

Limited biogeochemical modification of surface waters by kelp forest canopies: Influence of kelp metabolism and site-specific hydrodynamics

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Abstract

Climate change is causing decreases in pH and dissolved oxygen (DO) in coastal ecosystems. Canopy-forming giant kelp can locally increase DO and pH through photosynthesis, with the most pronounced effect expected in surface waters where the bulk of kelp biomass resides. However, limited observations are available from waters in canopies and measurements at depth show limited potential of giant kelp to ameliorate chemical conditions. We quantified spatiotemporal variability of surface biogeochemistry and assessed the role of biological and physical drivers in pH and DO modification at two locations differing in hydrodynamics inside and outside of two kelp forests in Monterey Bay, California in summer 2019. pH, DO, dissolved inorganic carbon (DIC), and temperature were measured at and near the surface, in conjunction with physical parameters (currents and pressure), nutrients, and metrics of phytoplankton and kelp biological processes. DO and pH were highest, with lower DIC, at the surface inside kelp forests. However, differences inside vs. outside of kelp forests were small (DO 6–8%, pH 0.05 higher in kelp). The kelp forest with lower significant wave height and slower currents had greater modification of surface biogeochemistry as indicated by larger diel variation and slightly higher mean DO and pH, despite lower kelp growth rates. Differences between kelp forests and offshore areas were not driven by nutrients or phytoplankton. Although kelp had clear effects on biogeochemistry, which were modulated by hydrodynamics, the small magnitude and spatial extent of the effect limits the potential of kelp forests to mitigate acidification and hypoxia.

Biogeochemistry of coastal ecosystems is highly dynamic, particularly in temperate eastern boundary current regions influenced by upwelling, which contributes to high ecosystem productivity (Brzezinski and Washburn 2011). Upwelling delivers cold, nutrient-rich, low oxygen, acidic water to the near-shore zone (Checkley and Barth 2009; Largier 2020) that fuels phytoplankton blooms (Kudela and Dugdale 2000; Pennington and Chavez 2000; Kahru et al. 2012) and lowers dissolved inorganic carbon (DIC) concentrations (Fassbender et al. 2011). Upwelling systems also support kelp and other submerged

vegetation that can draw down carbon and locally increase pH and dissolved oxygen (DO) (Kowek et al. 2017; Hoshijima and Hofmann 2019; Hirsh et al. 2020). *Macrocystis pyrifera* forms extensive kelp forests, which support diverse communities, provide food and habitat to many ecologically and economically important species (Dayton 1985), and can produce $670\text{--}1300\text{ g C m}^{-2}\text{ yr}^{-1}$ (Reed and Brzezinski 2009).

These dynamic systems are changing due to ocean acidification and warming. Global sea surface temperatures have increased by 1°C over the last century and pH has declined by 0.017–0.027 pH units per decade since the late 1980s (Poloczanska 2013; IPCC 2019). Ocean acidification is worsening with continued fossil fuel consumption, with further declines in pH of 0.1–0.3 units predicted over the 21st century (IPCC 2019). Ocean acidification will likely have large impacts on commercial fisheries (Cooley and Doney 2009) and ecosystem services (Doney et al. 2020). Because of their high productivity, there is great interest in the potential for submerged aquatic vegetation,

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such as kelp forests, to alleviate stressful water column conditions for nearshore marine organisms (Nielsen et al. 2018).

The potential for kelp forests to mitigate local acidic and hypoxic conditions will depend on biological activity of the kelp as well as physical processes such as upwelling and wave exposure which interact to shape local biogeochemistry. Regional upwelling can lower pH and aragonite saturation state (Feely et al. 2008; Fassbender et al. 2011). Simultaneously, low oxygen, low pH water can be brought to the nearshore by internal tides driven by mesoscale topography (Booth et al. 2012; Takeshita et al. 2015; Hirsh et al. 2020). As internal tides relax, hypoxic water can be retained within depressions in nearshore rocky reefs, contributing to high variability in oxygen conditions in the nearshore benthos (Leary et al. 2017). Furthermore, seasonal changes in the properties of source waters for upwelling can also lead to significant differences in pH and DO on the shelf (Nam et al. 2015). These physical processes create highly variable biogeochemical conditions for the organisms in the nearshore environment.

Kelp forests also modify the surrounding flow environment which can further influence biogeochemistry. The physical structure of the kelp forest leads to attenuation of flow within the bed, acceleration around the edges of kelp forests, and damping of internal motions and mixing within the bed (Gaylord et al. 2007, 2012; Rosman et al. 2007). The degree of physical modification depends on kelp forest characteristics (e.g., the magnitude of current attenuation scales with kelp forest size and density; Gaylord et al. 2007, 2012) as well as physical characteristics of the site. Longer water residence times within kelp forests may allow for increased uptake of CO₂ by giant kelp, increasing ambient pH and DO levels. In a kelp forest spanning wave-protected and wave-exposed nearshore areas Koweek et al. (2017) observed that benthic pH on the wave-protected side of the kelp forest was higher than benthic pH on the wave-exposed side, where pH was similar to that outside of the kelp forests due to high water motion. To fully assess the potential for kelp forests to provide refuge from acidification and hypoxia, it is important to interpret chemical changes in context of the physical environment (e.g., prevailing currents, exposure to upwelling and surface waves, and internal wave climate), which can overwhelm biological signals (Koweek et al. 2017; Hirsh et al. 2020).

Previous studies of kelp forest biogeochemistry have shown mixed evidence that kelp forests can ameliorate ocean acidification and hypoxia. Some comparisons between locations inside vs. outside of kelp forests demonstrate higher pH inside kelp forests (Pfister et al. 2019), while others show negligible differences or mixed results depending on depth (Hoshijima and Hofmann 2019; Hirsh et al. 2020; Murie and Bourdeau 2020). Several studies document clear biologically driven diel cycles in DO and carbonate chemistry near the surface in kelp forests (Delille et al. 2009; Hoshijima and Hofmann 2019; Pfister et al. 2019) and increased pH inside the forest that decline with

depth and distance from the canopy (Frieder et al. 2012; Hoshijima and Hofmann 2019; Hirsh et al. 2020). These studies showed inconclusive or negligible ability for kelp forests to modify pH at depth. Therefore, it is likely that if there were any amelioration effects they would be most pronounced at the surface. However, for all of these previous studies, the closest measurements to the surface were made 1 m below the surface, which is below the surface canopy. For example, in a kelp forest in Southern Monterey Bay, Hirsh et al. (2020) found little to no biological signature in the bottom part of the kelp forest, but an increase in pH, DO, and diel cycling toward the surface and the kelp canopy. While Hirsh et al. (2020) suspected potential for the kelp canopy to significantly alter surface biogeochemistry, they did not have data to conclusively test this.

