Annals of Botany **00**: 1–14, 2026
https://doi.org/10.1093/aob/mcag181, available online at www.academic.oup.com/aob

ANNALS OF BOTANY
Nonprofit since 1887

ORIGINAL ARTICLE

Giant kelp-associated variation in coastal seawater chemistry across contrasting sites in Chile and Tasmania

Elisabeth M. A. Strain[1,2,†], Pamela A. Fernández[3,*†], Scott Bennett[1,2], Alejandro H. Buschmann[3], Patricio Díaz[4], Hunter Forbes[1], Cayne Layton[1,2], Mauricio A. Urbina[5], Laura Gutiérrez[6] and Cristian A. Vargas[6]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania 7004, Australia, [2]Centre for Marine Socioecology, University of Tasmania, Hobart, Tasmania 7004, Australia, [3]Centro i∼mar, CeBiB & MASH, Universidad de Los Lagos, Puerto Montt, Chile, [4]Centro i∼mar & CeBiB, Universidad de Los Lagos, Puerto Montt, Chile, [5]Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción and Instituto Milenio de Oceanografía (IMO), Concepción, Chile and [6]Laboratorio de Ecosistemas Costeros & Cambio Ambiental Global (ECCALab), Departamento de Sistemas Acuáticos, Facultad de Ciencias Ambientales, Universidad de Concepción e Instituto Milenio en Socioecología Costera (SECOS), Concepción 4030000, Chile
[*]For correspondence. E-mail pamela.fernandez@ulagos.cl
[†]Joint first authors.

Received: 12 January 2026 Returned for revision: 08 June 2026 Accepted: 22 June 2026

• **Background and Aims** Widespread shifts in seawater chemistry are occurring across spatial and temporal scales, with important consequences for coastal ecosystems. Giant kelp (*Macrocystis pyrifera*) forests elevate seawater pH and dissolved oxygen (DO) through photosynthesis, potentially providing short-term refugia from ocean acidification and deoxygenation. However, whether these effects persist across contrasting environmental settings remains unclear. Here, we assess how biological and oceanographic conditions regulate giant kelp-mediated modification of seawater chemistry across multiple sites.
• **Methodology** Hourly measurements of seawater pH, DO and temperature were collected during spring–summer 2022–23 using paired deployments inside and outside giant kelp forests at one site in central Chile and four sites in Tasmania, Australia. The influence of giant kelp density was also evaluated at two sites in southern Chile and three sites in Tasmania. An upwelling index was calculated for the central Chile site to assess the influence of regional oceanographic forcing on kelp-associated seawater chemistry patterns.
• **Key Results** Hourly pH and DO were higher inside giant kelp forests than outside at the central Chile site and at one Tasmanian site. At these locations, stronger daytime pH–DO relationships indicated that photosynthetic carbon uptake exceeded night-time respiration, generating a net positive metabolic signal. In Tasmania, giant kelp density was positively associated with hourly pH and DO, whereas no such relationship was detected in southern Chile. At the central Chile site, kelp-associated effects intensified during a strong upwelling event, reducing the severity of low pH and DO conditions.
• **Conclusions** Giant kelp forests can locally buffer short-term fluctuations in seawater pH and DO, but this capacity is highly site-dependent and influenced by giant kelp density and environmental conditions. Overall, our findings suggest that continued loss of giant kelp forests in Tasmania may reduce their potential to provide short-term refugia, while in Chile the strength of kelp-mediated seawater chemistry modification is likely to remain strongly influenced by variability in upwelling and freshwater inputs.

Key words: Climate change, *Macrocystis pyrifera*, macrophytes, ocean acidification, photosynthesis–respiration, seawater chemistry.

INTRODUCTION

Local-scale fluctuations in seawater pH and dissolved oxygen (DO) are a natural feature of coastal ecosystems, driven by processes such as upwelling, freshwater inputs, organic matter loading and biological activity (Vargas *et al.*, 2016; Lowe *et al.*, 2019; Walter *et al.*, 2022; George *et al.*, 2024). These dynamics can create highly variable and sometimes extreme changes in seawater chemistry conditions over short spatial and temporal scales (Baumann *et al.*, 2015;

Gobler and Baumann, 2016; Baumann and Smith, 2018). However, these natural patterns now occur against the backdrop of long-term, anthropogenically driven changes in ocean chemistry. Ocean acidification, caused by the uptake of atmospheric CO_2 and the resulting increase in dissolved inorganic carbon, is reducing surface ocean pH globally (Feely *et al.*, 2004, 2010). At the same time, ocean warming is decreasing oxygen solubility, while shifts in geophysical and biogeochemical processes are increasing oxygen demand, driving widespread deoxygenation and, in some regions, hypoxia (Feely *et al.*, 2010; Diaz and Rosenberg, 2014; Breitburg *et al.*, 2018; Pitcher *et al.*, 2023). Globally, surface ocean pH has already declined by ∼0.02 units and DO by ∼2 %, with rates accelerating in recent decades (Pörtner *et al.*, 2019; Garcia-Soto *et al.*, 2021). In nearshore and estuarine environments, local biological and physical processes can generate substantial short-term variability in pH and DO that may intensify or mask broader long-term trends (Howarth *et al.*, 2011; Carstensen and Duarte, 2019; Kroeker *et al.*, 2023). Together, these shifts are expected to profoundly affect marine organisms and ecosystem functioning (Waldbusser and Salisbury, 2014; Doney *et al.*, 2020; Hurd *et al.*, 2020).

In response, a range of mitigation and adaptation strategies are being explored (Pörtner *et al.*, 2019), with growing attention to the capacity of marine macrophytes, particularly kelps, to potentially buffer short-term and local changes in seawater pH and DO (Kosek and Kukliński, 2023; Ross *et al.*, 2023; Strain *et al.*, 2024). Through photosynthesis, kelps take up inorganic carbon, primarily as aqueous CO_2 and/or bicarbonate (HCO_3^-), and release O_2, thereby elevating local seawater pH and DO when rates of carbon fixation exceed replenishment from surrounding waters (Delille *et al.*, 1997, 2000, 2009; Hofmann *et al.*, 2011; Cornwall *et al.*, 2015; Hirsh *et al.*, 2020; Strain *et al.*, 2024). Their complex and dense 3-D structure can further slow water exchange within the canopy, allowing the buffering chemical effect produced by macroalgae to persist for longer periods, although the magnitude of such effects varies with forest size, canopy density and exposure to waves, and other hydrodynamic conditions (Jackson and Winant, 1983; Gaylord *et al.*, 2003; Morris *et al.*, 2020; Kregting *et al.*, 2021; Elsmore *et al.*, 2024). At night, respiration and microbial remineralization release CO_2 and consume O_2, lowering pH and DO (Frieder *et al.*, 2012). However, because the solubility of CO_2 is roughly an order of magnitude greater than that of O_2 (Weiss, 1974), daytime CO_2 drawdown is often not fully counterbalanced by nocturnal respiration, allowing elevated pH and DO to persist across diel cycles, a pattern that has been documented in both natural kelp forests and macroalgae aquaculture systems (Murie and Bourdeau, 2020; Xiao *et al.*, 2021).

Despite this potential, empirical studies of kelp forests' effects on seawater chemistry have demonstrated mixed results (Kosek and Kukliński, 2023; Strain *et al.*, 2024). Some studies reported higher seawater pH and DO inside kelp forests than outside the forest (e.g. Delille *et al.*, 1997, 2000, 2009; Hofmann *et al.*, 2011; Frieder *et al.*, 2014; Pfister *et al.*, 2019; Hirsh *et al.*, 2020), while others observe no consistent patterns or high temporal variability (Kapsenberg and Hofmann, 2016; Koweek *et al.*, 2017; Traiger *et al.*, 2022). These discrepancies are widely attributed to differences in kelp biomass, forest structure, hydrodynamic forcing, freshwater inputs and anthropogenic influences (Krause-Jensen *et al.*, 2015; Strain *et al.*, 2024). However, most studies have been conducted at single sites or within one region, limiting the ability to examine how biological patterns and oceanographic conditions are associated with changes in seawater chemistry.

Giant kelp (*Macrocystis pyrifera*) is among the most productive macrophytes on Earth and occurs across a wide range of environmental settings, from strongly upwelling-dominated coasts to hydrographically stable temperate systems (Graham *et al.* 2007; Gonzalez-Aragon *et al.*, 2025). In eastern boundary current systems such as Chile, seasonal upwelling delivers cold, CO_2-rich and often oxygen-poor waters that can simultaneously stimulate giant kelp growth and abundance while reducing seawater pH and DO concentrations (Murie and Bourdeau, 2020; Guajardo-Rubilar *et al.*, 2026). In contrast, south-eastern Australia is characterized by relatively stable, oligotrophic waters, with giant kelp forests declining due to marine heatwaves and strengthening of the East Australian Current (Butler *et al.*, 2020).

Previous studies have also often relied on observations spanning multiple seasons or years, enabling broader assessment of temporal variability in giant kelp density and oceanographic forcing (e.g. Frieder *et al.*, 2012; Hirsh *et al.*, 2020) and reporting stronger effects during spring–summer and near-surface portions of the canopy, where biomass is concentrated. In contrast, our study uses shorter-term deployments across multiple sites and regions to examine whether consistent seawater chemistry patterns emerge across contrasting hydrographic conditions. While this design limits our ability to resolve seasonal and interannual variability fully or isolate mechanistic drivers, it provides an opportunity to evaluate the spatial consistency of giant kelp-associated seawater chemistry patterns across diverse environments.

