



Growth, survival, and metal content of marsh invertebrates fed diets of detritus from *Spartina alterniflora* Loisel. and *Phragmites australis* Cav. Trin. ex Steud. from metal-contaminated and clean sites

Judith S. Weis¹, Lisamarie Windham^{1,4}, Celine Santiago-Bass² & Peddrick Weis³

¹Department of Biological Sciences, Rutgers University, Newark New Jersey 07102; ²Langan Engineering and Environmental Services, Elmwood Park, New Jersey 07407; ³Department of Anatomy, Cell Biology & Injury Science, NJ Medical School, Newark, New Jersey 07103; ⁴Present address: Department of Earth and Environmental Sciences, Lehigh University, Bethlehem, Pennsylvania 18015

Received 13 April 2000; accepted in revised form 29 January 2001

Key words: crab, detritus, diet, growth, metal, *Phragmites*, regeneration, shrimp, *Spartina*, survival

Abstract

Marsh vegetation plays an important role in trophic ecology of estuaries. Once broken down to detritus, it is an important food source for many organisms. In Atlantic Coast marshes, the reed *Phragmites australis* has been invading many areas once dominated by smooth cordgrass, *Spartina alterniflora*. In this study we evaluated the growth of and trophic transfer of metals to estuarine invertebrates when fed diets of detritus from these different plant species. Decaying leaves from populations of *Phragmites*, natural *Spartina*, and restored *Spartina* from both the Hackensack Meadowlands, New Jersey, and the more pristine Accabonac Harbor of East Hampton, New York, were collected from the marsh surface in the spring. Decaying leaves were pureed and fed to the fiddler crabs *Uca pugnax* and *U. pugilator*, and to the grass shrimp *Palaemonetes pugio*. In fiddler crabs we monitored limb regeneration, molting and weight. *U. pugilator* regenerated limbs and molted equally well on all six diets. Most of the *U. pugnax* arrested growth midway through regeneration on all 6 diets. A repeat experiment with smaller crabs, which did complete the process, found no consistent differences among the six diets and control food, although control food and *Phragmites* detritus had higher N concentrations than the *Spartina* detritus. Grass shrimp fed all six diets did not survive beyond 3 weeks. In another experiment using HM sediments from each vegetation type (containing detritus, meiofauna, and microflora), survival was equally high among treatments and the shrimp fed sediments from the restored *Spartina* site or control food grew better than those fed sediments from the *Phragmites* or natural *Spartina* sites. Although metal concentrations in detritus varied between sites and plant species, the crabs of each group did not differ in metal concentrations after the feeding experiment. Our data do not support the general assumption that *Phragmites* leaf detritus is of poorer nutritional quality than *Spartina alterniflora* leaf detritus to estuarine consumers.

Introduction

Tidal wetlands are critical for estuarine function, as they are responsible for a high proportion of estuarine productivity. The marsh grass, *Spartina alterniflora* Loisel, typical in Atlantic coast estuaries, is not generally consumed by aquatic species until it has died and decayed. Decomposition processes in salt marshes fragment the original dead leaves and stems into smaller sizes. Colonization of the substrate by bacteria,

fungi, and protozoa (Odum and de la Cruz, 1967) makes the detritus more palatable to invertebrates (Barlocher and Newell, 1999). Using stable isotopes, Currin et al. (1995) found that the *S. alterniflora* detritus was utilized by several consumer species and noted that the isotopic signature for standing dead *S. alterniflora* was different from that of live or senescent plants, due to aerial decomposition by fungi.

In contaminated marshes, plants can take up pollutants from sediments, some of which may be stored in aboveground tissues (Giblin et al., 1980). After the plant dies, contaminants such as metals may be present in the detritus, which can serve as a trophic link in transferring metals to animal consumers.

