Foraging by the mud snail, *Ilyanassa obsoleta* (Say), modulates spatial variation in benthic community structure

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Abstract

We investigated the foraging behavior of the mud snail, *Ilyanassa obsoleta*, and its consequences for macrobenthic community structure on mud flats on Long Island, NY, USA. Field sampling demonstrated strong spatial heterogeneity in the population densities of *I. obsoleta*. We experimentally tested three hypotheses: (i) *I. obsoleta* are strongly attracted to areas with high levels of detritus; (ii) local abundances of deposit-feeding annelids are limited by detritus; and (iii) the foraging activities of *I. obsoleta* negatively affects annelid assemblages. We manipulated the density of mud snails using inclusion fences and the levels of detritus using dried *Ulva*. Results showed that high densities of *I. obsoleta* were attracted to areas enriched with *Ulva* detritus. In addition, high densities of snails negatively affected abundances of annelids, with the opportunistic species, *Capitella* spp. and *Paranais litoralis*, being most affected. The addition of *Ulva* detritus had more specific effects on annelid assemblages. Only *Capitella* spp. showed a significant positive response, although previous evidence has demonstrated that higher experimental detrital inputs stimulated growth of other species of annelids and microphytobenthos. In an experimental treatment with enhanced detritus and low densities of snails, we found population abundances of opportunistic annelids (up to 200,000 m^{-2}) substantially larger than has ever been recorded in 5 years of sampling. Because mud snails in natural areas actively search, locate and exploit areas with enhanced detritus and their foraging negatively affects abundances of opportunistic worms, *I. obsoleta* probably controls the upper limits of annelid abundance in the field. Foraging behavior of *I. obsoleta* therefore

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modulates spatial variation in benthic community structure in an environment where limiting resources are patchily distributed.

1. Introduction

Evaluating the consequences of foraging strategies has been a central theme in ecological research. Foraging behaviors influence patterns of distribution and abundance, habitat preference, reproductive success and, ultimately, natural selection and evolutionary processes (Pyke, 1984; Stephens and Krebs, 1986; Hughes, 1993; Perry and Pianka, 1997). As well as affecting the population dynamics of the species in question, foraging by some organisms can have disproportionately large effects on diversity and abundance of other taxa (Paine, 1969; Power et al., 1996). These so called 'keystone species' strongly influence community structure in terrestrial (Brown and Heske, 1990; Knapp et al., 1999), freshwater (Flecker, 1996; Ives et al., 1999) and marine systems (Paine, 1969; Estes and Palmisano, 1974; Castilla and Duran, 1985).

The foraging activities of gastropods often have large effects on benthic community structure (Lubchenco and Gaines, 1981; Castilla and Duran, 1985; Anderson and Underwood, 1997). Predatory snails that consume competitively dominant species increase local diversity by creating space for competitively inferior organisms (Connell, 1961; Menge et al., 1994). Furthermore, grazing by herbivorous snails can strongly influence the distribution, composition and biomass of micro- and macro-algal assemblages in rocky reefs (Underwood, 1980; Lubchenco and Gaines, 1981), seagrass (Jernakoff et al., 1996; Jernakoff and Nielsen, 1997) and soft-sediment habitats (Bianchi and Levinton, 1981; Connor and Edgar, 1982).

In this study, we focused on the foraging behaviour of the eastern mud snail, *Ilyanassa obsoleta* (Say), and its consequences for benthic community structure. *I. obsoleta* is extremely common in sheltered soft-sediment habitats on the East Coast of the United States, but lived in a broader range of habitats prior to the arrival of the periwinkle, *Littorina littorea* (Brenchley and Carlton, 1983). *I. obsoleta* are often found in dense aggregations of up to 1500 m^{-2} (Nichols and Robertson, 1979; Brenchley and Carlton, 1983). They feed prominently on microorganisms (e.g., bacteria, blue-green algae and diatoms) that grow in and on the surface of the sediment (Pace et al., 1979; Bianchi and Levinton, 1981; Connor and Edgar, 1982; Feller, 1984; Novak et al., 2001), but they will also scavenge carrion and actively feed on macroalgae when available (Britton and Morton, 1994; Giannotti and McGlathery, 2001). These snails also have well-developed sensory systems, which enables them to quickly locate food resources and conspecifics (Trott and Dimock, 1978; Zimmer et al., 1999; Rahman et al., 2000).

I. obsoleta are abundant on mud flats directly adjacent to salt marshes on the north shore of Long Island, NY, USA (Levinton et al., 1985, 1995). Trophic interactions on these flats are fueled by organic material from a number of sources (saltmarsh, macroalgae

or phytoplankton; see Nixon, 1980 for review). Some of this organic detritus can be consumed directly by deposit-feeding organisms (Findlay and Tenore, 1982; Peterson et al., 1986). Alternatively, bacteria break down the detritus (Rublee, 1982), which provides nutrients for benthic microorganisms that are then consumed by deposit feeders (Bianchi and Levinton, 1981; Lopez and Levinton, 1987). Because of the tightness of these links, the population abundances of common deposit feeders (e.g., *Capitella* spp. (Fabricius), *Paranais litoralis* (Muller) and *I. obsoleta*) are often limited by the availability of detritus (Levinton and Stewart, 1988; Cheng et al., 1993).

