

UC Davis

UC Davis Previously Published Works

Title

Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium

Permalink

<https://escholarship.org/uc/item/0xs3w4s5>

Journal

Ecology, 87(9)

Authors

Bracken, Matthew E S
Stachowicz, John J

Publication Date

2006-09-01

Peer reviewed

SEAWEED DIVERSITY ENHANCES NITROGEN UPTAKE VIA COMPLEMENTARY USE OF NITRATE AND AMMONIUM

MATTHEW E. S. BRACKEN^{1,2,3} AND JOHN J. STACHOWICZ²

¹*Bodega Marine Laboratory, University of California at Davis, P.O. Box 247, Bodega Bay, California 94923 USA*

²*Section of Evolution and Ecology, One Shields Avenue, University of California, Davis, California 95616 USA*

Abstract. The consequences of declining biodiversity remain controversial, in part because many studies focus on a single metric of ecosystem functioning and fail to consider diversity's integrated effects on multiple ecosystem functions. We used tide pool microcosms as a model system to show that different conclusions about the potential effects of producer diversity on ecosystem functioning may result when ecosystem functions are measured separately vs. together. Specifically, we found that in diverse seaweed assemblages, uptake of either nitrate or ammonium alone was equal to the average of the component monocultures. However, when nitrate and ammonium were available simultaneously, uptake by diverse assemblages was 22% greater than the monoculture average because different species were complementary in their use of different nitrogen forms. Our results suggest that when individual species have dominant effects on particular ecosystem processes (i.e., the sampling effect), multivariate complementarity can arise if different species dominate different processes. Further, these results suggest that similar mechanisms (complementary nutrient uptake) may underlie diversity–functioning relationships in both algal and vascular-plant-based systems.

Key words: ammonium; biodiversity; complementarity; ecosystem function; macroalgae; nitrate; nitrogen uptake; rocky intertidal; seaweeds.

INTRODUCTION

Because organisms differ in their impacts on biogeochemical processes, there is growing consensus that the diversity of species in an ecosystem influences that system's functioning (Loreau et al. 2001, Kinzig et al. 2002). Three major classes of mechanisms that link diversity with enhanced functioning have been identified: the sampling effect, which is the increased probability of including a dominant species in a more diverse assemblage (Huston et al. 2000); complementarity, which occurs when species partition limiting resources, reducing competitive overlap among community members and leading to enhanced resource use in systems containing more species (Loreau and Hector 2001); and facilitation, the enhancement of ecosystem-level processes due to beneficial interactions among species in the system (Cardinale et al. 2002). Considerable research has debated the relative importance of these mechanisms (particularly complementarity vs. the

sampling effect) and their conservation relevance. The dichotomy between these mechanisms may be, in part, a consequence of the deliberate focus on individual response variables as independent measures of ecosystem function (but see Hooper and Vitousek 1998). A recent analysis of the effects of crustacean-grazer diversity on a suite of ecosystem properties found that more diverse grazer assemblages maximized multiple ecosystem functions simultaneously, because different species had dominant effects on different ecosystem functions (Duffy et al. 2003). These results suggest that multivariate complementarity may emerge when multiple ecosystem functions are simultaneously considered, but the generality of this finding is unclear.

We explicitly tested this hypothesis of multivariate complementarity by evaluating the influence of tide pool seaweed diversity on the flux of nitrogen, the primary limiting nutrient in temperate nearshore marine systems (Ryther and Dunstan 1971). Inorganic nitrogen in northeastern Pacific tide pools occurs in two forms. (1) Ammonium is excreted as a waste product by invertebrates and accumulates in pools at low tide (Bracken 2004, Bracken and Nielsen 2004). (2) Nitrate is brought to the ocean surface by coastal upwelling and is

Manuscript received 9 September 2005; revised 3 January 2006; accepted 8 February 2006. Corresponding Editor: P. D. Steinberg.

