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Local-scale nutrient regeneration facilitates seaweed growth on wave-exposed rocky shores in an upwelling system

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Abstract

This study shows that, even on exposed, wave-swept, rocky shores in a nutrient-replete upwelling ecosystem, mussels (*Mytilus californianus*) facilitate the growth of the seaweed *Porphyra perforata* by enhancing nutrient concentrations in the nearby water column. In field surveys on emergent substrate in the mid-intertidal zone, we found ten times greater abundance of *P. perforata* on mussels than on adjacent rock. In field experiments, *P. perforata* accumulated and grew more quickly on mussels than on bare rock or on mussel mimics, suggesting that nutrients excreted by mussels might be responsible for greater *P. perforata* cover. At high tide, water column ammonium concentrations over mussel beds were nearly double those found over bare rock. Correspondingly, tissue nitrogen concentrations were higher, and carbon-to-nitrogen ratios were lower in *P. perforata* growing on mussels compared to bare rock. Given the dominance of mussels in mid-intertidal regions of temperate coasts worldwide, ammonium regeneration could be a general contributor to local-scale nutrient availability, even in high-flow systems characterized by high nutrient concentrations.

Variation in nutrient availability can affect the growth, composition, and biomass of primary producer communities (Tilman and Wedin 1991; Leibold 1999; Worm et al. 2002). However, the extent to which biologically important variation in nutrient availability emerges from inputs of new vs. regenerated nutrients is often uncertain. Regenerated nitrogen can compose a large proportion of nutrients in systems with low external inputs of nitrogen, but is generally thought to be less important in systems dominated by allochthonous nitrogen inputs (Miller 2004). It is possible that nutrient regeneration may be important in relatively high-nutrient systems open to flow; however, the

prevalence of ecologically important autochthonous nitrogen inputs, especially in very high-flow marine systems exposed to strong waves or currents, remains unclear.

In intertidal and shallow, subtidal marine systems, nutrient variation was historically ignored in favor of species interactions as explanations for patterns of species distribution and abundance (Menge 2000). However, recent studies have demonstrated that large-scale variation in allochthonous nutrients associated with coastal upwelling can alter species interactions and community structure in nearshore environments (Dayton et al. 1999; Blanchette et al. 2006). For example, Nielsen and Navarrete (2004) described how mesoscale (10 s of km) variation in nitrogen concentration associated with variability in the strength of upwelling along the Chilean coast affects the interaction between molluscan herbivores and macroalgae, altering algal community structure. Similarly, increases in anthropogenic nutrient input can favor fast-growing macroalgae in estuaries (Hauxwell 2001) and on rocky shores (Worm and Lotze 2006), altering the structure and composition of algal assemblages, which can have indirect effects on the structure of the entire community.

Whereas upwelling or anthropogenic inputs are important sources of nutrients over relatively large scales, small-scale nutrient inputs, such as nitrogen regeneration by invertebrates, also influence community structure and

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function in nearshore environments. However, most studies examining the effect of local-scale nutrient regeneration on marine benthic-producer assemblages have been performed in systems characterized by relatively low nutrient availability and/or low water flow (Bertness 1984; Peterson and Heck 2001; Gibbs et al. 2005). For example, mussels increase the vegetative growth of seagrasses via nutrient excretion in a shallow, protected seagrass beds with minimal wave energy and weak tidal currents (Peterson and Heck 2001). Similarly, mussel density positively correlates with height, biomass, and flowering of the cordgrass *Spartina alterniflora* (Bertness 1984). Ammonium excreted by mobile epifauna facilitates algal turfs in tide pools (Bracken et al. 2007) and has the potential to enhance algal growth in shallow subtidal seaweed beds (Taylor and Rees 1998). Additionally, there is growing recognition that sessile invertebrates facilitate algal growth and diversity in tide pools (Bracken 2004; Bracken and Nielsen 2004; Pfister 2007). Thus, whereas an increasing number of studies document significant effects of local-scale nutrient regeneration on algae, it is generally assumed that such inputs are overwhelmed in more open systems with more intense flow regimes (Probyn and Chapman 1983).

To assess whether regenerated nutrients might be important in systems with high flow, we evaluated the role of local-scale ammonium excretion on macroalgal growth on a wave-exposed, rocky shoreline on the northern California coast. This region is characterized by strong tides, large waves, and seasonal upwelling of cool, nutrient-rich water, which delivers high concentrations of nutrients (nitrate) to the nearshore area. These aspects of the physical environment suggest that the importance of invertebrate-regenerated nutrients on algal assemblages should be relatively minor in this system. Therefore, if invertebrate-derived nutrients contribute appreciably to local algal growth and/or species composition in such environments, then this is likely to be a ubiquitous phenomenon.