Effects of kelp forests on biogeochemistry should be most obvious at the surface where the bulk of the *M. pyrifera* biomass and biological production/respiration occurs and where light is greatest (Colombo-Pallotta et al. 2006). Therefore, it is necessary to monitor carbon chemistry and DO at the surface where photosynthetic biomass is greatest. It is also important to concurrently measure biological factors related to co-occurring primary producers that may contribute to these patterns (i.e., kelp growth, phytoplankton productivity) to separate the roles of various primary producers (Miller et al. 2011; Pfister et al. 2019). Here, we present a holistic study of the biogeochemical, physical, and biological conditions of surface waters inside and outside of two kelp forests differing in wave exposure and mean currents in southern Monterey Bay, California. Our objectives were to (1) describe the spatial and temporal variability in surface water biogeochemistry inside and outside of two kelp forests; (2) assess the role of the two dominant primary producers, kelp and phytoplankton, in altering surface biogeochemistry; and (3) understand the potential for water column pH and DO elevation in the context of site-specific environmental characteristics.

Methods

Study sites

Two locations, Otter Cove and McAbee Beach, in Southern Monterey Bay, California were monitored over a 9-week period from June to early August in 2019 (Fig. 1). Otter Cove is more wave-exposed than McAbee Beach (Graham et al. 1997), and we refer to Otter Cove as the high-flow location and McAbee Beach as the low-flow location. At each location we established sites within the center of the kelp forest (high-flow kelp site, mean depth 11.8 m; low-flow kelp site, mean depth 9.4 m) and 50 m offshore from the edge of the forested rocky reef (high-flow offshore site, mean depth 15.9 m; low-flow offshore site, mean depth 18.1 m; Table S1, Fig. 1).

Wave conditions and currents

From mid-July to early August, pressure loggers were deployed near moorings at kelp forest sites. At the low-flow kelp site an RBR SoloD³ pressure logger ($\pm 0.05\%$ accuracy) sampled at 1 Hz

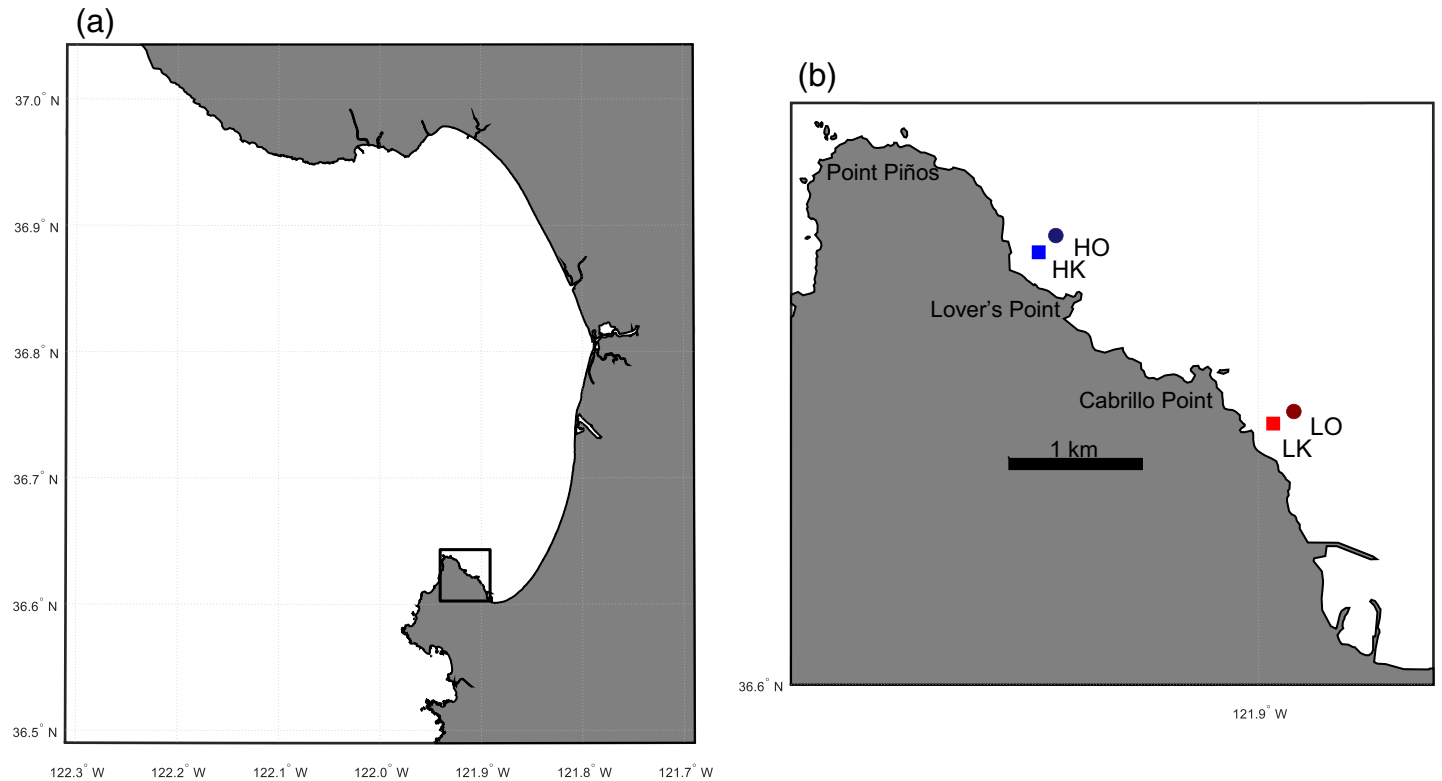


Fig. 1. Map of Monterey Bay, California (a) with the square indicating the study area shown in (b). Sites in (b) in blue are the high-wave kelp forest site (HK) and high-wave offshore site (HO), and in red are the low-wave kelp forest site (LK), and low-wave offshore site (LO).

Table 1. Mean overall, daytime, and nighttime DIC, DO, and pH (\pm std. err.) at each site and depth. For DO and pH, time periods were only used when there was overlap among all sensors. Differences between surface and subsurface parameters were standardized by depth.

