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Growth rates and response to nutrient variability in the green tide forming alga *Ulva stenophylloides* from Algarrobo Bay, Chile

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ABSTRACT

Blooms of green macroalgae have become a recurring phenomenon along many shores. Here, we conducted oceanographic surveys and field experiments to quantify daily growth rates of *Ulva stenophylloides,* the predominant species in the green tides that occur year-round at the southern end of the wave-protected open bay of Algarrobo, central Chile. We assessed the association between growth and nutrient availability, as well as other environmental variables, and compared growth rates between the south end of the bay and the north end (1.6 km away), where green tides are absent. Fronds of *U. stenophylloides* were suspended at ~3–4 m depth from moorings anchored at 10 m depth at both sites. Daily growth rates were high at both locations, ranging from a 9 %–121 % increase in wet biomass, but were significantly higher at the southern site. Nutrient concentrations in water samples collected once daily were not correlated with algal growth and showed no consistent differences between sites. However, high-frequency temperature records from moorings revealed rapid (minutes to hours) cold-water pulses at the southern end, which were nearly absent in the north. Given the strong inverse relationship between temperature and nitrate in the bay, we suggest that these cold-water intrusions—likely associated with internal waves—supply additional nutrients supporting higher growth rates at the southern site. Our findings indicate that once-daily water sampling may misrepresent the dynamic nutrient regimes experienced by fast-growing macroalgae, highlighting the need for high-frequency monitoring.

1. Introduction

Blooms of *Ulva* macroalgae have become a recurrent phenomenon on many shores worldwide (Joniver et al., 2021; Ye et al., 2011). These blooms occur when the plants detach from the hard substratum or release frond fragments that accumulate in the water column and end up stranded in massive quantities on sandy beaches (Gong et al., 2024; Liu et al., 2009). While *Ulva* species are the predominant in green tides, other green algae, such as *Cladophora*, *Codium*, and *Spyrogyra*, also form green tides (Gladyshev and Gubelit, 2019; Teichberg et al., 2010; Ye et al., 2011). In regions such as Brittany, France, and the Yellow Sea, China, extensive blooms of *U. prolifera* have led to severe ecological disturbances, negatively affecting tourism, marine biodiversity, and coastal industries (Charlier et al., 2008; Liu et al., 2009). Sustained high

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and persistent macroalgal biomass requires both high and persistent delivery of nutrients, which are rapidly taken up and assimilated into growth through photosynthesis, favorable light conditions, and release from natural controls. Massive *Ulva* green tides are, therefore, typically associated with regions where nutrient levels have shifted from oligotrophic/mesotrophic to eutrophic conditions due to natural and anthropogenic nutrient enrichment (Joniver et al., 2021). This pattern is evident in places like Brittany, the Yellow Sea, and the Baltic Sea. Historically, these regions had comparatively low nutrient levels, but agricultural runoff, urban wastewater discharges, and industrial activities have significantly elevated the availability of nitrogen and phosphorus (Li et al., 2017; Liu et al., 2009; Teichberg et al., 2010). However, although nutrient enrichment seems to be involved in sustaining high algal biomass in these regions, the proximate causes that trigger green tide events are more complex. Anthropogenic alteration of hard substratum availability (e.g., habitat modification by aquaculture, seawalls, piers, etc.), which is required for green tides' initial growth, is frequently implicated in green tides (Liu et al., 2009). Broader degradation of coastal ecosystems, which weakens the multiple environmental and ecological controls (e.g., grazing, competitors) that normally suppress fast-growing nuisance species, is also critical (Joniver et al., 2021; Lotze and Worm, 2002; Smetacek and Zingone, 2013; Valiela et al., 1997). Moreover, green algal blooms also occur in many oligotrophic environments, likely because the species involved in green tides exhibit high nutrient uptake efficiency, even under very low ($NO_3 < 1$ μM) nutrient levels (Cohen and Fong, 2006; Luo et al., 2012; Taylor and Rees, 1999; Teichberg et al., 2010). Therefore, nutrient enrichment alone cannot explain the massive proliferation of green tides, nor can mitigation plans be designed effectively without local information about the ecological controls that regulate algal growth (Smetacek and Zingone, 2013).

In naturally nutrient-rich environments, such as the Eastern Boundary Upwelling Systems (EBUS), nitrate and phosphate concentrations are naturally high, with peaks in spring-summer driven by equatorward winds that force the transport of cold and rich nutrient subsurface waters into the photic layer, triggering photosynthetic activity and fueling coastal trophic webs (Chavez and Messie, 2009; García-Reyes et al., 2014). Nutrient concentrations fluctuate strongly at seasonal, synoptic, and high-frequency (short-term: days, minutes) scales, but coastal surface waters consistently maintain high nitrate levels. Daily averages > 4–12 μmol/L in winter and reaching up to 35 μmol/L in spring are common in coastal waters along these regions (Farias and de la Maza, 2024; García-Reyes et al., 2014; Nielsen and Navarrete, 2004; Palacios et al., 2013; Pérez-Mayorga et al., 2011; Wieters, 2005), which explains the high biomass of large kelps and corticated algae, many of which are commercially and intensively exploited (Bularz et al., 2022; Carranza et al., 2024; Santelices, 1989; Vásquez, 2016). In upwelling systems, nitrate and phosphate concentrations are strongly and inversely related to temperature, typically resulting in inverse relationships between benthic algal growth rates, total macroalgal biomass, and water temperature (Nielsen and Navarrete, 2004; Pérez-Mayorga et al., 2011; Wieters, 2005). This contrasts with the notion that increased *Ulva* growth is associated with increased temperatures in regions where massive green tides occur. Indeed, along upwelling shores, episodes of nutrient-depleted waters (<5 μmol/L) occur when temperatures exceed a certain threshold, a halt in the advection of cold water, and nutrients are depleted by photosynthetic activity (García-Reyes et al., 2014; Palacios et al., 2013; Tapia et al., 2014). Although these high-temperature, low-nutrient events rarely last more than a few hours, cumulative exposure to nutrient-depleted waters can help explain differences in macroalgal biomass among sites along the shore (Tapia et al., 2014) and variations in the growth rates of suspended green algae (Pérez-Mayorga et al., 2011).

Along the Humboldt upwelling shores of central Chile, the southern end of the wave-protected Bay of Algarrobo has experienced year-round green tides for at least two decades (Inostroza, 2012). Beached algal biomass often covers approximately 1.5 km of shoreline and has negatively affected tourism, sparked socio-environmental conflicts, and caused significant economic strain on local government. Five *Ulva* species have been identified from these green tides, with *U. stenophylloides* being the predominant species and the most abundant on intertidal platforms across the low and mid intertidal zones (Mutizabal-Aros et al., 2024). Several potential causes have been proposed, including the introduction of exotic *Ulva* species from other regions or countries and the anthropogenic eutrophication of coastal waters (Inostroza, 2012). However, to date, no local environmental, oceanographic, or ecological data exist to support or refute these claims. A submarine sewage outfall, which has been operating since 1998 at the northern end of the bay (Fig. 1) and discharging untreated domestic wastewater, has been identified as a potential contributor of excess nutrients sustaining the green tides observed in the southern end of the bay. Yet, no systematic studies have been conducted to quantify nutrient availability and spatio-temporal dynamics in the bay and whether a submarine sewage discharge of ca. 220 L/s can alter the naturally high nutrient concentrations within the bay in this upwelling shore.

To address these knowledge gaps, we conducted intensive oceanographic surveys, characterized the nutrient-temperature relationship, and conducted a replicated field experiment to quantify the daily growth rates of *U. stenophylloides*. The experiment was conducted at the southern end of the bay, where the green tides occur, and at the northern end, closer to the submarine outfall, where green tides are absent (Navarrete et al., 2024). We tested the hypotheses: (a) *Ulva* growth rates are positively associated with daily variation in nutrient concentrations; (b) nutrient concentrations in the bay exhibit a persistent spatial pattern associated with a permanent source, such as the submarine outfall; and (c) if the sewage discharge significantly contributes to algal growth, *Ulva* growth rates would be faster at the experimental site closest to the outfall.

2. Materials and methods

2.1. Study site

The study was conducted in the north-facing open bay of Algarrobo on the central coast of Chile (Fig. 1a). Because predominant waves in Chile come from the south (Lucero et al., 2017; Winckler Grez et al., 2020), the Bay of Algarrobo is one of the few semi-protected bays in central Chile, which promotes nautical sports and tourism. Green tides of *Ulva* species, primarily *U. stenophylloides* (Mutizabal-Aros et al., 2024), have been observed on the south end of the bay at least since about 2002 (Inostroza, 2012) and have not expanded to the northern end of the bay (Fig. 1a and b). *Ulva* spp dominate (>70 % canopy cover) the mid and low intertidal zones of the sedimentary platforms at Playa Los Tubos and are also abundant (~40 %) at the rocky platforms in Cofradía, 500 m to the south. In comparison, they are scarce (<10 %) at the granite rocks of Bora Bora beach towards the northern end of the bay (Navarrete et al., 2024). In the subtidal habitat, *Ulva* spp cover >70 % of the hard substratum in front of Playa Los Tubos, which is mostly boulders and broken rocky outcrops interspersed with sand and shelly bottom. But *Ulva* does not extend beyond 10 m depth. In deeper waters and anywhere else in the bay, *Ulva* spp are scarce (<5 % canopy), and the hard substratum is covered by kelps, red algae, and barren ground (Henríquez, 2018).

The submarine sewage outfall of ESVAL S.A. starts near Bora Bora beach and extends 1200 m northwestward to evacuate sewage at about 26 m depth (Fig. 1). This operation started in 1998 and evacuates "primarily treated" sewage, i.e., solids, sand, and oils have been removed. The average peak flow was ca. 220 L/s between 2017 and 2020 (Navarrete et al., 2024).

