Marine Biology (2021) 168:166
https://doi.org/10.1007/s00227-021-03975-z

ORIGINAL PAPER

An evaluation of surge uptake capability in the giant kelp (*Macrocystis pyrifera*) in response to pulses of three different forms of nitrogen

Tiffany Hiroko Cedeno[1,2] · **Mark A. Brzezinski**[2,3] · **Robert J. Miller**[2] · **Daniel C. Reed**[2]

Received: 4 August 2021 / Accepted: 1 October 2021 / Published online: 22 October 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract
This study examined the capacity of the giant kelp, *Macrocystis pyrifera,* to exhibit surge uptake as a mechanism to enhance nitrogen assimilation during seasons when nitrate is depleted. Surge uptake of nitrate, ammonium, and urea was assessed in the spring and summer with whole-blade incubation experiments using ^{15}N tracers. The incubation experiments showed evidence of surge uptake lasting up to 5 min for ammonium and 1 min for nitrate during the summer only. Giant kelp showed little capacity for surge uptake of urea regardless of season. The ecological importance of the patterns of surge uptake observed for ammonium and nitrate, however, is questionable, given the small scale and ephemeral nature of ammonium pulses most likely experienced by giant kelp, and the longer duration pulses of nitrate associated with internal waves and upwelling. Rather it seems more likely that uptake of ammonium and urea at ambient concentrations, combined with normal uptake of nitrate during longer duration pulses of high concentrations, sustains giant kelp growth during seasons when ambient concentrations of nitrate are low.

keywords Ammonium · Kelp · Nitrate · Nitrogen · Surge uptake · Urea

Introduction

Nutrient availability is a primary factor controlling the species composition and performance of primary producers in many marine environments (Borum 1996; Pedersen and Borum 1997; Taylor et al. 1999; Lucas et al. 2011). In coastal systems strong seasonal variation in the supply of nitrogen is known to limit primary production by both phytoplankton and macroalgae, especially during prolonged periods of stratified conditions (Ryther and Dunstan 1971; Topinka and Robbins 1976; Chapman and Craigie 1977; Thomas and Harrison 1987; Phillips and Hurd 2004; Kim et al. 2007; Pérez-Mayorga et al. 2011; Baek et al. 2015; Ding et al. 2018). In the highly productive systems that occur on the inner shelf within eastern boundary currents, the annual net supply of nitrogen is dominated by nitrate-rich water transported to the inner shelf by wind-driven coastal upwelling (Chavez and Messie 2009; Washburn and McPhee-Shaw 2013; Messie and Chavez 2015).

During non-upwelling periods other oceanographic processes, including internal waves, sub-mesoscale eddies and aerial deposition serve as the major transporters of nitrate to the inner shelf of eastern boundary currents, especially in semi-arid regions with weak river inflows (Zimmerman and Kremer 1984; Paerl et al. 2002; Washburn and McPhee-Shaw 2013; Baek et al. 2015). However, these processes may collectively deliver only a small fraction of the annual net supply of nitrate in these regions (McPhee-Shaw et al. 2007), and have relatively little effect during the stratified conditions in summer and autumn when ambient concentrations of nitrate typically average < 1 μmol L^{-1} (Hepburn et al. 2007; Brzezinski et al. 2013). While these other oceanographic and aerial processes are not sufficient to maintain nitrate at high levels during stratified periods, they are capable of delivering high concentrations of nitrate in short pulses. Such is

Responsible Editor: M.Y. Roleda.

Daniel C. Reed
danreed@ucsb.edu

[1] Interdepartmental Graduate Program in Marine Science, University of California, Santa Barbara, CA 93106, USA

[2] Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

[3] Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA

the case for diurnal and semidiurnal internal waves, which periodically expose shallow waters of the inner shelf of eastern boundary currents to high concentrations of nitrate over periods lasting minutes to several hours (Lerczak et al. 2001; McPhee-Shaw et al. 2007; Ladah et al. 2017). Internal waves are most prominent during late spring and summer (Pineda 1995; Sharples et al. 2001; Brzezinski et al. 2013) and the nitrate that they supply is thought to sustain populations of phytoplankton and macroalgae in shallow coastal waters during periods of summer stratification (Zimmerman and Kremer 1984; Ladah et al. 2012, 2017; Villamaña et al. 2017).

In addition to nitrate, locally recycled forms of nitrogen such as ammonium and urea are present on the inner shelf throughout the year (Remsen 1971; Eppley et al. 1979; Herbert 1999; Smith et al. 2018) and both are known to be utilized by phytoplankton and at least some macrophytes (Smith et al. 2018). As opposed to the large diurnal pulses of nitrate, pulsed delivery of ammonium and urea is most likely to occur as high concentrations in small emphemeral patches created via excretion by consumers within the system (Corner and Newell 1967; Allen and Garrett 1971; Regnault 1987; Allgeier et al. 2017). The near continuous flux of these alternative forms of nitrogen may be important in helping to sustain primary production to varying degrees during periods of low nitrate availability (Fram et al. 2008; Brzezinski et al. 2013; Han et al. 2017).

Pulsed delivery of nitrogen is likely to be most advantageous to species that have the capacity to quickly increase their rate of nitrogen uptake. Such non-linear uptake that optimizes the use of ephemeral nutrient pulses is commonly referred to as surge uptake, enhanced uptake or transient uptake (Rosenberg et al. 1984; Thomas and Harrison 1987; Pedersen 1994; Dy and Yap 2001). Evidence for surge uptake by phytoplankton and macroalgae in low-nutrient conditions commonly comes from studies in which organisms have been previously starved of nitrogen (D'Elia and DeBoer 1978; Thomas and Harrison 1987). Results from these studies indicate that surge uptake is most beneficial to phytoplankton during the first two hours of pulsed delivery, whereas the capacity for surge uptake by macroalgae appears to diminish within the first 15–30 min of exposure to elevated nitrogen.

