [SST]) and relative zooplankton abundance for all sampling years where data were available (2016–2021; wind stress and SST data not available from NOAA buoy in 2018 and 2019). Gray cross marks: the mean for each year; black cross marks: the mean applied in model analysis. Note differences in the y-axis ranges

transition (ST) was the second contributor to the model (23.4%; Fig. 5b), where the greatest abundance of zooplankton occurred between values of ~0 and

150, after which zooplankton abundance decreased as CUTI accumulation increased. CUTI at a 3 d lag was the third-top predictor (12%; Fig. 5c), where strong upwelling 3 d prior to sampling increased zooplankton abundance. The amount of recent relaxation contributed 10.5% (Fig. 5d) to the model and indicated that 0–4 d of relaxation within the past 10 d is correlated with increased zooplankton abundance, with a decline in zooplankton abundance after 5 or more days of recent relaxation. The SST functional response curve (7.9%; Fig. 5e) illustrates high zooplankton abundance at both coldest and warmest temperatures, with greatest abundance at 14–16°C. Number of relaxation days since the ST (7.7%; Fig. 5f) shows a L-shaped curve, with high zooplankton when the cumulative relaxation days were <70 and increasing abundance when the number of relaxation days was >110. Wind stress at a 4 d lag contributed 6.5% to the model (Fig. 5g), with high zooplankton abundance occurring after strong upwelling favorable winds 4 d prior.

Strong interactions in the BRT_{zoop} model were detected between cumulative CUTI and number of relaxation days (Fig. 6a), as well as cumulative CUTI and kelp health (Fig. 6b). Pearson correlation between cumulative CUTI and number of relaxation days was low, while cumulative CUTI and kelp health were the most correlated pair (see Table S2). However, both interaction plots (Fig. 6a,b) illustrate the importance of low cumulative CUTI since the ST on increased zooplankton abundance, with an added positive influence on zooplankton abundance with extreme values of cumulative relaxation since the ST or if kelp is in good condition.

3.4. Gray whale response to environmental variables

For the BRT_{whale} model (Fig. 7), the same environmental variables from BRT_{zoop} were included as well as relative zooplankton abundance as a predictor. These variables combined explained 13.1% of the CrV deviance. Cross-fold correlation was 42.4% with an AUC score of 0.754, a learning rate of 5×10^{-4} , a total of 2900 trees, and a tree complexity of 2. Wind stress at a 4 d lag was the greatest contributor (28.7%; Fig. 7a) to the BRT_{whale} model, where strong upwelling-favorable winds correlated with increased whale foraging effort 4 d later. Cumulative CUTI since the ST was the second-top predictor (24.4%; Fig. 7b), where whale foraging effort was greatest between values of 0 and 150, after which whale foraging