Here, we provide the first multi-site assessment of how giant kelp forests locally influence seawater pH and DO across contrasting Southern Hemisphere environments. We focused on one site in central Chile, two in southern Chile and four in south-eastern Australia (Tasmania), which markedly differ in hydrographic forcing, from nutrient-rich, upwelling-influenced waters and freshwater affected systems in Chile (Vargas *et al.*, 2016; Vergara-Jara *et al.*, 2019; Molinet *et al.*, 2025) to oligotrophic and hydrographically stable environments in south-east Australia (Ridgway and Ling, 2023). Specifically, we examined whether (2) diel seawater pH and DO patterns differed inside versus outside giant kelp forests, (2) variation in adult giant kelp density was associated with variation in seawater pH and DO within forests; and (3) upwelling influenced seawater chemistry differently inside and outside giant kelp forests. Different subsets of sites were used to address these questions because paired inside–outside deployments, giant kelp density measurements and upwelling data were not consistently available or ecologically relevant across all study sites. Seawater chemistry measurements were collected in the upper 2–3 m of the water column, corresponding to the adult giant kelp height within forests and positioned above other kelp species both inside and outside the forest. By comparing seawater chemistry across multiple contrasting environments, this study provides new insights into the potential of giant kelp forests to

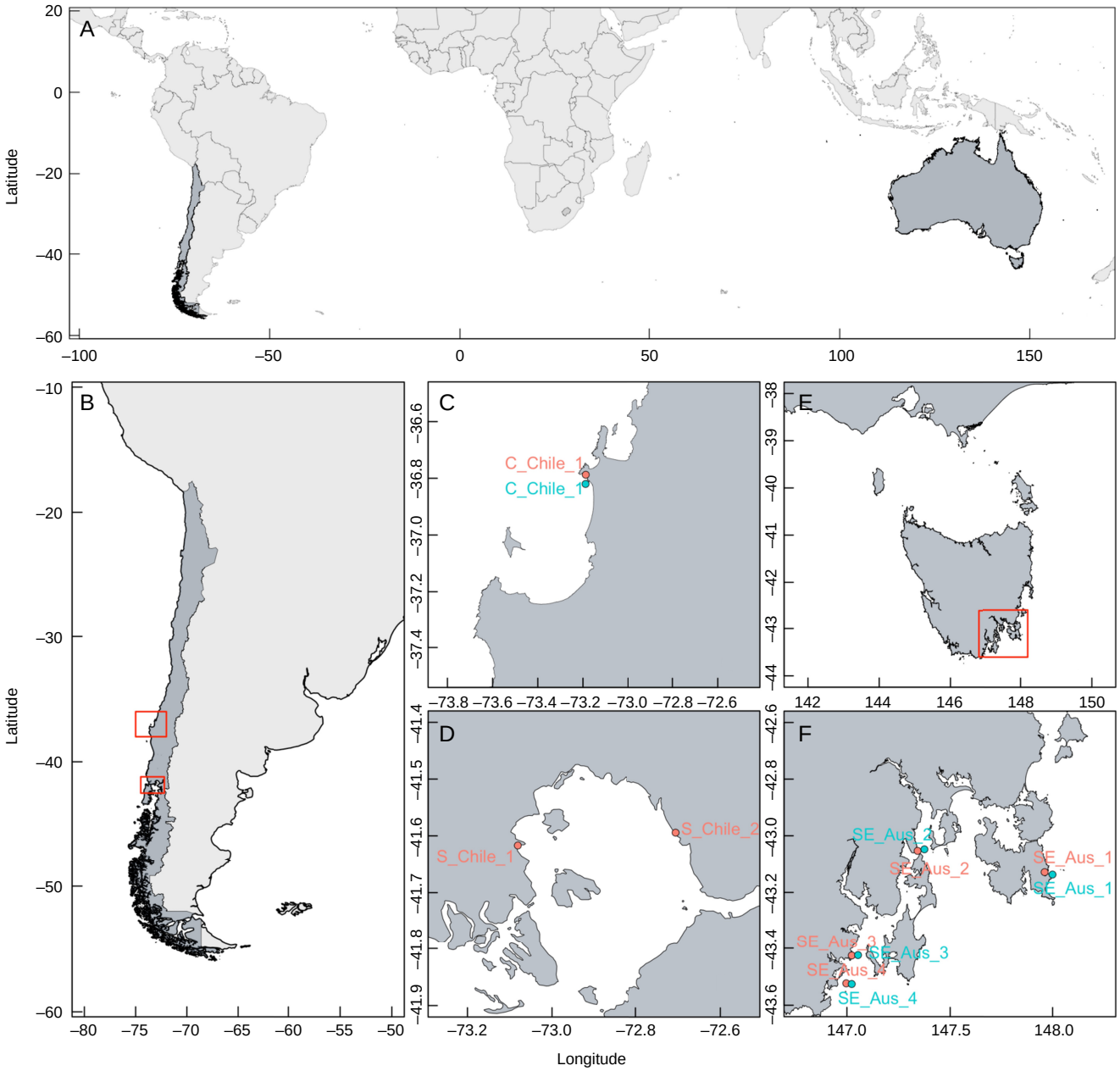

FIG. 1. Map showing sites where seawater chemistry measurements were conducted in south-east Australia and central and southern Chile. Points are coloured by location: aqua indicates sites located inside the giant kelp forest, while orange indicates sites outside the kelp forest. Insets display the broader geographical context with study areas outlined.

create short-term, localized refugia from low-pH and low DO conditions for associated marine organisms.

MATERIALS AND METHODS

Site and habitat descriptions

The study was conducted at seven sites: four in Tasmania (Australia), one in central Chile and two in southern Chile (Fig. 1). The giant kelp (*Macrocystis pyrifera*) forests at these sites varied in age and density and were exposed to contrasting oceanographic conditions. However, all sites were characterized by subtidal rocky reef habitat and influenced by wave action to some extent.

The Tasmanian sites were characterized by deeper rocky reefs (~9–11 m depth), varying levels of wave exposure and differences in the persistence of giant kelp forests (Forbes *et al.*, 2024). These sites are not influenced by coastal upwelling or major freshwater inputs, but instead by relatively oligotrophic conditions which are amplified by strengthening of the East Australian Current (Butler *et al.*, 2020; Forbes *et al.*, 2024). The central Chile site, located near the Gulf of Arauco, is characterized by shallow rocky reefs (~7–10 m depth) with giant kelp forest exhibiting heterogeneous interannual variation rather than pronounced seasonal variability

Table 1. Overview of measurements, sensors used and dates of collection for each site.

Site label	Site name	Sensor and site depth (m)	Location	Measurements	Sensor and measurement interval (min)	Dates and duration (d)
SE_Aus_1	Fortescue Bay	2.5 m (sensor), 11 m (site)	Inside and outside giant kelp forest	DO, pH, kelp density, temperature	PME miniDOT, HOBO pH (MX2501), 10 min	18/10/2022–1/11/2022 (15)
SE_Aus_2	Tinderbox	2 m (sensor), 9 m (site)	Inside and outside giant kelp forest	DO, pH, temperature	PME miniDOT, HOBO pH (MX2501), 10 min	24/01/2023–6/02/2023 (14)
SE_Aus_3	Sisters Bay	3 m (sensor), 10 m (site)	Inside and outside giant kelp forest	DO, pH, kelp density, temperature	PME miniDOT, HOBO pH (MX2501), 10 min	12/09/2023–24/09/2023 (14)
SE_Aus_4	Actaeon Islands	3 m (sensor), 11 m (site)	Inside and outside giant kelp forest	DO, pH, kelp density, temperature	PME miniDOT, HOBO pH (MX2501), 10 min	12/10/2023–6/11/2023 (26)
C_Chile_1	Concepcion	2 m (sensor), 8 m (site)	Inside and outside giant kelp forests	DO, pH, temperature	PME miniDOT, HOBO pH (MX2501), 60 min	3/11/2023–30/11/2023 (27)
S_Chile_1	Ilque	2 m (sensor), 8 m (site)	Inside giant kelp forest	DO, pH, kelp density, temperature	HOBO DO (U26-001), HOBO pH (MX2501), 20 min	9/11/2023–30/11/2023 (22)
S_Chile_2	Metri	2 m (sensor), 8 m (site)	Inside giant kelp forest	DO, pH, kelp density, temperature	HOBO DO (U26-001), HOBO pH (MX2501), 20 min	7/11/2023–29/11/2023 (23)

(Guajardo-Rubilar *et al.*, 2026). This region is strongly influenced by seasonal coastal upwelling driven by prevailing south–westerly winds during spring and summer (Arcos and Navarro 1986; Peterson *et al.*, 1988; Sobarzo *et al.*, 2007). In contrast, the southern Chilean sites are characterized by relatively shallow giant kelp forests (~6–8 m depth), annual kelp populations and moderate wave exposure (Buschmann *et al.*, 2004). Unlike central Chile, these systems are primarily influenced by freshwater inputs from the Reloncaví Estuary rather than by coastal upwelling (Castillo *et al.*, 2016; Pérez-Santos *et al.*, 2021; Pinilla *et al.*, 2024).

Seawater pH and DO diel patterns inside and outside giant kelp forests

To assess whether diel seawater pH and DO patterns differed between areas within and outside giant kelp forests, pH/temperature and DO/temperature sensors were deployed in central Chile and Tasmania. In central Chile, pH/temperature and DO/temperature sensors were deployed within giant kelp forests where *M. pyrifera* was interspersed with shorter stipated kelps (~4 m tall and 4 m below the sensors) and on adjacent rocky reefs without kelps (located >100 m away from the giant kelp site), In Tasmania, measurements were taken within forests where *M. pyrifera* was similarly interspersed with shorter stipitate kelps (~2 m tall and at least 4 m below the sensors), and on adjacent rocky reefs with comparable species composition and stipe densities but lacking giant kelp (Forbes *et al.*, 2024).

All sensors were deployed within giant kelp forests at ~2–3 m depth in the water column, for 14–27 d. At each site, seawater pH, DO and temperature were recorded at 10-, 20- or 60-min intervals using HOBO pH loggers and miniDOT or HOBO DO loggers (Table 1). Sensors were calibrated according to the manufacturer's instructions. To standardize measurements across sites with differing logger sampling intervals, all data were converted to hourly averages of pH and DO. Comparisons between higher-frequency measurements and hourly subsampling indicated that hourly averages produced comparable patterns in seawater chemistry across sites and habitats.

Giant kelp density effects on seawater pH and DO diel patterns

To assess whether adult giant kelp density provided a reasonable proxy for canopy structure at the depth of seawater chemistry measurements, additional information on kelp morphology and vertical distribution was collected.

