Vol. 482: 299–304, 2013
doi: 10.3354/meps10289

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 22

NOTE

Nitrogen transfers mediated by a perennial, non-native macroalga: a ^{15}N tracer study

Dana Gulbransen*, Karen McGlathery

Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904, USA

ABSTRACT: Mats of macroalgae can alter nutrient regimes in intertidal communities, such as mudflats, marshes and beaches, by transferring nutrients to the surrounding habitat. Previous work has focused on ephemeral species of macroalgae that decompose in these intertidal environments. However, unlike ephemeral macroalgae, perennial species can be long-lived, resident members of intertidal systems and hence their role in mediating nutrient transfers may therefore be different. In this study, we used a ^{15}N isotope tracer to determine if nitrogen from a perennial, non-native macroalga (*Gracilaria vermiculophylla*) could be found in other macrophytes and in higher trophic groups on salt marshes and mudflats in shallow coastal bays in Virginia. We found that sediment on marshes and mudflats, marsh cordgrass (*Spartina alterniflora*), and mudflat invertebrates all incorporated nitrogen from *G. vermiculophylla*, indicating that this perennial alga is important in the transfer of nutrients within, and between, trophic levels.

KEY WORDS: Nitrogen transfer · Isotope · Non-native · *Gracilaria vermiculophylla* · Perennial · Marsh · Mudflat

INTRODUCTION

Prior work on intertidal macroalgal mats has found that macroalgal communities can mediate nutrient transfers to higher trophic levels as well as to other macrophytes. However, until now, a distinction has not been made between ephemeral and perennial macroalgae. Ephemeral algae typically bloom in areas with high nutrient inputs and then collapse when they are limited by oxygen and/or light availability (Sfriso et al. 1992, Valiela et al. 1997). In contrast, perennial fucoids (brown macroalgae) and rhodophytes (red macroalgae) form mats that persist over longer time scales (Gerard 1999, Thomsen et al. 2006, Dijkstra et al. 2012). Due to their different growth cycles, information on both ephemeral and perennial macroalgae is needed to understand the potential role of macroalgae in nutrient transfers on marshes and mudflats.

Gerard (1999) hypothesized that mats of the perennial brown macroalga *Ascophyllum nodosum* enhanced the survival of marsh cordgrass *Spartina alterniflora* by releasing nutrients during senescence; however, this hypothesis was never tested experimentally. All prior studies that have experimentally documented intertidal macroalgal nutrient transfers have focused on ephemeral species (e.g. Boyer & Fong 2005, Rossi 2007). However, these results cannot be directly applied to ecosystems with perennial macroalgae that persist in intertidal environments.

Gracilaria vermiculophylla is a perennial rhodophyte that is native to Southeast Asia and has invaded temperate estuaries across North America and Europe (Kim et al. 2010, Gulbransen et al. 2012). It is a successful invader in the mid-Atlantic region due to its resistance to desiccation, sedimentation, and grazing relative to native macroalgal species, as

*Email: djg4j@virginia.edu

well as its association with a common mudflat polychaete, *Diopatra cuprea*, that stabilizes populations and facilitates asexual reproduction (Thomsen & McGlathery 2005, 2007). *G. vermiculophylla* has been the dominant macroalgal species in the coastal bays of Virginia since at least 1998 (Thomsen et al. 2006), and high densities on marshes (mats up to 3 cm deep, maximum biomass 88 g dry weight [DW] m^{-2}) and mudflats (mats up to 15 cm deep, maximum biomass 800 g DW m^{-2}) can persist on the order of months to years (D. Gulbransen pers. obs.).