We focused our investigation on a conspicuous, but previously undocumented, association between the mussel *Mytilus californianus* and the red alga *Porphyra perforata* in the mid-intertidal zone on the northern California coast. Abundant cover of species in the genus *Porphyra* on mussels compared to the surrounding substrate has also been documented on rocky shores elsewhere, such as *P. columbiana* on *Perumytilus purpuratus* in Chile (Santelices and Martínez 1988) and *Porphyra yezoensis* on *Septifer virgatus* in Japan (Miyamoto and Noda 2004). *P. perforata* is a fast-growing alga that reaches high abundances in the summer and early fall (J. J. Stachowicz, unpubl.). Mussels are prolific, forming extensive beds in the low- to mid-intertidal zones of temperate coasts across the world. Although most commonly thought of as competing with other primary space holders like algae (Paine 1974), the mussel's hard shell can support a diverse community of epibionts including many species of algae (Suchanek 1979).

Like many other marine invertebrates, mussels excrete ammonium (Bayne et al. 1976; Bracken 2004; Pfister 2007), which could increase algal growth by alleviating nutrient limitation. Because mussels form such extensive beds, the potential flux of mussel-derived nutrients is great. Yet mussels

have previously been documented to affect algal growth only in stagnant tide pools at low tide (Bracken 2004; Pfister 2007). Alternatively, associations with mussels could increase algal growth and/or survival by providing a refuge from some herbivores with morphologies that restrict the substrates on which they can graze effectively (Geller 1991). Using manipulative field experiments and surveys, we assessed the local effect of mussels on *P. perforata* recruitment, growth, and cover in the rocky intertidal zone. Specifically, we asked the following questions: (1) What is the growth rate, nitrogen content, and standing stock of *P. perforata* on mussels vs. adjacent bare rock? (2) Is the greater *P. perforata* growth and cover we observed on mussels due to a causal relationship, and if so, is it caused by live mussels or simply by the physical structure that mussels provide? (3) Do ammonium concentrations in the water column differ above mussel beds vs. bare rock areas? We synthesized our results to assess the potential importance of regenerated nutrients for algal distribution and abundance across rocky shores with high flow.

Methods

M. californianus and *P. perforata* are both conspicuous members of mid-intertidal communities from Alaska to Baja, California (Abbott and Hollenberg 1976; Morris et al. 1980). We conducted all experiments in the summers of 2005 and 2006 at the Bodega Marine Reserve on the northern coast of California (38°19.0'N, 123°4.1'W). Significant wave heights average 2 m during the summer months, when most of our experiments were performed (data provided by the University of California at Davis, Bodega Marine Laboratory). Given data from previous studies relating wave height to velocity on rocky shores, waves of this magnitude correspond to maximum water velocities of 4 m s⁻¹ to 10 m s⁻¹ (Bell and Denny 1994; Gaylord 1999). We surveyed algal cover on mussel beds vs. bare rock on emergent substrate in the mid-intertidal zone by haphazardly selecting 60 interspersed 20-cm × 20-cm quadrats at the same tidal elevation, 30 on mussel beds and 30 on adjacent bare-rock substrates. To establish ambient differences in cover between mussel and rock substrates, we visually estimated percent cover of each algal species present to the nearest 5% with the aid of four squares marked off within the quadrat frame. This procedure has been previously demonstrated to yield an accurate representation of relative algal cover, while also allowing for the assessment of understory as well as canopy cover, and better quantifying cover of rare species than estimates using the random-point-count method (Dethier et al. 1993).

To establish whether mussels affected *P. perforata* growth, we monitored the area of 30 *P. perforata* thalli growing on mussels and 30 growing on nearby patches of bare rock for 15 d by digitally photographing each thallus every 2 d, as tides permitted, and measuring thallus area using ImageJ (<http://rsb.info.nih.gov/ij/download.html>). We examined *P. perforata* thalli at similar tidal elevation, and chose thalli growing on bare rock that were interspersed with those growing on mussels and within 30 cm of the mussel bed. Differences in growth rates among algae on

the two substrates were analyzed using a repeated-measures analysis of variance (ANOVA).

