

# Threat of predation alters the ability of benthic invertebrates to modify sediment biogeochemistry and benthic microalgal abundance

Katherine M. Premo, Anna Christina Tyler\*

Program in Environmental Sciences, School of Life Sciences, Rochester Institute of Technology, 85 Lomb Memorial Drive, Rochester, New York 14623, USA

**ABSTRACT:** Benthic invertebrates alter estuarine ecosystem function by moderating benthic microalgal production and sediment biogeochemistry. While lethal predation eliminates the effect of invertebrates, non-consumptive effects of predation through trait-mediated indirect effects on behavior may reduce prey control of ecosystem function. Using microcosms, we investigated how chemical cues from the predatory mud crab *Panopeus herbstii* changed prey behavior and thereby affected the ability of the grazing-deposit feeding gastropod *Ilyanassa obsoleta* and filter-feeding bivalve *Mercenaria mercenaria* to regulate benthic ecosystem function. Sediment–water column fluxes of oxygen and nutrients, microscale profiles of sediment oxygen, benthic chlorophyll *a*, porewater ammonium and organic matter were measured after exposure to predator effluent. Both species had significant effects on sediment processes, with higher sediment oxygen consumption and release of ammonium to the water column, and lower porewater ammonium. However, individual effects were altered in the presence of chemical cues from *P. herbstii*. The negative effect of *M. mercenaria* on porewater ammonium was diminished by 26 % in predator treatments, suggesting less movement and therefore less sediment oxidation and nitrogen removal. For *I. obsoleta*, there was a 30 % increase in microalgal biomass and a 35 % decrease in sediment ammonium release in the predator treatments, possibly associated with decreased foraging activity. In these experiments, non-consumptive predator effects indirectly altered benthic biogeochemistry, benthic microalgae and nutrient fluxes. These results suggest that experiments conducted without predators may overestimate the impact of benthic fauna on ecosystem processes and that changes in community structure resulting in loss of predators may have indirect effects on benthic ecosystem function, leading to faster nitrogen turnover and release to the water column.

**KEY WORDS:** Trait-mediated interactions · Non-consumptive effects · Benthic invertebrates · Benthic microalgae · Sediment biogeochemistry

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Predators exert consumptive and non-consumptive controls on prey populations. Consumptive effects are the direct lethal effects of predation, while non-consumptive effects (NCE) refer to behavioral or morphological changes that occur to avoid predation (Lima 1998, Preisser et al. 2005). A number of marine studies have discussed the effects of predation on

phenotypic and behavioral change (e.g. Doering 1982, Leonard et al. 1999, O'Connor et al. 2008, Geraldi & Powers 2011). Consequences of non-consumptive predation on benthic invertebrates include increased burrowing depths (Doering 1982, Whitlow 2010), escape (Marko & Palmer 1991), increased shell thickness (Leonard et al. 1999), reduced size and growth rate (Nakaoka 2000), reduced feeding (Trussell et al. 2003, Smee & Weissburg 2006a,b,

Maire et al. 2010) and increased siphon lengths (Whitlow 2010). In some instances, NCE are as detrimental to prey as lethal effects (Trussell et al. 2004).

Only a few studies have explored how changes in prey behavior may indirectly affect the growth of primary producers, and fewer still have examined how these NCE may translate to changes in biogeochemical cycling. Macrobenthic invertebrates often regulate the abundance of micro- and macroalgae (e.g. Connor et al. 1982, Hauxwell et al. 1998, Bruno & O'Connor 2005, Engelsen & Pihl 2008). While it is well established that predation can result in trophic cascade effects (e.g. Silliman & Bertness 2002, Bruno & O'Connor 2005), NCE may also initiate trophic cascades by reducing grazing activities and allowing proliferation of primary producers (Schmitz et al. 1997, Molis et al. 2011). For example, consumption of *Fucus serratus* recruits by *Littorina littorea* decreased 15-fold in the presence of feeding *Carcinus maenus* (Molis et al. 2011). Similar NCE on primary producers probably occur in a multitude of marine ecosystems. As benthic microalgae (BMA) regulate inorganic nutrient fluxes and sediment oxygen utilization (Tyler et al. 2003, Vopel et al. 2012), NCE-induced reduction in BMA consumption may ultimately affect solute fluxes at the sediment–water interface.

Bioturbation through burrowing and grazing significantly alters sediment conditions, affecting oxygen penetration, oxygen consumption and mineralization, and nutrient release (e.g. Aller 1988, Gilbert et al. 1998, Mermillod-Blondin et al. 2004, Michaud et al. 2005, McLenaghan et al. 2011). Invertebrate activity also results in the redistribution of organic matter (OM) and porewater, altering the oxic–anoxic boundary and promoting OM degradation and nutrient cycling (e.g. Kristensen 2000 and references therein, Mermillod-Blondin et al. 2005). However, many of the above studies were conducted in single species assemblages that excluded predators, even though NCE-related behavioral changes may alter these key interactions. For example, bioturbation depth increases when the deposit-feeding bivalve *Macoma balthica* senses predatory shrimp (Maire et al. 2010). If bioturbation increases porewater oxidation, increased bioturbation depth may promote deeper OM mineralization. In contrast, in the presence of a predator, benthic chironomids exhibit avoidance behavior and spend significantly more time hiding in burrows than at the sediment surface, ultimately resulting in higher mineralization due to reduced subduction of freshly deposited OM into the sediment anoxic zone (Stief & Hölker 2006). Likewise, O'Connor et al. (2008) speculated that loss of

predators would increase sediment OM content because the presence of predatory crabs suppressed settlement of oyster larvae that produce OM-rich pseudofeces. It follows that NCE will indirectly influence many other benthic functions influenced by bioturbating prey, including BMA production, porewater solutes and sediment–water column nutrient fluxes, and that these indirect effects will depend on the lifestyle of the prey. To date, we know little about the role of NCE in soft-bottomed marine communities and how predators may alter the influence of benthic invertebrates, important ecosystem engineers (Levinton 1995), on benthic processes. A better understanding of the direct and indirect role of predators in the maintenance of ecosystem function is required (Preisser et al. 2005) and particularly important given the rapid loss of diversity and thereby ecosystem functions in degraded estuaries (Solan et al. 2004, Diaz & Rosenberg 2008).