In Tasmania, the number of giant kelps reaching the height of the seawater chemistry sensors was recorded along 2×50 m transects at each site, with an average of 75 % of individuals extending to the sensor depth. In southern Chile, adult giant kelp (>60 cm) density was quantified along four 10-m transects at each site using randomly placed 1-m^2 quadrats (16 quadrats per site), and ten adult kelps were collected at each site to estimate total length. Approximately 60 % of adult individuals ranged between 2 and 4 m in length, corresponding closely to the depth of the seawater chemistry sensors (~2 m below the surface). In central Chile, adult giant kelp density was not quantified; however, 20 adult kelps were collected and measured, with ~75 % of individuals ranging between 4 and 6 m in length. Although direct measurements of canopy biomass at sensor depth were unavailable, these observations indicated that most adult giant kelps extended into the upper water column where seawater chemistry measurements were collected.

Analysis

To characterize variation in seawater chemistry (pH and DO), hourly pH and DO values were firstly calculated across all sites. Linear mixed-effects models (LMs) were used to examine the effects of habitat (inside vs outside) and sites (four Tasmanian sites and one central Chile site) with day included as a random effect to account for temporal autocorrelation among repeated measurements. Hour of day was modelled as a second-degree polynomial term to capture diel patterns in seawater chemistry.

To examine whether relationships between pH and DO differ inside vs outside giant kelp forests during periods of active photosynthesis, additional LMs were conducted using daylight measurements only (0900–1700 h), with the same fixed and random effects structure as that described above.

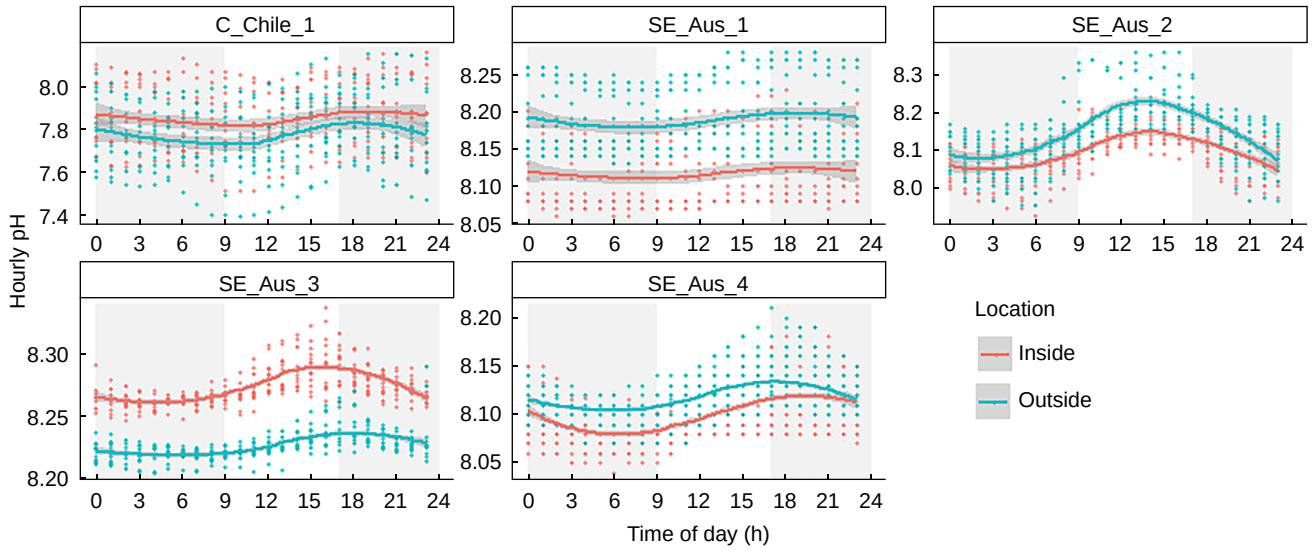

FIG. 2. Hourly pH inside (blue) and outside (orange) giant kelp forests at five sites. Coloured lines indicate mean values. Dark grey shading represents ±95 % confidence intervals; light grey shading highlights night-time hours (~1900–0800 h).

Within giant kelp forests, either LMs or generalized linear models (GLMs) with a quasi-Poisson distribution were used to examine relationships among hourly pH, DO and temperature at each site separately. Hour of day was included as a second-degree polynomial covariate to account for diel variability. Analyses were conducted for both the full 24-h period and daylight hours only (0900–1700 h).

To test whether adult giant kelp density was associated with seawater chemistry within forests in southern Chile and Tasmania, LMs were used to examine the effects of site, giant kelp density and hour of day on hourly pH and DO, with day included as a random effect. These analyses included the five sites where giant kelp density measurements were available (three Tasmanian sites and two southern Chilean sites).

To assess whether upwelling influenced seawater chemistry differently inside and outside giant kelp forests, we first determined the occurrence of coastal upwelling events at the central Chile sites (inside and outside giant kelp forests). To do this, wind data were obtained from MeteoChile for the period 3–30 November 2023. An upwelling index (UI) was calculated following Bakun (1973) (see Supplementary Data S1 for details), where positive values indicate winds favourable for upwelling (south-to-north winds). Upwelling index values were then compared with seawater pH and DO measured inside and outside giant kelp forests to assess short-term relationships between upwelling conditions and seawater chemistry.

For all models, assumptions of normality and homoscedasticity were assessed using diagnostic plots. Where necessary, data transformations were applied based on Box–Cox procedures. Significance of fixed effects was assessed using type III ANOVA implemented with the Anova function in the car package (Fox *et al.*, 2013), and post hoc comparisons were conducted using the emmeans package (Lenth *et al.*, 2019). All statistical analyses were performed in R version 4.5.0 (R Core Team, 2025) and figures were generated using ggplot2 (Wickham, 2011).

RESULTS

Effects of giant kelp forests on local seawater chemistry

The effects of giant kelp forests on hourly pH varied across sites (Fig. 2, Table 2). At central Chile 1 and Tasmania 3, pH was significantly higher inside the giant kelp forests than outside. In contrast, at all other sites hourly pH was higher outside than inside the giant kelp forests.

Similarly, the influence of giant kelp forests on seawater DO concentrations was site-specific (Fig. 3, Table 2). At central Chile 1, Tasmania 3 and 4, DO was significantly higher inside than outside the giant kelp forests. In contrast, Tasmania 2 had significantly lower DO inside the giant kelp forest relative to outside. At all other sites, there were no detectable differences in DO between inside and outside the giant kelp forests.

At all sites, hourly pH and DO were positively correlated during daylight hours, though the strength and nature of this relationship varied across sites and through time (Fig. 4, Table 3). At both central Chile 1 and Tasmania 3, the relationship between hourly pH and DO was steeper and there were higher R^2 values inside the giant kelp forest compared with outside (Fig. 4, Table 3). This relationship was stronger in Chile 1 than in Tasmania 3, with higher R^2 values. In contrast, at Tasmania 1 there was a steeper relationship and higher R^2 value outside relative to inside the giant kelp forest (Fig. 4, Table 3). At the remaining sites there were no significant differences between habitats (Fig. 4, Table 3).

Across all giant kelp sites (including southern Chile), seawater hourly pH and DO had significant and moderate to strong positive relationships (adjusted R^2 values 0.33–0.86), (Table 4). Most sites also showed weak to strong positive relationships between hourly DO and temperature (adjusted R^2 from 0.15 to 0.72), as well as between pH and temperature (adjusted R^2 from 0.12 to 0.85) (Table 4). Significant effects of time of day were observed, especially during the daylight period, reflecting diel cycles that influence these

TABLE 2. Results of LMs testing the effects of habitat (inside vs outside giant kelp forests), site (five levels) and time (hour, modelled as second-degree polynomial) on (A) hourly pH and (b) hourly DO (mg L^{-1}). Bold *P*-value indicated significant differences.

(A) Hourly pH

Effect	χ^2	d.f.	*P*-value
Intercept	418 759.40	1	**<0.0001**
Habitat	416.09	1	**<0.0001**
Site	811.01	4	**<0.0001**
Poly(time)	166.86	2	**<0.0001**
Habitat × site	1264.16	4	**<0.0001**

Site	Contrast	Estimate	Standard error	d.f.	*t*-Ratio	*P*-value
C_Chile_1	Inside–outside	0.0723	0.00354	3655	20.685	**<0.0001**
SE_Aus_1	Inside–outside	−0.0679	0.00342	3656	−20.143	**<0.0001**
SE_Aus_2	Inside–outside	−0.0523	0.00341	3655	−15.543	**<0.0001**
SE_Aus_3	Inside–outside	0.0464	0.00348	3655	13.138	**<0.0001**
SE_Aus_4	Inside–outside	−0.0217	0.00246	3656	−7.543	**<0.0001**

(B) Hourly DO

Effect	χ^2	d.f.	*P*-value
Intercept	5593.66	1	**<0.0001**
Habitat	540.91	1	**<0.0001**
Site	2030.16	4	**<0.0001**
Poly(time)	307.43	2	**<0.0001**
Habitat × site	434.48	4	**<0.0001**

Site	Contrast	Estimate	Standard error	*t*-Ratio	*P*-value
C_Chile_1	Inside–outside	0.9778	0.0420	23.257	**<0.0001**
SE_Aus_1	Inside–outside	−0.0314	0.0405	−0.774	0.4392
SE_Aus_2	Inside–outside	−0.1066	0.0405	−2.635	**0.0084**
SE_Aus_3	Inside–outside	0.2662	0.0427	6.236	**<0.0001**
SE_Aus_4	Inside–outside	0.1547	0.0292	5.297	**<0.0001**