The deposition of detritus is spatially and temporally patchy, which creates variation in benthic community structure (Levinton and McCartney, 1988; Cheng et al., 1993). This is best demonstrated in early spring on Long Island, when detrital resources are large but spatially variable because of low levels of winter benthic activity and the patchy growth and localized deposition of seaweed detritus over winter (Levinton, 1985; Cheng et al., 1993). When temperatures are adequately high (usually in March), populations of deposit-feeding annelids begin to increase in abundance (Levinton and Stewart, 1988; Nilsson et al., 1997). Because some species are more effective at using these resources than others, the spatial variation in detritus also stimulates spatial unevenness in community structure (Cheng et al., 1993).

At the same time, large groups of *I. obsoleta* are actively foraging on the mudflats and competing with deposit-feeding annelids for food (Levinton et al., 1985). Evidence from natural experiments and laboratory studies suggests that the foraging activities of *I. obsoleta* negatively affect abundances of annelids (Grant, 1965; Levinton and Stewart, 1982; Levinton et al., 1985). It is therefore likely that the interaction of patchy detrital enrichment and the foraging behavior of mud snails strongly influence the structure of benthic communities.

To evaluate how these factors affect diverse assemblages of annelids on Long Island mud flats, we evaluated spatial heterogeneity of population densities of *I. obsoleta* and experimentally tested three hypotheses: (i) *I. obsoleta* are strongly attracted to areas that are rich in organic detritus; (ii) the community structure of annelids is strongly affected by detrital inputs and the population abundances of opportunistic deposit-feeding species (e.g., *P. litoralis* and *Capitella* spp.) are limited by detrital levels; and (iii) the foraging activities of *I. obsoleta* negatively affects annelids. We focused on annelids because they represented approximately 90% of the total abundance of macrobenthic invertebrates on Long Island mud flats (J.S. Levinton, unpublished data). These annelids also constituted a trophically complex assemblage that included predators, deposit feeders, suspension feeders and scavengers.

2. Methods

2.1. Study site

This study was done on intertidal mud flats at Flax Pond, Long Island, NY, USA (see Levinton and Bianchi, 1981 for description). The mud flats were surrounded by salt marsh, dominated by *Spartina alterniflora* Loisel, and were protected from wave

action. As well as *Spartina* detritus, large amounts of macroalgae were commonly found growing and decomposing on these mud flats. While there is variation in the species composition of this seaweed, the green alga, *Ulva rotundata* Bliding, is generally the most abundant, especially over the winter months (Levinton, 1985; Cheng et al., 1993).

2.2. Variation in density of I. obsoleta and the effects of detritus enrichment

To test the hypothesis that the density of *I. obsoleta* varies from patch to patch, snails were quantified in six haphazardly chosen sites (25 m^2). Sites were separated by at least 20 m and were at a similar tidal height and distance from the *Spartina* zone. In each site, snails were counted in 10 randomly placed quadrats (0.25 m^2). The upper 2 cm of sediment in each replicate quadrat was washed through a sieve with 2 mm mesh to ensure buried snails were also included in counts. At least 90% of the snails found were greater than 10 mm and less than 30 mm in length.

To test the hypotheses that detrital enrichment affects local densities of *I. obsoleta*, a manipulative experiment was set up on a mud flat with low densities of snails (see Results) in March 2002. Ten plots (1 m^2) were haphazardly selected and randomly allocated to three treatments: a detritus enrichment treatment (4 plots) and an untouched (4 plots) and disturbance control (2 plots). Two hundred eight grams of dried shredded *U. rotundata* was hand-churned into the sediment of each plot in the detritus enrichment treatment. The individual pieces of *Ulva* varied between 0.5 and 2 mm in size. This amount of *Ulva* represents the average biomass per square meter deposited within *Ulva* patches on Flax Pond mud flats over the winter period (Levinton and Stewart, 1988). While these methods ensured equal *Ulva* enrichment among treatments, they did not entirely mimic natural algal deposition because the *Ulva* pieces were of similar size and similar state of decay. In natural deposition, algal frond size is variable and algal detritus often spends some time on the sediment surface before burial. As surface algae is quickly broken down and buried, it is unlikely that initial differences between natural and artificial enrichment have lasting effects on benthic fauna.

Previous studies have shown that adding *Ulva* detritus to sediment increases the biomass of microorganisms (e.g., bacteria and benthic diatoms) that are readily consumed by *I. obsoleta* (Levinton, 1985). In addition, *I. obsoleta* can also directly consume the *Ulva*, although it is a poor quality source of nutrition (Giannotti and McGlathery, 2001). The *Ulva* for this and other experiments (see below) was collected live from nearby areas and had a mean (S.D., $n = 2$) C/N ratio = 7.62 (0.10), which was slightly lower than *Ulva* that was washed up on the mudflat [C/N ratio = 7.90 (0.09)].

To control for the manual disturbance of adding *Ulva*, sediment in disturbance plots was also hand-churned, but no detritus was added. Only two plots were used in this treatment because pilot studies indicated that manual disturbances had few lasting effects on densities of *I. obsoleta* (B.P. Kelaher, unpublished data). Six weeks after the *Ulva* was added, the number of snails on the surface of mud in each plot was counted.

2.3. Effects of detritus enrichment and I. obsoleta density on annelids

To test the hypotheses that detrital input, the density of *I. obsoleta* and their interaction affect assemblages of annelids, a manipulative experiment was set up in April 2002. The experiment had four orthogonal treatments with: low densities of snails and ambient detritus; low densities of snails and added detritus, high densities of snails and ambient detritus and high densities of snails and added detritus. The experiment was done in part of the mud flat that had relatively low densities of *I. obsoleta* (average density (S.D.) = 42.1 (27.1) per m^2, $n = 10$ quadrats) because it is much easier to keep snails in experimental enclosures than it is to keep them out (B.P. Kelaher, personal observation).