We investigated how the chemical cues from the predatory mud crab *Panopeus herbstii* influence the ability of the eastern mud snail *Ilyanassa obsoleta* and the hard-shelled clam, or quahog, *Mercenaria mercenaria* to influence BMA biomass, benthic oxygen consumption (BOC), gross primary production (GPP), sediment–water column nutrient release, and sediment porewater nutrient concentrations and OM. These are cosmopolitan prey species in the western Mid-Atlantic region and are tolerant of eutrophic conditions to the extent that populations seem to increase in eutrophic estuaries, where they may find a refuge from predation by less tolerant predators (Altieri 2008, Fox et al. 2009, Johnson & Short 2013, Yarrington et al. 2013). Furthermore, both species influence sediment biogeochemistry and solute fluxes. *M. mercenaria* increases BOC (Murphy & Kremer 1985, Doering et al. 1987) and enhances denitrification (A. C. Tyler et al. unpubl. data). *I. obsoleta* increases nitrogen release directly through excretion and indirectly by bioturbation and feeding on BMA (McLenaghan et al. 2011, Yarrington et al. 2013). Finally, as prey, both react to chemical cues produced by predators. *M. mercenaria* reacts to a predator by increasing burrowing depth (Doering 1982) and reducing feeding time (Smee & Weissburg 2006a,b), resulting in lower growth rates (Nakaoka 2000). Smee & Weissburg (2006a) demonstrated that chemical cues elicit these behavioral responses. When presented with the scent of a predator, *I. obsoleta* shows increased 'alarm' and flees from the offensive odor (Rahman et al. 2000). Thus, these are ideal study organisms to better understand how chemical cues from predators impact prey behavior and

thereby control of benthic processes. We hypothesized that prey response to chemical cues would result in reduced sediment oxidation and nutrient fluxes and a build-up of nutrients and OM in the sediments relative to control treatments without predator influence. Furthermore, if NCE lead to decreased surface grazing by *I. obsoleta*, we expected to observe an increase in BMA and, because of increased BMA nutrient uptake, a decrease in nutrient efflux to the water column.

## MATERIALS AND METHODS

### Sediment collection and microcosm construction

Sediment, invertebrates and *Ulva* sp. were collected during August 2011 from West Falmouth Harbor (WFH; 41° 36' N, 70° 38' W), a shallow (average depth at mean low water 0.6 m), polyhaline estuary in southwestern Cape Cod, Massachusetts, USA (Howes et al. 2006). In the mid-1990s, a localized wastewater plume high in nitrogen began to enter the harbor, roughly doubling the nitrogen load relative to background levels. The mean grain size of sediments in the area of sediment collection is 1.0 mm, with an average composition of 0.1% gravel, 90.3% sand and 9.6% mud (Scheiner 2011).

Surface sediments (to ~10 cm depth) were collected using a 9.5 cm (inner diameter) × 30 cm (height) polycarbonate tube and sectioned at depths of 0–2, 2–5 and 5–10 cm. Sediment from each section was homogenized separately and larger invertebrates and gravel removed using a 1 mm sieve. Microcosms were constructed in similar tubes by filling the bottom 12 cm with sediment, leaving ~1 l headspace. Sediment strata were maintained during construction. Microcosms were maintained in a 'Living Stream' (FrigidUnits) flowing aquaculture system with artificial seawater (28 to 32 ppt, 18 to 22°C) and illuminated with full-spectrum fluorescent lights for 14 h d<sup>-1</sup>. Bubbles generated by an air pump were introduced continually to each microcosm to promote water circulation. Once assembled, the microcosms were allowed to acclimate under these conditions for 1 mo.

### Experimental set-up

The prey densities (3 small *Mercenaria mercenaria* [20 to 30 mm shell length] per microcosm [430 ind. m<sup>-2</sup>] or 4 *Ilyanassa obsoleta* [17 to 19 mm shell

length] per microcosm [570 ind. m<sup>-2</sup>]) were within the range found in WFH (0 to 572 ind. m<sup>-2</sup> for *M. mercenaria* and 0 to 1952 ind. m<sup>-2</sup> for *I. obsoleta*; Yarrington et al. 2013, N. A. McLenaghan unpubl. data). We used 4 replicates for each of the 5 treatments: *M. mercenaria* (Mer) (total biomass = 14.0 ± 0.5 g); *I. obsoleta* (Ily) (total biomass = 7.2 ± 0.5 g); *M. mercenaria* + *Panopeus herbstii* effluent (Mer+Pred) (total biomass = 13.8 ± 0.5 g); *I. obsoleta* + *P. herbstii* effluent (Ily+Pred) (total biomass = 7.1 ± 0.7 g); and a control with no animals or predator influence (Con). Following the acclimation period, we added 100 g dry weight m<sup>-2</sup> of dried, ground *Ulva* sp. to each microcosm to simulate the deposition of fresh detritus after the demise of a moderate macroalgal bloom. The quantity of detritus added was based on macroalgal standing stocks measured previously in nearby Waquoit Bay (Hauxwell et al. 1998). *M. mercenaria* and *I. obsoleta* were added to their designated microcosms 24 h later. *M. mercenaria* that did not rapidly bury were replaced with more active individuals.

Prey species acclimated in microcosms for 1 wk before implementing predator treatments. The mud crab *Panopeus herbstii* was chosen as the predator species because it is common in WFH (McLennaghan 2009) and preys on both *Mercenaria mercenaria* and *Ilyanassa obsoleta*. *P. herbstii* preys on *M. mercenaria* by either crushing or slowly chipping away at the shell (Whetstone & Eversole 1981). *P. herbstii* consumes *I. obsoleta* by reaching into the shell and picking away at the operculum (authors' pers. obs.). When predator treatments were imposed, all microcosms were raised so that the top of the microcosm was just above the water surface and sufficiently submerged to maintain a consistent temperature, but the headspace was isolated from the surrounding water. A siphon drip system was set up to create a flow-through system to maintain water turnover and allow crab effluent to flow into predator treatments (Fig. 1). Seawater flowed from a large reservoir into two 8.3 l containers, one containing no animals and another containing 5 *P. herbstii* (10 to 12 mm carapace width). Individual *P. herbstii* were isolated in separate screened containers within the larger tank to prevent fighting. Flow through the Tygon tubing was maintained at a rate of 1 ml min<sup>-1</sup> with gang valves, allowing for total headspace water exchange every ~17 h. Excess water spilled over the top of the microcosms and a siphon system was used to maintain the overall water level in the Living Stream. Smee & Weissburg (2006b) found that *M. mercenaria*'s predator response was only to chemical cues from damaged conspecifics or blue crabs that had

recently eaten. Thus, each *P. herbstii* was fed twice a week with approximately 1 g wet weight frozen *M. mercenaria* tissue. All microcosms were supplied with 5 ml of phytoplankton culture 3 times per week to provide an OM source and food supply for *M. mercenaria*. We measured the nutrient concentration in the tanks with and without *P. herbstii* periodically during the experiment and compared differences with a paired *t*-test.