Phragmites australis (Cav.) Trin. ex Steud. is an invasive reed that has replaced the extant *Spartina* spp. in many marshes on the Atlantic Coast of the US, particularly in those considered 'disturbed.' Historically found in the high marsh in mixed plant communities, it has been moving over the past century into low marsh areas forming dense, monotypic stands. *Phragmites* is considered less desirable because it reduces plant diversity, causes accumulation of sediments (Rooth and Stevenson, 1998), and alters patterns of water flow, reducing habitat heterogeneity and open water space (Buttery and Lambert, 1965; Shisler, 1990). Although it is considered a valuable plant in Europe (Silberhorn, 1982), in the USA *Phragmites* is considered a weedy invader by marsh managers. In recent years, many wetland restoration efforts have removed *Phragmites* and planted *Spartina*. However, restored and created marshes generally are less productive and diverse than natural marshes. Minello and Webb (1997) compared natural and created *Spartina* marshes (up to 15 years of age) on the Gulf Coast and found that benthic infauna density and species richness were lower in the created marshes. In addition, densities of most fishes and commercially-important crustaceans were lower in the restored marshes. Sacco et al. (1994) similarly found a decreased faunal community in restored marshes. Allen et al. (1994) found that mummichogs (*Fundulus heteroclitus*) in restored marshes consumed less food than fish inhabiting natural marshes. It may be that decades, rather than years, are needed before normal marsh functions can be restored. As has been pointed out by Levin et al. (1996), a process of succession takes place in created marshes. Therefore, replacing natural with created marshes will result in an overall loss of community productivity for a substantial period of time.

Despite the general dislike for and frequent removal of *Phragmites* in marsh management programs in the US, there is little known about the extent of its contribution to or effects on estuarine ecology and productivity. There is a general assumption that the plant has little ecological value. Wainwright et al. (2000) found that stable isotope ratios of mummichogs caught in *S. alterniflora* or *Phragmites*-dominated marshes reflected strongly the ratios found in these dominant

plant species, suggesting that *Phragmites* can contribute in a significant way to the food webs in areas where it predominates. Fell et al. (1998) found that *Phragmites*-dominated marshes have abundant tidal-marsh invertebrates (snails, amphipods, and isopods) which provide suitable food for mummichogs. Gut content analysis revealed that these fish moved onto the marshes at high tide and fed on the invertebrates, as they do in *Spartina* marshes (Kneib, 1984).

Two important consumers of detritus are grass shrimp (*Palaemonetes* spp.) and fiddler crabs (*Uca* spp.). Grass shrimp are among the most widely distributed, abundant and conspicuous species of shallow estuarine marshes (Welsh, 1975). They play a pivotal role in facilitating transport of energy and nutrients. The normal diet of the omnivorous *Palaemonetes pugio* consists of detritus as well as live food (Welsh, 1975). Fiddler crabs (*Uca* spp.) are integral components of many marsh systems. Their intertidal burrows serve to aerate the sediments, which is considered beneficial for the marsh grasses (Montague, 1980; Bertness, 1985). The crabs also benefit from the presence of the marsh vegetation, which provides detritus for food as well as cover to hide from predators (Nomann and Pennings, 1998).

Like other Brachyuran crabs, fiddler crabs can autotomize limbs at a preformed breakage plane and subsequently regenerate them. The regenerating limb bud grows within a layer of cuticle in a folded position, and at the time of ecdysis it unfolds and becomes functional. The regeneration of limbs is closely tied to the molt cycle, and factors that affect the molt cycle (such as environmental factors, toxicants, and nutrition) will also affect regeneration (Rao, 1965; Weis, 1976 a and b, 1977; Weis et al., 1992). Limb regeneration and ecdysis can be accelerated by the removal of a number of limbs, a process of multiple autotomy (Skinner and Graham, 1972). This can synchronize crabs that are in different stages of their molt cycle so that they generally will begin regenerating, enter proecdysis, and molt within a comparable period of time.