³ E-mail: mebracken@ucdavis.edu

available to seaweeds at high tide (Fujita et al. 1989), but can be rapidly depleted when pools are isolated at low tide (Bracken and Nielsen 2004). Because ammonium is primarily associated with local-scale regeneration, whereas nitrate availability is predominately determined by oceanographic processes in the adjacent nearshore ocean, these two nitrogen forms are usually considered separately in studies of nitrogen dynamics in coastal ecosystems (Dugdale and Goering 1967, Eppley and Peterson 1979). Therefore, in this study we treated nitrate and ammonium fluxes as separate, but potentially complementary, ecosystem processes. The physiological mechanisms by which each form is used differ substantially (Lobban and Harrison 1994), and different seaweed species show uptake and storage preferences for either nitrate or ammonium (Pedersen and Borum 1997, Naldi and Wheeler 1999), suggesting that seaweeds with different morphologies, physiological capabilities, and life-history strategies might differ in their abilities to utilize nitrate vs. ammonium (Wallentinus 1984, Pedersen and Borum 1997, Naldi and Wheeler 1999). If species are complementary in their use of nitrate and ammonium, nitrogen uptake by a multi-species assemblage may be enhanced when both nitrogen forms are available, providing a mechanistic link between producer diversity and nutrient use in marine ecosystems.

We measured nitrogen fluxes in outdoor tide pool microcosms, where we compared the abilities of eight seaweed species in monoculture and polyculture to take up nitrogen provided as nitrate, ammonium, or both nitrate and ammonium. We then compared the measured nitrogen uptake coefficients of the eight-species polycultures with those predicted by the component monocultures (Emmerson and Raffaelli 2000). We were unable to partition sampling vs. complementarity effects because it was not possible to measure individual species' uptake rates in the polycultures (Loreau and Hector 2001). However, the comparison of predicted and measured uptake coefficients provided a statistical test for nontransgressive overyielding, which occurs when a polyculture's impact on ecosystem functioning is greater than the weighted average effects of its component monocultures (Fridley 2001). This comparison allowed us to evaluate potential mechanisms underlying the positive correlation we previously observed between seaweed diversity and nitrogen uptake in natural tide pools (Bracken and Nielsen 2004). Because many terrestrial experiments linking producer diversity and ecosystem functioning have measured diversity effects on nitrogen pools and fluxes (Tilman et al. 1997, Hooper and Vitousek 1998, Tilman 1999), our study provides a direct analogue to terrestrial experiments, allowing us to address the generality of these relationships and mechanisms in a system where nutrient acquisition occurs via fundamentally different processes (i.e., algae lack roots). More generally, less than 3% of

published studies investigating the effect of diversity on ecosystem processes have been conducted in marine systems (Naeem and Wright 2003), and most of this work has focused on the effects of consumer diversity (e.g., Stachowicz et al. 1999, Emmerson et al. 2001, Duffy et al. 2003; but see Bruno et al. 2005). This makes it difficult to compare marine studies with studies in terrestrial ecosystems, where most research has quantified the effects of producer diversity.

METHODS

Eight species of intertidal seaweeds were collected from the Bodega Marine Reserve on the northern coast of California, USA (38°19.0' N, 123°4.1' W): five Rhodophytes (*Mastocarpus papillatus*, *Mazzaella flaccida*, *Microcladia borealis*, *Porphyra perforata*, and *Prionitis lanceolata*); one Heterokontophyte (*Fucus gardneri*); and two Chlorophytes (*Cladophora columbiana* and *Ulva taeniata*) (see Gabrielson et al. 2004 for authorities). The macroalgal species in our assemblages commonly occur in tide pools on northeastern Pacific rocky shores (Nielsen 2003), representing >80% of biomass in surveyed pools (Bracken and Nielsen 2004); our experimental assemblages included most of the species found in natural tide pools. These species spanned a range of morphologies, including filaments, thinly corticated species, thin blades, and thickly corticated species. Algae were kept outdoors under ambient daylight conditions in running seawater ($26.5 \pm 5.3 \mu\text{mol/L NO}_3^-$ and $2.3 \pm 0.6 \mu\text{mol/L NH}_4^+$) for <24 h before uptake trials were conducted. Immediately prior to uptake measurements, algae were rinsed in nitrogen-depleted seawater to remove sediment, epiphytes, and residual nitrogen.

