Urea as a source of nitrogen to giant kelp (*Macrocystis pyrifera*)

Jason M. Smith,1* Mark A. Brzezinski,1,2 John M. Melack,1,2,3 Robert J. Miller,1 Daniel C. Reed1

1Marine Science Institute, University of California, Santa Barbara, California; 2Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California; 3Bren School of Environmental Science and Management, University of California, Santa Barbara, California

Abstract

Nitrate concentrations routinely fall below levels required to sustain growth of giant kelp (*Macrocystis pyrifera*) during summer and autumn in the Santa Barbara Channel, yet growth continues. We found urea to be consistently present at concentrations of 0.48–1.82 μM, accounting for greater than 20% of the dissolved fixed nitrogen pool during summer (14% overall). Field experiments indicate direct uptake of urea by giant kelp at a rate of 0.19 μmol N g dw⁻¹ h⁻¹, comparable to rates for ammonium (0.18 μmol N g dw⁻¹ h⁻¹) but lower than for nitrate (0.39 μmol N g dw⁻¹ h⁻¹). Co-occurring phytoplankton took up nitrate, urea, and ammonium, 2-, 15-, and 39-fold faster than giant kelp; however, the nitrogen uptake advantage of phytoplankton varies by substrate and season. Together, our results suggest that urea is readily used by giant kelp and may help to sustain growth throughout the year.

Introduction of inorganic nitrogen (N) into coastal and oceanic systems is often met by concomitant increases in phytoplankton growth (Gruber 2008); nitrate is particularly important, given its association with new production (e.g., Eppley and Peterson 1979) and runoff-driven algal growth (Conley et al. 2009). Seasonal and interannual variations are also linked to nitrate availability in coastal upwelling systems (Messié et al. 2009), which could lead one to presume...
nitrate is important to sustaining the growth of all autotrophs in these environments. However, primary producers in upwelling and other coastal systems comprise a diverse range of autotrophs (Mann 1973), with growth strategies that differ from phytoplankton.

Giant kelp (Macrocystis sp.), the largest of the seaweeds, grows in dense forests off of North and South America, South Africa, Australia, and New Zealand (Graham et al. 2007). Along the coast of southern California, where kelp forests are dominated by Macrocystis pyrifera, the processes that deliver nitrate to kelp forests have strong seasonality (McPhee-Shaw et al. 2007), characterized by periods of low nitrate availability from July through November (Brzezinski et al. 2013) and sometimes longer (Parnell et al. 2010; Reed et al. 2016). Phytoplankton biomass fluctuates in response to variations in nitrate availability during these periods (Brzezinski and Washburn 2011; Goodman et al. 2012; Gómez-Ocampo et al. 2017). Giant kelp, in contrast, appears to maintain growth year around (Brzezinski et al. 2013), for reasons that are not well understood. We hypothesize that kelp sustain their growth in a manner similar to many marine phytoplankton (Mulholland and Lomas 2008), by accessing a larger range of nitrogenous compounds than ammonium and nitrate, the two primary forms examined to date.

The dissolved fixed nitrogen (DFN) pool in most aquatic environments is made up of three major components: ammonium, nitrate, and dissolved organic nitrogen (DON) (Gruber 2008). DON represents the largest pool of fixed nitrogen in many aquatic systems, with urea and amino acids considered the most readily available components for uptake (Berman and Bronk 2003). Urea is of particular interest as a potential source of N to giant kelp because it is linked to excretion by common marine consumers (Regnault 1987). Marine phytoplankton readily use urea to support their growth (Mulholland and Lomas 2008), at times preferring it over ammonium or nitrate (Horrigan and McCarthy 1982). Unlike for phytoplankton, evidence of urea use by most seaweeds, including giant kelp is limited. A number of studies confirm uptake of N from urea into seaweed biomass (Phillips and Hurd 2004; Tyler et al. 2005; Han et al. 2017, 2018; Ross et al. 2018), but whether this is following extracellular decomposition or by uptake of the entire molecule remains unclear.

In this study, we tested the potential for urea to serve as a source of N to giant kelp and phytoplankton during periods when the concentration of nitrate is low, by measuring monthly concentrations of nitrate, ammonium, and urea in surface waters adjacent to five giant kelp forests off the coastal of Santa Barbara, California, U.S.A., and performing field and laboratory experiments to determine whether urea uptake by giant kelp occurs, how its use compares to rates of ammonium and nitrate uptake, and how interactions with phytoplankton influence the ability of giant kelp to capture a particular N substrate.