### Oxygen microelectrode measurements

Microscale sediment O<sub>2</sub> concentrations were measured 20 d after the addition of *Panopeus herbstii* effluent using 50 µm diameter glass oxygen microelectrodes (OX-50, UNISENSE) connected to a picoammeter (PA2000, UNISENSE) and a manual micro-manipulator. The electrode was calibrated using the O<sub>2</sub> concentration in the water column as measured with a Hach HQ40d meter (LDO101 probe) and the concentration at the bottom of the profile, which was assumed to be completely oxygen depleted. Per treatment, 3 of the 4 microcosms were randomly selected and 1 profile measured in the light and dark roughly in the center of the chamber, but taking care to avoid obvious *Ilyanassa obsoleta* or *Mercenaria mercenaria* siphon holes. We acknowledge the potential heterogeneity in the sediment surface within and between microcosms, as demonstrated by studies utilizing planar oxygen optodes and visual imagery (i.e. Volkenborn et al. 2010, 2012). As the depth at which the probe crossed the sediment–water interface could not be determined visually due to the small tip size, the sediment–water interface was determined by inspecting the slope of the resulting profile. Sediment oxygen consumption (SOC) was calculated using the PROFILE model developed

and explained in Berg et al. (1998). GPP was calculated as the difference between the light and dark hourly fluxes of oxygen, assuming that respiration and non-microbial oxidation of reduced compounds were similar in the light and dark.

### Oxygen and nutrient flux measurements

Oxygen and nutrient flux measurements were taken 21 d after the addition *Panopeus herbstii* effluent according to the methods of Tyler et al. (2001). Two-thirds of the overlying water in each microcosm was gently siphoned off and replaced with fresh seawater. Replacement water for *P. herbstii* treatments comprised 50% effluent-containing water and 50% fresh seawater. The microcosms were sealed with a gas-tight polycarbonate lid fitted with a butyl rubber O-ring. One rotating (~60 rpm) Teflon®-coated magnet was used to mix the water column. The sealed microcosms were submerged in the aquarium and the temperature and light conditions were maintained as above. Five measurements were taken at 1 to 2 h intervals, the first 3 in the dark and the remaining 2 in the light. Oxygen was measured with a Hach HQ40d meter (LDO101 probe) and water samples for ammonium (NH<sub>4</sub><sup>+</sup>), nitrate (NO<sub>3</sub><sup>-</sup>) and phosphate (PO<sub>4</sub><sup>3-</sup>) were taken with a 60 cm<sup>3</sup> syringe. After sampling, water was replaced with a known fill volume.

All water samples were immediately filtered through Supor TM 0.45 µm membrane filters and frozen at -20°C. NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup> (hereafter NO<sub>3</sub><sup>-</sup>) and PO<sub>4</sub><sup>3-</sup> were analyzed on a Lachat Quikchem 8500 Autoanalyzer with the cadmium reduction and molybdate complex methods, respectively. Ammonium was analyzed according to Solorzano (1969) using the phenol-hypochlorite method. The initial concentration of nutrients in microcosms with and without predation effects were compared using a *t*-test to ensure no differences associated with crab effluent. Hourly BOC and nutrient fluxes were calculated based on changes in concentration over time after adjustment for the change in concentration associated with refilling the cores after each sample was removed (Tyler et al. 2001). To calculate daily fluxes, we used a 14 h light, 10 h dark cycle. The BOC measured here differs from SOC measured using microelectrodes because it also includes faunal and overlying water

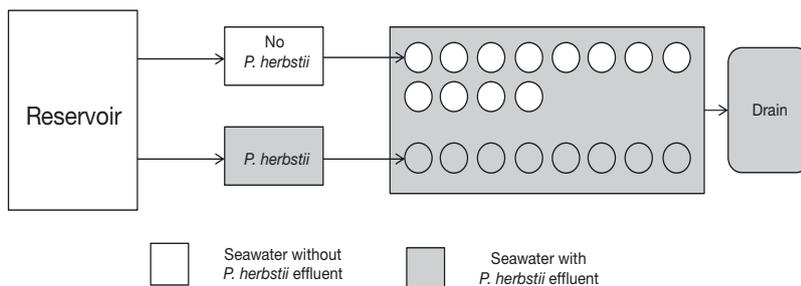


Fig. 1. Schematic diagram of tank set-up with siphon drip systems. Seawater flowed from the reservoir into designated tanks with or without *Panopeus herbstii*, then into specific cores. Water overflowed from microcosms into a tank whose water level was maintained by a siphon connected to the drain. Note: not to scale

metabolism. The use of both techniques allowed us to separate the effects of organisms on sediment metabolism alone from metabolism of the benthos (sediment plus fauna plus overlying water) as a whole.

### Sediment characteristics

Porewater NH<sub>4</sub><sup>+</sup> samples were taken according to Berg & McGlathery (2001). A 2 mm stainless steel probe was used to extract 2.5 ml of water at depths of 2, 5, 7 and 10 cm, which was immediately filtered with a 0.45 µm membrane filter and frozen at -20°C until analysis according to Solorzano (1969). Sediment samples for chlorophyll *a* (chl *a*), a proxy for BMA biomass, were taken with a modified 5 cm<sup>3</sup> syringe corer to the depth of 1 cm. Sediment was immediately placed in 15 ml centrifuge tubes, darkened and frozen at -80°C until analysis within 30 d using the methods of Strickland & Parsons (1972). Chl *a* concentrations were calculated using the Lorenzen (1967) equations. A modified 60 cm<sup>3</sup> syringe corer was used to collect 1 sample for OM analysis from each microcosm. The cores were then sectioned at depths of 0–1, 1–2, 2–5 and 5–12 cm. Porosity was determined gravimetrically following drying at 60°C and percent OM was determined by loss on ignition (Heiri et al. 2001). We calculated the depth-integrated porewater NH<sub>4</sub><sup>+</sup> inventory, a measure of the total ammonium in the porewater, based on the concentrations and porosity at each depth.

### Statistical analysis

All statistical analyses were conducted using SAS 9.2. Normality was determined in SAS using the Shapiro-Wilks test. Daily oxygen and nutrient fluxes, porewater NH<sub>4</sub><sup>+</sup>, chl *a*, OM and O<sub>2</sub> output parameters from the PROFILE model were tested for significant differences between treatments with either a 1-way ANOVA or a Kruskal-Wallis test for non-normally distributed data. When significant effects were found, a contrast analysis was run.