Having the capacity for surge uptake could be particularly beneficial for species like giant kelp, *Macrocystis pyrifera*, a perennial brown macroalgae that forms highly productive forests on shallow coastal reefs on eastern continental margins of North and South America, Australasia and in sub-Antarctic waters (Graham et al. 2007; Schiel and Foster 2015). The development of near-oligotrophic conditions during summer and autumn throughout much of *M. pyrifera*'s range (Wheeler and Srivastava 1984; Brown et al. 1997; Buschmann et al. 2004; Bell et al. 2015) coupled with its inability to accumulate nitrogen reserves sufficient to last more than a couple weeks (Gerard 1982a; Zimmerman and Kremer 1984) appear to contradict its demonstrated ability to sustain growth year round (Wheeler et al. 1981; González-Fragoso et al. 1991; Reed et al. 2008). Having the capacity to rapidly elevate the rate of nitrogen uptake to take advantage of short pulses of concentrated nitrogen (such as those associated with internal waves) could help sustain the growth of giant kelp during summer and autumn when ambient nitrate concentrations are critically low (i.e., $< 1\ \mu\text{mol L}^{-1}$), and help explain why nitrogen starvation in giant kelp appears to be uncommon (Gerard 1982b). Surge uptake of concentrated pulses of ammonium and urea might also enhance nitrogen assimilation in *M. pyrifera* as these recycled forms of nitrogen are readily taken up by giant kelp (Haines and Wheeler 1978; Hepburn et al. 2006; Smith et al. 2018, 2021).

Here we used laboratory incubation experiments to assess the physiological capacity of *M. pyrifera* for surge uptake as a mechanism to enhance nitrogen assimilation during seasons when nitrate is depleted. We examined this phenomena for three common forms of nitrogen, nitrate, ammonium, and urea, using whole kelp blades collected from the Santa Barbara Channel, a region where ambient nitrate concentrations average $< 1\ \mu\text{mol L}^{-1}$ during summer and autumn (Brzezinski and Washburn 2011; Brzezinski et al. 2013), and the pulsed delivery of nitrate, ammonium and urea are common (Fram et al. 2008; Stewart et al. 2009; Smith et al. 2018; Peters et al. 2019). Demonstrating the physiological capacity for surge uptake does not in of itself provide evidence of its adaptive value. Therefore, to gain insight into the ecological relevance of surge uptake by giant kelp we evaluated temporal changes in the uptake rates of nitrate, ammonium and urea in the context of the characteristic patterns of their pulsed delivery in nature.

Materials and methods

Sample collection and preparation

Actively growing *Macrocystis pyrifera* blades that were relatively free of epiphytes were collected during the nitrate replete spring (May) and the nitrate-deplete summer (September) from natural populations near Santa Barbara, California for use in incubation experiments of surge uptake. Five replicate experiments were conducted in both spring and summer 2019. For each experiment a single blade located ~ 2 m from the distal end of a growing frond was collected from 30 unique haphazardly chosen plants. Blades were placed in an insulated cooler upon collection and returned to the laboratory at the University of California Santa Barbara where they were placed in a tank with constantly flowing sand-filtered seawater illuminated with full spectrum LED lamps emitting 100–200 µmol m^{-2} s^{-1} on a 12:12 h day:night cycle for 1–2 days prior to each experiment.

Experimental design

Nitrogen uptake by *M. pyrifera* was measured in incubation experiments exposing entire blades to an isotopically labelled form (^{15}N) of one of three nitrogen sources (nitrate, ammonium or urea) for pre-determined amounts of time. In each replicate experiment, single blades were placed in 1 L trays filled with nitrogen-depleted filtered sea water. Nitrogen depleted sea water was obtained by inoculating translucent carboys of sand-filtered seawater with phytoplankton-enriched seawater and placing the carboys in ambient daylight (~ 30 µmol m^{-2} s^{-1}) at room temperature. After a minimum of 4 weeks, upon which nitrate plus nitrite concentrations were undetectable, the seawater was coarse filtered (10 µm) and then fine filtered (0.2 µm) using a gravitational filtration system, and stored at ambient seawater temperature until used in an experiment.

Each incubation tray was aerated with an aquarium pump and air stone to maintain constant water movement. Experimental pulses of nitrogen were simulated by introducing one of the three nitrogen isotope tracers into an incubation tray filled with 1 L of nitrogen-depleted seawater to achieve an initial concentration of 10 µM nitrogen prior to adding the kelp blade. A concentration of 10 µM nitrogen is representative of nutrient pulses delivered to giant kelp in southern California by internal waves (Brzezinski et al. 2013) and excretion (Bray et al. 1986). The length of exposure to labeled nitrogen was varied to determine how the rate of uptake changed as a function of the duration of the simulated pulse. Because previous studies have shown that surge uptake in macroalgae typically diminishes after 15–30 min (D'Elia and DeBoer 1978; Rosenberg et al. 1984; Thomas and Harrison 1987; Dy and Yap 2001) we tested exposure times of 1, 5, 15, and 45 min. Three replicate incubations of the four exposure times were done for each nitrogen form, resulting in simultaneous incubations of 36 unique blades for each of the ten replicate experiments (five in spring and five in summer). All experiments were done under conditions of saturating irradiance, > 170 µmol photons m-^{2} s^{-1}, to eliminate light as a potentially confounding factor influencing the rate of nitrogen uptake (Colombo-Pallotta et al. 2006).

Blades were removed from the incubation trays at the end of the designated exposure time, and cleaned of any remaining tracer and potential epiphytes by rinsing in 10% HCl and then deionized water. Each blade was blotted and weighed damp, and then dried overnight at 60 °C to obtain dry weight. Dried tissue was ground to a powder and subsamples were analyzed using an elemental analyzer isotope ratio mass spectrometer (EA-IRMS) to determine the atom % ^{15}N and the percent weight nitrogen (% N) of each blade, which was used to calculate uptake rates for each incubation treatment. For each experiment, five control blades, collected at the same time as the experimental blades, but not incubated in isotopically labeled ^{15}N, were processed and analyzed for ^{15}N to obtain an estimate of the initial nitrogen isotope composition and total nitrogen content (as a percent dry weight) of experimental blades prior to incubation.

Evaluating the physiological capacity for surge uptake

The uptake rate of nitrogen for nutrient pulses with different durations (V) in units of inverse time was calculated using a modified version of an equation by Legendre and Gosselin (1996):

$$V = \frac{(n_t - n_0)}{t(d_s - d_0)} \tag{1}$$

where n_t is the atom % ^{15}N in the blade after incubation; n_0 is the atom % ^{15}N in the control blades; d_s is the atom % ^{15}N of the substrate (nitrate, ammonium or urea) in the seawater at the start of the incubation after isotope tracer addition; d_0 is the atom % ^{15}N of the substrate in the seawater before isotope tracer was added; and t is the length of the incubation in minutes.

