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Predictable patterns within the kelp forest can indirectly create temporary refugia from ocean acidification

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HIGHLIGHTS

- Potential of kelp as ocean acidification refugia has been addressed through an integration of observations, modelling and mesocosm work.
- Kelp did not have a direct mitigating effect against OA in the low retentive habitats.
- Improved biological responses were observed in investigated calcifiers.
- Positive responses were related to increased predictability in pH autocorrelation signal and improved habitat provisioning through resource utilization.
- Kelp can improve ecosystem services

GRAPHICAL ABSTRACT

Outcomes:

Kelp in the low retentive water habitats do not mitigate against ocean acidification
Kelp creates more predictable habitat that improves fitness in marinecalcifiers

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ABSTRACT

Kelps are recognized for providing many ecosystem services in coastal areas and considered in ocean acidification (OA) mitigation. However, assessing OA modification requires an understanding of the multiple parameters involved in carbonate chemistry, especially in highly dynamic systems. We studied the effects of sugar kelp (*Saccharina latissima*) on an experimental farm at the north end of Hood Canal, Washington—a low retentive coastal system. In this field mesocosm study, two oyster species (*Magallana gigas*, *Ostrea lurida*) were exposed at locations in the mid, edge, and outside the kelp array. The Hood Head Sugar Kelp Farm Model outputs were used

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Oyster
Shell dissolution
Refugia

to identify dominating factors in spatial and temporal kelp dynamics, while wavelet spectrum analyses helped in understanding predictability patterns. This was linked to the measured biological responses (dissolution, growth, isotopes) of the exposed organisms. Positioned in an area of high (sub)-diel tidal fluxes with low retention potential, there were no measurable alterations of the seawater pH at the study site, demonstrating that the kelp array could not induce a direct mitigating effect against OA. However, beneficial responses in calcifiers were still observed, which are linked to two causes: increased pH predictability and improved provisioning through kelp-derived particulate organic resource utilization and as such, kelp improved habitat suitability and indirectly created refugia against OA. This study can serve as an analogue for many coastal bay habitats where prevailing physical forcing drives chemical changes. Future macrophyte studies that investigate OA mitigating effects should focus also on the importance of predictability patterns, which can additionally improve the conditions for marine calcifiers and ecosystem services vulnerable to or compromised by OA, including aquaculture sustainability.

Synopsis

Predictable autocorrelation signal within the kelp habitat can induce a more favorable environment for marine calcifiers despite not changing ocean acidification conditions.

1. Introduction

Ocean acidification (OA), predicted to significantly alter many marine ecosystems in the years ahead (Doney et al., 2020), is caused by the sustained absorption of anthropogenically derived atmospheric carbon dioxide (CO_2). The severity of OA depends on the baseline conditions and other anthropogenic stressors on the local and regional level (Feely et al., 2004, 2010; Kessouri et al., 2021; Bednaršek et al., 2020), impacting highly valued and culturally and economically important species and ecosystems (Doney et al., 2020; Bednaršek et al., 2021a.b; Waldbusser and Salisbury, 2014; Mostofa et al., 2016). As such, numerous mitigation and adaptation ocean-based solutions are being proposed for vulnerable marine coastal systems (IPCC, 2019). The use of coastal kelps could relate to such solutions from multiple perspectives.

Kelps (in the strict sense including only representatives of the order Laminariales) are brown macroalgae that have been recognized for its numerous roles in the coastal areas; it is considered a foundational primary producer and a critical habitat that supports higher trophic levels and protects coastal ecosystems, physically stabilizing substrate and providing biogenic structure, while enhancing species diversity and productivity (Dayton, 1985; Pfister et al., 2019; Nielsen et al., 2018; Krause-Jensen et al., 2018; Chung et al., 2013). Kelp canopy also supports diverse microbial communities, utilizing dissolved organic carbon excreted by kelp (Reed et al., 2010) and enhancing nitrogen cycling (Pfister et al., 2014). Massively produced kelp could be used for human consumption and animal feed, and on a large scale for biofuel production (Kumar et al., 2021). Kelps have also been considered for its potential to mitigate local acidic and hypoxic conditions (Hurd, 2015; Frieder et al., 2014; Koweek et al., 2017; Kapsenberg and Cyronak, 2019; Li et al., 2021). Although transient and confined to short-term periods during daylight and the most active growing season (e.g., Pfister et al., 2019), diel increases in pH demonstrated positive effects in some, but not all, marine species (Frieder et al., 2014; Hendriks et al., 2015; Hurd, 2015; Semesi et al., 2009; Wahl et al., 2018; Falkenberg et al., 2021; Young et al., 2022). Such effects sparked the discussion and emerging evidence of kelp as the OA management tool (Nielsen et al., 2018), applicable in protecting and restoring vulnerable habitats or serve in the aquaculture sustainability (Kaladharan et al., 2019; Ramajo et al., 2019; Saderne et al., 2015). However, it's becoming critically recognized that there is no uniformity in kelp-induced OA mitigation effect, because the scale of the buffering depends on the complex interactions of underlying physical processes (upwelling, currents, internal waves), kelp modifications of the flow attenuation and local physical characteristics and hydrodynamics patterns (Koweek et al., 2017; Hojishima and Hofmann, 2019; Traiger et al., 2022).

With such narrow focus on the OA mitigation, other, more complex effects of kelp on the change in the habitat specific parameters have been neglected so far, including the changes in the temporal variations of dominant periods (periodicity) and pH predictability, which can have impact biological responses (Bernhardt et al., 2020; Reed et al., 2015). Predictability, defined through the temporal pH autocorrelation, represents an important component of spatial and temporal variability at the coastal-estuarine interface. It indicates the extent to which the current environmental state allows the organisms to more efficiently predict future conditions and better adjust their responses through cue-based mechanisms, specifically in marine calcifiers (Bitter et al., 2021a, 2021b; Bednaršek et al., 2022).

Oysters are one of the most important aquaculture species that are directly impacted by OA and are a key foundation species, supporting key ecosystem services. The Pacific oyster, *Magallana gigas (previously called Crassostrea gigas)* is one of the most 'globalized' introduced species, while the native Olympia oyster (*Ostrea lurida*) remains an important contributor to regional oyster production. Because of their economic importance, Pacific oyster has been one of the most studied species, with well characterized OA responses from gene to shell, organismal and population level, which was determined as an integration of macro-physiological and micro-molecular sensitive pathways, transcriptional responses and identification of the tipping points (Dineshram et al., 2021; Meng et al., 2018; Ducker and Falkenberg, 2020; Chandra Rajan and Vengatesen, 2020; Chandra Rajan et al., 2021, 2023; Lutier et al., 2022). Shell dissolution has been recognized as a uniformed response, exemplifying that OA problem is mostly exacerbated as a shell dissolution, which is valid across marine calcifiers (Chandra Rajan et al., 2021, Bednaršek and Johnson, 2016; 2020, 2021; 2022), and only secondary, as a biomineralization problem (Fitzer et al., 2016). Shell dissolution was also impacted by pH variability and predictability (Meng et al., 2018; Bednaršek et al., 2022).

This study focuses on investigating the potential of a cold-water brown macroalgae, sugar kelp (*Saccharina latissima*), grown at an experimental kelp farm in the highly dynamic, low retentive coastal system at the north end of Hood Canal, Washington, USA that is seasonally impacted by low OA (Feely et al., 2010; Bednaršek et al., 2020; Bednaršek et al., 2021; Alin et al., 2024). The main objective of the study was (1) a temporal characterization of the biogeochemistry inside and outside of the kelp array, (2) and the identification of the changes related to the change in frequency and predictability that (3) are linked to the biological responses of two oyster species to examine how kelp-induced habitat changes could serve as a refuge from OA. The effects were tested on two juvenile oyster species, the Olympia (*Ostrea lurida*) and Pacific oysters (*Magallana gigas*), focusing on shell dissolution and growth, the two parameters that were explored in the preceding lab experimental study (Bednaršek et al., 2022). Oysters were kept in the mesocosms for 6 weeks along the transects of a kelp array, encountering pH conditions relative to the proximity of the sugar kelp, i.e., in the middle (mid), on the edge, and outside (out). Model outputs from the mathematical simulations *Hood Head Sugar Kelp Farm Model*, which has been validated by in situ field observations at various kelp array locations and used to determine the carbonate chemistry changes along the kelp pH gradients. We hypothesized that the metabolic activity of kelp would induce direct alterations in the carbonate system conditions, which would facilitate improved responses of the investigated oyster species, with such biological effect showing a gradient of beneficial responses from the middle of the-kelp array to its edges and outside. Instead, no mitigation of OA happened. Investigating biological responses focused on shell dissolution, growth, while stable isotope ratios of carbon and nitrogen (δ^{13}C, δ^{15}N) were used to trace the assimilation of organic matter sources, to identify if *Saccharina latissima* can be used as a food source for the two oyster species.

2. Methods

2.1. Seaweed farm infrastructure and monitoring

The sugar kelp (*Saccharina latissimi*) was cultivated in Hood Canal, located in Puget Sound, Washington (latitude 47.88, longitude −122.63). The site contained 38 grow lines that were suspended within a lattice at 3 m below the sea surface and aligned sensor buoys (Fig. S1). The kelp farm was installed in the fall of 2016 and monitored during the spring and early summer of 2017 and 2018. To supply the cultivation site, spools of seeded twine were produced at the seaweed propagation facility at NOAA Northwest Fisheries Manchester Research Station in Manchester, Washington. Seeded line with attached sporophytes of sugar kelp were transferred to the cultivation site and were attached to the cultivation lines (Fig. S1c).