Nitrogen uptake measurements were conducted in 0.4-L microcosms, which were maintained at ambient seawater temperatures ($12.9^\circ \pm 0.3^\circ\text{C}$; mean \pm SE). Previous studies have shown that nitrogen dynamics in microcosms of this size are similar to those in natural tide pools (Bracken 2004, Bracken and Nielsen 2004). All trials were conducted outside, under natural light conditions ($1345 \pm 87 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), to ensure that light availability did not limit nitrogen uptake.

We added 0.4 L of nitrogen-depleted seawater and 24 g (wet mass) of algae to each microcosm. Polycultures were composed of equal masses (3 g wet tissue) of each of the eight component species. One problem with replacement series designs like this one is that they confound changes in species composition with changes in intraspecific density. However, our previous field surveys of tide pools (Bracken and Nielsen 2004) found no relationship between seaweed diversity and biomass, suggesting that natural pools support a given amount of algal biomass, which is partitioned among the species present. This observation argues that the most ecologically relevant design is one in which total biomass

across all levels of diversity is constant. The density of algae in our microcosms was well within the range of densities recorded in natural tide pools (microcosms, 12.46 ± 0.11 g dry tissue/L; natural tide pools, 14.53 ± 6.10 g dry tissue/L; calculated from data in Bracken and Nielsen [2004]). By matching the seaweed densities in our microcosms to those measured in the field, we ensured that our experimental design was appropriate for quantifying the extent to which seaweeds partition nitrate and ammonium in tide pools (Sackville Hamilton 1994).

Nitrogen (as 100% NH_4Cl , 100% NaNO_3 , or 50% NH_4Cl and 50% NaNO_3) was added to the microcosms to supply macroalgae with initial nitrogen concentrations of 2, 4, 8, 12, 20, 30, 40, and 60 $\mu\text{mol/L}$. Initial nitrogen concentrations spanned the ranges of ammonium and nitrate concentrations observed in natural tide pools, where ammonium concentrations (associated with excretion by invertebrates) average 24.1 ± 6.4 $\mu\text{mol/L}$ and nitrate concentrations (associated with coastal upwelling and bacterial oxidation) average 29.2 ± 2.9 $\mu\text{mol/L}$ (Bracken and Nielsen 2004). Four replicate microcosms were sampled at each initial concentration, and we measured nitrogen uptake in a total of 32 microcosms for each combination of species and nitrogen form. Water samples were collected at 0, 15, and 30 min and analyzed for ammonium and nitrate concentrations (Parsons et al. 1984). The change in the nitrogen concentration in each microcosm over a 30-min incubation period was used to calculate the biomass-specific nitrogen uptake rate of the seaweeds in that microcosm ($\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) as a function of initial nitrogen concentration. Because of still water conditions in the microcosm (which occur in natural tide pools at low tide), nitrogen uptake rates did not saturate, and relationships between nitrogen uptake and concentration were linear. Regression constants (y -intercepts) for the relationships between uptake rates and initial nitrogen concentration were never significantly different from 0 (one-sample t tests, $P > 0.10$), so we used the slopes of these linear relationships as coefficients ($\text{L}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) describing the uptake capabilities of each of the monocultures and polycultures (Phillips and Hurd 2004).

The data were analyzed using one- and two-sample t tests and general linear models after verifying normal distributions and homogeneity of variances. The uptake coefficients of the component monocultures were used to predict the uptake coefficients of the polycultures for each nitrogen source (ammonium, nitrate, and ammonium and nitrate). Each species' contribution to a predicted uptake coefficient was weighted by its actual proportion of the dry tissue mass in each polyculture. This was necessary because uptake rates were normalized by dry tissue mass, but partitioning of biomass in polycultures was initially done using wet tissue mass.

However, expressing results in terms of wet tissue mass (assuming equal proportions of each species) did not affect the outcomes of any of the analyses. The variance associated with each monoculture uptake coefficient was calculated using regression analyses, and the predicted polyculture variances were calculated by normalizing the monoculture standard deviations by their proportion of the total biomass in each microcosm, then using those mass-normalized standard deviations to calculate pooled estimates of variance (Ramsey and Schafer 1997). Measured and predicted uptake coefficients were then compared using two-sample t tests. Actual sample sizes for these calculations ranged from $n = 29$ to 32, due to occasional sample loss during nitrogen analyses.

