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LETTER

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. Reed* [1]

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

Scientific Significance Statement

The giant kelp (*Macrocystis pyrifera*), the largest of the seaweeds, grows in dense forests that form the basis for development of diverse, productive temperate reef ecosystems. Multiple lines of evidence indicate giant kelp growth continues unhindered during sustained periods when nitrate concentrations are low enough to cause declines in primary productivity. To date, the only forms of dissolved nitrogen known to be used by giant kelp are ammonium and nitrate. Here, we have shown urea to be a ubiquitous and abundant component of dissolved fixed nitrogen in a coastal upwelling zone containing giant kelp forests and that urea is readily used by giant kelp and phytoplankton, introducing the potential for it to be used year-round to support primary production by both groups.

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

*Correspondence: jmsmith@ucsb.edu

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Data Availability Statement: Data are available in the LTER Network Data repository at https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sbc.109.2 (urea uptake data) and https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sbc.10.22 (monthly water chemistry data).

Additional Supporting Information may be found in the online version of this article.

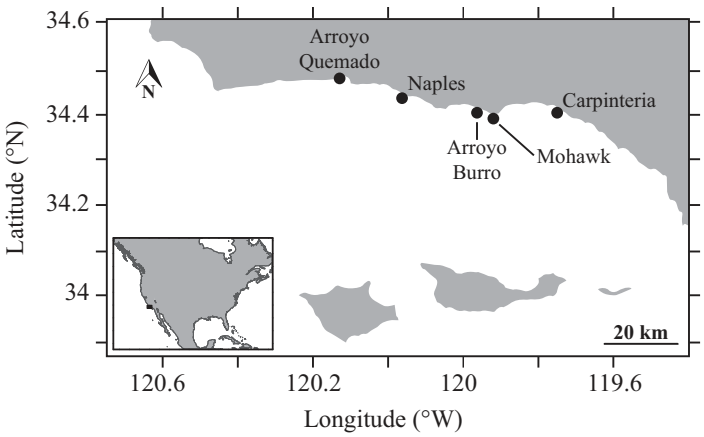

Fig. 1. Locations of kelp forest study sites off the coast of Santa Barbara, California, U.S.A. Monthly urea concentrations were measured at all sites. In situ uptake experiments were conducted at Mohawk (June 2016 and March 2017) and Carpinteria (August 2016 and December 2016).

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_x) 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 μM urea-N (0.025 μM 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 μM urea = 2 μM 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 ~ 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 pneumatocyst. Each experiment consisted of the following treatments: Control (no tracer), $^{15}NH_4^+$, ^{15}N-urea, and (on two occasions) $^{15}NO_3^-$ ($N = 7$ blades per treatment).

Experiments were started by injection of > 99 atom percent ^{15}N-urea (10 μM), $^{15}NH_4^+$ (10 μM) or $^{15}NO_3^-$ (20 μM) into each bag. Water samples (60 mL, 0.3 μm 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 within 1 h, then weighed, dried at 60°C for 72 h, reweighed, and ground to a fine powder. Water in each bag was transferred to acid-rinsed polycarbonate bottles and stored on ice. Particles were collected from ~ 0.5 L of seawater by filtration for analysis of chlorophyll or the concentration and isotopic composition of particulate organic carbon and particulate nitrogen, as described by Miller et al. (2011).

^{15}N uptake rates were determined based on accumulation of ^{15}N in giant kelp tissues or particulates (on filters) using the following equations (Dugdale and Wilkerson 1986):

$$V = \frac{(n_t - n_{t0})}{(n_S - n_{S0}) \times t}$$

$$\rho = V \times [\text{Tissue N}]$$

where V is the specific uptake rate (h^{-1}), n_t is the atom percent ^{15}N in the tissues at time (t), n_{t0} is the atom percent ^{15}N of tissues from control bags, n_S is the atom percent ^{15}N of the substrate pool following tracer addition, and n_{S0} is the atom percent ^{15}N enrichment of the ambient substrate pool, calculated by isotope mass balance based on concentrations in samples before and after tracer addition and assuming the ^{15}N activity of the unlabeled substrate pool to be that of nitrogen in air (0.3663 atom percent ^{15}N) (Legendre and Gosselin 1996). See the Supporting Information for calculation details.