2.1.1. Ulva growth rate experiments

We conducted a field experiment in the austral summer (January) of 2023 to assess whether algal growth responded to daily variability in

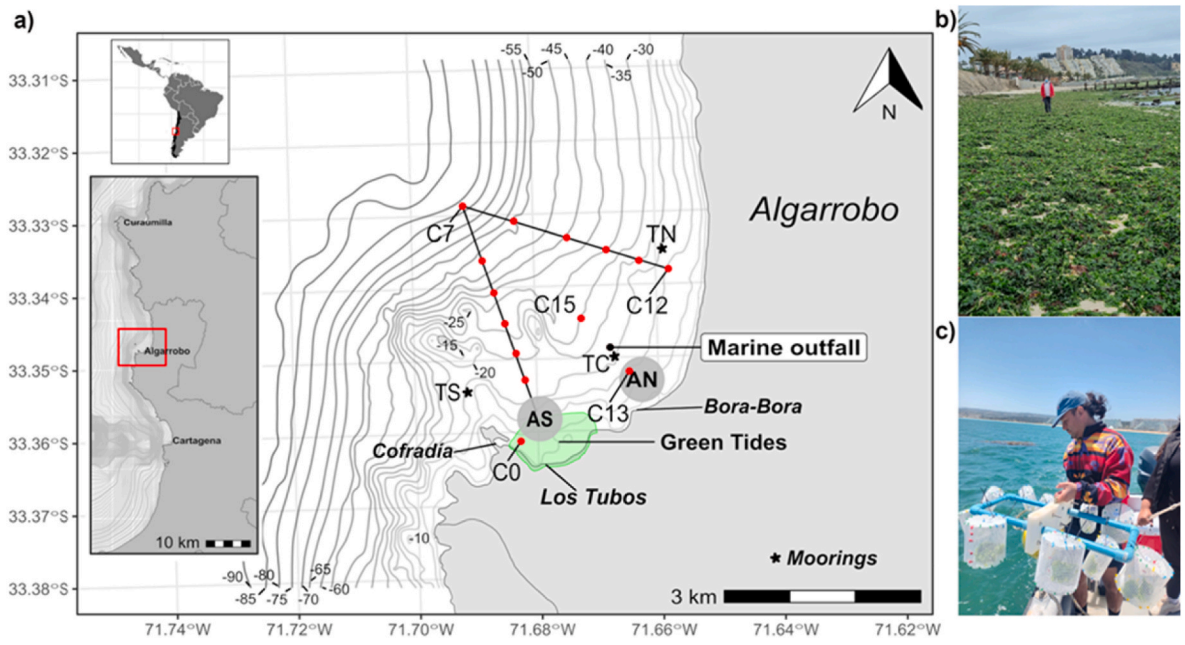


Fig. 1. A) Map and bathymetry of Algarrobo Bay in central Chile showing the location of green tides near Los Tubos, the orientation of the north-facing open bay (inset), study sites, and the mouth of the marine outfall. The algal growth experiment was conducted in the southern (AS) and northern (AN) ends with moorings anchored at ca. 10 m depth and cages suspended at ca. 3–4 m below the surface. The black lines show the oceanographic transects and survey stations (red dots) where water samples were collected at different depths on multiple occasions (see Table S1). Surveys were divided into the south transect (stations C0-C7), the north transect (stations C7-C12), and the stations nearest to the marine outfall. Positions of the three thermistor lines, with loggers moored at 5, 15, and 20 m depth, are labeled TS, TC, and TN. B) Beached *Ulva* fronds near Playa Los Tubos, Algarrobo. C) Experimental Vexar mesh cages used for the daily growth experiment, shown attached to the anchored PVC frame. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

nutrient concentrations and whether growth rates were different between two sites: AS and AN. Site AS is on the south end near Playa Los Tubos, where the *Ulva*-dominated green tides are recurrent. Site AN is located at the northern end, across from Bora Bora beach, where kelps and other macroalgae are common, but *Ulva* is scarce (Fig. 1). Fronds of *U. stenophylloides* were collected locally from AS and suspended at about 3-m depth inside white 8-cm diameter x 16-cm long Vexar-mesh cylinder cages. The cages were attached to moorings anchored at ca. 10-meter bottom depths (Fig. 1c). Five replicated cages containing one frond each were deployed at each mooring. Fronds were replaced daily with new ones collected from the Los Tubos site (Fig. 1). Although the experiment was planned for 10 days, weather conditions and logistical limitations allowed us to monitor only five consecutive days concurrently at both experimental sites.

Cages were individually labeled, and algal fronds were measured (maximum length and width), spun in a salad spinner to remove excess water, weighted in a precision scale (wet weight), and placed inside the experimental cages at the Estación Costera de Investigaciones Marinas (ECIM), about 20 km south of Algarrobo. Deployment and monitoring were conducted aboard ECIM's research boat, *Ilan*, and with the aid of a free diver. Each day, retrieved fronds were brought to the laboratory, measured again, weighed, oven-dried at 60 °C for 24 h, and weighed again to obtain dry weight. Here, we report wet weights (*W*) and include the wet-to-dry weight relationship as supplementary material (Fig. S1). Daily growth rate (*DGR*) was then expressed as the fraction (or percentage) of new growth from initial size after roughly 24 h in the field:

$$1)\ DGR = \frac{W_{t=1} - W_0}{W_0}$$

where, W_0 is the initial wet weight (g) of the frond at time t = 0 (before deployment in the field). $W_{t=1}$ is the wet weight of the same frond after approximately 24 h in the field (t = 1). Therefore, DRG represents the new biomass gained daily as a fraction of the original size (% if multiplied by 100), which accounts for variation in initial frond size (Fig. S1).

A preliminary experiment conducted under running seawater and direct sunlight (outdoor aquaria) at ECIM showed that *Ulva* fronds inside the cylinder cages can grow between 28 % and 166 % in 24 h under these conditions, i.e., unfiltered seawater pumped from ca. 1.5 m depth at the shoreline within the Las Cruces Marine Reserve, in Cartagena Bay (33°30.17′S, 71°38.08′W). Daily growth rates were compared between the two moorings (AS, AN) and between days, with five replicates per condition, using a two-way factorial ANOVA, considering mooring location as fixed and day as a random factor. Visual inspection of residual quantile plots suggested approximately normal distributions, and Levene's test indicated homogeneous variances among groups ($p > 0.05$).

In addition to daily growth rates, we measured cumulative growth to estimate the rate of frond loss over time. To this end, 25 *Ulva* fronds were measured, weighed, and placed in groups of five in each of five 20 cm diameter x 16 cm long replicate cages made of the same material described above. These larger cages were interspersed amongst the daily growth cages in the same moorings as the daily experiment. One frond was selected randomly and removed from each cage at 1, 2, 4, 9, and 16 days after deployment, brought to ECIM, and measured following the procedure described above. Due to the loss of cages and fronds from the AS mooring, cumulative growth could only be monitored for cages deployed at the north mooring (AN).

Algal growth rates in the cumulative experiment were calculated as the average differences between the frond wet weight (one from each cage) and the initial weight recorded at the time of deployment (time = 0), divided by the number of days (*d*) fronds were in the field. Thus, after one day had elapsed, algal growth rates were equivalent to those measured in the daily growth rate experiment described above, except for being in a group of five fronds. To estimate frond loss (*FL*) over time (grams of tissue lost), we assumed that frond loss is negligible after only one day and, therefore, the weight increments recorded over the initial 24 h of the experiment were a good indicator of net primary production. Then, we subtracted the observed algal weight measured after 2, 4, 9,

and 16 days in the field, W_d, from the weight expected for fronds after d days in the field, based on the initial weight ($W_{d\ =\ initial}$) and the average daily-growth rate (DGR) as

$$2)\ FL = \left(W_{d=initial}{}^{*}(1+DGR)^{d}\right) - W_d$$

When no data existed for the dates when fronds were in the field for more than 5 days, we used the overall mean DGR from the daily experiments. Since some frond loss indeed occurs within the first 24 h of deployment (e.g., Pérez-Mayorga et al., 2011), our estimates of net primary production and frond loss are considered conservative.

2.2. Oceanographic survey: environmental variables

2.2.1. Nutrients

As part of a larger oceanographic survey within the Bay of Algarrobo, we conducted CTD casts and collected water samples at multiple stations and depths in winter (August 2021, July 2022) and spring-summer (December 2021, January 2023) along two onshore-offshore transects spanning the southern and northern portions of the Bay (Fig. 1, Table S1). Additional stations were also surveyed daily during the experiment in January 2023 to provide a more detailed representation of spatial and daily variation. Water samples for chemical analyses were collected using a 1-liter Niskin bottle. Samples were collected in triplicate and stored in 15-ml tubes, filtered through 0.45 μm pore GF/F filters, and frozen (−20 °C) until laboratory analysis. Nitrate, nitrite, phosphate, and silicate were determined using colorimetric techniques with a Seal Autoanalyzer 3 (AA3) and following protocols described in Grasshoff et al., (1983). Samples for ammonium determinations (40 ml) were obtained in triplicate, stored in glass flasks, and fixed immediately with 10 ml of o-phthalaldehyde (OPA) reagent for fluorometric analysis (Holmes et al., 1999). The samples were kept in the dark and analyzed by fluorometry 3 h after fixing. A summary of the oceanographic surveys is presented by Navarrete et al. (2024). A full account of nutrient variability in Algarrobo Bay, including hydrographic sections from CTD profiles (Seabird SBE25), will be presented elsewhere. Here, we summarize spatial (horizontal) and depth nutrient patterns relevant to the algal growth experiments.

