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# MULTIPLE SOURCES AND FORMS OF NITROGEN SUSTAIN YEAR-ROUND KELP GROWTH

on the Inner Continental Shelf of the Santa Barbara Channel

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Figure 1. An underwater  
view of a giant kelp forest  
in southern California.  
Photo credit: R. McPeak

**ABSTRACT.** Forests of the giant kelp *Macrocystis pyrifera* found on coastal rocky reefs lack the large reservoirs for nutrient storage found in many terrestrial environments. Supporting their high year-round growth rates requires a continuous supply of nitrogen. Complementary timing of nutrient supply associated with the physical processes that deliver nitrate to reefs largely achieves this goal, but modeling studies indicate that the magnitude of nitrate delivery is inadequate to support the measured nitrogen demand of kelp forests during summer. Ammonium, from sediment efflux and excretion by reef consumers, likely fills the deficit. Together, the varied sources of inorganic nitrogen supplied to kelp forests support their high growth rates throughout the year. Kelp compensates for diminished nitrogen supply during summer by decreasing tissue nitrogen content, resulting in a doubling of kelp C:N ratios.

## INTRODUCTION

The production of organic matter in an ecosystem and the flow of energy derived from it are critically dependent on an adequate supply of inorganic nutrients. Nutrient storage is a common feature on land where the supply of nutrients that fuels primary production is most often controlled by the local recycling of organic matter in soils. By contrast, most marine systems tend to have a low capacity for nutrient storage (mangrove forests, salt marshes, and seagrass meadows are exceptions). Instead, primary production in the ocean is most often governed by external processes (e.g., mixing, currents, wind, tides, runoff) that deliver nutrients from surrounding areas through water motion. Under these conditions, the magnitude and timing of primary production may be limited by the rate and timing of nutrient delivery.

Shallow coastal reefs in temperate seas are considered to be among the most productive systems on Earth, and they are typically dominated by fast-growing

species of macroalgae (Mann, 2000; Reed and Brzezinski, 2009). Dissolved inorganic nitrogen (DIN) most often limits macroalgal growth, and it can be supplied as either nitrate or ammonium, both of which are readily taken up by seaweeds (Haines and Wheeler, 1978). Fast-growing species of macroalgae typically have a limited capacity for internal nitrogen storage, and the rocky substrata upon which they grow offer little potential to sequester nitrogen. Consequently, the high net productivity of temperate

reefs is maintained primarily by a continuous, but variable, supply of nitrogen (N) from the surrounding ocean and adjacent landscape.

The giant kelp, *Macrocystis pyrifera*, is one of the most conspicuous inhabitants of shallow coastal reefs in the eastern Pacific and Southern Oceans (Graham et al., 2007). It is the world's largest alga; it attains lengths of over 30 m as multiple fronds consisting of stipes with leaflike blades extend from the seafloor to the sea surface to produce a floating canopy (Figure 1). Aggregations of giant kelp form extensive forests whose iconic stature is recognized throughout the world. Growth of *M. pyrifera* in temperate zones occurs year-round (Gerard, 1976; van Tüssenbroek, 1993; Reed et al., 2008; Stewart et al., 2009), and the elongation rates of individual fronds can exceed 50 cm per day, which is among the fastest measured for any autotroph on land or in the ocean (Clendenning, 1971). The rapid growth of giant kelp and the dynamic oceanographic environment

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in which it lives dictate frequent and sustained measurements of growth and ocean physics in order to understand the processes delivering the nitrogen needed to sustain its growth throughout the year. Long-term research on giant kelp forests in the Santa Barbara Channel is contributing to significant advances in our understanding of giant kelp growth patterns and the environmental processes that control them.

## KELP NITROGEN DYNAMICS

Most in situ studies of nitrogen dynamics have focused on nitrate as the major form of DIN supporting the growth of *Macrocystis pyrifera* (Gerard, 1982a,b; Brown, 1997; Fram et al., 2008). A sense of the nitrate levels required to support giant kelp can be gained from in situ measurements of the alga's half-saturation constant for nitrate uptake (i.e., the nitrate concentration required to support uptake rates that are 50% of the

organism's physiological maximum). That value for giant kelp is  $2\text{--}3\ \mu\text{mol L}^{-1}\ \text{NO}_3^-$  (Gerard, 1982b), suggesting that nitrate must reach quite low levels before the kelp nitrate uptake rate becomes severely limited by its ambient concentration. That inference is consistent with model predictions that  $\text{NO}_3^-$  concentrations below  $1\text{--}2\ \mu\text{mol L}^{-1}$  cannot sustain growth rates that are typical of mainland populations of *M. pyrifera* in southern California (Gerard, 1982b). Much like other shallow reefs in southern California (Wheeler and North, 1981), seasonality in nitrate concentration on reefs in the Santa Barbara Channel is strong, with the highest concentrations during March and April when levels can exceed  $20\ \mu\text{mol L}^{-1}$  (Figure 2A). Concentrations may decline to less than the  $1\ \mu\text{mol L}^{-1}$  growth threshold at any time of the year, but do so most frequently during July through November when concentrations average  $< 0.5\ \mu\text{mol L}^{-1}$  (Figure 2A). Our 10-year time series of monthly estimates of the growth rate of the standing biomass of giant kelp at three reefs shows strong variability among years and reefs, but no noticeable decline during summer and autumn (Figure 2B), despite sustained low mean nitrate concentration during this time of year (Figure 2A). Instead, the lowest growth rates were most frequently observed during winter when nitrate concentrations tended to be higher and light levels lower.