Values of V calculated for pulses of different duration using Eq. (1) were compared to assess how the physiological uptake of different forms of nitrogen changed over time in response to exposure to a high-concentration pulse. A caveat of this calculation is that uptake is averaged over the total duration of the nitrogen pulse and thus does not provide instantaneous rates of uptake rate at any given point in time. To provide insight into the temporal evolution of uptake over a pulse lasting 45 min, average values of nitrogen uptake for specific time intervals during a 45-min pulse (V_I) were calculated as:

$$V_I = \frac{(V_f t_f) - (V_i t_i)}{t_{f-} t_i} \tag{2}$$

where V_i and V_{f} are the uptake rates measured at the start and end of a specific time interval and t_i and t_{f} are the durations of the time intervals over which V_i and V_{f} were calculated. Using Eq. (2) we calculated values of V_I for time intervals of 0–1 min, 1–5 min, 5–15 min, and 15–45 min for each of the three nitrogen forms.

Assessing the ecological relevance of uptake rates

The ecological implication of the uptake response to pulsed nitrogen was assessed by examining the biomass-normalized uptake rate ρ [µg N (g dw)$^{-1}$ min^{-1}] using Eq. (3):

$$\rho = V\left(\frac{m_N}{m_{dw}}\right) \tag{3}$$

where m_N is the mass of isotope in the subsample taken for isotope analysis (µg) and m_{dw} is the dried weight subsample (g) (Legendre and Gosselin 1997).

Values of ρ were used in combination with estimates of daily nitrogen uptake by *M. pyrifera* to evaluate the likelihood that nitrogen uptake during pulses, and surge uptake in particular, make a significant contribution to giant kelp's nitrogen demand. For this purpose, we estimated the number of pulses of a given concentration and duration that would be needed to meet the nitrogen demand of giant kelp in spring and summer. Estimates of the average daily nitrogen demand in spring and summer were derived from measurements of net primary production by giant kelp (in units of g kelp N produced m^{-2}d^{-1}) and standing biomass (in units of g dry mass m^{-2}) of *M. pyrifera* obtained from a 15-y monthly time series of three kelp forests in the Santa Barbara Channel collected by the Santa Barbara Long Term Ecological Research program (Rassweiler et al. 2018).

Examination of nitrogen status as a driver of surge uptake

Previous studies have found surge uptake by macroalgae to be more pronounced in specimens previously starved of nitrogen (D'Elia and DeBoer 1978; Rosenberg et al. 1984; Brinkhuis et al. 1989). Thus, we estimated the percent nitrogen of experimental blades to account for variation in surge uptake due to differences in nitrogen status. Because it was not possible to measure the nitrogen content of a blade prior to an experiment without damaging it, the percent nitrogen of a blade at the start of incubation (N_{t0}) was calculated as

$$N_{t0} = m_N - \frac{\rho t m_{dw}}{m_{dw} - 15\rho t m_{dw}} \tag{4}$$

where m_N is the mass of nitrogen present at the end of the experiments (µg) as measured by the EA-IRMS, m_{dw} is the dried weight subsample (g), ρ is the biomass-normalized uptake rate [µg N (g dw)$^{-1}$ min^{-1}] and t is the length of the incubation in minutes.

Statistical analysis

Linear mixed-effects models were used to estimate the effects of season, pulse duration, and the percent nitrogen of blades at the start of the incubation on nitrogen uptake rates. Separate models were used to predict responses in the specific uptake rate (V_d) of each of the three nitrogen forms as a function of season (fixed) and pulse duration (fixed) while controlling for experiment day (random nested within season) and initial percent N (covariate). Estimating uptake for specific pulse intervals required averaging replicate blades within a given pulse duration. Thus, the response of V_I to variation in season, pulse interval and initial percent N were assessed separately for the three forms of nitrogen using a linear model in which season and pulse interval were fixed and percent N a covariate. Pairwise comparisons of Tukey-adjusted least square means were used to determine differences among pulse durations (or pulse intervals) in cases where the effects of pulse duration (or pulse interval) were significant. Significantly higher uptake rates for pulse durations and pulse intervals of 15 min or less were considered as evidence of surge uptake as per previous studies of macroalgae (D'Elia and DeBoer 1978; Rosenberg et al. 1984; Thomas and Harrison 1987; Dy and Yap 2001).

Although variation in the nitrogen status of experimental blades was controlled for in the analyses of surge uptake it was nonetheless possible that this variation was not distributed equally among the different factors examined in our experiments. Thus, we tested whether the percent nitrogen of control blades collected at the same time as those used in the experiments differed with season using a linear mixed effects model with season (fixed) and experiment day (random nested within season). We also tested whether the percent nitrogen of experimental blades calculated at the beginning of an incubation (based on ρ and nitrogen content measured at the end of the experiment) differed with respect to pulse duration and nitrogen form using a linear fixed effects model.

Results

Patterns of surge uptake

The response of the specific uptake rate (V) by blades exposed to experimental pulses of nitrogen differed with incubation time and season for the three forms of nitrogen. The uptake of nitrate during pulses lasting 1 minute was on average 50% higher than that of pulses lasting 5–45 min ($F_{3,105} = 6.74$, $p < 0.001$ for main effect of pulse interval, Fig. 1a), indicating that the capacity for surge uptake of nitrate by giant kelp is restricted to very short pulses. The uptake of nitrate was on average 17% higher in summer

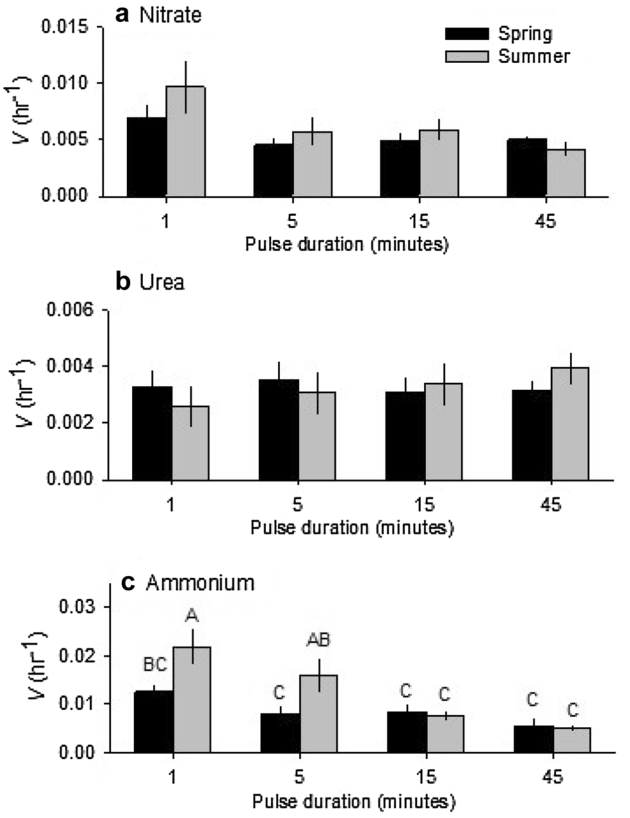

Fig. 1 The effects of pulse duration and season on the specific uptake rate (*V*) for **a** nitrate, **b** urea and **c** ammonium. Bars and errors represent least squared means and standard errors. Bars for ammonium that do not share the same letter were significantly different from each other based on Turkey post hoc comparisons ($\alpha = 0.05$)