To characterize the vertical variability of nutrient concentrations and the relationship between the different inorganic nutrients, we used data from all water samples collected from the surface down to 65 m depth. Since these are not continuous depth profiles, we present all nutrient observations across depths and Pearson linear correlations between nutrients across all water samples. For samples collected between January 10–30th, 2023, encompassing the *Ulva* growth experiment, we assessed whether there was a persistent spatial structure between the northern and southern ends of the bay, averaging samples in the surface layer (1–3 m depth, hereafter 1 m-layer) and subsurface layer (4–12 m depth, hereafter 10 m-layer) for every sampling day. We constrained the analysis to these depths because *Ulva* is rarely found below 10 m (Henríquez, 2018). Daily *Ulva* growth rates measured at AS and AN were then regressed on daily nutrient concentrations in the two depth layers defined above using OLS regressions. Since discrete water samples collected once per day may not represent well the variable nutrient regime to which macroalgae are exposed between daily deployments, we used (1) the nutrient concentrations measured the day before algae were retrieved and (2) the average of concentrations recorded the day before and the day of algal retrieval.

2.3. Surface continuous temperature and nitrate monitoring

To obtain high-frequency records of seawater temperature, in August 2021 we deployed three moorings with HOBO U22 temperature loggers at ca. 5, 15, and 20 m depths, recording every 10 min, at the southern (TS), center (TC), and northern (TN) sections of the study area (Fig. 1). The moorings were anchored at depths of 27–30 m and were periodically serviced for logger maintenance and data retrieval. Unfortunately, the lines at TN and TC could not be found and retrieved during the January 2023 surveys, but we have a semi-continuous time series for the previous two years (2021–2022). In addition to a visual comparison of the temperature time series, we used spectral analyses, applied separately to winter-spring and spring-summer, to assess the relative importance of synoptic-scale variability (mostly upwelling-related), diurnal (mostly sea breeze and tide-related), semi-diurnal (tide-related), and high-frequency (minutes) variability. Following (Ladah and Tapia, 2021), from each of the nine spectra (3 depths x 3 mooring lines), we calculated the percent of total spectral density (i.e., contribution to total variability) accounted for by signals in the following frequency bands: synoptic (0.1–0.5 cycles per day, cpd), diurnal (0.8–1.2 cpd), semi-diurnal (1.8–2.2 cpd), and high-frequency (>2.2 cpd).

As shown in most coastal areas of the world, including the Humboldt ecosystem, there is typically a tight inverse and nonlinear relationship between seawater temperature and nitrate concentration (Wieters, 2005; Pérez-Mayorga et al., 2011; Palacios et al., 2013). Therefore, using all the information collected during the study (Table S1), we constructed the relationship between measured nitrate concentration and seawater temperature for Algarrobo Bay and used it to predict nitrate concentration from the continuous temperature records collected at three depths from the TS and TN moorings. We also estimated the temperature above which nitrate concentration falls below 5 μmol/L, which we considered indicative of nutrient-depleted waters at our site (Tapia et al., 2014). Pérez-Mayorga et al. (2011) used 1 μmol/L as the threshold for depleted waters in Baja California. We then calculated the time (minutes) algae would be exposed to nutrient-depleted waters daily and through the spring-summer season (integrated) in the south and north ends of the bay. Finally, total solar radiation for the days of the experiment was obtained from the ECIM meteorological station.

3. Results

3.1. Nutrients in the Bay of Algarrobo

The mean concentrations of nitrate, nitrite, phosphate, and silicate from water samples collected daily between 10 and 30 January 2023 showed comparatively large fluctuations, with generally higher nutrient values at the beginning of the *Ulva* growth study (14 January) than later in the month, at both depths (Fig. 2). On 10 January, nitrate levels at 1 m and 10 m were > 4 μmol/L and >9 μmol/L, respectively, and increased thereafter to reach maximum values (>25 μmol/L) between 14 and 16 January. After the 16th, nitrate decreased rapidly in the surface layer and remained low (ca. 0.3–1.2 μmol/L) but decreased more slowly in the 10-m layer, remaining above 5 μmol/L throughout the growth experiment (Fig. 2). The temporal pattern of nutrient variation suggests the onset of upwelling during the beginning of the study followed by a period of calm, which is consistent with the wind conditions recorded during this period (not shown). There were no persistent spatial differences between the north and south sections of the bay (Fig. 2), and daily fluctuations were highly correlated between sections (Pearson $r = 0.92$, $p < 0.0001$). The concentration of all nutrients increased rapidly and significantly with depth from 1 m down to about 45 m, with only a moderate increase from there to 70 m depth (Fig. 3). Nutrient concentrations at stations near the submarine sewage outfall (blue open circles in Fig. 3) were not different from the more distant stations.

Strong ($r > 0.93$) and significant ($p < 0.05$) linear Pearson correlations were observed between nitrate, nitrite, phosphate, and silicate across dates and depths (Fig. S2). Given the tight correlation among all inorganic nutrients, we here present the relationship between algal growth rates and nitrate concentration.

3.1.1. Ulva growth rates

Daily growth rates (DGR) expressed as the percentage of increment

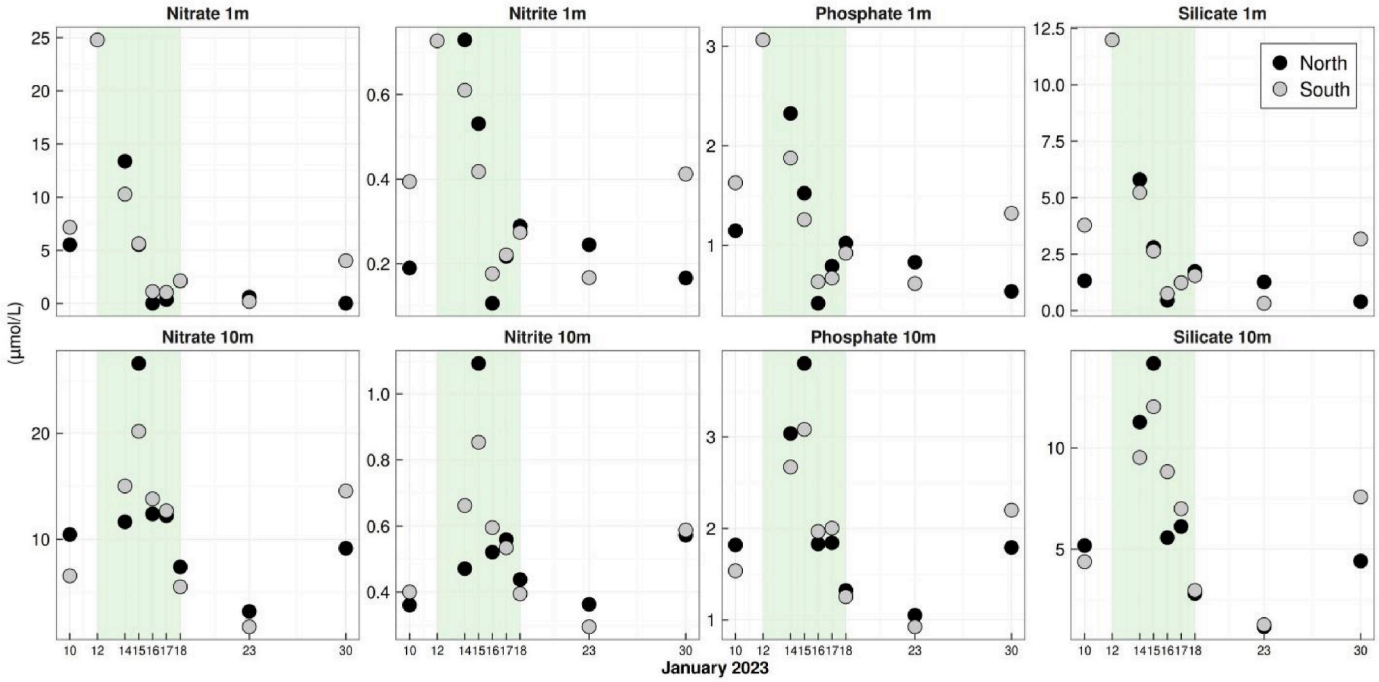


Fig. 2. Mean nutrient concentration per sampling date in January 2023 at the surface (1–3 m) and at ca.10 m (6–12 m) depths averaged for all stations in the north and south ends of the bay (see Fig. 1). The green shading indicates the growth rate experiment period. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

in wet weight in the field varied widely and significantly, from 9 % to 121 %, with similar patterns at both experimental sites (Fig. 4a, Table 1, significant Day effect). Daily growth rates were slightly but significantly higher at the southern site (AS) than at the northern site (AN), and this difference was persistent through the duration of the experiment (Fig. 4, Table 1, no significant interaction between mooring and day).

Growth rates decreased rapidly when fronds were exposed for 48 h or longer, compared with rates evaluated after 24 h, which we consider indicative of fragment loss from fronds over time. The expected loss of biomass (frond fragments) from a frond that starts at about 3 g wet weight is nearly 80 g of fresh biomass over 16 days (Fig. 4b). Also, this conservative estimate does not consider that those fragments could continue growing in the water column.

Nitrate concentrations measured from water samples collected once a day at ca. 10 m depth were not significantly correlated with *U. stenophylloides* daily growth rates (Fig. 5a). Using nutrient concentrations at 1 m depth, or values only at the closest station near the experimental moorings, did not improve these regressions. Total solar radiation measured at Las Cruces was unrelated to daily algal growth rates (Fig. 5c). However, a significantly negative, albeit weak (14 % explained variance) linear relationship was observed between daily growth rates and mean daily temperature (Fig. 5b).