We hypothesized that *Gracilaria vermiculophylla* would be present year-round on marshes and mudflats and would transfer nitrogen to the sediments, to *Spartina alterniflora*, and to invertebrates, including the marsh snail *Littorina irrorata*, the mud snail *Ilyanassa obsoleta*, gammarid amphipods, and the tube-building polychaete *Diopatra cuprea*, all of which are common in these systems. Using a natural abundance mixing model that incorporated ^{13}C, ^{15}N, and ^{2}H on a Virginia coastal bay marsh, we were unable to resolve trophic interactions because the isotopic composition of end-members in the community were not sufficiently different (D. Gulbransen unpubl. data). Therefore, we enriched *G. vermiculophylla* with a ^{15}N stable isotope tracer and recorded the changes in ^{15}N levels in sediments, macrophytes and invertebrates to determine if the macroalga mediated nitrogen transfers on marshes and mudflats.

MATERIALS AND METHODS

This study was conducted in coastal bays at the Virginia Coastal Reserve Long Term Ecological Research (VCR LTER) site. The coastal bays of Virginia extend 110 km along the mid-Atlantic coast and are bounded to the west by the Delmarva Peninsula and to the east by a series of barrier islands. They are shallow, with 50% < 1 m at mean low water, a tidal range of 1.2 to 1.5 m, and 37% of the benthic surface area covered by marsh and intertidal flats (Oertel 2001).

Seasonal macroalgal biomass was determined along transects at 5 marshes from June 2009 to January 2012 and 3 mudflats from December 2010 to January 2012 (Fig. 1). At each marsh site a 100 m transect was run perpendicular to the edge of the marsh–mudflat interface and 5 haphazard 0.25 m^2 samples were collected in each 20 m segment, for a total of 25 samples. Mudflat transects were conducted the same way but were 30 to 50 m in length, with samples collected in 10 m sections.

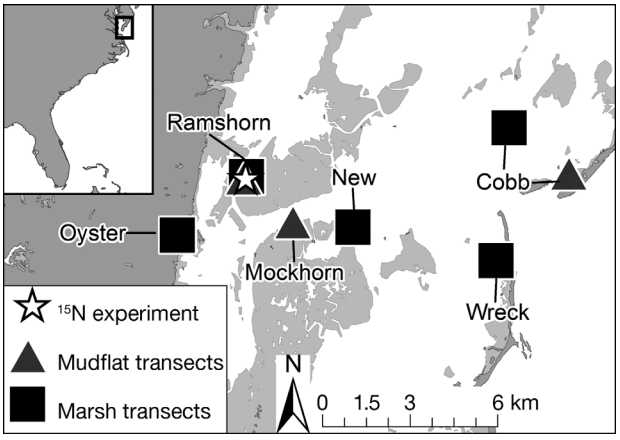

Fig. 1. Map of the seasonal transect locations and ^{15}N study at Virginia coastal bays

All macroalgal samples were rinsed with distilled (DI) water, identified, dried in a 60°C oven for at least 48 h, and weighed. A subset of samples were saved for C:N analysis, which was conducted on a Carlo Erba elemental analyzer. Biomass data from each sampling period were pooled seasonally and plotted relative to *Ulva* spp., another prominent macroalgal species in the region.

The ^{15}N enrichment studies were conducted on the Ramshorn channel marsh and mudflat (Fig. 1; 37° 18.133′ N, 75° 54.036′ W). Prior to the start of the experiment, *Gracilaria vermiculophylla* was labeled with 98% + $^{15}NO_3NH_4$ for 1 wk in the lab. Each day, enough 98% + $^{15}NO_3NH_4$ was added to fuel 0.05 g DW growth d^{-1} and a cumulative 1% tissue enrichment (i.e. 0.0312 mg N day^{-1} for 100 g algae).

For the marsh experiment, 20 paired control (no *Gracilaria vermiculophylla* added) and experimental (with added live, ^{15}N labeled *G. vermiculophylla*) cages (circular, 1/16 m^2) were anchored on the marsh on 17 May 2010 using PVC stakes. At each of 5 sampling periods (38, 71, 93, 138, and 249 d after initial launch), 4 replicate cages were collected. Within each cage, any remaining *G. vermiculophylla*, one sediment plug (30 cm^3 syringe, 5 cm depth), *Spartina alterniflora*, and all macrofauna were collected. In experimental cages that were not collected, all remaining algae was removed and replaced with enriched biomass that reflected seasonal variations. At 38 and 71 d into the experiment, the equivalent of 110 g DW m^{-2} of labeled *G. vermiculophylla* was added to experimental cages, followed by 45 g DW m^{-2} at 93 and 138 d, and 28 g DW m^{-2} at 249 d.