2.2. Buoy and sensor deployment with performance and discrete measurements

Two moorings were deployed within 6 m north and south of the kelp array, with upward-pointing, bottom-mounted current meters located at 2.5 m depth, adjacent to each surface buoy (Fig. S1). Both buoys were equipped with surface pCO_2 systems (measurement uncertainty ± 2 μatm), as well as SeaBird SeapHOx sensors at 3 m depth, which continuously measured DO, temperature, salinity and pH (measurement uncertainty ± 0.02). In addition, field cruises were conducted to obtain discrete samples of seawater (see Section S1). pH data (total scale) were obtained from both buoys, while pCO_2 data (μatm) were derived from the south buoy. Discrete and continuous data recorded from the moorings served to validate the model (see section S2.4, Fig. S5).

2.3. The hood head sugar kelp farm model: A 3-dimentional simulation of ecological dynamics

The Hood Head Sugar Kelp Farm Model is a 3-dimensional simulation of the ecological dynamics of a sugar kelp, Saccharina latissima. The aim of the model development was to document and test the capability of the farmed kelp to remove CO2 and increase pH in the ambient waters flowing through the farm. Fig. S1d shows the infrastructure of the sugar kelp farm at the Hood Head site. The model (Fig. S2) operated within the Environmental Analysis Systems (EASy) GIS software known as Seaweed AquaModel, was developed as a custom-made plug-in. The EASy GIS contains the software tools to plot and map a variety of outputs related to Saccharina latissima productivity, biomass, frond carbon and nitrogen content (Fig. S2, S4), as well as environmental parameters such as temperature, salinity, pH, current speed, oxygen concentrations, dissolved inorganic nitrogen (DIN), and DIC (Fig. S3). The boundary conditions of the computational grid are updated regularly according to external data input files ingested by the EASy. Model output was continuous at the grid points within the lease area (Fig. S1d, yellow dots within the black rectangle, representing the 'mid', 'out', 'edge' locations within the kelp array) (see also Supplementary Material section S2). The circulation model, plankton model, and kelp metabolic models, including state variables, equation description, and constants, are detailed in the Supplementary Material (sections S2.1–3).

2.4. Comparison of ΔpH based on modeled simulations

In order to extract information on the contribution of the cultured kelp to changes in concentration and spatial distribution of pH and DIC, we ran two simulations: one with the kelp farm and one without the farm (difference between the Kelp and NoKelp simulations; see Fig. S7). This was done at five virtual locations: one in the center, two at the edges located within the SW and NE corners, and two open boundary cells of the computational grid. All other conditions were identical. The time series for pH difference was depicted as a delta (ΔpH) for the entire simulation from late May to July, when the biological experiments were conducted. We distinguished between pH magnitude and amplitude, with pH *magnitude* referring to the strength of the frequency (shown in the magnitude scalograms; Figs. 2 and S8), and pH *amplitude* referring to the maximum absolute values of delta pH (ΔpH, here as the difference between the Kelp and NoKelp simulation; Fig. 1, S7).

2.5. Temporal autocorrelation and wavelet analysis of diel pH data to characterize predictability based on model outputs

The goal of the analysis was to characterize environmental predictability patterns to infer physiological response to pH variability. We used two approaches as surrogates for environmental predictability: wavelet analysis and temporal autocorrelation analysis (Bernhardt et al., 2020). We used the wavelet analysis to determine whether significant periods stand out in the data compared with random noise, in other words, to determine whether the data exhibit periodicity (i.e. data has significant periods). Wavelet analysis to identify dominant periods of cyclical periodicity in pH time series at different locations within and outside the kelp array (mid, NE edge, SW edge, outside the kelp array) was done using the MATLAB R2021a transform package developed by Grinsted et al. (2014). Wavelet analysis is a type of spectral analysis that shows how the variance spectrum of frequencies changes over time (e.g. Torrence and Compo, 1998), applicable to the evaluation of environmental predictability for sensitive marine organisms (Bernhardt et al., 2020; Bitter et al., 2021a, 2021b; Bednaršek et al., 2022). Using a continuous wavelet transform package, these results allowed us to identify the relative strengths of the frequency components, such as pH periodicity of the temporal window from February to July as compared to daily or sub-daily periodicity. We also calculated temporal pH autocorrelation using MATLAB R2021a.

2.6. Mesocosm deployment and biological analyses

Two different oyster species, Pacific (*Magallana gigas)* and Olympia *(Ostrea lurida)* were chosen in the experiments as they are naturally present in the coastal embayments of the Puget Sound. Healthy spat oysters were obtained from the nearby hatchery, where they were exposed to the same conditions, which is important for their exposure history not to interfere with their responses in the mesocosms. Oysters were exposed in the mesocosms in the form of tailor-made meshed boxes for 6 weeks to different conditions at the mid, edge and outside locations relative to the kelp array, with three mesocosms per oyster species per location. The total number of examined Pacific and Olympia oysters was $N = 515$ and $N = 379$, equally divided between the mesocosms at three investigated locations. Oysters were preserved for subsequent analyses.

2.6.1. Shell dissolution and growth analyses

To allow the examinations under SEM, oyster shells were cleaned with sterilized seawater and prepared (Section S4.2 and S5). We followed preparation processes described in prior studies (Bednaršek et al., 2022; Beniash et al., 2010; Dickinson et al., 2012) and in the Supplementary Material (section S5.1) to prepare and analyze 42 Olympia oysters (15 'out', 12 'edge', 15 'mid') and 42 Pacific oysters (15 'out', 10 'edge', 17 'mid'). Over the examined growing edge, approximately 20–30 SEM images were produced per oyster individual per entire

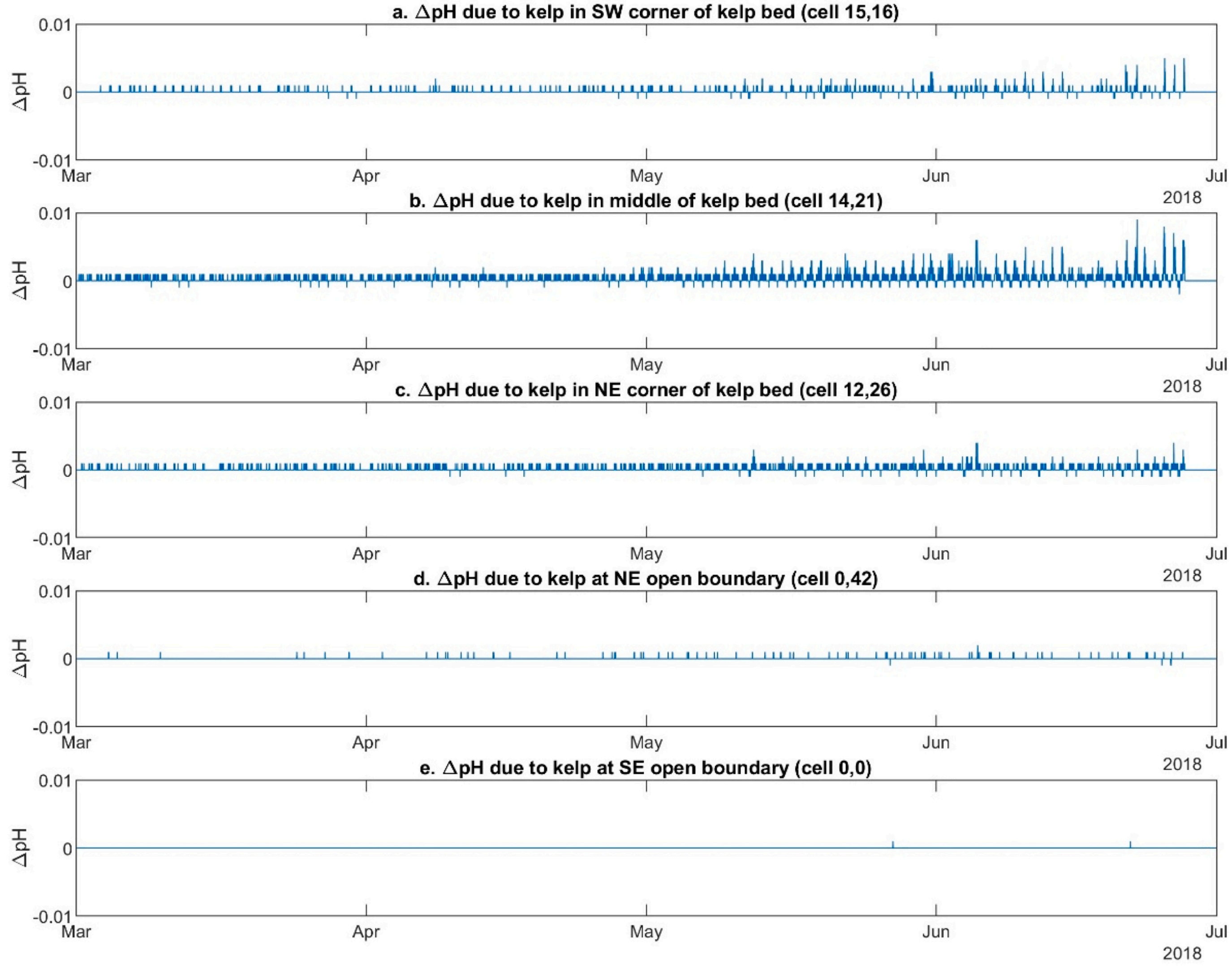

Fig. 1. Calculated ΔpH amplitude (calculated as the difference Δ pH between Kelp and NoKelp) based on the model outputs at different places within and around the kelp array (mid, edge, outside, see Fig. S1).

growing edge and each image was scored separately for the dissolution type (Type I, II, or III). The oyster dissolution categorization scheme over the growing edge is detailed in Bednaršek et al. (2022): ***Intact shell*** (*Type I*) indicates that the prism surfaces are mostly intact (*Type 0*) with a smooth appearance, or with surface dissolution in some organisms. ***Moderate dissolution*** (*Type II)* describes a partially eroded outer prismatic layer with exposed crystals. ***Severe dissolution*** (*Type III*) characterized a completely removed prismatic layer and partially exposed lower, cross-lamellar layer where the crystals are severely dissolved.