The nitrogen content of blades can be a useful index of the physiological status of giant kelp relative to nitrogen (Zimmerman and Kremer, 1986). Seasonality in the nitrogen content of kelp blades at our long-term study sites in the Santa Barbara Channel resembles that of the nitrate concentration in the

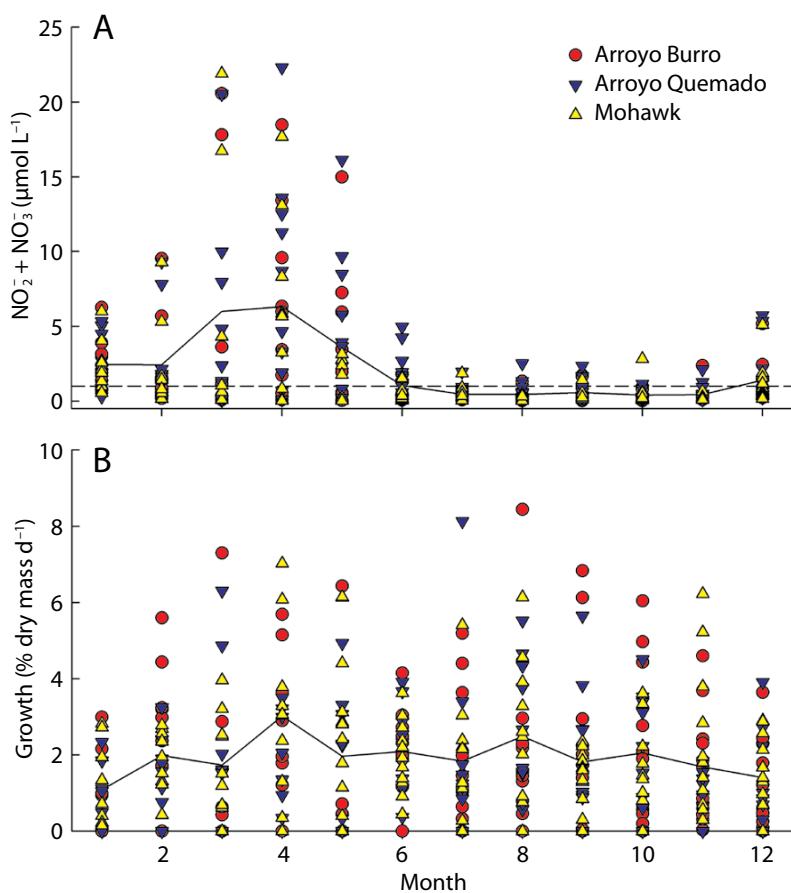


Figure 2. Annual cycle of (A) the average of the sum of nitrate and nitrite concentration (nearly 100% nitrate; each point is an average of measurements from two to three samples distributed vertically over the 10–15 m water column at each site), and (B) growth rate of the standing biomass of giant kelp as determined using the methods of Rassweiler et al. (2008). Individual data points are monthly measurements from 2002 through 2012 at the Arroyo Burro, Arroyo Quemado, and the Mohawk kelp forests. Solid lines represent the monthly means averaged over 11 years.

surrounding seawater with considerable interannual variability: a peak in spring and a minimum in summer and autumn (compare Figures 2A and 3A). Kelp survival is compromised when the nitrogen content of blades declines to less than 1% of dry mass, which indicates a depletion of internal nitrogen reserves (Gerard, 1982a). Surprisingly, this depletion was evident in only five of 360 measurements in 10 years of observation at our three study sites (Figure 3A).

Seasonal changes in blade nitrogen are decoupled from those of blade carbon, potentially altering the quality of kelp as a food resource to consumers across seasons. Much like blade nitrogen, blade carbon can vary among sites and years (Figure 3B). However, in contrast to nitrogen, blade carbon displays little seasonality, averaging about 30% of dry weight throughout the year (Figure 3B). The net result is that the mean monthly C:N mass ratio of kelp reaches an annual minimum of 10.3 when nitrate is abundant in April and May and increases to an annual maximum of 19.7 when nitrate is deficient in October (Figure 3C). The seasonal shifts in %N and in C:N mass ratio imply diminished nutritional value of giant kelp to consumers in fall when %N is low and C:N is high.