For the mudflat experiment, 30 cages (circular, 1/8 m^2), 10 control (without *Gracilaria vermiculo-*

phylla) and 20 experimental (live, ^{15}N labeled *G. vermiculophylla*) were anchored to the mudflat on 9 June 2010 using PVC stakes. All cages were collected after 1 month because maintaining accurate algal biomasses within cages on the mudflats for a longer period of time was not possible due to tidal effects. Algae were placed into experimental cages on the mudflat at densities between 90 to 500 g DW m^{-2} to represent estimates of patchy *in situ* conditions, which could be as low as 60 g DW m^{-2} and as high as 800 g DW m^{-2} (D. Gulbransen unpubl. data). At the completion of the study, all remaining algae, one sediment plug (30 cm^3 syringe, 5 cm depth), and all macrofauna were collected as described above.

Macroalgal samples were rinsed with DI water, dried in a 60°C oven, and weighed. Sediment samples were picked free of roots and invertebrates were placed into separate containers and allowed to expel their stomach contents for 24 h before drying. All samples were ground, packaged and shipped to the University of California Davis Stable Isotope Facility (UCD SIF) for ^{15}N tissue content analysis using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon).

Marsh data were analyzed using 3 mixed-model ANOVAs in SAS 9.2 to test the effects of sampling time since launch, the presence or absence of ^{15}N enriched *Gracilaria vermiculophylla*, and the interaction of these 2 factors on the ^{15}N levels detected in the sediment, *Spartina alterniflora*, and *Littorina irrorata*. Data for sediment and *L. irrorata* ^{15}N levels satisfied ANOVA assumptions, but data for *S. alterniflora* ^{15}N levels had to be natural log transformed in order to satisfy ANOVA assumptions. Data for sediment ^{15}N levels on the mudflat were log transformed and analyzed using a 1-way ANOVA. Amphipod, *Diopatra cuprea*, and *Ilyanassa obsoleta* ^{15}N data on the mudflat were all analyzed using non-parametric Wilcoxon tests.

RESULTS

Seasonal transects showed that *Gracilaria vermiculophylla* was a dominant member of the macroalgal community and was present year-round (Fig. 2, Table 1). Average *G. vermiculophylla* tissue nitrogen values at the marsh and mudflat sites varied seasonally, with highest values documented in fall (Table 2). In addition, tissue nitrogen values were higher, and C:N levels were lower on mudflats when compared to marshes year-round.