The foremost goal of the present study was to investigate the growth responses of the fiddler crabs, *Uca pugnax* Smith and *U. pugilator* Bosc, and the grass shrimp, *Palaemonetes pugio* Holthuis, to detritus from *Phragmites* (P) and from natural and restored *Spartina* (NS and RS). In order to ascertain their nutritional value to these species, we (1) examined the regeneration and molting (in fiddler crabs only), growth, and survival of animals consuming these diets, and (2) measured carbon and nitrogen concentrations

in the different diets. Our second goal was to compare the two plant species as agents of metal transfer into the marsh food web. Elevated metals in the food could have a toxic effect that reduces growth and/or survival in animals consuming it, irrespective of its nutritional value. We therefore investigated the concentrations of metals in detritus from a contaminated and a 'clean' reference site and the amounts transferred to the fiddler crab consumers.

Materials and methods

In April 1998, decaying leaf litter was collected from the marsh surface at a natural *Spartina* site (NS, Saw Mill Creek), a restored *Spartina* site (RS, Mill Creek), and a *Phragmites* site (P, Saw Mill Creek) in the Hackensack Meadowlands (HM), a contaminated area. Similar collections were made from the three vegetation communities in Accabonac Harbor (AC), East Hampton, New York, as a reference site. Saw Mill Creek, the source of the HM natural *Spartina* and *Phragmites*, is a 500-ha marsh of mudflats and shallow tidal bays along the west bank of the Hackensack River. *Phragmites* populations have been present at this site for decades. The site has been impacted over time by primary and secondary sewage effluent and landfill leachate, which has now ceased. Mill Creek, a 25-ha mitigation site completed over a decade ago, currently contains a mixture of open water areas that become mudflats at low tide, intertidal zones vegetated primarily by the planted *S. alterniflora*, and upland islands. The site in East Hampton is in a <1-ha low salinity cove ('pond') of Accabonac Harbor, which connects to Gardiner's Bay. This is a residential, non-industrialized area, although a road runs next to the marsh. After the *S. alterniflora* dominated pond was invaded by *Phragmites*, an area at one end was restored – that is, *Phragmites* was removed and *Spartina* was planted about five years ago. Thus, the three types of plants are all growing in close proximity.

After being brought into the laboratory, the leaves were placed in Nalgene[®] containers and allowed to decay in the dark for two additional months in small amounts of site water supplemented with synthetic estuarine water (Instant Ocean[®]). The water was gently aerated every other week with an air stone. The detrital leaves were then put into a blender and pureed. The purees from all six types of leaves were stored in jars and kept at 4 °C for use as food for the experimental animals. Samples were taken for metal

analyses (atomic absorption spectrophotometry). Additional experiments used sediment from the upper 1 cm of marsh (which includes detritus, microflora and meiofauna and contaminants) from the three HM sites as food for grass shrimp.

Fiddler crab experiments

In 1998, *Uca pugilator* were collected from East Hampton, New York and *U. pugnax* from Piles Creek in Linden, New Jersey. Autotomy of one chela and 5 walking legs was induced by pinching each merus, after which the crabs were blotted dry and weighed. All groups were arranged to have crabs with a comparable size range and sex distribution. Crabs of both species were generally 12–17 mm carapace width. One hundred twenty of each species were maintained in individual polystyrene containers in estuarine water (15 ppt, 25 °C) with twenty animals of each species receiving each of the six diets. Twice a week the water was changed and each animal was fed 0.1 g (wet weight) of detritus. Preliminary trials demonstrated that this amount was mostly (but not totally) consumed after 3–4 days. Previous studies had demonstrated that this amount was adequate to support growth and molting in these species (Weis, 1977; Callahan and Weis, 1983).