Our observations of kelp elemental composition and growth rate share the unusual feature of a large number of instances of relatively high growth rate and of high relative nitrogen content when ambient average nitrate levels are  $< 1 \mu\text{mol L}^{-1}$  (Figure 4). Others have observed similar patterns for the elongation rates of individual fronds in shorter time series and have suggested that other forms of nitrogen (e.g., ammonium)

may contribute to the nutritional needs of giant kelp (Wheeler and North, 1981; Gerard, 1982a; Zimmerman and Kremer,

1984). To help resolve this apparent discrepancy between nitrate concentration and the growth and N content of giant

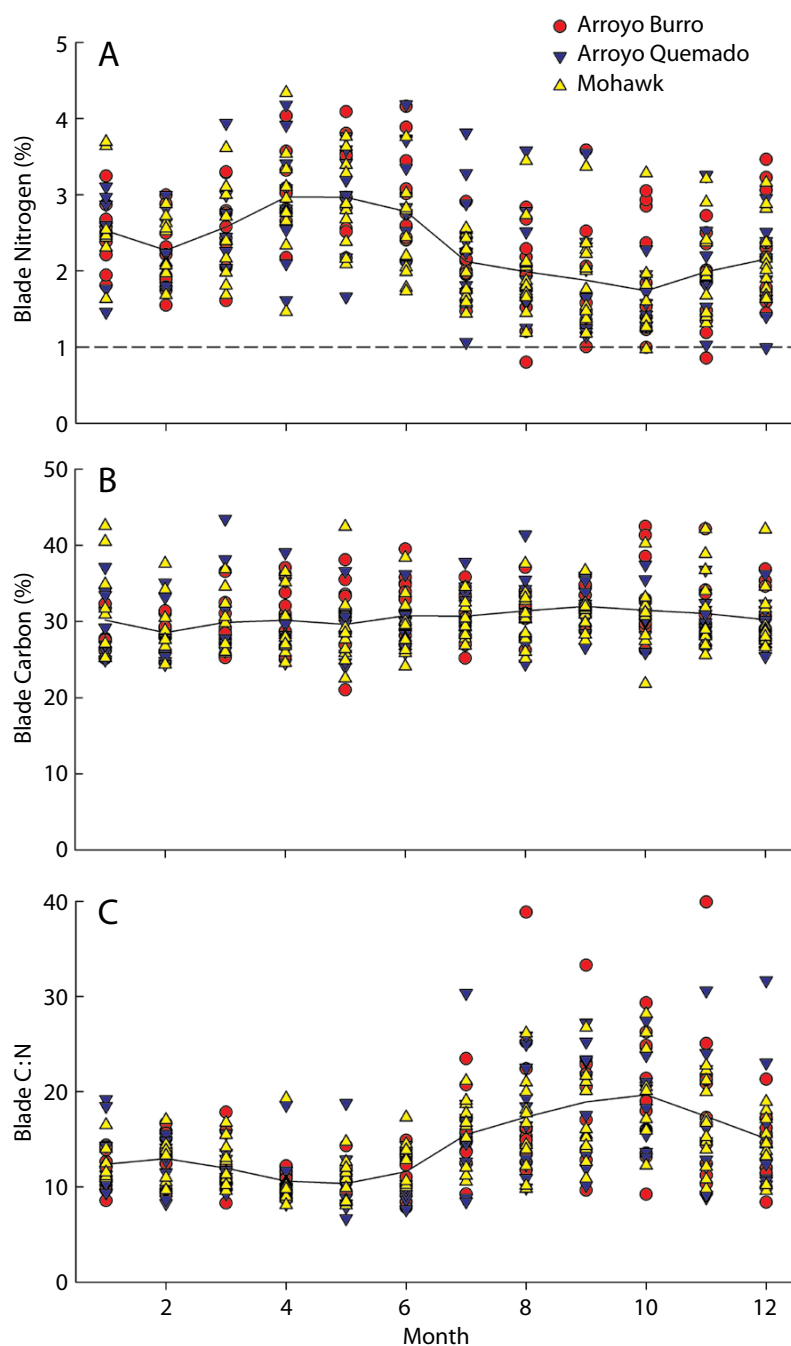


Figure 3. Annual cycle of (A) giant kelp blade nitrogen content as a percent of dry mass, (B) giant kelp blade carbon content as a percent of dry mass, and (C) kelp blade C:N weight ratio. Individual data points are monthly measurements from 2002 through 2012 at Arroyo Burro, Arroyo Quemado, and Mohawk kelp forests. The horizontal dashed line in (A) represents a concentration of  $1 \mu\text{mol L}^{-1} \text{NO}_3^-$ , below which kelp growth is not sustained.

kelp in the Santa Barbara Channel, we investigated several routes of nitrate supply. In particular, we considered the timing and magnitude of physical processes that can deliver nutrients to reefs and how nitrate delivery by each mechanism varies over time scales ranging from hours to weeks. Together, these supplies must be of sufficient magnitude and have enough complementarity over time to sustain the levels of kelp growth that we measured across seasons. If they are insufficient, then alternate DIN sources are likely involved.