Methods

Nearshore patterns of dissolved nitrogen availability

Monthly water samples were collected for nutrient analysis using Go-Flo bottles at 1 m and 5 m depth, < 50 m from the offshore edge of five giant kelp forests near Santa Barbara, California, U.S.A. (Fig. 1) (Washburn et al. 2018). Seawater (0.2 μm filtered) concentrations of ammonium and combined nitrate + nitrite (NO$_3^-$ + NO$_2^-$) were determined using flow injection techniques (http://msi.ucsb.edu/services/analytical-lab/seawater-nutrients-fia). The detection limit for both nitrate + nitrite (NO$_3^-$ + NO$_2^-$) and ammonium (NH$_4^+$) was 0.1 μM. For simplicity, the sum of NO$_3^-$ + NO$_2^-$ will hereafter be referred to as nitrate because nitrite in Santa Barbara Channel is typically < 0.2 μM in surface waters. Total dissolved nitrogen (referred to here as dissolved fixed nitrogen or DFN) was determined by flow injection measurement of nitrate + nitrite concentrations following persulfate digestion (Valderrama 1981). Urea concentrations were measured colorimetrically following the procedure described by Goeyens.
et al. (1998). The lower limit of detection for the assay was 0.05 \( \mu \text{M urea-N} \) (0.025 \( \mu \text{M urea} \)). All values for urea concentration are reported in terms of \( N \), concentrations of the urea molecule would be half the values reported here, as urea contains two \( N \) atoms (i.e., 1 \( \mu \text{M urea} = 2 \mu \text{M urea-N} \)).

**Dissolved nitrogen uptake**

In situ rates of \( N \) uptake by giant kelp blades and phytoplankton were measured during 4 h incubations conducted from \( \sim 10:00-14:00 \) h (local time) (Smith et al. 2017). Mature, epiphyte-free giant kelp blades were enclosed in clear polyethylene bags equipped with sampling ports, as described by Reed et al. (2015). Each bag was filled with ambient seawater from the upper 1 m of the canopy. Bags were then slipped over individual giant kelp blades and sealed with a cable tie at the base of the pneumocystoc. Each experiment consisted of the following treatments: Control (no tracer), \( ^{15}\text{NH}_4 \), \( ^{15}\text{N-urea} \), and (on two occasions) \( ^{15}\text{NO}_3 \) (\( N = 7 \) blades per treatment).

Experiments were started by injection of \( > 99 \) atom percent \( ^{15}\text{N-urea} \) (10 \( \mu \text{M} \)), \( ^{15}\text{NH}_4 \) (10 \( \mu \text{M} \)) or \( ^{15}\text{NO}_3 \) (20 \( \mu \text{M} \)) into each bag. Water samples (60 mL, 0.3 \( \mu \text{M} \) filtered) were taken by syringe before and after tracer addition and at the end of the experiment. Blades were severed from fronds at the end of the experiment, transported to the laboratory in a cooler and stations, ranged from 0.48 \( \pm 0.1 \) \( \mu \text{M} \) to 1.82 \( \pm 0.39 \ \mu \text{M} \) and varied from the overall average of 1.06 \( \pm 0.09 \ \mu \text{M} \), with no apparent seasonality (Fig. 2A). The only environmental variable measured at the time of sampling that correlated with urea concentration was temperature; however, it explained only a small fraction of the variability (\( R^2 = 0.16; p < 0.001 \)).

Concentrations of DFN, ammonium, and nitrate were quantified in order to better assess the potential importance of urea as a nitrogen source. Average (\( \pm 1 \) SE) DFN concentrations showed no seasonality, varying 6.8 \( \mu \text{M} \) to 10.5 \( \mu \text{M} \) about the overall mean of 8.5 \( \pm 0.3 \ \mu \text{M} \). The contribution of all three constituents (ammonium, nitrate, urea) to the DFN pool varied temporally. Urea comprised 7–23% of DFN, with some of the highest contributions occurring during spring and summer (Fig. 2B). Opposite that of nitrate (concentration range: 0.1–2.1 \( \mu \text{M} \)), which tended to make up <1% of DFN during summer months and as much as 25% during winter. No temporal patterns in ammonium concentrations (range: 0.2–1.3 \( \mu \text{M} \)) or its contribution to DFN, ranging 3–19%, were evident.