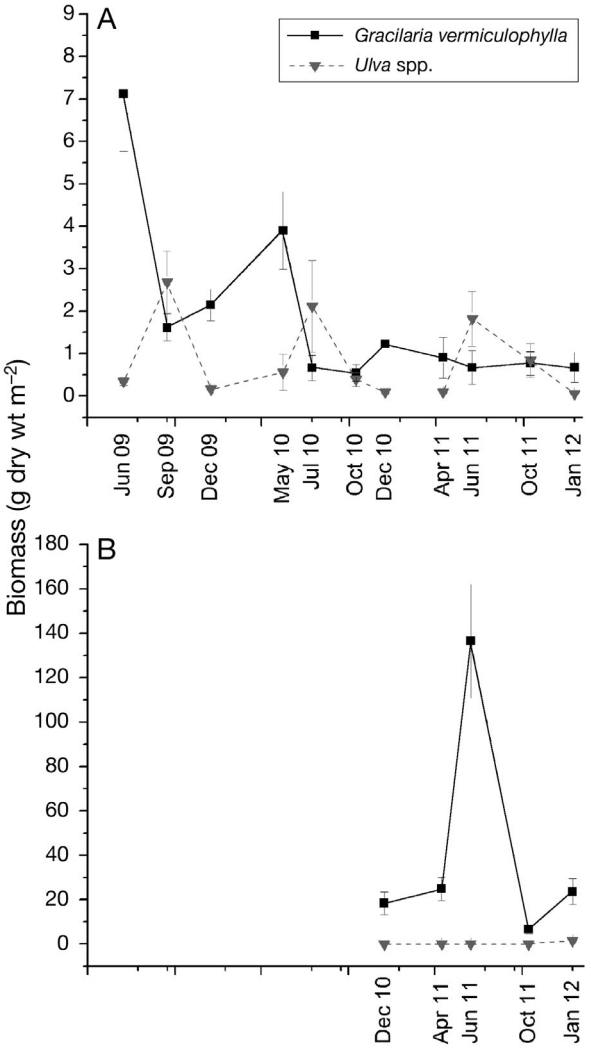

Fig. 2. Mean ± SE macroalgal biomass collected on (A) marshes and (B) mudflats seasonally from June 2009 to January 2012. For more detailed information, see Table 1

Over the course of the ^{15}N experiment, *Gracilaria vermiculophylla* on the marsh lost biomass (Table 3). In addition, $\delta^{15}N$ tissue levels were always lower at the end of the experiment than at the beginning, but this difference was only significant in the third sampling period (27 July to 18 August 2010, $p = 0.0396$, Table 3). Cages with labeled *G. vermiculophylla* had significantly higher $\delta^{15}N$ levels in marsh sediment ($p < 0.0001$) and *Spartina alterniflora* ($p < 0.0001$), but there were no significant differences in *Littorina irrorata* tissue ($p = 0.2127$, Fig. 3A). Differences in $\delta^{15}N$ levels in sediment, *S. alterniflora*, and *L. irrorata* were not significantly affected by the number of days after launch before the samples were collected ($p = 0.2369$, 0.0780, and 0.0651, respectively). In addition, the interaction between enriched treatment and sam-

Table 1. *Gracilaria vermiculophylla* biomass (mean ± SE g dry wt m^{-2}) on marshes sampled from June 2009 to January 2012 and mudflats sampled December 2010 to January 2012. na: not applicable

Date	Cobb Marsh	New Marsh	Oyster Marsh	Ramshorn Marsh	Wreck Marsh	Cobb Mudflat	Ramshorn Mudflat	Mockhorn Mudflat
Jun 09	6.72±2.06	1.02±0.35	16.04±5.44	11.29±3.70	2.33±1.02	na	na	na
Sep 09	4.60±1.27	0.91±0.46	1.00±0.45	1.11±0.30	0.40±0.14	na	na	na
Dec 09	1.89±0.69	0.80±0.42	5.09±1.48	2.26±0.57	0.66±0.20	na	na	na
May 10	3.12± 0.90	7.94±3.80	6.01±2.06	0.90±0.43	1.52±0.39	na	na	na
Jul 10	0	0.32±0.25	2.86±1.43	0.11±0.10	0.02 ±0.01	na	na	na
Oct 10	0.26±0.21	1.26±0.46	1.29±0.86	0	0.01±0.01	na	na	na
Dec 10	0.16±0.07	2.80±2.10	2.61±1.88	0.03±0.02	0.82±0.69	18.78±6.96	17.98±7.38	na
Apr 11	0.10±0.05	0.83±0.32	2.44±2.06	0	1.24±1.24	10.46±3.35	13.86±5.07	58.90±14.24
Jun 11	0.14±0.13	0.22±0.16	2.71±1.87	0.14±0.10	0.04±0.03	1.11±0.53	57.77±11.96	336.36±51.08
Oct 11	0.57±0.24	0.03±0.03	0.71±0.31	2.41±1.22	0	0.12±0.09	2.84±0.60	16.04±5.44
Jan 12	0.52±0.30	2.12±1.99	0.73±0.67	0.03±0.02	0.27±0.17	9.12±5.87	52.51±14.66	12.76±5.39

pling time was not significant for sediment ($p = 0.2735$) or *L. irrorata* ($p = 0.2246$), indicating that their $\delta^{15}N$ levels changed at the same rate in each enrichment treatment. The enrichment treatment and sampling time interaction was significant for *S. alterniflora* measurements ($p = 0.0492$).