## SOURCES AND SEASONALITY IN NITRATE SUPPLY

A number of physical mechanisms supply nitrate to nearshore reefs, including upwelling, internal waves, and terrestrial runoff (McPhee-Shaw et al., 2007); other lesser known oceanographic processes also play a role (e.g., coastal eddies and coastal trapped waves; Washburn and McPhee-Shaw, 2013, in this issue). The physical mechanisms supplying nitrate to reefs on the inner continental shelf show a high level of temporal complementarity. Terrestrial runoff in the Santa

Barbara Channel is highly seasonal. Seventy-four creeks flow from the Santa Ynez Mountains along the northern coast of Santa Barbara Channel. Rainfall is largely confined to the winter months in this Mediterranean climate, and most stream discharge is associated with a small number of storms from December through April (Figure 5A). Upwelling-favorable wind stress is present year-round, with a clear annual cycle. Wind stress is generally lowest during winter and highest during spring and summer, with the transition to higher stress occurring during February through March (Figure 5A). Internal waves that drive the seasonal thermocline and its high nitrate content onto the continental shelf show a seasonal cycle similar to that of upwelling-favorable wind stress, with internal wave activity being relatively low in winter, transitioning to a seasonal high in April through May, with a slow decline for the remainder of the year (Figure 5A). Thus, at least one physical mechanism that can deliver nitrate to reefs is operating throughout the year, creating the potential for a near-continuous supply of nitrate to giant kelp forests. However, the magnitude of nitrate delivery among mechanisms varies, and within each mechanism, the nitrate content of waters delivered to kelp forests also varies through time such that the potential for a continuous significant supply of nitrate implied by Figure 5A is not always realized.

Figure 5B shows the seasonal patterns in nitrate delivery associated with each supply mechanism. Upwelling is the dominant source of nitrate to kelp from March through May. Temperature records at Arroyo Quemado show little evidence of the presence of cold

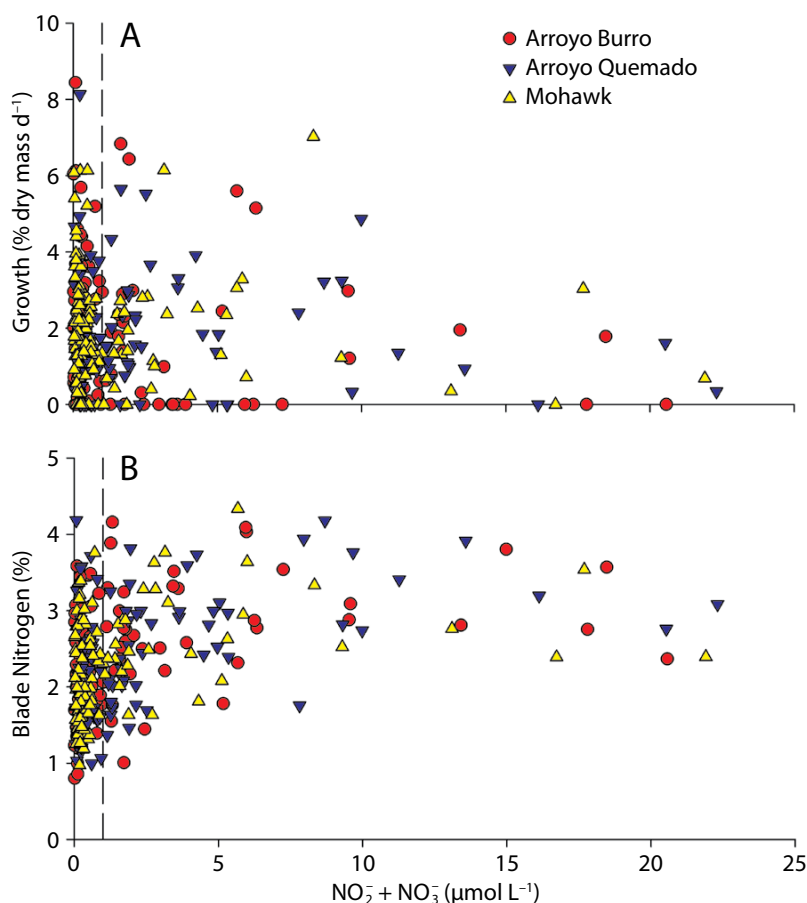


Figure 4. Relationship between the average of the sum of nitrate and nitrite concentrations (nearly 100% nitrate; each point is an average of measurements from two to three samples distributed vertically over the 10–15 m water column at each site) and (A) the growth rate of the standing biomass of giant kelp and (B) kelp blade nitrogen content. Vertical dashed lines represent a concentration of  $1 \mu\text{mol L}^{-1}$   $\text{NO}_3$ , below which kelp growth is not sustained.

nitrate-rich upwelled waters entering the kelp forests during other times of the year, despite wind stress remaining upwelling favorable (compare Figures 5A and 5B). An explanation may lie in the analysis of Brzezinski and Washburn (2011), who examined seasonal changes in surface nitrate concentrations over a wide area of the Santa Barbara Channel for six years. They concluded that upwelling was often ineffective at increasing nitrate concentrations in surface waters across the Santa Barbara Channel after spring, and they suggested that upwelling later in the year often drove relatively warm, and thus nitrate-poor, waters to the surface.