**Results**

**Time series of DFN and its constituents**

Urea was consistently detected in all water samples (\( n = 180 \)). Monthly means (\( \pm 1 \) SE) averaged over all depths and stations, ranged from 0.48 \( \pm 0.1 \) \( \mu \text{M} \) to 1.82 \( \pm 0.39 \ \mu \text{M} \) and varied from the overall average of 1.06 \( \pm 0.09 \ \mu \text{M} \), with no apparent seasonality (Fig. 2A). The only environmental variable measured at the time of sampling that correlated with urea concentration was temperature; however, it explained only a small fraction of the variability (\( R^2 = 0.16; p < 0.001 \)).

Concentrations of DFN, ammonium, and nitrate were quantified in order to better assess the potential importance of urea as a nitrogen source. Average (\( \pm 1 \) SE) DFN concentrations showed no seasonality, varying 6.8 \( \mu \text{M} \) to 10.5 \( \mu \text{M} \) about the overall mean of 8.5 \( \pm 0.3 \ \mu \text{M} \). The contribution of all three constituents (ammonium, nitrate, urea) to the DFN pool varied temporally. Urea comprised 7–23% of DFN, with some of the highest contributions occurring during spring and summer (Fig. 2B). Opposite that of nitrate (concentration range: 0.1–2.1 \( \mu \text{M} \)), which tended to make up <1% of DFN during summer months and as much as 25% during winter. No temporal patterns in ammonium concentrations (range: 0.2–1.3 \( \mu \text{M} \)) or its contribution to DFN, ranging 3–19%, were evident.

**In situ uptake of urea, ammonium, and nitrate by giant kelp and phytoplankton**

Nutrient concentrations in blade bags were determined at the start of each experiment (prior to isotope tracer addition). Nitrate concentration was <0.3 \( \mu \text{M} \) during all experiments except December when it was 1.4 \( \pm 0.1 \ \mu \text{M} \). Urea-N ranged from 0.5 \( \pm 0.1 \ \mu \text{M} \) to 1.0 \( \pm 0.2 \ \mu \text{M} \), within the range observed for ammonium (0.4 \( \pm 0.1 \ \mu \text{M} \) to 1.7 \( \pm 0.2 \ \mu \text{M} \)). Nitrogen content of giant kelp blades in control bags ranged from 0.9% to 2% of dry weight.

Uptake of urea-N by giant kelp blades was detected during all experiments, with the lowest rate observed in July and
the highest in March (Fig. 3A). Similar patterns of uptake were observed for ammonium. Nitrate was taken up by giant kelp blades at a rate that was approximately twice that of urea and ammonium during December and then again in March. Across all experiments, rates ($q$) of urea uptake ($0.19 \pm 0.03$ $\mu$mol N g dw$^{-1}$ h$^{-1}$) were similar to those of ammonium ($0.18 \pm 0.06$ $\mu$mol N g dw$^{-1}$ h$^{-1}$), both of which were lower than rates of nitrate uptake ($0.39 \pm 0.01$ $\mu$mol N g dw$^{-1}$ h$^{-1}$).

Urea, ammonium, and nitrate were consistently taken up by planktonic organisms (phytoplankton, microorganisms > 0.3 $\mu$m; hereafter referred to as phytoplankton) during our experiments, however, in ways that varied inversely from those of giant kelp. In contrast to giant kelp, the uptake of urea (range: $8.0 \times 10^{-4} \pm 4 \times 10^{-5}$ h$^{-1}$ to $23.6 \times 10^{-4}$ h$^{-1}$) and ammonium (range: $16.1 \times 10^{-4} \pm 2.64 \times 10^{-4}$ h$^{-1}$ to $52.9 \times 10^{-4}$ h$^{-1}$) by phytoplankton was greatest in July and August and lowest in March. Moreover, the uptake of nitrate (range: $2.3 \times 0.39 \times 10^{-4}$ $\mu$mol L$^{-1}$ h$^{-1}$ to $2.7 \times 0.36 \mu$mol L$^{-1}$ h$^{-1}$) by plankton was substantially lower than that of urea and ammonium during December and March, opposite the pattern observed for giant kelp.

Specific uptake rates ($V$) for giant kelp and phytoplankton varied with the form of N and the date of the experiment. Phytoplankton rates ranged fourfold across N forms, from $(\pm 1$ SE $) 8 \times 10^{-4} \pm 4 \times 10^{-5}$ h$^{-1}$ for nitrate to $3 \times 10^{-3} \pm 2 \times 10^{-4}$ h$^{-1}$ for urea and ammonium, and $2 \times 10^{-3}$ h$^{-1}$ for nitrate.

Fig. 2. Time series of average monthly (A) dissolved urea-N concentrations and (B) relative contributions of urea, ammonium, and nitrate + nitrite to the DFN pool. Error bars represent the standard error about each monthly mean.