On the mudflat, $\delta^{15}N$ levels in *Gracilaria vermiculophylla* collected at the completion of the experiment were significantly lower than initial levels ($p = 0.0013$, Table 4). Sediments underlying cages with labeled *G. vermiculophylla* added had significantly higher $\delta^{15}N$ levels ($p < 0.0001$), as well as significantly higher amphipod ($p < 0.0001$), *Ilyanassa obsoleta* ($p = 0.0007$), and *Diopatra cuprea* ($p = 0.0002$) tissue levels when compared to cages without labeled *G. vermiculophylla* (Fig. 3B).

Table 2. Seasonal percent nitrogen and carbon (mean ± SE) in *Gracilaria vermiculophylla* collected on marshes and mudflats

Season	Marsh			Mudflat		
	%N	%C	C:N	%N	%C	C:N
Spring	1.69±0.09	34.78±0.81	20.58	2.29±0.08	33.76±0.22	14.74
Summer	1.95±0.05	34.31±0.14	17.59	2.93±0.11	33.72±0.24	11.51
Fall	2.51±0.10	34.13±0.21	13.60	3.16±0.09	35.08±0.50	11.10
Winter	2.33±0.10	34.80±0.19	14.94	2.60±0.16	34.03±0.35	13.09

DISCUSSION

We present evidence of nitrogen transfers from the perennial macroalga *Gracilaria vermiculophylla,* to sediment on the marsh and mudflat, to the marsh cordgrass *Spartina alterniflora*, and to mudflat invertebrates. *G. vermiculophylla* nitrogen could be entering the marsh and mudflat systems either via leakage of nitrogen during active growth or by release during decomposition of the algae (Tyler & McGlathery 2006). This released nitrogen may have been subsequently incorporated into cordgrass on the marsh (Gerard 1999) or benthic microalgae (BMA) and bacteria and then further transferred through the trophic food web via consumption by macrofauna. Alternately, direct consumption of *G. vermiculophylla* by macrofauna could result in the incorporation of the tracer into the system.

Table 3. Percent dry wt lost d^{-1}, initial and final $\delta^{15}N$, atom% ^{15}N, and %N tissue levels (all mean ± SE) of *Gracilaria vermiculophylla* in each sampling period of the marsh study. p-values reported for *t*-test between initial and final $\delta^{15}N$ values in each sampling period

Sample date	% dry wt lost d^{-1}	$\delta^{15}N$ of caged algae		p for $\delta^{15}N$	Atom% ^{15}N		%N	
		Initial	Final		Initial	Final	Initial	Final
24 Jun 10	1.90 ± 0.29	2402.11 ± 798.60	599.27 ± 51.52	0.0871	1.55 ± 0.09	1.60 ± 0.09	1.23 ± 0.28	0.58 ± 0.02
27 Jul 10	3.02 ± 0.01	1289.05 ± 226.31	156.46 ± 0	0.1106	2.48 ± 0.06	2.21 ± 0	0.83 ± 0.08	0.42 ± 0
18 Aug 10	3.44 ± 0.46	506.45 ± 56.82	279.86 ± 71.24	0.0396	3.12 ± 0.23	2.66 ± 0.15	0.55 ± 0.02	0.47 ± 0.03
12 Oct 10	1.33 ± 0.31	693.06 ± 244.90	346.10 ± 160.89	0.3560	3.07 ± 0.30	3.09 ± 0.08	0.62 ± 0.09	0.49 ± 0.06
31 Jan 11	0.19 ± 0.17	431.58 ± 103.67	256.20 ± 167.22	0.3822	3.23 ± 0.24	2.38 ± 0.09	0.52 ± 0.04	0.46 ± 0.06