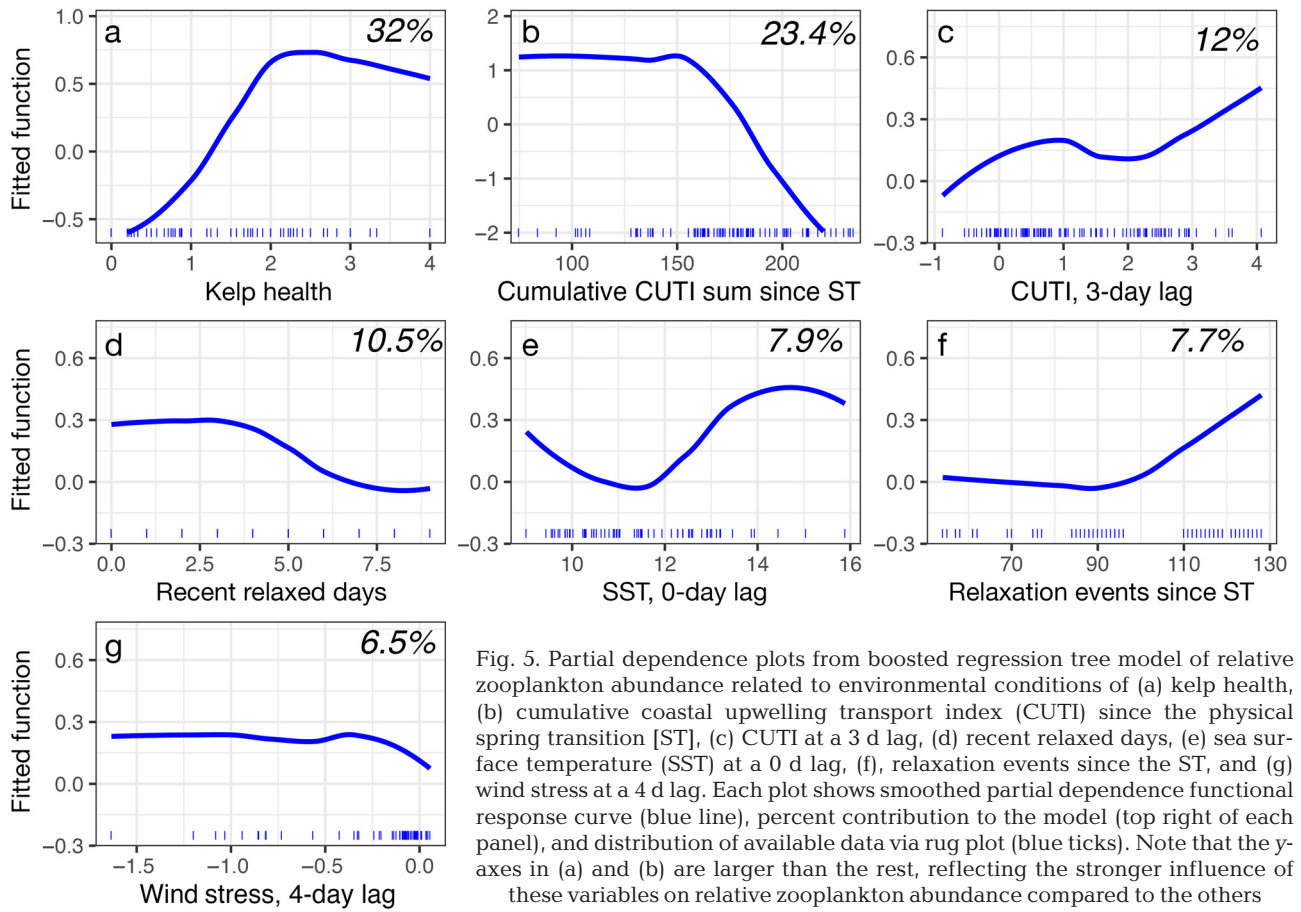


Fig. 5. Partial dependence plots from boosted regression tree model of relative zooplankton abundance related to environmental conditions of (a) kelp health, (b) cumulative coastal upwelling transport index (CUTI) since the physical spring transition [ST], (c) CUTI at a 3 d lag, (d) recent relaxed days, (e) sea surface temperature (SST) at a 0 d lag, (f), relaxation events since the ST, and (g) wind stress at a 4 d lag. Each plot shows smoothed partial dependence functional response curve (blue line), percent contribution to the model (top right of each panel), and distribution of available data via rug plot (blue ticks). Note that the y-axes in (a) and (b) are larger than the rest, reflecting the stronger influence of these variables on relative zooplankton abundance compared to the others