Fig. 3. Box and whisker plot showing (A) rates of urea, ammonium, and nitrate uptake by kelp and (B) ratios of specific uptake rates ($V$) for phytoplankton and kelp for urea, ammonium, and nitrate during four in situ experiments. Data in panel B are plotted on a Log$_{10}$ axis to emphasize order of magnitude differences. Whiskers show the full range of data; boxes show the 25–75% range, and the horizontal line is the mean.
for urea. Nitrate uptake averaged $3 \times 10^{-4} \pm 4 \times 10^{-5}$ h$^{-1}$, comparable to urea ($2 \times 10^{-4} \pm 3 \times 10^{-5}$ h$^{-1}$) and ammonium ($2 \times 10^{-4} \pm 2 \times 10^{-5}$ h$^{-1}$). Specific uptake rates of phytoplankton exceeded those of giant kelp, irrespective of N form or experiment (Fig. 3B). However, the degree to which phytoplankton rates exceeded those of giant kelp for different N forms varied considerably, from a low of 1.3 $\pm$ 0.1-fold higher for nitrate in March to a high of 52 $\pm$ 6-fold for ammonium in July.

**Direct urea uptake by giant kelp and phytoplankton**

Rates of urea uptake measured following exposure of giant kelp blades to 10 $\mu$M $^{13}$C,$^{15}$N-urea for 15 min and up to 4 h were used to assess the potential for direct urea uptake. Urea contains a single carbon and two nitrogen atoms. Therefore, if the entire molecule is taken up, and the C and N components remain in the cells, the ratio of urea uptake calculated based on $^{13}$C and $^{15}$N tissue enrichments should be two. Nevertheless, ratios well above or below two do not negate the possibility of direct uptake, particularly over time scales of minutes when the likelihood of urea being broken down and taken up in parts is very low.

$^{15}$N and $^{13}$C enrichment was detected in giant kelp tissues and in surface-water particles. Mean rates of uptake based on $^{15}$N and $^{13}$C enrichment were fairly consistent for giant kelp, varying only 1.4- and 1.6-fold between experiments, respectively. The overall mean ($\pm$ 1 SE) ratio (N : C) of urea uptake rates for our experiments was 1.95 $\pm$ 0.01, close to the expected value of 2 for direct uptake. Phytoplankton uptake of $^{15}$N and $^{13}$C from urea was also detected in all experiments. Rates tended to be more variable than for giant kelp; N-based rates of urea uptake decreased twofold across experiments, while $^{13}$C-based rates decreased 2.9-fold (Table 1). The ratio of urea uptake based on $^{15}$N and $^{13}$C enrichment in particles was greater than two in all experiments (average = 3.98 $\pm$ 0.59).

**Discussion**

Urea is found in a variety of aquatic environments (Berman and Bronk 2003), a condition unlikely to be reversed given its global use as a fertilizer (Gilbert et al. 2006). Here we report urea to be a readily available N substrate in nearshore waters of the Santa Barbara Channel (Fig. 2A), that accounts for a substantial (14% $\pm$ 1%) portion of DFN—exceeding, on average, ammonium (7% $\pm$ 1%) and nitrate (7% $\pm$ 2%), the most widely studied forms of DFN (the remainder of the pool is comprised of uncharacterized non-urea DON). While we do acknowledge the pitfalls of using concentration to infer flux, the consistent (Fig. 2A), and relatively high (Fig. 2B) concentrations of urea in the Santa Barbara Channel (Fig. 1) introduce the potential for it to be an important N source to support primary production.

Urea use by phytoplankton is well documented (Mulholland and Lomas 2008) but its use by seaweeds is understudied. It has been shown to be a source of N to Ulva lactuca (Tyler et al. 2005) and other intertidal seaweeds (Phillips and Hurd 2003). However, the kelp Ecklonia maxima appears to use only ammonium and nitrate (Probyn and McQuaid 1985). In contrast, our field experiments indicate urea to be a consistent source of N to the giant kelp, _M. pyrifera_, throughout the year (Fig. 3A).

An important question is whether N from urea is acquired by direct uptake of the molecule or indirectly following decomposition, because direct uptake represents a diversification in metabolism and a potential competitive advantage, whereas the indirect pathway is a usual aspect of regenerated N uptake (Solomon et al. 2010). The distinction has been made for many phytoplankton and microbes but not for seaweeds (Mulholland and Lomas 2008; Solomon et al. 2010). The results of our laboratory experiments indicate both N and C from urea are incorporated into giant kelp and phytoplankton tissues (Table 1). Rates of urea uptake, calculated from $^{15}$N enrichment were approximately twofold higher than those based on $^{13}$C enrichment of giant kelp blade tissues, indicating direct uptake of the urea molecule (Table 1). Once in the cell, urea must be processed into a useable form before it can be used in biosynthesis. Many organisms, including some seaweeds (Bekheet and Syrett 1977; Bekheet et al. 1984), do so using the enzyme urease. Urease activity in _M. pyrifera_ has not been documented, but our results predict its presence.