## RESULTS

The benthic community for all microcosms was net heterotrophic, and as anticipated, treatments with invertebrates had significantly greater (3 to 4 times) daily BOC than the control (Tables 1 & 2). Invertebrate treatments also yielded significant results for

Table 1. Mean values (±SE) for sediment water column oxygen fluxes in the light and dark, the calculated gross primary production (GPP), the daily sediment oxygen consumption (SOC) based on microelectrode measurements, and the benthic oxygen consumption (BOC) based on whole microcosm flux measurements; microalgal chlorophyll *a* (chl *a*) and the ratio of GPP to chl *a* based on the microelectrode measurements; sediment-water column fluxes of ammonium (NH<sub>4</sub><sup>+</sup>), nitrate (NO<sub>3</sub><sup>-</sup>) and phosphate (PO<sub>4</sub><sup>3-</sup>); and depth-integrated porewater NH<sub>4</sub><sup>+</sup>. Negative values for flux measurements represent uptake of solute by the sediment. Treatments are control (Con), *Mercenaria mercenaria* (Mer), *M. mercenaria* and *Panopeus herbstii* influence (Mer+Pred), *Ilyanassa obsoleta* (Ily) and *I. obsoleta* and *P. herbstii* influence (Ily+Pred). Different superscripted letters indicate significance between treatments. Values for each variable that share a superscripted letter are not significantly different from one another (p > 0.05)

	Light		Dark		Oxygen flux		SOC		BOC		Benthic microalgae		Nutrient flux		Porewater		
	(mmol m <sup>-2</sup> h <sup>-1</sup> )	GPP (mmol m <sup>-2</sup> h <sup>-1</sup> )	Dark (mmol m <sup>-2</sup> h <sup>-1</sup> )	GPP (mmol m <sup>-2</sup> h <sup>-1</sup> )	(mmol m <sup>-2</sup> d <sup>-1</sup> )	(mmol m <sup>-2</sup> d <sup>-1</sup> )	chl <i>a</i> (mg m <sup>-2</sup> )	GPP:chl <i>a</i> (µmol h <sup>-1</sup> mg chl <i>a</i> <sup>-1</sup> )	NH <sub>4</sub> <sup>+</sup> (mmol m <sup>-2</sup> d <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> (mmol m <sup>-2</sup> d <sup>-1</sup> )	PO <sub>4</sub> <sup>3-</sup> (mmol m <sup>-2</sup> d <sup>-1</sup> )	NH <sub>4</sub> <sup>+</sup> (mmol)	Whole core (mmol)				
Con	-0.02 ± 0.01 <sup>a</sup>	-0.01 ± 0.01 <sup>a</sup>	-0.01 ± 0.01 <sup>a</sup>	-0.01 ± 0.01 <sup>a</sup>	0.01 ± 0.03 <sup>a</sup>	-0.4 ± 0.16 <sup>a</sup>	-0.4 ± 0.16 <sup>a</sup>	-0.4 ± 0.16 <sup>a</sup>	-9.35 ± 0.63 <sup>a</sup>	69.2 ± 4.0 <sup>a</sup>	0.1 ± 0.4 <sup>a</sup>	0.15 ± 0.03 <sup>a</sup>	-2.36 ± 6.18 <sup>a</sup>	-0.08 ± 0.02 <sup>a</sup>	0.31 ± 0.06 <sup>a</sup>		
Mer	-0.72 ± 0.13 <sup>b</sup>	-0.83 ± 0.18 <sup>b</sup>	-0.83 ± 0.18 <sup>b</sup>	-0.83 ± 0.18 <sup>b</sup>	0.11 ± 0.10 <sup>a</sup>	-18.37 ± 3.48 <sup>b</sup>	-18.37 ± 3.48 <sup>b</sup>	-18.37 ± 3.48 <sup>b</sup>	-28.41 ± 4.83 <sup>b</sup>	93.2 ± 3.7 <sup>a</sup>	1.1 ± 1.1 <sup>a</sup>	0.32 ± 0.02 <sup>ab</sup>	1.65 ± 1.53 <sup>a</sup>	-0.02 ± 0.03 <sup>a</sup>	0.19 ± 0.06 <sup>a</sup>		
Mer+Pred	-0.9 ± 0.15 <sup>b</sup>	-1.15 ± 0.12 <sup>b</sup>	-1.15 ± 0.12 <sup>b</sup>	-1.15 ± 0.12 <sup>b</sup>	0.24 ± 0.26 <sup>ab</sup>	-24.08 ± 1.06 <sup>b</sup>	-24.08 ± 1.06 <sup>b</sup>	-24.08 ± 1.06 <sup>b</sup>	-40.11 ± 5.85 <sup>b</sup>	84.5 ± 12.4 <sup>a</sup>	2.2 ± 2.5 <sup>ab</sup>	0.41 ± 0.08 <sup>b</sup>	-4.28 ± 1.02 <sup>a</sup>	-0.09 ± 0.04 <sup>a</sup>	0.27 ± 0.03 <sup>a</sup>		
Ily	0.06 ± 0.05 <sup>a</sup>	-0.81 ± 0.05 <sup>b</sup>	-0.81 ± 0.05 <sup>b</sup>	-0.81 ± 0.05 <sup>b</sup>	0.87 ± 0.09 <sup>b</sup>	-7.25 ± 0.73 <sup>a</sup>	-7.25 ± 0.73 <sup>a</sup>	-7.25 ± 0.73 <sup>a</sup>	-32.26 ± 3.87 <sup>b</sup>	119.2 ± 17.9 <sup>b</sup>	7.4 ± 0.4 <sup>b</sup>	0.72 ± 0.06 <sup>c</sup>	-2 ± 3.34 <sup>a</sup>	-0.02 ± 0.05 <sup>a</sup>	0.32 ± 0.03 <sup>a</sup>		
Ily+Pred	-0.09 ± 0.07 <sup>a</sup>	-0.72 ± 0.06 <sup>b</sup>	-0.72 ± 0.06 <sup>b</sup>	-0.72 ± 0.06 <sup>b</sup>	0.63 ± 0.03 <sup>ab</sup>	-8.38 ± 1.49 <sup>a</sup>	-8.38 ± 1.49 <sup>a</sup>	-8.38 ± 1.49 <sup>a</sup>	-33.77 ± 4.32 <sup>b</sup>	167.7 ± 15.4 <sup>c</sup>	3.8 ± 0.3 <sup>ab</sup>	0.46 ± 0.04 <sup>b</sup>	-5.06 ± 0.60 <sup>a</sup>	-0.06 ± 0.04 <sup>a</sup>	0.32 ± 0.03 <sup>a</sup>		

Table 2. Results from 1-way ANOVA or, when necessary, Kruskal-Wallis, for dissolved oxygen fluxes, including benthic oxygen consumption (BOC) measured during flux experiments, and sediment oxygen consumption (SOC) and gross primary production (GPP) based on microelectrode measurements, benthic microalgal chl *a*, GPP:chl *a* (based on microelectrode measurements of GPP), daily nutrient fluxes of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$ ; porewater  $\text{NH}_4^+$  concentrations for the whole core and at individual depths, and sediment percent organic matter (OM) at different depths. **Bold** values indicate significance at  $p < 0.05$