For each treatment, four experimental plots (45 cm in diameter, 0.16 m^2) were established. Each plot was approximately 4–5 m from it nearest neighbor and enclosed by a fence to maintain snails at different densities. Fences were constructed with a double barrier of 15 cm high aluminum mesh (5 mm), with an inside and outside facing perpendicular lip (2 cm in length) at the top. Each fence was pushed 6 cm into the sediment and anchored by stakes of PVC pipe.

For treatments with elevated levels of detritus, 9 g of dried shredded *Ulva* was evenly added to the sediment in each plot. This amount of *Ulva* is a quarter the average biomass deposited within *Ulva* patches on mud flats at Flax Pond over the winter period (Levinton and Stewart, 1988). The remaining treatments had ambient (naturally occurring) levels of detritus. A proportionally smaller of amount of *Ulva* was used than in the first experiment to avoid anoxic effects observed in the field and shown by previous laboratory studies (Levinton, 1985) and to a lesser extent in the first *Ulva* manipulation. To control for the manual disturbance of adding *Ulva*, the sediment in the other plots was also hand-churned, regardless of treatment.

All *I. obsoleta* were removed from plots, while the sediment was disturbed. After this, seven snails and 90 adult snails were added to plots in treatments defined as low and high densities of *I. obsoleta*, respectively. The length of these snails varied between 10 and 30 mm. The treatment with low densities of snails represented the natural average density of snails in the area where the experiment was done. The number of snails in the high-density treatments represented the average density in areas with high densities of snails at Flax Pond, but was well within the natural range for *I. obsoleta* (Nichols and Robertson, 1979; Levinton et al., 1995).

The experimental methods used had the potential to cause large artifacts that may confound interpretations. To determine if the fences or the manual disturbance of adding *Ulva* or their interaction affected annelid assemblages, a second experiment was set up with four orthogonal treatments: a natural control; a fence only treatment; a disturbance only treatment; and a treatment with fences, disturbances and average densities of snails found in surrounding areas (e.g., seven snails per plot). The fences for these treatments were identical to those described above and the manual disturbance added to plots was similar to the disturbance caused by adding *Ulva* detritus to the sediment. Four experimental plots (0.16 m^2) of each treatment were set up amongst the other experimental plots and at the same time.

Thirty days after the experiment began, four cores (5 cm in diameter and 5 cm deep, ≈ 100 cm^3) were collected from each plot and the total number of snails
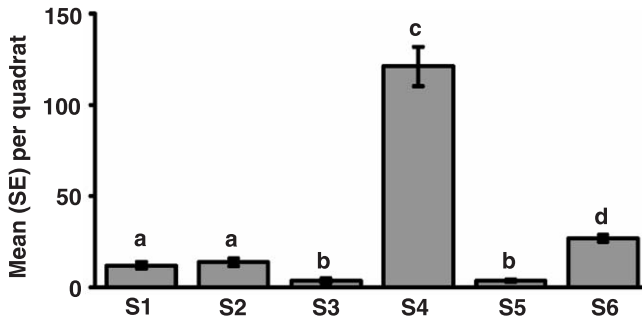
Fig. 1. Mean (S.E., $n = 10$ replicate 0.25 m² quadrats) density of *I. obsoleta* in sites separated by at least 20 m. Lower case letters above bars indicate results of Tukey HSD tests. Sites marked with different letters are significantly different ($P < 0.05$) and sites with the same letters are not significantly different ($P > 0.05$).

quantified. The experiment was kept relatively short to reduce the possibility of fence artifacts. Thirty days is, however, long enough for populations of deposit-feeding worms at Flax Pond to respond significantly to increased availability of detritus (Levinton and Stewart, 1988). The plots were only sampled at one time to avoid artifacts associated with repeated sampling (Skilleter, 1996). Each core was washed in a 500-μm sieve and the material retained was preserved in a 7% formalin solution. The material from each sieved core was then carefully sorted under ×16 magnification and all annelids identified to species. In total, 18 different species were identified from the 14,206 annelids that were found.

2.4. Statistical analyses

Analyses of variance (ANOVA) were used to test hypotheses about abundances of *I. obsoleta*, univariate measures of annelid assemblages and the most common species of annelids. Tukey HSD tests were used for a posteriori comparisons among means (Day and
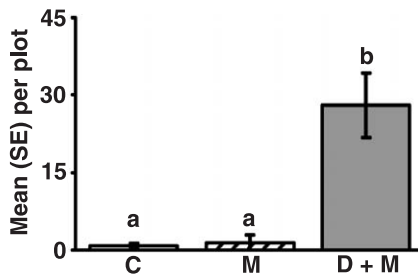

