Vol. 426: 171–184, 2011
doi: 10.3354/meps09029

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 28

Benthic macroinvertebrate functional diversity regulates nutrient and algal dynamics in a shallow estuary

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ABSTRACT: Proliferation of macroalgal blooms is regulated by grazing pressure and nutrient availability, which may be mediated directly by benthic macroinvertebrates or indirectly through feedback mechanisms. Using invertebrates common to a shallow estuary in Cape Cod, Massachusetts (USA), we determined effects of faunal diversity on benthic microalgae, net ecosystem metabolism, sediment nutrient fluxes, and macroalgal biomass and productivity. Laboratory microcosms contained sediments with single- and mixed-species invertebrate assemblages, in the presence of (1) no macroalgae, (2) a macroalgal monoculture, and (3) a realistic macroalgal polyculture. The deposit-feeding gastropod *Ilyanassa obsoleta* suppressed benthic microalgae, enhanced nitrate efflux from sediments, and maintained macroalgal standing stocks. Conversely, the burrowing, omnivorous polychaete *Alitta* (formerly *Nereis*) *virens* stimulated benthic microalgal growth, inhibited efflux of ammonium, and drastically reduced macroalgal biomass via grazing and translocation of thalli below the sediment surface. In the polyculture experiment, *A. virens* sequentially removed *Gracilaria* sp. (Rhodophyta), *Ulva* sp. (Chlorophyta), and finally *Fucus vesiculosus* (Phaeophyta). The bivalve *Mya arenaria* exhibited limited effects on benthic dynamics. In mixed-fauna assemblages, biomass and productivity of benthic microalgae and macroalgae were consistently lower than predicted, revealing non-additive effects of biodiversity. Communities dominated by *I. obsoleta* or other surficial grazers could indirectly promote macroalgal blooms via sustained release of sediment-derived nutrients and reduction of benthic microalgae. In contrast, omnivorous burrowers such as *A. virens* may buffer symptoms of eutrophication through inhibition of ammonium supply and direct grazing of bloom-forming macroalgae. Overall, our results highlight species-specific effects on key ecosystem functions, and demonstrate important feedbacks between top-down and bottom-up controls in shallow estuaries.

KEY WORDS: Benthic invertebrates · Macroalgae · Benthic microalgae · Nutrient supply · Grazing · Biodiversity · Ecosystem function · Eutrophication

INTRODUCTION

Macroalgal distribution and abundance in shallow estuaries is regulated by a complex suite of biotic and abiotic factors that incorporate feedbacks with resource availability and consumer pressure (Valiela et al. 1997, Hauxwell et al. 1998, Worm et al. 2000), coupled with competition among autotrophs (Havens et al. 2001, Sundbäck et al. 2003). In shallow coastal systems, accelerated nutrient loads have alleviated limitation of primary production (Howarth 1988) and prompted the proliferation of ephemeral seaweeds capable of dimin-

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ishing or replacing perennial macroalgae, seagrasses, and benthic microalgae (Valiela et al. 1997 and references therein). In concurrence with allochthonous inputs, macroalgal growth can be fueled by nutrient regeneration from underlying sediments (Sundbäck et al. 2003, Tyler et al. 2003, Kamer et al. 2004). This internal loading to bottom waters is controlled by a number of linked indirect and direct factors, including macroinvertebrates and benthic microalgae.

Sediment biogeochemical processes are strongly regulated by bioturbation and irrigation of biogenic structures (Rhoads 1974), and mediation of solute fluxes may vary according to invertebrate functional characteristics (Mermillod-Blondin et al. 2004, Karlson et al. 2005) that relate to feeding behavior and mobility within the benthos. Nereidid polychaetes dwelling in burrows, for example, can flush porewater ammonium to the water column (Andersen & Kristensen 1988, Michaud et al. 2006) and stimulate coupled nitrification-denitrification (Henriksen et al. 1983), while bioturbators active near the sediment surface, such as mollusks and tubiculous amphipods, may enhance oxygen penetration and thereby impact mineralization processes (Henriksen et al. 1983, Mermillod-Blondin et al. 2004, Michaud et al. 2006). Nutrient regeneration may further be mediated by benthic microalgal communities that intercept nitrogen (N) and phosphorus (P) at the sediment–water interface (Sundbäck et al. 1991, Tyler et al. 2003), stimulate nitrification potential (An & Joye 2001), and either augment or inhibit N removal by modifying denitrification rates (Rysgaard et al. 1995, Sundbäck et al. 2004). While a limited number of investigations have explicitly tested effects of species or functional diversity on biogeochemical cycling in marine systems (e.g. Emmerson et al. 2001, Waldbusser et al. 2004, Norling et al. 2007), the need remains for greater empirical understanding of complex interactions across multiple trophic levels (Bruno et al. 2008).

In conjunction with controls on sediment properties and nutrient supply, benthic fauna may also exert direct pressure on seaweed growth via top-down reduction of biomass (Hauxwell et al. 1998, Worm et al. 2000). Furthermore, invertebrates can influence macroalgal community structure and diversity through preferential consumption of palatable, annual taxa (Lubchenco 1978) with high nutrient content and negligible defense compounds (Hay & Fenical 1988). Most research to date, however, has focused on the roles of crustaceans and gastropods as dominant seaweed grazers. The few studies that have examined top-down impacts of omnivorous polychaetes (e.g. Raffaelli 2000, Nordstrom et al. 2006, Engelsen & Pihl 2008) did not explore effects within diverse faunal or macroalgal assemblages.

Our study investigated feedbacks between biodiversity and ecosystem functioning as related to bottom-up and top-down controls on algal growth. The approach employed a series of microcosm experiments representing a shallow, temperate estuary undergoing rapid eutrophication. We hypothesized that the functional characteristics of common invertebrates would differentially influence net ecosystem metabolism, nutrient supply, and biomass of benthic microalgae and macroalgae. Moreover, we tested the relationship between functional diversity and ecosystem processes in multispecies assemblages of both fauna and seaweeds.

MATERIALS AND METHODS

Site and organism descriptions. West Falmouth Harbor (WFH; 41° 36′ N, 70° 38′ W) is a shallow, polyhaline (from 20 to 30 ppt) embayment in SW Cape Cod, Massachusetts (USA), with an average depth of 0.6 m at mean low water (Howes et al. 2006). Since 1994, migration of a localized wastewater plume into the harbor has doubled the current N load compared with background levels (Howes et al. 2006). In the degraded inner reaches of the estuary, macroalgal standing stocks are dominated by annual, opportunistic seaweeds during early summer, although perennial fucoids are still present (K. McGlathery and A. C. Tyler unpubl. data). Macroalgae used in the current study included the following co-occurring taxa: the rhodophyte *Gracilaria* sp. (Gracilariaceae; hereafter *Gracilaria*), the (laminar form) chlorophyte *Ulva* sp. L. (Ulvales; hereafter *Ulva*), and the phaeophyte *Fucus vesiculosus* L. (Fucales; hereafter *Fucus*). We selected 3 macroinvertebrate species common to the WFH benthos (McLenaghan 2009, T. Duncan pers. comm.), each with a cosmopolitan distribution along the NW Atlantic coast (Gosner 1971). *Ilyanassa obsoleta* Say, the eastern mudsnail, inhabits the sediment–water interface and is a mobile, omnivorous deposit-feeder that primarily consumes micro-flora and -fauna (Curtis & Hurd 1979). *Mya arenaria* L., the soft-shelled clam, is a sub-surface (<8 cm depth) suspension-feeder. *Alitta* (formerly *Nereis*) *virens* Sars, the king ragworm, constructs and irrigates semi-permanent burrows and exhibits a diverse diet that includes detritus, benthic microalgae, macroalgae, and fauna (Pettibone 1963).

