Macroalgal-mediated transfers of water column nitrogen to intertidal sediments and salt marsh plants

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Abstract

In many temperate estuaries, mats of opportunistic macroalgae accumulate on intertidal flats and in lower elevations of salt marshes, perhaps playing a role in linking water column nitrogen (N) supply to these benthic habitats. Using a flow-through seawater system and tidal simulator, we varied densities (equivalent to 0, 1, 2, or 3 kg m⁻² wet mass) of ¹⁵N-labelled macroalgae (Enteromorpha intestinalis) on estuarine sediments in microcosms with/without pickleweed (Salicornia virginica) to assess N transfers from algae. In the 6-week experiment, macroalgal biomass increased from initial levels in the lower density treatments but all algae lost N mass, probably through both leakage and decomposition. With all densities of algae added, sediments and pickleweed became enriched in ¹⁵N. With increasing mat density, losses of algal N mass increased, resulting in stepwise increases in ¹⁵N labeling of the deeper sediments and pickleweed. While we did not detect a growth response in pickleweed with macroalgal addition during the experiment, N losses from algal mats that persist over many months and/or recur each year could be important to the mineral nutrition of N-limited marsh plants. We conclude that N dynamics of intertidal sediments and lower salt marsh vegetation are linked to the N pools of co-occurring macroalgae and that further study is needed to assess the magnitude and importance of N transfers.

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1. Introduction

Many studies have documented algal-mediated linkages between nutrient dynamics of the water column and sediments in the subtidal zone of estuaries. For example, phytoplankton and macroalgae suspended in the water column influence benthic nutrient processes through interception of
light and water column nutrients (Fong et al., 1993; McGlathery et al., 1997; Hauxwell et al., 2001). Macroalgae can also intercept nutrients fluxing from the sediments (Bierzychudek et al., 1993) and promote such fluxes by depleting water column nutrients (Thybo-Christesen et al., 1993; Fong and Zedler, 2000). In addition, macroalgae have been found to release nutrients and organic matter to underlying sediments when decomposing (Hansen and Kristensen, 1997; Tyler et al., 2001), fueling remineralization, and nutrient fluxes back to the water column (Lavery and McComb, 1991; Hansen and Blackburn, 1992; Enoksson, 1993).

While many of the same processes are at work in the intertidal zone of estuaries, alternating immersion and emersion of the sediment surface may uniquely influence the relationship between algae and benthic/pelagic nutrient exchanges. For example, benthic microalgae at the surface of intertidal flats access both the water column and sediment nutrient supply when submerged, but direct deposition of N from the air during exposure can be several orders of magnitude higher (Paerl, 1997). Further, macroalgae in the intertidal become desiccated when exposed at low tide, resulting in reduction of photosynthesis, light attenuation within the compressed algal mat, and inorganic carbon limitation (Pregnall, 1983; Pregnall and Rudy, 1985). These stresses are likely to influence nutrient dynamics both within and outside of the algal mat.

Growth and accumulation of macroalgae on intertidal flats are common in many estuaries throughout the world, with percent cover up to 100%, especially where anthropogenic N supply is pronounced (e.g., Pregnall and Rudy, 1985; Sfriso et al., 1992; Hernández et al., 1997; Kamer et al., 2001; Kennison et al., 2003). Opportunistic macroalgae, typically species in the green (Division Chlorophyta) genera Ulva, Enteromorpha, Cladophora, and Chaetomorpha, have rapid nutrient uptake, high growth rates, and the capacity to store “excess” nutrients for future growth (Rosenberg and Ramus, 1984; Fujita, 1985; Fong et al., 1994; Peckol et al., 1994). Such bloom-forming macroalgae represent a large pool of nutrients potentially available for release, and perhaps more prone to be released in the stressful intertidal zone.