Because ammonium uptake coefficients were virtually always higher than nitrate coefficients for each species (see *Results*), we used relative uptake ratios (r) to evaluate each species' uptake of nitrate and ammonium relative to other species:

$$r = \frac{\text{NO}_3^- / \overline{\text{NO}_3^-}}{\text{NH}_4^+ / \overline{\text{NH}_4^+}},$$

where NO_3^- and NH_4^+ are a species' nitrate and ammonium uptake coefficients, respectively, and $\overline{\text{NO}_3^-}$ and $\overline{\text{NH}_4^+}$ are the average nitrate and ammonium uptake coefficients of all eight seaweed species. This ratio provides an index that reflects the ability of each species to take up nitrate and ammonium relative to the other species in the eight-species assemblage. Thus, if $r > 1$, a species is relatively more effective at nitrate uptake, whereas if $r < 1$, then a species is relatively more effective at ammonium uptake. In general, if ratios of most species are very different from 1, then species that are more effective at nitrate uptake are less effective at ammonium uptake and vice versa. Conversely, if most ratios are close to one, then species tend to be similar in their uptake of both nitrogen forms.

RESULTS

For uptake of either ammonium or nitrate alone, the polycultures' measured uptake coefficients were no different than those predicted by the monocultures (Table 1; for NH_4^+ , $t = 0.589$, $\text{df} = 60$, $P = 0.552$; for NO_3^- , $t = 0.927$, $\text{df} = 58$, $P = 0.356$). However, when equal proportions of ammonium and nitrate were provided, the eight-species polycultures were 22% more effective at nitrogen uptake than predicted based on the uptake abilities of the individual species composing those polycultures (Table 1; $t = 3.104$, $\text{df} = 59$, $P = 0.003$) and 27% more effective than predicted, based on the polycultures' uptake of nitrate and ammonium alone ($t = 4.351$, $\text{df} = 60$, $P < 0.0001$), indicating that overyielding occurred when both nitrate and ammonium were available (Tilman 1999, Fridley 2001).

This nonadditive effect of diversity on nitrogen uptake indicated that one or more seaweed species

TABLE 1. Nitrogen uptake coefficients (means \pm SE) of tide pool macroalgae.

Species	Uptake coefficients ($L \cdot h^{-1} \cdot g^{-1}$)		
	NH_4^+	NO_3^-	NH_4^+ and NO_3^-
Monocultures			
<i>Cladophora</i>	0.116 \pm 0.019	0.017 \pm 0.016	0.049 \pm 0.009
<i>Microcladia</i>	0.148 \pm 0.008	0.032 \pm 0.004	0.104 \pm 0.006
<i>Ulva</i>	0.155 \pm 0.010	0.033 \pm 0.008	0.117 \pm 0.010
<i>Porphyra</i>	0.150 \pm 0.004	0.074 \pm 0.007	0.139 \pm 0.005
<i>Fucus</i>	0.066 \pm 0.004	0.037 \pm 0.002	0.067 \pm 0.003
<i>Mastocarpus</i>	0.089 \pm 0.006	0.057 \pm 0.002	0.045 \pm 0.003
<i>Prionitis</i>	0.098 \pm 0.008	0.067 \pm 0.005	0.085 \pm 0.004
<i>Mazzaella</i>	0.096 \pm 0.005	0.080 \pm 0.005	0.089 \pm 0.004
Polycultures†			
Predicted	0.112 \pm 0.007	0.053 \pm 0.005	0.086 \pm 0.005
Observed	0.117 \pm 0.005 ^{NS}	0.047 \pm 0.003 ^{NS}	0.105 \pm 0.003 ^{**}

† Statistical comparisons of predicted vs. observed polyculture uptake coefficients are indicated: NS, not significant ($P > 0.355$ in both cases); ** $P = 0.003$.