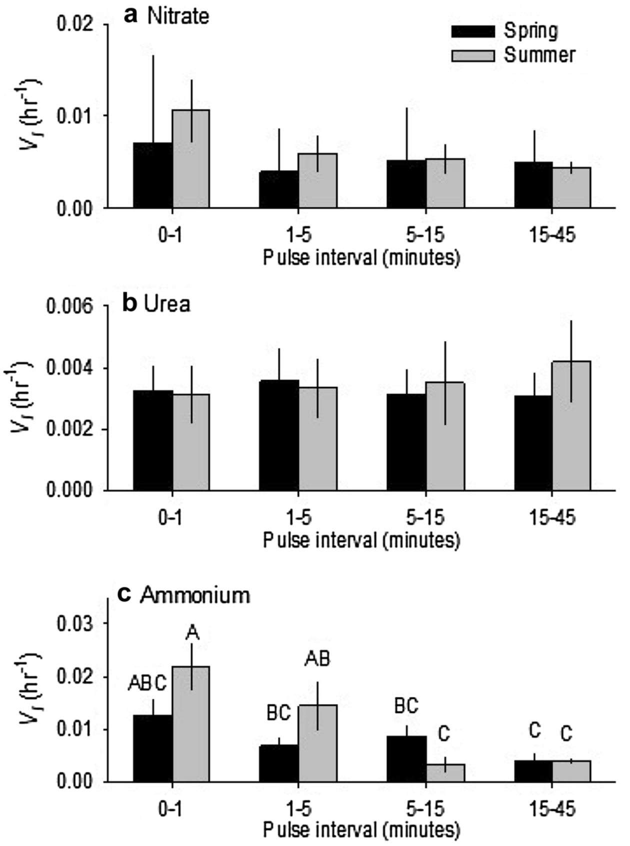

Fig. 2 The effects of pulse interval and season on the specific uptake rate (*V*) for **a** nitrate, **b** urea and **c** ammonium. Bars and errors represent least squared means and standard errors. Bars for ammonium that do not share the same letter were significantly different from each other based on Turkey post hoc comparisons ($\alpha = 0.05$)

(when conditions tend to be nitrate depleted) irrespective of the duration of the nitrate pulse ($F_{3,105} = 5.08$, $p = 0.026$ for main effect of season). Significantly higher uptake rates in summer were also observed for pulses of urea ($F_{3,104} = 5.24$, $p = 0.024$ for main effect of season), but *V* was unaffected by pulse duration ($F_{3,104} = 0.97$, $p = 0.410$) indicating little capacity for surge uptake of urea (Fig. 1b).

The specific uptake rate of ammonium was generally 2–3 times higher than that of nitrate and urea, and kelp blades displayed a higher capacity for surge uptake of this nitrogen form (Fig. 1c vs. a and b). The effects of pulse duration on the uptake of ammonium varied significantly with season ($F_{3,105} = 4.04$, $p = 0.009$ for season* pulse duration interaction). The uptake rate of ammonium by blades exposed to 1- and 5-min pulses in summer was about three times higher than that observed for longer pulses irrespective of season, and ~ 50% higher than that of blades exposed to a one-minute pulse in spring (Fig. 1c). The effects of pulse duration and season on the uptake of nitrate, urea and ammonium were qualitatively similar for ρ (Fig. S1).

Uptake rates of nitrate, urea and ammonium averaged over specific time intervals of a nitrogen pulse (V_I) were similar to those averaged over the entire duration of a pulse (Figs. 2 vs. 1). The only exceptions were a lack of significance of the effects of season for urea ($F_{12,\,38} = 2.16$, $p = 0.154$, Fig. 2b) and minor differences in the statistical significance between pairs of season-pulse interval combinations for ammonium (Figs. 2c vs. 1c).

Response of uptake to variation in blade nitrogen

The specific uptake rate of all three forms of nitrogen generally declined linearly with increasing blade nitrogen content (Fig. 3). In the cases of nitrate and ammonium the rate of decline in *V* with blade nitrogen content varied with pulse duration ($F_{3,105} = 4.21$, $p = 0.008$ and $F_{3,105} = 5.37$, $p = 0.002$ for the pulse duration * percent nitrogen interaction for nitrate and ammonium, respectively). The rate of decline in *V* with blade nitrogen tended to increase with pulse duration for nitrate and decrease with pulse duration for ammonium.

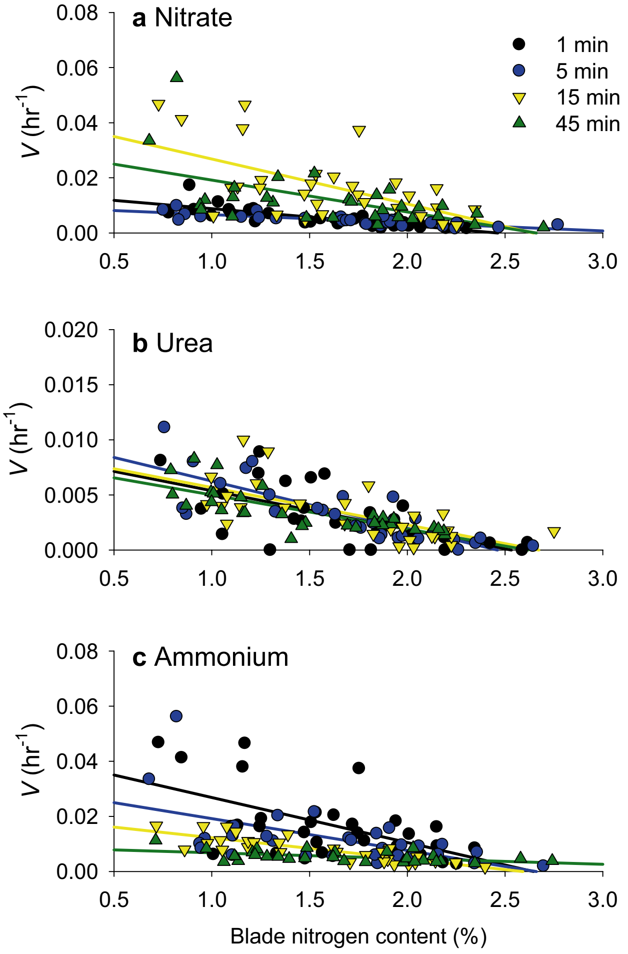

Fig. 3 Results showing the relationship between blade percent nitrogen and specific uptake rate (*V*) for different durations of concentrated pulses of **a** nitrate, **b** urea and **c** ammonium