Starting on day 7 after autotomy and twice a week thereafter, the first walking leg (as a representative limb) of each crab was measured under a stereomicroscope with a calibrated ocular micrometer. To standardize measurements on crabs of different sizes, the millimeter value of the limb bud was converted to an 'R-value' (Bliss, 1956), which is limb bud length \times 100/carapace width. Mean R-values were calculated for each group on each measurement day. To ascertain the extent to which they were eating the detritus, counts of fecal pellets were made on two occasions before changing the water to assure that crabs were feeding. Mortalities and time to ecdysis for each individual were recorded. After they molted, surviving crabs were blotted dry and reweighed; the dry weight of the exuvium was added to the weight of the crab, and the carapace width was again measured. At the end of the experiment, crabs that had not molted were reweighed. All crabs were frozen for metal analysis. The experiment was repeated in 1999 with smaller *U. pugnax*. This trial included a 7th group fed the same amount of moistened Purina 'Fly Chow,' the usual lab fiddler crab diet, and did not include metal analysis.

Elemental analysis

Nutritional quality was assessed by comparing carbon and nitrogen concentrations of each plant species (Rietsma, 1988). Detrital leaves of *Phragmites*, natural *Spartina*, and restored *Spartina* from HM were oven-dried at 70 °C and finely ground with a Wiley mill (#40 mesh), and percentages of carbon and nitrogen measured with a CarloErba elemental analyzer (CHNS).

Metal analyses were performed on the detritus samples and fiddler crabs. Crab soft tissue and detritus was dried at 90°C, weighed, and prepared for analysis, except for those for mercury (Hg) analysis, which were analyzed wet so as not to volatilize organomercurials. Hg content was determined by cold vapor atomic absorption spectrophotometry (AAS), the method originally proposed by Hatch and Ott (1968), in a Coleman MAS-50D mercury analyzer, following mineralization in 4:1 H₂SO₄/HNO₃. For the other metals, samples were mineralized in 3:1 HNO₃/HClO₄, the acids boiled off, and the residue redissolved in 1% HNO₃. All reagents were 'for trace metal analysis.' Copper (Cu), zinc (Zn), and chromium (Cr) were analyzed using flame aspiration AAS in a Perkin Elmer 603 system. Lead (Pb) was analyzed by electrothermal atomization in a Perkin-Elmer 503. Quality control was maintained by analyzing commercially prepared standards, methods blanks, and standard reference materials (orchard leaf powder – NIST SRM 1571) at the beginning and after every 10–12 samples in each analytical run. For QA in animal tissues, National Research Council of Canada Certified Reference Material dogfish muscle (DORM-2) was analyzed along with the organisms. Quality control is assured by achieving measurements within the 95% confidence limits provided by N.I.S.T.

Shrimp experiments

Three trials were run to assess the effects of diet on shrimp growth. In 1998, *Palaemonetes pugio* were collected using umbrella nets in East Hampton New York, and Tuckerton, New Jersey. Their total length was measured to the nearest mm, and they were weighed on a digital balance to the nearest mg after being blot-dry for 5 sec. They were divided into 6 groups, comparable in length and weight, which received the detritus diets (0.1 g / shrimp / 3 days). When the experiment was repeated we included a 7th group that was fed commercial flake food (Tetramin®). In the first

trial, 20 of each group (in two replicates of 10) were kept together in a common tank. When cannibalism was noted, we modified the second trial to have each shrimp in a separate smaller container (polystyrene cup). Each cup had holes on the side to allow for water movement, and they were placed in groups in large aerated aquaria. Twice a week, the water was changed and animals were fed with 0.1 g (wet weight) of detritus. This was a surplus of food, since there was always some left over. Mortalities were recorded. We had planned to measure and weigh them after two and four weeks, but since mortality was high, these experiments focused on mortality rates rather than growth.

Since these experiments showed that the detritus diets were inadequate to support shrimp growth and survival, additional experiments were performed in which shrimp were provided with sediment collected from the upper 1 cm from *Phragmites* and *Spartina* marshes in the Hackensack Meadowlands. This would provide them with additional food from microflora and meiofauna as well as the specific type of decayed vascular plant material. Replicate 10-l tanks were set up with 10 shrimp each in 5 ppt salinity water (the salinity of HM in the early summer). 30 g of sediment from the particular site was placed in a watch glass, which was put at the bottom of the tank. Water and sediment was changed twice a week. The sediment was stored in a refrigerator prior to use and allowed to come to room temperature before introducing it into the tanks. A control group fed commercial flake food (Tetramin®) was included. Shrimp were weighed and measured at the beginning of the experiment and after two, four, and six weeks.