To elucidate the mechanism underlying enhanced abundance and growth of *P. perforata* on mussels (see Results) we performed a factorial experiment examining the effects of herbivores and substrate on *P. perforata*. In 15-cm \times 15-cm plots, ambient and reduced herbivore treatments were crossed with three substrates: live mussels, mussel mimics, and bare rock. The experiment was performed in eight blocks, each containing one plot of each treatment. We randomly assigned treatments to individual plots within each block that were arranged in a 2 \times 3 grid and separated by 10 cm. We cleared the area surrounding each plot of algae and mussels; however, each block was surrounded by an intact community that included mussels and algae growing both on the mussels and on the natural substrate to provide an ample source of recruits of both herbivores and algae into the plots. We cleared the interior of bare and mimic plots and removed all algae from live mussels, scraping algae from the surface of the mussel shells as necessary. We removed all visible herbivores from herbivore exclusion plots. To separate the effects of structure and substrate provided by mussels from biological effects of mussels (e.g., nutrient excretion), we used mussel mimics made of mussel shells scraped bare of algae. We filled the shells with nontoxic silicone and attached them to the substrate using a marine epoxy (Z-Spar A-788 Splash-Zone compound). Splash-Zone compound is non-toxic after it cures, and we have commonly observed seaweeds growing on unpainted epoxy (K. M. Aquilino, unpubl.). Furthermore, we controlled for any potential negative effects of the epoxy by including it in all treatments. To reduce herbivore abundance in plots, we surrounded them with a border of marine epoxy covered with copper paint, which reduces access by limpets and chitons but not by littorine snails or arthropod herbivores (Cubit 1984; Johnson 1992). We therefore manually removed littorines and arthropods from herbivore exclusion plots during sampling. We avoided using full cages to exclude herbivores because the mesh size required to restrict access by small, but abundant, herbivores in this system would have altered light and water flow, confounding interpretation of the results. Plots with herbivore access had marine epoxy and copper paint at each corner as a control for their potential effects. We visually estimated the percent cover of all algal species present in each plot to the nearest 5% each week for 7 weeks. To assess whether the facilitation of *P. perforata* by live mussels that we observed in the first 7 weeks of the experiment persisted once sufficient time was allowed for perennial species to colonize and establish, we revisited the plots after a year of algal recruitment and succession, reassessed algal percent cover, and harvested all algae growing within each plot. Herbivore reduction treatments were maintained only during the first 7 weeks of the experiment. To analyze data collected over the first 7 weeks, we used a repeated-measures ANOVA. We used a one-way ANOVA to compare effect of substrate treatment (bare rock, mussel mimics, and live mussels) after one year on algal cover, comparing individual treatment means using Tukey's Honestly Significant Differences (HSD) test.

To estimate the magnitude of potential fertilization of algae by mussels, we compared concentrations of ammonium in the

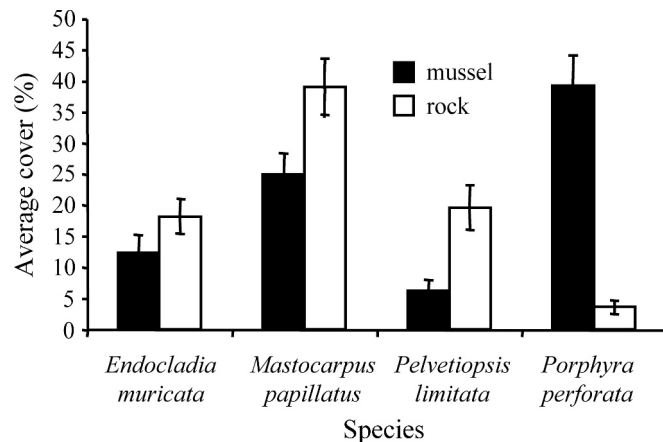


Fig. 1. Mean \pm standard error percent cover of most abundant algal species by substrate in 30-cm \times 30-cm plots over mussel beds and adjacent patches of bare rock ($n = 30$).

water column over mussel beds and over bare rock using the phenol-hypochlorite method (Solórzano 1969). We collected water samples during the incoming tide at 12 mid-intertidal sites where most of the cover consisted of mussels, and at 12 interspersed sites that had very low cover of invertebrates and were primarily bare rock. Although there may have been inherent differences between mussel- and bare-rock-dominated sites other than the presence or absence of mussels alone, we chose sites with similar tidal elevation, slope, and wave exposure in order to minimize these potential differences. We collected samples using a small cup attached to the end of a stick that was dipped into the water as the first waves of the incoming tide washed over the site. Offshore significant wave height on the day of collection was 1.07 m (NOAA standard meteorological data, Station 46013, Bodega Bay, California). We also collected tissue samples of 18 *P. perforata* thalli growing on mussels and 17 *P. perforata* thalli growing on bare rock (one sample was lost during analysis) to analyze carbon (C) and nitrogen (N) content (%N and C:N ratios).

Results

Of the 21 algal species observed, four species occurred in more than half of the plots we surveyed: *Mastocarpus papillatus* (98% of plots), *Endocladia muricata* (83% of plots), *P. perforata* (71% of plots), and *Pelvetiopsis limitata* (60% of plots). These species were also the only species that had a mean percent cover of $>5\%$ in the plots (Fig. 1; mean \pm standard error, $32 \pm 3\%$ for *M. papillatus*, $21 \pm 3\%$ for *P. perforata*, $15 \pm 2\%$ for *E. muricata*, and $13 \pm 2\%$ for *P. limitata*). Of these four algal species, only *P. perforata* exhibited significantly greater frequency of occurrence or cover on mussels than on bare rock: *P. perforata* was present in 28 of 30 survey plots on mussel compared to 15 of 30 survey plots on rock, and average *P. perforata* cover was 10 times higher on mussels ($39 \pm 5\%$) than on bare rock ($4 \pm 1\%$; paired t -test, $t = 7.13$; $df = 58$; $p < 0.0001$), suggesting that mussels might facilitate *P. perforata*. Of the other three common species, two were less abundant on mussels than bare rock: *M. papillatus* ($25 \pm 3\%$ and $39 \pm 5\%$ on mussels and bare rock, respectively; paired t -test, $t = 2.50$; $df = 58$; p