Source	df	F or $\chi^2$	p
<b>Oxygen fluxes</b>			
Daily BOC	4	<b>5.66</b>	<b>0.006</b>
Dark SOC	4	<b>15.96</b>	<b>&lt;0.001</b>
Light SOC	4	<b>20.52</b>	<b>&lt;0.001</b>
Daily SOC	4	<b>21.87</b>	<b>&lt;0.001</b>
GPP (based on SOC)	4	<b>6.31</b>	<b>0.011</b>
<b>Benthic microalgae</b>			
Chl <i>a</i>	4	<b>12.99</b>	<b>&lt;0.001</b>
GPP:chl <i>a</i>	4	<b>4.49</b>	<b>0.028</b>
<b>Daily nutrient flux</b>			
$\text{NH}_4^+$	4	<b>10.72</b>	<b>&lt;0.001</b>
$\text{NO}_3^-$	4	0.66	0.630
$\text{PO}_4^{3-}$	4	0.83	0.531
<b>Porewater <math>\text{NH}_4^+</math></b>			
Whole core depth integrated	4	1.56	0.239
2 cm	4	<b>4.57</b>	<b>0.014</b>
4 cm	4	1.39	0.288
7 cm	4	1.83	0.180
10 cm	4	0.83	0.529
<b>OM</b>			
0–1 cm	4	<b>4.20</b>	<b>0.026</b>
1–2 cm	4	0.23	0.918
2–5 cm <sup>a</sup>	4	1.88	0.759
5–10 cm	4	1.15	0.387

<sup>a</sup>Kruskal-Wallis test

SOC, modeled from oxygen microelectrode measurements (Tables 1 & 2). In the dark, SOC was significantly greater in all treatments without regard to the species, but in the light Mer significantly increased SOC while Ily did not. These trends in the light and dark are reflected in the daily SOC, where both Mer and Mer+Pred had significantly greater daily SOC than the other treatments.

GPP was the smallest for Con and only Ily+Pred was significantly greater than the Con and Mer treatments (Tables 1 & 2). *Mercenaria mercenaria* had no effect on chl *a*, but *Ilyanassa obsoleta* significantly increased chl *a* concentrations in both Ily (40% higher) and Ily+Pred (58%) treatments relative to the control (Tables 1 & 2). Interestingly, there was a significant difference in the GPP (based on SOC) per unit chl *a* between treatments, with higher chl *a* efficiency in the Ily treatments, particu-

larly in the *I. obsoleta* treatment without predation (Tables 1 & 2).

Porewater  $\text{NH}_4^+$  concentrations were significantly lower in the top 2 cm of sediment in both Mer and Ily alone relative to Con, but this effect disappeared in the presence of a predator (Fig. 2a, Table 2). Although not significant, the total porewater  $\text{NH}_4^+$  inventory in the sediments was also reduced by 38% in treatments with Mer but only by 12% in the presence of a predator (Tables 1 & 2). Total porewater inventory was similar in Con and both Ily and Ily+Pred treatments, suggesting little influence of Ily below the sediment surface. Sediment OM was higher in both predator treatments relative to Con or prey-alone treatments but only significantly so in the case of Ily (Fig. 2b, Table 2).

The most substantial difference in nutrient fluxes was observed for  $\text{NH}_4^+$  (Tables 1 & 2). Ily had a significantly greater efflux of  $\text{NH}_4^+$  compared with the other treatments and was 3 times higher than the Con. Ily+Pred was significantly higher than the Con but 43% lower than Ily alone. Mer+Pred was significantly different from the Con yet not significantly different from the Mer treatment alone. No significant differences were observed in  $\text{NO}_3^-$  or  $\text{PO}_4^{3-}$  fluxes (Tables 1 & 2). Ammonium concentrations in the outflow from the 2 intermediate reservoir tanks (Fig. 1) did not vary significantly between tanks with and without *Panopeus herbstii* ( $0.62 \pm 0.16$  (SE) and  $0.46 \pm 0.04$  (SE)  $\mu\text{M}$ , respectively;  $p = 0.80$ ,  $t = 0.57$ ). Likewise, there was no significant difference in microcosm headspace ammonium concentrations at the start of the flux measurements, in spite of the fact that 50% of the headspace water in the +Pred treatments was from tanks containing *P. herbstii* ( $0.73 \pm 0.10$   $\mu\text{M}$  with and  $0.53 \pm 0.19$   $\mu\text{M}$  without;  $p = 0.13$ ,  $t = 1.62$ ).

## DISCUSSION

Individual benthic organisms strongly affect sediment characteristics and the release of nutrients, as we have demonstrated here. However, in the presence of a predator, non-lethal predation appears to alter the interaction between the prey organisms and their environment. The effect of *Mercenaria mercenaria* and *Ilyanassa obsoleta* activity on sediment biogeochemistry and benthic–pelagic coupling depends on the presence or absence of *Panopeus herbstii*, illustrating the need to take into account higher trophic levels when describing the net effect of benthic organisms on sediment biogeochemistry.

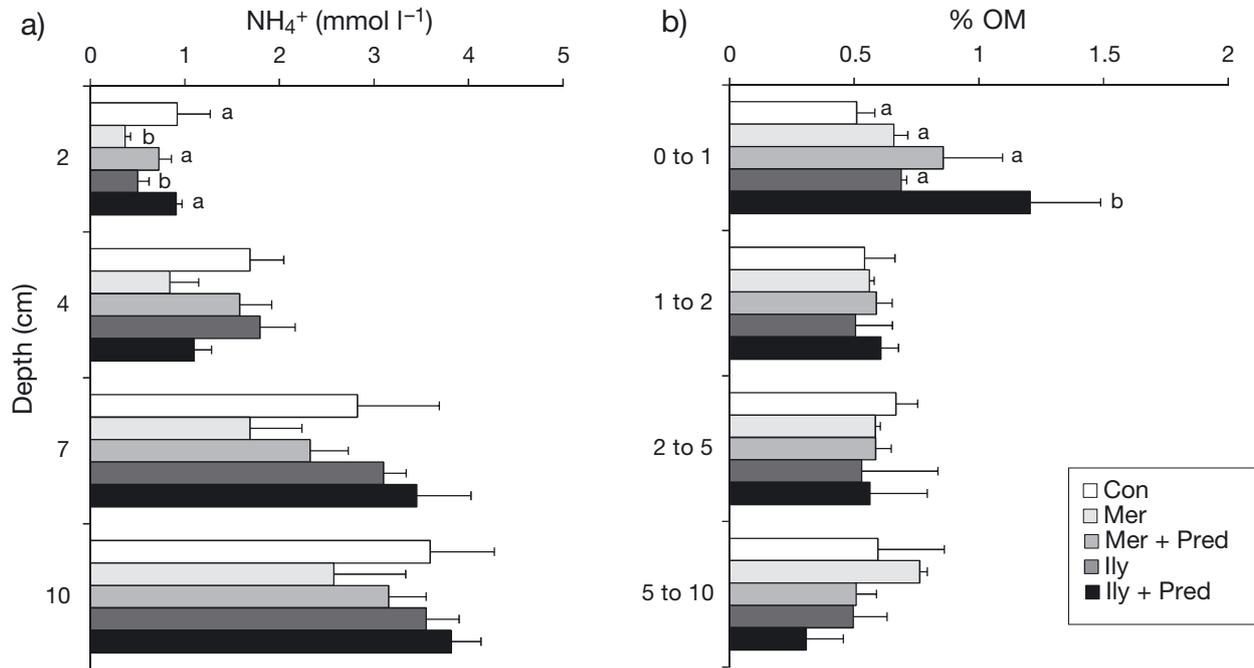


Fig. 2. (a) Porewater  $\text{NH}_4^+$  ( $\pm$ SE) and (b) sediment organic matter (OM) at each depth for control (Con), *Mercenaria mercenaria* (Mer), *M. mercenaria* and *Panopeus herbstii* influence (Mer+Pred), *Ilyanassa obsoleta* (Ily) and *I. obsoleta* and *P. herbstii* influence (Ily+Pred) treatments. Different letters indicate significance ( $p < 0.05$ ) between treatments