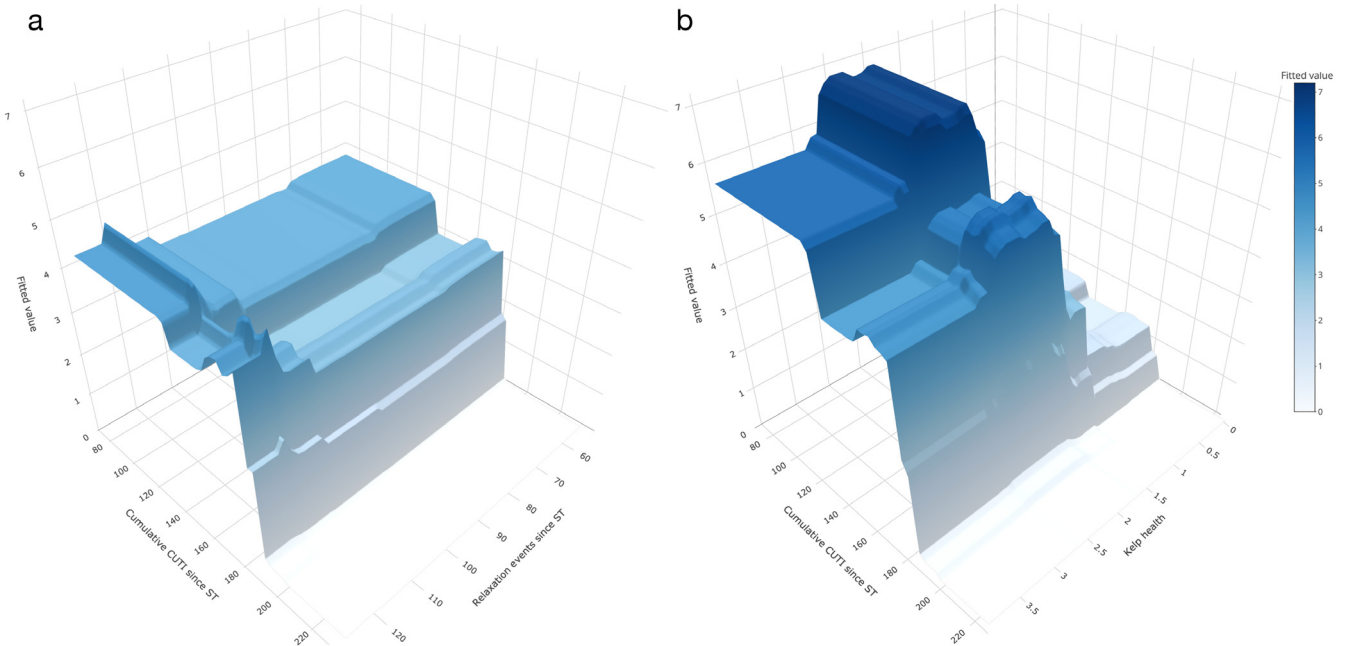


Fig. 6. Three-dimensional partial dependence plot showing the top interactions from boosted regression tree model of zooplankton relative abundance, showing (a) interaction between cumulative coastal upwelling transport index (CUTI) since the physical spring transition (ST) and relaxation events since the ST and the fitted value (marginal effect) on relative zooplankton abundance; and (b) interaction between cumulative CUTI since the ST and kelp health and the fitted value (marginal effect) on relative zooplankton abundance