3.1.2. *High-frequency temperature records and nutrient regimes*

Our high-frequency temperature records showed that, during the spring and summer months, rapid temperature drops (occurring over minutes to hours) were observed at the southern mooring, while they were rare at the central mooring and completely absent at the northern mooring (Fig. 6). These temperature drops were more frequent at 15 m and at 20 m deep. Occasionally, rapid temperature drops exceeding 2.7 °C were recorded at 4 and 15 m.

Spectral analyses of the high-frequency temperature records allowed us to assess the intensity (based on the power spectral density) of different signals contributing to temperature variability separately for the spring and summer months (Figs. S3–S4). Synoptic-scale fluctuations accounted for the largest fraction of temperature variability, with greater importance during winter-spring (>15 %) compared to spring-summer (Fig. 7). There was minimal variation in the strength of synoptic signals among the three depths and mooring sites within the bay (Fig. 7). Diurnal-scale temperature variability tended to be higher (4–5 %) at the surface than at subsurface depths, and was larger at the northern compared to the central and southern moorings (Fig. 7). Semi-diurnal temperature variability generally represented less than 2 % of the total variability, except during the spring summer months at the south end of the bay, where a clear increase was observed at 10 and 15 m depth (Fig. 7). High-frequency variability was the second most important timescale of temperature variability, following synoptic variability, particularly during summer (Fig. 7). In this case, the fraction of high-frequency variability observed at the southern-end of the bay was twice that recorded at the central and northern moorings during the summer months (Fig. 7), consistent with the increased frequency of short-lived cold-spells observed in the raw data.

As expected from previous studies in the region (e.g., Wieters, 2005), a tight nonlinear relationship was observed between temperature and nitrate concentration, explaining more than 82 % of nitrate variability ($p < 0.0001$) characterized the relationship (Fig. 8a). Predicted nitrate concentrations derived from the high-frequency temperature records exhibited large fluctuations during spring-summer months of 2021–2022, with both hourly and synoptic-scale variations at both ends of the bay (Fig. 8b and c). Nitrate levels were, on average, about 20 µmol/L between September and early December, then decreased to about 15 µmol/L between late December and March (Fig. 8b and c). Concentrations were generally higher at 15 m than at 4 m and occasionally dropped below 5 µmol/L, particularly between December and February. The total duration of exposure (in minutes) to nutrient-depleted waters throughout the spring-summer season (Fig. 8d), as well as the daily exposure to these waters (Fig. 8e), was higher and more prolonged in the northern than the southern end of the bay.

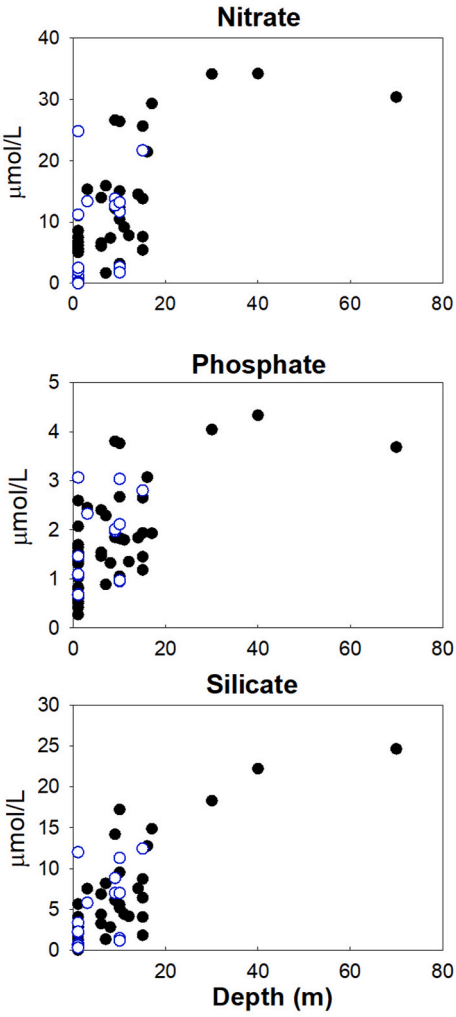


Fig. 3. Depth variation in nutrient concentrations measured within the bay of Algarrobo. Blue open circles correspond to measurements conducted near the submarine sewage outfall (see Fig. 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

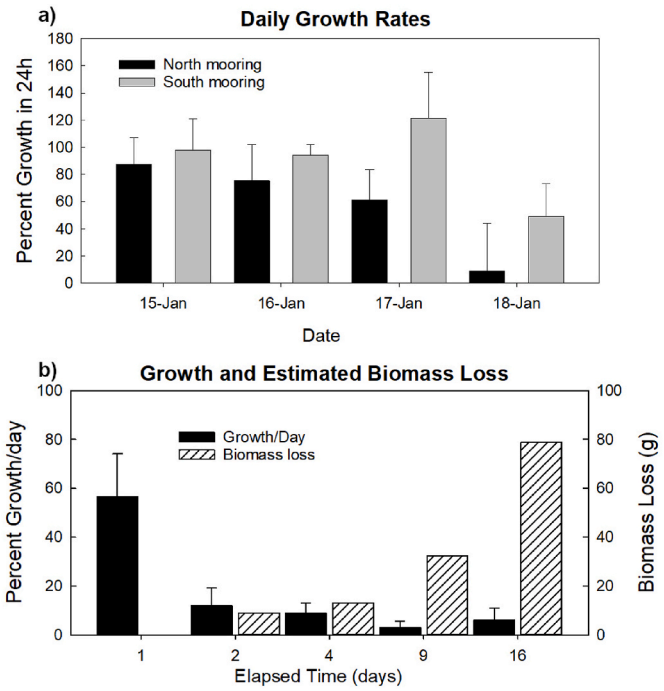


Fig. 4. a) Mean (+SE) daily growth rate (DGR, %) of *Ulva stenophylloides*, expressed as a percentage of new biomass (wet weight) at the north (black bars) and south (gray bars) experimental sites. Replicate fronds were replaced daily. b) Mean (+SE) growth of *U. stenophylloides* at the north site (black bars) in the cumulative growth experiment, expressed as percent growth per day over the days that fronds were in the field (elapsed time). The hatched bars indicate the cumulative biomass lost from the fronds (FL) over that period in the field.

Table 1
Results of a two-way mixed model ANOVA using type III sum of squares on *Ulva stenophylloides* daily growth (ca. 24 h).

Source	DF	Type III SS	MS	F	P-value
Day	3	24,603.00	8201.07	10.88	**0.040**
Mooring	1	14,323.00	14,323.00	19.00	**0.022**
Day*Mooring	3	2261.82	753.94	0.25	0.861
Error	32	96,897.00	3028.04		

4. Discussion

Our results demonstrate that fronds of *Ulva stenophylloides*, the main species associated with green tides in Algarrobo Bay (Mutizabal-Aros et al., 2024), can more than double their wet weight within 24 h and produce over 80 g of biomass released into the water column within two weeks (>26 times their initial size), thus explaining the high biomass of beached fronds found at the southern end of Algarrobo Bay. The field experiment further showed that *Ulva* fronds grew consistently and significantly faster at the bay's southern end compared to the northern end, despite the closer proximity to a submarine outfall at the latter site. While surface nutrient concentrations varied daily, apparently in response to changes in upwelling intensity, they were generally high (>10 µmol/L) at depths greater than 3 m. During the field experiment, nutrient concentrations in seawater samples collected once per day were not significantly correlated with daily variations in algal growth rates but were weakly and negatively correlated with water temperature, prompting further investigation into nutrient variability within the bay. High-frequency temperature records revealed that brief (minutes to hours) cold spells, with a periodicity akin to internal tide activity, occur frequently at the southern end of the bay during spring and summer but were nearly absent at the northern end, approximately 3 km away. Predicted local regimes of nitrate variability, derived from the temperature records, showed higher cumulative nitrate concentrations and substantially reduced exposure to nutrient-depleted waters at the southern end compared to the northern end of the bay. We therefore speculate that internal tides contribute to the faster *Ulva* growth at the southern end of the bay. Here, we discuss these results in the context of potential factors promoting green tides in Algarrobo Bay.

4.1. Field measurements of Ulva growth rates and ambient nutrients

The fast growth rates of *U. stenophylloides* observed in our study are comparable to those reported for *Ulva lactuca* in a similar experiment conducted at the Bay of Todos Santos, located near Ensenada along the upwelling coast of Baja California. Pérez-Mayorga et al. (2011) experimentally measured *U. lactuca* growth rates at 12-h intervals over eight consecutive days and at three depths along a mooring anchored at a bottom depth of 10 m. They documented significant daily variability in growth rates (ca. 20–80 % per 12 h), with faster growth rates observed near the bottom at a depth of 10 m, where nitrate concentrations were persistently higher than at 5 m depth or the surface. The average growth rates and magnitude of daily variability observed at 10 m depth in *U. lactuca* were like those recorded in our experiment with *U. stenophylloides* over 24 h at 3–4 m depth. Water temperatures recorded at a 10-m depth in the Bay of Todos Santos (ca. 16–17 °C) were