Microcosm set-up and experimental design. For all experiments, we constructed microcosms in transparent, polycarbonate tubes (i.d. = 9.5 cm, length = 30 cm), sealed at the bottom with rubber stoppers. Fine-grained sands were collected from WFH using core-tubes and were partitioned into 3 depth intervals (from 0 to 2, from 2 to 5, and from 5 to 13 cm). To avoid downward mixing of surface biota and organic matter,

respective vertical sections were sieved (1 mm mesh) and homogenized separately prior to reconstruction. Organic matter (OM) content of surface sediments (from 0 to 2 cm) was 1.3% in 2007 and 0.7% in 2008 (loss-on-ignition at 500°C). Tubes were wrapped with opaque material below the sediment–water interface to inhibit light penetration at depth, then incubated in indoor, flowing seawater tables (from 28 to 30 ppt; from 17 to 20°C) with full-spectrum fluorescent bulbs on a 14 h light:10 h dark (14:10 L/D) daily photoperiod. Photosynthetically active radiation in experiments (sediment surface: 200 µmol m^{-2} s^{-1}; LI-192 underwater quantum sensor, LI-COR®) was consistent with the lower range of daytime light levels in WFH (M. Hayn pers. comm.), and an integrated aeration system enhanced water mixing in each microcosm and ensured adequate oxygenation. We augmented surficial sediments with oven-dried (60°C), finely ground macroalgal thalli collected from WFH (100 g dry weight [dwt] m^{-2}) to simulate deposition of a moderate-sized bloom (Hauxwell et al. 1998). Prior to organism additions, microcosms were acclimated for ~3 wk (see timeline in Fig. 1).

We executed the first and second experiments (Expt I and Expt II, respectively) simultaneously from June to July 2007, and the third experiment (Expt III) from June to August 2008. In Expt I, we investigated invertebrate regulation of nutrient fluxes, net ecosystem metabolism, benthic microalgae, and N_2 fixation in microcosms with sediments but without macroalgae. Expts II and III explored faunal effects on the biomass, productivity, and nutrient content of macroalgae, using a seaweed monoculture (*Gracilaria*; Expt II) and a seaweed polyculture (*Gracilaria*, *Ulva*, and *Fucus*; Expt III). Treatments included defaunated controls and single- and mixed-species invertebrate additions.

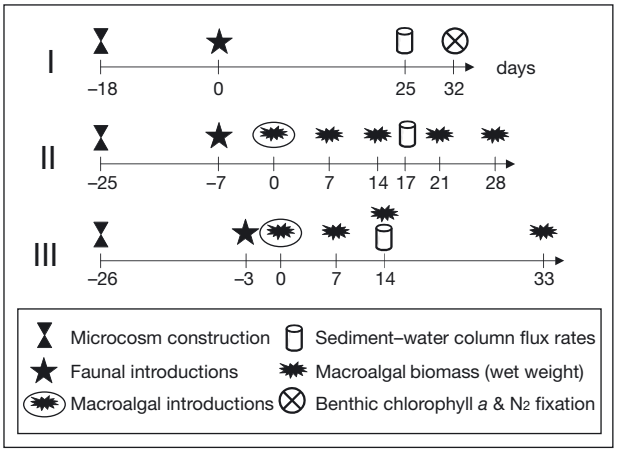

Fig. 1. Timelines for procedures (left column in key) and measurements (right column in key) in Expts I to III. 'Day 0' marks introduction of fauna in Expt I, while 'Day 0' in Expts II and III marks introduction of macroalgae

Expts I and II each contained *Ilyanassa obsoleta* ('*Ilyanassa*' treatment; 430 ind. m^{-2}), *Mya arenaria* ('*Mya*' treatment; 290 ind. m^{-2}), and *Alitta virens* ('*Alitta*' treatment; 290 ind. m^{-2}) in monospecific microcosms and in a 3-species assemblage ('Mix' treatment; 430 ind. m^{-2}) (n = 4). Expt III consisted of *I. obsoleta* (*Ilyanassa*; 860 ind. m^{-2}) and *A. virens* (*Alitta*; 290 ind. m^{-2}) in 1- and 2-species (Mix; 570 ind. m^{-2}) treatments (n = 5). We equalized microcosms according to total organism biovolume (Expts I and II = 4.6 ± 0.3 ml; Expt III = 7.3 ± 0.5 ml). See McLenaghan (2009) for relative abundances of invertebrates used in experiments and in WFH, and Michaud et al. (2006) for justification of using biovolume as a means to compare faunal treatments. Following a 4 d laboratory acclimation in WFH sediments, fauna were introduced to microcosms and they burrowed immediately. Macroalgae were collected manually, rinsed to remove epibiota, and acclimated in seawater tanks for 5 d prior to inclusion in experiments. Initial wet weights (wwt) per microcosm (Expt II: 4.65 g; Expt III: 1.45 g $species^{-1}$ = 4.35 total g) corresponded to densities in local estuaries with moderate nutrient loads (Hauxwell et al. 1998). We secured screens (5 mm mesh) atop each microcosm to prevent faunal and macroalgal migration; screens did not substantially impede light penetration.

Sediment–water column nutrient and oxygen exchange. In Expt I, flux rates of dissolved inorganic nitrogen (DIN = NO_2^- + NO_3^- [hereafter, NO_3^-] and NH_4^+), PO_4^{3-}, and dissolved O_2 (DO) were measured on Day 25. DO fluxes (only) were recorded 17 and 14 d following addition of macroalgae in Expts II and III, respectively. We incubated microcosms according to Tyler et al. (2001), with dark conditions preceding light conditions. Overlying water was carefully siphoned and refilled with fresh seawater prior to sealing with a gas-tight lid, and mixing was maintained with a Teflon-coated magnetic stir-bar (60 rpm) suspended in the water column of each microcosm. Seawater-only microcosms were analyzed simultaneously to correct for water-column activity. DO measurements (WTW Oxi 330i meter with galvanic probe for Expts I and II; Hach HQ40d meter with LBOD101 probe for Expt III) were recorded regularly to prevent depletion. Water samples for nutrient analyses were filtered immediately (0.45 µm; Whatman GF/F) and NH_4^+ reacted within 1 h of collection using the phenol-hypochlorite method (Solorzano 1969). PO_4^{3-} was analyzed according to Murphy & Riley (1962) and NO_3^- samples were frozen (–40°C) prior to measurement on an Alpkem 'continuous flow' Autoanalyzer (OI Analytical). Hourly flux rates across the sediment–water interface were calculated based on changes in concentration over time, with corrections for water-column activity and seawater replacement following sample extraction (see Tyler et al.

2001). Gross primary productivity (GPP) was determined by subtracting hourly rates of benthic oxygen consumption (BOC) measured in the dark from hourly flux rates in the light. Net ecosystem metabolism (NEM) represents the combined daily total of light and dark fluxes. We used a seasonal 14:10 L/D photoperiod to estimate daily GPP, BOC, and NEM. Our calculations assume constant daily rates of community O_2 consumption and thus do not account for possible diurnal variability. For Expts II and III, GPP values reflect the combined productivity of macroalgae and benthic microalgae. Potential DIN assimilation by benthic microalgae in Expt I was calculated using 80% GPP and carbon (C):N of 9:1, according to Sundbäck et al. (2004).

Benthic microalgal biomass and N_2 fixation rates. After 32 d, sediments from Expt I were extruded, sectioned and homogenized, then sub-sampled for benthic photopigments (from 0 to 1 cm) and N_2 fixation rates (surface: from 0 to 1 cm; sub-surface: from 3 to 4 cm). Samples for photopigment analysis were frozen (–80°C) in darkness prior to spectrophotometric measurement (Strickland & Parsons 1972), and concentrations calculated according to Lorenzen (1967). Benthic chlorophyll *a* (chl *a*) was used as a proxy for biomass of photosynthetic microalgae, and chl *a*: phaeopigments (natural degradation products of chl *a*) provided an indication of microalgal turnover. N_2 fixation rates were determined on a subset of treatments (surface: control, *Ilyanassa*, *Alitta*; sub-surface: control, *Alitta*). Assays utilized the acetylene-reduction method with the slurry technique (Stewart et al. 1967) under the following sediment incubations: light (280 µmol m^{-2} s^{-1}; surface only), dark, and dark + sodium molybdate (+Mo: 40 mM Na_2MoO_4). Molybdate is a specific inhibitor of sulfate reduction (Smith & Klug 1981), and its inclusion enables evaluation of sulfate-reducing bacteria contributions in N_2-fixing communities. Detailed assay methods are described in McLenaghan (2009).

Macroalgal properties. Macroalgal biomass was measured periodically (see Fig. 1) by temporarily removing thalli from microcosms, rinsing in seawater and blotting with paper towels, and recording wwt. At the end of experiments, thalli were briefly rinsed in deionized water and oven-dried (60°C) to obtain dwt. When sufficient biomass remained, macroalgae were finely ground to determine tissue C and N content (Carlo-Erba NA-2500 Elemental Analyzer).