Site	Depth	DIC		DO			pH		
		Day	Overall	Day	Night	Overall	Day	Night	
HK	Surface	1996 \pm 11	315 \pm 1.4	326 \pm 1.9	298 \pm 1.6	8.14 \pm 0.003	8.16 \pm 0.004	8.10 \pm 0.004	
	Subsurface	2006 \pm 8	298 \pm 1.3	297 \pm 1.8	300 \pm 1.8	8.07 \pm 0.002	8.06 \pm 0.003	8.07 \pm 0.003	
	Surface–subsurface	-9 \pm 3	13 \pm 0.9	22 \pm 1.2	-1.3 \pm 0.5	0.057 \pm 0.002	0.075 \pm 0.003	0.03 \pm 0.003	
HO	Surface	2032 \pm 8	305 \pm 1.2	305 \pm 1.7	305 \pm 1.5	8.11 \pm 0.002	8.11 \pm 0.003	8.11 \pm 0.003	
	Subsurface	2031 \pm 8	294 \pm 1.3	291 \pm 1.8	298 \pm 1.7	No data	No data	No data	
	Surface–subsurface	0.7 \pm 2	8 \pm 0.5	9 \pm 0.7	5 \pm 0.5	No data	No data	No data	
LK	Surface	1974 \pm 9	331 \pm 1.8	346 \pm 2.4	307 \pm 1.7	8.14 \pm 0.003	8.16 \pm 0.004	8.11 \pm 0.003	
	Subsurface	1990 \pm 9	314 \pm 1.3	312 \pm 1.8	316 \pm 1.6	8.12 \pm 0.002	8.11 \pm 0.003	8.13 \pm 0.003	
	Surface–subsurface	-14 \pm 3	13 \pm 1.0	26 \pm 1.2	-7 \pm 0.4	0.016 \pm 0.002	0.03 \pm 0.002	-0.01 \pm 0.001	
LO	Surface	2013 \pm 7	319 \pm 1.2	319 \pm 1.7	320 \pm 1.6	No data	No data	No data	
	Subsurface	2010 \pm 7	308 \pm 1.2	304 \pm 1.7	315 \pm 1.7	No data	No data	No data	
	Surface–subsurface	3 \pm 2	6 \pm 0.4	7 \pm 0.6	3 \pm 0.4	No data	No data	No data	

continuously. At the high-flow kelp site an RBR quartz³ pressure logger (\pm 0.01% accuracy) sampled at 6 Hz in 20 min bursts every hour. A low-pass 2nd-order Butterworth filter was applied to filter out the tidal signal. Wave properties and significant wave heights were inferred spectrally from 20 min sample periods (Holthuijsen 2007).

To capture water-column velocity, bottom-mounted Acoustic Doppler Current Profilers (ADCP) were placed at each site (high-flow outside site: RD Instruments, 600 kHz Workhorse Sentinel; low-flow kelp site and outside site: Nortek Signature 1000). Due to instrument failure, no data are available from the high-flow kelp site. Data were collected in 0.5-m bins

extending from ~ 1 m above the bottom to ~ 1.5 m below the surface that sampled in 5-s intervals at the high-flow outside site, 10-min intervals at the low-flow outside site, and 5-min intervals at the low-flow kelp site. Velocity measurements were used to calculate residence time for the low-flow kelp site (see Supporting Information).

Temperature, oxygen, and pH sensor measurements

Sensors were placed at the surface, subsurface, and 1 m above the bottom. pH and DO were measured using PME miniDOTs, custom pH sensors utilizing the DuraFET combination electrode (Martz et al. 2010), SeaFETs (Seabird Electronics), and SeapHOxs (Seabird Electronics). Some data were lost due to sensor failures (Supporting Information Table S1). For details on sensor placement, data coverage, and calibration protocols see Supporting Information and Tables S1 and S2.

Discrete DIC and nitrate

Discrete water samples were collected for DIC and nitrate concentrations at each site twice weekly between 11:00 and 14:00. Water samples were collected at the surface and 1 m below the surface using 1.75-L Niskin bottles. Thirty milliliter water samples for DIC were preserved with saturated mercuric chloride solution (0.1% by volume until 05 July, 0.05% by volume for remainder of study) and analyzed at Stanford University using a custom-built instrument based on designs of O'Sullivan and Millero (1998). Certified reference materials (batches 177 and 187) were used to standardize measurements approximately hourly. DIC precision was estimated to be $\pm 2.1 \mu\text{mol kg}^{-1}$.

Bottom and surface nitrates were collected to provide context for phytoplankton and kelp growth rates. *M. pyrifera* can translocate nitrate vertically (Jackson 1977; Stephens and Hepburn 2014); however, kelp growth has been related to surface nitrate (Cavanaugh et al. 2011; Bell et al. 2018) and is limited by nitrate if only available near the bottom (Gerard 1982). Sixty milliliter water samples were collected at the surface and 1 m above the bottom and stored in a dark cooler until frozen (< 4 h). Nitrate was measured with a WestCo SmartChem 200 discrete auto-analyzer (NO_3^- , $N = 57$). Precision on standards was ± 0.06 ($N = 29$) $\mu\text{mol kg}^{-1}$. Internal control seawater was used on each run sequence and was run after approximately every 10 unknowns with a precision of ± 0.02 ($N = 33$).

Phytoplankton abundance and species composition

Surface water samples for chlorophyll *a* (Chl *a*) concentration were collected at each site twice per week, at the same time DIC and nitrate samples were collected. Water samples were filtered onto 47-mm Whatman GF/F filters (0.7 μm pore size) upon return to the laboratory. Filters were frozen at -80°C until Chl *a* extraction. Five hundred milliliter samples were used in June, and 100 mL samples were used for the rest of the study. Chl *a* was extracted for two replicate samples following the EPA Method 445 protocol and measured using a calibrated Trilogy Laboratory Fluorometer (Turner Designs).

Phytoplankton community composition was monitored at the same time as the Chl *a* samples using a vertical tow with a 20- μm plankton net lowered five times to 5 m depth. Two hundred fifty milliliter plankton samples were transported in a cooler and stored in a refrigerator until analyzed (less than 3 d). Samples were gently inverted then subsampled. Phytoplankton were identified to the lowest taxonomic level and relative abundance of each group was scored (absent, rare < 1%, present 1–10%, common 10–50%, and abundant > 50%) (Fischer et al. 2020).

Kelp density, growth, and fouling

M. pyrifera density was measured in July at each kelp forest site in four 2×30 m transects running parallel to shore centered around the mooring. Two transects were 1 m inshore of the mooring and two were 1 m offshore of the mooring. *M. pyrifera* individuals with at least one stipe > 1 m in length and the number of stipes per individual were counted.

Kelp growth was quantified weekly at each kelp forest site using three metrics: production of new fronds, frond growth, and blade growth following modifications of the methods of Brown et al. (1997) and Fox (2016). Growth was measured for individuals inside a 20 m circumference circle centered on the moorings (nine individuals at the low-flow kelp site, eight individuals at the high-flow kelp site). For detailed methods see Supplementary Information.