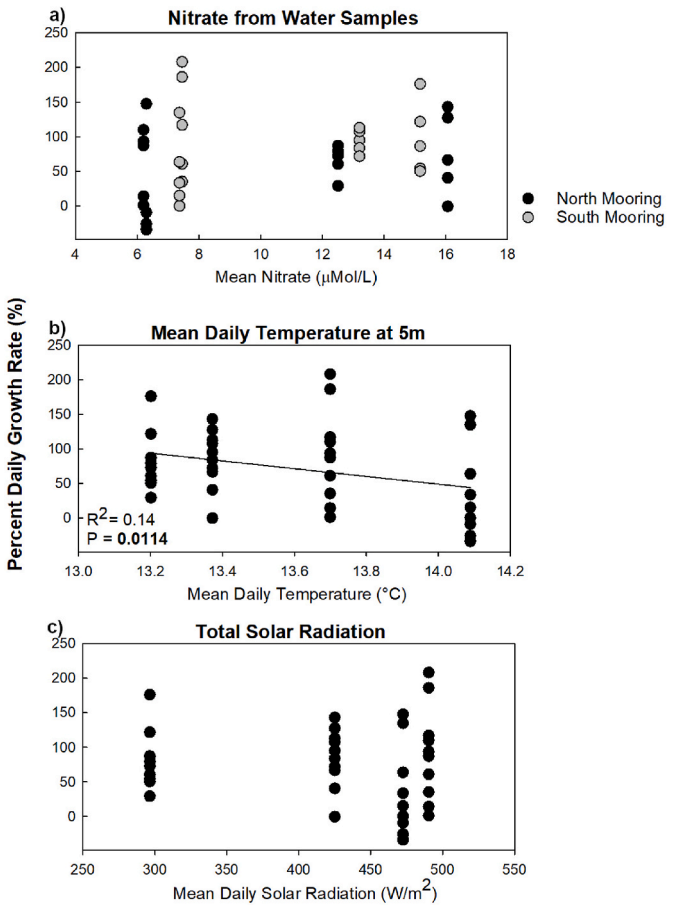


Fig. 5. Relationship between *Ulva* daily growth rates and a) mean nitrate concentration from water samples collected once daily between 7 and 10 m depth, b) mean daily temperature at ca. 5 m depth recorded at the south mooring (see Fig. 1), and c) mean daily solar radiation recorded at ECIM, 20 km south of Algarrobo.

higher than those recorded at a 4-m depth in Algarrobo Bay between 2021 and 2023 (ca. 12–13 °C). Consequently, ambient nutrient levels in Algarrobo were higher than in the Baja California site throughout these two summertime studies. As in our study, Pérez-Mayorga et al. (2011) did not find a correlation between the growth rates of *U. lactuca* and mean nitrate concentrations but identified a strong and significant inverse relationship between growth rates and the time algae were exposed to nutrient-depleted waters (defined in their case as concentrations below 1 µmol/L). In other words, algae grew faster when they were least exposed to nutrient-depleted conditions between measurements. Although we did not have high-frequency temperature records for the northern site during the experiment of January 2023, using only data from the southern end to estimate nitrate concentration and exposure to nutrient-depleted waters (see below), we observed a significant positive relationship between *Ulva* growth rates and the predicted daily integrated nitrate concentration (Fig. S5a) and a significant negative relationship with the total time of algal exposure to nutrient-depleted waters (Fig. S5b). Thus, our results corroborate Pérez-Mayorga et al. (2011) conclusions that nutrient levels obtained from low-frequency (one per day) samples are not good indicators of the nutrient regimes experienced by fast-growing *Ulva* in these upwelling shores and that the predicted time algae are exposed to depleted waters is a good indicator of algal daily growth rates.

The study by Teichberg et al. (2010), conducted at seven sites on different continents, although none in upwelling areas, showed that *Ulva* green tides can occur at sites with a wide range of ambient nutrient concentrations, with annual means for nitrate ranging from 0.11 to 79.8 µmol/L (Table S1 in Teichberg et al., 2010). In that study, the authors did not measure daily nutrient levels to assess their relationship with daily *Ulva* growth; however, they found a significant positive correlation between mean annual nitrate levels at the site and *Ulva* growth rates recorded in 13-day-long field incubation experiments. However, all of their experimentally measured daily growth rates were substantially lower (4–24 %) than those reported here for Algarrobo and by Pérez-Mayorga et al. (2011) for Baja California. The low growth rates recorded by Teichberg et al. (2010) could be the result of measuring growth over a 13-day period, which can underestimate actual growth rates due to the loss of frond fragments, as we show here for *U. stenophylloides* (Fig. 4b, and see Gong et al., 2024 for *U. prolifera*). Alternatively, the experimental cages used by Teichberg et al. (2010),

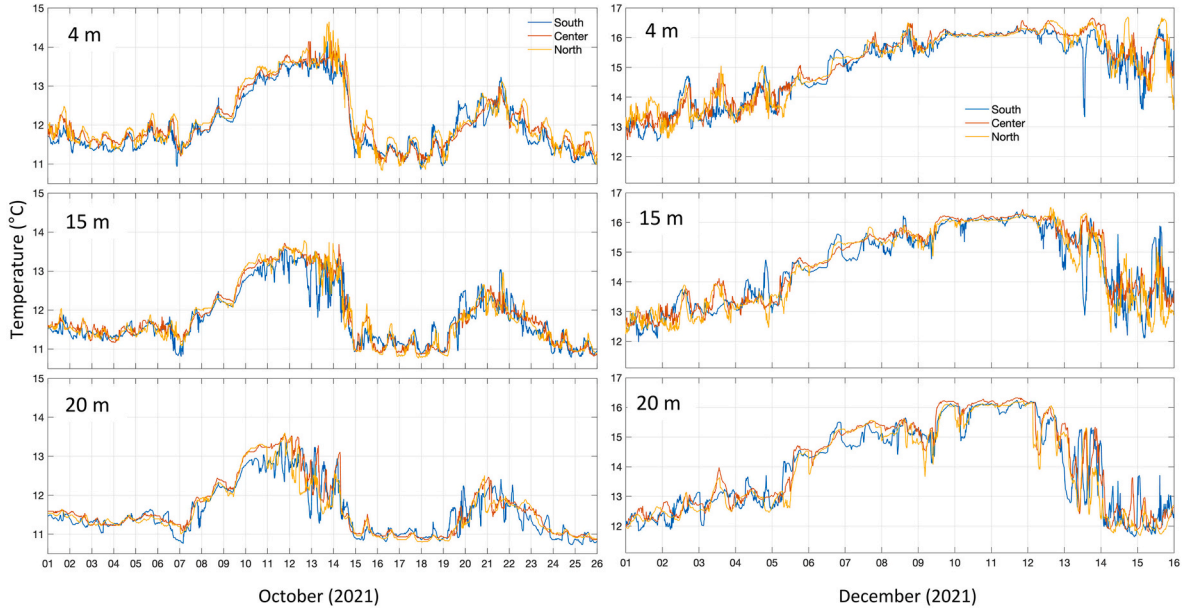


Fig. 6. High-frequency temperature records at the north, center, and south moorings (TN, TC, TS in Fig. 1) at three depths during the spring (October, left panels) and summer (December, right panels) in Algarrobo Bay.

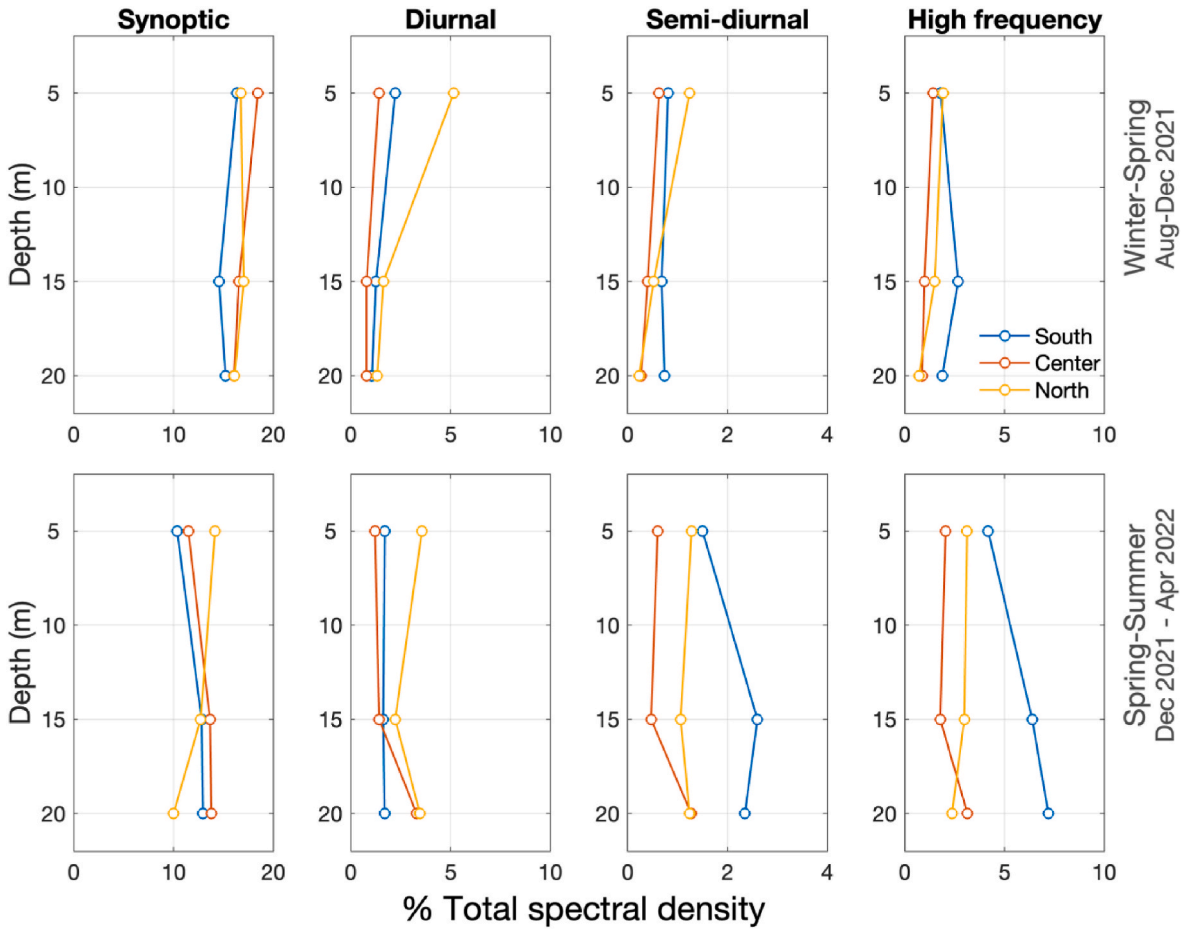


Fig. 7. Fraction of total spectral density (%) accounted for by variability in the synoptic (2–10 d), diurnal (20–30 h), semi-diurnal (10.9–13.3 h), and high frequency (<10.9 h) time scales obtained from the spectral analysis of 10-min temperature records at three sites (Fig. 1) in the bay of Algarrobo during the austral spring (top panels) and summer (bottom panels) of 2021–2022. Separate analyses were conducted for different depths. Note the different x-axis scales for better visualization.

with four solid sides and two sides with fine mesh (1 mm), may have restricted water flow inside the cage and limited growth. While this was not a problem for their nutrient enrichment experiment and main conclusions, it makes it difficult to compare rates directly with our study.