Internal waves have been proposed as a mechanism for sustaining the growth of giant kelp during summer at Catalina Island, located ~ 130 km southwest of the Santa Barbara Channel (Zimmerman and Kremer, 1984). Nitrate pulses supplied by internal waves have frequencies ranging between the inertial period (about 22 hours at the latitude in our study area) down to the buoyancy period (several minutes depending on stratification). The delivery of nitrate by internal waves at Arroyo Quemado was most prevalent from March through September (Figure 5B). When expressed as a daily average delivery rate (Figure 5B), internal waves appear to supply relatively little nitrate to the kelp forest (Figure 5B). However, in situ measurements of nitrate concentrations at 20-minute resolution show increases in nitrate concentrations on the reef of 5–10  $\mu\text{mol L}^{-1}$  for periods of 20–60 minutes due to internal waves during summer (McPhee-Shaw et al., 2007; Fram et al., 2008). Such pulses could contribute to kelp growth and survival by

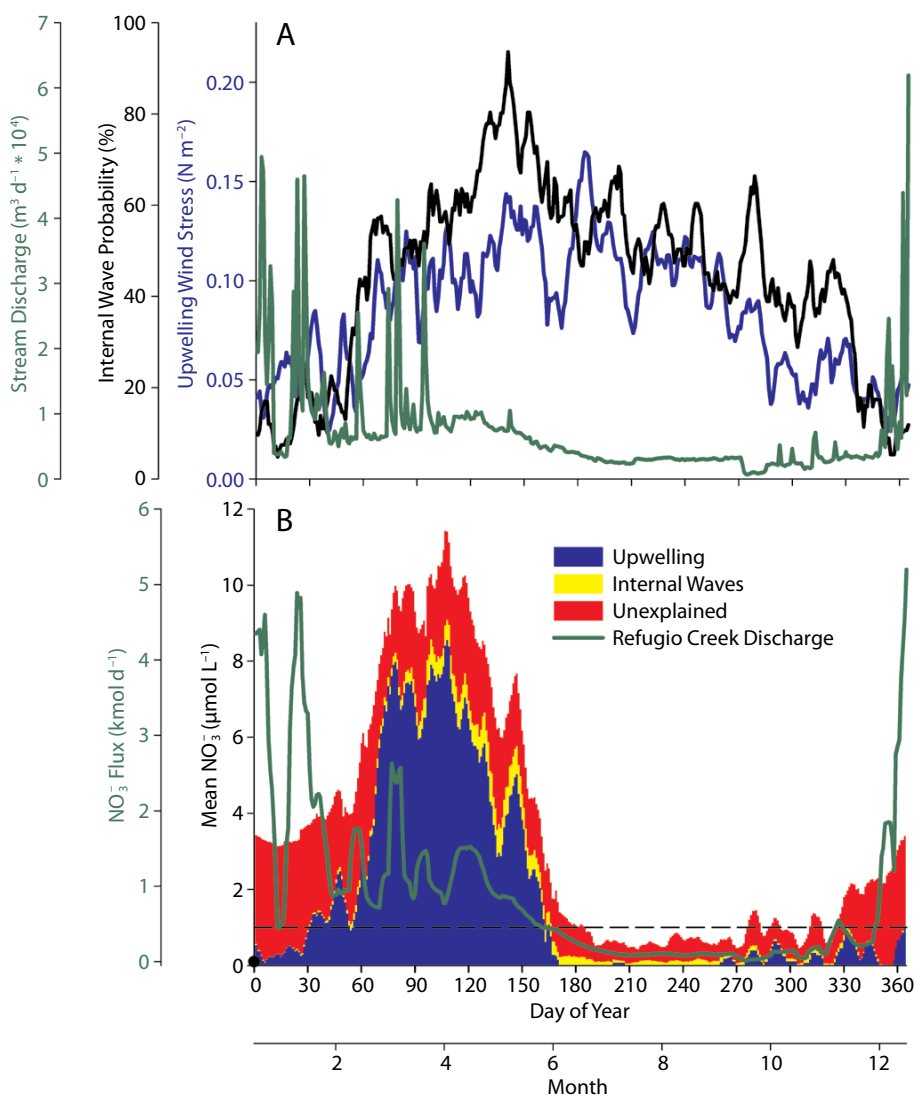


Figure 5. (A) Seasonality in the mechanisms delivering nitrate to nearshore reefs. Mean daily stream discharge measured at Refugio Creek ( $34^{\circ}27'54.3''\text{N}$ ,  $120^{\circ}4'8.4''\text{W}$ ) was calculated following Goodridge and Melack (2012). Mean daily probability of internal wave occurrence at Arroyo Quemado Reef ( $34^{\circ}27.897'\text{N}$ ,  $120^{\circ}07.179'\text{W}$ ) was calculated as the percent of days that an internal wave was detected, using the McPhee-Shaw et al. (2007) definition of a  $0.7^{\circ}\text{C}$  variance in daily temperature as indication of an internal wave. Mean daily upwelling (equatorward) wind stress was calculated from winds measured at National Oceanic and Atmospheric Administration station 46054 ( $34^{\circ}16.28'\text{N}$ ,  $120^{\circ}27.42'\text{W}$ ). Values for discharge at Refugio Creek represent mean daily discharge calculated for each day of the year from 2002–2012; values for upwelling wind stress and internal wave probability represent seven-day running averages for each day of the year from 2002–2012. (B) Nearshore ocean nitrate concentrations in  $\mu\text{mol L}^{-1}$  delivered from upwelling, internal waves, and unexplained marine sources at Arroyo Quemado Reef. Concentrations represent seven-day running averages for each day of the year from 2002–2012. Nitrate concentrations were calculated using the relationship between seawater temperature and nitrate developed for Arroyo Quemado by McPhee-Shaw et al. (2007). Nitrate delivered by upwelling was defined as nitrate in water  $< 13^{\circ}\text{C}$  (as per McPhee-Shaw et al., 2007) on days when upwelling wind stress during the preceding two days averaged  $< 0.05 \text{ N m}^{-2}$ . Nitrate delivered by internal waves was calculated using the hourly temperature for times when internal waves were present. The category “Unexplained” represents marine sources of nitrate not accounted for by upwelling and internal waves. Stream nitrate flux was measured daily at Refugio Creek and calculated following Goodridge and Melack (2012). The contribution of runoff to nitrate levels at reefs is not calculated separately as this quantity is difficult to estimate given uncertainties in the dilution of freshwater inputs in the coastal zone.