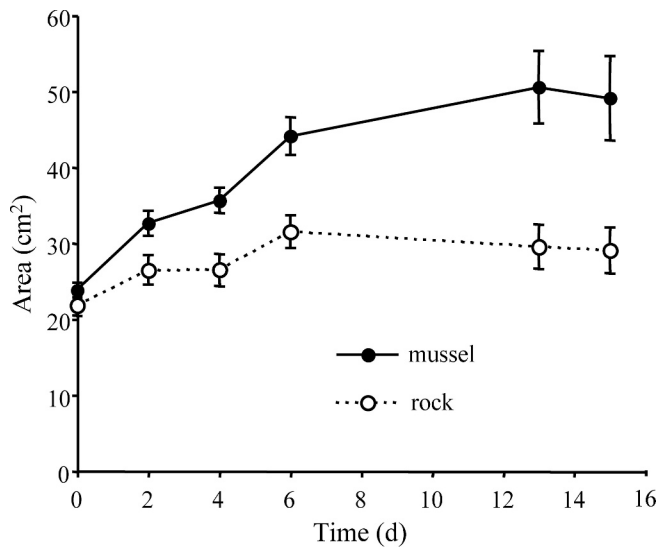


Fig. 2. Mean \pm standard error thallus area of *Porphyra perforata* growing on mussel beds ($n = 26$) and *P. perforata* growing on adjacent bare rock ($n = 23$) over 15 d.

= 0.015) and *P. limitata* ($6 \pm 2\%$ and $20 \pm 4\%$; paired *t*-test, $t = 3.30$, $df = 58$, $p = 0.002$). There was no difference in percent cover of *E. muricata* between the substrates ($12 \pm 3\%$ and $18 \pm 3\%$ on mussels and bare rock, respectively; paired *t*-test, $t = 1.50$; $df = 58$; $p = 0.140$).

P. perforata grew three times faster on mussels than on bare rock (Fig. 2; repeated measures ANOVA: $F_{1,47} = 8.84$; $p = 0.0046$). *P. perforata* thalli measured on bare rock were on average 9.1 ± 1.0 cm away from the nearest mussel and a maximum of 26 cm from the nearest mussel, whereas *P. perforata* thalli measured growing on mussels were completely surrounded by mussels.

Our field experiment suggested that mussels did indeed facilitate *P. perforata* and that the effects on *P. perforata* were mediated by live mussels rather than by the physical structure or refuge from herbivores that mussel beds might provide. Over the first 7 weeks of the experiment, *Ulva* spp.—ephemeral algae, which typically colonize disturbed areas during the summer months (J. J. Stachowicz, unpubl.)—dominated the experimental plots with an average cover of $50.5 \pm 5.3\%$. However, *Ulva* cover did not vary among treatments (repeated measures ANOVA: $F_{5,42} = 0.49$; $p = 0.7784$). Of the other algal species observed, *P. perforata* was the only macroalga to achieve an average cover $>1\%$ ($4.4 \pm 1.6\%$). The substrate affected the percent cover of *P. perforata* (Fig. 3; repeated measures ANOVA: $F_{2,45} = 12.18$; $p < 0.0001$). Although the average percent cover of *P. perforata* was generally higher in herbivore exclusion treatments, this trend was not significant ($F_{1,46} = 0.725$; $p = 0.3988$). Furthermore, there was no herbivore by substrate interaction ($F_{5,42} = 1.03$; $p = 0.3642$). The effect of substrate on *P. perforata* cover persisted at 1 yr (Fig. 4; ANOVA on power-transformed data, $F_{2,42} = 9.29$; $p = 0.0006$). Because herbivore exclusions were not maintained between 7 weeks and 1 yr, we did not report tests of the effect of herbivore treatment or its interaction with substrate after 1 yr