exhibited enhanced, biomass-specific uptake in polyculture, but only when both nitrate and ammonium were available. While non-additivity could be associated with facilitation (Cardinale et al. 2002), this is an unlikely explanation in this case, as facilitation would likely involve enhancement of either nitrate or ammonium uptake, and polyculture uptake coefficients were predicted by component monocultures for both nitrate and ammonium alone (Table 1). This pattern could also arise if species exhibited nonlinear responses to changes in nitrogen concentration, as the concentrations of nitrate and ammonium added in combination were half the concentrations of each added separately. We therefore compared the nitrate and ammonium uptake coefficients of monocultures when one vs. both nitrogen forms were available. We found that the range of initial concentrations (1–30 $\mu\text{mol/L}$ or 2–60 $\mu\text{mol/L}$) did not influence the uptake coefficient ($P > 0.15$ for all combinations of species and nitrogen forms). Instead, the overyielding we describe here is consistent with reduced interspecific competition for each nutrient in microcosms where both forms of nitrogen were available (Jolliffe 2000). There was overyielding in uptake of both nitrate ($t = 2.831$, $df = 59$, $P = 0.006$) and ammonium ($t = 2.816$, $df = 59$, $P = 0.007$) in polyculture when both chemical forms of nitrogen were present, suggesting that competition for both nitrate and ammonium was reduced in diverse assemblages.

Evaluations of each species' ability to utilize nitrogen suggested that the mechanism underlying the observed overyielding was, indeed, reduced competition associated with complementary uptake of nitrate and ammonium. All species had greater rates of ammonium uptake than nitrate uptake (Table 1), but species that were the most effective at utilizing ammonium were among the poorest at taking up nitrate, and those that were the strongest at nitrate uptake were among the weakest at using ammonium (Table 1, Fig. 1). For example, *Microcladia* was more effective than *Mazzaella* at

utilizing ammonium (ammonium \times species interaction; $F_{1,57} = 32.2$, $P < 0.0001$), whereas *Mazzaella* was better than *Microcladia* at nitrate uptake (nitrate \times species interaction; $F_{1,46} = 31.8$; $P < 0.0001$). In general, species could be divided into two functional groups that were relatively better at utilizing either nitrate or ammonium. *Cladophora*, *Microcladia*, and *Ulva* were more effective at ammonium uptake (relative uptake ratio < 1 ; $P < 0.01$), whereas *Prionitis*, *Fucus*, *Mastocarpus*, and *Mazzaella* were better at nitrate uptake (relative uptake ratio > 1 ; $P < 0.001$) (Fig. 1). Results of these analyses were qualitatively the same regardless of whether relative or absolute uptake ratios were used. Only *Porphyra* was equally effective at utilizing nitrate and ammonium ($P = 0.174$). While this species was characterized by relatively high uptake of both nitrate and ammonium (it was the only species with combined nitrate and ammonium uptake rates greater than the polyculture [$t = 5.72$, $df = 60$, $P < 0.001$; Table 1]), the low fraction of each species' biomass in the polycultures prevented any one species from dominating nitrogen uptake.

DISCUSSION

Our results suggest that when both functional groups of macroalgae, those preferring ammonium and those preferring nitrate, co-occur in tide pools, and both forms of nitrogen are present, niche partitioning can reduce competition and lead to greater nitrogen fluxes into intertidal ecosystems. This study provides a simple example of how measuring additional response variables can lead to different conclusions about the influences of diversity on ecosystem functioning. If we had assessed nitrate or ammonium uptake separately, we would have mistakenly concluded that the uptake rate of a diverse assemblage is a simple weighted average of the uptake rates of the component species and that diversity affects nitrogen uptake only via a sampling effect. However, measuring uptake of both nitrogen forms simultaneously revealed that multivariate complementarity can