2.6.2. *Stable isotope analyses*

Kelp and oyster tissue were preserved on ice until arriving to the lab and frozen at −80 °C until further analyses. 18 oysters (9 Olympia and 9 Pacific individuals) were selected for stable carbon isotope determination (δ^{15}N & δ^{13}C) at three (mid, edge, out) different locations, i.e., three individuals per species per location. Preparation methods are described in the Supplementary Material (section S5.2). The isotope analysis of oyster gills was conducted at the Stable Isotope Facility at the University of California, Davis, measured on a EuroEA3000 element analyzer and an Iso-Prime stable isotope mass spectrometer, with mean SD for reference material replicates and the mean absolute accuracy for calibrated reference material for δ^{15}N ± 0.06 ‰ and ± 0.03 ‰, respectively, and for δ^{13}C ± 0.04 ‰ and ± 0.02 ‰, respectively.

2.7. *Statistical analyses of the oyster data*

Changes in shell dissolution for each oyster species per each meshed box were evaluated using a one-way analysis of variance (ANOVA) using location—mid, edge, or out—as a single predictor. The average dissolution score combining all three dissolution score types (I, II, and III) for an individual was used as the single response measure. Model-estimated means of the average dissolution at each location and the contrasts comparing results between locations were estimated from the ANOVA model using the *estimate_means* and *estimate_contrasts* functions, respectively, of the model-based R package, v0.8.6 (Makowski et al., 2020). The growth after 6 weeks was determined as a measurement of the length (mm) and wet weight (g) for each oyster species. Using a two-way ANOVA, we evaluated the interacting effects of location ('mid', 'edge/out') and treatment (pre- or post- experiment) to determine the effect of location on the biological responses. Initial analyses showed no significant differences among locations using three separate factor levels for the middle, edge, and outside locations. Therefore, the edge and outside locations were pooled to further evaluate potential differences in growth attributed to kelp and to increase the power of the statistical test. The estimated means from the ANOVA analysis are shown as delta length and weight, as the difference between pre- and post-exposure conditions. Multiple comparison tests evaluating all combinations of the predictor variables from the original ANOVA were evaluated using the Tukey HSD test as part of the base R stats package (R Core Team, 2022), including a p-value correction to account for increased likelihood of type I (false positive) error rates. All dissolution and growth analyses were conducted using the R Statistical Programming Language, R version 4.1.3 (R Core Team, 2022). Plots were created using the ggplot2 R package, v3.3.6 (Wickham, 2016). Differences were considered significant at alpha = 0.05.

3. Results

3.1. Physical-chemical characterization of the kelp system

Saccharina latissima grew most intensely during April to mid-June period, followed by a rapid degradation of material in the weeks followed because of increased blade loss due to erosion, epibiont fouling and the leakage of dissolved organic material (DOM) from kelp blades (Fig. S2). Carbon and nitrogen content in *Saccharina latissimi* indicated no statistically significant differences in carbon and nitrogen content in kelp fronds during the growth period, with mean carbon and nitrogen content for kelp blades of 20.4 % and 2.09 % and high correlation between the two elements.

Time series from February through early July recorded the water properties as its passes through the kelp array from the north or south depending upon the tidal cycle, which is based on mooring observations depicting changes in the amplitude of the following biogeochemical variables (Fig. S6): temperature, salinity, pH, and oxygen. Seasonal temperature showed a steady increase over the observed period, reaching values up to 12–13 °C, after which diel temperature variations prevailed. Salinity dynamics also changed over weekly to monthly timescales, with salinity ranging from 27 to 29 psu. pH in waters passing the farm ranged from 7.73 to 8.30 units and varied by as much as 0.2 units within a single day. The lowest pH occurred during winter and increased with the initial onset of phytoplankton productivity in March (Bednaršek et al., 2021a). The two other peaks in primary productivity occurred in early May and from late May to early June (Fig. S5, S6), with pH ranging between 8 and 8.3, which was related to increased kelp biomass and productivity (Fig. S2). Mid-June was characterized by a pH decline of about 0.2 units, when the pH dropped to around 7.9. The large, short-term variations in pH are diel and are largest during periods when pH is high. The oxygen concentration ranged from 8 to 14 mg/l and varied as much as 2 mg/l within a single day, with an important feature of a positive correlation between pH and oxygen (Fig. S6).

3.2. Comparison of ΔpH amplitude and magnitude change based on modeled simulations

In addition to the time series, model outputs were also recorded at five virtual stations specifically to delineate the pH change. Over the entire period, the largest pH amplitude (ΔpH) began to increase in May,

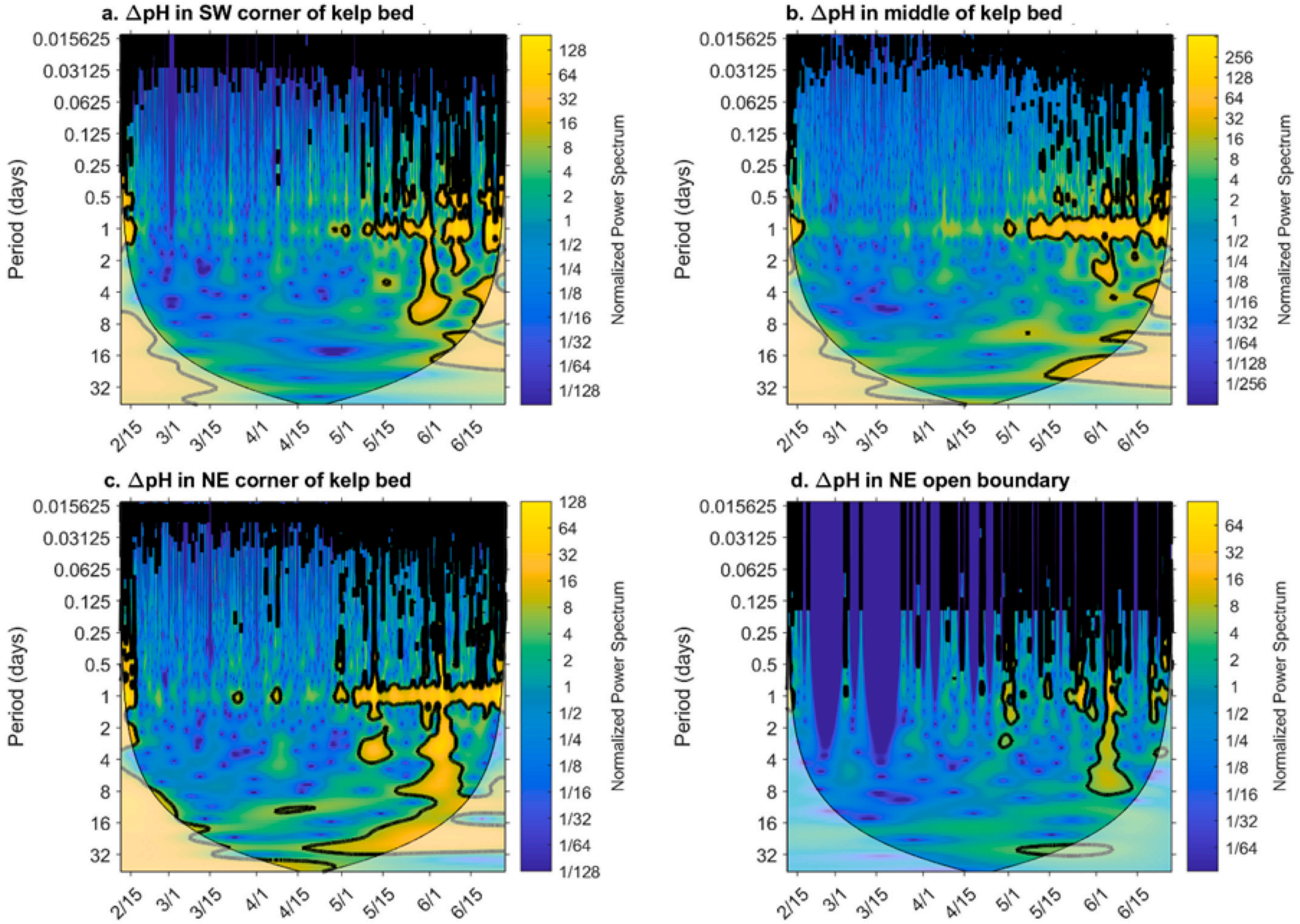

Fig. 2. The results of a wavelet analysis with the Hood Head Sugar Kelp Farm Model in which the difference between the pH conditions at the middle of the kelp array in the absence of the farm is subtracted from the presence of kelp array. Clockwise from upper left: SW edge corner, middle of kelp array, NE open boundary cell, NE edge corner of kelp array). Areas highlighted in yellow represent significant values at the high end of the normalized power spectrum – that is, the dates (x-axis) and temporal periods (y-axis) of the simulation, which have the greatest strength of environmental predictability.