Data analysis. Effects of faunal treatments were evaluated with ANOVA (SPSS 11.0) after checking for normality (Shapiro-Wilk's test) and homogeneity of variance (Levene's test). Data were transformed if assumptions were violated. When significant effects were established ($p < 0.05$), we used post hoc pairwise comparisons (Tukey's HSD) to determine treatment differences. One-way ANOVA was used for benthic photopigments, macroalgal biomass and tissue nutrients, GPP, BOC, and NEM. Two-way ANOVA was performed for N_2 fixation and nutrient flux rates, with faunal treatment and incubation condition as fixed and interaction factors. Macroalgal biomass data did not consistently achieve normality or homoscedasticity, and we therefore applied the rank transformation (RT-1) procedure outlined by Conover & Iman (1981). Pearson correlation analyses were used to evaluate relationships between (1) GPP and light-associated nutrient uptake (L subtracted from D hourly flux rates), (2) GPP and benthic chl *a*, and (3) GPP and macroalgal biomass (dwt calculated from wwt at time of flux measurements). To compare predicted and observed results of diversity in the mixed-faunal assemblage, we applied yielding equations according to Waldbusser et al. (2004). Measurable contributions to an effect (e.g. flux rate) per individual organism (E_i) of species *i* were calculated as:

$$E_i = (M_i - A) / p_i \quad (1)$$

where M_i is the value measured in the monospecific treatment, A is the value measured in the control, and p_i is the number of individuals in the treatment. The predicted value for the mixed-faunal assemblage (E_T) was then determined by:

$$E_T = A + \sum_i (E_i\ p_i) \quad (2)$$

Yielding (D_T) values were derived from differences between observed (O_T) and predicted (E_T) values for the mixed-species treatment:

$$D_T = (O_T - E_T) / E_T \quad (3)$$

Non-zero values for D_T represent over-yielding (positive) or under-yielding (negative), indicating that organism effects in diverse assemblages are not simple, additive functions of performance in single-species treatments.

RESULTS

Organism recovery at the termination of each experiment was 100%, with the exception of a failed acclimation in one *Alitta* microcosm (Expt III) that was subsequently omitted from statistical analysis. In Expt I only, an unintended polychaete colonization altered the number of replicates per treatment: the control was reduced to n = 3 and *Alitta* increased to n = 5.

Nutrient release and benthic microalgae

Sediments were a consistent source of NH_4^+ and PO_4^{3-} to the water column in Expt I, but NH_4^+ efflux

was substantially reduced in *Alitta* (Table 1A, Fig. 2A). Daily NO_3^- fluxes were positive (i.e. equaling net efflux) for *Alitta* and *Ilyanassa*, and negative (i.e. equaling net uptake) for the control, *Mya*, and Mix (hourly rates displayed in Fig. 2). Daily fluxes were highest in *Ilyanassa,* by 1.7-fold for total DIN and 3.4-fold for PO_4^{3-} with respect to *Alitta*. Nutrient release was significantly lower in the light relative to the dark (Table 1A), with the following reductions under illumination: from 20 to 53% (NH_4^+), from 43 to 93% (DIN), and from 64 to 93% (PO_4^{3-}). An interaction between faunal treatment and L/D condition was observed for NO_3^- (Table 1A), with dark efflux and light influx in all treatments except *Ilyanassa*, which exhibited constant efflux (Fig. 2B).

Table 1. Expt I. Results of 2-way ANOVA for (A) flux rates across the sediment–water interface for dissolved inorganic nitrogen (DIN) compounds and PO_4^{3-}. Results of 1-way ANOVA for (B) dissolved oxygen (DO) flux rates, including benthic oxygen consumption (BOC), net ecosystem metabolism (NEM), and gross primary productivity (GPP), in addition to (C) benthic microalgal chlorophyll *a* (chl *a*). Results of 2-way ANOVA for (D) N_2 fixation rates. Significant results ($p < 0.05$) in **bold**

Source	df	*F*	p
(A) Nutrient flux rates			
NH_4^+			
Faunal treatment	4, 28	6.58	**0.001**
Incubation condition	1, 28	23.16	**<0.001**
Treatment × Condition	4, 28	0.39	0.815
NO_3^-			
Faunal treatment	4, 24	0.73	0.580
Incubation condition	1, 24	48.94	**<0.001**
Treatment × Condition	4, 24	4.18	**0.010**
DIN (total)			
Faunal treatment	4, 24	1.72	0.179
Incubation condition	1, 24	88.04	**<0.001**
Treatment × Condition	4, 24	2.53	0.066
PO_4^{3-}			
Faunal treatment	4, 28	2.14	0.103
Incubation condition	1, 28	23.93	**<0.001**
Treatment × Condition	4, 28	0.48	0.749
(B) DO flux rates			
BOC	4, 15	2.58	0.080
NEM[a]	4, 15	3.26	**0.041**
GPP[b]	4, 15	2.33	0.104
(C) Benthic microalgae			
Chl *a*[b]	4, 15	4.24	**0.017**
Chl *a*: phaeopigments	4, 15	2.84	0.062
(D) N_2 fixation rates			
Surface sediments			
Faunal treatment	2, 26	1.11	0.345
Incubation condition	2, 26	51.44	**<0.001**
Treatment × Condition	4, 26	0.36	0.837
Sub-surface sediments			
Faunal treatment	1, 12	0.24	0.635
Incubation condition	1, 12	61.06	**<0.001**
Treatment × Condition	1, 12	0.09	0.767

[a]$\log(x + 10)$; [b]$1/x$

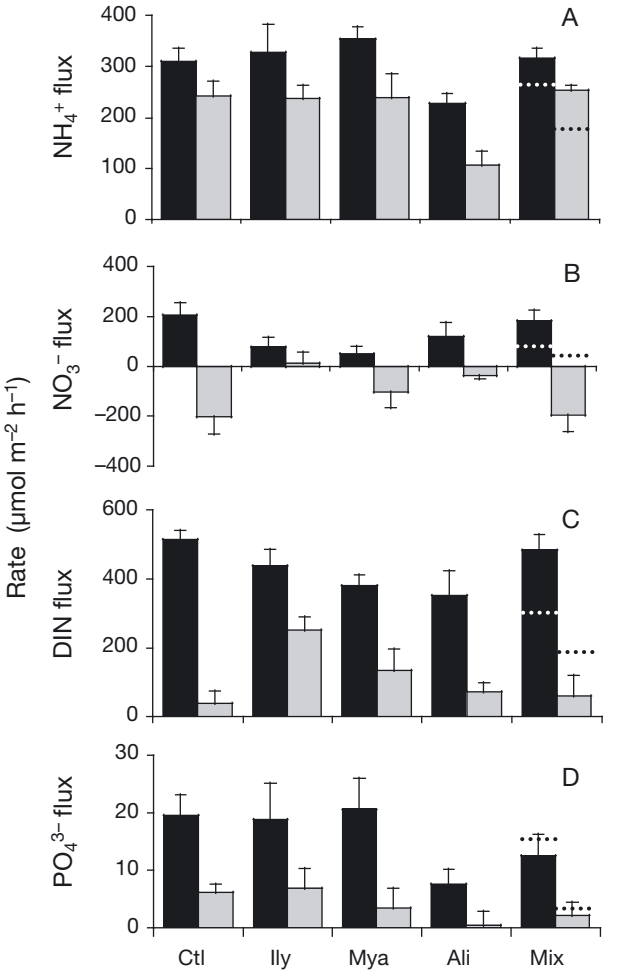

Fig. 2. Expt I. Sediment–water column hourly flux rates (mean ± SE) during dark (black bars) and light (gray bars) incubations for (A) NH_4^+, (B) NO_3^-, (C) total dissolved inorganic nitrogen (DIN), and (D) PO_4^{3-}. Positive values = sediment release; negative values = sediment uptake. Treatment codes: Ctl, control; Ily, *Ilyanassa obsoleta*; Mya, *Mya arenaria*; Ali, *Alitta virens*; Mix, mixed-fauna. Dotted lines in Mix indicate expected values based on yielding calculations. Note different scales on *y*-axes

All Expt I treatments were net heterotrophic, and BOC in microcosms containing fauna was enhanced from 7 to 30% relative to the control (Fig. 3A). NEM was most negative in Mix (Fig. 3B), which was significantly more heterotrophic than *Alitta* (Table 1B). GPP was greatest in *Alitta* and lowest in Mix (Fig. 3C), although differences were not significant (Table 1B). Light-associated reductions (D minus L hourly values) in NH_4^+ efflux were positively correlated with GPP (Pearson's $R = 0.74$, $p < 0.001$), but there were no parallel correlations between GPP and NO_3^- (Pearson's $R = 0.02$, $p > 0.99$) or PO_4^{3-} (Pearson's $R = -0.13$, $p = 0.61$). Light-associated uptake of sediment-derived DIN could meet from 90 to 100% of calculated daytime