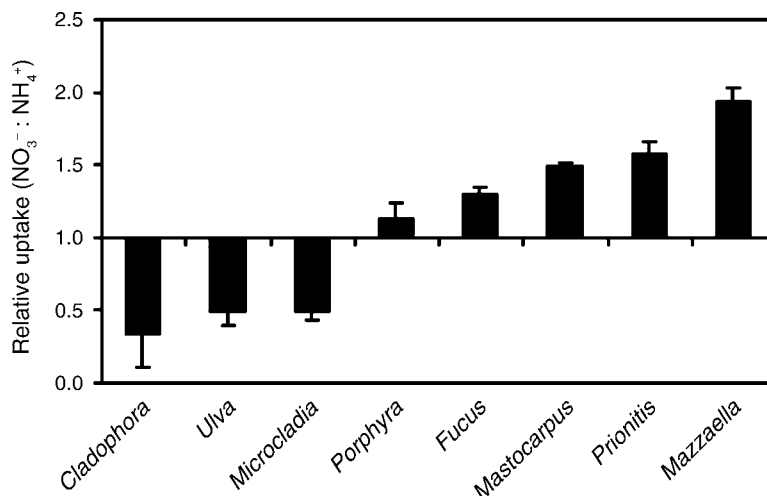


FIG. 1. Relative uptake of NO_3^- and NH_4^+ by tide pool seaweed species. Ratios (mean \pm SE) represent each species' relative ability to take up NO_3^- vs. NH_4^+ . Values >1 indicate that a species is more effective than average at NO_3^- uptake, and values <1 indicate that a species is more effective at NH_4^+ uptake.

lead to non-transgressive overyielding (Table 1). As a corollary, our results predict that if one nitrogen form is rare or absent, diversity will only affect nitrogen uptake via a sampling effect.

While *Porphyra* monocultures outperformed the polycultures when both nitrate and ammonium were available, this species never dominates tide pools in the Bodega Marine Reserve ($<1\%$ of algal cover in 50 pools surveyed; C. Gonzalez-Dorantes, M. Bracken, and J. Stachowicz, unpublished data), perhaps because it is highly susceptible to grazing by molluscs present in the pools. In fact, the best-performing monocultures (*Porphyra* and *Ulva*; Table 1) are both preferentially consumed by herbivores (Lubchenco 1978, Harley 2002), which suggests a possible trade-off between a seaweed's ability to sequester nitrogen and its tolerance to herbivory. In most high-zone tide pools, herbivores are abundant (Nielsen 2003, Bracken and Nielsen 2004), which likely limits the abilities of species like *Ulva* and *Porphyra* to dominate the pools. The importance of diversity in mediating nitrogen uptake by seaweed assemblages may therefore be context dependent. Where herbivore densities are high, complementarity links diversity and nitrogen use, but where herbivores are less abundant, one or a few dominant species may be responsible for the majority of nitrogen uptake. Like other recent work in marine systems (Duffy et al. 2005, Byrnes et al. 2006), this result highlights the importance of including higher trophic levels in evaluating the relationship between diversity and ecosystem functioning.

In fact, the majority of tide pools in the Bodega Marine Reserve are dominated by *Cladophora*, which has a strong preference for ammonium, and *Prionitis*, which is relatively better at taking up nitrate (Fig. 1). These two species collectively comprise 65% of macroalgal cover, and each has a lower nitrogen uptake rate

than the polyculture when both nitrate and ammonium are available (Table 1). Thus, in natural tide pools, where nitrate concentrations (associated with nearshore oceanographic conditions at high tide and bacterial oxidation at low tide) can exceed $70 \mu\text{mol/L}$, and invertebrate-mediated ammonium concentrations can reach $44 \mu\text{mol/L}$ (Bracken and Nielsen 2004), complementary use of nitrate and ammonium likely plays an important role in linking algal diversity and nitrogen fluxes. Because the dominant form of available nitrogen changes over tidal and seasonal cycles (Fujita et al. 1989, Bracken and Nielsen 2004), this mechanism of complementarity may commonly enhance the consistency of nitrogen inputs into diverse intertidal systems. However, because seaweeds' relative uptake preferences for nitrate and ammonium vary in time and space (Hanisak and Harlin 1978, Phillips and Hurd 2003), the multivariate complementarity effect we describe may also depend to some extent on time of day, season, and location. Finally, our uptake calculations are based on 30-min incubations and may not be representative of uptake over longer periods of time (Pedersen 1994), though maintaining the algae in ambient high-nitrogen seawater during the brief period between collection and uptake trials should have minimized depletion of internal nitrogen pools, reducing the potential for initial transient enhancement of nitrogen uptake.