Another distinguishing feature of the intertidal zone of estuaries is the presence of emergent vascular plants. In many locations, macroalgae can be found growing or deposited among the bases of the stems of these marsh plants at their lower elevations. One or more species of macroalgae can be observed among culms of smooth cordgrass (Spartina alterniflora Loisel) in many areas of the US, including the coastal bays of Maryland and Delaware (J. Gallagher, pers. comm.), Jamaica Bay, New York (D. Franz, pers. comm.), Bogue Sound, North Carolina (K. Boyer, pers. obs.), and Waquoit Bay, Massachusetts (P. Peckol, pers. comm.). In southern California, the major bloom-forming genera Enteromorpha and Ulva are found among Salicornia virginica L. (pickleweed), Salicornia bigelovii Torr. (annual pickleweed), Spartina foliosa Trin. (Pacific cordgrass), Batis maritima L. (saltwort), and Distichlis spicata L. (saltgrass) (K. Boyer, pers. obs., H. Page, pers. comm., Zedler, 1980).

While such associations may be fairly common in the lower marsh, we know of only one study that has explicitly examined the effects of macroalgae occurring on sediments among salt marsh plants. Gerard (1999) found lower biomass of S. alterniflora in plots where the brown alga Ascophyllum nodosum Scorpiodes was removed experimentally; algal nutrient releases to sediments upon decomposition were suggested, but not assessed, as the mechanism for enhancement of cordgrass growth.

If macroalgae release substantial quantities of nutrients in the intertidal zone, then enhancement of the nutrient supply to intertidal sediments and the plants rooted therein is plausible. In view of the fact that lower marsh plants are typically N limited (e.g., Broome et al., 1975; Boyer et al., 2001), access to water column N formerly sequestered in algal tissues could be important to marsh plant mineral nutrition where macroalgae co-occur. However, flooding tides may wash algal-derived nutrients out of the intertidal zone, limiting their accumulation in sediments and their uptake by associated vascular plants. Further, algal mats in the intertidal may initiate nutrient fluxes from sediments as can occur subtidally (e.g., Lavery and McComb, 1991), reducing sediment nutrient pools. Even if N is being supplied to the sediments by algal mats, if algal decomposition depletes oxygen and leads to accumulation of hydrogen sulfide in
sediments, marsh plant productivity may be reduced 
(Koch et al., 1990).

We are particularly interested in the fate of macro-
algal N in tidal flats and marshes dominated by coarse 
sediments. Where such habitats are created for 
restoration purposes, sediments are often sandy due 
to terrestrial origin or as a product of dredging (Langis 
et al., 1991; Craft et al., 1999). Coarse-grained 
sediments can also be found in marshes and tidal 
flats in geologically young systems such as those that 
form along barrier islands (Tyler and Zieman, 1998), 
in areas of estuaries where storms episodically deposit 
sandy terrestrial or dune/beach-derived sediments 
(Osgood and Zieman, 1993, 1995), or in areas where 
there are higher velocity flows (e.g., Bolam et al., 
2000). Sandy sediments lack the nutrient adsorption 
capacity of clay particles, and store and supply N 
poorly (Brady and Weil, 1999). Therefore, processes 
that supply N from external sources, e.g., advective 
flux of enriched tidal water through sediments 
(Osgood and Zieman, 1998), can be especially 
important to nutrient dynamics of coarse sediment 
systems. Macroalgal mats on sandy tidal flats could 
similarly act as an external N source.

The objective of our study was to investigate the 
potential role of macroalgal mats in influencing N 
supply to intertidal sand flats and salt marsh habitats. 

2. Methods

We performed a 4×2 factorial experiment varying 
E. intestinalis (hereafter called macroalgae) mat 
density (0, 1, 2, or 3 kg macroalgae m⁻², see below) 
and presence/absence of S. virginica (hereafter called 
pickleweed) in pots subjected to simulated tides (Fig. 
1). In April 2000, we collected sediment and 
pickleweed from a sandy restoration marsh at Mugu 
Lagoon in Ventura County, California. Sediments 
were collected from an unvegetated slope at a point 
just below the highest tidal elevation. Lower on the 
slope, a trowel was used to collect pickleweed 
recruits and soil surrounding their roots (~4 cm 
diameter, 4 cm deep).

Sediments were added to nursery pots and half were 
planted with pickleweed. Five extra pots were planted 
for later analysis of initial conditions. To acclimate 
plants, pots were set into pans of low nutrient (<3.57 
\(\mu M\) NO₃, <1.61 \(\mu M\) PO₄) seawater in a greenhouse at 
the University of CA Los Angeles for three weeks; de-
ionized water was added to counter evaporation.