with the greatest increase recorded in June, occurring in the middle of the kelp array (cell 14,21). This is because kelp uses carbon, resulting in a decrease in modeled DIC, as well as an increase in pH, compared to the run without kelp (Figs. 1, S6, S7). Lower ΔpH amplitude was observed at the SW and NW edges of the array, while there was no ΔpH observable at the open boundaries outside the kelp array (E and NE open boundary cells; Figs. 1, 2, S6 and S7). Despite the spatial difference across three locations, the maximum amplitude of the ΔpH over the April–July period was generally <0.01 pH units at all locations, with the average ΔpH <0.01 (Fig. 1, S7). Such a trend was observed over the entire season, as well as during the most productive season that coincided with the mesocosm co-cultivation experiment (May–July), signifying a negligible impact of the kelp patch on ΔpH diel amplitude (Fig. S9). Moreover, the diel ΔpH variations between the kelp and its surrounding habitat were also insignificant (Fig. S9). This indicates that the signals with the farm are dominated by the ambient conditions of water flowing through the farm rather than the metabolism of the cultured kelp.

We also identified the temporal variations of dominant periods in the pH time-series from February–June (Fig. 2, S8). Wavelet analysis, a type of spectral analysis, shows temporal variations in the variance spectrum of frequencies and identifies the magnitude of the frequency components (e.g. seasonal, daily, or sub-daily periodicity). Significant periods that are depicted in wavelet scalograms indicate the temporal scales of environmental predictability that are present for marine organisms (Bernhardt et al., 2020). Based on the pH wavelet scalograms depicting ΔpH at four model capture cells ('mid', 'NW', 'NE', 'out'), the strongest oscillations were observed with a period of one day. We observed that the 'mid' kelp array location had the greatest daily ΔpH magnitude of frequency, while these oscillations were weak or absent from the capture cells most distant from the farm. These oscillations were weak at the start of the simulation and strengthened at the beginning of May (Fig. 2, S8), coinciding with the greatest diel cycle of photosynthesis (kelp) productivity (Figs. S2, S6), here demonstrated by the high-power levels spreading out horizontally at the one-day period. Moreover, the wavelet plots for Δoxygen are similar to those of ΔpH (Fig. S8). This pattern can only be explained by the diel cycle of photosynthesis and respiration and the increases in the amplitude of this diel cycle with increases in the biomass of the kelp array, further supported by the patterns observed for the changes in DIC and pH (Fig. S7). Outlined areas in yellow (Fig. 2) show the occurrence of periods that are statistically significant – that is, the dates (x-axis) and temporal periods (y-axis) of the simulation that have the greatest environmental predictability at the scale of the significant periods.

3.2.1. ΔpH autocorrelation signal

Autocorrelation plots, which were generated from the model outputs (Fig. 3) show ΔpH autocorrelation differences between the Kelp and NoKelp monthly simulations at four capture cells from March to June. The ΔpH autocorrelation pattern became noticeable in the April–May period, with a significant increase in June, when kelp productivity was at its peak (Fig. S2, S6), leading to higher ΔpH autocorrelation. ΔpH autocorrelation at 24- and 48-h lag was the highest in the middle of the kelp array, while considerably smaller on its edge, and almost negligible outside the array (Fig. 3). This suggested that ΔpH associated with changes in productivity due to the kelp bed is the most predictable in the center of the kelp array and the least predictable at the boundaries.

3.3. Biological responses

3.3.1. Biological responses: Shell dissolution in two oyster species

Biological responses, including shell dissolution, growth, stable isotopes (Figs. 4–6) in two oyster species (Pacific and Olympia) positioned at three different locations ('mid', 'edge', and 'out') were reported after the 6-week exposure from mid-May to the end of June. For both of the

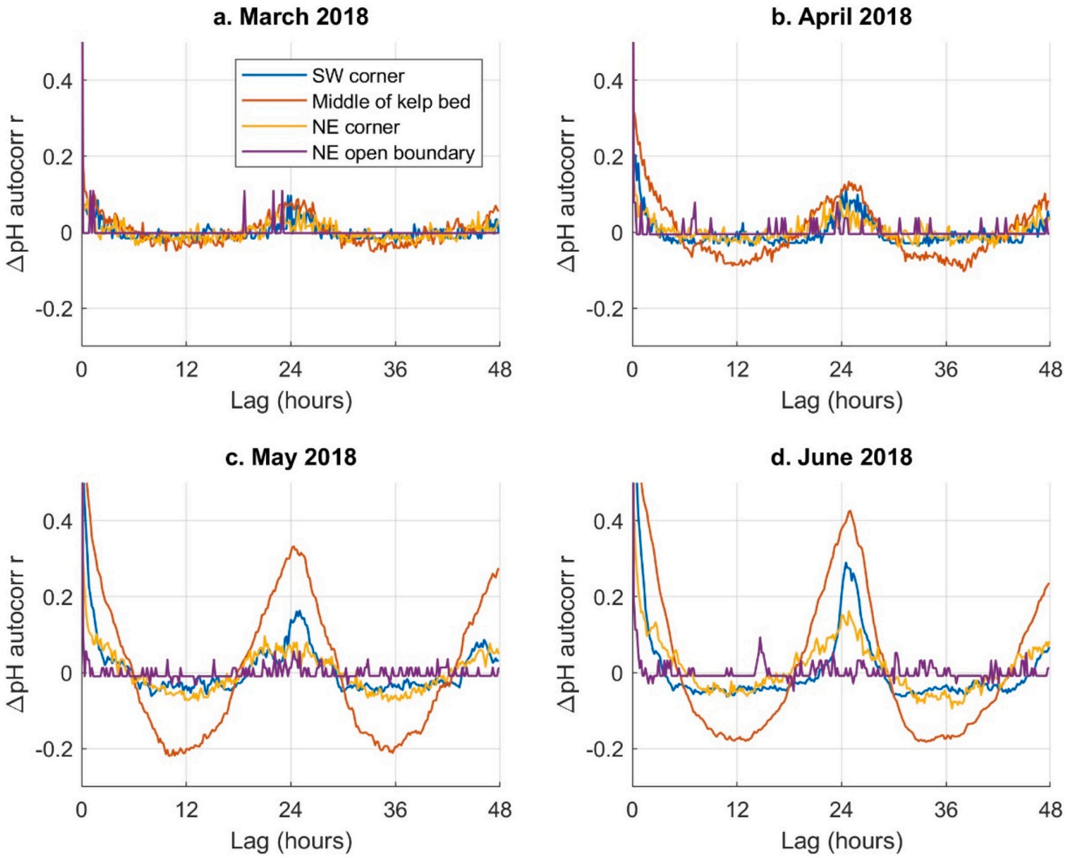

Fig. 3. ΔpH autocorrelation plot of the difference between simulations with and without kelp (Kelp and NoKelp) during the March – June period.

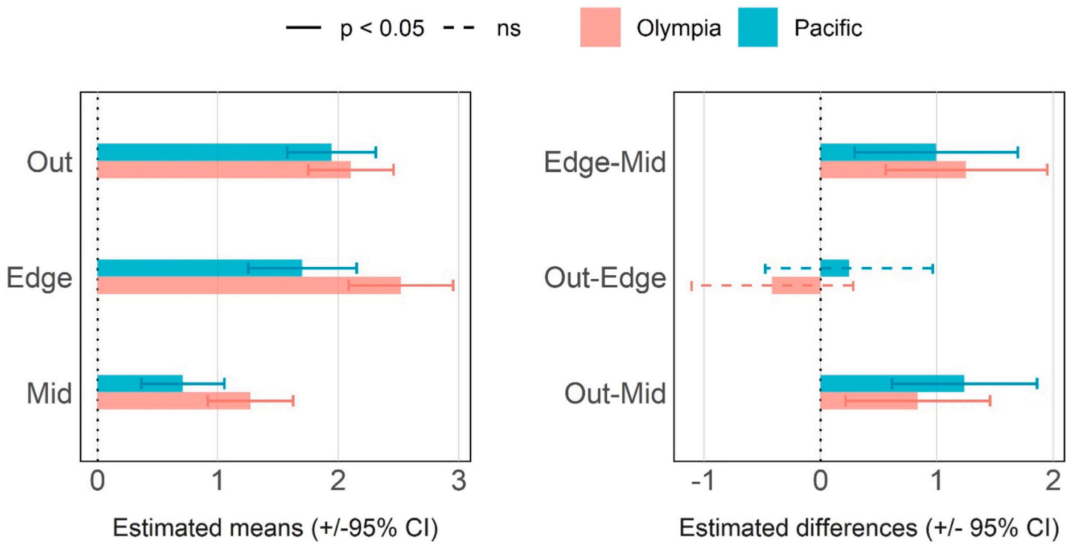

Fig. 4. Shell dissolution across the various locations (‘mid’, ‘out’, ‘edge’) for both Pacific and Olympia oyster species. Model estimates of mean dissolution by treatment (location) are shown in (a) and pairwise comparisons between treatments are shown in (b). Treatment comparisons in (b) that are significantly different are indicated as dotted lines.