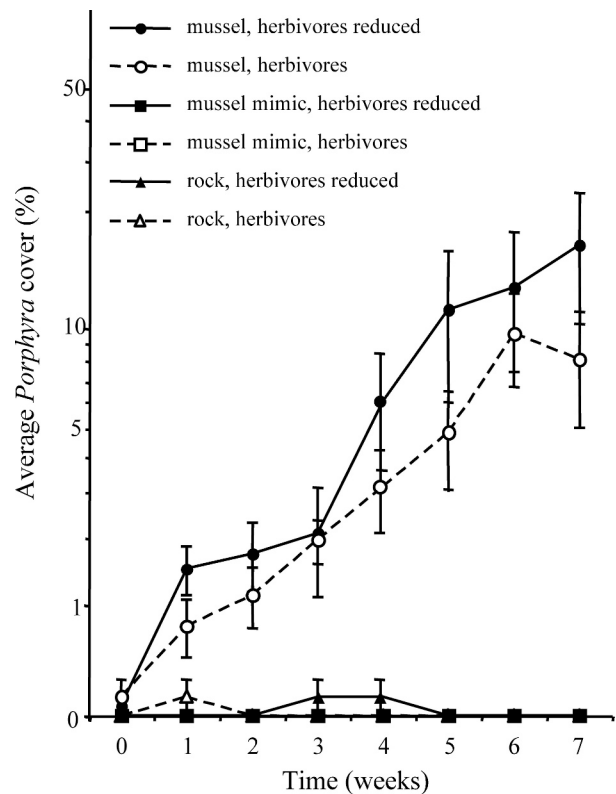


Fig. 3. Mean \pm standard error *Porphyra perforata* percent cover on mussels, mussel mimics, and bare rock over 7 weeks ($n = 8$). Data are presented on a log scale to show small values in non-live mussel plots. Cover in mussel mimic plots was never significantly greater than zero.

(although neither was significant). There was significantly higher *P. perforata* cover on live mussels than on mussel mimics or on bare rock (Tukey's HSD test, $p = 0.0002$ and $p = 0.001$, respectively), and there was no difference between cover on mussel mimics and bare rock ($p = 0.830$). Similar results were obtained for the effects of substrate when we measured *P. perforata* abundance as wet mass ($F_{2,42} = 10.92$; $p = 0.0002$ for cover on live mussels vs. mussel mimics or bare rock, and $F_{1,42} = 2.96$; $p = 0.093$ for cover on mussel mimics vs. bare rock) or dry mass ($F_{2,42} = 10.09$; $p = 0.0003$; and $F_{1,42} = 2.67$, $p = 0.110$).

After 1 yr, other algal species had recruited into our plots, allowing us to compare the effect of treatments on *P. perforata* to their effect on other species. In addition to the increased cover of *P. perforata* on live mussels described previously, cover also differed between substrate treatments for *E. muricata* and *Ulva* at 1 yr (Fig. 4; $F_{2,45} = 3.621$, $p = 0.035$ and $F_{2,45} = 3.261$, $p = 0.048$, respectively). There was significantly higher cover of *E. muricata* on live mussels than on bare rock (Tukey's HSD test, $p = 0.027$), but cover did not differ between mussel mimics and live mussels or bare rock ($p = 0.506$ and $p = 0.274$, respectively). The greater cover of *Ulva* on live mussels compared to mussel mimics was marginally significant (Tukey's HSD test, $p = 0.061$), and there was no difference between cover on bare rock and live mussels or mussel mimics ($p = 0.110$ and $p = 0.959$, respectively). *M. papillatus* and *P. limitata* both had greater abundance on bare

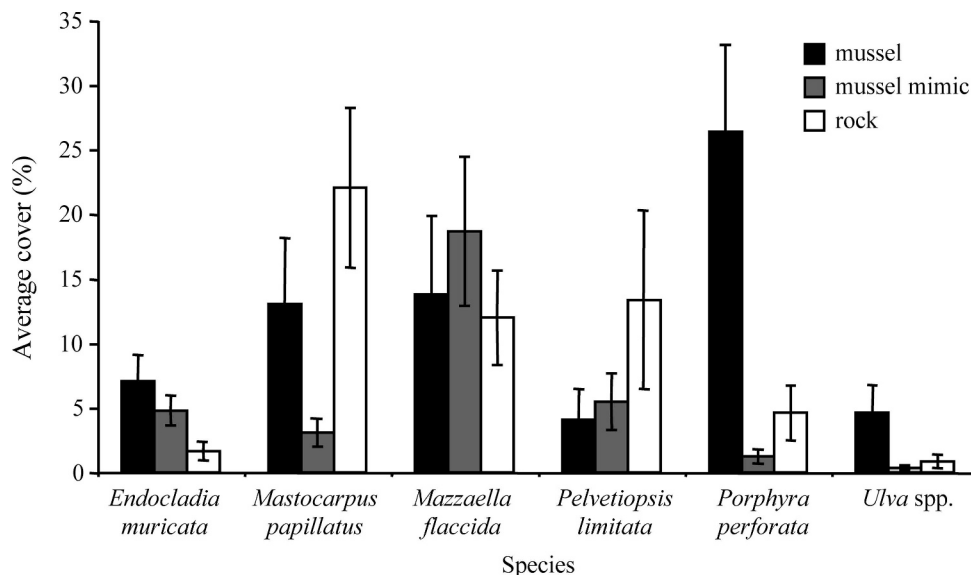


Fig. 4. Mean \pm standard error percent cover of most abundant algal species on live mussels, mussel mimics, and bare rock 1 yr after experiment establishment ($n = 16$).

rock than on mussels or mussel mimics, but this difference was only significant for *M. papillatus* (Tukey's HSD test $p = 0.017$).