Macroalgae were also collected at Mugu Lagoon, 
cleaned of visible fauna and debris, and cultured in 
low nutrient seawater to equalize internal nutrient 
stores. After 1 week, \(^{15}\text{N}\)-labelled NaNO₃ was added 
to produce a 200 \(\mu M\) culture solution, to simulate 
moderately enriched conditions common to southern 
CA estuarine waters (concentrations can exceed 800 
\(\mu M\) in upper Newport Bay (Boyle et al., 2004) and 
3000 \(\mu M\) at Carpinteria marsh, near Santa Barbara 
(Kennison et al., 2003)). Two more equivalent nitrate 
additions were made over the next 2 weeks, along 
with deionized water to counter evaporation.

The 6-week experiment was conducted outdoors 
at the Redondo Beach Generating Station in 
Redondo Beach, CA, from early May to mid-June 
2000. Algal tissue was spun for 1 min in a lettuce 
spinner, then divided into 20, 40, or 60 g portions 
(equivalent to 1, 2, or 3 kg algae m⁻²) to reflect the 
range in densities typical of estuaries in southern 
CA and elsewhere where algal blooms occur (e.g., 
Pregnall and Rudy, 1985; Hernández et al., 1997; 
Kamer et al., 2001; Tyler et al., 2001). Algal tissues 
were spread evenly on the sediment surface and the 
pots were placed in a random array on a table. With 
5-fold replication, there were a total of 40 pots, each 
independently plumbed with seawater using drip 
irrigation tubing and emitters (Fig. 1B). A swim-
ming pool timer controlled a pump to simulate 
twice-daily tides of equal length. Pots were 
scrubbed weekly to reduce algal/bacterial films, 
then re-randomized.

At the start of the experiment, water samples were 
collected from the seawater system, filtered through 
Whatman GF/C filters, and frozen for later analysis of 
total Kjeldahl N (TKN), NH₄⁻N, NO₃⁻N, and total P 
at the University of CA, Davis Division of Agriculture 
and Natural Resources (DANR) laboratory using 
standard methods. As the TKN method does not 
digest N from oxidized forms (e.g., nitrate and nitrite),
dissolved organic N was calculated by subtraction of NH$_4$–N from TKN. Water nutrients (Table 1) were extremely low compared to levels in southern CA estuaries (Fong, 1986; Fong and Zedler, 2000; Boyle et al., 2004; Kennison et al., 2003).

Initial sediment subsamples were dried (55 °C), ground, and sieved (1-mm sieve), and grain size distribution, organic matter, and total N and P concentration were determined at DANR (Table 1). The high proportion of sand particles was comparable to that of other marshes formed naturally on sandy deposits or newly constructed from dredged material (Osgood and Zieman, 1993, Boyer and Fong, unpublished data). There had been little accumulation of organic matter in these sediments (Table 1; compare to 0.8–3% in sandy marshes >10 years old, Osgood and Zieman, 1993; Craft et al., 1999). As expected for coarse sediments, N concentration was at the low end of the range for low elevation marshes (often greater than 0.2% dry mass and as high at 0.8%; reviewed in Boyer et al., 2001), but similar to other constructed and natural coarse grained sites (Boyer and Zedler, 1998; Craft et al., 1999). Total P was in the middle of the range found in lower elevation marshes (0.01–0.14% dry mass: Mendelssohn and Marcellus, 1976; Ellison et al., 1986;