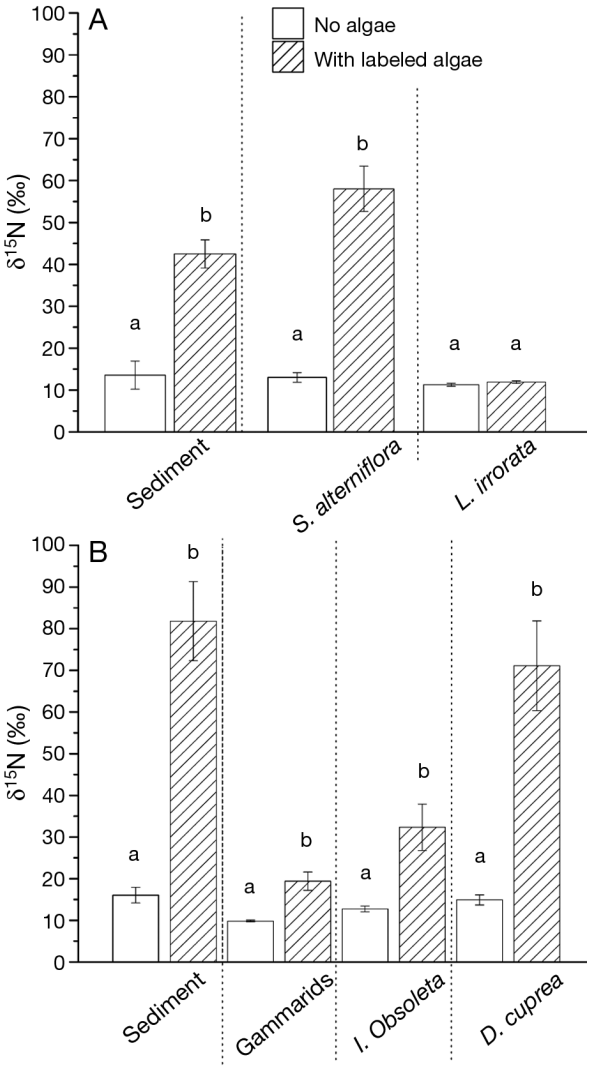

Fig. 3. Compiled $\delta^{15}N$ (mean ±SE) results for (A) marsh sediment, *Spartina alterniflora*, and *Littorina irrorata* and (B) mudflat sediment, gammarids, *Ilyanassa obsoleta*, and *Diopatra cuprea* in cages with and without labeled *Gracilaria vermiculophylla*. Significant differences within each category are denoted by different lowercase letters

Table 4. Initial and final $\delta^{15}N$, atom% ^{15}N, and %N tissue levels (all mean ± SE) of *Gracilaria vermiculophylla* in the mudflat study

Sample time	$\delta^{15}N$	Atom% ^{15}N	%N
Initial	2060.54 ± 454.70	1.11 ± 0.16	2.33 ± 0.05
Final	233.49 ± 25.47	0.45 ± 0.009	2.47 ± 0.08

On the mudflat, the mechanisms of trophic transfer of ^{15}N tissue from *Gracilaria vermiculophylla* to invertebrates were likely direct consumption of the labeled *G. vermiculophylla* or BMA, and/or other invertebrates that were enriched in ^{15}N from *G. vermiculophylla*. For amphipods, many species, including gammarids, have been shown to consume *Gracilaria* spp. tissue in both laboratory and *in situ* studies (e.g. Mancinelli & Rossi 2001). Other studies have found that amphipods prefer to eat diatoms (e.g. Kanaya et al. 2007). Thus, it is likely that the amphipods in our experiments had elevated ^{15}N levels from eating labeled *G. vermiculophylla* and/or BMA. The mud snail *Ilyanassa obsoleta* is a non-selective omnivore (Feller 1984). Therefore, it is probable that mud snails assimilated ^{15}N either directly by consuming labeled *G. vermiculophylla* (Giannotti & McGlathery 2001) or indirectly by grazing on labeled BMA (Connor & Edgar 1982). Finally, our data indicate that the polychaete worm *Diopatra cuprea* consumed labeled *G. vermiculophylla*, BMA, and/or invertebrate tissue. This is supported by prior work that examined gut contents of *D. cuprea* and found that it is omnivorous and will consume animal tissue, microalgae, and macroalgae (Mangum et al. 1968).