Membranipora spp. is among the most common epibionts on *M. pyrifera* in Monterey Bay and has been demonstrated to affect kelp physiology (Dixon et al. 1981; Hurd et al. 2000; Hepburn et al. 2012). At each site surface blades were sampled for *Membranipora* spp. weekly from early July to early August. On each of 10 randomly selected fronds, percent cover of *Membranipora* spp. was categorized (absent, < 1% cover, 1–50% cover, > 50% cover) for every 5th blade from the 1st blade below the apical scimitar over the portion of the frond in the surface canopy.

Data analysis

Temperature, DO, and pH values were compared among sites (fixed, 4 levels for temperature and DO, 3 levels for pH) and between depths (fixed, 2 levels) using separate PERMANOVA tests with 999 permutations based on Euclidean distance matrix using Primer (v6). Power spectral density was estimated for temperature, DO, and pH using the Matlab function `pwelch` with five Hamming windows overlapping at 50% (R2018b; Mathworks). DIC was compared among sites (fixed, 4 levels) and depths (fixed, 2 levels) using PERMANOVA with 9999 permutations based on Euclidean distance matrix in Primer.

Phytoplankton community composition was compared among sites (fixed, 4 levels) and weeks (random, 8 levels) using PERMANOVA with 9999 permutations based on Bray Curtis similarity matrix in Primer. Log transformed frond growth, blade growth, and new fronds per individual were compared between sites (fixed, 2 levels) and weeks (random, 8 levels) with separate generalized linear mixed effects models

using a gamma distribution in R (version 3.6.2). For frond growth, frond number and *M. pyrifera* individual number were included as nested random blocking factors and frond length was included as a fixed factor. For blade growth, the length of time since the hole was initially punched was included as a fixed factor, and blade number, frond number, and *M. pyrifera* individual number were included as nested random blocking factors. For new fronds per individual, *M. pyrifera* individual number was included as a random blocking factor. All factors included in each model improved model fit based on AIC and BIC. Separate Kruskal-Wallis tests were used to compare Chl *a* concentration, kelp individual and stipe density, and NO_3^- concentration among sites. *Membranipora* spp. cover was compared among sites (fixed, 2 levels) and weeks (fixed, 5 levels) using PERMANOVA with 9999 permutations based on Euclidean distance similarity matrix in Primer.

Results

Spatial patterns

Sites inside kelp forests had higher DO and pH and lower DIC than offshore sites, although the differences were small. Overall mean as well as daytime mean surface DO and pH were significantly higher at the kelp forest than at the offshore site (Table 1; Supporting Information Tables S3, S4) and nighttime mean surface DO and pH were significantly lower (Supporting Information Table S4). Mean daytime surface DO was 6% and 8% higher in the kelp forest than at the paired offshore site at the high-flow and low-flow location, respectively (Table 1). At night, surface DO was 4% lower at the low-flow kelp site than at the low-flow outside site and 2% lower at the high-flow kelp site than outside. Surface pH was higher at the high-flow kelp site than outside by 0.03 and 0.05 units overall and during the day, respectively. Mean nighttime surface pH was 0.01 units higher at the high-flow outside site than the high-flow kelp site (offshore pH not available for low-flow location). Examining 1 week of continuous pH and DO data, we see higher pH and DO in the kelp forest compared to offshore during the day and similar or slightly lower values at night (Fig. 2). At each location DIC, which was only measured during the day, was slightly lower at the kelp forest than at its paired offshore site (Table 1; mean DIC 2% higher offshore than in the kelp forest at both locations).

Patterns in biogeochemical parameters with depth varied between the kelp and offshore stations. At the offshore stations, mean DO significantly declined with depth across the time series, and for daytime and nighttime periods separately (Table 1; Supporting Information Tables S3, S4). Within the kelp forest, overall and daytime mean DO declined with depth at the high-flow kelp site and the low-flow kelp site, but at night was similar between depths at the high-flow kelp site and was higher at the subsurface location than at the surface at the low-flow kelp site. At the high-flow kelp forest, mean pH was 0.1 units higher at the surface than the subsurface

during the day and 0.03 units higher at night. At the low-flow kelp site, overall and daytime mean pH was 0.05 higher at the surface than at the subsurface, but at night mean pH was 0.02 higher at the subsurface than at the surface. Looking at the full continuous time series (Supporting Information Fig. S3) and zooming in on 1 week of data (Supporting Information caption Fig. S4), pH and DO were almost always lower at the subsurface than at the surface at all sites, including at night. DIC did not vary between the surface and 1 m below the surface, although there was a nonsignificant trend toward lower DIC at the surface than at 1 m below the surface in the kelp forests (Table 1; Supporting Information Table S3). Temperature decreased with depth, and did so similarly between all sites (Supporting Information Tables S3, S5).

The high-flow kelp forest site was characterized by lower surface temperature, greater wave energy, and higher cross-shore and alongshore current velocities than the low-flow kelp forest site. Mean surface temperature was 0.9°C lower at the high-flow kelp site than at the low-flow kelp site (Supporting Information Table S5). Significant wave heights were greater at the high-flow than the low-flow kelp site for most of the time series (Fig. 3). Direct comparisons of currents at the high- and low-flow kelp sites were not possible, due to instrument failure. Depth-averaged alongshore current velocities within the upper water column were lower at the low- than the high-flow offshore site, and were much lower at the low-flow kelp site than at either offshore site, often by an order of magnitude (Fig. 3). Depth-averaged cross-shore velocities within the upper water column were also lower at low-flow than the high-flow outside site and were reduced inside the kelp forest, but to a lesser extent than alongshore velocities (Fig. 3). Residence time, T_r , at the low-flow kelp site showed substantial temporal variability with a median value of $T_r = 2.4$ h, and 5% and 95% exceedance values of 0.78 and 9.8 h, respectively (Supporting Information Fig. S5).

Comparing the two kelp forest sites, biogeochemical parameters were equal or slightly higher at low-flow than at the high-flow kelp site. Mean daytime surface DO was 6% ($20 \mu\text{mol kg}^{-1}$) higher at low-flow than the high-flow kelp site, while the mean daytime and overall surface pH at the high-flow kelp site was essentially equal to that at the low-flow kelp site (Table 1). Nighttime mean surface DO was 3% higher at the low-flow kelp site, and pH was similar between the two sites (0.01 units higher at the low-flow kelp site). Discrete daytime surface DIC samples were not significantly different between the low-flow kelp site (mean of $1974 \mu\text{mol kg}^{-1}$) and the high-flow kelp site (mean of $1996 \mu\text{mol kg}^{-1}$), although values from individual sampling days were generally lower at the low-flow kelp site (Table 1; Supporting Information Fig. S3).