Fig. 1. (A) Schematic of experimental design with four levels of algal addition (0–3 kg m$^{-2}$) and presence/absence of pickleweed in pots of sediments. (B) Cross-sectional view; water entered and exited the outer pots through irrigation tubing and emitters, and the inner pot through holes (covered with mesh to retain sediments) in the bottom. Wooden blocks elevated the shorter inner pots such that water did not reach their top edges, and so that the water level dropped below the inner pots at simulated low tide. Pump timing permitted approximately equal periods of submergence and exposure of the sediment surface.
Prior to the experiment, samples of the enriched algae were rinsed in de-ionized water, dried (60 °C), and ground. Stable isotope ratios of nitrogen were measured by continuous flow isotope ratio mass spectrometry at the UC Davis Stable Isotope Facility. Sample peak areas and isotope ratios were compared to those of standard samples for calculation of atom% $^{15}$N. Stable isotope ratios of nitrogen were measured by continuous flow isotope ratio mass spectrometry at the UC Davis Stable Isotope Facility. Sample peak areas and isotope ratios were compared to those of standard samples for calculation of atom% $^{15}$N. Samples were also analyzed for total P (Table 1). Pickleweed N and P concentrations were similar to those found in other studies (0.9–2.5% N, 0.15–0.17% P; Sullivan and Zedler, 1999; Boyer et al., 2001; Boyer and Fong, unpublished data). For the experimental pickleweed replicates, we recorded initial branch number and lengths and calculated total branch length per pot (grand mean=178.4±18.1 cm).

At the end of the experiment, redox potential ($E_h$) was measured at 2- and 6-cm sediment depths (two replicates each, averaged) using platinum electrodes. The potential of a calomel reference electrode against a standard hydrogen electrode (+245 mV) was added to each measured value.

Algae were removed, rinsed, spun in a lettuce spinner for 1 min, weighed, dried at 60 °C, and reweighed. Dried samples were processed and analyzed for $^{15}$N (as atom%) and total N. The mean wet:dry mass ratio (9.3) was used to estimate initial dry mass of algae, which was used to calculate the initial N mass as %N/2C to initial dry mass. Final dry mass and N content were used to calculate percentage change in N mass from initial values. Initial and final $^{15}$N mass were calculated as atom% $^{15}$N/2C on initial dry mass and used to calculate percentage change in $^{15}$N mass.

Sediments cores (2.5-cm diameter×6 cm deep) were subdivided into 0–2 cm and 2–6 cm sections, dried, weighed, ground, and analyzed for $^{15}$N, total N, and total P. Soil salinity was estimated using a refractometer on saturated soil pastes prepared from dried soils. Organic matter (loss on ignition) was determined for the 0–2-cm depth; deeper sediments were not expected to change in 6 weeks.

Final pickleweed branch lengths and numbers were recorded and tissues were divided into “succulent” (fleshy tissue on stems) and “woody” (older stems over which the fleshy covering had senesced and shed). Roots were rinsed of sediments, and all tissues were analyzed as for the initial samples.

Two-factor ANOVA was used to test for the effects of algal density, presence/absence of pickleweed, and interaction. When one factor was not significant, mean squares were pooled and re-evaluated through one-factor ANOVA. One-factor ANOVA was also used to compare algal treatment effects on N and P concentration in pickleweed tissues. Following a significant

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Table 1
Initial conditions of (A) incoming seawater for the tidal simulator, (B) sediments, and (C) macroalgae after culturing, and pickleweed

<table>
<thead>
<tr>
<th>A. Water (all μM)</th>
<th>Macroalgae</th>
<th>Pickleweed</th>
<th>roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>DON²</td>
<td>24.29 (3.27)</td>
<td>1.22 (0.08)</td>
<td>1.02 (0.15)</td>
</tr>
<tr>
<td>NO₃-N</td>
<td>7.00 (1.24)</td>
<td>0.3704 (0.0002)</td>
<td>0.3695 (0.0002)</td>
</tr>
<tr>
<td>NH₄-N</td>
<td>7.14 (1.24)</td>
<td>6.55 (0.4)</td>
<td>8.7 (0.6)</td>
</tr>
<tr>
<td>Total P</td>
<td>&lt;1.56b</td>
<td>0.11 (0.01)</td>
<td>Not measured</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>B. Sediments</th>
<th>Macroalgae</th>
<th>Pickleweed</th>
<th>roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total N (% dry mass)</td>
<td>3.41 (0.19)</td>
<td>1.22 (0.08)</td>
<td>1.02 (0.15)</td>
</tr>
<tr>
<td>Total P (% dry mass)</td>
<td>0.05 (0.00)</td>
<td>Not measured</td>
<td></td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>0.05 (0.00)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand (%)</td>
<td>96 (0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Silt (%)</td>
<td>1 (0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clay (%)</td>
<td>3 (0)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>C. Macroalgae and pickleweed</th>
<th>Macroalgae</th>
<th>Pickleweed</th>
<th>roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total N (% dry mass)</td>
<td>1.22 (0.08)</td>
<td>0.3704 (0.0002)</td>
<td>0.3695 (0.0002)</td>
</tr>
<tr>
<td>$^{15}$N (atom%)</td>
<td>N/A</td>
<td>11.1 (0.4)</td>
<td>8.7 (0.6)</td>
</tr>
<tr>
<td>$^{15}$N (%)</td>
<td>0.33 (0.01)</td>
<td>Not measured</td>
<td></td>
</tr>
</tbody>
</table>