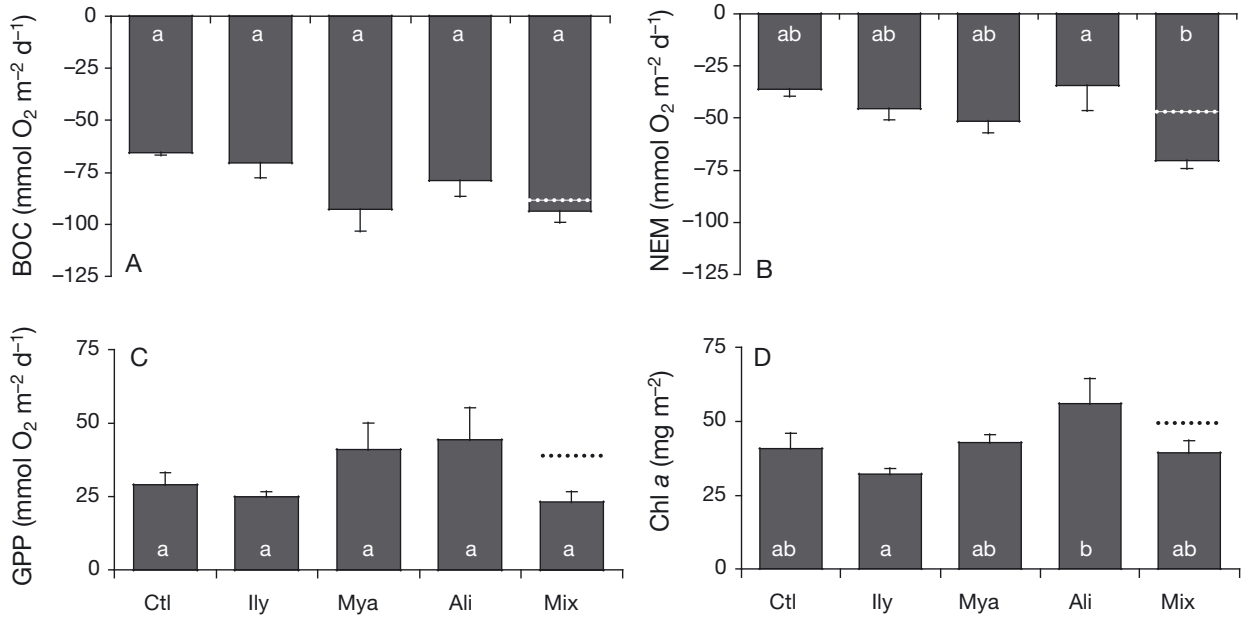

Fig. 3. Expt I. Daily rates (mean ± SE) for (A) benthic oxygen consumption (BOC), (B) net ecosystem metabolism (NEM), and (C) gross primary productivity (GPP), in addition to (D) benthic chlorophyll *a* (chl *a*) in surface sediments. Treatment codes: Ctl, control; Ily, *Ilyanassa obsoleta*; Mya, *Mya arenaria*; Ali, *Alitta virens*; Mix, mixed-fauna. Dotted lines in Mix indicate expected values based on yielding calculations. Dissimilar lower-case letters inside bars denote significant differences (Tukey's HSD) between treatments

benthic microalgal N demand, which ranged from 2.6 ± 0.4 (Mix) to 4.9 ± 1.2 (*Alitta*) mmol m^{-2} d^{-1}.

Benthic chl *a* was also positively correlated with GPP (Pearson's R = 0.71, $p < 0.001$) and was significantly higher in *Alitta* than *Ilyanassa* (Table 1C, Fig. 3D). Microalgal turnover (chl *a*:phaeopigments) was highest in *Alitta*, although not significantly so (Table 1C). N_2 fixation was greater in the dark than in the light (Table 1D) and was generally higher in surface sediments, although the relative importance of sulfate-reducing bacteria to total N_2 fixation (from 60 to 70% contribution) was similar between sediment depths (Table 2). Faunal effects on N_2 fixation, however, were negligible (Table 1D).

Macroalgal biomass and productivity

While *Gracilaria* biomass declined over time in all treatments in Expt II (Fig. 4A), the decline was greatest in *Alitta* and Mix and least in *Ilyanassa*. Macroalgae in microcosms containing *A. virens* displayed clear evidence of grazing, coupled with redistribution of thalli into burrows; remaining thalli became increasingly fragmented and pigmentation shifted from dark red to pale yellow-brown until complete disappearance — in *Alitta* by Day 21 and in Mix by Day 28. In contrast, mean *Gracilaria* biomass in *Ilyanassa* was 2.4-fold greater than the control on Day 28, although values were similar at prior time-points. The significant pattern of higher biomass in the control and *Ilyanassa* relative to *Alitta* and Mix at each measurement (Table 3A) was reflected in the close correlation between GPP and macroalgal biomass (Pearson's R = 0.97, $p < 0.001$). We did not find any clear effects on macroalgae in *Mya*. Microcosms containing *A. virens* were net heterotrophic, and in comparison with *Ilyanassa* we observed greater rates of BOC and significantly lower NEM values (Table 3B, Fig. 5). At the termination of Expt II, only the control and *Ilyanassa* retained sufficient macroalgal tissue for elemental analyses, but no differences in %N or in C:N were observed (McLenaghan 2009).

In Expt III, total macroalgal biomass increased in *Ilyanassa* (+6%) yet ultimately declined in all other treatments (control: –21%, Mix: –56%, *Alitta*: –80%). There were significant treatment effects on total biomass

Table 2. Expt I. N_2 fixation rates (µmol N m^{-2} h^{-1}) in surface (0 to 1 cm) and sub-surface (3 to 4 cm) sediments in light, dark, and dark + sodium molybdate (+Mo) incubation conditions. Values are mean ± SE

Treatment	Surface sediments			Sub-surface sediments	
	Light	Dark	Dark+Mo	Dark	Dark+Mo
Control	22.8 ± 2.2	32.5 ± 4.3	11.7 ± 2.1	17.3 ± 0.9	5.2 ± 1.7
Alitta	18.2 ± 1.8	30.4 ± 2.4	9.6 ± 0.8	16.1 ± 1.9	5.0 ± 0.7
Ilyanassa	21.2 ± 4.6	28.8 ± 1.9	11.5 ± 1.7		

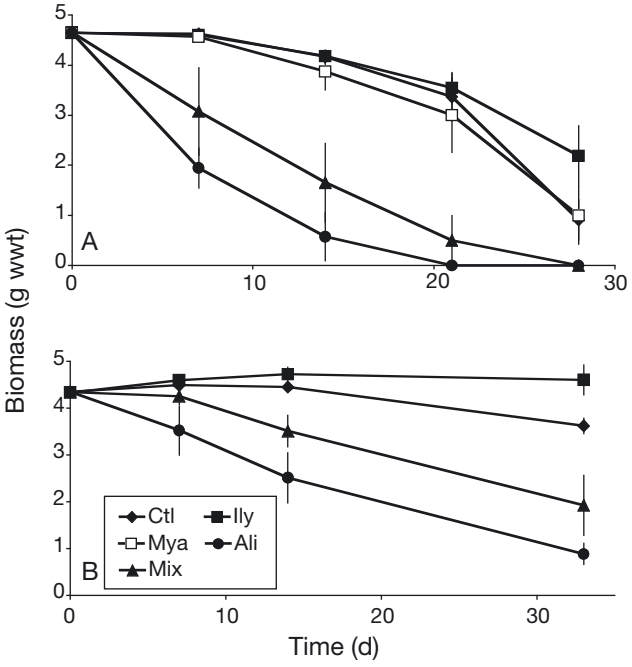

Fig. 4. (A) Biomass (mean ± SE) over time of *Gracilaria* sp. in the Expt II macroalgal monoculture and (B) total biomass of the 3-species macroalgal polyculture in Expt III. Treatment codes: Ctl, control; Ily, *Ilyanassa obsoleta*; Mya, *Mya arenaria* (Expt II, only); Ali, *Alitta virens*; Mix, mixed-fauna; wwt: wet weight