### *Mercenaria mercenaria*

As anticipated, *Mercenaria mercenaria* had a substantial effect on sediment oxygen demand, with an increase in consumption for the microcosm as a whole and at the sediment surface. The 3- to 4-fold difference in oxygen consumption relative to the control for both *M. mercenaria* treatments is much higher than the 20% (Doering et al. 1987) to 59% (Murphy & Kremer 1985) increases previously observed but may be attributed to the higher density of organisms in our microcosms. While some of the greater consumption is certainly clam respiration, the microelectrode results suggest increased oxygen demand in the top few mm of sediment. This increase is likely explained by the decomposition of organic carbon supplied to the sediment surface through biodeposition of pseudofeces (Hibbert 1977, Doering et al. 1986).

The increase in sediment oxygen demand in the presence of *Mercenaria mercenaria* was echoed by an increase in sediment release of  $\text{NH}_4^+$ , as previously observed (Murphy & Kremer 1985, Doering et al. 1987). Doering et al. (1986) suggested that this increased flux is the result of remineralization of biodeposits and excretion. In oyster reefs, biodeposit nitrogen is returned directly to the water column,

rather than incorporated into sediments (Dame 2011). This concurs with our observations: an increase in  $\text{NH}_4^+$  release but no accumulation in surface or deep sediments. Instead, the vertical movements and siphon extension and retraction by bivalves that redistribute porewater nutrients lowered the porewater  $\text{NH}_4^+$  (Mermillod-Blondin et al. 2005). In a parallel study in WFH, we demonstrated that *M. mercenaria* can lower porewater  $\text{NH}_4^+$  and result in net removal of reactive nitrogen through increased denitrification and nitrogen release to the water column (A. C. Tyler et al. unpubl. data). Clam movement through the sediment may increase oxygen availability, promoting nitrification of  $\text{NH}_4^+$ . Active vertical movement and siphon extension and retraction may also lead to more efficient degradation of OM through increased porosity, porewater translocation and nutrient supply to sediment microbes (Aller 1994).

However, these values may overestimate the effect of *Mercenaria mercenaria* on porewater chemistry in a natural setting where predators are present. When *M. mercenaria* senses a predator, feeding ceases and their siphons retract while the predator remains in the vicinity (Smee & Weissburg 2006a), an effect that may persist over extended periods of time (Nakaoka 2000). Feeding activities resume once the predator is

removed (Smee & Weissburg 2006b, Maire et al. 2010). As this response is limited to living predators and their effluent (no response to an empty carapace), chemical, rather than mechanical, cues are involved in prey detection by this species (Smee & Weissburg 2006a). Although we did specifically record behavioral responses, these previous works support the idea that our observations are the result of decreased activity by *M. mercenaria* due to predatory chemical cues. The higher concentration of porewater  $\text{NH}_4^+$  in surface sediments when predation is included suggests less clam movement. While the effluent water contained  $\text{NH}_4^+$ , the concentration was not significantly different from control tank water, and we believe that decreased clam movement caused the higher porewater  $\text{NH}_4^+$  rather than the effluent. The absence of predators thus suggests the potential for not only increased feeding but also more frequent siphon retraction and vertical movement, increasing translocation of solutes, sediment oxygen uptake and removal of OM.

Bivalve prey may react differently to tactile and vibrational cues or the temporary presence of chemical cues. For example, *Macoma balthica* ceases feeding and increases bioturbation activity when in the same physical location as a predatory shrimp, even if the shrimp is not actively foraging (Maire et al. 2010). However, the lack of response with chemical cues alone suggests that this response is driven more by tactile than chemical cues for *M. balthica* (Maire et al. 2010), in contrast to *Mercenaria mercenaria*. Thus, caution is warranted in expanding results to other types of bivalves that may exhibit different behavior. Furthermore, in our experiment, where the predation threat was constant, the effect of predation may have been exaggerated above what may occur in a field situation where predators come and go. In a field setting, we may observe Turner & Montgomery's (2003) 'behavioral landscape', where prey exhibit reversible behavior in the presence of a predator, thus modulating the effect observed herein.

### *Ilyanassa obsoleta*

Previous studies have attributed the positive effect of *Ilyanassa obsoleta* on sediment efflux of dissolved nitrogen to direct release through excretion, and indirect release through bioturbation and feeding at the sediment surface (McLenaghan et al. 2011, Yarrington et al. 2013). By disturbing surface sediments, porewater is mixed with the overlying water column and solutes are released. Furthermore, by

consuming BMA, *I. obsoleta* are removing the living 'filter' that prevents the flux of nutrients from the sediment to the water column (Tyler et al. 2003, McLenaghan et al. 2011). This, coupled with excretion and bioturbation, enhances the release of nitrogen to the water column.

In contrast to McLenaghan et al. (2011), we found greater chl *a* and greater sediment GPP in treatments with *Ilyanassa obsoleta*. Our microelectrode measurements allowed us to measure the effect of snails on benthic primary production, which was not visible in the whole-microcosm BOC estimates. Although the net effect of snails is to drive up daily BOC, at the microscale, we observed greater primary production, a phenomenon that was swamped by snail activity in the whole-microcosm measurements. At low densities ( $<80 \text{ ind. m}^{-2}$ ), *I. obsoleta* may stimulate microalgal growth, through either fertilization effects or increased nutrient regeneration (Connor 1980) and inhibit growth of BMA at higher densities due to increased grazing pressures (McLenaghan et al. 2011). Our results suggest that grazing had a balanced effect on BMA through the effect of consumption, which possibly reduced self-shading, and the facilitative effect of nutrient provision, with a net effect of higher photosynthetic efficiency (as GPP: chl *a*) in *I. obsoleta* treatments.