Statistical analyses

All data from experiments with different diets were analyzed with ANOVAs followed by Bonferroni multiple comparison tests (Statistix®). When appropriate, two-way ANOVAs were performed to detect separate effects of site and detritus species. Differences in metal concentrations between *Uca* species were compared with t-tests.

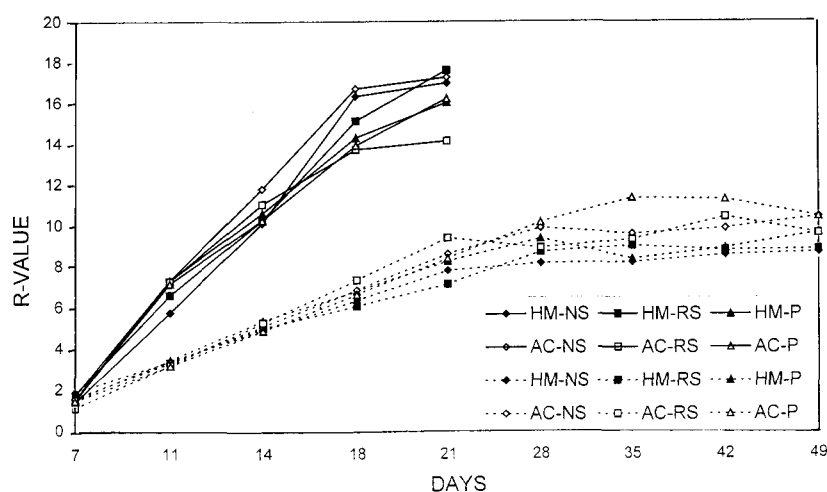


Figure 1. Regenerative growth (R-values) of the first walking legs of *U. pugilator* (solid lines) over three weeks, and *U. pugnax* (dotted lines) over seven weeks, fed diets of detritus from different plants. HM= Hackensack Meadowlands, AC = Acabonac Harbor, NS = natural *Spartina*, RS = restored *Spartina*, P = *Phragmites*.

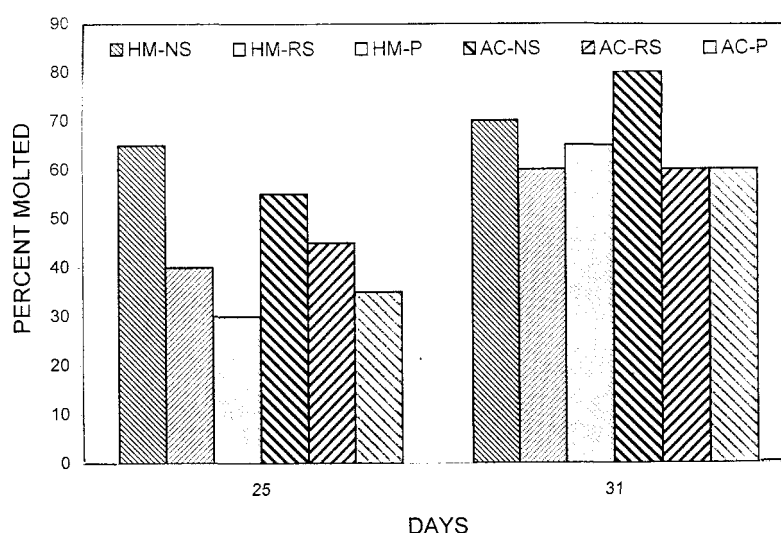


Figure 2. Percent of *U. pugilator* molting by 25 and 31 days after being fed different detritus diets. See Figure 1 for legend.