In contrast to the mudflat, on the marsh we found that the dominant periwinkle snail, *Littorina irrorata*, did not incorporate labeled nitrogen from *Gracilaria vermiculophylla*. Previous studies have shown that periwinkle snails consume macroalgae (Norton et al. 1990), BMA (Sommer 1999), live *Spartina alterniflora* tissue (Bertness 1984, Silliman & Zieman 2001), detritus (Newell & Bärlocher 1993, Currin et al. 1995), and fungi growing on standing dead *S. alterniflora* stems (Newell & Bärlocher 1993, Silliman & Newell 2003). We often collected *L. irrorata* on *S. alterniflora* shoots, but since the snails did not incorporate the ^{15}N signal, we conclude that these snails were likely consuming fungi on *S. alterniflora* stems rather than the enriched cordgrass tissue directly. This scenario would account for the *L. irrorata* ^{15}N signal that was not significantly different from controls. Unfortunately, the inefficiency of collecting all fungi mycelia, as documented in Newell et al. (1986), prevented us from measuring fungal isotopic signatures.

Variations in *Gracilaria vermiculophylla* total nitrogen content followed the trend previously documented for algal species in the coastal bays, with highest nitrogen availability in late summer and early fall (Anderson et al. 2003, Tyler et al. 2003). The tissue nitrogen and C:N levels in *G. vermiculophylla* also indicated nitrogen was likely more limiting to macroalgae on the marsh compared to the mudflat.

This study demonstrates that a perennial, nonnative macroalga is important in the transfer of nitrogen to sediments, *Spartina alterniflora,* and invertebrate consumers. It differs from prior studies which

used ephemeral macroalgae in microcosms or buried as detritus in intertidal sediments. Our study was done under more realistic environmental conditions for perennial macroalgae and confirmed that the non-native macroalga can transfer nitrogen to marshes and mudflats during both active growth and decomposition.

In order to determine if macroalgal-mediated nutrient transfers can result in nutrient subsidies to a system, researchers need to know how macroalgae move in space and time and if the addition of macroalgae results in increased growth and production of flora and fauna in recipient communities. Before the ultimate effects of *Gracilaria vermiculophylla* nutrient mediation on marshes and mudflats can be determined, more information is needed on these dynamics.

Acknowledgements. Funding for this work was provided by the Virginia Coastal Reserve Long Term Ecological Research Grant DEB-0621014 and DEB-1237733. Thank you to the Nature Conservancy in the VA coastal reserve for research permits. Also thanks to the staff of the Anheuser-Busch Coastal Research Center and R. Gonzalez for field support.

LITERATURE CITED

Anderson IC, McGlathery KJ, Tyler AC (2003) Microbial mediation of 'reactive' nitrogen transformations in a temperate lagoon. Mar Ecol Prog Ser 246:73–84

Bertness MD (1984) Habitat and community modification by an introduced herbivorous snail. Ecology 65:370–381

Boyer KE, Fong P (2005) Macroalgal-mediated transfers of water column nitrogen to intertidal sediments and salt marsh plants. J Exp Mar Biol Ecol 321:59–69

Connor MS, Edgar RK (1982) Selective grazing by the mud snail *Ilyanassa obsoleta*. Oecologia 53:271–275

Currin CA, Newell SY, Paerl HW (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Mar Ecol Prog Ser 121:99–116

Dijkstra JA, Boudreau J, Dionne M (2012) Species-specific mediation of temperature and community interactions by multiple foundation species. Oikos 121:646–654

Feller RJ (1984) Dietary immunoassay of *Ilyanassa obsoleta*, the Eastern mud snail. Biol Bull 166:96–102

Gerard VA (1999) Positive interactions between cordgrass, *Spartina alterniflora*, and the brown alga, *Ascophyllum nodosum* ecad *scorpioides*, in a mid-Atlantic coast salt marsh. J Exp Mar Biol Ecol 239:157–164