Although *Ilyanassa obsoleta* are highly sensitive to the chemical cues of predators and flee when they encounter the scent (Rahman et al. 2000), in our experiment they were unable to escape and possibly were less active (authors' pers. obs.). Some studies in both terrestrial and marine systems suggest that the indirect effects of predators on biomass of primary producers are negligible, because of compensation within the primary producer community and shifts in species assemblages (e.g. Schmitz 2006, O'Connor & Bruno 2007). Others have demonstrated a substantial effect of predators on the consumption of new algal recruits, suggesting higher survival of juveniles and later mature biomass (Molis et al. 2011). We observed that predator cues led to proliferation of BMA but lower GPP. Reduced GPP per unit chl *a* in the predator treatment may be the result of lower turnover of BMA and self-shading within the surface mat. Despite the marginally higher levels of  $\text{NH}_4^+$  in *Panopeus herbstii* effluent, we did not observe a difference in chl *a* between *Mercenaria mercenaria* treatments and believe that the higher biomass here is due to the stimulation provided by *I. obsoleta* excretion. Thus, the predator effluent created an effect similar to a lower density of snails, promoting the accumulation of BMA. Higher sediment OM within

the top 2 cm also indicates an accumulation of OM not seen in any other treatment, again supporting the idea that predators reduce OM turnover in surface sediments.

The high BMA biomass in the predator treatment can also be linked to the decrease in  $\text{NH}_4^+$  efflux, with the greatest reduction occurring in the light when BMA are most actively assimilating nitrogen (not shown). Like the rocky shore grazing gastropod *Littorina littorea*, which reduces feeding and metabolic activity and thus grows more slowly in the presence of a predator (Trussell et al. 2003), the metabolic production of the more cautious *Ilyanassa obsoleta* probably slowed, producing less nitrogenous waste. In previous laboratory experiments, *I. obsoleta* facilitated macroalgal growth through grazing on BMA (McLenaghan et al. 2011), production of nitrogen (Yarrington et al. 2013) or removal of epiphytes from algal thalli (Guidone et al. 2010, 2012). Although the facilitation of macroalgal growth has not been successfully confirmed through field experiments (Guidone et al. 2012, Yarrington et al. 2013), *I. obsoleta* has a clear effect on sediment biogeochemistry and benthic–pelagic coupling. This effect is muted in the presence of a predator such as *Panopeus herbstii*, suggesting that the loss of predators through eutrophication or over-harvesting may be a positive feedback that enhances sediment nutrient release and leads to further proliferation of primary producers.

## CONCLUSION

Much of our understanding of the impact of benthic invertebrates on benthic ecosystem function is based on laboratory microcosm experiments, or field experiments, where predators have been excluded. While predator exclusion has clearly been necessary to prevent consumption of the organism of interest during the experiment, our results suggest that omission of predators may lead to the overestimation of the true influence of invertebrates on the benthic environment. Furthermore, we consider that changes in benthic communities due to anthropogenic pressures will lead to a complex array of direct and indirect effects, suggesting the need for a better understanding of the effects of community interactions on benthic ecosystem function.

*Acknowledgements.* A. Giblin, K. Foreman and M. Hayn provided logistical support in Woods Hole. B. Bourdon, M. Bida, C. Yarrington and A. Abdul Rahman provided invaluable assistance in the field and laboratory. A. Altieri

and P. Berg provided valuable input related to the design of experiments and sampling. We thank E. Hane, S. Smith Pagano and 2 anonymous reviewers for comments that improved the manuscript. This material is based on work funded by the National Science Foundation (OCE 0727642).

## LITERATURE CITED

- Aller RC (1988) Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In: Blackburn TN, Sorensen J (eds) Nitrogen cycling in coastal marine environments. Wiley, New York, NY, p 301–338
- Aller RC (1994) Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chem Geol* 114:331–345
- Altieri AH (2008) Dead zones enhance key fisheries species by providing predation refuge. *Ecology* 89:2808–2818
- Berg P, McGlathery KJ (2001) A high-resolution pore water sampler for sandy sediments. *Limnol Oceanogr* 46: 203–210
- Berg P, Risgaard-Petersen N, Rysgaard S (1998) Interpretation of measured concentration profiles in sediment pore water. *Limnol Oceanogr* 43:1500–1510
- Bruno JF, O'Connor MI (2005) Cascading effects of predator diversity and omnivory in a marine food web. *Ecol Lett* 8: 1048–1056
- Connor M (1980) Snail grazing effects on the composition and metabolism of benthic diatom communities and subsequent effects on fish growth. PhD dissertation, Massachusetts Institute of Technology and Woods Hole Oceanographic Institution, Woods Hole, MA
- Connor MS, Teal JM, Valiela I (1982) The effect of feeding by mud snails, *Ilyanassa obsoleta* (say), on the structure and metabolism of a laboratory benthic algal community. *J Exp Mar Biol Ecol* 65:29–45
- Dame RF (2011) Ecology of marine bivalves: an ecosystem approach, 2nd edn. CRC Press, Boca Raton, FL
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–929
- Doering PH (1982) Reduction of sea star predation by the burrowing response of the hard clam *Mercenaria mercenaria* (Mollusca: Bivalvia). *Estuaries* 5:310–315
- Doering PH, Oviatt CA, Kelly JR (1986) The effects of the filter-feeding clam *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms. *J Mar Res* 44:839–861
- Doering PH, Kelly JR, Oviatt CA, Sowers T (1987) Effect of the hard clam *Mercenaria mercenaria* on benthic fluxes of inorganic nutrients and gases. *Mar Biol* 94:377–383
- Engelsen A, Pihl L (2008) Grazing effects by *Nereis diversicolor* on development and growth of green algal mats. *J Sea Res* 59:228–236
- Fox SE, Teichberg M, Olsen YS, Heffner L, Valiela I (2009) Restructuring of benthic communities in eutrophic estuaries: lower abundance of prey leads to trophic shifts from omnivory to grazing. *Mar Ecol Prog Ser* 380:43–57
- Geraldi NR, Powers SP (2011) Subtle changes in prey foraging behavior have cascading effects in a shallow estuary. *Mar Ecol Prog Ser* 427:51–58
- Gilbert F, Stora G, Bonin P (1998) Influence of bioturbation on denitrification activity in Mediterranean coastal sediments: an *in situ* experimental approach. *Mar Ecol Prog Ser* 163:99–107