Results

Fiddler crabs

The *U. pugilator* regenerated limbs (Figure 1), and by four weeks most crabs in all six groups (60–80%) had molted (Figure 2). There were no significant differences among the groups in R-value at any given day, nor in weight gain or mortality (Figure 3). In contrast, the *U. pugnax* began regenerating normally, but at around three weeks, most reached a plateau at R-

values of 8–12, about half grown (Figure 1). A few of the smallest crabs in each group (11–12 mm carapace width) did complete regeneration and molting, but the majority remained at the plateau until the experiment was discontinued at seven weeks. This indicates that all six diets were inadequate to support regeneration in these crabs. There were no significant differences in R-values among the groups except at the five-week measurement, crabs eating AC-P detritus had higher R-values than the other groups ($F = 4.51$; $p = 0.0136$). Mortality in all groups was very low (0–5%). The

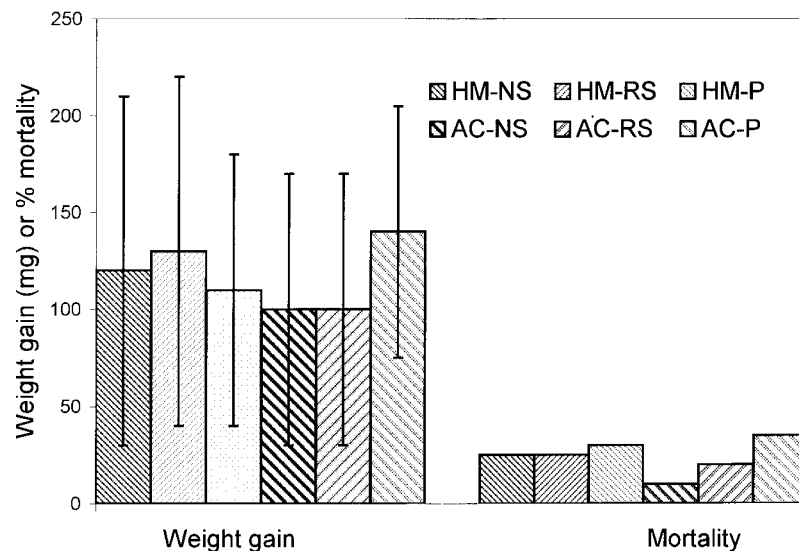


Figure 3. Weight gain (wet weight \pm SD) and percent mortality of *U. pugilator* on the different detritus diets (see Figure 1 for legend).

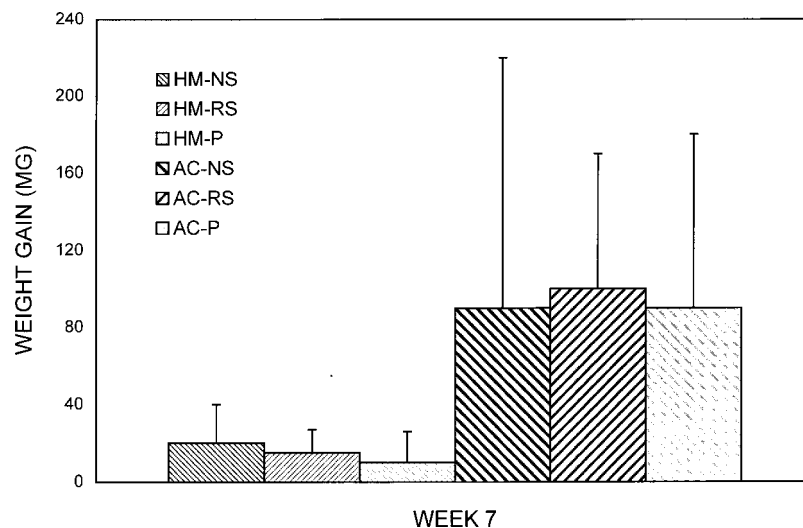


Figure 4. Weight gain of *U. pugnax* (wet weight \pm SD) on the different detritus diets (see Figure 1 for legend).

crabs fed the three diets from HM appeared to gain less weight than those fed the detritus from AC but the variability was high within treatments and differences were not significant (Figure 4; $F = 1.18$; $p = 0.2852$). There were no significant differences among crabs fed NS, RS, or P ($F = 0.9607$; $p = 0.418$). Fecal pellet production was also comparable among the groups.