Ambient seawater nitrate concentrations were $13.07 \pm 2.26 \mu\text{mol L}^{-1}$ at the time of our nutrient sampling. Ammonium concentrations were an order of magnitude higher over mussel beds than over bare rock (Fig. 5A; $1.26 \pm 0.03 \mu\text{mol L}^{-1}$ and $0.08 \pm 0.04 \mu\text{mol L}^{-1}$, respectively; paired t -test $t = 30.14$; $\text{df} = 22$; $p < 0.0001$). The percentage of nitrogen in tissue was higher in *P. perforata* growing on mussels than in individuals growing on bare rock (Fig. 5B; $2.56 \pm 0.72\%$ and $1.85 \pm 0.07\%$, respectively; paired t -test, $t = 6.93$; $\text{df} = 33$; $p < 0.0001$), and C:N tissue ratios were lower on mussels than on bare rock (Fig. 5C; 14.7 ± 0.5 and 20.3 ± 0.6 , respectively; paired t -test, $t = -7.06$; $\text{df} = 33$; $p < 0.0001$).

Discussion

Our data indicate that nutrient fertilization by mussels was probably responsible for increased growth and cover of *P. perforata* on *M. californianus* compared to adjacent bare rock in an exposed, rocky intertidal ecosystem. Higher growth, cover, and nitrogen content of *P. perforata* on mussels were correlated with higher ammonium availability above mussel beds at high tide. Neither the structure of mussel beds nor the presence of herbivores influenced *P. perforata* cover in our field experiment. Herbivore species composition and abundance often differs between mussel beds and bare rock (Lohse 1993), with some herbivores being more abundant within mussel beds (Miyamoto and Noda 2004). Although *P. perforata* is readily consumed by several abundant herbivores, including limpets and turban snails (Harley 2002), we saw no differences in algal cover between herbivore treatments. The lack of a grazing effect in our study is consistent with a similar experiment crossing

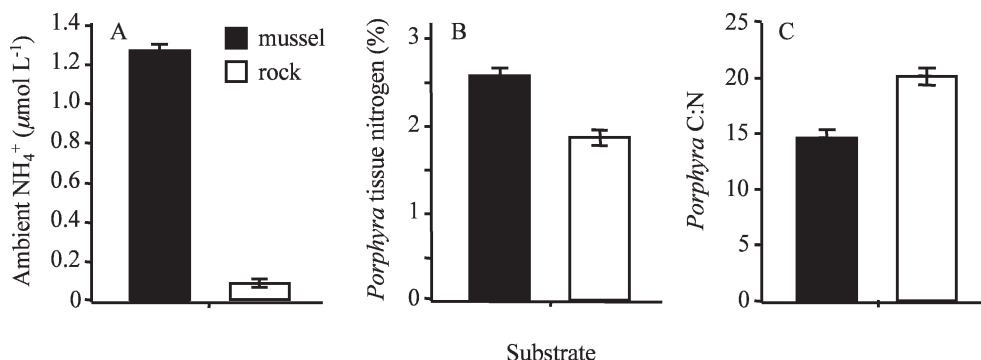


Fig. 5. (A) Mean \pm standard error ammonium concentration in the water column as the incoming tide washed over mussel beds and bare rock ($n = 12$); (B) Mean \pm standard error tissue percent nitrogen in *Porphyra perforata* fronds growing on mussel beds and bare rock ($n = 18$ and $n = 17$, respectively); (C) Mean \pm standard error carbon-to-nitrogen ratio of *P. perforata* fronds growing on mussel beds and bare rock ($n = 18$ and $n = 17$, respectively).

treatments of undisturbed mussels, herbivores, and algae with removals of each (Miyamoto and Noda 2004). In fact, Miyamoto and Noda (2004) found greater percent cover of *P. yezoensis* on the mussel *S. virgatus* despite a greater abundance of herbivores in mussel environments, supporting our contention that mussel facilitation of *P. perforata* is not mediated through a reduction in grazing rates. The close association of both herbivores and *P. perforata* with mussel beds suggests that mussels may benefit these herbivores both directly, by providing habitat, and indirectly, by facilitating a palatable algal species.