Fig. 2. Mean (S.E.) density of *I. obsoleta* in untouched control plots (C) and plots with added *Ulva* detritus and manual disturbance (D+M) and with manual disturbance only (M). Treatments are significantly different (ANOVA, $F_{2,7} = 27.43$, $P < 0.01$). Lower case letters above bars indicate results of Tukey HSD tests. Treatments with different letters are significantly different ($P < 0.05$) and treatments with the same letters are not significantly different ($P > 0.05$).
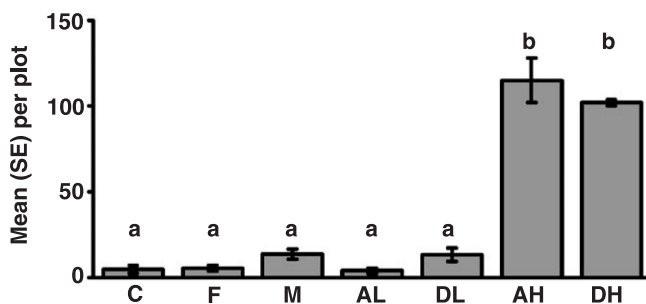
Fig. 3. Mean (S.E., $n=4$ replicate 0.16 m^2 plots) density of *I. obsoleta* in experimental plots after 30 days. C, untouched control; F, fence control; M, manual disturbance control; AL, ambient detritus and low densities of snails; DL, *Ulva* added and low densities of snails; AH, ambient detritus and high densities of snails; DH, *Ulva* added and high densities of snails (treatments a, b, c, d, e, f, g in Fig. 1, respectively). Lower case letters above bars indicate results of Tukey HSD tests. Treatments with different letters are significantly different ($P<0.05$) and treatments with the same letters are not significantly different ($P>0.05$).

Quinn, 1989). The variances of *I. obsoleta* densities were mostly heterogeneous (Cochran's tests, $P<0.05$). To reduce heterogeneity of variances, these data were transformed using a $\ln(x+1)$ function prior to analysis (Underwood, 1997), after which no Cochran's test was significant ($P>0.05$). Unbalanced ANOVAs and Tukey HSD comparisons were used to test for effects of enhanced detritus on abundances of *I. obsoleta* (Winer et al., 1991).

Non-parametric multivariate analyses of variance (NP-MANOVA) were used to test hypotheses about differences in annelid assemblages (Anderson, 2001; McArdle and

Table 1

NP-MANOVAs of assemblages of annelids ($n=4$ replicates cores) in (a) comparisons of controls (a, b, c, d in Fig. 1) and (b) between experimental treatments (d, e, f, g in Fig. 1)

	df	Permutable units	MS	Pseudo-F	P
(a) Tests of disturbance and fence effects					
M	1	16 plot units	2978.40	1.33	0.25
F	1	16 plot units	1458.99	0.65	0.62
M × F	1	16 plot units	192.50	0.09	0.99
P(M × F)	12	64 sample units	2241.16	4.68	<0.01
Residual	48		479.32		
(b) Tests of food and snail effects					
S	1	16 plot units	11,126.96	5.21	<0.01
D	1	16 plot units	13,178.13	6.17	<0.01
S × D	1	16 plot units	3644.23	1.71	0.16
P(S × D)	12	64 sample units	2136.26	5.74	<0.01
Residual	48		371.91		

'M' is the fixed comparison between treatments with and without manual disturbance; 'F' is the fixed comparison of treatments with and without a fence. 'S' is the fixed comparison between treatments with high and low densities of snails; 'D' is the fixed comparison between treatments with ambient and enhanced levels of detritus; and 'P' is the comparisons of randomly located plots within the interaction of fixed effects.
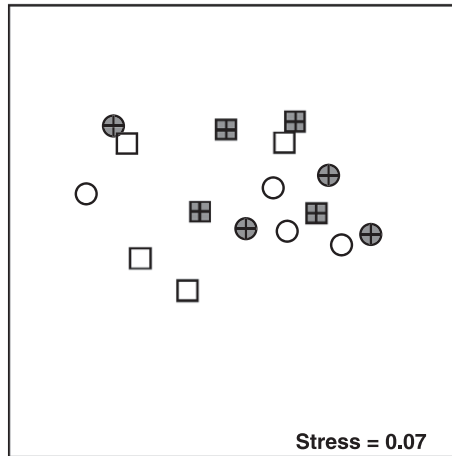
Fig. 4. Two-dimensional nMDS ($n = 4$) ordination comparing annelid assemblages in natural controls □, fence control ○, disturbance control ▣, and the experimental treatment with ambient detritus and low densities of snails ⊕ (a, b, c, d in Fig. 1, respectively). Data are averaged for each plot.

Anderson, 2001). These analyses test for overall multivariate changes in community structure, which may include differences in composition, richness and/or abundances of individual species. We used these methods because the designs of experiments were relatively complex (involving three factors) and, similar to most other studies on diverse communities, the data did not meet the assumptions of traditional multivariate statistical analyses (e.g., MANOVA). Like other non-parametric multivariate methods (e.g., ANO-
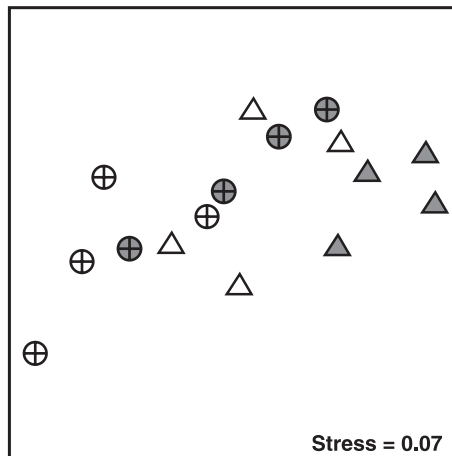

Fig. 5. Two-dimensional nMDS ($n = 4$) ordination comparing annelid assemblages among experiment treatments with ambient detritus and low densities of snails ⊕, with *Ulva* added and low densities of snails ▲, ambient detritus and high densities of snails ⊕, and with *Ulva* added and high densities of snails △, (d, e, f, g in Fig. 1, respectively). Data are averaged for each plot.