Nitrogen- and carbon-based urea uptake rates for phytoplankton consistently diverged from the expected ratio of 2 throughout the experiment, a common result of field studies comparing uptake of urea C and N by phytoplankton (e.g.,

### Table 1. Results of direct urea uptake experiments with giant kelp blades and phytoplankton. Rates were calculated from $^{13}$C and $^{15}$N enrichment of tissues following exposure to 10 $\mu$M $^{15}$N,$^{13}$C-urea for periods of minutes to hours.

| Time  | N-based rate (mol g dw$^{-1}$ h$^{-1}$) | C-based rate (mol g dw$^{-1}$ h$^{-1}$) | Ratio (N : C) | N-based rate (mol L$^{-1}$ h$^{-1}$) | C-based rate (mol L$^{-1}$ h$^{-1}$) | Ratio (N : C) |
|-------|--------------------------------------|--------------------------------------|--------------|--------------------------------------|--------------------------------------|--------------|
| 15 min | 3.71 $\pm$ 0.13*                     | 2.06 $\pm$ 0.02                      | 1.80 $\pm$ 0.08 | 9.54 $\pm$ 0.69                      | 2.78 $\pm$ 0.40                      | 3.43 $\pm$ 0.66 |
| 45 min | 3.20 $\pm$ 0.21                      | 1.76 $\pm$ 0.12                      | 1.92 $\pm$ 0.01 | 6.71 $\pm$ 0.05                      | 2.04 $\pm$ 0.26                      | 3.28 $\pm$ 0.37 |
| 4 h    | 2.72 $\pm$ 0.34                      | 1.27 $\pm$ 0.34                      | 2.14 $\pm$ 0.05 | 4.97 $\pm$ 0.57                      | 0.95 $\pm$ 0.05                      | 5.23 $\pm$ 0.54 |

*Values are the standard error about the mean.
The possibility exists that some of the $^{13}$C and $^{15}$N enrichment in kelp and phytoplankton is due to incorporation of $^{15}$N- and $^{13}$C-labeled compounds produced by in vitro decomposition of urea, particularly with increasing incubation time (Table 1). The likelihood of the N- and C-based urea uptake rates being ~2 or even consistent over time, as observed for giant kelp (Table 1), is much less likely if this is the primary mechanism by which the tissues become $^{13}$C and $^{15}$N enriched. Following processing by extracellular ureases, the CO$_2$ from urea would enter a dissolved inorganic carbon pool that is several orders of magnitude larger than that of the ammonium pool, where urea-N would initially end up (Gruber 2008). In other words, the probability of uptake of a $^{13}$C-labeled carbon molecule is substantially lower than that for a $^{15}$N, were the majority of urea to first be subject to extracellular decomposition.

The ability of giant kelp to exploit urea as a source of N broadens our understanding of the factors influencing its growth. Contrary to prior evidence of resource selectivity in seaweeds (Probyn and McQuaid 1985; Harrison and Hurd 2001), urea uptake rates were similar in magnitude to those for ammonium, typically the preferred N substrate for primary producers (Harrison and Hurd 2001; Mulholland and Lomas 2008) and twofold lower than those for nitrate (Fig. 3A). While we have not demonstrated a direct linkage between urea use and giant kelp growth, these data, together with the time series results (Fig. 2A), introduce the possibility of urea being an important source of N for sustaining kelp productivity and growth.

The potential importance of urea to giant kelp stems from long-term monitoring of giant kelp growth in the Santa Barbara Channel. Prior research indicates giant kelp to have a limited capacity to store N (Gerard 1982a) and that net growth is sustained only when ambient “available” N concentrations are >1 μM (Gerard 1982b). Off the coast of Santa Barbara, this demand is easily met during winter and spring when rates of advective nitrate supply are highest (McPhee-Shaw et al. 2007). However, it is difficult to rectify how giant kelp sustain their growth during summer and autumn (Reed et al. 2008) when nitrate availability is consistently below the growth threshold (Fram et al. 2008; Brzezinski et al. 2013). It is during this period that urea could potentially be an important source of N to giant kelp. However, urea is probably not the sole underlying factor in sustained kelp growth during periods of low N availability. Giant kelp plants may also alter their growth strategy (Stephens and Hepburn 2016) and gain N in the form of ammonium from epibions that often colonize their tissues (Gerard 1982b; Hepburn and Hurd 2005; Hepburn et al. 2012).