Values are means (S.E.); n=5.

² Dissolved organic nitrogen.

b Below this detection limit.
one-factor ANOVA, multiple comparisons were made using Fisher’s PLSD method. Data not meeting assumptions of ANOVA after transformation were analyzed using the non-parametric Kruskal–Wallis (K–W) test. When one factor was not significant, mean squares were pooled for analysis by K–W or Mann–Whitney U tests. Non-parametric multiple comparisons by simultaneous test procedure followed significant K–W tests. All errors presented are ± 1 S.E.

3. Results

3.1. Changes in macroalgae

There was no effect of pickleweed presence on any of the algal response variables. During the 6-week experiment, wet mass of macroalgae increased from initial values in the 1- and 2- kg algal density treatments (Fig. 2A), by 39 and 6%, respectively. In contrast, the 3-kg treatment decreased in algal wet mass by 33%. We observed small patches of bleached tissue in all the treatments; these were most evident on the underside of mats in the 3-kg treatment.

N concentration in algal tissues declined during the experiment in all treatments (Fig. 2B). The greatest decrease (68%) occurred in the 1-kg treatment, at least partly due to dilution of N over increased mass. The 2- and 3-kg treatments decreased significantly less, by 56 and 50%, respectively (not significantly different from each other). The N pool in the algae (N mass) decreased in all algal addition treatments (Fig. 2C). Both mass of N and mass of $^{15}$N in the algae (Fig. 2D) decreased significantly more with each increasing level of initial algal density. Algal $^{15}$N mass decreased by 2, 4, and nearly 8 mg/pot in the 1-, 2-, and 3-kg treatments, respectively.

Algal $^{15}$N concentration increased in all density treatments, suggesting a preferential loss of the lighter isotope, $^{14}$N. Isotopic enrichment of macroalgae was similar (~14%) regardless of mat density, increasing to 6.7 ± 0.1 atom% (grand mean) from an initial value of 5.9 atom%.

3.2. $^{15}$N transfer to soils and plants

The presence of pickleweed had no effect on sediment $^{15}$N concentration (atom%) at either sediment depth (Fig. 3). With all densities of algae added, $^{15}$N concentration at the surface (0–2 cm) was $4 \times$ greater.

Fig. 2. Change from initial macroalgal (A) wet mass, (B) N concentration, (C) mass of N, and (D) mass of $^{15}$N. Panels B–D are based on dry mass. $p$ values are shown from pooled (± pickleweed) analysis by one-factor ANOVA, with results of multiple comparisons indicated by letters (bars with shared letters are not different).

Fig. 3. $^{15}$N (atom%) of soils at (A) 0–2 cm depth and (B) 2–6 cm depth, with $p$ values from Kruskal–Wallis tests on pooled (± pickleweed) data and results of simultaneous test procedure indicated by letters (bars with shared letters are not different).
than natural abundance levels (0-kg treatment) (Fig. 3A). There was no significant difference in sediment \( ^{15}N \) concentration in the 1- to 3-kg treatments. \( ^{15}N \) levels at depth (2–6 cm) were 2 \( \times \) lower than at the surface, but increased significantly with increasing algal density (Fig. 3B). \( ^{15}N \) ranked highest in the 3-kg treatment, but was not significantly different than in the 2-kg treatment.