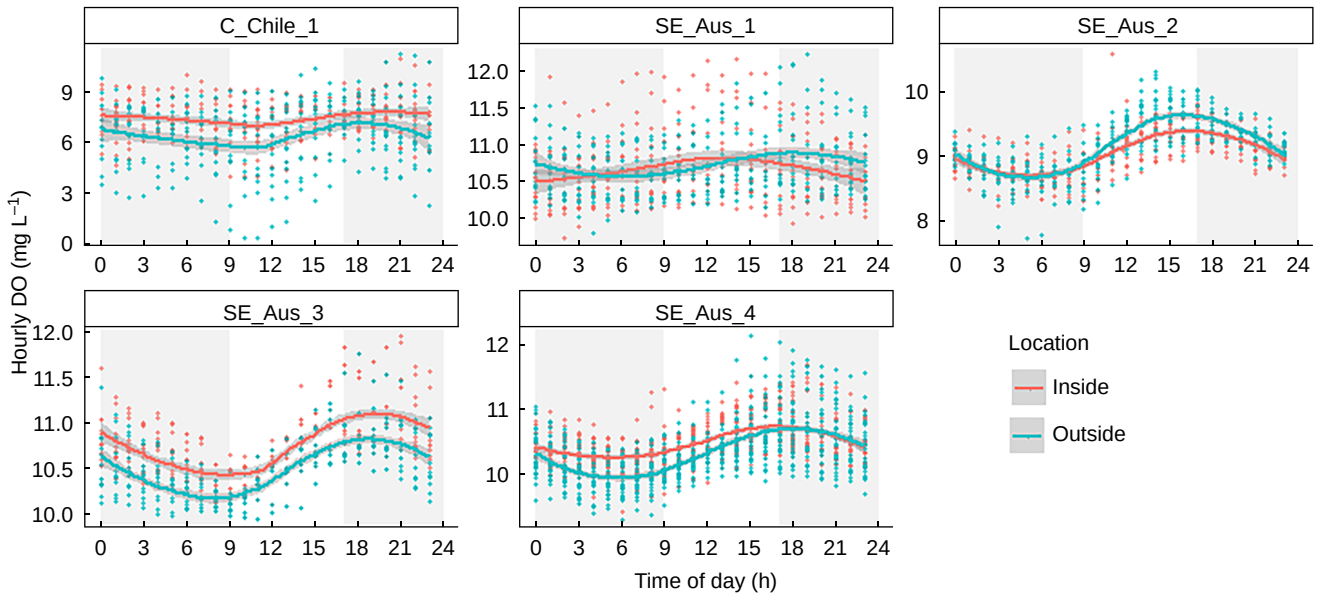

FIG. 3. Hourly DO concentrations inside (blue) and outside (orange) giant kelp forests at five sites. Coloured lines indicate mean values. Dark grey shading represents ±95 % confidence intervals; light grey shading highlights night-time hours (~1900–0800 h).

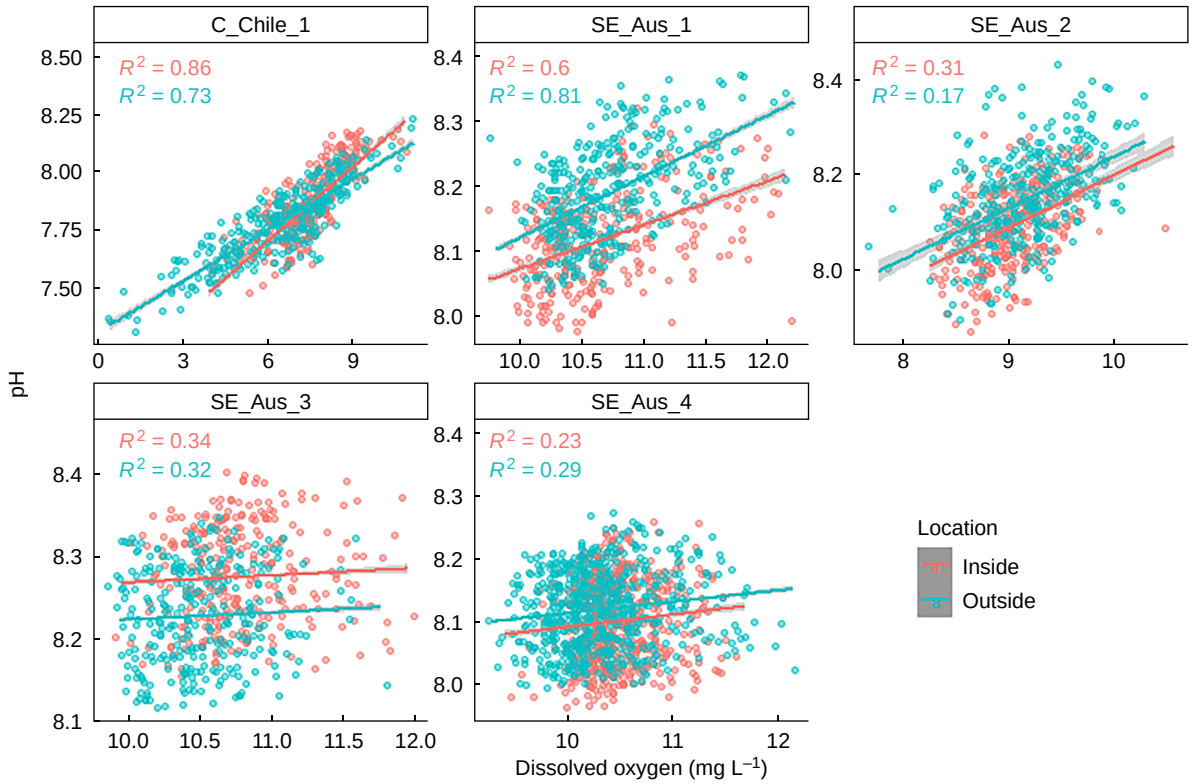

FIG. 4. Relationships between hourly pH and DO inside (aqua) and outside (orange) giant kelp forests at five sites, in daylight hours (0900–1700 h). Coloured lines indicate mean values: shading represents ±95 % confidence intervals.

TABLE 3. Results of LMs testing the effects of habitat (inside vs outside giant kelp forests), site (five) and time (hour, modelled as a second-degree polynomial) on the relationships between hourly seawater pH and DO (mg L^{-1}) during daylight hours (0900–1700 h). Bold *P*-value indicate significant differences.

Factor	χ^2	d.f.	*P*-value
(Intercept)	156 493.171	1	**<0.0001**
Habitat	40.600	1	**<0.0001**
DO	872.658	1	**<0.0001**
Site	279.092	4	**<0.0001**
Poly(time)	61.967	2	**<0.0001**
DO × habitat	56.789	1	**<0.0001**
DO × site	221.402	4	**<0.0001**
Habitat × site	50.098	4	**<0.0001**
DO × habitat × site	70.817	4	**<0.0001**

Site pairwise contrasts	Estimate	Standard error	*t*-Ratio	d.f.	*P*-value
C_Chile_1 inside–outside	0.0201	0.0018	11.144	3658	**<0.0001**
SE_Aus_1 inside–outside	−0.0144	0.0056	−2.545	3658	**0.0110**
SE_Aus_2 inside–outside	−0.005	0.006	−0.740	3651	0.4591
SE_Aus_3 inside–outside	0.0102	0.0724	1.1411	3649	**0.0465**
SE_Aus_4 inside–outside	0.002	0.0047	0.294	3654	0.7689

seawater chemistry parameters (Table 4). At most sites, temperature-related relationships (both pH–temperature and DO–temperature) had higher R^2 values during daylight hours (0900–1700 h) compared with the full 24-h period, with these effects more pronounced in central and southern Chile than in the Tasmanian sites (Table 4). Additionally, four sites (Tasmania 3, central Chile 1 and southern Chile 1 and 2), had higher R^2 values for the relationship between

TABLE 4. Results of GLMs assessing relationships among hourly pH, temperature (temp) and DO (mg L^{-1}), and the effect of time (hour, modelled as a second-degree polynomial) inside giant kelp forests. Bold *P*-value significant diferrences.

Site	Factor	χ^2 24 h	d.f.	Adjusted R^2	*P*-value	χ^2 0900–1700 h	d.f.	Adjusted R^2	*P*-value
C_Chile_1	DO × temp	44.846	1	0.1552	**<0.0001**	9.003	1	0.242	**0.0027**
	Hour	1.940	2	–	0.379	72.559	1	–	**<0.0001**
	pH × temp	36.803	1	0.1228	**<0.0001**	33.698	1	0.2581	**<0.0001**
	Hour	1.440	2	–	0.4867	6.479	2	–	**0.0394**
	pH × DO	1029.56	1	0.7792	**<0.0001**	289.714	1	0.8583	**<0.0001**
	Hour	2.05	2	–	0.3595	0.355	2	–	0.8374
S_Chile_1	DO × temp	1224.50	1	0.7177	**<0.0001**	178.756	1	0.4987	**<0.0001**
	Hour	16.21	2	–	**0.0004**	15.579	2	–	**0.0004**
	pH × temp	1342.45	1	0.7313	**<0.0001**	749.82	1	0.8132	**<0.0001**
	Hour	22.19	2	–	**<0.0001**	8.33	2	–	**0.0155**
	pH × DO	272.469	1	0.3645	**<0.0001**	129.655	1	0.4487	**<0.0001**
	Hour	50.603	2	–	**<0.0001**	28.975	2	–	**<0.0001**
S_Chile_2	DO × temp	476.43	1	0.5309	**<0.0001**	100.409	1	0.3637	**<0.0001**
	Hour	66.99	2	–	**<0.0001**	0.976	2	–	0.6138
	pH × temp	955.33	1	0.6446	**<0.0001**	442.56	1	0.7126	**<0.0001**
	Hour	16.46	2	–	**0.0002**	39.23	2	–	**<0.0001**
	pH × DO	274.906	1	0.3549	**<0.0001**	162.09	1	0.5636	**<0.0001**
	Hour	89.827	2	–	**<0.0001**	112.12	2	–	**<0.0001**
SE_Aus_1	DO × temp	119.339	1	0.3075	**<0.0001**	66.829	1	0.3825	**<0.0001**
	Hour	31.116	2	–	**<0.0001**	4.896	2	–	0.0865
	pH × temp	182.245	1	0.3716	**<0.0001**	78.707	1	0.4246	**<0.0001**
	Hour	0.394	2	–	0.812	0.397	2	–	0.8202
	pH × DO	460.09	1	0.5969	**<0.0001**	157.146	1	0.5921	**<0.0001**
	Hour	30.86	2	–	**<0.0001**	9.945	2	–	**0.0069**
SE_Aus_2	DO × temp	8.17	1	0.2957	**0.0043**	0.013	1	0.3576	0.9080
	Hour	110.39	2	–	**<0.0001**	59.628	2	–	**<0.0001**
	pH × temp	19.63	1	0.2991	**<0.0001**	0.8214	1	0.1765	0.3648
	Hour	112.58	2	–	**<0.0001**	25.2885	2	–	**<0.0001**
	pH × DO	202.02	1	0.5435	**<0.0001**	29.9092	1	0.3087	**<0.0001**
	Hour	85.32	2	–	**<0.0001**	3.5443	2	–	0.1700
SE_Aus_3	DO × temp	0.853	1	0.2684	0.3556	0.092	1	0.4813	0.7620
	Hour	101.633	2	–	**<0.0001**	123.869	2	–	**<0.0001**
	pH × temp	34.234	1	0.3456	**<0.0001**	3.03	1	0.4380	0.0817
	Hour	55.529	2	–	**<0.0001**	39.99	2	–	**<0.0001**
	pH × DO	7.875	1	0.2888	**0.0050**	2.012	1	0.3331	**0.0100**
	Hour	101.041	2	–	**<0.0001**	35.951	2	–	**<0.0001**
SE_Aus_4	DO × temp	3.603	1	0.1577	0.0577	33.871	1	0.3135	**<0.0001**
	Hour	115.288	2	–	**<0.0001**	86.365	2	–	**<0.0001**
	pH × temp	3.479	1	0.2248	0.0622	2.566	1	0.2319	0.1092
	Hour	161.339	2	–	**<0.0001**	69.396	2	–	**<0.0001**
	pH × DO	8.16	1	0.2305	**0.0043**	0.585	1	0.2253	0.4444
	Hour	138.19	2	–	**<0.0001**	57.602	2	–	**<0.0001**