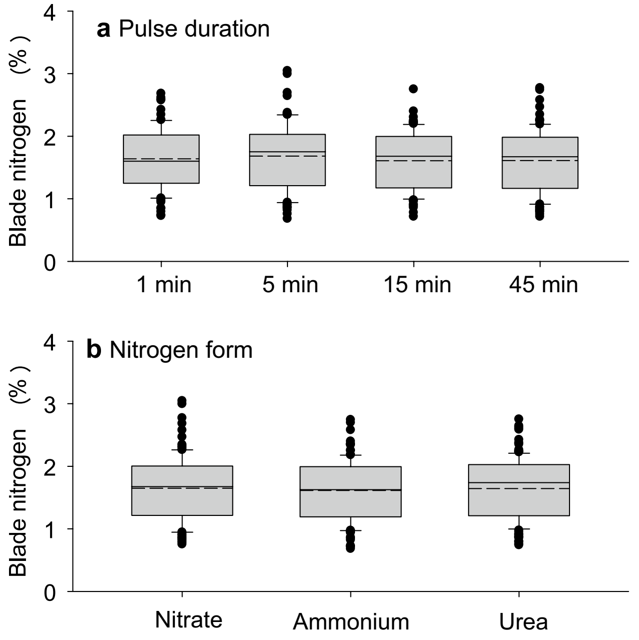

Fig. 4 Box plots showing the variation in the initial nitrogen content of experimental blades (expressed as % dry mass) as a function of **a** pulse duration and **b** nitrogen form. The solid horizontal line represents the median, the dashed line the mean, the boundary of the box indicates the 25th and 75th percentile, the whiskers (error bars) indicate the 10th and 90th percentiles and the solid points are values that lie outside the 10th and 90th percentiles

By contrast, the rate of decline in *V* with blade nitrogen content for urea was unaffected by pulse duration ($F_{3,104} = 0.55$, $p = 0.646$ for the pulse duration * percent nitrogen interaction), which is not unexpected given that *V* for urea did not vary with pulse duration (Fig. 1).

The nitrogen status of control blades collected at the same time as those used in the experiments varied substantially, even within a season (range 0.7–2.3% nitrogen dry weight), despite standardized collections that targeted blades of similar age and condition. Nonetheless, the average percent nitrogen content of control blades collected in spring when conditions tend to be nitrate replete was similar to that of blades collected in summer when conditions tend to be nitrate depleted (mean = 1.65% ± 0.08 SE and 1.51 ± 0.09 SE for spring and summer, respectively; $F_{1,46} = 0.07$, $p = 0.799$). Comparisons of calculated values of the initial percent N of experimental blades showed that the average percent nitrogen of blades used in uptake experiments did not differ significantly among pulse durations (Fig. 4a, $F_{3,347} = 0.43$, $p = 0.730$) or nitrogen forms (Fig. 4b, $F_{2,347} = 0.20$, $p = 0.820$). Collectively, these results indicate that variation in the initial nitrogen status of blades was similar among the experimental treatments and did not influence the significance of treatment effects.

Discussion

Using laboratory incubation experiments of entire blades, we found that the capacity for surge uptake by *Macrocystis pyrifera* varied with nitrogen form, season and blade nitrogen content (measured as a percent of dry mass). The strongest evidence of surge uptake as a potential strategy for N acquisition came from incubation experiments in summer involving ammonium, when pulses produced a 2 to three-fold increase in *V* and *ρ* for the first 5 min. Giant kelp tissue N content in the study region is typically lower in summer (Reed et. al. 1996; Brzezinski et al. 2013), but highly variable, and we found no significant difference between the mean % N of blades collected for our experiments in spring and summer. Our analysis, moreover, removed this effect on uptake rates, suggesting that the higher surge uptake we observed in summer is driven by factors other than tissue N content. Taken together this suggests that the seasonal differences in surge uptake that we detected in our experiments could be magnified at the population level when lower tissue N content in summer is evident.

The extent to which surge uptake by *M. pyrifera* is influenced by acclimation to its recent history of nitrogen exposure (as opposed to its current nitrogen status) was not examined in our study. Such acclimation could account for the seasonal differences in uptake that we observed as ambient nitrogen concentrations in the Santa Barbara Channel and elsewhere throughout *M. pyrifera*'s range tend to be highest in winter and spring and lowest in summer, with corresponding seasonal patterns in blade nitrogen content (Wheeler and Srivastava 1984; Van Tussenbroek 1989; Brown et al. 1997; Brzezinski et al. 2013). Such seasonal differences would afford greater advantage to surge uptake of ammonium in summer given that *V* varied inversely with blade nitrogen content.

Our finding that surge uptake of ammonium by *M. pyrifera* was influenced by the nitrogen content of its tissues is consistent with that observed in other macroalgae. Short-term (5 min) uptake rates of ammonium by nitrogen starved specimens of the red algae *Neoagardhiella baileyi* and *Gracilaria foliifera* were twice that of more N-replete specimens (D'Elia and DeBoer 1978). Similarly, individuals of the brown algae *Chordaria flagelliformis and Fucus distichus* with the lowest thalli N content displayed the highest rates of nonlinear uptake of ammonium (Rosenberg et al. 1984).

Much like ammonium, urea is produced locally via excretion by consumers. However, unlike ammonium, we found no evidence of surge uptake of urea by *M. pyrifera*. In the case of nitrate which is advected into the kelp forest from deeper water, both V and ρ were 50% higher during the 1-min exposure compared to 5 to 45-min exposures, indicating that *M. pyrifera* may exhibit some capacity for surge uptake of nitrate for a very short duration. However, it is unlikely that such short-term increases in the rate of nitrate uptake significantly alter the N content and growth of *M. pyrifera* during the nitrate depleted summer. Therefore, instead of relying on surge uptake to increase its acquisition of nitrate during this oligotrophic period, giant kelp may simply increase its uptake capacity of nitrate in response to prolonged exposure to low nitrogen conditions as found by Fernandez et al. (2017) for *M. pyrifera* in New Zealand, and as suggested by our result that nitrate uptake was higher in summer compared to spring.