Because our data suggest that the availability of urea is not strongly coupled to that of nitrate, or to the advective processes that deliver nitrate to giant kelp forests (McPhee-Shaw et al. 2007), a potential role for urea in sustaining giant kelp growth seems plausible during the 2014–2016 El Niño event, which led to the influx and prolonged residence of warm, nutrient-poor waters in the northeastern Pacific Ocean (Di Lorenzo and Mantua 2016) including the shallow coastal waters inhabited by giant kelp (Reed et al. 2016). As expected, a concomitant decline in planktonic primary productivity was observed during this period (Gómez-Ocampo et al. 2017). Surprisingly, giant kelp biomass remained within its historical range (Reed et al. 2016), despite being believed to be sensitive to prolonged exposure to warm, low nutrient waters (Graham et al. 2007). Urea may also be an important N source to M. pyrifera off of New Zealand, where, at times, growth appears to be decoupled from nitrate availability (e.g., Stephens and Hepburn 2014).

In many aquatic environments, the growth of phytoplankton and macroalgae is constrained by the availability of “accessible” N forms (Harrison and Hurd 2001; Gruber 2008). Our results show that giant kelp and phytoplankton utilize the same major forms of DFN, suggesting that they may compete for the same sources of N. In agreement with prior theoretical assertions (Hein et al. 1995), our data indicate phytoplankton are more efficient than giant kelp in taking up ammonium, nitrate, and urea. However, the uptake advantage of phytoplankton over giant kelp appears to vary by substrate type and time of year (Fig. 3B). The size and structure of phytoplankton communities are temporally variable in many aquatic environments which may also influence N demand or preference for a given substrate (Mulholland and Lomas 2008). Spatial and temporal variations in seaweed N metabolism are not well understood. However, our data suggest a lack of preference for a given N substrate and a relative consistency in rates of N acquisition (Fig. 3A). This contrasts with the often-plastic physiological response to changing nutrient availability found in terrestrial plants (Hodge 2004), and suggests that the degree of environmental heterogeneity and plasticity costs do not favor this strategy in giant kelp (Menge et al. 2011). Future work should focus on understanding the environmental and biological factors that influence the outcome of resource competition between planktonic and sessile primary producers, with a goal of developing more comprehensive models through which we interpret aquatic primary production.

**References**

Andersson, M. I., P. van Rijswijk, and J. J. Middelburg. 2006. Uptake of dissolved inorganic nitrogen, urea and amino acids in the Scheldt estuary: Comparison of organic carbon and nitrogen uptake. Aquat. Microb. Ecol. **44**: 303–315. doi:10.3354/ame044303
Goeyens, L., N. Kindermans, M. Abu Yusuf, and M. Elskens. 1998. A room temperature procedure for the manual determination of urea in seawater. Estuar. Coast. Shelf Sci. 47: 415–418. doi:10.1006/ecss.1998.0357

Gómez-Ocampo, E., G. Gaxiola-Castro, R. Durazo, and E. Beier. 2017. Effects of the 2013–2016 warm anomalies on the California Current phytoplankton. Deep-Sea Res. Part II Top. Stud. Oceanogr. doi:10.1016/j.dsr2.2017.01.005

Goodman, J., M. A. Brzezinski, E. R. Halewood, and C. A. Carlson. 2012. Sources of phytoplankton to the inner continental shelf in the Santa Barbara Channel inferred from cross-shelf gradients in biological, physical and chemical parameters Cont. Shelf Res. 48: 27–39. doi:10.1016/j.csr.2012.08.011

Graham, M. H., J. A. Vásquez, and A. H. Buschmann. 2007. Global ecology of the giant kelp Macrocystis: From ecotypes to ecosystems. Oceanogr. Mar. Biol. Ann. Rev. 45: 39–88. doi:10.1201/9781420050943.ch2

Gruber, N. 2008. The marine nitrogen cycle: Overview and challenges, p. 1–50. In D. G. Capone, D. A. Bronk, M. R. Mulholland, and E. J. Carpenter [eds.], Nitrogen in the marine environment. Academic Press.