Models were run separately for each of the seven sites, across both the full 24-h period and the daylight hours (0900–1700 h).

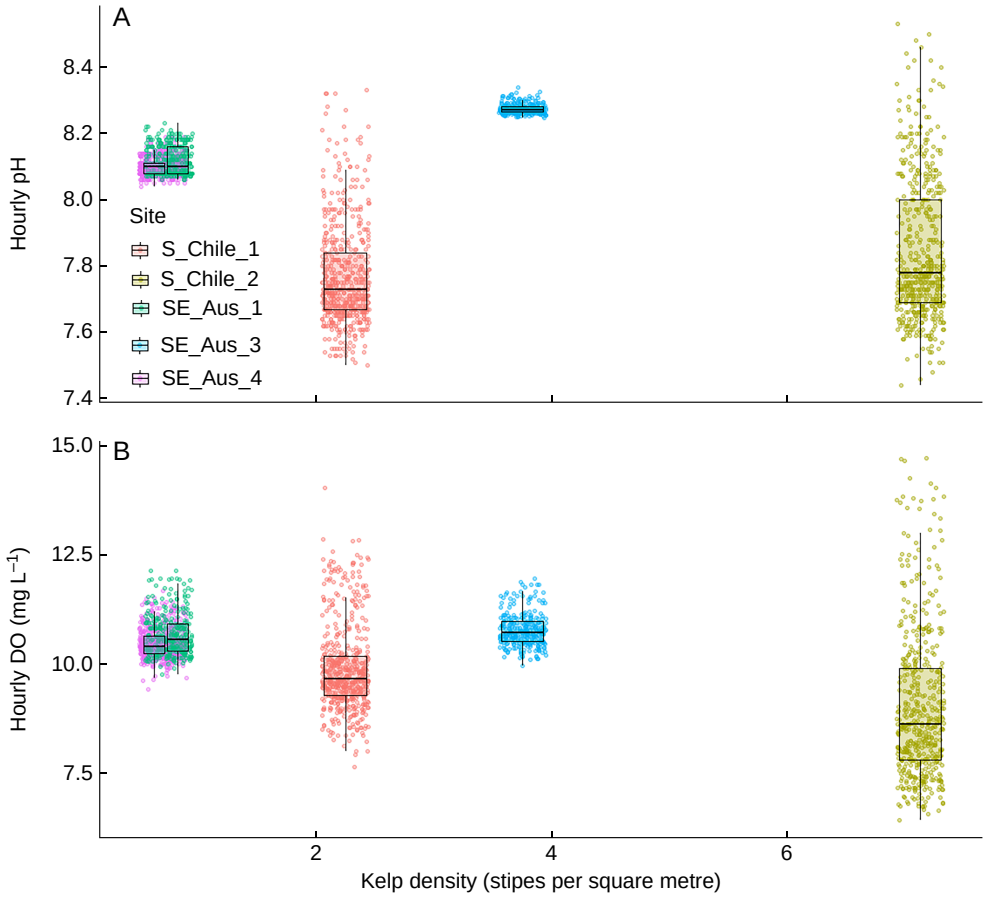

FIG. 5. Relationships between kelp density and (A) hourly pH and (B) hourly DO for five sites in two regions. Raw data points are shown with jitter for visibility. Boxplots represent the median and interquartile range with 95 % confidence intervals.

hourly pH and DO in daylight hours than over the full day, consistent with increased photosynthetic activity driving these patterns (Table 4).

Effects of giant kelp density on local seawater chemistry

Both hourly pH and DO increased with giant kelp density, though these relationships differed between regions and through time (Fig. 5, Table 5). Pairwise comparisons indicated that the positive effect of increasing giant kelp density on hourly pH was stronger in Tasmania than in southern Chile. Similarly, higher giant kelp density was associated with elevated hourly DO concentrations in Tasmania, whereas this effect was weaker or not evident in southern Chile.

Effects of upwelling on seawater chemistry in central Chile

The UI for central Chile indicated several wind-driven upwelling pulses during the deployment period, particularly between 11 and 17 November 2023 (Supplementary Data S1). During this event, positive UI values (>100 $m^3\ s^{-1}\ km^{-1}$) corresponded to marked declines in seawater pH and DO outside the giant kelp forest, reaching minima of 7.40 and 0.43 mg L^{-1}, respectively. In contrast, inside the giant kelp forest, minimum values were slightly higher (pH 7.52; DO 3.92 mg L^{-1}), suggesting a moderate and localized buffering effect associated with giant kelp photosynthesis and reduced mixing. Following the relaxation of upwelling (negative UI values), both seawater pH and DO increased rapidly in both habitats, indicating a strong short-term coupling between wind-driven upwelling intensity and nearshore seawater chemistry.

DISCUSSION

This study provides a multi-site assessment of seawater pH and DO diel patterns associated with giant kelp forests across contrasting Southern Hemisphere habitats. Clear increases in pH and DO were observed within the giant kelp forest in central Chile and at one site in Tasmania, whereas no consistent differences were detected at other sites. At Tasmania 3, hourly pH and DO inside the canopy were elevated by ~0.05 units and ~0.3 mg L^{-1}, respectively, while at central Chile 1, increases were greater ~0.07 pH units and ~0.97 mg L^{-1} DO. These values fall within the global ranges reported for other kelp forests (pH ≈ 0.01–0.8 and DO ≈ 0.13–2.89 mg L^{-1}, (Strain *et al.*, 2024)), with the effects unsurprisingly concentrated during daylight hours (Frieder *et al.*, 2014; Traiger *et al.*, 2022; Strain *et al.*, 2024). Overall, our results indicate that the influence of giant kelp forests on seawater pH and DO vary substantially among sites and regions, and these differences are context-dependent. Similar spatial variability has been reported at sites within California (Koweek *et al.*, 2017; Traiger *et al.*, 2022; Kroeker

TABLE 5. Results of LMs testing the effects of giant kelp density (m^2), region (SE Australia and southern Chile) and time (hour, modelled as a second-degree polynomial) on hourly seawater pH and DO (mg L^{-1}). Bold *P*-value indicate significant differences.

(A) Hourly pH

Factor	χ^2	**d.f.**	***P*-value**
(Intercept)	260 226.11	1	**<0.0001**
Region	208.59	1	**<0.0001**
Density	46.53	1	**<0.0001**
Poly(time)	19.88	2	**<0.0001**
Region × giant kelp density	25.87	1	**<0.0001**

Contrast	Estimate	Standard error	d.f.	*t*-Ratio	*P*-value
Australia–Chile	0.0419	0.0082	84	5.087	**<0.0001**

(B) Hourly DO

Factor	χ^2	d.f.	*P*-value
(Intercept)	7626.81	1	**<0.0001**
Region	1.60	1	0.2055
Density	1.35	1	0.2458
Poly(time)	212.56	2	**<0.0001**
Region × giant kelp density	16.37	1	**<0.0001**

Contrast	Estimate	Standard error	d.f.	*t*-Ratio	*P*-value
Australia–Chile	0.253	0.0626	83.8	4.046	**0.0001**

et al., 2023) and specific regions in Australia (Britton *et al.*, 2016; Ling *et al.*, 2020; Strain *et al.*, 2024), reinforcing that the potential of kelp forests to provide short-term refuges from changes in pH and DO must be evaluated within their specific ecological and physical contexts.

Effects of giant kelp forests on seawater chemistry in south-east Australia

In Tasmania, Australia, there was only one site where giant kelp forests significantly altered surrounding seawater pH and DO relative to outside. The minimum and maximum hourly values recorded inside that giant kelp forest were 8.24 and 8.34 for pH and 9.89 and 12.07 mg L^{-1} for DO, compared with 8.19 and 8.32 (pH) and 9.81 and 11.86 mg L^{-1} (DO) outside. Positive relationships between pH and DO were most evident during the daylight hours, and there was a stronger influence of photosynthetic activity inside the giant forest than outside. Moreover, the consistently positive hourly range in pH and DO within this giant kelp forest suggests that net photosynthesis might have outweighed respiration.

Several factors may explain why buffering was only evident at this site. Remnant Tasmanian giant kelp forests are typically smaller, younger, less dense and more transient than they were historically (Johnson *et al.*, 2011; Butler *et al.*, 2020; Forbes *et al.*, 2024), largely due to the increasing penetration of the East Australian Current and marine heatwaves (Mabin *et al.*, 2019; Hurd *et al.*, 2023; Ridgway and Ling, 2023). Consequently, differences in giant kelp density may have contributed to weaker seawater chemistry differences at Tasmania 1, 2 and 4 relative to Tasmania 3 or compared with the more extensive and persistent giant kelp forests in central Chile (Mora-Soto *et al.*, 2021; Guajardo-Rubilar *et al.*, 2026) and elsewhere globally (Wernberg *et al.*, 2019).