Temporal patterns

Temperature, DO, and pH varied most strongly at diurnal and semidiurnal frequencies (Supporting Information Fig. S6) with all parameters dominated by diurnal variability. Daily fluctuations in temperature, DO, and pH were

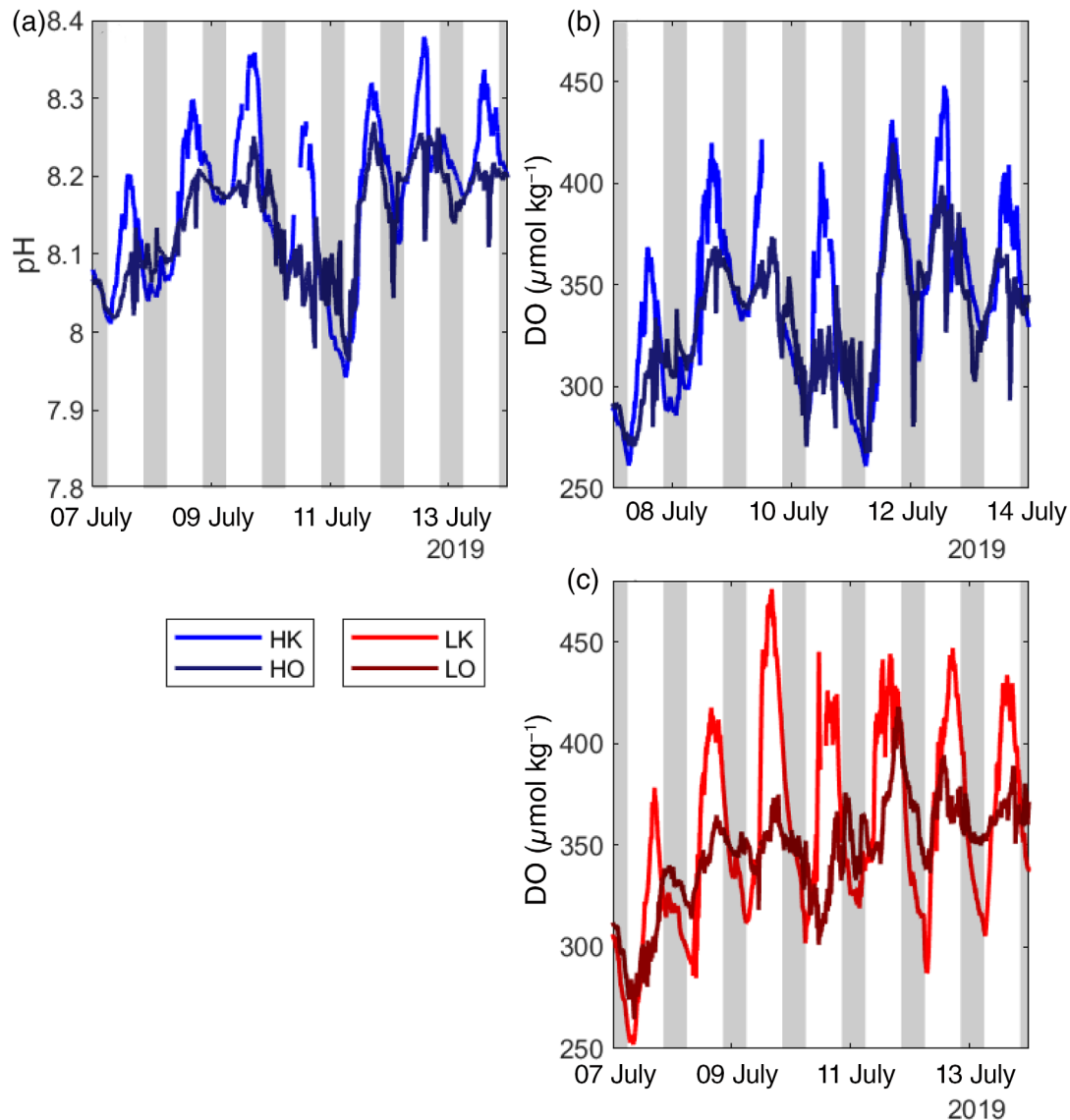


Fig. 2. One week of surface pH and DO sensor data. **(a)** Surface pH data at the high-flow kelp site and high-flow offshore site, **(b)** surface DO data from the high-flow kelp site and high-flow outside site, and **(c)** surface DO data from the low-flow kelp site and low-flow outside site. Gray boxes indicate nighttime period between sunset and sunrise (21:00–05:00).

largest at the surface at the kelp forest sites and were much weaker below the surface and at offshore sites (Fig. 4). Surface temperature increased above subsurface levels from late morning to afternoon in the kelp forest, but the increase above subsurface levels was much smaller at the offshore sites (Fig. 4). DO and pH was higher at the surface than subsurface during the day but concentrations were similar between depths at night (Fig. 4). On most days, DO saturation was above 100% across all sites; DO saturation at the subsurface fell below 100% more often than at the surface (Fig. 4).

Nutrients

There were no differences in NO_3^- concentration among sites at the surface (Kruskal-Wallis, $\chi^2 = 6.03$, $p = 0.110$) or 1 m above

the bottom (Kruskal-Wallis, $\chi^2 = 2.62$, $p = 0.455$). Surface NO_3^- concentrations ranged from 0.073 to 9.446 $\mu\text{mol L}^{-1}$ and bottom NO_3^- concentrations ranged from 1.171 to 25.259 $\mu\text{mol L}^{-1}$. NO_3^- concentrations of 1–2 $\mu\text{mol L}^{-1}$ are required to sustain typical kelp growth rates (Gerard 1982; Parnell et al. 2010). Surface NO_3^- concentrations were sometimes below 1 $\mu\text{mol L}^{-1}$ at all sites. Nitrate depletion occurred more frequently at the surface within the kelp canopy at the low-flow site than at the high-flow site; however, NO_3^- concentrations were always above 1 $\mu\text{mol L}^{-1}$ at the bottom.