There was a significant positive effect of algal density on concentration of \( ^{15}N \) (atom\%) in all portions of pickleweed tissues (Fig. 4). The stepwise pattern of enrichment resembled that of the sediments in the rooting zone (2–6 cm), and was opposite that of algal N mass declines. In all portions, \( ^{15}N \) concentration of pickleweed in the highest density algal treatment was 250–300\% greater than in the 0-kg treatment. Effects of algal density on pickleweed \( ^{15}N \) labeling were more pronounced in the succulent and root tissues than in the stem tissues.

3.3. Pickleweed and sediment responses

Biomass of pickleweed succulent, woody, and root portions did not differ by algal density treatment (grand means=1.5 \( \pm \) 0.2, 1.0 \( \pm \) 0.1, and 1.9 \( \pm \) 0.3 g dry mass pot\(^{-1}\), respectively), nor did total length or number of branches. Total branch length increased by 22\% overall from initial measures, although change per individual plant was highly variable (range=–29 cm to 126 cm). The number of branches per pot stayed approximately the same despite the new growth we observed on all plants.

Macroalgal additions had no effect on N concentration of pickleweed tissues. Mean N levels dropped from initial concentrations by 31\% in succulent tissues and by 13\% in root tissues. P in succulent tissues did not differ by algal treatment or change from initial levels.

Pots with pickleweed had significantly higher soil N concentrations at both the 0–2 and 2–6 cm depths than pots without pickleweed (Fig. 5A,B). At the 0–2-cm depth, there was no significant effect of algal treatment. However, at 2–6 cm, soil N concentration was significantly lower in the two higher density treatments than in the 0- or 1-kg \( m^{-2} \) treatments (PLSD, \( p<0.05 \)). Sediment P did not differ by treatment (grand mean=0.05 \( \pm \) 0.00\%).

Organic matter in surface sediments was significantly higher with pickleweed present (grand mean=0.22 \( \pm \) 0.02\%) than without (grand mean=0.13 \( \pm \) 0.02\%), reflecting sediment N patterns. Sediment organic matter did not differ by algal density treatment.

Sediments at the end of the experiment ranged from well oxygenated to moderately reduced (Patrick et al., 1996). Redox potential at both the 2- and 6-cm depths decreased significantly with pickleweed present (Fig. 5C,D). At the 6-cm depth, the 3-kg algae treatment led to more reduced conditions than both the 0- and 1-kg treatments (PLSD, \( p<0.05 \)), while the 2-kg treatment had an intermediate potential. The presence of pickleweed appeared to influence the degree to which macroalgal mats led to declines in redox potential; however, we found no significant interactions at either depth to support this.

The flow-through seawater system kept sediments well flushed of salts. Grand means of soil salinity were 34 \( \pm \) 1 ppt at the 0–2 cm depth and 31 \( \pm \) 0.5 ppt at 2–6 cm depth. There were no differences by treatment.

4. Discussion

The use of \( ^{15}N \) as a tracer allowed us to document that macroalgae play a role in transferring N from the water column to sediments and vascular plants of the intertidal zone. Algal N lost from all mat density
treatments was discernible through isotopic enrichment of sediments and pickleweed in our experimental units. Further, patterns of $^{15}$N labeling of both the sediments and pickleweed suggest that algal mat density is important to N transfers, with thicker mats supplying a greater quantity of N.

While we hypothesized that N would be released from decomposing algal tissue, our data suggest that N entered the sediment/plant pool from live macroalgae as well. Leakage of dissolved organic N can occur during macroalgal growth (e.g., Tyler et al., 2001; Fong et al., 2003), and thus may have contributed to N releases in the 1- and 2-kg density treatments, in which algae grew during the experiment. The large decreases in algal biomass in the 3-kg treatment suggest that decomposition was probably most important as a mechanism for N loss in this treatment.