providing brief periods of enhanced N supply when little nitrate is supplied by other mechanisms.

While upwelling and internal waves account for a high fraction of the nitrate measured on reefs during spring, a considerable fraction of the nitrate present in winter and summer is not explained by these supply mechanisms. It is important to note that seawater concentrations of nitrate shown in Figure 5B were derived from a relationship between nitrate concentration and seawater temperature that was developed for the Santa Barbara Channel (McPhee-Shaw et al., 2007). Thus, the nitrate in the “unexplained” category represents nitrate supplied by oceanographic processes other than upwelling and internal waves (e.g., coastal trapped waves, coastal eddies; Washburn and MCPhee-Shaw, 2013, in this issue). It does not include nitrate delivered by runoff, as the nitrate concentrations were reconstructed from temperature, and there is little reason to believe that the relationship between temperature and nitrate in runoff is similar to that in the ocean. Thus, the nitrate supplied by runoff is in addition to the unexplained nitrate rather than part of the unexplained nitrate. The nitrate flux from streams provides an additional source of nitrate to the coastal ocean.

A time series of nitrate flux from Refugio Creek, a representative stream that enters the ocean ~ 6 km to the east of the Arroyo Quemado kelp forest, shows the delivery of nitrate into the coastal ocean from runoff to be highest during the winter months, with significant inputs continuing through June. Translating this flux into the fraction of nitrate on reefs attributable to freshwater influence was not attempted because

of the complexities of intermittent and highly variable freshwater plumes mixing into the wave and tidally influenced nearshore waters. Changes in salinity on reefs at 3–4 m depth (tide dependent) during periods of high runoff indicate that stream inputs reach kelp beds, but it is unclear whether these sensors accurately capture the full influence of buoyant freshwater plumes. Direct observations of nitrate concentrations in the upper 3 m on the continental shelf during a storm in February 2004 revealed nitrate concentrations of  $50 \mu\text{mol L}^{-1}$  associated with runoff plumes (recent work of author M. Brzezinski and Libe Washburn, University of California, Santa Barbara). Given the  $K_s$  value of  $2\text{--}3 \mu\text{mol L}^{-1}$  for nitrate uptake in *M. pyrifera* (Gerard, 1982b), pulses of nitrate during storms (Figure 5B) have the potential to increase uptake rates. Observations of  $^{15}\text{N}$  enrichment in sea urchins and tube worms in kelp forests located near sources of runoff in the Santa Barbara Channel suggest that terrestrially derived nitrogen enters the nearshore food web (Page et al., 2008).