In addition to affecting herbivores, the complex structure provided by mussels can influence abiotic conditions experienced by algae such as water flow (Gutiérrez et al. 2003) and desiccation stress (Bertness and Leonard 1997). Changes due to mussel bed structure could facilitate *P. perforata* directly or release *P. perforata* from competition with dominants such as *M. papillatus* or *P. limitata* if these species perform poorly on mussels. However, if mussel bed structure were responsible for differences in *P. perforata* cover, we should have seen equal cover of *P. perforata* on mussels and on mussel mimics. Though it is possible that the arrangement of our mussel mimics varied enough from live mussels to influence abiotic conditions (Santelices and Martínez 1988), there were no obvious differences in abiotic conditions on the areas of shell surfaces where *P. perforata* grows.

Whereas many *Porphyra* species can reproduce asexually via monospores, *P. perforata* reproduction requires an alternate filamentous *Conchocelis* phase. Although this phase is common on mollusk shells, the lack of a difference in foliose *P. perforata* cover between bare rock and mussel mimics, especially after one year, suggests that the presence of *Conchocelis* on mussels within the experimental plots did not contribute to greater cover of *P. perforata* blades on mussels. Additionally, the *Conchocelis* stage is associated with intertidal barnacles (Abbott and Hollenberg 1976; Matamala et al. 1985), which were present in bare plots. Even if the *Conchocelis* stage remained more abundant on live mussels than on mussel mimics or on bare rock at the start of the experiment, our experimental blocks were embedded within larger mussel beds with an abundance of epibiotic *P. perforata*. Therefore, adjacent spore sources were plentiful, and *P. perforata* would have colonized live mussels and mussel mimics equally, especially after an entire year (Fig. 4). Furthermore, although the *Conchocelis* stage of *P. perforata* does occur in the intertidal zone (Martínez 1990; Pacheco-Ruiz et al. 2005), its abundance declines dramatically with increasing tide height and is not correlated with cover of upright *P. perforata* blades (Martínez 1990), suggesting that mid-intertidal *P. perforata* is primarily seeded from *Conchocelis* at lower tidal elevation.

Ammonium excretion by mussels probably generated the difference in *P. perforata* cover between mussels and bare rock. Greater tissue nitrogen and lower tissue C:N ratios in *P. perforata* growing on mussels indicate that the enhanced growth of *P. perforata* on mussel beds was probably due to increased nutrient utilization. Higher ammonium concentrations above mussel beds suggest that

these nutrients were generated via ammonium excreted by mussels. These increases are noteworthy considering the high rates of water flow during sampling. Based on data from previous studies relating wave height to velocity on rocky shores, waves of 1 m—the average offshore significant wave height during our ammonium sampling—correspond to maximum water velocities of 2 m s⁻¹ to 4 m s⁻¹ (Bell and Denny 1994; Gaylord 1999). While there can be a small pulse of ammonium release during the first 15 min of re-emersion for *Mytilus* species, ammonium excretion typically increases after a few hours of emersion, suggesting that near-bed ammonium concentrations probably remain elevated throughout the high tide (Bayne et al. 1976; Widdows and Shick 1985). In addition to excretion variation within tidal cycles, the amount of ammonium excreted by *Mytilus* species can vary seasonally, with higher excretion rates during the summer and lower rates during the winter (Bayne and Scullard 1977). If *Porphyra* species are nutrient limited, variation in seasonal ammonium abundance could contribute to temporal variation in *Porphyra* abundance.

Many studies of open-coast macroalgae have focused on the use of nitrate by seaweeds because it is associated with upwelling. For example, Wootton et al. (1996) found that adding nitrate and phosphate to emergent substrate affected the abundance of molluscan grazers during periods of nutrient stress, but had no effect on total algal biomass. Our data indicate that ammonium is also an important source of nitrogen in nearshore environments. This is surprising given that nearshore waters along the northern California coast are generally considered to be especially nutrient-replete during upwelling periods. Though facilitation of algae via ammonium excretion by invertebrates has been documented in habitats within upwelling systems, such as tide pools (Bracken 2004; Pfister 2007), allochthonous nutrients in these habitats are depleted during low tide. This is the first study to our knowledge to demonstrate nutrient limitation outside of tide pools in the exposed rocky intertidal during strong upwelling.

Even when nitrate concentrations are high (e.g., during upwelling events), many algal species more readily use nitrogen in the form of ammonium (Bracken and Stachowicz 2006). *P. perforata* has the highest rate of ammonium uptake of the three most common species found on live mussels in the field experiment: *P. perforata*, *M. papillatus*, and *Mazzaella flaccida* (Bracken and Stachowicz 2006). Thus, in addition to increasing the concentration of nitrogen available to *P. perforata*, mussels provide nitrogen in a form that is more readily utilized by algae. When ambient mesoscale nutrient concentrations are high, *P. perforata* may be less nutrient-limited. However, nitrate concentrations were an order of magnitude higher than ammonium concentrations over mussel beds during our experiments, and we still observed effects of mussels on *P. perforata* growth. During upwelling events, nitrate concentrations are approximately 20 times that of the ammonium concentrations we measured over mussel beds ($21.5 \pm 1.8 \mu\text{mol L}^{-1}$ vs. $1.26 \pm 0.03 \mu\text{mol L}^{-1}$), whereas during non-upwelling conditions, nitrate concentrations ($4.7 \pm 0.9 \mu\text{mol L}^{-1}$) are only three to four times the ammonium