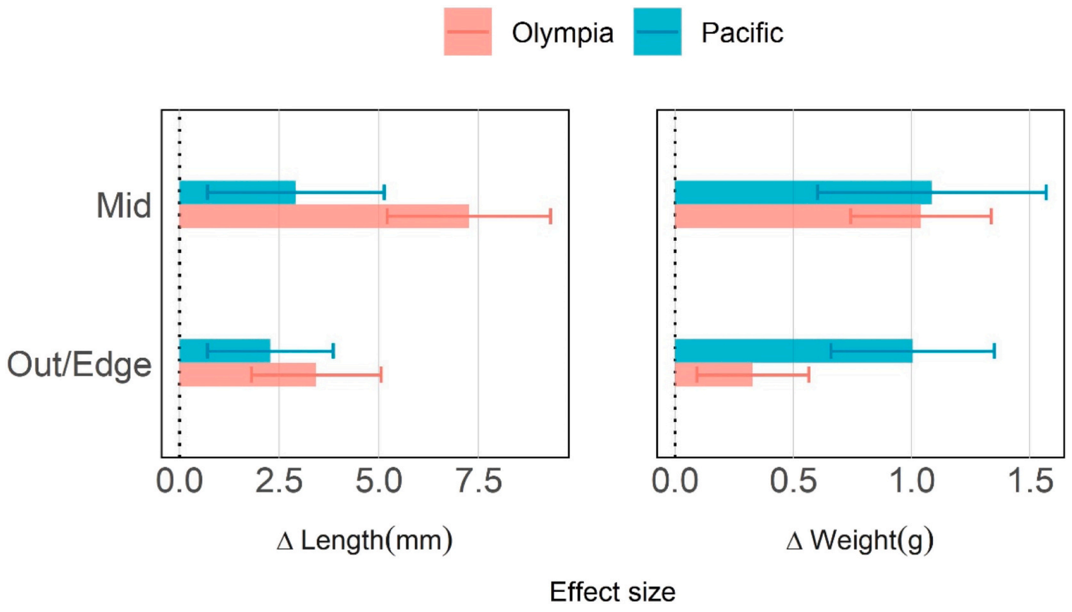

Fig. 5. Statistical outcomes for Olympia and Pacific oyster biological responses (shell growth (length, wet weight) at three investigated locations (‘mid’, ‘out’, ‘edge’).

oyster species, there were significant differences in shell dissolution among locations ($F = 13.6$; $df = 2, 39$; $p < 0.001$ for Pacific; $F = 11.4$; $df = 2, 37$; $p < 0.001$ for Olympia). Pairwise comparisons among the locations for both species showed significantly more dissolution observed outside compared to the middle of the kelp array ($t = 5.0$; $p < 0.001$ for Pacific; $t = 3.4$; $p = 0.004$ for Olympia), as well as in the middle compared to the edge ($t = 3.5$; $p = 0.002$ for Pacific; $t = 4.5$; $p < 0.001$ for Olympia), while neither species exhibited significant differences between the array’s edge and outside (Fig. 4).

3.3.2. *Oyster growth analysis*

For both oyster species, growth parameters, i.e., length and wet weight, of each individual oyster were investigated at all three locations (‘mid’, ‘edge’, and ‘out’) and were compared to their initial (pre-exposure) length and wet weight. Both length and weight were significantly greater after the cultivation irrespective of the locations for two species (Fig. 5). Specifically, Olympia oysters showed significant increase in both length and weight within the middle of the kelp array compared to outside and the edge, indicating a faster growth in the middle of the kelp array (Fig. 5). For the Pacific oyster, although more variable in the pre-exposed samples, significantly greater length extension was observed over time in the mid compared to outside and the edge. The same was observed for the weight increase in the edge treatment compared to the outside, while the shells in the middle were not significantly different from the outside (Fig. 5).

3.3.3. *Stable isotope analyses to identify oysters’ food source*

There were distinctive differences between the stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ between the two oyster species and the location of the exposure (‘mid’, ‘out’, and ‘edge’). The $\delta^{13}C$ and $\delta^{15}N$ isotope values

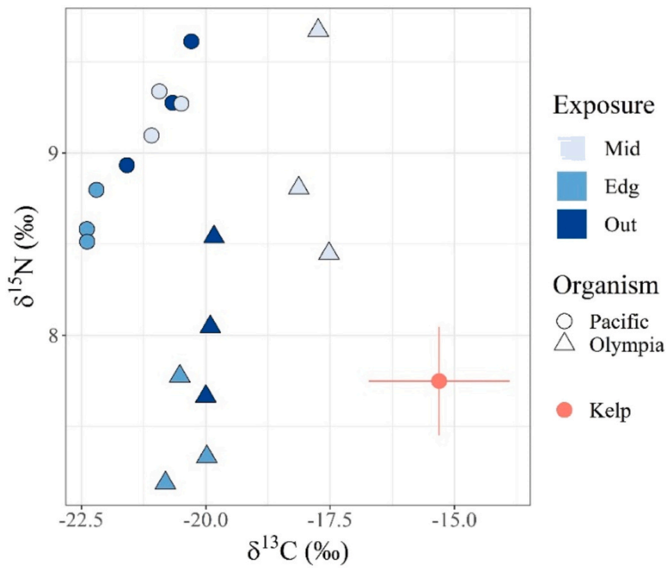

Fig. 6. Isotope ratios in the tissue of both oyster species (Pacific as circles, Olympia as triangles) colored by various locations ('mid', 'out', 'edge') relative to the isotope ratio of kelp (mean and standard deviation).

ranged between −17.5 to −22.5 ‰ and 6.5 to 10 ‰, respectively, whereas kelp particulate organic matter (POM) ranged from −11.5 ‰ for $\delta^{13}C$ and 7.5 ‰ for $\delta^{15}N$ (Fig. 5). The range in the isotopic values between the oysters was different, much greater in Olympia compared to the Pacific oyster, especially within the 'mid' kelp location. The $\delta^{13}C$ isotope ratios in the Olympia show 2 ‰ ('mid') to 4.5 ‰ ('out', 'edge') depletion, and 0 ‰ ('out', 'edge') to 1 ‰ ('mid') in $\delta^{15}N$ enrichment compared to the POM in the kelp (Fig. 6). Similarity in $\delta^{13}C$ and trophic shift smaller than 2 ‰ in $\delta^{15}N$ in the oysters from the 'mid' location indicate that POM of the kelp served as one of the food sources for Olympia oyster. The isotopic signature of Olympia oysters at the edge and outside showed that sources other than kelp were contributing to their food diet. Conversely, a much greater trophic shift in both $\delta^{13}C$ and $\delta^{15}N$ in Pacific oysters compared to kelp across all locations indicated that kelp did not contribute to their diet as a food source. Overall, the isotope ratio between Pacific and Olympic oysters seems to reflect different food sources between the two oysters within the mid kelp array.

4. Discussion and conclusion

Macroalgae ecosystems have received a lot of attention as a potential mitigating strategy against OA, which was previously demonstrated for the highly retentive areas, while our results show that OA mitigation is not an efficient strategy in the highly dynamic systems with low retentive capacity. However, observed positive biological responses in this show the kelp to play a role in improving habitat suitability though increased pH predictability pattern that allows organisms to improve their fitness. As such, kelp induced pH predictability represents an important indirect benefit, which has not been accounted for before as the ecosystem service.

4.1. Hydrodynamics impacting pH dynamics

The importance of hydrodynamic conditions and thus related site-specific conditions, altering the range of chemical conditions, has been recognized before in the context of the biological effects. The strength of seawater chemistry modifications depends on the residence time and current speed of the water within the macrophyte habitat (e.g., Truchot and Duhamel-Jouve, 1980; Hurd, 2015; Mostofa et al., 2016; Traiger et al., 2022). Our results show that whatever pH modifications were induced by the kelp metabolism there was no measurable signal of the pH amplitudes and diel pH change (Fig. 1, S7, S9). In model simulations of the kelp farm dynamics during the spring and summer, the largest decreases in DIC and pH (Figs. S7) were found in the middle of the kelp array during periods of weak currents, yet the differences in the middle of the array compared to the outside were insignificant. In fact, the highest ΔpH amplitude were around ±0.004 and were more than five times lower than the uncertainty of pH observations (±0.02), i.e. below the range of detection given the measurement uncertainties by the best available oceanographic instruments. The lack of observable changes was attributed in part to high average current velocities at the Hood Head site (Fig. S6), which was driven by the high (sub)-diel tidal fluxes and resulted in low residence time of seawater within the kelp farm, eliminating any OA mitigation effects as well as positive effects on the co-exposed or co-cultured species. Given the importance of the hydrodynamics-related pH conditions, the design, location, and scaling of an effective cultivation kelp layout is critically dependent on a prevailing hydrodynamic regime (Kaladharan et al., 2019). In addition, accurate and cost-effective methods for measuring carbon uptake and OA buffering need to be implemented at the low retentive testing sites.