## UTILIZATION OF N SOURCES

The residence times of waters flowing through the modest-sized kelp forests along the mainland in the Santa Barbara Channel are on the order of 1–2 hours (Gaylord et al. 2007), and uptake by kelp is insufficient to significantly deplete nitrate concentrations in the forest with this rate of exchange. As water flows through the forest, turbulence from currents and waves transports nutrient molecules across the diffusive boundary layer surrounding kelp blades where nutrient transporters then move nutrient molecules into kelp tissue. This process

was incorporated into a biophysical model that combined temporal changes in ambient nitrate concentrations with turbulence estimates to predict kelp nitrate uptake (Fram et al., 2008). Comparison of measured seasonal kelp N production with predicted nitrate uptake showed that, for most of the year, the concentration of nitrate over the reef was adequate to meet the forest’s measured N demand. The exception was the summer and autumn when estimated kelp N production exceeded the ambient nitrate supply, suggesting that other forms of nitrogen are required to support production rates during the period of low nitrate concentration.

## Alternate DIN sources

Nitrate is a major form of new nitrogen that can support autotrophic production in the sea (Eppley and Peterson, 1979). However, in shallow habitats where coastal waters interact with bottom sediments, benthic biota, and beaches, other forms of DIN, such as ammonium, may be a significant source of DIN supporting macrophyte production during summer and autumn when nitrate concentrations are low. Ammonium can be supplied through a variety of mechanisms. The remineralization of organic matter of marine and terrestrial origin that accumulates on the bottom within sediments may elevate concentrations of ammonium in shallow waters. Excretion by consumers may serve as an important source of nitrogen for reef ecosystems and other nearshore benthic ecosystems (Bray et al., 1988; Holbrook et al., 2008; Allgeier et al., 2013; Burkepile et al., 2013). Recent work of the Santa Barbara Coastal Long Term Ecological Research Project indicates that a majority of



consumer biomass in kelp forests of the Santa Barbara Channel consists of filter feeding invertebrates and fish. The excretion of ammonium by these planktivores could enhance primary productivity in kelp forests during conditions of low nitrate as has been observed on coral reefs (Holbrook et al., 2008; Burkepile et al., 2013).

Part of the DIN pool within giant kelp forests may be the result of recycling between giant kelp forests and beaches. Kelp forests export large quantities of drift kelp to sandy beaches (Hayes, 1974; Griffiths and Stenton-Dozey, 1981; Koop et al., 1982; Dugan et al., 2003, 2011). Once stranded on beaches, intertidal invertebrate detritivores rapidly consume kelp wrack (Lastra et al., 2008) and microbes decompose it, creating high concentrations of DIN in the underlying beach aquifer (Dugan et al., 2011). Ammonium is the dominant form of DIN in beach pore water efflux to the nearshore ocean (recent work of authors Goodridge and Melack). The inorganic nitrogen produced in the beach pore water is flushed from the sands into the surf zone by the action of receding waves and falling tides, becoming available to nearshore primary producers (Swarzenski and Izbicki, 2009). It is difficult to estimate the fraction of the nitrogen from beaches entering the coastal ocean that may actually reach kelp forests due to uncertainties in the extent of dilution of this nitrogen and its consumption by other nearshore autotrophs (seagrasses, macroalgae, and phytoplankton).

Monthly monitoring of ammonium and nitrate concentrations at our kelp forest sites shows that, on average, the ambient concentrations of ammonium

rivals that of nitrate during summer (Figure 6A). This approximate doubling in DIN is sufficient to account for the apparent deficit in N supply

needed to balance kelp N production during summer (Fram et al., 2008) and bring total DIN concentrations above the  $1 \mu\text{mol L}^{-1}$  growth threshold