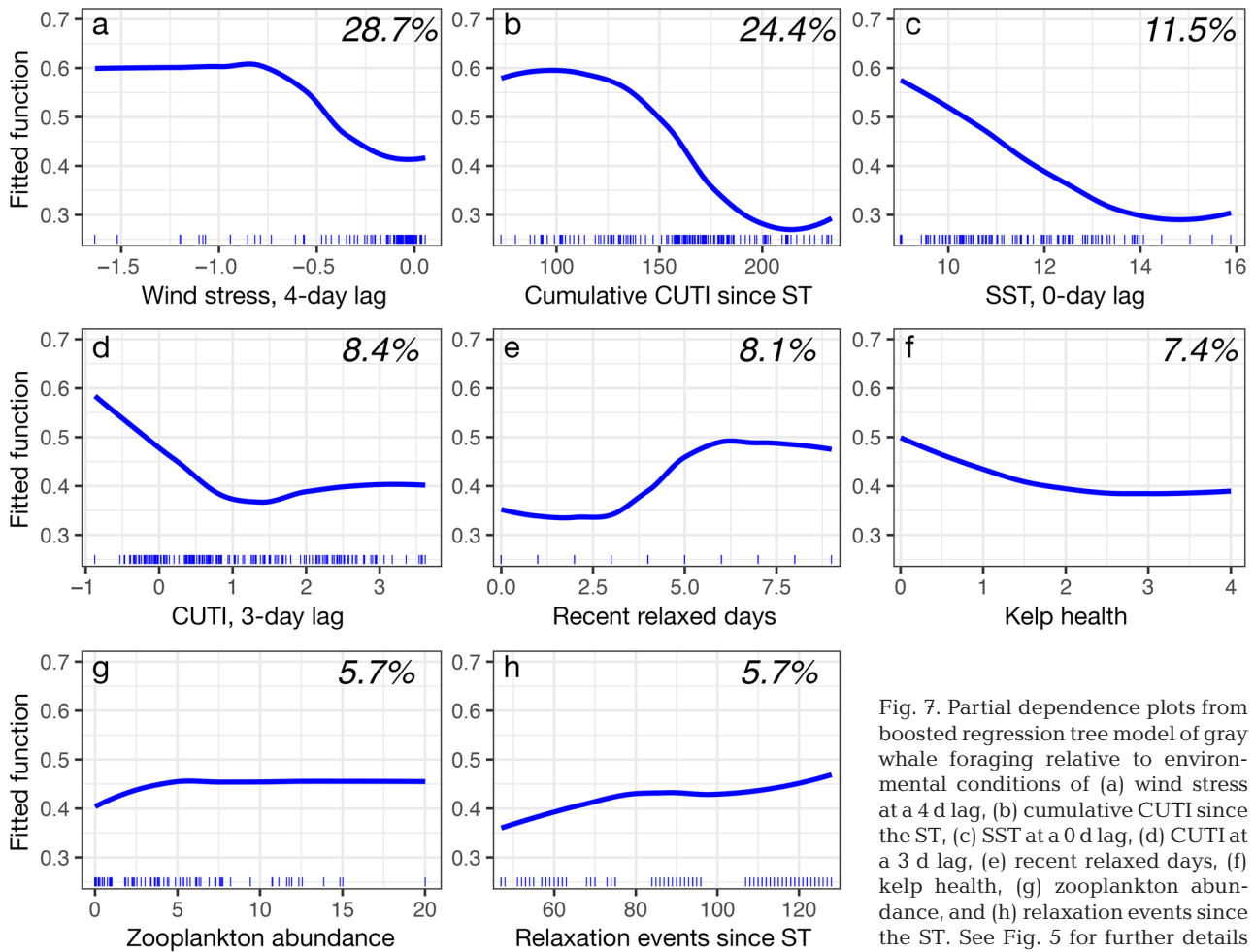


Fig. 7. Partial dependence plots from boosted regression tree model of gray whale foraging relative to environmental conditions of (a) wind stress at a 4 d lag, (b) cumulative CUTI since the ST, (c) SST at a 0 d lag, (d) CUTI at a 3 d lag, (e) recent relaxed days, (f) kelp health, (g) zooplankton abundance, and (h) relaxation events since the ST. See Fig. 5 for further details

decreased as upwelling accumulation increased. The SST functional response curve (11.5%; Fig. 7c) illustrates that high foraging effort occurred at cold temperature ranges (9–11°C). CUTI at a 3 d lag (8.4%; Fig. 7d) showed that whale foraging effort increased 3 d after CUTI values were above average. Five to 10 consecutive days of recent relaxation (8.1%; Fig. 7e) within the previous 10 d correlated with increased whale foraging, as did kelp condition (7.4%, Fig. 7f). The zooplankton abundance response curve (5.7%; Fig. 7g) showed a slight increase in whale foraging after zooplankton values rose above 0; otherwise, all values of relative zooplankton abundance above 5 contributed to whale foraging equally. Lastly, the number of relaxation days since the ST (5.7%; Fig. 7h) correlated with an increase in whale foraging. The top-ranked interactions between environmental variables found in the BRT_{whale} model were between SST and recent relaxation (Fig. 8a), cumulative CUTI and kelp health (Fig. 8b), and cumulative CUTI and the number of relaxation days (Fig. 8c; see also Table S2).

Unlike the interaction in the BRT_{zoop} model, the interaction between cumulative CUTI and kelp health showed that at every value of kelp health, whale foraging is high with a slight increase in foraging if kelp health was low.

4. DISCUSSION

Our results, derived from a 6 yr data set, contribute to the understanding of environmental drivers of both zooplankton availability and gray whale foraging response in nearshore areas of the Northern CCS. Results from BRT analysis demonstrate that predators and prey are influenced by the same environmental factors with similar functional relationships (Figs. 5 & 7), although these environmental factors had greater explanatory power for the prey model. We assessed the dynamics between upwelling and relaxation, as suggested by the IUH, and found that an intermittent state produced maximal predator and prey occur-