4.1.1. *High-frequency nutrient regimes*

Given the high-frequency and fortnightly variability in seawater temperature, it was concluded that in the Bay of Todos Santos, Baja California, *U. lactuca* can rapidly assimilate nutrients delivered to shore by internal tides, thereby enhancing growth rates. As we show below, we suggest that the generally high growth rates of *U. stenophylloides* observed in Algarrobo Bay can be further enhanced by frequent cold spells that exhibit features (i.e., timing and periodicity) consistent with tidally forced internal waves. Indeed, internal waves are subsurface oscillations that occur at density interfaces (e.g., pycnocline or thermocline). Similar to surface gravity waves, they oscillate vertically and can propagate over extensive distances before dissipating along continental margins. In coastal areas, they are often generated by tidal currents interacting with topography. This process facilitates the transport of deep ocean water onto the continental shelf, supplying nutrients essential for photosynthesis (Alford et al., 2015; Woodson, 2018). Since internal waves have been linked to onshore nutrient delivery and increased green algal growth in other coastal areas (Leichter et al., 1998; Pérez-Mayorga et al., 2011), their more frequent occurrence in the south end of Algarrobo Bay could explain the faster algal growth at that site.

We showed that brief (minutes to hours) cold spells occurred frequently at the bay's southern end and most apparently at mid-depths, while they were nearly or completely absent at the center and northern sections of the bay. This thermal pattern is suggestive of internal waves, with horizontal extensions of less than 2–3 km, which could be entering the bay from the south, where the bathymetry is notably more complex than at the northern end (see isobaths in Fig. 1). We do not have high-frequency salinity records to corroborate the transport of deep water onshore. However, CTD casts conducted on different seasons showed that, during summer months, the nutrient-rich Equatorial Subsurface Waters (ESSW), characterized by a density of 26.2 kg/m^3 (Aiken et al., 2011), are found at depths around 20 m or less, and within 500 m from the shoreline in Algarrobo Bay (Figs. S6–S7). The shoaling of the ESSW and thermal stratification observed nearshore during spring-summer in the area make it feasible for internal waves to transport these waters onshore. However, additional observations and analyses are needed to determine whether the cold spells in Algarrobo are indeed driven by onshore-propagating internal waves or by other hydrodynamic features.

The high-frequency thermal phenomenon was well captured by the spectral analyses of our temperature records, which clearly showed the increased importance of the high-frequency variability in the bottom half of the water column at the southern end of Algarrobo Bay. The strong temperature-nutrient relationship established for Algarrobo Bay, consistent with patterns observed in other coastal regions (Chavez et al., 1996; García-Reyes et al., 2014; Palacios et al., 2013), allowed us to convert temperature measurements into nitrate concentrations. Using these temperature records, we were able to compute the duration of algal exposure to nutrient-depleted waters, defined here as waters with nitrate concentration below 5 μmol/L. This analysis revealed large differences between the bay's north and south ends, with higher nutrient concentrations and, especially, lower exposure to nutrient-depleted

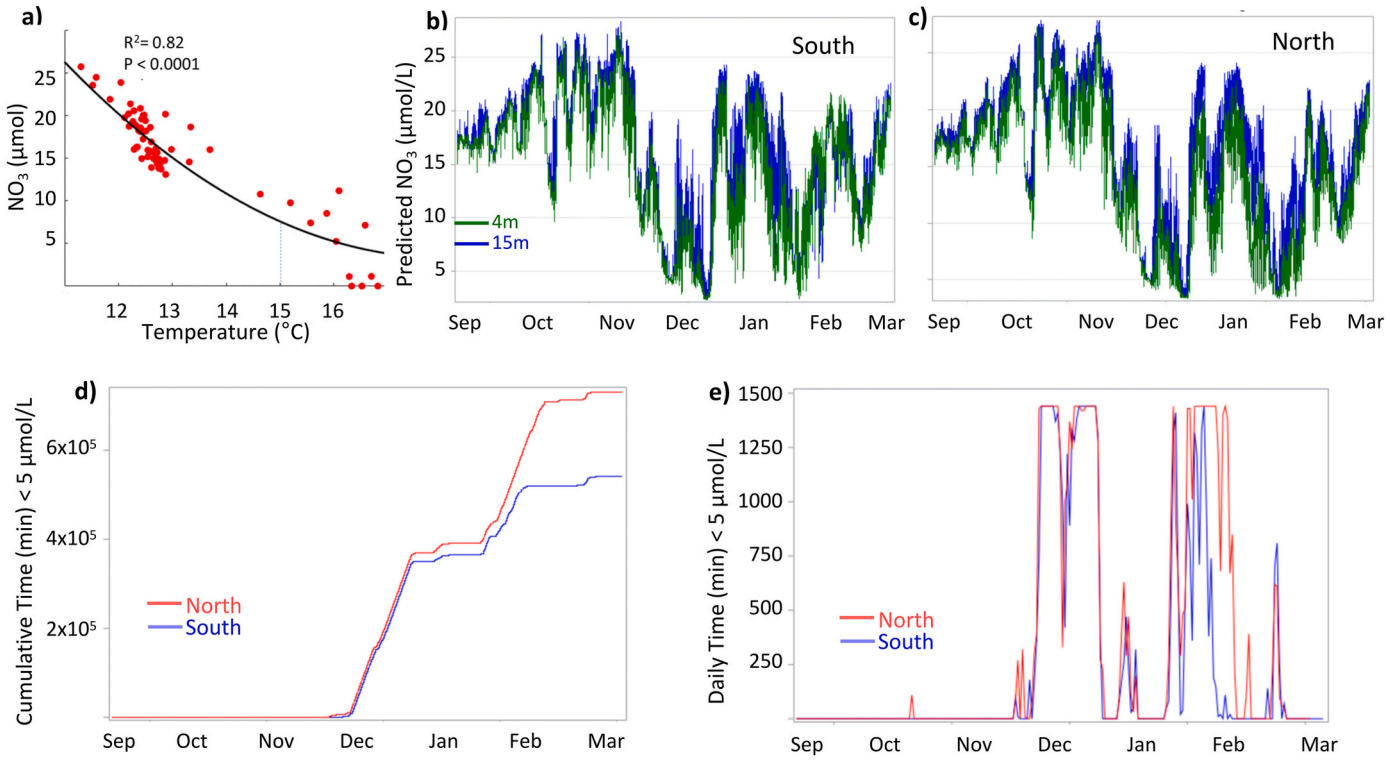


Fig. 8. a) Relationship between nitrate concentration and seawater temperature in the bay of Algarrobo. b) Predicted nitrate concentration at 4 m and 15 m depths for September 2022 through March 2023 at the southern mooring (TS), and c) at the northern mooring (TN). d) Cumulative time (minutes) that algae are exposed to nutrient-depleted waters (i.e., temperature >14.5 °C) at the southern and northern moorings through the spring-summer season. e) The time that algae are exposed to nutrient-depleted waters each day during the spring-summer season at the southern and northern moorings.

waters at the southern end. As expected, at the south end, these two indicators of nutrient regimes show significant correlations with daily *Ulva* growth rates.

Considering the tight inverse relationship between water temperature and nutrient concentration in all upwelling ecosystems as well as in several other temperate and tropical coastal habitats (Chavez et al., 1996), increased water temperatures nearshore should signal a drop in nutrient delivery and, consequently, decreasing algal growth rates. In laboratory experiments, where researchers supply nutrients to experimental units, temperature is usually positively correlated with algal growth, following the universal effect of temperature on anabolic processes (Arroyo et al., 2022). However, under most natural conditions, water temperature is strongly and inversely correlated with nutrients, which rapidly become the limiting factor for algal growth. This prediction applies over the mesoscale of upwelling intensification, i.e., 10s of Km (Nielsen and Navarrete, 2004; Wieters, 2005), over regional scales of 100s of Km (Tapia et al., 2014; Navarrete et al., 2022), and over interannual timescales (e.g., Martínez et al., 2003).