(Table 3C), with differences between *Ilyanassa* and *Alitta* at each time-point and between the control and *Alitta* on Days 14 and 33. As in Expt II, grazing and translocation of thalli by *A. virens* substantially diminished macroalgal standing stocks (Fig. 4B) and diversity by eliminating 2 of the 3 species from the seaweed polyculture. Individual macroalgal species displayed distinct chronological variations in biomass (Fig. 6). *Fucus* biomass peaked after 7 to 14 d in all treatments and then either remained constant (control and *Ilyanassa*) or declined to 61% (*Alitta*) or 74% (Mix) of the initial biomass by Day 33. In treatments that excluded *A. virens*, *Gracilaria* grew steadily throughout the experiment. *Ulva* declined slowly from Day 0 to 14, followed by a more rapid reduction in biomass (from Day 14 to 33) that coincided with emergence of enlarged, circular perforations in thalli from all treatments. Although the control and *Ilyanassa* were statistically similar at all time-points, the final biomass of all macroalgal species was greatest in *Ilyanassa*. In sharp contrast, grazing by *A. virens* (Fig. 7) radically altered the patterns exhibited in the control (Table 3C), with maximum reductions in each species occurring sequentially in *Alitta*: (1) *Gracilaria* biomass decreased first (from Day 0 to 7), (2) *Ulva* was next (from Day 7 to 14), and (3) *Fucus* was last (from Day 14 to 33).

Table 3. Results of 1-way ANOVA for Expt II: (A) *Gracilaria* sp. biomass and (B) dissolved oxygen (DO) flux rates, including benthic oxygen consumption (BOC), net ecosystem metabolism (NEM), and gross primary productivity (GPP). Results of 1-way ANOVA for Expt III: (C) macroalgal biomass, (D) DO flux rates, and (E) tissue carbon:nitrogen (C:N) ratios and %N of *Fucus vesiculosus* (all treatments) and *Gracilaria* sp. (control and *Ilyanassa*). Significant results ($p < 0.05$) in **bold**

Source	df	*F*	p
(A) Expt II: *Gracilaria* sp. biomass[a]			
Day 7	4,15	12.29	**<0.001**
Day 14	4,15	8.71	**0.001**
Day 21	4,15	10.22	**<0.001**
Day 28	4,15	10.25	**<0.001**
(B) Expt II: DO flux rates			
BOC	4,15	7.04	**0.028**
NEM	4,15	9.23	**0.016**
GPP	4,15	7.33	**0.025**
(C) Expt III: Macroalgal biomass[a]			
Gracilaria sp.			
Day 7	3,15	9.42	**0.001**
Day 14	3,15	9.87	**0.001**
Day 33	3,15	8.50	**0.002**
Ulva sp.			
Day 7	3,15	2.69	0.084
Day 14	3,15	4.53	**0.019**
Day 33	3,15	3.21	0.053
Fucus vesiculosus			
Day 7	3,15	0.36	0.785
Day 14	3,15	1.16	0.356
Day 33	3,15	6.07	**0.006**
Total macroalgal biomass			
Day 7	3,15	5.34	**0.011**
Day 14	3,15	8.69	**0.001**
Day 33	3,15	12.13	**<0.001**
(D) Expt III: DO flux rates			
BOC	3,15	16.87	**<0.001**
NEM	3,15	15.98	**<0.001**
GPP	3,15	5.69	**0.008**
(E) Expt III: tissue nutrients			
Fucus vesiculosus C:N	3,15	12.38	**<0.001**
Fucus vesiculosus %N	3,15	13.61	**<0.001**
Gracilaria sp. C:N	1,8	0.35	0.568
Gracilaria sp. %N	1,8	5.23	0.051

[a]Rank-transformation according to Conover & Iman (1981)

In Expt III, *Alitta* again displayed significant trends of enhanced BOC, net heterotrophic metabolism, and lower GPP (Table 3D, Fig. 5). Although the effect of *A. virens* on BOC and total macroalgal biomass in Mix was apparent, we surprisingly observed greater GPP and slightly higher *Ulva* biomass in this treatment than in the control; GPP in Mix was most similar to *Ilyanassa* (Fig. 5F). The relationship between GPP and total macroalgal biomass in Expt III (Pearson's $R = 0.47$, $p = 0.04$) was weaker than the correlation displayed in the Expt II monoculture. The best predictor of GPP was *Ulva* biomass (Pearson's $R = 0.59$, $p = 0.01$), while *Gracilaria* (Pearson's $R = 0.32$, $p = 0.18$) and *Fucus*

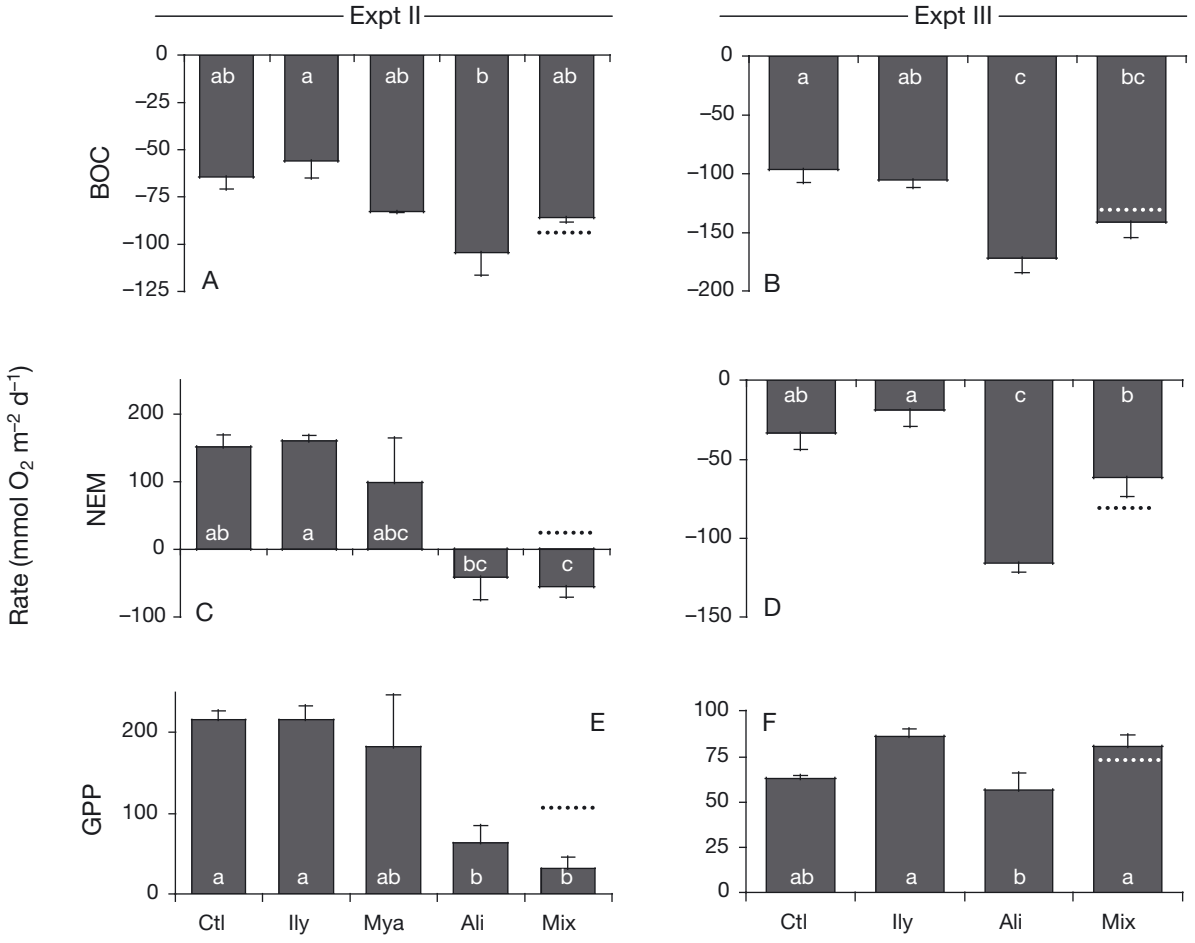

Fig. 5. Daily rates (mean ± SE) for benthic oxygen consumption (BOC) in (A) Expt II and (B) Expt III; for net ecosystem metabolism (NEM) in (C) Expt II and (D) Expt III, and for gross primary productivity (GPP) in (E) Expt II and (F) Expt III. Treatment codes: Ctl, control; Ily, *Ilyanassa obsoleta*; Mya, *Mya arenaria* (Expt II, only); Ali, *Alitta virens*; Mix, mixed-fauna. Dotted lines in Mix indicate expected values based on yielding calculations. Note different scales on *y*-axes. Dissimilar lower-case letters inside bars denote significant differences (Tukey's HSD) between treatments

(Pearson's R = –0.10, p = 0.68) were not correlated. Sufficient tissue for elemental analysis was present in all microcosms for *Fucus*, and in *Ilyanassa* and the control for *Gracilaria*. We could not obtain adequate tissue for *Ulva*. Both *Alitta* and Mix showed significantly lower %N and higher C:N in *Fucus* relative to the control and *Ilyanassa* (Table 3E, Fig. 8). Tissue %N of *Gracilaria* was marginally higher in *Ilyanassa* (Table 3E; p = 0.051).