Assessing the ecological significance of surge uptake by *M. pyrifera* requires interpreting its capacity for surge uptake in the context of the amount of nitrogen uptake required to account for its production as well as the concentration, size, duration and frequency of naturally occurring pulses of different forms of nitrogen. Using estimates of the net nitrogen production (g N $m^{-2}d^{-1}$) and standing biomass (g dry mass m^{-2}) of giant kelp obtained from a 15-year record of monthly observations at three kelp forests near Santa Barbara (Rassweiler et al. 2018), we calculated the average daily nitrogen uptake of *M. pyrifera* in summer to be 270 µg N g dry $mass^{-1}$ d^{-1}. The most common form of nitrate pulses in kelp forests off California USA and Mexico during summer are delivered via diurnal to semidiurnal internal waves (Zimmerman and Kremer 1984; Ladah et al. 2012, 2017), which have been estimated to account for 27% of the summertime nitrogen demand of *M. pyrifera* in the Santa Barbara Channel (Fram et al. 2008). Abrupt increases in nitrate associated with steep leading edges of internal waves can elevate bottom (i.e., 12 m depth) nitrate concentrations in kelp forests to 5–10 µmol L^{-1} for 30–60 min with concentrations of 3 µmol L^{-1} persisting for up to 6–9 h (McPhee-Shaw et al. 2007). Internal waves in this region have an along-shelf coherence scale of at least 50 km (Cudaback and McPhee-Shaw 2009), which is more than sufficient to elevate nitrate concentrations of entire kelp populations. However, it is unlikely that surge uptake significantly enhances *M. pyrifera's* ability to maximize its uptake of nitrate during internal waves given that it is limited to a 50% increase in uptake during the first few minutes.

As mentioned above, naturally occurring pulses of ammonium and urea commonly occur sporadically as biproducts of excretion by consumers. Raikar and Wafar (2006) described such pulses as being highly localized and extremely short-lived, dissipating within minutes. Nonetheless, excretion by reef consumers has been implicated as a readily available source of nitrogen for macroalgae including giant kelp (Bray et al. 1986; Bracken 2004; Bracken and Nielsen 2004; Hepburn et al. 2006). The extent to which surge uptake of ammonium contributes to *M. pyrifera's* acquisition of nitrogen, however, is also questionable. Using the average value for ρ determined for 1 and 5-min exposure to a 10 µmol L^{-1} pulse to represent the response of *M. pyrifera* to patches of excreted ammonium, we estimated that 71 1-min pulses or 18 5-min pulses of ammonium would be required each day to meet *M. pyrifera*'s total nitrogen demand in summer. These estimates are based on the assumption that a pulse of ammonium encompasses an entire plant. Scaling down to the millimeter or centimeter scale associated with an ammonium excretion event by an individual consumer would increase these estimates by orders of magnitude, diminishing the ecological importance of surge uptake for an alga that can be many meters in length.

Although surge uptake of such small patches of ammonium are likely irrelevant to satisfying the nitrogen needs of *M. pyrifera* it should still be noted that both ammonium and urea exist at low, relatively constant concentrations (0.2–1.5 μmol L^{-1} N) in coastal waters (Eppley et al. 1979; Herbert 1999; Smith et al. 2018). The near constant uptake of this background concentration, rather than surge uptake of smaller pulses, likely plays a significant role in sustaining giant kelp's nitrogen demand during periods of low nitrate supply (Fram et al. 2008; Brzezinski et al. 2013), and may explain why nitrogen starvation in giant kelp is a rare occurrence in Southern California (Gerard 1982a).

Understanding the physiological capacity of *M. pyrifera* for surge uptake and its ecological significance in accounting for the abundance and growth of this iconic foundation species is important given its limited capacity to store nitrogen (Gerard 1982a) and its routine exposure to prolonged periods of nitrate depletion throughout much of its range (Wheeler and Srivastava 1984; Brown et al. 1997; Buschmann et al. 2004; Bell et al. 2015). Our results suggest that during prolonged periods of low nitrate, surge uptake of ammonium or direct exploitation of small patches of elevated ammonium and urea excreted by consumers hold little potential for meeting giant kelp's N demand. Moreover, modest surge uptake of nitrate on timescales of a few minutes such as we observed would not contribute appreciably to giant kelp's ability to exploit pulses of elevated nitrate delivered by internal waves lasting a few hours. Instead, our findings suggest that a combination of uptake of ammonium and urea at ambient concentrations with normal uptake of nitrate during diurnal to semidiurnal internal waves is a more likely explanation for the sustained growth of giant kelp during prolonged periods with low ambient concentrations of nitrate.

Ongoing climate change is likely to lead to increase in the frequency and duration of low nitrate conditions as oceans continue to warm. Understanding how giant kelp will respond and adapt to these changing conditions will become increasingly important when developing management strategies aimed at mitigating climate change effects on this important foundation species. Much still remains unknown about the complexities of nitrogen uptake and demand by *Macrocystis pyrifera,* but the results presented here suggest that surge uptake will not be an important factor influencing the adaptation of this species to future conditions of nitrogen availability.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-021-03975-z.

Acknowledgements We thank Jason Smith for stimulating discussions on nitrogen physiology in marine algae and guidance during our preliminary investigations of surge uptake, and C. Nelson and S. Sampson for assistance with field and laboratory sampling and logistics. We are grateful to G. Paradis for providing access and technical training in EA-IRMS. Funding was provided by the U. S. National Science Foundation in support of the Santa Barbara Coastal Long Term Ecological Research program and the U. S, Department of Energy Advanced Research Projects Agency–Energy (ARPA-E) MARINER program.

Author's contributions THC performed the experiments and chemical analyses. THC and DCR analyzed the data. All authors contributed to the study design and manuscript preparation.

Funding Funding was provided by the U. S. National Science Foundation in support of the Santa Barbara Coastal Long Term Ecological Research program and the U. S, Department of Energy Advanced Research Projects Agency–Energy (ARPA-E) MARINER program.

Availability of data and materials Data and metadata are available from the data portal of the Environmental Data Initiative at https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-sbc&identifier=142

Code availability Not applicable.