Another potential explanation is the high diversity and cover of the macroalgal subcanopy in Tasmania giant kelp forests, which may mask the signal of giant kelp. In this region, up to ten species of large, brown, canopy-forming macroalgae co-occur, forming a mixed canopy both inside and outside remnant giant kelp forests (S. Bennett, unpubl. data). Species such as *Ecklonia radiata*, *Phyllospora comosa* and several others fucoids, can obtain substantial sizes and biomass, and their photosynthetic activity likely contributes significantly to seawater pH and DO variability (Britton *et al.*, 2016; Ling *et al.*, 2020; Strain *et al.*, 2024). This interpretation is supported by the relatively high pH values recorded outside giant kelp forests at Tasmania 1, 2 and 4, where similar densities of other canopy-forming kelps were recorded inside and outside the giant kelp forest (E. M. A. Strain, unpubl. data).

The strongest seawater chemistry effects occurred at the youngest and densest giant kelp forest, consistent with previous studies showing that dense kelp forests are often associated with higher daytime pH and DO than sparse forests (Krause-Jensen *et al.*, 2015; Traiger *et al.*, 2022; Strain *et al.*, 2024). This pattern parallels terrestrial forests, where younger, regenerating stands or plantations often exhibit the highest rates of carbon uptake as the rapidly growing, dense stands of trees actively fix CO_2 through photosynthesis (Pan *et al.*, 2024).

Effects of giant kelp forests on seawater chemistry in central Chile

Along the Chilean coast, strong seasonal upwelling results in large fluctuations in seawater chemistry particularly during spring and summer (Aguirre *et al.*, 2021; Muñoz *et al.*, 2023). At central Chile 1, seawater pH and DO were consistently higher inside than outside the giant kelp forest, with the strongest correlations occurring during an upwelling pulse. During a major upwelling period, the minimum hourly values outside the forest dropped to pH 7.40 and DO 0.43 mg L^{-1}, whereas inside the forest they remained higher (pH 7.52; DO 3.92 mg L^{-1}). Mean daily offsets between inside and outside the forest ranged from 0.03 to 0.27 pH units and from 0.41 to 4.03 mg L^{-1} DO, comparable to values reported for other macroalgal habitats along upwelling-influenced coastlines (Koweek *et al.*, 2017; Pfister *et al.*, 2019). Similar short-term differences have also been reported in giant kelp forests in California and seagrass meadows in Tanzania (Pfister *et al.*, 2019; George *et al.*, 2024).

These stronger differences during upwelling periods may reflect interactions between nutrient-rich waters, canopy photosynthesis and lower pH and DO conditions outside forests. In central Chile, *M. pyrifera* biomass typically peaks during spring, coinciding with the upwelling season (Gonzalez-Aragon *et al.*, 2025), suggesting that seasonal changes in canopy structure may influence seawater chemistry patterns and that changes associated with upwelling events might promote the growth of *M. pyrifera* (Guajardo-Rubilar *et al.*, 2026). However, the present study was limited to a relatively short

deployment period and did not directly quantify canopy biomass or seawater nutrients concentration.

Freshwater inputs could also have influenced the seawater chemistry at this site through both physical and biogeochemical pathways (Salisbury *et al.*, 2009; Vargas *et al.*, 2016; Breitburg *et al.*, 2018). River discharge and precipitation can reduce seawater pH directly by diluting total alkalinity and indirectly by delivering organic matter that stimulates microbial respiration and CO_2 production (Borgesa and Gypensb, 2010; Duarte *et al.*, 2013). For example, Vargas *et al.* (2016) recorded nearshore pH values as low as 7.60 during peak Biobío River discharge in winter, compared with 7.95–8.15 in more oceanic waters, while higher pH values of ~8.15 were observed near the river plume during spring upwelling due to dense algal blooms. In mixed environments where upwelling and freshwater plumes periodically reduce pH and DO while elevating nutrient concentrations, photosynthetic activity by *M. pyrifera* may locally and temporarily moderate exposure to low pH and low DO conditions.

Effects of giant kelp forests on seawater chemistry in southern Chile

At the southern Chile sites, minimum hourly DO values inside giant kelp forests consistently exceeded 6 mg L^{-1} and were generally higher than those recorded in central Chile. Relationships between pH and DO were weaker than those observed at the central Chile site, suggesting that seawater chemistry dynamics differed between these regions. However, stronger daytime correlations between pH and DO relative to the full 24-h cycle suggest that daytime photosynthesis by giant kelp contributed to increases in both variables.

In contrast to the upwelling-dominated systems in central Chile, southern Chilean coastal ecosystems are strongly influenced by freshwater inputs and exhibit strong salinity-driven pycnoclines resulting from river discharge (Molinet *et al.*, 2025). Freshwater inputs can reduce alkalinity and buffering capacity (Salisbury *et al.*, 2009; Vargas *et al.*, 2016), while organic and nutrient inputs may stimulate microbial respiration and CO_2 production in subsurface waters (Borgesa and Gypensb, 2010; Cai *et al.*, 2011). Consequently, the relatively low pH values recorded in this region likely reflect combined freshwater and biogeochemical influences rather than upwelling.

Contrary to our expectations, giant kelp density was not strongly associated with seawater pH or DO at the southern Chile sites. This suggests that adult density alone may not adequately represent canopy structure or standing biomass in these systems. Although southern Chile site 2 supported higher adult densities than site 1, the forest was younger with a marked seasonality, with smaller individuals and reduced canopy extent (A. H. Buschmann *et al.*, unpubl. data). These observations suggest that differences in canopy structure, size distribution and local physical conditions may have contributed more strongly to seawater chemistry variation than adult density alone.

Conclusions

Across seven sites spanning Tasmania and Chile, seawater chemistry patterns associated with giant kelp forests differed substantially among regions with contrasting environmental conditions. Higher pH and DO inside giant kelp forests were most evident at central Chile 1 and Tasmania 3, where hourly pH was elevated by ~0.05–0.07 units and DO by ~0.3–0.9 mg L^{-1} relative to surrounding waters. Although modest in magnitude, these short-term differences may locally reduce exposure to low pH and low DO conditions for organisms associated with giant kelp habitats, such as amphipods, calcifiers, grazers and gastropods (Almanza *et al.*, 2012; Forbes *et al.*, 2024), which can be found in giant kelp fronds.

However, our measurements were limited to relatively short deployments (14–27 d), restricted to spring–summer conditions (peak growing season), and focused within the upper portion of giant kelp canopies. In addition, direct measurements of canopy biomass and hydrodynamic forcing were unavailable for most sites. Quantifying kelp biomass across multiple sites is logistically challenging, as it typically requires intensive diver-based surveys, underwater imaging, or destructive sampling, which can be constrained by wave exposure, currents, limited accessibility and the complex structure of rocky reef habitats (Kartveit *et al.*, 2022). Consequently, biomass was estimated using available structural proxies rather than direct measurements. While these estimates provide a useful approximation of forest structure, future studies incorporating efficient, non-destructive assessments of both subsurface and surface canopy biomass, as well as high-resolution remote sensing approaches would improve our understanding of the relationship between kelp biomass, forest structure, and seawater chemistry modification.

Moreover, because measurements were restricted to the spring–summer period, our results may not capture the full temporal variability in kelp-mediated seawater chemistry modification. The magnitude of these effects is likely to vary seasonally in response to changes in environmental conditions (Frieder *et al.*, 2012; Kosek and Kukliński, 2023), including light availability, temperature, nutrient supply and hydrodynamic conditions, as well as seasonal fluctuations in kelp biomass, canopy structure and photosynthetic activity. Consequently, the patterns observed during the peak growing season may not be representative of other times of the year. Long-term studies spanning multiple seasons are therefore needed to better understand how temporal variation in environmental forcing and kelp population dynamics influences the capacity of giant kelp forests to modify local seawater chemistry.

Importantly, we found the continued loss of giant kelp in Tasmania will likely further erode the short-term capacity of giant kelp forests to increase seawater pH and DO, while changes in coastal upwelling and freshwater regimes in Chile will continue to modulate the strength and direction of giant kelp–seawater chemistry feedback. Understanding the physical and biological mechanisms underlying these regional contrasts is essential for predicting how giant kelp forests will influence nearshore carbonate dynamics and ecosystem functioning under future ocean conditions.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. S1: details of the methods used to calculate the upwelling index.

FUNDING

Research in south-east Australia was supported by the Australian Academy of Science Thomas Davis Award and by the SeaForest Foundation, which funded work led by S.B., C.L. and E.M.A.S. Research in Chile was supported by The University of Los Lagos grant ULA RED21992, Packard Foundation grant 2022-74310 to M.A.U. and C.A.V., ANID–Millennium Science Initiative Program–Code ICN2019_015 to C.A.V. and Fondecyt grants 1250048 to C.A.V., 1221161 to A.B. and 1250526 to P.A.F., Centre of Biotechnology and Bioengineering (CeBiB, FB-0001 and AFB240001), and Nucleo Millenium Marine Agronomy and Seaweed Holobiont (MASH, NCN2024_037), given by the Chilean National Agency of Research and Development (ANID-Chile) to A.H.B. and P.A.F.

ACKNOWLEDGEMENTS

We thank all those who contributed to fieldwork for this study.

AUTHOR CONTRIBUTIONS

Conceptualization: E.M.A.S., P.A.F., C.A.V., M.A.U., L.C. Data curation: E.M.A.S., P.A.F., C.A.V., M.A.U., L.C. Formal analysis: E.M.A.S., P.A.F. Methodology: E.M.A.S., P.A.F., C.A.V., M.A.U. Visualization: E.M.A.S., P.A.F., C.A.V., M.A.U. Writing – original draft: E.M.A.S., P.A.F., C.A.V. Writing – review and editing: all authors.