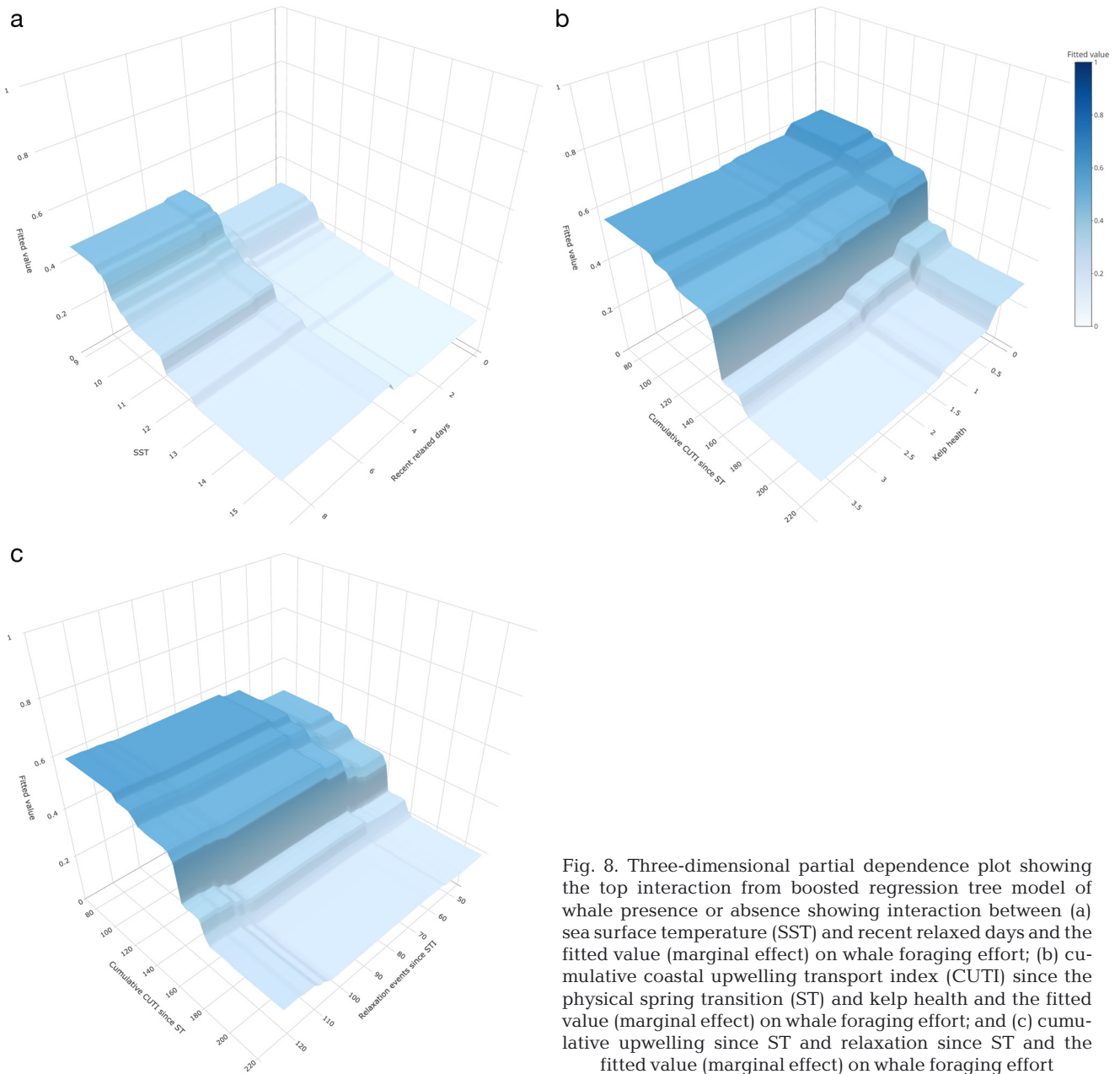


Fig. 8. Three-dimensional partial dependence plot showing the top interaction from boosted regression tree model of whale presence or absence showing interaction between (a) sea surface temperature (SST) and recent relaxed days and the fitted value (marginal effect) on whale foraging effort; (b) cumulative coastal upwelling transport index (CUTI) since the physical spring transition (ST) and kelp health and the fitted value (marginal effect) on whale foraging effort; and (c) cumulative upwelling since ST and relaxation since ST and the fitted value (marginal effect) on whale foraging effort