Declarations

Conflict of interest Giant kelp blades used in experiments were collected under the California Department of Fish and Wildlife Scientific Collecting Permit no. 11964 to SBC LTER.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Allen JA, Garrett MR (1971) The excretion of ammonia and urea by *Mya arenaria* L. (Mollusca: Bivalvia). Comp Biochem Phys Part A Physiol. 39:633–642

Allgeier JE, Burkepile DE, Layman CA (2017) Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Glob Change Biol 23:2166–2178

Baek SH, Kim D, Son M, Yun SM, Kim YO (2015) Seasonal distribution of phytoplankton assemblages and nutrient-enriched bioassays as indicators of nutrient limitation of phytoplankton growth in Gwangyang Bay, Korea. Estuar Coast Shelf Sci 163:265–278

Bell TW, Cavanaugh KC, Reed DC, Siegel DA (2015) Geographical variability in the controls of giant kelp biomass dynamics. J Biogeog 42:2010–2021

Borum J (1996) Shallow waters and land/sea boundaries. In: Barker Jorgensen B, Richardson K (eds) Eutrophication in coastal marine systems. American Geophysical Union, Washington DC, pp 179–203

Bracken MES (2004) Invertebrate-mediated nutrient loading increases growth of an intertidal macroalga. J Phycol 40:1032–1041

Bracken MES, Nielsen KJ (2004) Diversity of intertidal macroalgae increases with nitrogen loading by invertebrates. Ecology 85:2828–2836

Bray RN, Purcell LJ, Miller AC (1986) Ammonium excretion in a temperate-reef community by a planktivorous fish, *Chromis punctipinnis* (Pomacentridae), and potential uptake by young giant kelp, *Macrocystis pyrifera* (Laminariales). Mar Biol 90:327–334

Brinkhuis BH, Renzhi L, Chaoyuan W, Xun-sen J (1989) Nitrite uptake transients and consequences for in vivoalgal nitrate reductase assays. J Phycol 25:539–545

Brown MT, Nyman MA, Keogh JA, Chin NKM (1997) Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. Mar Biol 129:417–424

Brzezinski MA, Washburn L (2011) Phytoplankton primary productivity in the Santa Barbara Channel: effects of wind-driven upwelling and mesoscale eddies. J Geophys Res 116:C12013. https://doi.org/10.1029/2011JC007397

Brzezinski MA, Reed DC, Harrer S, Rassweiler A, Melack JM, Goodridge BM, Dugan JE (2013) Multiple sources and forms of nitrogen sustain year-round kelp growth on the inner continental shelf of the Santa Barbara Channel. Oceanogr 26:114–123

Buschmann AH, Väsquez JA, Osorio P, Reyes E, Filún L, Hernández-González MC, Vega A (2004) The effect of water movement, temperature and salinity on abundance and reproductive of patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. Mar Biol 145:849–862

Chapman ARO, Craigie JS (1977) Seasonal growth in *Laminaria longicruris*: Relations with dissolved inorganic nutrients and internal reserves of nitrogen. Mar Biol 40:197–205

Chavez FP, Messié M (2009) A comparison of eastern boundary upwelling ecosystems. Prog Oceanogr 83:80–96

Colombo-Pallotta MF, García-Mendoza E, Ladah LB (2006) Photosynthetic performance, light absorption, and pigment composition of *Macrocystis pyrifera* (Laminariales, phaeophyceae) blades from different depths. J Phycol 42:1225–1234

Corner EDS, Newell BS (1967) On the nutrition and metabolism of zooplankton IV. The forms of nitrogen excreted by *Calanus*. J Mar Biol Assoc UK 47:113–120

Cudaback CN, McPhee-Shaw E (2009) Diurnal-period internal waves near point conception, California. Estuar Coast Shelf Sci 83:349–359

D'Elia CF, DeBoer JA (1978) Nutritional studies of two red algae. II. kinetics of ammonium and nitrate uptake. J Phycol 14:266–272

Ding S, Chen M, Gong M, Fan X, Qin B, Xu H, Gao SS, Jin Z, Tsang DCW, Zhang C (2018) Internal phosphorus loading from sediments causes seasonal nitrogen limitation for harmful algal blooms. Sci Total Envir 625:872–884

Dy DT, Yap HT (2001) Surge ammonium uptake of the cultured seaweed, *Kappaphycus alvarezii* (Doty) Doty (Rhodophyta: Gigartinales). J Exp Mar Biol Ecol 265:89–100

Eppley RW, Render EH, Harrison WG, Cullen JJ (1979) Ammonium distribution in southern California coastal waters and its role in the growth of phytoplankton. Limnol Oceanogr 24:495–509

Fernandez PA, Roleda MY, Leal PP, Hurd HCD, CL, (2017) Tissue nitrogen status does not alter the physiological responses of *Macrocystis pyrifera* to ocean acidification. Mar Biol 164:177

Fram JP, Stewart HL, Brzezinski MA, Gaylord B, Reed DC, Williams SL, MacIntyre S (2008) Physical pathways and utilization of nitrate supply to the giant kelp, *Macrocystis pyrifera*. Limnol Oceanogr 53:1589–1603

Gerard VA (1982a) Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low-nitrogen environment. Mar Biol 66:27–35

Gerard VA (1982b) In situ rates of nitrate uptake by giant kelp, *Macrocystis pyrifera* (L.) C. Agardh: tissue differences, environmental effects, and predictions of nitrogen-limited growth. J Exp Mar Biol Ecol 62:211–224

González-Fragoso J, Ibarra-Obando SE, North WJ (1991) Frond elongation rates of shallow water *Macrocystis pyrifera* (L.) Ag. in northern Baja California Mexico. J Appl Phycol 3:311–318

Graham MH, Vasquez JA, Buschmann AH (2007) Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. Oceanogr Mar Biol Ann Rev 45:39–88

Haines KC, Wheeler PA (1978) Ammonium and nitrate uptake by the marine macrophytes *Hypnea musciformis* (rhodophyta) and *Macrocystis pyrifera* (phaeophyta). J Phycol 14:319–324

Han T, Qi Z, Huang H, Fu G (2017) Biochemical and uptake responses of the macroalga *Gracilaria lemaneiformis* under urea enrichment conditions. Aquatic Bot 136:197–204

Hepburn CD, Hurd CL, Frew RD (2006) Colony structure and seasonal differences in light and nitrogen modify the impact of sessile epifauna on the giant kelp *Macrocystis pyrifera* (L.) C Agardh. Hydrobiologia 560:373–384

Hepburn C, Holborow J, Wing S, Frew R, Hurd C (2007) Exposure to waves enhances the growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera*. Mar Ecol Prog Ser 339:99–108

Herbert RA (1999) Nitrogen cycling in coastal marine ecosystems. FEMS Microbiol Rev 23:563–590

Kim JK, Kraemer GP, Neefus CD, Chung IK, Yarish C (2007) Effects of temperature and ammonium on growth, pigment production and nitrogen uptake by four species of *Porphyra* (Bangiales, Rhodophyta) native to the New England coast. J Appl Phycol 19:431–440

Ladah LB, Filonov A, Lavín MF, Leichter JJ, Zertuche-González JA, Pérez-Mayorga DM (2012) Cross-shelf transport of sub-thermocline nitrate by the internal tide and rapid (3–6h) incorporation by an inshore macroalga. Continental Shelf Res 42:10–19