4.1.2. *Green tides and anthropic nutrient enrichment*

Nutrient concentrations along the coast of central Chile, where Algarrobo Bay is located, are naturally variable at most timescales (hours, days, synoptic, seasons) but remain generally high in waters just below 3 m depth (Nitrate >10 µmol/L, Fig. 3), which contrasts sharply with non-upwelling shores (Chavez and Messie, 2009; Trujillo and Thurman, 2013). Such high nutrient levels explain the high kelp biomass that is harvested daily by fishers from these shores (Vásquez, 2016; Carranza et al., 2024). It is therefore not entirely surprising that the nutrient contribution by the comparatively small submarine outfall (discharging <300 L/s) was not apparent in any of our surveys (Navarrete et al., 2024), nor in previous studies about nutrients and phytoplankton conducted in the bay (Ferreira et al., 2020). In fact, we found that *Ulva* growth rates were consistently lower at the northern site (AN), closer to the outfall, compared to the southern site (AS). Thus, regardless of potential pollution (e.g., coliforms, toxins, emergent chemicals) associated with the outfall, its contribution to inorganic nutrient levels does not appear to play a role in the outbreak or maintenance of green tides in Algarrobo Bay. Some yet unidentified pollutants released at the outfall could potentially suppress algal growth and prevent green tides from occurring at the northern end. However, surveys of metals and potential pollutants conducted at multiple stations did not reveal concentrations above the Chilean and EPA norms or a pattern attributable to the marine outfall (Navarrete et al., 2024).

It should be noted that although green tides have been typically associated with anthropogenic nutrient enrichment (Li et al., 2017; Teichberg et al., 2010), it is evident that nutrients alone cannot explain the onset or persistence of green tide events (Valiela et al., 1997; Liu et al., 2009; Joniver et al., 2021). Several laboratory and field experiments have shown that *Ulva* growth rates increase with rising concentrations of dissolved inorganic nitrogen (DIN), sometimes without any indication of saturation (but see Teichberg et al., 2010). Such results have often been mistakenly interpreted as evidence that nutrients control the onset of green tide events and/or that *Ulva* can outcompete other algae solely through faster growth rates. First, virtually all micro- and macro-algae exhibit increased growth rates when exposed to higher nutrient concentrations, particularly when other ecological controls (e.g., grazing, competitors) are removed under experimental settings. However, this response does not imply that these species can overcome natural ecological constraints and produce blooms. Second, *Ulva* species are capable of rapidly capturing nitrate and ammonium at very low concentrations, generally faster than most other macroalgae (Kennison et al., 2011; Luo et al., 2012). This capability confers a competitive advantage at very low nutrient levels and helps explain the presence of green tides in meso- and oligotrophic waters with DIN concentrations below 1 µmol/L (Teichberg et al., 2010). However, this ability does not confer any competitive advantage at high nutrient levels, only faster

growth rates. Indeed, green algae are rapidly outcompeted by most late successional macroalgal species, as shown repeatedly in field experiments along temperate and tropical shores (Lubchenco, 1978; Lubchenco et al., 1984; Nielsen and Navarrete, 2004; Santelices, 1990). This suggests that while reducing nutrient inputs in coastal ecosystems affected by green tides may lower total green tide biomass, it may have a more negative effect on other macroalgae that require higher nutrient concentrations to sustain their biomass.

Finally, *Ulva* species are rapidly consumed by most intertidal and subtidal grazers (Lubchenco and Gaines, 1981; Muñoz and Ojeda, 1998; Nielsen and Navarrete, 2004; Santelices, 1990), which, under most conditions, can control *Ulva* cover and biomass. Therefore, while moderate nutrient levels are necessary to maintain high biomass, *Ulva* blooms are more likely associated with a lack of top-down control and the ability of this species to continue generating biomass from detached floating fragments, as shown here for *U. stenophylloides* and by Gong et al. (2024) for *U. prolifera* in the Yellow Sea. We did not measure grazing by local benthic species, including those currently present at the site or those that have been functionally removed by harvesting (e.g., large limpets). This aspect should be a priority for future studies. The calm water conditions within Algarrobo Bay, which are rare in central Chile, undoubtedly also favor the retention of floating *Ulva* biomass within the bay, allowing fronds to grow before beaching and producing a green tide event. Thus, more attention should be paid to the multiple anthropic disturbances that degrade coastal ecosystems by removing or inhibiting competitors, harvesting effective consumers, and providing hard artificial substrates, which functionally eliminate natural biological controls and favor green algal blooming.

5. Conclusions

In conclusion, understanding temporal and spatial variability in growth rates of green tide-forming macroalgae requires high-resolution estimates of nutrient regimes, which cannot be adequately captured through discrete nutrient sampling conducted once per day. The high rate of frond tissue loss, together with whole-plant detachment (not observed in our study), can explain the high *Ulva* biomass observed in the water column, highlighting that growth rates should be measured at intervals of no more than 24 h. Finally, the naturally high nutrient concentrations in coastal waters of upwelling regions, such as those of the Humboldt Current ecosystem, are sufficient to maintain high macroalgal biomass. Therefore, the occurrence of green tides in these regions is likely not associated with anthropogenic nutrient enrichment of coastal waters but rather with a suite of local ecological factors indicative of overall ecosystem degradation, including the loss of competitors and the removal of grazers.

CRediT authorship contribution statement

Navarrete S.A.: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Andrés E. González:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Juan Faúndez:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Loretto Contreras-Porcia:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis. **Alejandra Núñez:** Writing – review & editing, Methodology, Investigation. **Jorge Rivas:** Writing – review & editing, Methodology, Investigation. **Sofia Chacano:** Writing – review & editing, Formal analysis, Data curation. **Laura Farías:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Gonzalo S. Saldías:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Fabián J. Tapia:** Writing – review & editing, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

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

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The current contribution forms part of a collective three-year effort to improve oceanographic and ecological knowledge of Algarrobo Bay, to provide baseline information in aid of management decisions for multiple environmental issues afflicting the bay, especially green tides. This effort was possible thanks to the Coastal Social-Ecological Millennium Institute (SECOS), the Center for Oceanographic Research COPAS-COASTAL, the Center for Applied Ecology and Sustainability (CAPES), and the Núcleo Milenio NUTME.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107338.

Data availability

We have attached the primary datasets supporting this study. Additional data and analysis code are available upon request.

References

Aiken, C.M., Navarrete, S.A., Pelegrí, J.L., 2011. Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. J. Geophys. Res. 116. https://doi.org/10.1029/2011JG001731.

Alford, M.H., Peacock, T., MacKinnon, J.A., Nash, J.D., Buijsman, M.C., Centurioni, L.R., Chao, S.-Y., Chang, M.-H., Farmer, D.M., Fringer, O.B., Fu, K.-H., Gallacher, P.C., Graber, H.C., Helfrich, K.R., Jachec, S.M., Jackson, C.R., Klymak, J.M., Ko, D.S., Jan, S., Johnston, T.M.S., Legg, S., Lee, I.-H., Lien, R.-C., Mercier, M.J., Moum, J.N., Musgrave, R., Park, J.-H., Pickering, A.I., Pinkel, R., Rainville, L., Ramp, S.R., Rudnick, D.L., Sarkar, S., Scotti, A., Simmons, H.L., St Laurent, L.C., Venayagamoorthy, S.K., Wang, Y.-H., Wang, J., Yang, Y.J., Paluszkiewicz, T., Tang, T.Y., 2015. The formation and fate of internal waves in the South China Sea. Nature 521, 65–69. https://doi.org/10.1038/nature14399.

Arroyo, J.I., Díez, B., Kempes, C.P., West, G.B., Marquet, P.A., 2022. A general theory for temperature dependence in biology. Proceedings of the National Academy of Sciences. https://doi.org/10.1073/pnas.2119872119.

Bularz, B., Fernández, M., Subida, M.D., Wieters, E.A., Pérez-Matus, A., 2022. Effects of harvesting on subtidal kelp forests (*Lessonia trabeculata*) in central Chile. Ecosphere 13, e3958. https://doi.org/10.1002/ecs2.3958.

Carranza, D.M., Wieters, E.A., Vásquez, J.A., Stotz, W.B., 2024. Exploring the consequences of kelp removal: a review shows we are missing a broader perspective. Biodivers. Conserv. 33, 401–437. https://doi.org/10.1007/s10531-023-02769-7.

Charlier, R.H., Morand, P., Finkl, C.W., 2008. How Brittany and Florida coasts cope with green tides. Int. J. Environ. Stud. 65, 191–208. https://doi.org/10.1080/00207230701791448.

Chavez, F.P., Service, S.K., Buttrey, S.E., 1996. Temperature-nitrate relationships in the central and eastern tropical Pacific. J. Geophys. Res. Oceans 101, 20553–20563. https://doi.org/10.1029/96JC01943.

Chavez, F.P., Messie, M., 2009. A comparison of eastern boundary upwelling ecosystems. Prog. Oceanogr. 83, 80–96. https://doi.org/10.1016/j.pocean.2009.07.032.

Cohen, R.A., Fong, P., 2006. Using opportunistic green macroalgae as indicators of nitrogen supply and sources to estuaries. Ecol. Appl. 16, 1405–1420. https://doi.org/10.1890/1051-0761(2006)016[1405:UOGMAI]2.0.CO;2.

Farias, L., de la Maza, L., 2024. Understanding the impacts of coastal deoxygenation in nitrogen dynamics: an observational analysis. Sci. Rep. 14, 11826. https://doi.org/10.1038/s41598-024-62186-w.

Ferreira, A., Sá, C., Silva, N., Beltrán, C., Dias, A.M., Brito, A.C., 2020. Phytoplankton community dynamics in a coastal bay under upwelling influence (central Chile). Estuar. Coast Shelf Sci. 245, 106968. https://doi.org/10.1016/j.ecss.2020.106968.

García-Reyes, M., Largier, J.L., Sydeman, W.J., 2014. Synoptic-scale upwelling indices and predictions of phyto- and zooplankton populations. Prog. Oceanogr. 120, 177–188. https://doi.org/10.1016/j.pocean.2013.08.004.