When the experiment was repeated in 1999 we used smaller crabs (carapace width ~ 12 mm) and included a control group fed normal lab diet. While a

larger percentage of these crabs completed regeneration and molted, and controls tended to grow faster and molt sooner, there were no consistent differences among groups fed the different types of detritus. At weeks 3 and 4, the group fed the AC-NS had R values (9.45 ± 3.82 SD and 10.86 ± 4.60) significantly lower than the controls and those fed AC-RS (15.09 ± 5.98 and 15.55 ± 6.38 respectively, at week 3, and 19.03 ± 4.54 and 17.36 ± 6.79 at week 4.) All other groups had intermediate R-values. By week 5, R values among

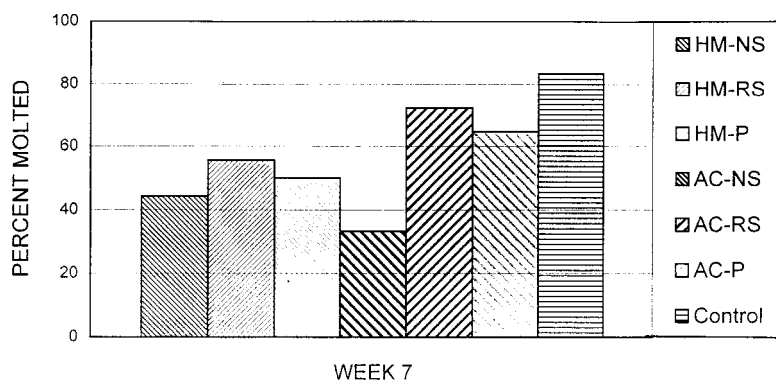


Figure 5. Percent of small sized *U. pugnax* in Trial 2 that molted by Week 7 (see Figure 1 for legend).

all groups were not significantly different. By week 7, the percent that had molted was greatest in the control group (83%; Figure 5). There were no significant differences in weight gain among crabs fed the different diets ($F = 1.22$; $p = 0.3088$).

Metal content

In general, the detritus from the HM had, as expected, higher levels of the metals than the detritus from AC, but levels in the crabs were unrelated to the levels in their diets. The statistical results of the metal analyses of the plant detritus and of the fiddler crabs are presented in Tables 1 and 2. Two-way ANOVAs on metal concentrations detected site, species, and interaction effects (Table 3). AC detritus had metal concentrations that were quite consistent among plant types and lower than the HM detritus for all metals except Zn.

For Cu, three groups were detected among which the means were significantly different: HM-P and HM-RS had the highest levels, and AC-P, AC-RS and AC-NS the lowest levels. For Zn, there were also three groups, with HM-NS having the highest level and AC-NS, HM-RS, and HM-P the lowest. For Cr, there were 2 groups: HM-RS and HM-P were higher than HM-NS, AC-P, AC-NS, and AC-RS. For Pb, there were 3 groups with HM-RS and HM-P the highest, and AC-RS, AC-P, AC-NS, and HM-NS the lowest. For Hg, there were 2 groups: HM-RS and HM-P were higher, and HM-P, HM-NS, AC-NS, AC-P, and AC-RS were lower. Thus, within the HM samples, the RS (Mill Creek) detritus had the highest levels of Cr, and had Cu, Zn, and Pb levels comparable to HM-P. The HM-NS had the lowest levels of Cu, Cr, and Pb, but the highest level of Zn.