Table 2
Total average Bray–Curtis dissimilarities for comparisons among experimental treatments (d, e, f, g in Fig. 1)

	AL	DL	AH
DL	40.97		
AH	40.49	58.28	
DH	33.09	40.38	41.93

AL, ambient detritus and low densities of snails; DL, detritus added and low densities of snails; AH, ambient detritus and high densities of snails; and DH, detritus added and high densities of snails.

SIM, Clarke, 1993), np-MANOVA has less stringent assumptions than traditional tests. Unlike other methods, NP-MANOVA allows direct additive partitioning of variation, which enables tests of multivariate interactions in complex experimental designs. Non-metric multidimensional scaling (nMDS, Field et al., 1982) was used to produce two-dimensional ordination plots to show relationships among assemblages of annelids. All multivariate analyses were done using Bray–Curtis similarity coefficients (Bray and Curtis, 1957).

Analyses of annelids were divided into orthogonal comparisons to test (i) for effects of detrital enrichment and densities of snails and (ii) for effects of fences and manual disturbances. For each analysis, there were two treatment factors, which were fixed

Table 3
Analyses of variance of univariate measures of annelid assemblages in experimental treatments (d, e, f, g in Fig. 1, $n = 4$ replicates cores)

	df	MS	F	P
(a) Species richness				
S	1	4.00	0.68	0.42
D	1	0.56	0.10	0.76
S × D	1	0.25	0.04	0.84
P(S × D)	12	5.84	4.71	<0.01
Residual	48	1.24		
(b) Total abundance				
S	1	253,009.00	16.48	<0.01
D	1	180,837.56	11.78	<0.01
S × D	1	16,900.00	1.10	0.3148
P(S × D)	12	15,352.70	4.97	<0.01
Residual	48	3089.95		
(c) Evenness				
S	1	0.19	3.89	0.07
D	1	0.64	13.10	<0.01
S × D	1	0.00	0.08	0.78
P(S × D)	12	0.05	7.76	<0.01
Residual	48	0.01		

'S' is the fixed comparison between treatments with high and low densities of snails; 'D' is the fixed comparison between treatments with ambient and enhanced levels of detritus. 'P' is the comparisons of randomly located plots within the interaction of fixed effects.

effects with two levels, and four plots nested in the interaction term of the treatments ($n = 4$).

3. Results

3.1. Variation in density of I. obsoleta and the effects of detritus addition

The density of *I. obsoleta* significantly varied among sites (ANOVA, $F_{5,54} = 95.33$, $P < 0.01$, Fig. 1). Of the six sites sampled, there were four significantly different groups indicating the substantial variation among sites (Fig. 1). For the most part, the densities varied between 15 and 100 snails m^{-2}. In one site, however, densities reached nearly 500 m^{-2}. *I. obsoleta* also responded strongly to enrichment of *Ulva* detritus (Fig. 2). There were significantly more snails in the plots with added *Ulva* than other treatments. After 6 weeks, there were also no detectable effects of experimental sediment disturbance on
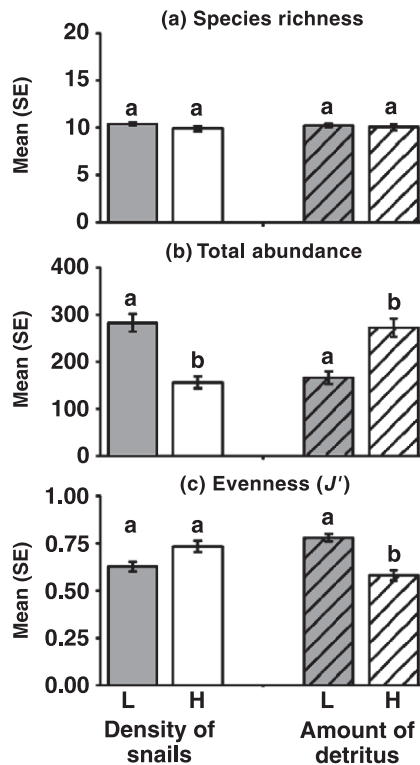

Fig. 6. Average univariate measures of annelid assemblages in treatments with (a) low ▬ and high ☐ densities of snails and with (b) ambient ▨ and enhanced ▨ detritus (d, e, f, g in Fig. 1, respectively). Data represent tests of main effects in Table 3. Lower case letters above bars indicate results of ANOVAs. Comparisons with different letters are significantly different and those with the same letters are not significantly different.

abundances of *I. obsoleta* because abundances of snails in natural and disturbance controls did not significantly differ (Fig. 2).

3.2. Effects of detritus addition and I. obsoleta density on annelids

At the end of the experiment, snail densities also varied among experimental treatments (ANOVA, $F_{6,21} = 70.82$, $P < 0.01$, Fig. 3), but were similar to initial conditions. There were no significant differences in the density of snails between natural controls, treatments with low densities of snails and the fence and disturbance controls (Fig. 3). The abundances of *I. obsoleta* in high-density treatments were marginally larger than initial values, but well within natural ranges (Fig. 3).