Han, T., Z. Qi, H. Huang, and G. Fu. 2017. Biochemical and uptake responses of the macroalga Gracilaria lemaneiformis under urea enrichment conditions. Aquat. Bot. 136: 197–204. doi:10.1016/j.aquabot.2016.09.012

Han, T., Z. Qi, H. Huang, X. Liao, and W. Zhang. 2018. Nitrogen uptake and growth responses of seedlings of the brown seaweed Sargassum hemiphyllum under controlled culture conditions. J. Appl. Phycol. 30: 507. doi:10.1007/s10811-017-1216-1

Harrison, P. J., and C. L. Hurd. 2001. Nutrient physiology of seaweeds: Application of concepts to aquaculture. Cah. Biol. Mar. 42: 71–82. doi:10.1016/S0007-4243(04)00020-9

Hein, M., M. F. Pedersen, and K. San-Jensen. 1995. Size-dependent nitrogen uptake in micro- and macroalgae. Mar. Ecol. Prog. Ser. 118: 247–253. doi:10.3354/meps118247

Hepburn, C. D., and C. L. Hurd. 2005. Conditional mutualism between the giant kelp Macrocystis pyrifera and colonial epifauna. Mar. Ecol. Prog. Ser. 302: 37–48. doi:10.3354/meps302037

Hepburn, C. D., R. D. Frew, and C. L. Hurd. 2012. Uptake and transport of nitrogen derived from sessile epifauna in the giant kelp Macrocystis pyrifera. Aquat. Biol. 14: 121–128. doi:10.3354/ab00382

Hodge, A. 2004. The plastic plant: Root responses to heterogeneous supplies of nutrients. New Phytol. 162: 9–24. doi:10.1111/j.1469-8137.2004.01015.x

Horrigan, S. G., and J. J. McCarthy. 1982. Phytoplankton uptake of ammonium and urea during growth on oxidized forms of nitrogen. J. Plankton Res. 4: 379–389. doi:10.1093/plankt/4.2.379