Chl *a* and phytoplankton community composition

Chl *a* concentrations were similar among sites (Kruskal-Wallis, $\chi^2 = 2.33$, $p = 0.508$). There were no significant

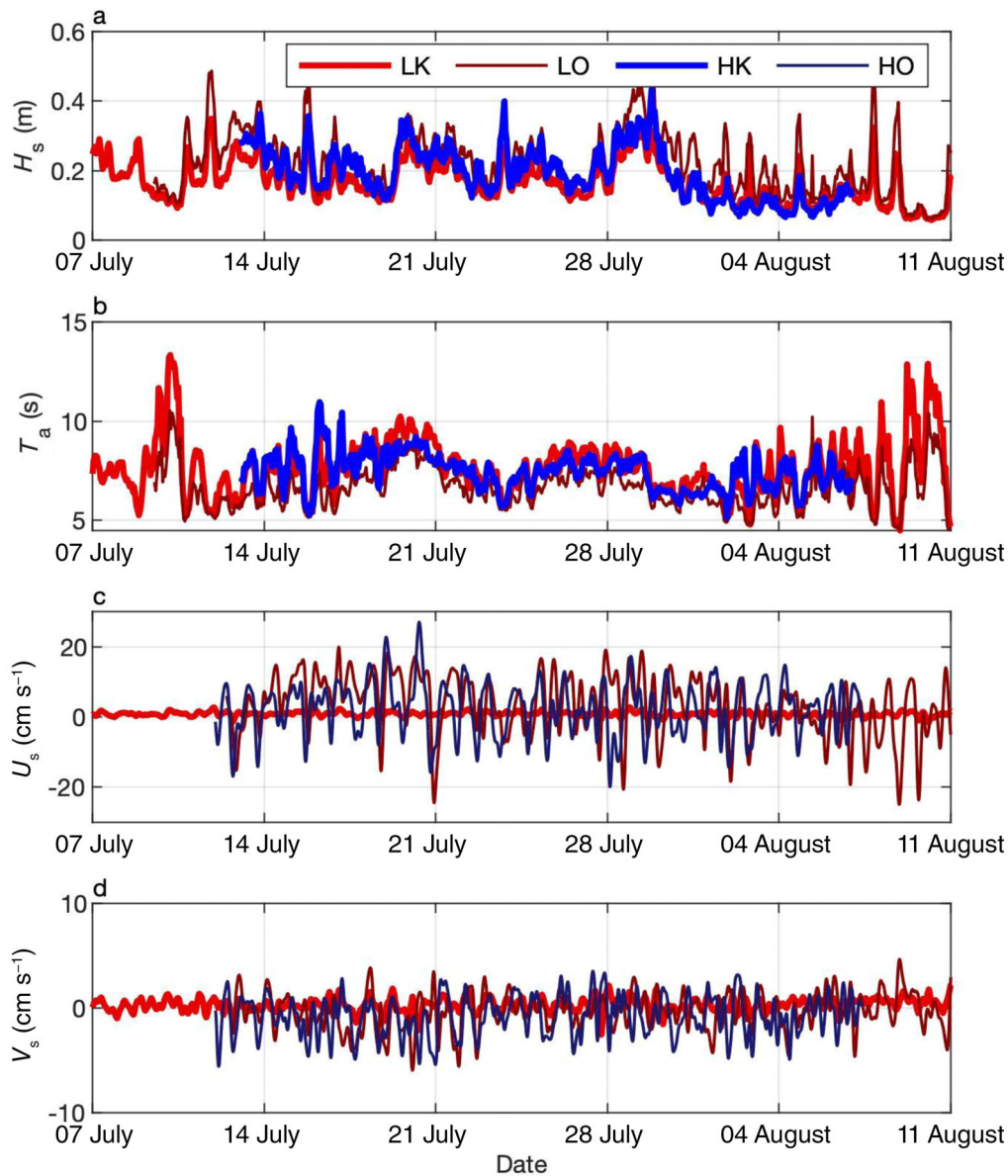


Fig. 3. Significant wave height (a), period (b), near-surface long-shore velocities (c), and near-surface cross-shore velocities (d). Dark red lines are the low-flow offshore site (LO), light red is the low-flow kelp site (LK), dark blue is the high-flow offshore site (HO), and light blue is the high-flow kelp site (HK, only shown in panels a and b).

relationships between DIC and Chl *a* concentration across all sites, at individual sites, or when offshore and nearshore sites were pooled ($p > 0.05$).

Phytoplankton community composition did not vary among sites or between offshore and kelp locations (PERMANOVA, Pseudo- $F = 1.316$, $p = 0.197$); however, it did vary significantly from week to week (Pseudo- $F = 8.160$, $p < 0.001$) with three main shifts in the phytoplankton community. These shifts did not correspond to notable changes in Chl *a* or biogeochemical parameters. For descriptions of the shifts in community composition, see the Supplementary Information (Supplementary Results, Table S6; Fig. S7).

Kelp density, growth, and epibionts

There were no significant differences in kelp density (Kruskal-Wallis, $\chi^2 = 2.08$, $p = 0.149$) or stipe density ($\chi^2 = 0.75$, $p = 0.387$) between sites (at the site level and in the immediate area around each mooring), but there were differences in frond and blade growth between sites and over time (Table 2; Supporting Information Table S7, Fig. S8). Frond growth was higher and more variable at the high-flow kelp site at $16 \text{ cm d}^{-1} \pm 1$ (mean \pm std. err.) than at the low-flow kelp site ($11 \text{ cm d}^{-1} \pm 0.8$, Table 2). At both sites longer fronds grew at faster rates and there was not a significant interaction between site and frond length (Supporting Information