This study highlights the lessons that can be learned by conducting analogous measurements of diversity effects on ecosystem functioning in different ecosystems. While diversity influences nitrogen uptake in both terrestrial (Tilman et al. 1997, Hooper and Vitousek 1998) and marine (Bracken and Nielsen 2004, Hughes and Stachowicz 2004) ecosystems, differences in nutrient diffusion and acquisition mean that the mechanisms linking

diversity and ecosystem functioning in these systems can be very different. For example, vascular plant species vary with respect to rooting depth and root morphology (Tilman et al. 1997, Hooper and Vitousek 1998, Loreau 1998), allowing plants to spatially partition nitrogen in the soil, such that spatial complementarity can link plant diversity and uptake of either nitrate or ammonium alone (Tilman et al. 1997, Loreau 1998, Fargione and Tilman 2005). In contrast, rapid diffusion of nitrate and ammonium in marine systems precludes a spatial distribution of resources for marine algae, which obtain nutrients from the fluid medium in which they are bathed (Phillips and Hurd 2003). Previously observed links between seaweed diversity and uptake of either ammonium or nitrate alone (Nielsen 1998, Bracken and Nielsen 2004) may therefore be associated with the sampling effect, because species with high capacities for nitrogen uptake occurred in more diverse tide pools but not in species-poor ones. However, when both forms of nitrogen are present, different species are more effective at obtaining nitrate or ammonium, reducing interspecific competition and resulting in enhanced total nitrogen uptake (Table 1). Multivariate nitrogen complementarity is also likely to occur in terrestrial ecosystems, where specialization by plant species on different nitrogen forms (nitrate, ammonium, and free amino acids) influences plant species diversity and community composition (McKane et al. 2002).

Our results suggest that a more complete understanding of the influence of diversity on ecosystem functioning can emerge when multiple ecosystem functions are considered simultaneously. Most studies have focused on links between diversity and a narrow range of ecosystem functions, such as primary production and nutrient retention (Loreau et al. 2001), but each ecosystem is characterized by a multitude of biogeochemical transformations and fluxes. When different species or functional groups maximize different ecosystem functions (Petchey and Gaston 2002, Duffy et al. 2003), these independent effects can combine to generate multivariate complementarity.

ACKNOWLEDGMENTS

We thank S. Williams for advice, lab space, and equipment; A. Carranza, E. Jones, and C. Sorte for research assistance; and J. Byrnes, M. Graham, C. Harley, E. Sanford, and several anonymous reviewers for helpful comments on the manuscript. This research was supported by the National Science Foundation (OCE-0351778 to J. Stachowicz). This is contribution number 2303 of the Bodega Marine Laboratory, University of California, Davis, California, USA.