There were no detectable artifacts associated with fences and the manual disturbance of adding *Ulva* because there were no significant differences among annelid assemblages in the natural, disturbance and fence controls and the treatment with low densities of snails

Table 4
Analyses of variance of common annelids in experimental treatments (d, e, f, g in Fig. 1, $n = 4$ replicates cores)

	df	MS	F	P	MS	F	P
		(a) Capitella spp.			*(b) Paranais litoralis*		
S	1	125,581.64	16.72	<0.01	17,755.56	6.91	0.02
D	1	171,499.52	22.84	<0.01	689.06	0.27	0.61
S × D	1	28,266.02	3.76	0.08	126.56	0.05	0.83
P(S × D)	12	7509.07	4.53	<0.01	2568.23	8.14	<0.01
Residual	48	1656.13			315.41		
		(c) Leitoscolopolos robustus			*(d) Nereis succinea*		
S	1	47.27	8.10	0.01	141.02	0.69	0.42
D	1	11.39	1.95	0.19	147.02	0.72	0.41
S × D	1	4.52	0.77	0.40	23.77	0.12	0.74
P(S × D)	12	5.84	0.83	0.62	204.42	7.74	<0.01
Residual	48	7.06			26.40		
		(e) Tubificoides brownae			*(f) Polydora cornuta*		
S	1	50.77	0.28	0.60	76.56	9.44	<0.01
D	1	337.64	1.88	0.20	0.25	0.03	0.86
S × D	1	15.02	0.08	0.78	7.56	0.93	0.35
P(S × D)	12	179.54	3.19	<0.01	8.11	2.67	<0.01
Residual	48	56.30			3.04		
		(g) Prionospio heterobranchia			*(h) Streblospio benedicti*		
S	1	95.06	0.50	0.49	0.77	0.01	0.91
D	1	1.56	0.01	0.93	3.52	0.06	0.81
S × D	1	0.25	0.00	0.97	47.27	0.79	0.39
P(S × D)	12	190.64	10.50	<0.01	59.79	1.81	0.07
Residual	48	18.16			33.09		

'S' is the fixed comparison between treatments with high and low densities of snails; 'D' is the fixed comparison between treatments with ambient and enhanced levels of detritus. 'P' is the comparisons of randomly located plots within the interaction of fixed effects.

and ambient levels of detritus (Table 1a). These results are further supported by an MDS plot that showed substantial overlap among annelid assemblages in treatments and controls (Fig. 4). Analyses of univariate community measures and individual abundances of common species also showed no significant differences among treatments. For brevity, these non-significant results are not presented.

The density of snails and enrichment of detritus, however, had significant effects on the structure of annelid assemblages (Table 1). These effects were relatively consistent in direction and magnitude because there was no significant interaction between the
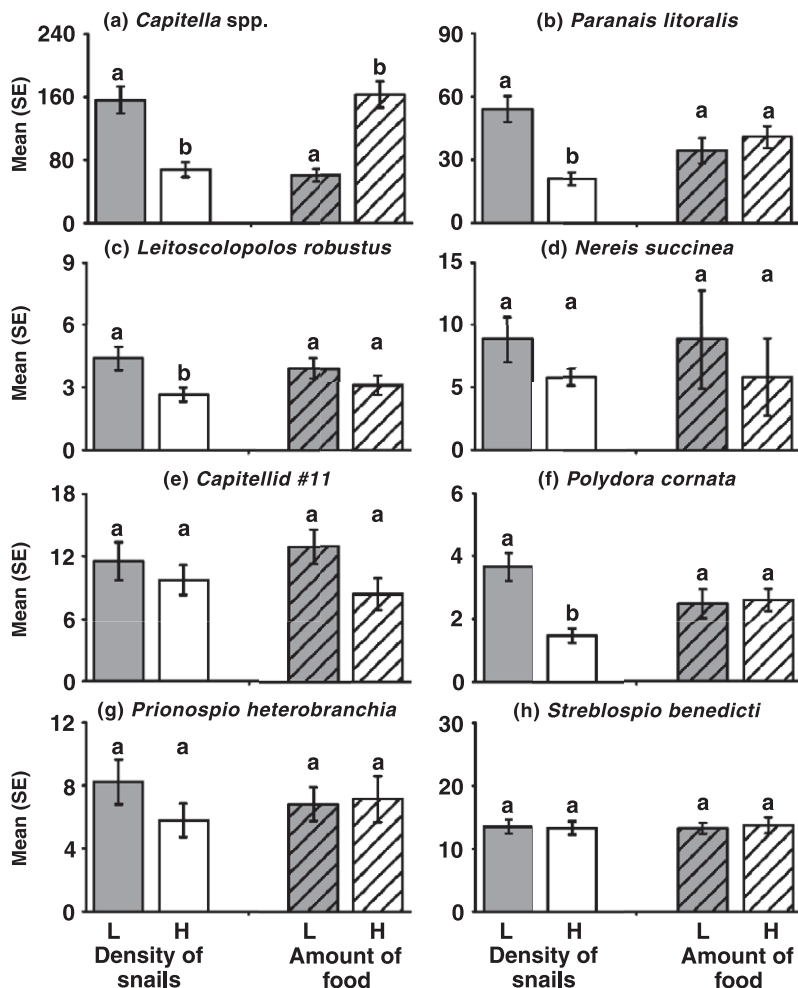

Fig. 7. Mean density of common annelids in treatments with (a) low ▮ and high � densities of snails and with (b) ambient ▨ and enhanced ▨ detritus (d, e, f, g in Fig. 1, respectively). Data represent tests of main effects in Table 3. Lower case letters above bars indicate results of ANOVAs. Comparisons with different letters are significantly different and those with the same letters are not significantly different.

orthogonal factors (Table 1b). Fig. 5 not only graphically demonstrates these effects, but also clearly shows a remarkable similarity between annelid assemblages in the treatment with ambient levels of detritus and low densities of snails and the treatment with detritus added and high density of snails. This result is further confirmed by the average Bray–Curtis dissimilarity values, which show this particular comparison to be substantially less dissimilar than all others (Table 2).