REFERENCES

Aguirre C, **Garreaud R**, **Belmar L**, **Farías L**, **Ramajo L**, **Barrera F. 2021**. High-frequency variability of the surface ocean properties off central Chile during the upwelling season. *Frontiers in Marine Science* **8**: 124. doi: 10.3389/fmars.2021.702051

Almanza V, **Buschmann AH**, **Hernández-González MC**, **Henríquez LA. 2012**. Can giant kelp (*Macrocystis pyrifera*) forests enhance invertebrate recruitment in southern Chile? *Marine Biology Research* **8**: 855–864. doi:10.1080/17451000.2012.692159

Arcos D, **Navarro N. 1986**. Análisis de un índice de surgencia para la zona de Talcahuano Chile (Lat. 37° S). *InvestigaciÃ³n Pesquera* **33**: 91-98.

Bakun A. 1973. Coastal upwelling indices, West Coast of North America, 1946–71. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Baumann H, **Smith EM. 2018**. Quantifying metabolically driven pH and oxygen fluctuations in US nearshore habitats at diel to interannual time scales. *Estuaries and Coasts* **41**: 1102–1117. doi:10.1007/s12237-017-0321-3

Baumann H, **Wallace RB**, **Tagliaferri T**, **Gobler CJ. 2015**. Large natural pH, CO_2 and O_2 fluctuations in a temperate tidal salt marsh on diel, seasonal, and interannual time scales. *Estuaries and Coasts* **38**: 220–231. doi:10.1007/s12237-014-9800-y

Breitburg D, **Levin LA**, **Oschlies A**, ***et al.* 2018**. Declining oxygen in the global ocean and coastal waters. *Science* **359**: eaam7240. doi:10.1126/science.aam7240

Britton D, **Cornwall CE**, **Revill AT**, **Hurd CL**, **Johnson CR. 2016**. Ocean acidification reverses the positive effects of seawater pH fluctuations on growth and photosynthesis of the habitat-forming kelp, *Ecklonia radiata*. *Scientific Reports* **6**: 26036. doi:10.1038/srep26036

Buschmann A, **Vásquez JA**, **Osorio P**, ***et al.* 2004**. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. *Marine Biology* **145**: 849–862. doi:10.1007/s00227-004-1393-8

Borgesa AV, **Gypensb N. 2010**. Carbonate chemistry in the coastal zone responds more strongly to eutrophication than ocean acidification. *Limnology and Oceanography* **55**: 346–353. doi:10.4319/lo.2010.55.1.0346

Butler CL, **Lucieer VL**, **Wotherspoon SJ**, **Johnson CR. 2020**. Multi-decadal decline in cover of giant kelp *Macrocystis pyrifera* at the southern limit of its Australian range. *Marine Ecology Progress Series* **653**: 1–18. doi:10.3354/meps13510

Cai W-J, **Hu X**, **Huang W-J**, ***et al.* 2011**. Acidification of subsurface coastal waters enhanced by eutrophication. *Nature Geoscience* **4**: 766–770. doi:10.1038/ngeo1297

Carstensen J, **Duarte CM. 2019**. Drivers of pH variability in coastal ecosystems. *Environmental Science & Technology* **53**: 4020–4029. doi:10.1021/acs.est.8b03655

Castillo MI, **Cifuentes U**, **Pizarro O**, **Djurfeldt L**, **Caceres M. 2016**. Seasonal hydrography and surface outflow in a fjord with a deep sill: the Reloncaví fjord, Chile. *Ocean Sci Discuss* **12**: 533–544. doi:10.5194/os-12-533-2016

Cornwall CE, **Pilditch CA**, **Hepburn CD**, **Hurd CL. 2015**. Canopy macroalgae influence understorey corallines' metabolic control of near-surface pH and oxygen concentration. *Marine Ecology Progress Series* **525**: 81–95. doi:10.3354/meps11190

Delille B, **Borges AV**, **Delille D. 2009**. Influence of giant kelp beds (*Macrocystis pyrifera*) on diel cycles of pCO_2 and DIC in the Sub-Antarctic coastal area. *Estuarine, Coastal and Shelf Science* **81**: 114–122. doi:10.1016/j.ecss.2008.10.004

Delille B, **Delille D**, **Fiala M**, **Prevost C**, **Frankignoulle M. 2000**. Seasonal changes of pCO_2 over a subantarctic *Macrocystis* kelp bed. *Polar Biology* **23**: 706–716. doi:10.1007/s003000000142

Delille D, **Marty G**, **Cansemi-Soullard M**, **Frankignoulle M. 1997**. Influence of subantarctic *Macrocystis* bed metabolism in diel changes of marine bacterioplankton and CO_2 fluxes. *Journal of Plankton Research* **19**: 1251–1264. doi:10.1093/plankt/19.9.1251

Diaz RJ, **Rosenberg R. 2014**. Introduction to environmental and economic consequences of hypoxia. In: **Biswas A**, **Tortajada C**, **Izquierdo R.** eds. *Water quality management*. Milton Park, Abingdon, Oxon, UK: Routledge, 71-82.

Doney SC, **Busch DS**, **Cooley SR**, **Kroeker KJ. 2020**. The impacts of ocean acidification on marine ecosystems and reliant human communities. *Annual Review of Environment and Resources* **45**: 83–112. doi:10.1146/annurev-environ-012320-083019

Duarte CM, **Hendriks IE**, **Moore TS**, ***et al.* 2013**. Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. *Estuaries and Coasts* **36**: 221–236. doi:10.1007/s12237-013-9594-3

Elsmore K, **Nickols KJ**, **Miller LP**, **Ford T**, **Denny MW**, **Gaylord B. 2024**. Wave damping by giant kelp, *Macrocystis pyrifera*. *Annals of Botany* **133**: 29–40. doi:10.1093/aob/mcad094

Feely RA, **Alin SR**, **Newton J**, ***et al.* 2010**. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. *Estuarine, Coastal and Shelf Science* **88**: 442–449. doi:10.1016/j.ecss.2010.05.004

Feely RA, **Sabine CL**, **Lee K**, ***et al.* 2004**. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* **305**: 362–366. doi:10.1126/science.1097329

Forbes H, **Strain EMA**, **Bennett S**, **Ling SD**, **Layton C. 2024**. Endangered giant kelp forests support similar fish and macroinvertebrate communities to sympatric stipitate kelp forests. *Biodiversity and Conservation* **33**: 2503–2525. doi:10.1007/s10531-024-02867-0

Fox J, **Friendly M**, **Weisberg S. 2013**. Hypothesis tests for multivariate linear models using the car package. *The R Journal* **5**: 39-52. doi: 10.32614/RJ-2013-00

Frieder C, **Nam SH**, **Martz TR**, **Levin LA. 2012**. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences* **9**: 3917–3930. doi:10.5194/bg-9-3917-2012

Frieder CA, **Gonzalez JP**, **Bockmon EE**, **Navarro MO**, **Levin LA. 2014**. Can variable pH and low oxygen moderate ocean acidification outcomes for mussel larvae? *Global Change Biology* **20**: 754–764. doi:10.1111/gcb.12485

Garcia-Soto C, **Cheng L**, **Caesar L**, ***et al.* 2021**. An overview of ocean climate change indicators: sea surface temperature, ocean heat content, ocean pH, dissolved oxygen concentration, Arctic sea ice extent, thickness and volume, sea level and strength of the AMOC (Atlantic Meridional Overturning Circulation). *Frontiers in Marine Science* **8**: 642372. doi:10.3389/fmars.2021.642372

Gaylord B, **Denny MW**, **Koehl MAR. 2003**. Modulation of wave forces on kelp canopies by alongshore currents. *Limnology and Oceanography* **48**: 860–871. doi:10.4319/lo.2003.48.2.0860

George R, **Job S**, **Semba M**, ***et al.* 2024**. High-frequency dynamics of pH, dissolved oxygen, and temperature in the coastal ecosystems of the Tanga-Pemba Seascape: implications for upwelling-enhanced ocean acidification and deoxygenation. *Frontiers in Marine Science* **10**: 1286870. doi:10.3389/fmars.2023.1286870

Gobler CJ, **Baumann H. 2016**. Hypoxia and acidification in ocean ecosystems: coupled dynamics and effects on marine life. *Biology Letters* **12**: 20150976. doi:10.1098/rsbl.2015.0976

Gonzalez-Aragon D, **Muñoz R**, **Houskeeper H**, ***et al.* 2025**. Seasonal and inter-annual dynamics of a *Macrocystis pyrifera* forest in Concepcion Bay, Chile. *Ecological Informatics* **87**: 103103. doi:10.1016/j.ecoinf.2025.103103

Graham MH, **Vásquez JA**, **Buschmann AH. 2007**. Global ecology of the giant kelp Macrocystis: from ecotypes to ecosystems. *Oceanography and Marine Biology: An Annual Review* **45**: 39-88.

Guajardo-Rubilar E, **Mora-Soto A**, **Buschmann AH**, **Faugeron S. 2026**. Spatio-temporal dynamics of giant kelp forests in the Humboldt current system revealed by satellite data and hierarchical Bayesian modeling. *Ecological Informatics* **95**: 103746. doi:10.1016/j.ecoinf.2026.103746

Hirsh HK, **Nickols KJ**, **Takeshita Y**, ***et al.* 2020**. Drivers of biogeochemical variability in a central California kelp forest: implications for local amelioration of ocean acidification. *Journal of Geophysical Research: Oceans* **125**: e2020JC016320. doi:10.1029/2020JC016320

Hofmann GE, **Smith JE**, **Johnson KS**, ***et al.* 2011**. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS One* **6**: e28983. doi:10.1371/journal.pone.0028983

Howarth R, **Chan F**, **Conley DJ**, ***et al.* 2011**. Coupled biogeochemical cycles: eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems. *Frontiers in Ecology and the Environment* **9**: 18–26. doi:10.1890/100008

Hurd CL, **Beardall J**, **Comeau S**, ***et al.* 2020**. Ocean acidification as a multiple driver: how interactions between changing seawater carbonate parameters affect marine life. *Marine & Freshwater Research* **71**: 263–274. doi:10.1071/MF19267

Hurd CL, **Wright JT**, **Layton C**, ***et al.* 2023**. From Tasmania to the world: long and strong traditions in seaweed use, research, and development. *Botanica Marina* **66**: 1–36. doi:10.1515/bot-2022-0061