rence at both broad and fine temporal scales. While BRT_{zoop} and BRT_{whale} model results differed in what predictor had the greatest contribution in the model (kelp health for zooplankton relative abundance and wind stress at a 4 d lag for whale foraging effort), we found that the broad-scale accumulation of upwelling since the ST was the second-most important predictor in both models. Moreover, accumulation of relaxation days at the broad seasonal scale and the duration of relaxation days at the fine scale during the sampling period also contributed to models of both species occurrence in our nearshore study sys-

tem. These results provide further support for the importance of considering lag times and scale in the context of predator space use within hierarchical, dynamic marine environments (Torres 2017, Barlow et al. 2021). This knowledge gained can further inform investigations regarding top predator sensory cues and foraging strategies (Abrahms et al. 2019), especially in the very nearshore, where an understanding of the cross-shore transport of zooplankton is limited but may be influenced by similar velocity gradients found along the coastal boundary layer (Nickols et al. 2012).

4.1. Cross-correlation of fine-scale environmental variables with zooplankton and gray whales

Cross-correlation results revealed important lags between wind stress (4 d), CUTI (3 d), and SST (0 d) and relative zooplankton abundance (Fig. 4). Model results for both BRT_{zoop} and BRT_{whale} show that both zooplankton abundance and whale foraging effort increase 4 d after an upwelling-favorable wind event (Figs. 5g & 7a). Our results also describe increased zooplankton abundance and whale foraging effort 3 d after high CUTI values. Findings in Menge & Menge's (2013) study showed upwelling magnitude accounted for ~50% of the variance in ecological patterns in rocky intertidal regions, and our study also found upwelling magnitude to be a strong predictor, with CUTI at a 3 d lag as the third-top predictor in the BRT_{zoop} (12%) and fourth in the BRT_{whale} model (8.4%) (Figs. 5c & 7d). The variable-specific lags used in our analyses are within the ranges previously documented in the literature that describes wind-driven upwelling as a driver for larval transport in nearshore systems (Mace & Morgan 2006, Narváez et al. 2006, Papastephanou et al. 2006, Wilkerson et al. 2006, Roegner et al. 2007).

4.2. Cumulative upwelling and relaxation days as drivers of zooplankton and gray whales

On the broad, seasonal temporal scale, cumulative upwelling was the second-greatest driver of both zooplankton abundance and whale foraging effort. However, it is important to note that more upwelling since the ST was not always beneficial for predator–prey response. Indeed, we see a decline in zooplankton abundance and whale foraging effort after a cumulative CUTI value of approximately 150.

We also document that relaxation days, at both the fine temporal scale (recent relaxation within 10 d window) and at the broad seasonal scale (total number of relaxation days since the ST), impacted prey and predator occurrence. However, it is important to note these results differ between prey and predator. For recent relaxation, the highest zooplankton abundance occurred during 0–5 d of recent relaxation, while increased gray whale foraging effort was associated with relaxation 3 d prior, indicating that the greatest overlap in prey and predator species occurrence likely occurs when there are 3–5 d of relaxation within the past 10 d.

Cumulative relaxation days since ST and SST functional response curves illustrate increasing relative

zooplankton abundance at the extremes of both variables, yet whale foraging effort showed a positive relationship between the broad-scale number of cumulative relaxation days since ST and a negative relationship with fine-scale SST temperature (Figs. 5 & 7). Zooplankton abundance at higher temperatures may be caused by the retention of warmer water that is not advected during relaxation days, as zooplankton response to wind stress at a 1–3 d lag is positive, and warmer waters are associated with these events. Cooler temperatures in upwelling systems have been shown to be a reliable predictor of whale foraging behavior (Heyning 2001, Munger et al. 2009), and in this study, model results showed a negative relationship between gray whale foraging effort and increasing SST temperatures (Fig. 7). Additionally, the interaction between SST and number of recent relaxation days (Fig. 8A) shows that gray whale foraging was correlated with cool, upwelled waters after a recent relaxation period of approximately 5–8 d.