- Guidone M, Thornbe CS, Field E (2010) Snail grazing facilitates growth of a bloom-forming alga. *Mar Ecol Prog Ser* 420:83–89
- Guidone M, Thornbe CS, Vincent E (2012) Snail grazing facilitates growth of two morphologically similar bloom-forming *Ulva* species through different mechanisms. *J Ecol* 100:1105–1112
- Hauxwell J, McClelland J, Behr PJ, Valiela I (1998) Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. *Estuaries* 21:347–360
- Heiri O, Lotter AF, Lemcke G (2001) Loss on ignition as a method for estimating organic and carbonate content in sediment: reproducibility and comparability of results. *J Paleolimnol* 25:101–110
- Hibbert CJ (1977) Energy relations of the bivalve *Mercenaria mercenaria* on an intertidal mudflat. *Mar Biol* 44:77–84
- Howes BL, Kelley SW, Ramey JS, Samimy RI, Schlezinger DR, Eichner EM (2006) Linked watershed-embayment model to determine critical nitrogen loading thresholds for West Falmouth Harbor, Falmouth, Massachusetts. Massachusetts Estuaries Project, Massachusetts Department of Environmental Protection, Boston, MA
- Johnson DS, Short MI (2013) Chronic nutrient enrichment increases the density and biomass of the mudsnail, *Nassarius obsoletus*. *Estuaries* 36:28–35
- Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426:1–24
- Leonard GH, Bertness MD, Yund PO (1999) Crab predation waterborne cues and inducible defenses in the blue mussel *Mytilus edulis*. *Ecology* 80:1–14
- Levinton J (1995) Bioturbators as ecosystem engineers: control of the sediment fabric, inter-individual interactions and material fluxes. In: Jones CG, Lawton JH (eds) *Linking species and ecosystems*. Chapman & Hall, San Diego, CA, p 29–36
- Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48:25–34
- Lorenzen CJ (1967) Vertical distribution of chlorophyll and phaeo-pigments: spectrophotometric equations. *Limnol Oceanogr* 12:343–346
- Maire O, Merchant JN, Bulling M, Teal LR, Grémare A, Duchêne JC, Solan M (2010) Indirect effects of non-lethal predation on bivalve activity and sediment reworking. *J Exp Mar Biol Ecol* 395:30–36
- Marko PB, Palmer AR (1991) Response of a rocky shore gastropod to the effluents of predatory and non-predatory crabs: avoidance and attraction. *Biol Bull* 181:363–370
- McLenaghan NA (2009) Benthic macroinvertebrate diversity in a shallow estuary: controls on nutrient and algal dynamics. MS thesis, Rochester Institute of Technology, Rochester, NY
- McLenaghan NA, Tyler AC, Mahl UH, Howarth RH, Marino RM (2011) Benthic macroinvertebrate functional diversity regulates nutrient and algal dynamics in a shallow estuary. *Mar Ecol Prog Ser* 426:171–184
- Mermillod-Blondin F, Rosenberg R, Francois-Carcaillet F, Norling K, Mauclair L (2004) Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. *Aquat Microb Ecol* 36:271–284
- Mermillod-Blondin F, François-Carcaillet F, Rosenberg R (2005) Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experimental study. *J Exp Mar Biol Ecol* 315:187–209
- Michaud E, Desrosiers G, Mermillod-Blondin F, Sundby B, Stora G (2005) The functional group approach to bioturbation: the effects of biodiffusers and gallery-diffusers of the *Macoma balthica* community on sediment oxygen uptake. *J Exp Mar Biol Ecol* 326:77–88
- Molis M, Preuss I, Firmenich A, Ellrich J (2011) Predation risk indirectly enhances survival of seaweed recruits but not intraspecific competition in an intermediate herbivore species. *J Ecol* 99:807–817
- Murphy RC, Kremer JN (1985) Bivalve contribution to benthic metabolism in a California lagoon. *Estuaries* 8:330–341
- Nakaoka M (2000) Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology* 81:1031–1045
- O'Connor NE, Bruno JF (2007) Predatory fish loss affects the structure and functioning of a model marine food web. *Oikos* 116:2027–2038
- O'Connor NE, Grabowski JH, Ladwig LM, Bruno JF (2008) Simulated predator extinctions: predator identity affects survival and recruitment of oysters. *Ecology* 89:428–438
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effect of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509
- Rahman YJ, Forward RB, Rittschof D (2000) Responses of mud snails and periwinkles to environmental odors and disaccharide mimics of fish odor. *J Chem Ecol* 26:679–696
- Scheiner CA (2011) Scaling-up in estuaries: the feasibility of using small scale results to draw large scale conclusions. MS thesis, Rochester Institute of Technology, Rochester, NY
- Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology* 87:1432–1437
- Schmitz OJ, Beckerman AP, O'Brien KM (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399
- Silliman BR, Bertness MD (2002) A trophic cascade regulates salt marsh primary production. *Proc Natl Acad Sci USA* 99:10500–10505
- Smee DL, Weissburg MJ (2006a) Clamming up: environmental forces diminish the perceptive ability of bivalve prey. *Ecology* 87:1587–1598
- Smee DL, Weissburg MJ (2006b) Hard clams (*Mercenaria mercenaria*) evaluate predation risk using chemical signals from predators and injured conspecifics. *J Chem Ecol* 32:605–619
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180
- Solorzano L (1969) Determination of ammonia in natural waters by the phenol hypochlorite method. *Limnol Oceanogr* 14:799–801
- Stief P, Hölker F (2006) Trait-mediated indirect effects of predatory fish on microbial mineralization in aquatic sediments. *Ecology* 87:3152–3159
- Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd edn. *Bull Fish Res Board Can* 167:1–310
- Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains: predator

- risk cues alter prey feeding rates. *Ecology* 84:629–640
- Trussell GC, Ewanchuk PJ, Bertness MD, Silliman BR (2004) Trophic cascades in rocky shore tide pool: distinguishing lethal and nonlethal effects. *Oecologia* 139:427–432
- Turner AM, Montgomery SL (2003) Spatial and temporal scales of predator avoidance: experiment with fish and snails. *Ecology* 84:616–622
- Tyler AC, McGlathery KJ, Anderson IC (2003) Benthic algae control sediment–water column fluxes of organic and inorganic nitrogen compound in a temperate lagoon. *Limnol Oceanogr* 48:2125–2137
- Tyler AC, McGlathery KJ, Anderson IC (2001) Macroalgae mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuar Coast Shelf Sci* 53:155–168
- Volkenborn N, Polerecky L, Wetthey DS, Woodin SA (2010) Oscillatory porewater bioadvection in marine sediments induced by hydraulic activities of *Arenicola marina*. *Limnol Oceanogr* 55:1231–1247
- Volkenborn N, Polerecky L, Wetthey DS, DeWitt TH, Woodin SA (2012) Hydraulic activities by ghost shrimp *Neotrypaea californiensis* induce oxic–anoxic oscillations in sediments. *Mar Ecol Prog Ser* 455:141–156
- Vopel K, Wilson PS, Zeldis J (2012) Sediment–seawater solute flux in a polluted New Zealand estuary. *Mar Pollut Bull* 64:2885–2891
- Whetstone JM, Eversole AG (1981) Effects of size and temperature on mud crab, *Panopeus herbstii*, predation on hard clams, *Mercenaria mercenaria*. *Estuaries* 4:153–156
- Whitlow WL (2010) Changes in survivorship, behavior and morphology in native soft-shell clams induced by invasive green crab predators. *Mar Ecol* 31:418–430
- Yarrington CS, Altieri AH, Tyler AC (2013) Do snails facilitate bloom-forming macroalgae in a eutrophic estuary? *J Exp Mar Biol Ecol* 446:253–261

Editorial responsibility: Matthias Seaman,  
Oldendorf/Luhe, Germany

Submitted: March 4, 2013; Accepted: September 12, 2013  
Proofs received from author(s): November 26, 2013