Jackson GA, **Winant CD. 1983**. Effect of a kelp forest on coastal currents. *Continental Shelf Research* **2**: 75–80. doi:10.1016/0278-4343(83)90023-7

Johnson CR, **Banks SC**, **Barrett NS**, ***et al.* 2011**. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* **400**: 17–32. doi:10.1016/j.jembe.2011.02.032

Kapsenberg L, **Hofmann GE. 2016**. Ocean pH time-series and drivers of variability along the northern Channel Islands, California, USA. *Limnology and Oceanography* **61**: 953–968. doi:10.1002/lno.10264

Kartveit KH, **Filbee-Dexter K**, **Steen H**, **Christensen L**, **Norderhaug KM. 2022**. Efficient spatial kelp biomass estimations using acoustic methods. *Frontiers in Marine Science* **9**: 1065914. doi:10.3389/fmars.2022.1065914

Kosek K, **Kukliński P. 2023**. Impact of kelp forest on seawater chemistry – a review. *Marine Pollution Bulletin* **196**: 115655. doi:10.1016/j.marpolbul.2023.115655

Koweek DA, **Nickols KJ**, **Leary PR**, ***et al.* 2017**. A year in the life of a central California kelp forest: physical and biological insights into biogeochemical variability. *Biogeosciences* **14**: 31–44. doi:10.5194/bg-14-31-2017

Krause-Jensen D, **Duarte CM**, **Hendriks IE**, ***et al.* 2015**. Macroalgae contribute to nested mosaics of pH variability in a subarctic fjord. *Biogeosciences* **12**: 4895–4911. doi:10.5194/bg-12-4895-2015

Kregting L, **Britton D**, **Mundy CN**, **Hurd CL. 2021**. Safe in my garden: reduction of mainstream flow and turbulence by macroalgal assemblages and implications for refugia of calcifying organisms from ocean acidification. *Frontiers in Marine Science* **8**: 693695. doi:10.3389/fmars.2021.693695

Kroeker KJ, **Donham EM**, **Vylet K**, ***et al.* 2023**. Exposure to extremes in multiple global change drivers: characterizing pH, dissolved oxygen, and temperature variability in a dynamic, upwelling dominated ecosystem. *Limnology and Oceanography* **68**: 1611–1623. doi:10.1002/lno.12371

Lenth R, **Piaskowski J**, **Banfai B**, ***et al.* 2019**. emmeans: estimated marginal means, aka least-squares means. R package version 1.3.4. https://CRAN.R-project.org/package=emmeans.

Ling SD, **Cornwall CE**, **Tilbrook B**, **Hurd CL. 2020**. Remnant kelp bed refugia and future phase-shifts under ocean acidification. *PLoS One* **15**: e0239136. doi:10.1371/journal.pone.0239136

Lowe AT, **Bos J**, **Ruesink J. 2019**. Ecosystem metabolism drives pH variability and modulates long-term ocean acidification in the northeast Pacific coastal ocean. *Scientific Reports* **9**: 963. doi:10.1038/s41598-018-37764-4

Mabin CJ, **Johnson CR**, **Wright JT. 2019**. Physiological response to temperature, light, and nitrates in the giant kelp *Macrocystis pyrifera* from Tasmania, Australia. *Marine Ecology Progress Series* **614**: 1–19. doi:10.3354/meps12900

Molinet C, **Soto D**, **León-Muñoz J**, ***et al.* 2025**. Climate-driven changes in freshwater inputs to a northern Patagonia fjord and overfishing of wild mussel seed could threaten Chilean mussel farming. *Climatic Change* **178**: 119. doi:10.1007/s10584-025-03956-x

Mora-Soto A, **Capsey A**, **Friedlander AM**, ***et al.* 2021**. One of the least disturbed marine coastal ecosystems on Earth: spatial and temporal persistence of Darwin's sub-Antarctic giant kelp forests. *Journal of Biogeography* **48**: 2562–2577. doi:10.1111/jbi.14221

Morris RL, **Graham TDJ**, **Kelvin J**, **Ghisalberti M**, **Swearer SE. 2020**. Kelp beds as coastal protection: wave attenuation of *Ecklonia radiata* in a shallow coastal bay. *Annals of Botany* **125**: 235–246. doi:10.1093/aob/mcz127

Muñoz R, **Vergara OA**, **Figueroa PA**, **Mardones P**, **Sobarzo M**, **Saldías GS. 2023**. On the phenology of coastal upwelling off central-southern Chile. *Dynamics of Atmospheres and Oceans* **104**: 101405. doi: 10.1016/j.dynatmoce.2023.101405

Murie KA, **Bourdeau PE. 2020**. Fragmented kelp forest canopies retain their ability to alter local seawater chemistry. *Scientific Reports* **10**: 11939. doi:10.1038/s41598-020-68841-2

Pan Y, **Birdsey RA**, **Phillips OL**, ***et al.* 2024**. The enduring world forest carbon sink. *Nature* **631**: 563–569. doi:10.1038/s41586-024-07602-x

Pérez-Santos I, **Díaz PA**, **Silva N**, ***et al.* 2021**. Oceanography time series reveals annual asynchrony input between oceanic and estuarine waters in Patagonian fjords. *The Science of the Total Environment* **798**: 149241. doi:10.1016/j.scitotenv.2021.149241

Peterson WT, **Arcos DF**, **McManus GB *et al.* 1988**. The nearshore zone during coastal upwelling: Daily variability and coupling between primary and secondary production off central Chile. *Progress in Oceanography* **20**: 1-40. doi: 10.1016/0079-6611(88)90052-3

Pfister CA, **Altabet MA**, **Weigel BL. 2019**. Kelp beds and their local effects on seawater chemistry, productivity, and microbial communities. *Ecology* **100**: e02798. doi:10.1002/ecy.2798

Pinilla E, **Ross L**, **Pérez-Santos I. 2024**. Exchange flow in a highly stratified fjord in drought conditions. *Frontiers in Marine Science* **11**: 1458758. doi:10.3389/fmars.2024.1458758

Pitcher GC, **du Randt A**, **Seanego KG**, **Tsanwani M. 2023**. Variability and controls of the ocean acidification metrics pH and pCO_2 in a large embayment of an eastern boundary upwelling system (EBUS). *Estuarine, Coastal and Shelf Science* **292**: 108473. doi:10.1016/j.ecss.2023.108473

Pörtner H-O, **Roberts DC**, **Masson-Delmotte V**, ***et al.* 2019**. *IPCC special report on the ocean and cryosphere in a changing climate*. Cambridge, UK and New York, NY, USA: Cambridge University Press. https://doi.org/10.1017/9781009157964.

R Core Team**. 2025**. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Ridgway K, **Ling S. 2023**. Three decades of variability and warming of nearshore waters around Tasmania. *Progress in Oceanography* **215**: 103046. doi:10.1016/j.pocean.2023.103046

Ross FW, **Boyd PW**, **Filbee-Dexter K**, ***et al.* 2023**. Potential role of seaweeds in climate change mitigation. *The Science of the Total Environment* **885**: 163699. doi:10.1016/j.scitotenv.2023.163699

Salisbury J, **Vandemark D**, **Hunt C**, ***et al.* 2009**. Episodic riverine influence on surface DIC in the coastal Gulf of Maine. *Estuarine, Coastal and Shelf Science* **82**: 108–118. doi:10.1016/j.ecss.2008.12.021

Sobarzo M, **Bravo L**, **Donoso D**, **Garcés-Vargas J**, **Schneider W. 2007**. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. *Progress in Oceanography* **75**: 363-382. doi: 10.1016/j.pocean.2007.08.022

Strain EM, **Swearer SE**, **Ambler I**, **Morris RL**, **Nickols KJ. 2024**. Assessing the role of natural kelp forests in modifying seawater chemistry. *Scientific Reports* **14**: 22386. doi:10.1038/s41598-024-72801-5

Traiger SB, **Cohn B**, **Panos D**, ***et al.* 2022**. Limited biogeochemical modification of surface waters by kelp forest canopies: influence of kelp

metabolism and site-specific hydrodynamics. *Limnology and Oceanography* **67**: 392–403. doi:10.1002/lno.11999

Vargas CA, **Contreras PY**, **Pérez CA**, **Sobarzo M**, **Saldías GS**, **Salisbury J. 2016**. Influences of riverine and upwelling waters on the coastal carbonate system off central Chile and their ocean acidification implications. *Journal of Geophysical Research: Biogeosciences* **121**: 1468–1483. doi:10.1002/2015JG003213

Vergara-Jara MJ, **DeGrandpre MD**, **Torres R**, ***et al.* 2019**. Seasonal changes in carbonate saturation state and air-sea CO_2 fluxes during an annual cycle in a stratified-temperate fjord (Reloncaví Fjord, Chilean Patagonia). *Journal of Geophysical Research: Biogeosciences* **124**: 2851–2865. doi:10.1029/2019JG005028

Waldbusser GG, **Salisbury JE. 2014**. Ocean acidification in the coastal zone from an organism's perspective: multiple system parameters, frequency domains, and habitats. *Annual Review of Marine Science* **6**: 221–247. doi:10.1146/annurev-marine-121211-172238

Walter RK, **Huie SA**, **Abraham JCP**, ***et al.* 2022**. Seasonal controls on nearshore dissolved oxygen variability and hypoxia in a coastal embayment. *Estuarine, Coastal and Shelf Science* **278**: 108123. doi:10.1016/j.ecss.2022.108123

Weiss RF. 1974. Carbon dioxide in water and seawater: the solubility of a non-ideal gas. *Marine Chemistry* **2**: 203–215. doi:10.1016/0304-4203(74)90015-2

Wernberg T, **Krumhansl K**, **Filbee-Dexter K**, **Pedersen MF. 2019**. Status and trends for the world's kelp forests. In: **Sheppard C.** ed. *World seas: an environmental evaluation*. London, UK: Academic Press (Elsevier), 57-78.

Wickham H. 2011. ggplot2. *WIREs Computational Statistics* **3**: 180–185. doi:10.1002/wics.147

Xiao X, **Agustí S**, **Yu Y**, ***et al.* 2021**. Seaweed farms provide refugia from ocean acidification. *The Science of the Total Environment* **776**: 145192. doi:10.1016/j.scitotenv.2021.145192