LITERATURE CITED

- Bracken, M. E. S. 2004. Invertebrate-mediated nutrient loading increases growth of an intertidal macroalga. *Journal of Phycology* **40**:1032–1041.
- Bracken, M. E. S., and K. J. Nielsen. 2004. Diversity of intertidal macroalgae increases with nutrient loading by invertebrates. *Ecology* **85**:2828–2836.
- Bruno, J. F., K. E. Boyer, J. E. Duffy, S. C. Lee, and J. S. Kertesz. 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecology Letters* **8**:1165–1174.
- Byrnes, J., J. J. Stachowicz, K. M. Hultgren, A. R. Hughes, S. V. Olyarnik, and C. S. Thornber. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecology Letters* **9**:61–71.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**:426–429.
- Duffy, J. E., J. P. Richardson, and E. A. Canuel. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters* **6**:637–645.
- Duffy, J. E., J. P. Richardson, and K. E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters* **8**:301–309.
- Dugdale, R. C., and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography* **12**:196–206.
- Emmerson, M. C., and D. G. Raffaelli. 2000. Detecting the effects of diversity on measures of ecosystem function: experimental design, null models and empirical observations. *Oikos* **91**:195–203.
- Emmerson, M. C., M. Solan, C. Emes, D. M. Paterson, and D. Raffaelli. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* **411**:73–77.
- Eppley, R. W., and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* **282**:677–680.
- Falkowski, P. G., R. T. Barber, and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science* **281**:200–206.
- Fargione, J., and D. Tilman. 2005. Niche differences in phenology and rooting depth promote coexistence with a dominant C₄ bunchgrass. *Oecologia* **143**:598–606.
- Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281**:237–240.
- Fridley, J. D. 2001. The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos* **93**:514–526.
- Fujita, R. M., P. A. Wheeler, and R. L. Edwards. 1989. Assessment of macroalgal nitrogen limitation in a seasonal upwelling region. *Marine Ecology Progress Series* **53**:293–303.
- Gabrielson, P. W., T. B. Widdowson, and S. C. Lindstrom. 2004. Keys to the seaweeds and seagrasses of Oregon and California, north of Point Conception. PhycOID, Hillsborough, North Carolina, USA.
- Hanisak, M. D., and M. M. Harlin. 1978. Uptake of inorganic nitrogen by *Codium fragile* subsp. *tomentosoides* (Chlorophyta). *Journal of Phycology* **14**:450–454.
- Harley, C. D. G. 2002. Light availability indirectly limits herbivore growth and abundance in a high rocky intertidal community during the winter. *Limnology and Oceanography* **47**:1217–1222.
- Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**:121–149.
- Hughes, A. R., and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences (USA)* **101**:8998–9002.
- Huston, M. A., L. W. Aarssen, M. P. Austin, B. S. Cade, J. D. Fridley, E. Garnier, J. P. Grime, J. Hodgson, W. K. Lauenroth, K. Thompson, J. H. Vandermeer, and D. A.

- Wardle. 2000. No consistent effect of plant diversity on productivity. *Science* 289:1255a.
- Jolliffe, P. A. 2000. The replacement series. *Journal of Ecology* 88:371–385.
- Kinzig, A., S. W. Pacala, and D. Tilman. 2002. The functional consequences of biodiversity. Princeton University Press, Princeton, New Jersey, USA.
- Lobban, C. S., and P. J. Harrison. 1994. Seaweed ecology and physiology. Cambridge University Press, New York, New York, USA.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: a mechanistic model. *Proceedings of the National Academy of Sciences (USA)* 95:5632–5636.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112: 23–39.
- McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, K. Kielland, B. L. Kwiatkowski, J. A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415:68–71.
- Naeem, S., and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6:567–579.
- Naldi, M., and P. A. Wheeler. 1999. Changes in nitrogen pools in *Ulva fenestrata* (Chlorophyta) and *Gracilaria pacifica* (Rhodophyta) under nitrate and ammonium enrichment. *Journal of Phycology* 35:70–77.
- Nielsen, K. J. 1998. Bottom-up and top-down forces in tidepools: the influence of nutrients, herbivores, and wave exposure on community structure. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Nielsen, K. J. 2003. Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. *Proceedings of the National Academy of Sciences (USA)* 100:7660–7665.
- Parsons, T. R., Y. Maita, and C. M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon, New York, New York, USA.
- Pedersen, M. F. 1994. Transient ammonium uptake in the macroalga *Ulva lactuca* (Chlorophyta): nature, regulation, and the consequences for choice of measuring technique. *Journal of Phycology* 30:980–986.
- Pedersen, M. F., and J. Borum. 1997. Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. *Marine Ecology Progress Series* 161:155–163.
- Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402–411.
- 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. *Marine Ecology Progress Series* 264:31–48.
- Phillips, J. C., and C. L. Hurd. 2004. Kinetics of nitrate, ammonium, and urea uptake by four intertidal seaweeds from New Zealand. *Journal of Phycology* 40:534–545.
- Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, California, USA.
- Ryther, J. H., and W. M. Dunstan. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* 171:1008–1013.
- Sackville Hamilton, N. R. 1994. Replacement and additive designs for plant competition studies. *Journal of Applied Ecology* 31:599–603.
- Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455–1474.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Wallentinus, I. 1984. Comparisons of nutrient uptake rates for Baltic macroalgae with different thallus morphologies. *Marine Biology* 80:215–225.