Gladyshev, M., Gubelit, Y., 2019. Green tides: new consequences of the eutrophication of natural waters (invited review) introduction: bloom of natural waters. Contemp. Probl. Ecol. 12, 135–156. https://doi.org/10.1134/S1995425519020057.

Grasshoff, K., Ehrhardt, M., Kremling, K., 1983. Methods of Seawater Analysis, second ed. Verlag Chemie, Weinhein, New York, NY.

Gong, N., Shao, K., Shen, L., Wang, Z., Han, X., Zhou, K., Kong, D., Pan, X., 2024. How did the floating *Ulva prolifera* develop into the world's largest green tide? Mar. Environ. Res. 202, 106763. https://doi.org/10.1016/j.marenvres.2024.106763.

Henríquez, G., 2018. Prospección Submarina en la rada de Algarrobo: batilitología, comunidad bentónica e identificación de macrófitas indicadoras. Departamento de Medio Ambiente de la Ilustre Municipalidad de Algarrobo, Algarrobo, Chile.

Holmes, R., Aminot, A., Kérouel, R., Hooker, B.A., Peterson, B.J., 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Can. J. Fish. Aquat. Sci. 56, 1801–1808. https://doi.org/10.1139/f99-128.

Inostroza, M., 2012. Diagnóstico y Plan de Contingencia para las floraciones del alga Ulva sp. en la bahía de Algarrobo. Departamento de Medio Ambiente, Algarrobo, Región de Valparaíso, Chile, p. 37.

Joniver, C.F.H., Photiades, A., Moore, P.J., Winters, A.L., Woolmer, A., Adams, J.M.M., 2021. The global problem of nuisance macroalgal blooms and pathways to its use in the circular economy. Algal Res. 58, 102407. https://doi.org/10.1016/j.algal.2021.102407.

Kennison, R.L., Kamer, K., Fong, P., 2011. Rapid nitrate uptake rates and large short-term storage capacities may explain why opportunistic green macroalgae dominate shallow eutrophic estuaries. J. Phycol. 47, 483–494. https://doi.org/10.1111/j.1529-8817.2011.00994.x.

Ladah, L.B., Tapia, F.J., 2021. Internal wave intensity and angle of propagation modulate small-scale settlement patterns of intertidal barnacles during peak recruitment. Mar. Ecol. Prog. Ser. 678, 81–93. https://doi.org/10.3354/meps13876.

Li, H., Zhang, Y., Tang, H., Shi, X., Rivkin, R.B., Legendre, L., 2017. Spatiotemporal variations of inorganic nutrients along the Jiangsu coast, China, and the occurrence of macroalgal blooms (green tides) in the southern Yellow Sea. Harmful Algae 63, 164–172. https://doi.org/10.1016/j.hal.2017.02.006.

Liu, D., Keesing, J.K., Xing, Q., Shi, P., 2009. World's largest macroalgal bloom caused by expansion of seaweed aquaculture in China. Mar. Pollut. Bull. 58, 888–895. https://doi.org/10.1016/j.marpolbul.2009.01.013.

Lotze, H.K., Worm, B., 2002. Complex interactions of climatic and ecological controls on macroalgal recruitment. Limnol. Oceanogr. 47, 1734–1741. https://doi.org/10.4319/lo.2002.47.6.1734.

Lubchenco, J., 1978. Plant species diversity in marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112, 23–39. https://doi.org/10.1086/283250.

Lubchenco, J., Gaines, S.D., 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annu. Rev. Ecol. Systemat. 12, 405–437. https://doi.org/10.1146/annurev.es.12.110181.002201.

Lubchenco, J., Menge, B.A., Garrity, S.D., Lubchenco, P.J., Ashkenas, L.R., Gaines, S.D., Emlet, R., Lucas, J., Strauss, S., 1984. Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). J. Exp. Mar. Biol. Ecol. 78, 23–73. https://doi.org/10.1016/0022-0981(84)90069-8.

Lucero, F., Catalan, P.A., Ossandon, A., Beya, J., Puelma, A., Zamorano, L., 2017. Wave energy assessment in the central-south coast of Chile. Renew. Energy 114, 120–131. https://doi.org/10.1016/j.renene.2017.03.076.

Luo, M.B., Liu, F., Xu, Z.L., 2012. Growth and nutrient uptake capacity of two co-occurring species, *Ulva prolifera* and *Ulva linza*. Aquat. Bot. 100, 18–24. https://doi.org/10.1016/j.aquabot.2012.03.006.

Martínez, E.A., Cárdenas, L., Pinto, R., 2003. Recovery and genetic diversity of the intertidal kelp *Lessonia nigrescens* (Phaeophyceae) 20 years after El Niño 1982/83. J. Phycol. 39, 504–508. https://doi.org/10.1046/j.1529-8817.2003.02191.x.

Muñoz, A.A., Ojeda, F.P., 1998. Guild structure of carnivorous intertidal fishes of the central Chilean coast: implications of ontogenetic dietary shifts. Oecologia 114, 563–573. https://doi.org/10.1007/s004420050481.

Mutizabal-Aros, J., Ramírez, M.E., Haye, P.A., Meynard, A., Pinilla-Rojas, B., Núñez, A., Latorre-Padilla, N., Search, F.V., Tapia, F.J., Saldías, G.S., Navarrete, S.A., Contreras-Porcia, L., 2024. Morphological and molecular identification of *ulva* spp. (Ulvophyceae; Chlorophyta) from Algarrobo Bay, Chile: understanding the composition of green tides. Plants 13, 1258. https://doi.org/10.3390/plants13091258.

Navarrete, S.A., Martínez, C., Troncoso, W., Tapia, F.J., 2024. Mareas verdes en la Bahía de Algarrobo: Conocimiento Ecológico y Oceanográfico para informar sobre sus causas y potenciales medidas de mitigación. https://doi.org/10.6084/m9.figshare.29276213ISBN:978-956-420-310-2. Santiago, Chile, p. 100.

Nielsen, K.J., Navarrete, S.A., 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecol. Lett. 7, 31–41. https://doi.org/10.1046/j.1461-0248.2003.00542.x.

Palacios, D.M., Hazen, E.L., Schroeder, I.D., Bograd, S.J., 2013. Modeling the temperature-nitrate relationship in the coastal upwelling domain of the California Current. J. Geophys. Res. Oceans 118, 3223–3239. https://doi.org/10.1002/jgrc.20216.

Pérez-Mayorga, D.M., Ladah, L.B., Zertuche-González, J.A., Leichter, J.J., Filonov, A.E., Lavín, M.F., 2011. Nitrogen uptake and growth by the opportunistic macroalga *Ulva lactuca* (Linnaeus) during the internal tide. J. Exp. Mar. Biol. Ecol. 406, 108–115. https://doi.org/10.1016/j.jembe.2011.05.028.

Santelices, B., 1989. Algas marinas de Chile. Distribución, ecología, utilización y diversidad. Universidad Católica de Chile.

Santelices, B., 1990. Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. Hydrobiologia 192, 35–57. https://doi.org/10.1007/BF00006226.

Smetacek, V., Zingone, A., 2013. Green and golden seaweed tides on the rise. Nature 504, 84–88. https://doi.org/10.1038/nature12860.

Tapia, F.J., Largier, J.L., Castillo, M., Wieters, E.A., Navarrete, S.A., 2014. Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. PLoS One 9, e110841. https://doi.org/10.1371/journal.pone.0110841.

Taylor, M.W., Rees, T.A.V., 1999. Kinetics of ammonium assimilation in two seaweeds, *Enteromorpha* sp. (Chlorophyceae) and *Osmundaria colensoi* (Rhodophyceae). J. Phycol. 35, 740–746. https://doi.org/10.1046/j.1529-8817.1999.3540740.x.

Teichberg, M., Fox, S.E., Olsen, Y.S., Valiela, I., Martinetto, P., Iribarne, O., Muto, E.Y., Petti, M.A.V., Corbisier, T.N., Soto-Jiménez, M., Páez-Osuna, F., Castro, P., Freitas, H., Zitelli, A., Cardinaletti, M., Tagliapietra, D., 2010. Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. Glob. Change Biol. 16, 2624–2637. https://doi.org/10.1111/j.1365-2486.2009.02108.x.

Trujillo, A., Thurman, H., 2013. Essentials of Oceanography, eleventh ed. Pearson.

Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42, 1105–1118. https://doi.org/10.4319/lo.1997.42.5_part_2.1105.

Vásquez, J.A., 2016. The brown seaweeds fishery in Chile. In: Mikkola, H. (Ed.), Fisheries and Aquaculture in the Modern World. InTech. https://doi.org/10.5772/62876.

Wieters, E., 2005. Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. Mar. Ecol. Prog. Ser. 301, 43–54. https://doi.org/10.3354/meps301043.

Winckler Grez, P., Aguirre, C., Farías, L., Contreras-López, M., Masotti, Í., 2020. Evidence of climate-driven changes on atmospheric, hydrological, and oceanographic variables along the Chilean coastal zone. Clim. Change 163, 633–652. https://doi.org/10.1007/s10584-020-02805-3.

Woodson, C.B., 2018. The fate and impact of internal waves in nearshore ecosystems. Annu. Rev. Mar. Sci. 10, 421–441. https://doi.org/10.1146/annurev-marine-121916-063619.

Ye, N., Zhang, X.-w., Mao, Y., Liang, C.-w., Xu, D., Zou, J., Zhuang, Z.-m., Wang, Q.-y., 2011. 'Green tides' are overwhelming the coastline of our blue planet: taking the world's largest example. Ecol. Res. 26, 477–485. https://doi.org/10.1007/s11284-011-0821-8.