Because there was no significant difference in species richness among any of the treatments (Table 3, Fig. 6) and the composition of species was relatively consistent among samples, the relative abundances of individual species probably had the largest contribution to multivariate effects. This is reflected in an analysis of the combined abundances of all annelids, which showed a significant decrease in response to increasing snail density and a significant increase in response to *Ulva* addition (Table 3, Fig. 6). Snails decreased the annelid abundance by about 50% and the addition of food increased abundance by about 40%. These differences were not, however, equally distributed among species because the evenness (J', Pielou, 1975) of assemblages also changed. The evenness of annelid assemblages in treatments enriched with *Ulva* was significantly less than treatments with ambient detritus. Although not significant ($P=0.07$, Table 3), the average evenness of treatments with high densities of snails was substantially larger than treatments with low densities of snails (Table 3, Fig. 6).

The most abundant species of annelid, *Capitella* spp., showed the strongest response to treatments (Table 4). Its abundance significantly increased to more than double ambient densities with addition of *Ulva* and significantly decreased by about the same magnitude with higher density of snails (Fig. 7). The small oligochaete, *P. litoralis* showed similar responses, although the effect of *Ulva* addition was not significant (Fig. 7). Overall high densities of snails had a consistent negative effect on annelids from a number of genera (Fig. 7). Seven out of eight of the most common annelids showed decreases in average abundance in response to greater snail densities, which is more that can be expected by chance (Binomial test, $P<0.05$). However, only four of these species were significant when individual abundances were tested (Table 4, Fig. 7). Other than *Capitella* spp., there were no significant effects of detrital enrichment on common annelids (Table 4, Fig. 7).

4. Discussion

The density of *I. obsoleta* and the enrichment of organic matter had clear and interpretable effects on assemblages of annelids that were independent of experimental caging and disturbance effects. Artifacts associated with cages in soft-sediment habitats have been well documented (Virnstein, 1978; Dayton and Oliver, 1980; Peterson and Black, 1994). The non-significant fence effects in our study are probably related to the relatively short length of the experiment, the sluggish water flow over the mud flat and the open access to predatory crabs and fish, which were frequently observed in the enclosures. Regardless, the results clearly demonstrate the usefulness of our snail inclusion fences for testing hypotheses on sheltered mudflats and validate the results of previous studies that have used these fences at Flax Pond (e.g., Levinton, 1985).

The control treatments not only showed minimal effects of fences, but also the ability of annelids to recover quickly from short-term mechanical disturbances. Localized physical disturbances from burrowing crustaceans and benthic fish are common in soft sediment habitats (Levin, 1984; Thrush et al., 1991). In some areas, these disturbances have short-term effects with long-term implications for benthic community structure (e.g., Thrush et al., 1991). Nevertheless, our results show that annelid communities at Flax Pond are relatively resilient to these localized disturbances at the intensity used in our treatments because hand-churning the sediment had no detectable effects on community structure.

Enrichment of detritus led to the creation of areas with high- and low-densities of foraging snails, similar to natural distributions found at Flax Pond. Because sediment rich in diatoms represents a high quality food source for *I. obsoleta* (Connor and Edgar, 1982), the increase in local densities of mud snails was probably related to the greater productivity of microorganisms that follows addition of *Ulva* to marine sediments (Levinton, 1985). Observations of these plots showed the increase in snail abundance did not occur immediately after the *Ulva* was added, but several weeks into the experiment. This delay was partially caused by a lag time required for populations of microorganisms to respond to the *Ulva* addition and a short period of anoxia that occurred in enriched plots at the beginning of the experiment (Levinton, 1985; Levinton and Stewart, 1988).

The *I. obsoleta* found in the unfenced *Ulva* enriched plots were mostly full sized adults, rather than recently recruited juveniles. It is therefore likely that foraging adult snails located the enriched plots and remained in these areas to exploit the enhanced food resources. The ability of *I. obsoleta* to quickly locate these areas was not surprising because they are extremely effective at detecting odors from food sources (Zimmer et al., 1999; Rahman et al., 2000). These snails also can follow mucus trails. Rather than following their own trails, *I. obsoleta* is biased toward following the trails of conspecifics, which can lead to aggregation (Trott and Dimock, 1978). It has been hypothesized that this trail-following behavior can help foraging snails locate high quality sources of food (Trott and Dimock, 1978).