4.2. Predictability-induced indirect benefits

Observed significant temporal pH variations of dominants frequencies indicate the temporal scales of environmental predictability that are present with the mid kelp array. The greatest daily ΔpH magnitude of frequency was most significant in the May–June period (Figs. 2, 3), coinciding with intense kelp growth and production (Fig. S2), creating significant positive temporal ΔpH autocorrelation. Based on the lab experimental results conducted previously (Bednaršek et al., 2022), where lower predictability negatively impacted oyster responses, this provided a cue that the higher pH autocorrelation was a significant signal affecting in situ biological response, contributing towards improved conditions for these aquaculture species. In general, habitats with more predictable patterns allow the organism to effectively track and anticipate future conditions more accurately (Reed et al., 2010, 2015; Bitter et al., 2021a, 2021b; Bernhardt et al., 2020), potentially reversing negative effects triggered with enhanced OA in the coastal areas (Bednaršek et al., 2022). Higher pH autocorrelation signal within the kelp likely allowed organisms to adjust their responses compared to the outside the kelp habitat with lower predictability. For example, organisms within the kelp would likely pre-activate less stress-related signaling pathways compared to the outside where the baseline gene expression might be elevated (Bitter et al., 2021a). As such, predictability as a parameter should be considered for more comprehensive predictions of responses in coastal kelp habitats. Here, we also emphasize that the background environmental conditions could not have influenced the results of this study for the following reasons: first, this was well-executed control experimental trial with randomized experimental design, with clearly delineated control (out) and perturbed (mid kelp array) conditions; second, the entire area of the kelp array and outside (control) site all experienced the same background conditions, which was verified from the observations through the entire duration of the experiments, with no deviations in data that could in any unintended or uncontrollable way impact biological responses; third, all spat oysters were derived from the nearby hatchery, removing any confounding effects of their exposure history, and were all healthy and in intact condition prior to mesocosm deployment.

4.3. Shell dissolution as a primary driver of calcifiers vulnerability

Shell dissolution is one of the most sensitive and well-studied responses in oysters (Chandra Rajan et al., 2021; Bednaršek et al., 2022), with the application as a field parameter for the monitoring of the impact of OA in the field. Recent studies agree that Pacific oysters can retain their biomineralization capacity and organismal vulnerability occurs below pH of 7.4 (Lutier et al., 2022), however severe shell dissolution seems to be a prevailing problem that occurs at higher pH. This is assumed to be related to the reduction in organic shell content originating from the loss of periostracal proteins and prismatic layer proteins, further enhancing shell dissolution and reducing the function of periostracum protection (Chandra Rajan et al., 2021). This pattern of OA-triggered dissolution as a reason for concern is not pertaining only to various groups of oysters, but is generalizable across many calcifiers, particular in their early stage, and was demonstrated among others in pteropods, scallops, clams (Talmage and Gobler, 2010; Dickinson et al., 2013; Bednaršek and Johnson, 2016). The fact that increased predictability in the kelp reduces the level of dissolution thus addresses a primary concern for marine calcifiers. The results of this study show a decline in dissolution in both oyster species within the mid kelp characterized by higher compared to lower pH autocorrelation outside (Figs. 3, 4) and previously validated by the lab study (Bednaršek et al., 2022), where the benefits were observed after 2 to 4 weeks of exposure, which is comparable to the timeframe observed in the studied kelp array. There was also some underlying shell dissolution observable on the shell in all samples, which is likely related to the occurrence of lower than 7.7 pH values (Bednaršek et al., 2022), which occurred the beginning of June and, more sporadically, also in July (Fig. S5, S6), rather than the effects of the diel variability (sensu Garner et al., 2022), which was negligible in this study (Fig. S9).

4.4. Kelp provisional services for marine species and ecosystems

In addition to reduced shell dissolution, Olympia oyster grew faster within the kelp than outside and faster than Pacific oyster. Such observable difference was not the case for the Pacific oyster. The most likely reason for location-specific growth differences is due to differential utilization of the kelp as a feeding resource. Kelp detritus has been shown to provide a food source for various marine species (Duggins and Eckman, 1997; Levinton et al., 2002). Our results show that Olympia oysters fed on POM and this likely enhanced its growth, while the Pacific oyster show an absence of any kelp-related isotopic signature, and this lack of POM utilization might be linked to slower growth. We note that our data serve as preliminary results, with a large isotope range indicating that oysters are feeding on other sources, e.g., Pacific oyster isotope signatures in δ^{13}C and δ^{15}N are similar to the sedimentary organic material and benthic macroalgae, as reported by Yang and Hoon (2009). In general, studies are still lacking on the importance of kelp-derived POM as a potential food source for suspension feeders with ecological or integrated multi-trophic aquaculture systems (Bustamante and Branch, 1996; Xu and Yang, 2007; Walton et al., 2022; Xu et al., 2016), with such contribution of seaweed arrays being demonstrated in bivalves (Bustamante and Branch, 1996; Xu and Yang, 2007), while this qualitative study is the first one showing *Saccharina latissima* to provide a food source to the filter-feeding Olympia oysters. Such relationships would be further supported with additional isotope data on alternative feeding sources outside of the kelp beds, as well as to quantitatively establish importance of kelp as a food source. Finally, given the importance of removal of the kelp POM through filter feeding, the co-cultivation of shellfish and seaweed could indirectly take up a volume of coastal ocean carbon.

4.5. Kelp-induced direct and indirect benefits

Kelp carries multiple direct and indirect benefits, especially during low pH conditions and/or in combination with high food availability in the natural environment. The negative impacts of low in situ pH could be offset by the higher predictability, while the availability of kelp as a food resource can have a booster effect at the end of the spring and summer, when other food sources are scarce. This study thus infers that for these regions, kelp's natural presence or cultivation would indirectly improve habitat suitability conditions, making such areas less vulnerable. The role of kelp could thus be explored in the context of future adaptive strategies to climate change specifically related to vulnerable species and OA-related habitats, including marine protected areas, and in support of the co-cultivation with aquaculture industry and for the carbon fixation (Tang et al., 2011; Nielsen et al., 2018; Fernández et al., 2019; Xiao et al., 2021).

5. Conclusions

We conclude that a complex combination of physical, chemical, and biological processes determines the efficacy of kelp farms for creating direct or indirect mitigating effects with respect to OA and broader. Being focused on an area of high (sub)-diel tidal fluxes with low retention potential, this study can serve as a comparative site for many coastal bay habitats with prevailing physical forcing on the carbonate chemistry and carbon sequestration. Cultivating kelp in highly dynamic systems does not exert a direct mitigating effect on the carbonate chemistry (sensu Hurd, 2015; Gattuso et al., 2018); OA mitigation capacity is dependent on the size, location, and scaling potential. Indirectly, kelp improved habitat conditions for marine calcifiers through the positive pH autocorrelation signal related to increased predictability and food provisioning. Based on the predictability-induced positive effects, kelp could provide low-cost spatial refugia and a future adaptive strategy for mitigating negative effects, which would likely not be limited to OA. We stress the importance of conducting a priori comprehensive kelp array design to gain the full benefits of the local setting to achieve combined mitigation and adaptation effects. Future macrophyte studies should focus more on the importance of predictability patterns, with the preliminary results of this study suggesting for the predictability to be potentially added to the list of kelp attributes as a nature-based solution. Cumulatively, this can improve the scope of the natural climate solution, and further reduce the impact of anthropogenic signature across the coastal oceans (sensu Corrigan et al., 2022; Farghali et al., 2023). Given the plentitude of ecosystem services, natural kelp forests need to be urgently monitored (García-Reyes et al., 2022), protected and restored given their fast, climate-change induced decline (Smale et al., 2013).

Abbreviations

OA	ocean acidification
POM	particulate organic materials

CRediT authorship contribution statement

Nina Bednaršek: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing – original draft, Writing – review & editing. **Greg Pelletier:** Data curation, Formal analysis, Investigation, Visualization, Writing – review & editing. **Marcus W. Beck:** Formal analysis, Software, Visualization, Writing – review & editing. **Richard A. Feely:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Supervision, Validation, Writing – review & editing. **Zach Siegrist:** Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – review & editing. **Dale Kiefer:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Supervision, Validation, Writing – review & editing. **Jonathan Davis:** Conceptualization, Data curation, Funding acquisition, Project administration. **Betsy Peabody:** Conceptualization, Funding acquisition, Project administration, Writing – review & editing. **Jonathan davis:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.174065.

References

Alin, S.R., Newton, J.A., Feely, R.A., Siedlecki, S., Greeley, D., 2024. Seasonality and response of ocean acidification and hypoxia to major environmental anomalies in the southern Salish Sea, North America (2014–2018). Biogeosciences 21 (7), 1639–1673.

Bednaršek, N., Newton, J.A., Beck, M.W., Alin, S.R., Feely, R.A., Christman, N.R., Klinger, T., 2021. Severe biological effects under present-day estuarine acidification in the seasonally variable Salish Sea. Sci. Total Environ. 765, 142689.