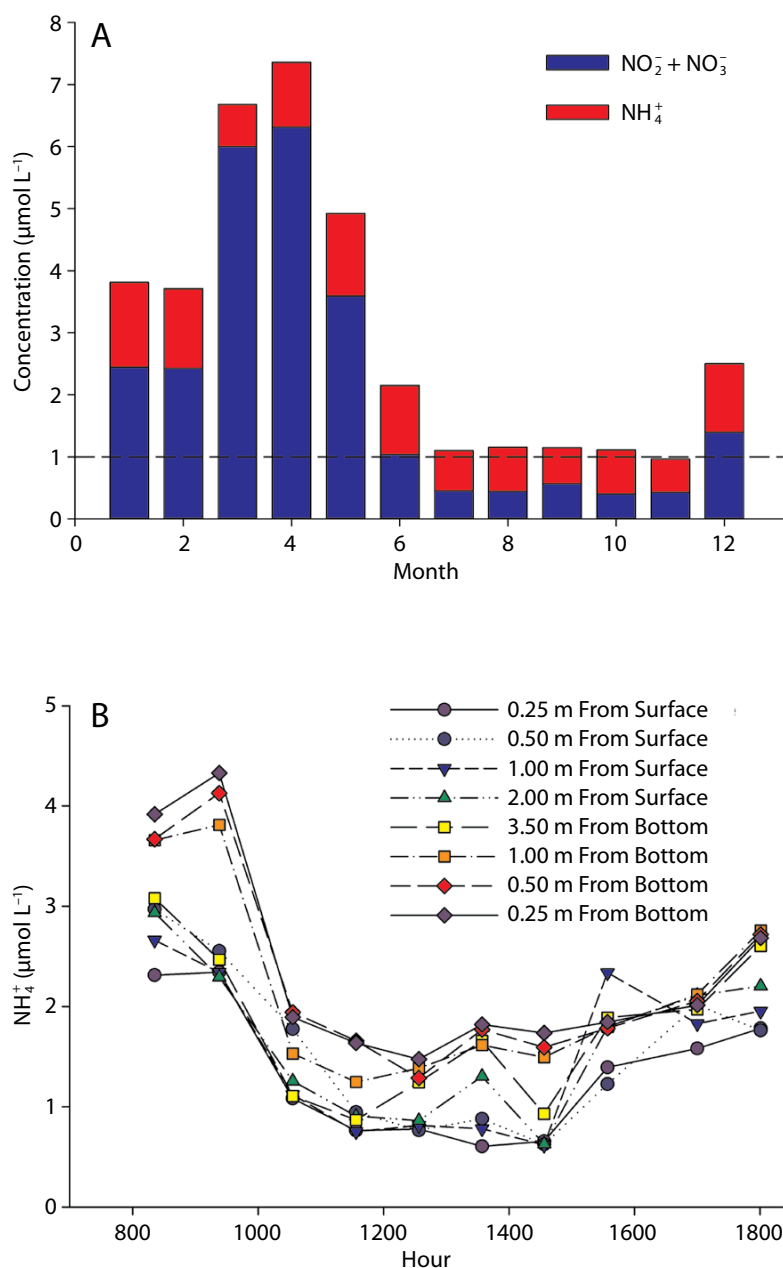


Figure 6. (A) Depth-averaged concentrations of the sum of nitrate and nitrite (nearly 100% nitrate) and ammonium from water samples collected monthly at Arroyo Burro, Arroyo Quemado, and Mohawk kelp forests from 2002 through 2012. (B) Time course of ammonium concentration in the water column obtained from water samples in the Mohawk kelp forest. Water was pumped to the surface through plastic tubing using multichannel peristaltic pumps and sampled continuously over 60 minute intervals to obtain integrated samples.

(Gerard, 1982b). Other data suggest that the ammonium concentrations in Figure 6A may significantly underestimate the actual concentrations near our study reefs. Ammonium distributions observed on cross-shelf transects off-

in shallow estuarine systems where significant light penetrates to the bottom (Rysgaard et al., 1995; Thornton et al., 1999). If this is the mechanism operating at our study sites, then our measures of ammonium concentrations underes-

pecially that arising from sediment efflux and excretion by reef consumers. Together, these DIN sources support high kelp growth rates throughout the year, but kelp adjust to the low N supply during summer by decreasing tissue nitrogen, resulting in a doubling of kelp C:N ratios.

“ LONG-TERM RESEARCH ON GIANT KELP FORESTS IN THE SANTA BARBARA CHANNEL IS CONTRIBUTING TO SIGNIFICANT ADVANCES IN OUR UNDERSTANDING OF GIANT KELP GROWTH PATTERNS AND THE ENVIRONMENTAL PROCESSES THAT CONTROL THEM. ”


shore of Mohawk Reef point to a benthic source with ammonium concentrations of 2–4  $\mu\text{mol L}^{-1}$  occasionally observed near the bottom (Goodman et al., 2012). Fine-scale vertical profiles of ammonium sampled continuously during daylight hours within the kelp forest at Mohawk Reef show a diurnal cycle in ammonium concentration, with the strongest amplitude and highest concentrations observed near the bottom (Figure 6B). Additional sampling throughout the day during spring and neap tides indicates that this cycle is tied to the photocycle rather than to the tidal cycle (not shown). One mechanism that could give rise to this pattern is a near continuous efflux of ammonium from sediment or from excretion by benthic reef consumers that is taken up by benthic biofilms and macroalgae during the day, but passes into the water column at night when ammonium use is less efficient. The phenomenon has been observed

estimate the supply as both the monthly reef measurements and the cross-shelf transects were conducted mid-day when ammonium concentration in the water column would be at their daily minimum due to biological consumption by micro- and macro-algae.

## SUMMARY

The limited ability of *Macrocystis* to store nitrogen, its lack of a dormant period, and the lack of large reservoirs of nitrogenous nutrients on rocky reefs together create the need for a continuous supply of adequate nitrogen to support the observed high growth rates of giant kelp throughout the year. Though the timing of stream discharge, upwelling winds, internal wave activity, and other oceanographic processes are complementary, nitrate delivery is nevertheless inadequate to meet the N demand of kelp forests during summer. A likely second DIN source appears to be ammonium,

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