Ladah LB, Leichter JJ, Filonov A, Tereshchenko I (2017) Diurnal frequency internal waves in the southern part of the California Current ecosystem as a nutrient source. Cienc Mar 43:203–215

Legendre L, Gosselin M (1997) Estimation of N or C uptake rates by phytoplankton using ^{15}N or ^{13}C: revisiting the usual computation formulae. J Plankton Res 19:263–271

Lerczak JA, Hendershott MC, Winant CD (2001) Observations and modeling of coastal internal waves driven by a diurnal sea breeze. J Geophys Res: Oceans 106:19715–19729

Lucas AJ, Dupont CL, Tai V, Largier JL, Palenik B, Franks PJS (2011) The green ribbon: multiscale physical control of phytoplankton productivity and community structure over a narrow continental shelf. Limnol Oceanogr 56:611–626

McPhee-Shaw EE, Siegel DA, Washburn L, Brzezinski MA, Jones JL, Leydecker A, Melack J (2007) Mechanisms for nutrient delivery to the inner shelf: observations from the Santa Barbara Channel. Limnol Oceanogr 52:1748–1766

Messié M, Chavez FP (2015) Seasonal regulation of primary production in eastern boundary upwelling systems. Progr Oceanogr 134:1–18

Paerl HW, Dennis RL, Whitall DR (2002) Atmospheric deposition of nitrogen: implications for nutrient over-enrichment of coastal waters. Estuaries 25:677–693

Pedersen MF (1994) Transient ammonium uptake in the macroalga *Ulva lactuca* (Chlorophyta): nature, regulation, and the consequences for choice of measuring technique. J Phycol 30:980–986

Pedersen MF, Borum J (1997) Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. Mar Ecol Prog Ser 161:155–163

Pérez-Mayorga DM, Ladah LB, Zertuche-González JA, Leichter JJ, Filonov AE, Lavín MF (2011) Nitrogen uptake and growth by the opportunistic macroalga *Ulva lactuca* (Linnaeus) during the internal tide. J Exp Mar Biol Ecol 406:108–115

Peters JR, Reed DC, Burkepile DE (2019) Climate and fishing drive regime shifts in consumer-mediated nutrient cycling in kelp forests. Glob Change Biol 25:3179–3192

Phillips JC, Hurd CL (2004) Kinetics of nitrate, ammonium, and urea uptake by four intertidal seaweeds from New Zealand. J Phycol 40:534–545

Pineda J (1995) An internal tidal bore regime at nearshore stations along western U.S.A.: predictable upwelling within the lunar cycle. Continental Shelf Res 15:1023–1041

Raikar V, Wafar M (2006) Surge ammonium uptake in macroalgae from a coral atoll. J Exp Mar Biol Ecol 339:236–240

Rassweiler A, Reed DC, Harrer SL, Nelson JC (2018) Improved estimates of net primary production, growth, and standing crop of *Macrocystis pyrifera* in Southern California. Ecology 99:2132

Reed DC, Ebeling AW, Anderson TW, Anghera M (1996) Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. Ecology 77:300–316

Reed DC, Rassweiler A, Arkema KK (2008) Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology 89:2493–2505

Regnault M (1987) Nitrogen excretion in marine and fresh-water Crustacea. Biol Rev 62:1–24

Remsen CC (1971) The distribution of urea in coastal and oceanic waters. Limnol Oceanog 16:732–740

Rosenberg G, Probyn TA, Mann KH (1984) Nutrient uptake and growth kinetics in brown seaweeds: response to continuous and single additions of ammonium. J Exp Mar Biol Ecol 80:125–146

Ryther JH, Dunstan WM (1971) Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171:1008–1013

Schiel DR, Foster MS (2015) The biology and ecology of giant kelp forests. University of California Press, Oakland

Sharples J, Moore CM, Abraham ER (2001) Internal tide dissipation, mixing, and vertical nitrate flux at the shelf edge of NE New Zealand. J Geophys Res 106:14069–14081

Smith JM, Brzezinski MA, Melack JM, Miller RJ, Reed DC (2018) Urea as a source of nitrogen to giant kelp (*Macrocystis pyrifera*). Limnol Oceanogr Lett 3:365–373

Smith JM, Blasco G, Brzezinski MA, Melack JM, Reed DC, Miller RJ (2021) Factors influencing urea use by giant kelp (*Macrocystis pyrifera*, Phaeophyceae). Limnol Oceanogr 66:1190–1200

Stewart H, Fram J, Reed D, Williams S, Brzezinski M, MacIntyre S, Gaylord B (2009) Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA. Mar Ecol Prog Ser 375:101–112

Taylor DI, Nixon SW, Granger SL, Buckley BA (1999) Responses of coastal lagoon plant communities to levels of nutrient enrichment: a mesocosm study. Estuaries 22:1041–1056

Thomas TE, Harrison PJ (1987) Rapid ammonium uptake and nitrogen interactions in five intertidal seaweeds grown under field conditions. J Exp Mar Biol Ecol 107:1–8

Topinka JA, Robbins JV (1976) Effects of nitrate and ammonium enrichment on growth and nitrogen physiology in *Fucus spiralis*. Limnol Oceanogr 21:659–664

Van Tussenbroek BI (1989) Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falkland Islands. Mar Biol 100:419–430

Villamaña M, Mouriño-Carballido B, Marañón E, Cermeño P, Chouciño P, da Silva JCB, Díaz PA, Fernández-Castro B, Gilcoto M, Graña R, Latasa M, Magalhaes JM, Luis Otero-Ferrer J, Reguera B, Scharek R (2017) Role of internal waves on mixing, nutrient supply and phytoplankton community structure during spring and neap tides in the upwelling ecosystem of Ría de Vigo (NW Iberian Peninsula). Limnol Oceanogr 62:1014–1030

Washburn L, McPhee-Shaw E (2013) Coastal transport processes affecting inner-shelf ecosystems in the California Current System. Oceanography 26:34–43

Wheeler WN, Srivastava LM (1984) Seasonal nitrate physiology of *Macrocystis integrifolia* Bory. J Exp Mar Biol Ecol 76:35–50

Wheeler PA, North WJ, Keck WM (1981) Nitrogen supply, tissue composition and frond growth rates for *Macrocystis pyrifera* off the coast of Southern California. Mar Biol 64:59–69

Zimmerman RC, Kremer JN (1984) Episodic nutrient supply to a kelp forest ecosystem in Southern California. J Mar Res 42:591–604

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.