Bednaršek, N., Beck, M.W., Pelletier, G., Applebaum, S.L., Feely, R.A., Butler, R., Byrne, M., Peabody, B., Davis, J., Štrus, J., 2022. Natural analogues in pH variability and predictability across the coastal Pacific estuaries: extrapolation of the increased oyster dissolution under increased pH amplitude and low predictability related to ocean acidification. Environ. Sci. Technol. 56 (12), 9015–9028. https://doi.org/10.1021/acs.est.2c00010.

Bednaršek, N., Feely, R.A., Beck, M.W., Alin, S.R., Siedlecki, S.A., Calosi, P., Norton, E.L., Saenger, C., Štrus, J., Greeley, D., Nezlin, N.P., 2020. Exoskeleton dissolution with mechanoreceptor damage in larval Dungeness crab related to severity of present-day ocean acidification vertical gradients. Sci. Total Environ. 716, 136610.

Bednaršek, N., Johnson, J., 2016. And Feely, R.A., 2016. Comment on peck et al: vulnerability of pteropod (Limacina helicina) to ocean acidification: shell dissolution occurs despite an intact organic layer. Deep-Sea Res. II Top. Stud. Oceanogr. 127, 53–56.

Beniash, E., Ivanina, A., Lieb, N.S., Kurochkin, I., Sokolova, I.M., 2010. Elevated level of carbon dioxide affects metabolism and shell formation in oysters Crassostrea virginica. Mar. Ecol. Prog. Ser. 419, 95–108.

Bernhardt, J.R., O'Connor, M.I., Sunday, J.M., Gonzalez, A., 2020. Life in fluctuating environments. Philos. Trans. R. Soc. B 375 (1814), 20190454.

Bitter, M.C., Kapsenberg, L., Silliman, K., Gattuso, J.P., Pfister, C.A., 2021a. Magnitude and predictability of pH fluctuations shape plastic responses to ocean acidification. Am. Nat. 197 (4), 486–501.

Bitter, M.C., Wong, J.M., Dam, H.G., Donelan, S.C., Kenkel, C.D., Komoroske, L.M., Nickols, K.J., Rivest, E.B., Salinas, S., Burgess, S.C., Lotterhos, K.E., 2021b. Fluctuating selection and global change: a synthesis and review on disentangling the roles of climate amplitude, predictability and novelty. Proc. R. Soc. B 288 (1957), 20210727.

Bustamante, R.H., Branch, G.M., 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. J. Exp. Mar. Biol. Ecol. 196 (1–2), 1–28.

Chandra Rajan, K., Vengatesen, T., 2020. Molecular adaptation of molluscan biomineralisation to high-CO2 oceans–the known and the unknown. Mar. Environ. Res. 155, 104883.

Chandra Rajan, K., Li, Y., Dang, X., Lim, Y.K., Suzuki, M., Lee, S.W., Vengatesen, T., 2023. Directional fabrication and dissolution of larval and juvenile oyster shells under ocean acidification. Proc. R. Soc. B 290 (1991), 20221216.

Chandra Rajan, K., Meng, Y., Yu, Z., Roberts, S.B., Vengatesen, T., 2021. Oyster biomineralization under ocean acidification: from genes to shell. Glob. Chang. Biol. 27 (16), 3779–3797.

Chung, I.K., Oak, J.H., Lee, J.A., Shin, J.A., Kim, J.G., Park, K.S., 2013. Installing kelp forests/seaweed arrays for mitigation and adaptation against global warming: Korean project overview. ICES J. Mar. Sci. 70 (5), 1038–1044.

Corrigan, S., Brown, A.R., Ashton, I.G., Smale, D.A., Tyler, C.R., 2022. Quantifying habitat provisioning at macroalgal cultivation sites. Rev. Aquac. 14 (3), 1671–1694.

Dayton, P.K., 1985. Ecology of kelp communities. Annu. Rev. Ecol. Syst. 16, 215–245.

Duggins, D.O., Eckman, J.E., 1997. Is kelp detritus a good food for suspension feeders? Effects of kelp species, age, and secondary metabolites. Mar. Biol. 128, 489–495. https://doi.org/10.1007/s002270050115.

Dickinson, G.H., Ivanina, A.V., Matoo, O.B., Pörtner, H.O., Lannig, G., Bock, C., Beniash, E., Sokolova, I.M., 2012. Interactive effects of salinity and elevated CO_2 levels on juvenile eastern oysters. Crassostrea virginica. J. Exp. Biol. 215 (1), 29–43.

Dickinson, G.H., Matoo, O.B., Tourek, R.T., Sokolova, I.M., Beniash, E., 2013. Environmental salinity modulates the effects of elevated CO2 levels on juvenile hard-shell clams, Mercenaria mercenaria. J. Exp. Biol. 216 (14), 2607–2618.

Dineshram, R., Xiao, S., Ko, G.W.K., Li, J., Smrithi, K., Thiyagarajan, V., Zhang, Y., Yu, Z., 2021. Ocean acidification triggers cell signaling, suppress immune and calcification in the Pacific oyster larvae. Front. Mar. Sci. 8, 782583.

Doney, S.C., Busch, D.S., Cooley, S.R., Kroeker, K.J., 2020. The impacts of ocean acidification on marine ecosystems and reliant human communities. Annu. Rev. Environ. Resour. 45 (1), 83–112.

Ducker, J. and Falkenberg, L.J. How the Pacific oyster responds to ocean acidification: development and application of a meta-analysis based Adverse Outcome Pathway. 2020. Frontiers in Marine Science, 7, p.597441.

Falkenberg, L.J., Scanes, E., Ducker, J., Ross, P.M., 2021. Biotic habitats as refugia under ocean acidification. Conserv. Physiol. 9 (1), coab077.

Farghali, M., Mohamed, I.M., Osman, A.I., Rooney, D.W., 2023. Seaweed for climate mitigation, wastewater treatment, bioenergy, bioplastic, biochar, food, pharmaceuticals, and cosmetics: a review. Environ. Chem. Lett. 21 (1), 97–152.

Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero, F.J., 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305 (5682), 362–366. https://doi.org/10.1126/science.1097329.

Feely, R.A., Alin, S.R., Newton, J., Sabine, C.L., Warner, M., Devol, A., Krembs, C., Maloy, C., 2010. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. Estuar. Coast. Shelf Sci. 88 (4), 442–449.

Fernández, P.A., Leal, P.P., Henríquez, L.A., 2019. Co-culture in marine farms: macroalgae can act as chemical refuge for shell-forming molluscs under an ocean acidification scenario. Phycologia 58 (5), 542–551.

Fitzer, S.C., Chung, P., Maccherozzi, F., Dhesi, S.S., Kamenos, N.A., Phoenix, V.R., Cusack, M., 2016. Biomineral shell formation under ocean acidification: a shift from order to chaos. Sci. Rep. 6 (1), 21076.

Frieder, C.A., Gonzalez, J.P., Bockmon, E.E., Navarro, M.O., Levin, L.A., 2014. Can variable pH and low oxygen moderate ocean acidification outcomes for mussel larvae? Glob. Chang. Biol. 20 (3), 754–764.

García-Reyes, M., Thompson, S.A., Rogers-Bennett, L., Sydeman, W.J., 2022. Winter oceanographic conditions predict summer bull kelp canopy cover in northern California. PLoS One 17 (5), e0267737.

Garner, N., Ross, P.M., Falkenberg, L.J., Seymour, J.R., Siboni, N., Scanes, E., 2022. Can seagrass modify the effects of ocean acidification on oysters? Mar. Pollut. Bull. 177, 113438.

Gattuso, J.P., Magnan, A.K., Bopp, L., Cheung, W.W., Duarte, C.M., Hinkel, J., Mcleod, E., Micheli, F., Oschlies, A., Williamson, P., Billé, R., 2018. Ocean solutions to address climate change and its effects on marine ecosystems. Front. Mar. Sci. 5, 337. https://doi.org/10.3389/fmars.2018.00337.

Grinsted, A., Moore, J.C., Jevrejeva, S., 2014. Application of the cross wavelet transform and wavelet coherence to geophysical time series. Nonlinear Process. Geophys. 11, 561–566. https://doi.org/10.5194/npg-11-561-2004.

Hendriks, I.E., Duarte, C.M., Olsen, Y.S., Steckbauer, A., Ramajo, L., Moore, T.S., Trotter, J.A., McCulloch, M., 2015. Biological mechanisms supporting adaptation to ocean acidification in coastal ecosystems. Estuar. Coast. Shelf Sci. 152, A1–A8.

Hojishima, U., Hofmann, G.E., 2019. Variability of seawater chemistry in a kelp forest environment is linked to in situ transgenerational effects in the purple sea urchin. Strongylocentrotus purpuratus. Front. Mar. Sci. 6, 62.

Hurd, C.L., 2015. Slow-flow habitats as refugia for coastal calcifiers from ocean acidification. J. Phycol. 51 (4), 599–605.

IPCC. Pörtner, H.-O., Roberts, D. C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., et al., Eds.; IPCC Special Report on the Ocean and Cryosphere in a Changing Climate, IPCC, 2019, Geneva.