Effects of faunal diversity

Comparison of observed vs. predicted values for measured properties revealed that the effects of increasing diversity were highly variable (Table 4). For daily nutrient fluxes, NO_3^- under-yielded by 270% as net uptake occurred rather than efflux; NH_4^+ release over-yielded by 25%; and PO_4^{3-} efflux was close to expected values (–8%). Oxygen consumption was within 3 to 7% of predictions across experiments, while NEM deviated from predictions by –53% (Expt I) and –270% (Expt II), as driven by low productivity in faunal assemblages. In Expt III, however, NEM was 8% greater and GPP was 13% higher than expected. Benthic chl *a* under-yielded (16%), as did final *Gracilaria* biomass in both the seaweed monoculture (100%) and seaweed polyculture (61%). Other macroalgal taxa, however, were within 5% (*Ulva*) to 15% (*Fucus*) of predicted biomass at the end of Expt III.

DISCUSSION

The invertebrates in our experiments exhibited species-specific controls over benthic algal communities

and sediment nutrient release, with effects that have direct implications for ecosystem functioning. The polychaete *Alitta virens* created a series of negative feedbacks with macroalgal growth through (1) enhancement of resource competition via stimulation of benthic microalgae, (2) inhibition of bottom-up nutrient supply (in particular, NH_4^+), and (3) direct grazing of thalli. In contrast, the gastropod *Ilyanassa obsoleta* supported macroalgal growth through (1) suppression of benthic microalgal communities, (2) maintenance of sediment nutrient release with promotion of continuous NO_3^- efflux, and (3) moderate increases in macroalgal tissue %N, specifically of *Gracilaria* in the seaweed polyculture. The bivalve *Mya arenaria*, in isolation, did not substantially alter nutrient or algal dynamics. In diverse faunal assemblages, benthic microalgal biomass and productivity appeared to be disproportionately reduced by *I. obsoleta*, while *A. virens* exerted dominant, negative controls on the proliferation of *Gracilaria*.

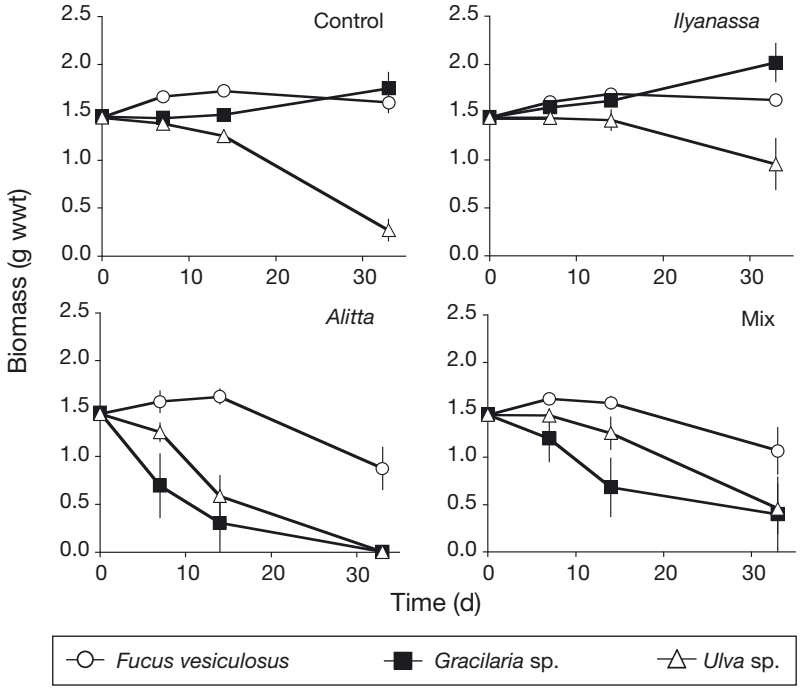

Fig. 6. Expt III. Biomass (mean ± SE) of *Fucus vesiculosus*, *Gracilaria* sp., and *Ulva* sp. over time in the control, *Ilyanassa obsoleta* treatment (*Ilyanassa*), *Alitta virens* treatment (*Alitta*), and the mixed-fauna treatment (Mix). wwt: wet weight

Faunal feedbacks with nutrient supply and benthic microalgae

Expt I demonstrated that invertebrates could act to either depress (*Ilyanassa obsoleta*) or stimulate (*Alitta virens*) benthic microalgal communities (Fig. 3), but that responses in faunal

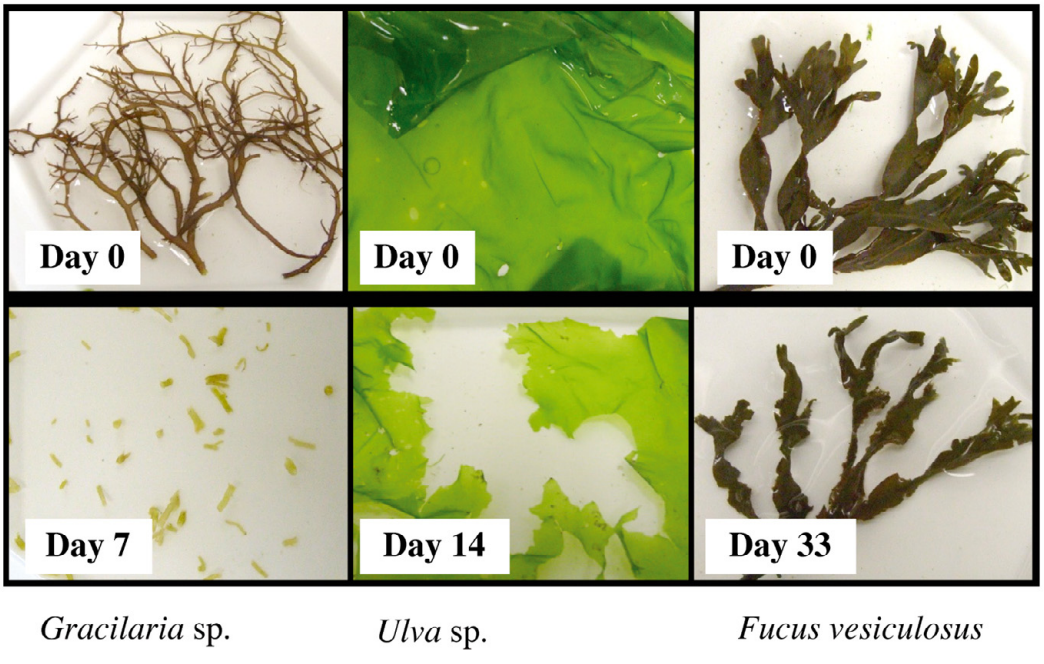

Fig. 7. Expt III. Evidence of grazing by the polychaete *Alitta virens* upon thalli of *Gracilaria* sp. 7 d following addition of macroalgae to microcosms, *Ulva* sp. after 14 d, and *Fucus vesiculosus* after 33 d