Giannotti AL, McGlathery KJ (2001) Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta* (Say). J Phycol 37:209–215

Gulbransen DJ, McGlathery KJ, Marklund M, Norris JN, Gurgel CFD (2012) *Gracilaria vermiculophylla* (Rhodophyta, Gracilariales) in the Virginia Coastal Bays, USA: *cox*1 analysis reveals high genetic richness of an introduced macroalga. J Phycol 48:1278–1283

Kanaya G, Takagi S, Nobata E, Kikuchi E (2007) Spatial dietary shift of macrozoobenthos in a brackish lagoon revealed by carbon and nitrogen stable isotope ratios. Mar Ecol Prog Ser 345:117–127

Kim SY, Weinberger F, Boo SM (2010) Genetic data hint at a common donor region for invasive Atlantic and Pacific populations of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta). J Phycol 46:1346–1349

Mancinelli G, Rossi L (2001) Indirect, size-dependent effects of crustacean mesograzers on the Rhodophyta *Gracilaria verrucosa* (Hudson) Papenfuss: evidence from a short-term study in the Lesina Lagoon (Italy). Mar Biol 138: 1163–1173

Mangum CP, Santos SL, Rhodes WR Jr (1968) Distribution and feeding in the onuphid polychaete, *Diopatra cuprea* (Bosc). Mar Biol 2:33–40

Newell SY, Bärlocher F (1993) Removal of fungal and total organic matter from decaying cordgrass leaves by shredder snails. J Exp Mar Biol Ecol 171:39–49

Newell SY, Fallon RD, Miller JD (1986) Measuring fungal-biomass dynamics in standing-dead leaves of a salt marsh vascular plant. In: Moss ST (ed) The biology of marine fungi. Press Syndicate of the University of Cambridge, New York, NY, p 19-25

Norton TA, Hawkins SJ, Manley NL, Williams GA, Watson DC (1990) Scraping a living: a review of littorinid grazing. Hydrobiologia 193:117–138

Oertel GF (2001) Hypsographic, hydro-hypsographic and hydrological analysis of coastal bay environments, Great Machipongo Bay, Virginia. J Coast Res 17:775–783

Rossi F (2007) Recycle of buried macroalgal detritus in sediments: use of dual-labeling experiments in the field. Mar Biol 150:1073–1081

Sfriso A, Pavoni B, Marcomini A, Orio AA (1992) Macroalgae, nutrient cycles, and pollutants in the lagoon of Venice. Estuaries 15:517–528

Silliman BR, Newell SY (2003) Fungal farming in a snail. Proc Natl Acad Sci USA 100:15643–15648

Silliman BR, Zieman JC (2001) Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. Ecology 82:2830–2845

Sommer U (1999) The susceptibility of benthic microalgae to periwinkle (*Littorina littorea*, Gastropoda) grazing in laboratory experiments. Aquat Bot 63:11–21

Thomsen MS, McGlathery KJ (2005) Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*. Estuar Coast Shelf Sci 62:63–73

Thomsen MS, McGlathery KJ (2007) Stress tolerance of the invasive macroalgae *Codium fragile* and *Gracilaria vermiculophylla* in a soft-bottomed turbid lagoon. Biol Invasions 9:499–513

Thomsen MS, McGlathery KJ, Tyler AC (2006) Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. Estuaries Coasts 29:470–478

Tyler AC, McGlathery KJ (2006) Uptake and release of nitrogen by macroalgae *Gracilaria vermiculophylla* (Rhodophyta). J Phycol 42:515–525

Tyler AC, McGlathery KJ, Anderson IC (2003) Benthic algae control sediment-water column fluxes of organic and inorganic nitrogen compounds in a temperate lagoon. Limnol Oceanogr 48:2125–2137

Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K (1997) Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnol Oceanogr 42:1105–1118

Editorial responsibility: Just Cebrian, Dauphin Island, Alabama, USA

Submitted: September 26, 2012; Accepted: January 28, 2013
Proofs received from author(s): April 27, 2013