Legendre, L., and M. Gosselin. 1996. 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. doi:10.1093/plankt/19.2.263
Mann, K. H. 1973. Seaweeds: Their productivity and strategy for growth. Science 182: 975–981. doi:10.1126/science.182.4116.975
McPhee-Shaw, E. E., D. A. Siegel, L. Washburn, M. A. Brzezinski, J. L. Jones, A. Leydecker, and J. Melack. 2007. Mechanisms for nutrient delivery to the inner shelf: Observations from the Santa Barbara Channel. Limnol. Oceanogr. 52: 1748–1766. doi:10.4319/lo.2007.52.5.1748
Menge, D. N. L., F. Ballantyne, IV, and J. S. Weitz. 2011. Dynamics of nutrient uptake strategies: Lessons from the tortoise and the hare. Theor. Ecol. 4: 163–177. doi:10.1007/s12080-010-0110-0
Messié, M., J. Ledesma, D. D. Kolber, R. P. Michisaki, D. G. Foley, and F. P. Chavez. 2009. Potential new production estimates in four eastern boundary upwelling ecosystems. Prog. Oceanogr. 83: 151–158. doi:10.1016/j.pocean.2009.07.018
Miller, R. J., D. C. Reed, and M. A. Brzezinski. 2011. Partitioning of primary production among giant kelp (Macrocystis pyrifera), understory macroalgae, and phytoplankton on a temperate reef. Limnol. Oceanogr. 56: 119–132. doi:10.4319/lo.2011.56.1.0119
Mulholland, M. R., G. Boneillo, and E. C. Minor. 2004. A comparison of N and C uptake during brown tide (Aureococcus anophagefferens) blooms from two coastal bays on the east coast of the USA. Harmful Algæ 3: 361–376. doi:10.1016/j.hal.2004.06.007
Mulholland, M. R., and M. W. Lomas. 2008. Nitrogen uptake and assimilation, p. 303–384. In D. G. Capone, D. A. Bronk, M. R. Mulholland, and E. J. Carpenter [eds.], Nitrogen in the marine environment. Academic Press.
Parnell, P. E., E. F. Miller, C. E. L. Cody, P. K. Dayton, M. L. Carter, and T. D. Stebbinsd. 2010. The response of giant kelp (Macrocystis pyrifera) in southern California to low-frequency climate forcing. Limnol. Oceanogr. 55: 2686–2702. doi:10.4319/lo.2010.55.6.2686
Phillips, J. C., and C. L. Hurd. 2003. Nitrogen ecophysiology of intertidal seaweeds from New Zealand: N uptake, storage and utilisation in relation to shore position and season. Mar. Ecol. Prog. Ser. 264: 31–48. doi:10.3354/meps264031
Phillips, J. C., and C. L. Hurd. 2004. Kinetics of nitrate, ammonium, and urea uptake by four intertidal seaweeds from New Zealand. J. Phycol. 40: 534–545. doi:10.1111/j.1529-8817.2004.03157.x
Price, N. M., and P. J. Harrison. 1988. Uptake of urea C and urea N by the coastal marine diatom Thalassiosira pseudonana. Limnol. Oceanogr. 33: 528–537. doi:10.4319/lo.1988.33.4.0528
Probyn, T. A., and C. D. McQuaid. 1985. In-situ measurements of nitrogenous nutrient uptake by kelp (Ecklonia maxima) and phytoplankton in a nitrate-rich upwelling environment. Mar. Biol. 88: 149–154. doi:10.1007/BF00397162
Reed, D., L. Washburn, A. Rassweiler, R. Miller, T. Bell, and S. Harrer. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. Nat. Commun. 7: 1–7. doi:10.1038/ncomms13757
Reed, D. C., A. Rassweiler, and K. K. Arkema. 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology 89: 2493–2505. doi:10.1890/07-1106.1
Reed, D. C., C. A. Carlson, E. R. Halewood, J. C. Nelson, S. L. Harrer, A. Rassweiler, and R. J. Miller. 2015. Patterns and controls of reef-scale production of dissolved organic carbon by giant kelp Macrocystis pyrifera. Limnol. Oceanogr. 60: 1996–2008. doi:10.1002/lio.10154
Regnault, M. 1987. Nitrogen excretion in marine and freshwater Crustacea. Biol. Rev. 62: 1–24. doi:10.1111/j.1469-185X.1987.tb00623.x
Ross, M. E., K. Davis, R. McColl, M. S. Stanley, J. G. Day, and A. J. C. Semião. 2018. Nitrogen uptake by the macro-algae Cladophora coelothrix and Cladophora parrilaudii: Influence on growth, nitrogen preference and biochemical composition. Algal Res. 30: 1–10. doi:10.1016/j.algal.2017.12.005
Smith, J., M. Brzezinski, J. Melack, R. Miller, and D. Reed. 2017. SBC LTER: Reef: Kelp Nitrogen uptake in Carpenteria and Mohawk kelp forests, 2016–2017. Environmental Data Initiative; [accessed 2018 April 26]. Available from https://doi.org/10.6073/pasta/a1fec15da1cb9ca108089e65d4da
Solomon, C. M., J. L. Collier, G. M. Berg, and P. M. Gilibert. 2010. Role of urea in microbial metabolism in aquatic systems: A biochemical and molecular review. Aquat. Microb. Ecol. 59: 67–88. doi:10.3354/ame01390
Stephens, T. A., and C. D. Hepburn. 2014. Mass-transfer gradients across kelp beds influence Macrocystis pyrifera growth over small spatial scales. Mar. Ecol. Prog. Ser. 515: 97–109. doi:10.3354/meps10974
Stephens, T. A., and C. D. Hepburn. 2016. A kelp with integrity: Macrocystis pyrifera prioritises tissue maintenance in response to nitrogen fertilisation. Oecologia 182: 71–84. doi:10.1007/s00442-016-3641-2
Tyler, A. C., K. J. McGlathery, and S. A. Macko. 2005. Uptake of urea and amino acids by the macroalgae Ulva Lactuca (Chlorophyta) and Gracilaria Vermiculophylla (Rhodophyta). Mar. Ecol. Prog. Ser. 294: 161–172. doi:10.3354/meps294161
Valderrama, J. C. 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural waters. Mar. Chem. 10: 109–122. doi:10.1016/0304-4203(81)90027-X
Washburn, L., M. Brzezinski, C. Carlson, and D. Siegel. 2018. SBC LTER: Ocean: Ocean currents and biogeochemistry: Nearshore water profiles (monthly CTD and chemistry). Environmental Data Initiative; [accessed 2018 March 12].
Available from https://doi.org/10.6073/pasta/5871aa141afe5d393af7483e658622c7

Acknowledgments
The authors thank Shannon Harrer, Janice Jones, and Clint Nelson for technical expertise and logistical support. Tiffany Cedeno, Michael DeNicola, Jordan Gallagher, Allie Kahler, Samuel Lewis, Heili Lowman, Maria McCausland, and Andrew Truong provided assistance with field experiments acquisition and sample analysis. The research was supported by the U.S. National Science Foundation’s Long Term Ecological Research program (OCE 9982105, 0620276, and 1232779).

Submitted 04 December 2017
Revised 13 March 2018
Accepted 24 April 2018