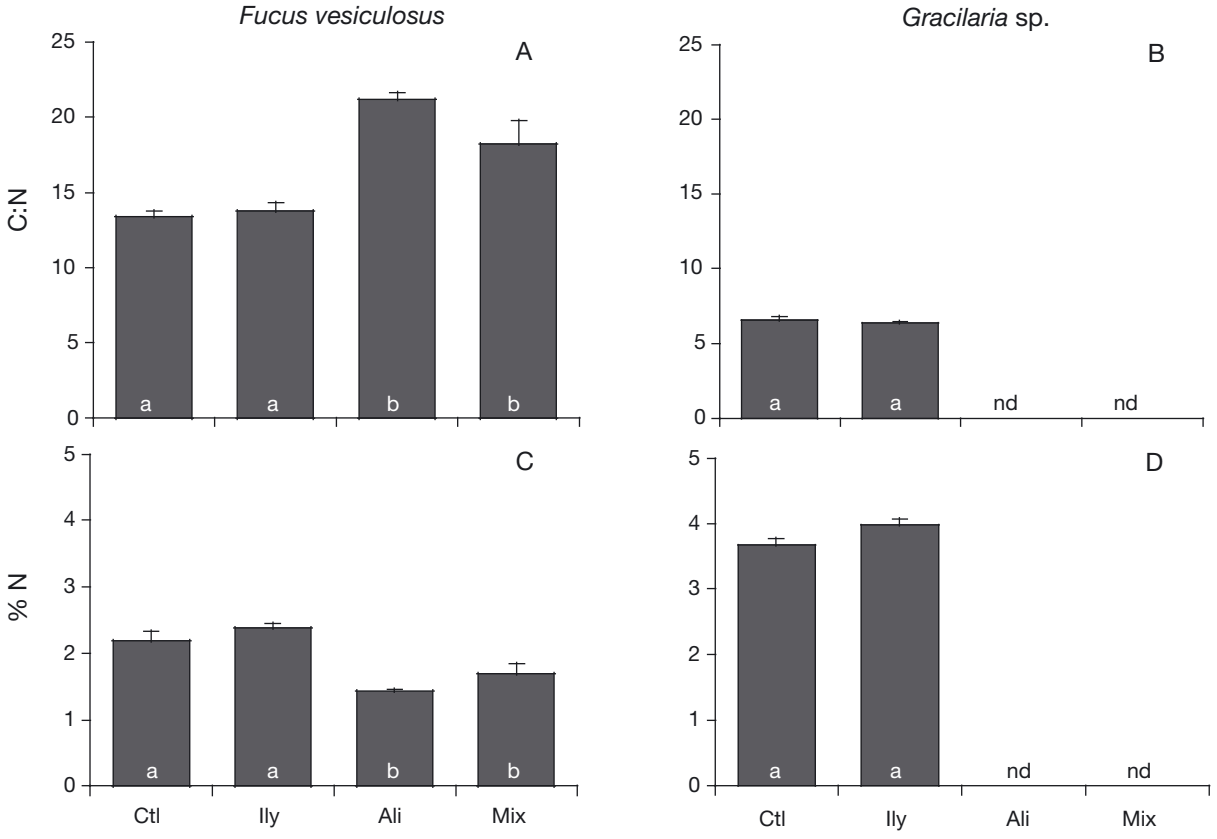

Fig. 8. Expt III. Mean values (+SE) for tissue carbon:nitrogen (C:N) and %N content in *Fucus vesiculosus* and *Gracilaria* sp. at final measurements. Treatment codes: Ctl, control; Ily, *Ilyanassa obsoleta*; Ali, *Alitta virens*; Mix, mixed-fauna. nd: no data. Dissimilar lower-case letters inside bars denote significant differences (Tukey's HSD) between treatments

mixtures were not simple additive functions of performance in monospecific microcosms (Table 4). Our finding that *A. virens* supported the highest levels of benthic microalgal biomass, primary production, and turnover could be a result of intermediate-level disturbance of the sediment surface, potentially with selective removal of senescent microalgae. Others have found that nereidid polychaetes prompt higher turnover of benthic microalgal C and photopigments (Tang & Kristensen 2007), which may have implications for succession in benthic microalgal communities if polychaetes promote new production. In contrast to these effects, our study and others using *I. obsoleta* at similar densities show effective decrease in benthic microalgal chl *a* and primary productivity (Pace et al. 1979, Connor et al. 1982). Moreover, *I. obsoleta* reduced GPP in our mixed-faunal assemblages despite the stimulatory effects of *A. virens*, and our yielding calculations (Table 4) suggest a particularly strong interaction between invertebrate diversity and benthic microalgal productivity, with an amplification of inhibitory effects by *I. obsoleta*. Andersen & Kristensen (1988) also documented reduced primary production within assemblages that included *A. virens* and mudsnails (*Hydrobia* sp.), and attribute the decrease to interspecific competition. Field evidence further suggests that the foraging behavior and superior mobility of *I. obsoleta* enable the snail to more effectively compete for food resources and in turn reduce abundances of deposit-feeding polychaetes, thereby structuring the benthic community (Kelaher et al. 2003).

Regulation of benthic microalgal production also translates into indirect faunal control of nutrient uptake, as evidenced by the tight correlations between GPP and both (1) chl *a* and (2) L/D differences in NH_4^+ efflux. Benthic microalgal communities exercise a critical role in regulating nutrient fluxes at the sediment–water interface (Tyler et al. 2001, 2003), and the depression of NH_4^+ release by *Alitta virens* after 25 d (Fig. 2A) may be partially attributed to enhancement of microalgal uptake. Our observations of NH_4^+ efflux reduction differ from others that have demonstrated stimulatory effects by nereidid polychaetes over shorter experimental time scales (from 1 to 20 d; e.g. Andersen & Kristensen 1988, Hansen & Kristensen 1997, Mermillod-Blondin et al. 2004, Michaud et al.

Table 4. Results of yielding calculations performed according to Waldbusser et al. (2004), comparing observed vs. expected values in the mixed-faunal treatment (Mix). Positive values indicate over-yielding (i.e. greater magnitude than predicted in Mix, based upon single-species treatments). Negative values represent under-yielding. BOC: benthic oxygen consumption; NEM: net ecosystem metabolism; GPP: gross primary productivity. Values for macroalgal biomass were calculated from final measurements. In Expts I and II; under-yielding indicates that Mix was more heterotrophic than predicted, and over-yielding indicates that Mix was less heterotrophic

Source	Yielding (%)
Expt I	
BOC	7
NEM	−53
GPP	−44
NH_4^+ flux (daily)	25
NO_3^- flux (daily)	−270
PO_4^{3-} flux (daily)	−9
Chlorophyll *a*	−16
Expt II	
BOC	−5
NEM	−270
GPP	−75
Gracilaria sp. biomass	−100
Expt III	
BOC	3
NEM	8
GPP	13
Gracilaria sp. biomass	−61
Ulva sp. biomass	−5
Fucus vesiculosus biomass	−15
Total macroalgal biomass	−30

2006). Measurements performed shortly after polychaete colonization may capture a period of enhanced mineralization and mobilization of solutes to the water column, as Hansen & Kristensen (1997) observed: initial pulses of nutrient release and oxygen consumption with *Hediste* (formerly *Nereis*) *diversicolor*, followed by a decrease and relative stabilization after 15 to 20 d. While early effects may be driven by the initial stimulation of sediment microbial communities (e.g. Andersen & Kristensen 1988, Mermillod-Blondin et al. 2004), coupled with effective burrow flushing (Henriksen et al. 1983, Hansen & Kristensen 1997, Mermillod-Blondin et al. 2004), *A. virens* might also diminish longer-term efflux through promotion of benthic microalgal N uptake. Moreover, nereidids could decrease nutrient release via reduction of microbial mineralization (Henriksen et al. 1983), through direct consumption of sediment OM. A companion investigation by Mahl (2009) showed that after 1 mo, *A. virens* density was negatively correlated with both porewater NH_4^+ and flux of sediment-derived NH_4^+ (excluding faunal excretion), potentially due to increased competition for OM among polychaetes and microbes, or enhancement of NH_4^+ transformation to NO_3^-.

Our results suggest that NO_3^- exchange was affected by feedbacks between the benthic microbial community and species-specific functional characteristics of invertebrates (Table 1A), as depth of bioturbation and formation of burrows can dictate the extent of nitrification and subsequent denitrification (Henriksen et al. 1983, Michaud et al. 2006). Continuous release of NO_3^- in *Ilyanassa* throughout both dark and light periods is likely attributable to disturbance of benthic microalgae and enhanced oxygenation of surface sediments, thus promoting nitrifying bacteria in this zone. In contrast, deeper-dwelling burrowers like *Alitta virens* and *Mya arenaria* may either increase (*A. virens*) or decrease (*M. arenaria*) the net daily efflux of NO_3^- by altering NH_4^+ production, sediment oxygenation, and coupled nitrification-denitrification.