Zooplankton abundance as a driver in the BRT_{whale} model was one of the lowest predictors for whale foraging effort, explaining 5.7%. While prey metrics alone may not be sufficient for predictive modeling of gray whale habitat suitability, predators likely cue into environmental drivers that regulate zooplankton variability (Torres 2008). The difference in CrV deviance explained between the BRT_{zoop} and BRT_{whale} models (52.6 and 13.1%, respectively) show that while environmental factors explain much of the variance in zooplankton response, gray whale foraging effort is likely influenced by more drivers not evaluated in this study. However, these results demonstrate that environmental variables are influential bottom-up drivers of zooplankton abundance and subsequent gray whale foraging effort. While top-down predation pressure may impact zooplankton community structure, including potential gray whale predation impacts on zooplankton availability (Feyrer & Duffus 2011, Burnham & Duffus 2018), bottom-up regulation of zooplankton by environmental conditions likely plays a large role (Largier et al. 2006). However, documenting this relationship in very nearshore systems (<1 km from shore) is often prohibited by challenging survey conditions not conducive to traditional boat-based sampling. Whether prey abundance is regulated by top-down or bottom-up forcings is situation-dependent, and neither should be ruled out as a significant mechanism unless otherwise demonstrated (Ottersen et al. 2010). While the zooplankton abundance during our sampling season may have been impacted by top-down forcing on an hourly or daily scale, there appears to be no discern-

able pattern between whale foraging effort and zooplankton abundance across years (Fig. 2). Further investigation of environmental drivers of mobile gray whales at broader spatiotemporal scales can provide a more holistic understanding of these nuanced ecosystem dynamics across the PCFG foraging range.

4.3. Interactive effects of environmental variables on zooplankton and gray whales

Several variables revealed interesting interactive effects for both the BRT_{zoop} and BRT_{whale} models. The interaction between cumulative upwelling and number of relaxation days was important in both models but with different marginal effects on response. For BRT_{zoop} , it is clear that low broad-scale cumulative upwelling relative to values observed earlier in the field season paired with a low number of relaxation days resulted in high zooplankton abundance. However, if cumulative upwelling was high, as long as the number of relaxation days was sufficiently high as well, zooplankton abundance increased. Results from both interactions appear to align with the IUH where prey and predator response will be maximal at intermittent states of upwelling. In the BRT_{whale} model, whale foraging effort was at its maximum where cumulative upwelling since the ST was low to moderate, and the number of relaxation days since the ST was moderate to high (Fig. 7). The interaction between these variables demonstrates the balance needed between upwelling and relaxation (Fig. 8A). These results similarly align with the IUH, with predator foraging effort increasing with upwelling intermittency. Relaxation days are known to increase temperatures in the system; however, the interaction between SST and recent relaxed days shows that the system must be both relaxed and cool at the fine scale (days to weeks) to be positively related to whale foraging (Fig. 8a). While Menge & Menge (2013) proposed this hypothesis to address barnacle colonization and mussel growth rates, our results suggest this hypothesis may also hold for other zooplankton prey as well as whale predators in the nearshore system of Port Orford, Oregon.

The functional response curves for recent relaxed days and wind stress (Fig. 7) indicate how gray whale foraging effort increases when the system has been recently relaxed for 3–10 d or if there was a strong upwelling-favorable wind event 4 d prior. While these findings may seem contradictory, they in fact demonstrate that whales are sensitive to shifts in wind stress, as seen with blue whales (Barlow et al. 2021, Ryan et

al. 2022), where both upwelling-favorable winds and relaxation days drive productive foraging opportunities. This balance between upwelling and relaxation conditions was also found to be a strong predictor of PCFG gray whale density at the scale of the Northern CCS across 31 yr (Barlow et al. 2024).