Isotopic enrichment of the algal tissue in all treatments during the 6-week experiment indicates that the low nutrient supply of the seawater and sediments could have supported little uptake of “new” nitrogen as $^{14}$N to dilute the $^{15}$N concentration. Several processes could have led to preferential loss of the lighter isotope, $^{14}$N, and thus the enrichment of macroalgal $^{15}$N during the experiment. Leakage across cell walls is related to diffusion rates, which may be faster for the lighter than heavier isotope (Flynn and Berry, 1999). In addition, portions of the algal mats undergoing decomposition, nitrification, and denitrification could have been enriched in $^{15}$N through preferential release of $^{14}$N associated with these bacterial transformations (Macko and Ostrom, 1994). As isotopic enrichment of algae during the experiment was similar across algal addition treatments, it should not have influenced our ability to detect transfers of N through isotopic enrichment of sediments and pickleweed.

At both the surface and deeper sediment depths, elevated $^{15}$N concentrations trace the path of algal N into the sediment N pool. Especially great isotopic enrichment of the surface layer may have been due to proximity to the algal N supply, and perhaps to the incorporation of isotopically-enriched macroalgal...
detritus into the sediment surface layer. Ammonia volatilization, which results in preferential release of $^{14}$N (Wada et al., 1981), may have further enhanced $^{15}$N concentration in the surface sediments. Conditions suitable for ammonia volatilization were perhaps provided by the heightened pH that can result in water during algal photosynthesis and the position of the NH$_4$–N source (the algal mat) on the sediment surface as it dried during simulated low tide (Brady and Weil, 1999). If so, this process was not differentially affected by algal mat density, but rather led to statistically similar isotopic signatures across algal addition treatments.

With increasing macroalgal mat density, a striking stepwise $^{15}$N enrichment of the deeper sediment zone suggests that sediments intercepted a greater supply of N from denser macroalgal mats. Our data are not supportive of an alternative explanation for this pattern, that denitrification beneath thicker mats led to isotopic enrichment of sediments (Handley and Raven, 1992). Redox potential fell to levels associated with denitrification ($<$250 mV; Patrick and Jugsujinda, 1992) in some of the pickleweed pots with higher density algal additions, but sediment $E_h$ explained little of the variation in $^{15}$N (regression on sediments from pickleweed pots with 1–3 kg/m$^2$ of algae; in surface sediments, $n=15$, $p=0.8740$, $R^2=0.002$; at depth, $n=15$, $p=0.1290$, $R^2=-0.168$).

Pickleweed enrichment in $^{15}$N with Enteromorpha present at all three densities suggests that N transferred from this alga may contribute to the plant’s mineral nutrition whenever algal mats occur on sediments in close proximity. Increased isotopic enrichment with increasing mat density provides evidence that a greater quantity of N was available to pickleweed in the presence of the thickest algal mats.

As macroalgal presence/density did not lead to differences in pickleweed total branch length or tissue N concentration, the contribution of macroalgal N to pickleweed productivity over short time periods remains uncertain. In this study, pickleweed declined in N concentration due, in part, to growth, which would have “diluted” N across biomass. However, growth was highly variable among individuals, with some even decreasing in total length. In a study at Mugu Lagoon, Onuf (unpublished manuscript) found that only ~30% of new branch tips survived for >3 months and that biomass loss by shedding of branches could be up to 4× the amount of new biomass produced. Greater sediment N and organic matter where pickleweed was present further suggests that the plant contributed detritus to the sediments. With high variability in growth and uncertainty about tissue losses, we are unable to adequately assess pickleweed productivity or, therefore, to estimate the absolute contribution of algal N to it.

In conclusion, this experiment provides evidence that mats of an opportunistic green macroalgae link water column and benthic N pools through uptake of water column N and transfers to underlying tidal flat or vegetated saltmarsh sediments. Transfers of N occurred from algal mats that were both growing and declining in biomass, suggesting that macroalgae may contribute N to sediments and marsh plants whenever mats are present. In addition, the persistence of algal blooms in the intertidal zone of estuaries over periods of months may have a cumulative effect on N pools of both sediments and emergent vascular plants, perhaps over many years of recurring algal blooms. As has been suggested previously for a US Atlantic coast marsh (Gerard, 1999), the N dynamics of intertidal sediments and marsh plants appear to be linked to the N pools of co-occurring macroalgae, and further study is needed to assess the significance of N transfers.

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