We anticipated that grazing pressure and controls on N availability would impact benthic N_2 fixation, as top-down limitations on fixation have been illustrated in pelagic systems (zooplankton grazers; Marino et al. 2002) and in lacustrine benthos (snails; Gettel et al. 2007), yet we detected no effects. Benthic N_2 fixation was negligible compared with net NH_4^+ fluxes (<10% of overall release), and in general, rates within non-vegetated, estuarine sediments of low to moderate organic content are considered to be of minor importance (Howarth et al. 1988). Below the sediment surface, nereidids may influence microbial communities by favoring aerobes over sulfate-reducers in burrow structures (Mermillod-Blondin et al. 2004), although we observed no such effects on N_2 fixation by sulfate reducers. Faunal regulation of nutrient availability did not appear to be linked with direct or indirect controls on sediment N_2 fixation.

Faunal mediation of macroalgal dynamics

Sediments function as a significant internal reservoir of nutrients to support primary production (Tyler et al. 2003, Sundbäck et al. 2003, Kamer et al. 2004), and active control of sediment nutrient release by invertebrates may be important in determining macroalgal proliferation. The promotion of continuous NO_3^- efflux in *Ilyanassa* (Fig. 2) appeared to stimulate growth (or to slow decline) of all macroalgal species (Figs. 4 & 6), and the marginally higher *Gracilaria* tissue N content in Expt III (Table 3E) suggests that nutrient enhancement played a role. Facilitation of macroalgae by bioturbating gastropods has been reported elsewhere, as Fong & Desmond (1997) noted that horn snails *Cerithidea californica* increased growth and N content of

Ulva expansa tissue via excretion and transfer of nutrients from the benthos. Furthermore, Giannotti & McGlathery (2001) illustrated that *I. obsoleta* enhanced tissue N content of *U. lactuca* by 40 to 80%, although the snails ultimately prompted the demise of the macroalgae. In our study, autogenic reduction in *Ulva* biomass caused in part by emergence of circular perforations (in presence and absence of fauna) was unrelated to grazing effects. Perforations in *Ulva* fronds are associated with reproduction and subsequent biomass loss occurs in mid-summer (Niesenbaum 1988), coinciding with the timing of our experiments. Using the same genera of annual seaweeds as the present study, Teichberg et al. (2008) demonstrated that early-summer growth of *Ulva* in the Waquoit Bay estuaries near WFH is superior to *Gracilaria* under enriched conditions, yet *Gracilaria* can rely on internal nutrient stores in depleted waters. While thalli of both taxa have a higher affinity for NH_4^+, *Ulva* can grow quickly with addition of either NO_3^- or NH_4^+ (Teichberg et al. 2008), which may partially explain why loss of *Ulva* biomass in Expt III was stemmed in the presence of *I. obsoleta*.

In contrast to the fertilization effect of snails, changes in *Gracilaria* pigmentation in the presence of *Alitta virens* suggest a reduction of tissue N. This could not be confirmed by elemental analyses due to complete removal of thalli by polychaetes, but is supported by our observation of reduced NH_4^+ supply in Expt I. Others have shown that N-deficient *Gracilaria* thalli lose phycoerythrin (red-brown pigment) in both laboratory (Ryther et al. 1981) and field populations (Tyler & McGlathery 2006). Furthermore, reduced %N and increased C:N in *Fucus* from microcosms containing *A. virens* (Fig. 8) could be related to higher phlorotannin concentrations. These secondary metabolites tend to be inversely correlated with tissue N content (Pavia & Toth 2000), with phlorotannin production increasing under low-nutrient conditions and in response to grazing (Yates & Peckol 1993). The observed decrease in tissue %N might be explained by reduction of sediment NH_4^+ release or consumption of high-N apical tissues. We recommend further research to clarify the potentially complex relationship between polychaetes, nutrient availability, and chemical defenses.

The few studies to report on seaweed grazing by nereidid polychaetes have documented substantial reductions in biomass, with results varying according to macroalgal taxa. For example, others have observed biomass declines and/or translocation of *Ulva* spp. due to activities of *Hediste diversicolor* (Raffaelli 2000, Nordstrom et al. 2006, Engelsen & Pihl 2008), while a 7 d experiment showed a non-significant decrease in *Fucus vesiculosus* in monoculture (Nordstrom et al. 2006). In our Expt III, grazing on *Fucus* was not documented until Days 14 to 33, when other species were either absent or less abundant, thus illustrating the importance of longer-term monitoring and inclusion of multiple seaweed taxa. Despite substantial redistribution of macroalgae into sediments, no subsequent increases in OM content were documented (McLenaghan 2009). Tissue not consumed directly by polychaetes likely was subject to rapid decomposition, as remaining thalli showed intensive fragmentation (Fig. 7).

Grazers tend to prefer macroalgal taxa with relatively higher nutrient content (Hauxwell et al. 1998, Worm et al. 2000), and furthermore, may selectively consume N- and P-rich specimens when presented with both ambient and enriched thalli of the same species (Kraufvelin et al. 2006). While grazers tend to restrict dominance of palatable taxa under oligotrophic conditions, annuals may displace perennials as nutrient loads to estuaries increase and grazing potential is overwhelmed (Worm et al. 2000). Of the seaweeds included in our polyculture experiment, dominance patterns in the field are likely dictated by a combination of nutrient availability, potential growth rates, timing of reproduction, and susceptibility to grazing.

Biodiversity and ecosystem functioning

Community composition of autotrophs can be a critical determinant of ecosystem processes such as primary productivity, in both terrestrial systems (Hooper & Vitousek 1997) and marine environments (Bruno et al. 2005). We have demonstrated that manipulation of faunal and seaweed diversity has both direct and indirect consequences for ecosystem functions, particularly in relation to productivity and composition of the autotrophic community. In simple systems including either zero or 1 seaweed species, there were substantial effects of faunal diversity on benthic microalgae and macroalgae, as well as ecosystem metabolism. When we incorporated multi-species assemblages of seaweeds, total macroalgal biomass and productivity in the mixed-fauna microcosms were close to predicted values, and clear species-specific patterns emerged: we consistently observed swift reduction of *Gracilaria* by *Alitta virens*, while *Ilyanassa obsoleta* promoted bloom-forming taxa such as *Ulva*. Moreover, species identity may be a more important factor than macroalgal richness in regulating overall production (Kraufvelin et al. 2010), as opportunistic taxa such as *Ulva* can be more productive in the absence of other macroalgae (Bruno et al. 2005). In support of these prior findings on the importance of macroalgal species identity, we found that GPP during Expt III was best explained by the biomass of a single taxon (*Ulva*) within assem-

blages. Total macroalgal biomass was only correlated with GPP in a seaweed monoculture (Expt II), as inclusion of multiple macroalgal species confounded this relationship. Our experiments highlight important species-specific effects and emphasize the need to incorporate increasingly complex assemblages across multiple trophic levels in biodiversity studies.

In conclusion, these results help to further our understanding of feedbacks between functional traits of invertebrates and ecosystem processes. *Ilyanassa obsoleta*, a common bioturbator, may accelerate eutrophication by diminishing benthic microalgal biomass, sustaining efflux of nutrients, and indirectly promoting macroalgal growth. Conversely, the bioirrigating polychaete *Alitta virens* may buffer initial impacts of nutrient enrichment by stimulating benthic microalgae, inhibiting NH_4^+ release, and efficiently reducing bloom-forming seaweeds through grazing. Other species, such as *Mya arenaria*, may produce only limited effects on nutrient and algal dynamics. In light of increasing eutrophication and widespread changes in species distribution on a global scale, particularly in coastal regions, it is increasingly urgent to clarify the mechanistic relationships between ecosystem functioning and both invertebrate and macroalgal diversity.

Acknowledgements. We are grateful to M. Hayn, C. Funk, S. Kelsey, M. Ferdie Muth, L. Reynolds, M. Kozlowski, and C. Scheiner for assistance in the field and laboratory, and to T. Duncan for sharing his knowledge of benthic invertebrate distributions within the study site. The Marine Biological Laboratory provided logistical support, and we especially thank the following people: A. Giblin, K. Foreman, K. McGlathery, and P. Berg. The manuscript was improved by the comments of 3 anonymous reviewers. This material is based on work funded by the National Science Foundation under grants awarded to A.C.T. (OCE 0727642) and R.W.H. (EAR 0420575).

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Editorial responsibility: Morten Pedersen, Roskilde, Denmark

Submitted: June 14, 2010; Accepted: January 10, 2011
Proofs received from author(s): March 11, 2011