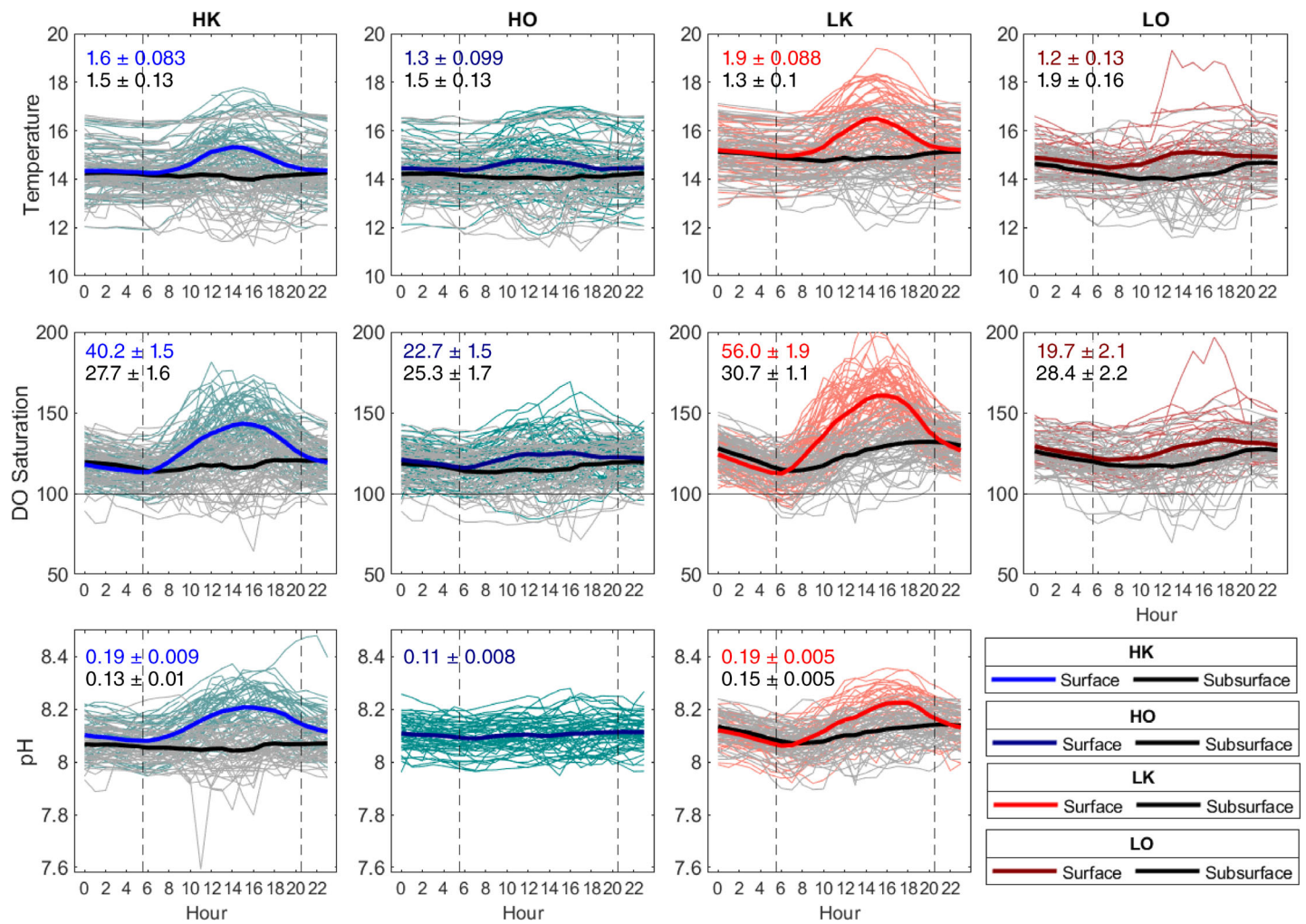


Fig. 4. Diel patterns of temperature (top row), DO (middle row), and pH (bottom row) at each site (high-flow kelp (HK), high-flow offshore (HO), low-flow kelp (LK), and low-flow offshore (LO)). Thin colored and gray lines are hourly averaged values for each day of the sampling period from the surface and subsurface, respectively. Thick lines are means of hourly averages across the entire sampling period. Dashed vertical lines indicate average sunrise and sunset times during the sampling period. Numbers in upper left of each panel are the mean daily range of the variable (± std. err.) for the surface (colored) and subsurface (black).

Table S7). Differences in frond growth rates between sites were likely related to differences in depth (mean depth was 11.8 m at the high-flow site and 9.4 m at the low-flow kelp site) and on average fronds used for frond growth measurements were longer at the high-flow kelp site ($10.600 \text{ m} \pm 4.868$, mean ± std. err.) than at the low-flow kelp site ($9.165 \text{ m} \pm 4.376$) (Kruskal-Wallis, $\chi^2 = 9.94$, $p = 0.002$). Blade growth also varied over time and between sites (Supporting Information Table S7). Blade growth declined over time since the hole used to track growth was punched. Mean blade growth was higher at the high-flow kelp site at $4.5 \text{ mm d}^{-1} \pm 0.4$ (mean ± std. err.) than at the low-flow kelp site at $2.8 \text{ mm d}^{-1} \pm 0.3$ (Table 2). There was not a significant difference in new fronds per individuals between sites; however, there was significant variation over time, with new fronds highest in early August (Supporting Information Table S7; Fig. S8). Increased surface

Table 2. Density of *Macrocystis pyrifera* within the 20 m circumference area centered around the mooring, mean (± std. err.) site-level kelp density, kelp growth metrics, and percent of blades with 0% *Membranipora* spp. at the high-flow kelp site (HK) and the low-flow kelp site (LK).

	HK	LK
<i>M. pyrifera</i> individuals m^{-2} next to mooring	0.249	0.280
<i>M. pyrifera</i> individuals m^{-2}	0.354 ± 0.117	0.217 ± 0.095
Stipes m^{-2}	6.029 ± 3.015	3.708 ± 1.854
Frond growth (cm d^{-1})	16 ± 1	11 ± 0.8
Blade growth (mm d^{-1})	4.5 ± 0.3	2.8 ± 0.18
New fronds per individual	0.672 ± 0.084	0.651 ± 0.082
Percent of surface blades with 0% <i>Membranipora</i> spp.	46 ± 2	53 ± 5

NO_3^- concentrations at the high-flow kelp site in mid-June, mid-July, and early August were not followed by increased kelp growth.

The cover of *Membranipora* spp. on surface blades did not differ significantly between sites (PERMANOVA, Pseudo- $F = 1.388$, $p = 0.250$). At both sites, there was generally low cover of *Membranipora* spp. throughout the study period (at least 33% of surface blades with no *Membranipora* spp. cover; Supporting Information Fig. S9). There was a slight increase in the percent of blades with 1–50% cover of *Membranipora* spp. in the 2nd half of July (Supporting Information Fig. S9).

Discussion

We observed slightly higher pH and DO, and slightly lower DIC near the surface inside kelp forests as compared to outside kelp forests. Inside the kelp forests we also observed increased pH, and DO, and lower DIC at the surface relative to the subsurface that appear to be related to kelp productivity. We also saw slight differences between the two kelp forest sites—with the low-flow kelp site having higher oxygen and lower DIC than the high-flow kelp site—on a scale similar to the inside-outside forest comparison. Differences between sites were not related to nutrients, kelp abundance, growth rates, fouling by epibionts, phytoplankton abundance, or phytoplankton community composition. Rather, they likely correspond to differences in water residence time between the two sites as seen in the higher wave energy and stronger currents at the high-flow site compared to the low-flow site. Our study adds to the growing body of literature showing biogeochemical modification inside marine vegetated habitats as compared to outside (Frieder et al. 2012; Krause-Jensen et al. 2015; Murie and Bourdeau 2020); however, these differences were small (6–8% increase in daytime DO, 0.05 increase in daytime pH units). This work demonstrates the importance of considering the physical context of vegetated marine habitats in assessing the drivers and variability of biogeochemistry, while also underscoring the limited potential of kelp forests to alleviate acidification and hypoxia stress.