High densities of *I. obsoleta* negatively affected annelid abundances. The magnitudes of these effects were not consistent across species, with the numerically dominant annelids, *Capitella* spp. and *P. litoralis*, having proportionally greater losses than other species. There are several mechanisms by which these negative interactions may have occurred. First, both *I. obsoleta* and deposit feeding annelids mostly consume benthic microorganisms and are, therefore, in direct competition for limited food resources (Levinton and Stewart, 1982, 1988). Second, the foraging activities of mud snails, which involves lots of burrowing and mucus production (Edwards and Welsh, 1982), may interfere with annelid feeding, reproduction or larval settlement (Curtis and Hurd, 1979; Dunn et al., 1999) or resuspend existing worms into the water column (Hunt et al., 1987; Dunn et al., 1999). Finally, *I. obsoleta* may unintentionally consume or dislodge small numbers of worms (Curtis and Hurd, 1979; Feller, 1984).

Compared to the generalized effects of *I. obsoleta*, the addition of detritus had more specific effects on annelid community structure because only *Capitella* spp. showed a significant positive response to enrichment of detritus. *Capitella* spp. is a group of sibling species that have relatively similar morphology, but different life histories (Grassle and

Grassle, 1976). Most of the *Capitella* spp. types (especially type 1) have eggs and larvae that develop relatively rapidly, which enables them to quickly take advantage of organic enrichment (Grassle and Grassle, 1977; Chesney and Tenore, 1985), as shown in experimental treatments.

It was somewhat unexpected that other annelid species did not respond strongly to the addition of algal detritus. Laboratory studies have demonstrated that populations of the oligochaete, *P. litoralis*, grow rapidly in *Ulva* enriched sediments (Levinton and Stewart, 1982, 1988), with each worm asexually producing a new individual every 4 days (Nilsson et al., 1997). Because these effects were not found in the field, it is possible these opportunistic oligochaetes were less effective at utilizing resources than *Capitella* spp. Alternatively, the quantity of detritus in the sediment may have been an important factor because the amount of *Ulva* used in our field experiment was a quarter of amount used in the laboratory experiments that showed positive effects (see Levinton and Stewart, 1982, 1988).

For more sedentary polychaetes that recruit mostly via larval settlement, such as the spionid polychaetes, *Polydora cornuta* (Bosc), *Prionospio heterobranchia* (Moore) and *Streblospio benedicti* (Webster) the experiment may not have been long enough for a substantial larval settlement. Nevertheless, adults of these species are often found in the water column and thereby could have moved into the experiment enclosures (Dauer et al., 1981; Levin, 1984). Similarly, more mobile worms, such as *Leitoscolopolos robustus* (Verrill) and *Tubificoides brownae* (Brinkhurst and Baker), could easily have crawled through the mesh of the fences from adjacent sediment. The unchanged abundances of the less opportunistic worms probably indicate their population abundances were not limited by food during the experiment. Alternatively, settling larval, juvenile or adult worms may actively avoid areas with *I. obsoleta*, even when snails are in low densities (see discussion in Dewitt and Levinton, 1985; Hunt et al., 1987).

Extremely large densities of opportunistic deposit feeding annelids (up to 200,000 m^{-2}) were found in plots with enhanced *Ulva* detritus and low densities of snails. This density of worms has never been recorded in 5 years of sampling unmanipulated areas at Flax pond (J.S. Levinton, unpublished data; Cheng et al., 1993). One possible explanation for these extreme abundances is that the opportunistic worms are food limited and levels of organic detritus never naturally reached those in the *Ulva* enriched treatments. This scenario is unlikely, however, because patches of anoxic sediment associated with high organic content are common in early spring at Flax Pond, but were not found in experimental plots testing hypotheses about annelid assemblages. An alternative explanation could be related to the foraging behavior of *I. obsoleta*. Experiments showed mud snails actively searched for and exploited areas with high levels of organic material. High densities of *I. obsoleta* associated with such areas would negatively affect abundances of annelids, especially the opportunistic species, *Capitella* spp. and *P. litoralis*. Consequently, the foraging behavior of snails could limit populations of opportunistic worms in areas with high levels of detritus, where they would normally dominate benthic assemblages.

Support for this *I. obsoleta* control hypothesis comes from community level analyses. The nMDS ordinations showed remarkable similarity between annelid assemblages in areas with low resources and low densities of snails and areas with high resources and high densities of snails. In addition, detrital enrichment decreased community evenness by

favoring opportunistic species, whereas mud snails tended to increase the evenness of annelid assemblages ($P = 0.07$) by negatively affecting a greater proportion of the dominant opportunistic species. These experimental results indicate, therefore, that the ability of *I. obsoleta* to locate and forage within areas with high detrital resources should substantially reduce the spatial variation in annelid community structure on natural mudflats.

It is well known that the mud snail, *I. obsoleta*, plays an important role in estuarine intertidal soft-sediment ecosystems in the eastern United States. It strongly influences the structure of microbial communities and accelerates nutrient cycling in the benthos (Pace et al., 1979; Connor and Edgar, 1982; Levinton and Bianchi, 1981; Levinton, 1985). Our experiments further demonstrate its major influence in structuring benthic communities (see also Grant, 1965; Nichols and Robertson, 1979; Levinton and Stewart, 1982, 1988; Hunt et al., 1987). Rather than increasing spatial variation in benthic community structure, we hypothesize that foraging by *I. obsoleta* smoothes out variation in an environment where limiting resources, in the form of detrital inputs, are patchily distributed. Because many environments are strongly affected by spatially localized input processes (e.g., macroalgal decomposition or invertebrate recruitment), the foraging behavior of many mobile consumers, like *I. obsoleta,* may even out patchiness in many natural communities (Schneider, 1978, 1992). Certainly, the potential top-down stabilizing effect of mobile consumers warrants further investigation.

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