The direct uptake and utilization of urea by giant kelp and phytoplankton

Direct urea uptake was tested by incubating surface water and whole giant kelp blades together in 10 L chambers fitted with recirculating aquarium pumps (40 L h^{-1} flow rate), under full spectrum LED lamps emitting ~ 1000 μmol m^{-2} s^{-1} of photosynthetically active radiation. Chambers were submerged in flowing seawater (~ 15°C) to control temperature. Experiments began upon addition of 10 μM ^{15}N,^{13}C-urea and ended upon the removal of blades and water samples (~ 1 L) after 15 min, 45 min, and 4 h (three blades per treatment). A parallel set of three control blades were incubated under the same conditions, except that no $^{15}N^{13}$C-urea was added. All samples for measurement of giant kelp and particle C and N concentrations and stable isotopes, dissolved macronutrients and urea were collected and analyzed as described above. ^{15}N and ^{13}C uptake rates were determined based on accumulation of tracer in giant kelp tissues or particulates using the equations of Dugdale and Wilkerson (1986). See the Supporting Information for calculation details.

Results

Time series of DFN and its constituents

Urea was consistently detected in all water samples ($n = 180$). Monthly means (± 1 SE) averaged over all depths and stations, ranged from 0.48 ± 0.1 μM to 1.82 ± 0.39 μM and varied from the overall average of 1.06 ± 0.09 μM, 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 (± 1 SE) DFN concentrations showed no seasonality, varying 6.8 μM to 10.5 μM about the overall mean of 8.5 ± 0.3 μM. 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 μM), 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 μM) 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 μM during all experiments except December when it was 1.4 ± 0.1 μM. Urea-N ranged from 0.5 ± 0.1 μM to 1.0 ± 0.2 μM, within the range observed for ammonium (0.4 ± 0.1 μM to 1.7 ± 0.2 μM). 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

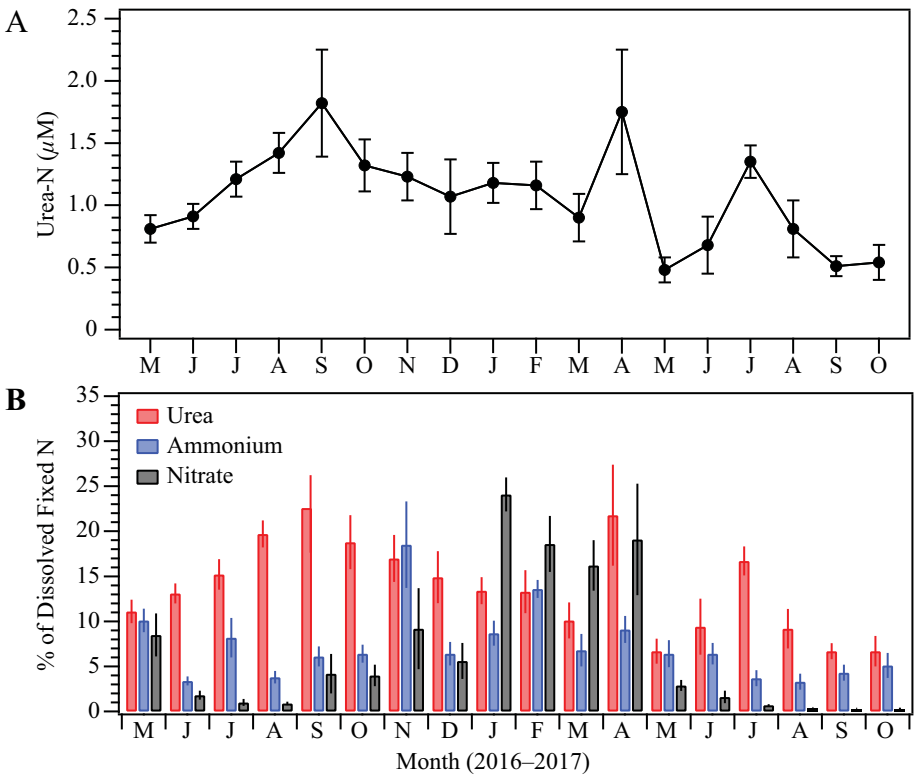

Fig. 2. Time series of average monthly (**A**) dissolved urea-N concentrations and (**B**) relative contributions of urea, ammonium, and nitrate + nitrite to the DFN pool. Error bars represent the standard error about each monthly mean.