4.4. Kelp condition as a driver of zooplankton and gray whales

Describing the relationship between intermittent upwelling and the biological response of prey and predator in our study area contributes to our understanding of how environmental variation affects multiple trophic levels (Hildebrand et al. 2024), especially as kelp systems are undergoing changes due to a rise in urchin barrens and environmental change (Rogers-Bennett & Catton 2019). Our results highlight the role of kelp condition as a primary driver for zooplankton abundance (Fig. 5), which aligns with the findings of Hildebrand et al. (2024). Kelp populations require the cold, nutrient-rich waters provided by upwelling in order to grow (Tegner et al. 1996), and here we find that fine-scale zooplankton abundance is maximized by an interaction between kelp and broad-scale seasonal upwelling accumulation (Fig. 6B). Our results suggest whales forage in areas of lower kelp condition; however, it should be noted this was a very low interactive effect compared to the BRT_{zoop} model. The interactive effect between kelp condition and cumulative CUTI shows that as long as cumulative CUTI remained moderate, whale foraging was elevated at every value of kelp condition (Fig. 8B). These findings suggest that environmental drivers may have an interactive effect with kelp condition to provide optimal conditions for whale foraging. Further investigation of the interactions between kelp condition and environmental variability may be useful in these nearshore systems where trophic relationships depend largely on kelp but where kelp abundance becomes less relevant as habitat complexity increases (Choat & Ayling 1987, Anderson 1994, Trebilco et al. 2015).

4.5. Future research directions

While our models of relative zooplankton abundance and PCFG gray whale foraging effort relative to environmental drivers perform well, these models are certainly not comprehensive. PCFG foraging effort should also be considered in the context of different prey availability metrics such as aggregation and

patch density, especially as these relate to shifts in upwelling conditions. For example, prey patch structure has been shown to change in response to variance in upwelling, where zooplankton aggregations swarm during upwelling events and scatter during relaxation (Benoit-Bird et al. 2019). There is also a mosaic of interconnected nearshore dynamics that future studies should investigate to better understand this study system, including the roles of fine-scale topography (Shanks & Morgan 2018, Killeen et al. 2023) and habitat complexity (Darling et al. 2017, Richardson et al. 2017), which would contribute to the current paucity of literature linking rugosity to marine mammal foraging (Cimino et al. 2020). Additionally, Shanks et al. (2003) investigated holoplankton retention in Port Orford and noted that the headland that forms the Port Orford Bight causes an 'upwelling shadow', which is a region of water protected from upwelling-favorable winds. This shadow results in a small-scale warm water feature in the lee of the Port Orford Bight, which may serve as an important retention and recirculation zone for primary productivity (Graham & Largier 1997). Indeed, PCFG whale density is elevated in the lee of prominent headlands along the Northern CCS (Barlow et al. 2024). 'Upwelling shadows' can act as convergence zones associated with greater zooplankton biomass (Woodson et al. 2007, Morgan & Fisher 2010, Ryan et al. 2010) and thus may be an important feature for future studies considering spatial analyses of prey availability for PCFG gray whales along the Northern CCS coastline with prominent headlands. On larger spatiotemporal scales, bottom-up mechanisms that produce a seasonal response in zooplankton life history are known to be sensitive to climate warming. Winder et al. (2009) documented a shift in zooplankton annual recruitment over 44 yr from predictable patterns to much more stochastic patterns due to climate warming. Thus, ecosystem shifts due to climate change pose an increasing threat to nearshore predator–prey dynamics and could impact prey abundance and distribution patterns, with subsequent impacts on predator health and vital rates.

4.6. Conclusions

PCFG whales are currently facing a range of threats, from loss of bull kelp habitat (Hildebrand et al. 2024), to increased physiological stress from vessel traffic and noise (Lemos et al. 2022b, Pirotta et al. 2023), behavioral disturbance from vessel traffic (Sullivan & Torres 2018), and low (Torres et al. 2022) and

variable (Lemos et al. 2020, Akmajian et al. 2021) body condition. Lower body condition has been linked to higher cortisol stress levels (Lemos et al. 2022a), indicating nutritionally compromised whales may not be as resilient to additional environmental stressors. Especially in a rapidly changing environment, continued monitoring and identification of the relationships between upwelling dynamics and prey is crucial to support the adaptive management of PCFG gray whales and their ecosystem. As this study presents new findings on the IUH relative to zooplankton prey and whale predators, future work should further investigate the influence of intermittent upwelling on prey availability and top predator foraging effort in upwelling systems across a range of spatiotemporal scales. Due to the dynamic and hierarchical nature of biological drivers in the nearshore environment, uncovering empirical relationships between drivers of habitat use and prey response metrics can be difficult (Folt & Burns 1999). However, results and methods from this study can help inform future research and management decisions concerning this small subgroup of gray whales by identifying the important scales of environmental processes that influence the distribution and availability of their primary prey.

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