Kaladharan, P., Amalu, A.M., Revathy, S., 2019. Role of seaweeds in neutralizing the impact of seawater acidification-a laboratory study with beached shells of certain bivalves and spines of a sea urchin. J. Mar. Biol. Assn. India 61 (1), 94–99.

Kapsenberg, L., Cyronak, T., 2019. Ocean acidification refugia in variable environments. Glob. Chang. Biol. 25 (10), 3201–3214.

Kessouri, F., McWilliams, J.C., Bianchi, D., Sutula, M., Renault, L., Deutsch, C., Feely, R. A., McLaughlin, K., Ho, M., Howard, E.M., Bednaršek, N., 2021. Coastal eutrophication drives acidification, oxygen loss, and ecosystem change in a major oceanic upwelling system. Proc. Natl. Acad. Sci. 118 (21), e2018856118.

Koweek, D.A., Nickols, K.J., Leary, P.R., Litvin, S.Y., Bell, T.W., Luthin, T., Lummis, S., Mucciarone, D.A., Dunbar, R.B., 2017. A year in the life of a Central California kelp forest: physical and biological insights into biogeochemical variability. Biogeosciences 14 (1), 31–44.

Krause-Jensen, D., Lavery, P., Serrano, O., Marbà, N., Masque, P., Duarte, C.M., 2018. Sequestration of macroalgal carbon: the elephant in the blue carbon room. Biol. Lett. 14 (6), 20180236.

Kumar, D., Pugazhendi, A., Bajhaiya, A.K., Gugulothu, P., 2021. Biofuel production from macroalgae: present scenario and future scope. Bioengineered 12 (2), 9216.

Li, J., Zhang, W., Ding, J., Xue, S., Huo, E., Ma, Z., Yu, W., Jiang, Z., Fang, J., Mao, Y., 2021. Effect of large-scale kelp and bivalve farming on seawater carbonate system variations in the semi-enclosed Sanggou Bay. Sci. Total Environ. 753, 142065.

Levinton, J., Ward, J., Shumway, S., 2002. Feeding responses of the bivalves Crassostrea gigas and Mytilus trossulus to chemical composition of fresh and aged kelp detritus. Mar. Biol. 141, 367–376.

Lutier, M., Di Poi, C., Gazeau, F., Appolis, A., Le Luyer, J., Pernet, F., 2022. Revisiting tolerance to ocean acidification: insights from a new framework combining physiological and molecular tipping points of Pacific oyster. Glob. Chang. Biol. 28 (10), 3333–3348.

Makowski, D.; Ben-Shachar, M. S.; Patil, I.; Lüdecke, D. Estimation of model-based predictions, contrasts and means. R package v.0.7.0, 2020. (Comprehensive R Archive Network (CRAN).

Meng, Y., Guo, Z., Fitzer, S.C., Upadhyay, A., Chan, V.B., Li, C., Cusack, M., Yao, H., Yeung, K.W., Thiyagarajan, V., 2018. Ocean acidification reduces hardness and stiffness of the Portuguese oyster shell with impaired microstructure: a hierarchical analysis. Biogeosciences 15 (22), 6833–6846.

Mostofa, K.M., Liu, C.Q., Zhai, W., Minella, M., Vione, D., Gao, K., Minakata, D., Arakaki, T., Yoshioka, T., Hayakawa, K., Konohira, E., 2016. Reviews and syntheses: ocean acidification and its potential impacts on marine ecosystems. Biogeosciences 13 (6), 1767–1786.

Nielsen, K.; Stachowicz, J.; Carter, H.; Boyer, K.; Bracken, M.; Chan, F.; Chavez, F.; Hovel, K.; Kent, M.; Nickols, K.; Ruesink, J.; Tyburczy, J.; Wheeler, S. Emerging understanding of the potential role of seagrass and kelp as an ocean acidification management tool in California. California Ocean Science Trust, 2018**,** Oakland, California,.

Pfister, C.A., Altabet, M.A., Post, D., 2014. Animal regeneration and microbial retention of nitrogen along coastal rocky shores. Ecology 95 (10), 2803–2814.

Pfister, C.A., Altabet, M.A., Weigel, B.L., 2019. Kelp arrays and their local effects on seawater chemistry, productivity, and microbial communities. Ecology 100 (10), e02798.

R Core Team R, 2022. A Language and Environment for Statistical Computing, v4.1.3. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramajo, L., Lagos, N.A., Duarte, C.M., 2019. Seagrass Posidonia oceanica diel pH fluctuations reduce the mortality of epiphytic forams under experimental ocean acidification. Mar. Pollut. Bull. 146, 247–254.

Reed, D.C., Carlson, C.A., Halewood, E.R., Nelson, J.C., Harrer, S.L., Rassweiler, A., Miller, R.J., 2015. Patterns and controls of reef-scale production of dissolved organic carbon by giant kelp Macrocystis pyrifera: DOC production by giant kelp. Limnol. Oceanogr. 60, 1996–2008.

Reed, T.E., Waples, R.S., Schindler, D.E., Hard, J.J., Kinnison, M.T., 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. Proc. R. Soc. B 277 (1699), 3391–3400. https://doi.org/10.1098/rspb.2010.0771.

Saderne, V., Fietzek, P., Aßmann, S., Körtzinger, A., Hiebenthal, C., 2015. Seagrass arrays as ocean acidification refuges for mussels? High resolution measurements of pCO_2 and O_2 in a Zostera marina and Mytilus edulis mosaic habitat. Biogeosci. Discuss. 12 (14), 11423–11461.

Semesi, I.S., Kangwe, J., Björk, M., 2009. Alterations in seawater pH and CO_2 affect calcification and photosynthesis in the tropical coralline alga, Hydrolithon sp. (Rhodophyta). Estuar. Coast. Shelf Sci. 84, 337–341.

Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N., Hawkins, S.J., 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a Northeast Atlantic perspective. Ecol. Evol. 3 (11), 4016–4038.

Talmage, S.C., Gobler, C.J., 2010. Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. Proceedings of the National Academy of Sciences, **2010** 107 (40), 17246–17251.

Tang, Q., Zhang, J., Fang, J., 2011. Shellfish and seaweed mariculture increase atmospheric CO_2 absorption by coastal ecosystems. Mar. Ecol. Prog. Ser. 424, 97–104.

Torrence, C., Compo, G.P., 1998. A practical guide to wavelet analysis. Bull. Am. Meteorol. Soc. 79, 61–78.

Traiger, S.B., Cohn, B., Panos, D., Daly, M., Hirsh, H.K., Martone, M., Gutierrez, I., Mucciarone, D.A., Takeshita, Y., Monismith, S.G., Dunbar, R.B., 2022. Limited biogeochemical modification of surface waters by kelp forest canopies: influence of kelp metabolism and site-specific hydrodynamics. Limnol. Oceanogr. 67 (2), 392–403.

Truchot, J.P., Duhamel-Jouve, A., 1980. Oxygen and carbon dioxide in the marine intertidal environment: diurnal and tidal changes in rockpools. Respir. Physiol. 39 (3), 241–254.

Young, C.S., Sylvers, L.H., Tomasetti, S.J., Lundstrom, A., Schenone, C., Doall, M.H., Gobler, C.J., 2022. Kelp (Saccharina latissima) mitigates coastal ocean acidification and increases the growth of North Atlantic bivalves in lab experiments and on an oyster farm. Front. Mar. Sci. 9, 881254.

Wahl, M., Schneider Covachã, S., Saderne, V., Hiebenthal, C., Müller, J.D., Pansch, C., Sawall, Y., 2018. Macroalgae may mitigate ocean acidification effects on mussel calcification by increasing pH and its fluctuations. Limnol. Oceanogr. 63 (1), 3–21.

Waldbusser, G.G., Salisbury, J.E., 2014. Ocean acidification in the coastal zone from an organism`s perspective: multiple system parameters, frequency domains, and habitats. Annu. Rev. Mar. Sci. 6, 221–247.

Walton, M.E.M., Browne, R., Griffiths, J.N., Cartwright, D., Robins, P., Malham, S.K., Le Vay, L., 2022. Kelp detritus: unutilized productivity or an unacknowledged trophic resource? Sci. Total Environ. 820, 153191.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Xiao, X., Agustí, S., Yu, Y., Huang, Y., Chen, W., Hu, J., Li, C., Li, K., Wei, F., Lu, Y., Xu, C., 2021. Seaweed farms provide refugia from ocean acidification. Sci. Total Environ. 776, 145192.

Xu, Q., Yang, H.S., 2007. Food sources of three bivalves living in two habitats of Jiaozhou bay(Qingdao, China): indicated by lipid biomarkers and stable isotope analysis. J. Shellfish Res. 26 (2), 561–567. https://doi.org/10.2983/0730-8000(2007)26[561:FSOTBL]2.0.CO;2.

Xu, Q., Gao, F., Yang, H., 2016. Importance of kelp-derived organic carbon to the scallop Chlamys farreri in an integrated multi-trophic aquaculture system. Chin. J. Oceanol. Limnol. 34 (2), 322–329.

Yang, J.-Y., Hoon, K., 2009. Identification of the food sources-metabolism of the Pacific oyster Crassostrea gigas using carbon and nitrogen stable isotopic ratios. Korean J. Environ. Biol. 27 (3), 279–284.