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 (ρ) of urea uptake (0.19 ± 0.03 μmol N g dw^{-1} h^{-1}) were similar to those of ammonium (0.18 ± 0.06 μmol N g dw^{-1} h^{-1}), both of which were lower than rates of nitrate uptake (0.39 ± 0.01 μmol N g dw^{-1} h^{-1}).

Urea, ammonium, and nitrate were consistently taken up by planktonic organisms (phytoplankton, microorganisms > 0.3 μm; 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 ± 1 SE: 9.11 ± 1.47 μmol L^{-1} h^{-1} to 23.62 ± 7.17 μmol L^{-1} h^{-1}) and ammonium (range: 16.17 ± 2.64 μmol L^{-1} h^{-1} to 52.91 ± 5.24 μmol L^{-1} h^{-1}) by phytoplankton was greatest in July and August and lowest in March. Moreover, the uptake of nitrate (range: 2.33 ± 0.39 μmol L^{-1} h^{-1} to 2.71 ± 0.36 μmol 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 (± 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}

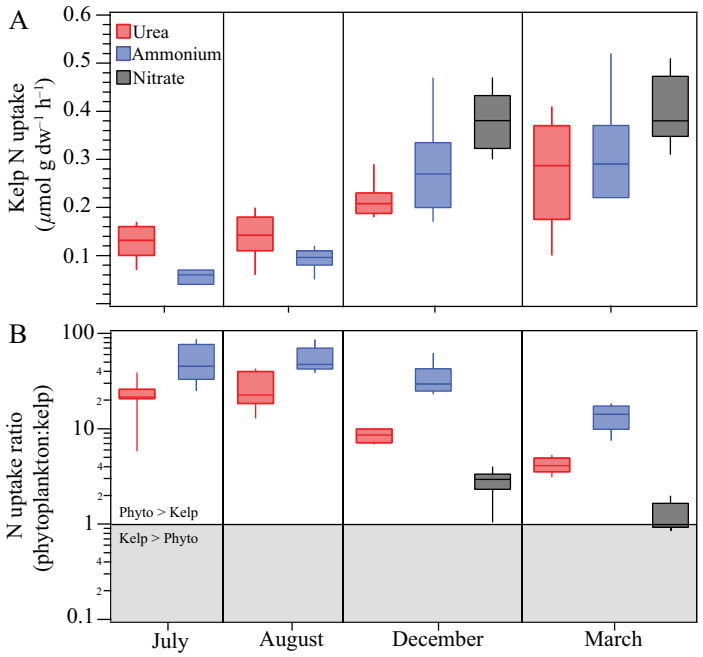

Fig. 3. Box and whisker plot showing (**A**) rates of urea, ammonium, and nitrate uptake by kelp and (**B**) ratios of specific uptake rates (V) for phytoplankton and kelp for urea, ammonium, and nitrate during four in situ experiments. Data in panel **B** are plotted on a Log_{10} axis to emphasize order of magnitude differences. Whiskers show the full range of data; boxes show the 25–75% range, and the horizontal line is the mean.

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 μM ^{15}N,^{13}C-urea for periods of minutes to hours.

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

*Values are the standard error about 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 ± 0.1-fold higher for nitrate in March to a high of 52 ± 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 μM ^{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 (± 1 SE) ratio (N : C) of urea uptake rates for our experiments was 1.95 ± 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 ± 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 (Glibert 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% ± 1%) portion of DFN—exceeding, on average, ammonium (7% ± 1%) and nitrate (7% ± 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.,

Mulholland et al. 2004; Fan and Glibert 2005; Andersson et al. 2006). More than likely the results reflect that not all planktonic taxa take up urea (Mulholland and Lomas 2008), and even those that do may not always retain its C and N constituents in a similar manner (Price and Harrison 1988). 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 1982*a*) and that net growth is sustained only when ambient "available" N concentrations are > 1 μM (Gerard 1982*b*). 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 epibionts that often colonize their tissues (Gerard 1982*b*; 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.

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