Although we found elevated surface pH and DO inside of the kelp relative to outside, particularly during the daytime, the ability for kelp forests to alleviate OA or hypoxia stress is limited and is unlikely to be biologically relevant. Furthermore, acidification and hypoxia stress reduction by the surface kelp canopy is mismatched from where it is most needed - in the nearshore benthic environment (Booth et al. 2012; Hirsh et al. 2020) where pH and DO can be as low as 7.64 and $68.7 \mu\text{mol kg}^{-1}$, respectively. Currently, at the surface, stress from ocean acidification and hypoxia is not low enough for detrimental effects, and kelp effects rapidly decreased over the 1st 1–2 m of the water column. While there are grazers in the kelp canopy (i.e., the kelp crab, *Pugettia producta*) that could be stressed by low oxygen or pH, these conditions do not occur in the kelp canopy or at the

surface outside kelp forests (Murie and Bourdeau 2020). Negative effects of lower pH have been demonstrated for juvenile rockfish (7.5 pH units, Hamilton et al. 2017) and sea urchin larvae (7.7 pH units, Yu et al. 2011), which may inhabit the canopy or pass through surface waters (Morton and Anderson 2013). In our study, pH of 7.5 was never observed at the surface or subsurface and pH of 7.7 was only rarely observed. The effect of kelp on seawater pH and DO could become important following further acidification, but at current surface pH levels the kelp effect is negligible. Because the biggest effect of kelp forests on biogeochemistry is expected in surface waters within the canopy, where we found only a minor change in biogeochemistry, it is unlikely that kelp will modify biogeochemistry on a meaningful scale for amelioration.

While signals were small, we did see evidence of kelp-mediated changes in biogeochemistry. In addition to slightly higher mean pH and DO in kelp forests at the surface, where the *M. pyrifera* canopy is located, strong diel fluctuations in temperature stratification and biogeochemistry were observed in kelp forest sites at the surface, and these patterns were absent at offshore sites and at the subsurface within kelp forest sites. These observations demonstrate that the *M. pyrifera* canopy modifies both the physics and biogeochemistry. Attenuated currents inside kelp forests increase residence time of water, leading to solar heating and retention of warm water as increased stratification prevents mixing. The increased water residence time allows more time for chemical modification by kelp. As tidal influences generally increase with depth (Valle-Levinson et al. 2000; Kumar et al. 2016), the surface peak in diurnal frequencies is likely due to biological processes of photosynthesis and respiration strengthened by reduced water movement. Declining biogeochemical modification by kelp with depth was indicated by our previous study of a Monterey kelp forest (Hirsh et al. 2020) and in Santa Barbara, CA (DO only, Hoshijima and Hofmann 2019), the sub-Antarctic (Delille et al. 2009), and in subsurface canopies in the sub-Arctic (Krause-Jensen et al. 2015). Chl *a* concentrations and phytoplankton community composition were not significantly different among sites; therefore, the increased daily range in DO and pH at the kelp forest sites is likely due to photosynthesis and respiration by *M. pyrifera* rather than phytoplankton. Previous studies have also found no difference in surface Chl *a* concentration between kelp forests and offshore locations (Pakhomov et al. 2002) or before and after kelp canopy removal (Miller et al. 2011, but see Delille et al. 2009).

Hydrodynamic conditions are important for determining the degree of biogeochemical modification by kelp and can affect differences in biogeochemistry among different kelp forests. The slight differences in biogeochemistry between the two kelp forest sites were better explained by differences in the physical aspects of the sites than by differences in biological characteristics. The increased wave energy and current velocities at the high-flow kelp site likely leads to lower residence time at this site, dampening the in-situ biogeochemical

signature of kelp metabolism, despite higher kelp productivity at the high-flow kelp site. This effect of local flow regime on biogeochemical patterns is similar to what was observed in a neighboring kelp forest studied in Koweek et al. (2017). To date, only one other study has compared the effects of kelp forests on biogeochemistry between nearby (km-scale) kelp forests. Pfister et al. (2019) compared pH, carbonate chemistry, and DO inside and outside of kelp forests and the greatest differences were observed at the most exposed site on the outer coast, which may have been related to high water retention within the kelp forest compared to the high-flow environment outside the kelp forest as well as its proximity to an upwelling center. Since upwelling and internal bores are important drivers of water column biogeochemistry (Hirsh et al. 2020), proximity to geographical features such as headlands that affect these hydrodynamic processes are important in determining biogeochemical mean values and variance. Differences in current profiles associated with local bathymetry and topographical features will also impact water residence time (Nickols et al. 2012), and therefore, biogeochemistry. The extent to which sites within a region vary in their hydrodynamic environments may be as important as their biological characteristics in driving patterns of biogeochemistry.

Our observations demonstrate that the portion of the kelp forest that most significantly modifies seawater biogeochemistry is limited to the canopy itself, with rapid attenuation outside of the forest and with depth below the canopy. Given that the canopy tends to be the densest within the 1st 0.5 m from the surface, and DIC concentrations were higher 1 m below the surface than at the surface, the layer of water significantly modified by kelp photosynthesis at our sites was likely less than 1 m thick. The “kelp signal” was also not observable at either of our outside moorings which were located only several hundred meters from the edge of the kelp forest. This suggests that not only the magnitude, but also the spatial extent of biogeochemical modifications by kelp forests are limited. Given the very minor biogeochemical modification by *M. pyrifera* observed at the surface in this study and throughout the water column in previous studies (Hoshijima and Hofmann 2019; Hirsh et al. 2020), it seems unlikely that other kelp species which form less dense canopies (e.g., bull kelp, *Nereocystis luetkeana*) would have strong mitigation potential. However, Murie and Bourdeau (2020) observed larger daytime differences in DO and pH at the surface between bull kelp forests and adjacent urchin barrens (DO 16%, pH 0.08 higher in kelp forest) than we did (DO 6–8%, pH 0.04 higher in kelp forests). The greater kelp effect observed by Murie and Bourdeau (2020) may be explained by shallower site depths in that study or differences in hydrodynamics and water residence time, which were not measured.

The results of our study demonstrate that *M. pyrifera* has a limited role in altering nearshore biogeochemistry at the surface, particularly when considering physical drivers like upwelling, wave exposure, and current attenuation. The limited magnitude and spatial extent of the effect of kelp on

biogeochemistry makes natural kelp forests unlikely to provide important protection against acidification. Any further evaluation of the potential of kelp forests to mitigate stressful conditions must take an interdisciplinary mechanistic approach to decipher the roles of biology and physics in the chemical signal. Our results suggest that kelp forests in semi-enclosed bays or other low-flow locations would have the largest effects on seawater chemistry; however, sites with reduced flushing may potentially see a higher respiration signal. Although the potential for kelp to modify biogeochemistry in ways that are beneficial to kelp forest organisms appears to be very limited, kelp forests provide important ecosystem services and these provide many other reasons to protect and restore these habitats (Wernberg et al. 2019).

Data availability statement

The data presented here are available through the Biological and Chemical Oceanography Data Management Office (<https://www.bco-dmo.org/project/748778>).

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Conflict of Interest

None declared.

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