concentrations we measured over mussel beds. However, in moving water, ammonium uptake rates by *P. perforata* are about three times higher than those for nitrate (Thomas and Harrison 1985). Based on this, we estimate that mussel-derived ammonium may provide as much as half of the nitrogen used by *P. perforata* under non-upwelling conditions, but provide only one sixth of required nitrogen during upwelling. Because upwelling and non-upwelling events occur with approximately equal frequency on the northern California coast, on average, approximately one third of *P. perforata*'s nitrogen may come from ammonium, most of which probably comes from local-scale excretion by animals.

Local-scale autochthonous nutrient inputs from sessile invertebrates are most likely to influence algal species like *P. perforata* that are fast growing and have high ammonium-uptake rates. Of eight common intertidal algal species tested by Bracken and Stachowicz (2006), *P. perforata* has the second greatest uptake rate of ammonium relative to nitrate (after *Ulva* spp.) and the fourth highest absolute uptake rate of ammonium after *Cladophora columbiana*, *Microcladia borealis*, and *Ulva*. Although these other ammonium-preferring species were not present in high abundances in our experiment, they showed trends similar to *P. perforata*. In the field experiment, *M. borealis* was only present in live-mussel plots and not in bare-rock plots or mussel-mimic plots, and *C. columbiana* and *Ulva* were both more abundant in live-mussel plots than in bare rock or mussel mimic plots. In contrast, *M. papillatus* and *M. flaccida*, species characterized by Bracken and Stachowicz (2006) as relatively poorer at ammonium uptake, did not show the same cover patterns as *P. perforata*. Even if these other species can utilize ammonium excreted by mussels, *P. perforata* probably does so to a greater degree and thus interspecific competition from *P. perforata* may preclude increases in cover of other species on mussels.

Because *P. perforata* cover was 10 times higher on mussels than on bare rock in surveys (Fig. 1), but grew only three times faster on mussels than bare rock (Fig. 2), biotic effects of mussels unexplored here, such as those that influence algal settlement rather than algal growth, could also affect algal abundance on mussels. In addition to the facilitative effects of mussels on algae, it is possible that there are reciprocal effects of algae on mussels. Negative effects such as increased frequency of dislodgement due to greater drag and interference with mussel filtration activities are well known (Dayton 1973; Suchanek 1979); however, algae may also have positive effects on mussels via shading. Shading by algae can lower mussel temperatures (M. N. Faubel, unpubl.) and decrease desiccation, increasing mussel survival rates (Bertness and Leonard 1997). Though mussels, along with other sessile invertebrates, have long been established as structuring aquatic communities via competitive exclusion (Connell 1961; Menge 1976), more recent evidence has demonstrated that sessile invertebrates can greatly increase nutrient concentrations (Pfister et al. 2007) and that these increased nutrients have facilitative effects on other species (Hurd et al. 1994; Williamson and Rees 1994; Bracken 2004). Thus,

the net effect of sessile invertebrates on other sessile species, particularly epibiotic species, may be positive when nutrient facilitation is considered. Although *P. perforata* may compete with mussels for space on primary substrates, our results indicate that facilitation by mussels may be as important as competition for space in determining growth and abundance of some algal species.

While the facilitation of mobile species by mussels via habitat provision is well documented (Suchanek 1979; Lohse 1993), nutrient provision to epibionts on a relatively competition-free substrate is an additional mechanism of facilitation for sessile species that has not been previously demonstrated outside low-flow environments. It is likely that this type of facilitation extends to other invertebrates that act as substrate for epibionts with high ammonium affinity. Because changing nutrient ratios due to excretion by consumers can affect relative growth rates of different species, altering competitive outcomes (Vanni et al. 1997), invertebrate nutrient inputs may have important implications for algal community composition and structure. Even under relatively high-flow conditions (i.e., wave heights of ~1 m and flow speeds approaching 4 m s⁻¹; Bell and Denny 1994; Gaylord 1999), ammonium concentrations remained higher over mussel beds than adjacent bare rock. This is striking because a substantial portion of the world's marine nearshore environments experience considerable flow, leading some to question whether local-scale use of animal-derived nutrient subsidies is a general phenomenon. Our data demonstrate that local-scale nutrient regeneration can affect algal growth rates and algal species composition over tens of centimeters. Because suspension-feeding, sessile invertebrates, and mussels in particular, often dominate intertidal habitats characterized by high wave action, their influence on local nutrient content (and algal species abundance and composition) by fertilization in high-flow environments may be widespread and will need to be considered, along with their other ecological effects, in models of nearshore benthic community structure.

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