The differences in metal content of the plant detritus from the different sites had little or no effect on the growth and molting or on the metal levels of the crabs (Table 2). No significant differences in metal levels were detected among the groups of *U. pugnax* receiving the different diets, nor among the groups of *U. pugilator*. A t-test comparing the two crab species regardless of diet showed that there were species differences in the level of metals in their tissues. *U. pugilator* had significantly more of the biologically important metals, Cu ($t = 5.08$, $p < 0.0001$) and Zn ($t = 11.09$, $p < 0.0001$). On the other hand, *U. pugnax* had significantly higher concentrations of the more toxic metals, Cr ($t = 2.12$, $p < 0.05$), Pb ($t = 6.84$, $p < 0.0001$), and Hg ($t = 13.63$, $p < 0.0001$). Because the crabs were collected from different sites, the differences may reflect either site or species differences.

The nitrogen and carbon concentrations in the three types of detritus from HM and the control diet ('Fly Chow') are presented in Table 4. The nitrogen content of *Phragmites* leaf detritus is similar to the control diet, and significantly greater than the two types of *Spartina* leaf detritus. Carbon:nitrogen ratios are similarly lower in *Phragmites* and control diets than in the two *Spartina* diets.

Grass shrimp

Measures of mortality in trial 1 are depicted in Figure 6. The survivors decreased steadily until day 24 when there were no survivors in any group. On day 17, there were significantly more survivors in the group eating AC-P than any other group. When the experiment was repeated with each animal in an individual container to prevent cannibalism (trial 2), mortality

Table 1. Metal contents ($\mu\text{g/g} \pm \text{SD}$) in detritus. HM = Hackensack Meadowlands, AC = Accabonac Harbor, NS = natural *Spartina*, RS = restored *Spartina*, P = *Phragmites*. For each metal, groups with the same superscript are not significantly different from one another.

Site	Plant	Cu	Zn	Cr	Pb	Hg
HM	NS	48.0 \pm 0.5 ^b	124 \pm 2.6 ^a	43.5 \pm 5.9 ^b	4.7 \pm 0.4 ^c	0.30 \pm 0.37 ^b
	RS	104 \pm 8.5 ^a	42.1 \pm 2.0 ^c	138 \pm 10 ^a	9.8 \pm 2.3 ^a	2.22 \pm 1.13 ^a
	P	107 \pm 9.4 ^a	34.8 \pm 9.2 ^b	108 \pm 24.5 ^a	9.2 \pm 2.4 ^{ab}	1.63 \pm 1.27 ^a
AC	NS	23.4 \pm 3.6 ^c	54.8 \pm 7.7 ^{bc}	16.2 \pm 4.8 ^b	4.7 \pm 0.4 ^c	0.09 \pm 0.04 ^b
	RS	25.1 \pm 1.9 ^{bc}	67.4 \pm 3.3 ^b	13.0 \pm 1.6 ^b	5.3 \pm 0.2 ^{bc}	0.04 \pm 0.03 ^b
	P	28.2 \pm 14.7 ^{bc}	62.5 \pm 8.1 ^b	17.2 \pm 5.2 ^b	5.3 \pm 0.7 ^{bc}	0.04 \pm 0.02 ^b
SRM		4.02 \pm 0.31	17.7 \pm 0.6	0.97 \pm 0.02	0.42 \pm 0.02	2.05 \pm 0.12
(expected)		3.7 \pm 0.4	17.9 \pm 0.4	1.0 (n.c.)*	0.87 \pm 0.03	1.99 \pm 0.10

* not certified.

Table 2. Metal concentrations ($\mu\text{g/g}$ dry weight) in fiddler crabs, *U. pugnator* and *U. pugnax*, that ate different detritus diets. HM = Hackensack Meadowlands, AC = Accabonac Harbor, NS = natural *Spartina*, RS = restored *Spartina*, P = *Phragmites*.

Site/Plant	Crab	Cu	Zn	Cr	Pb	Hg
HM-NS	<i>pugnax</i>	280 \pm 30	80.4 \pm 12.5	2.38 \pm 0.12	5.3 \pm 1.49	0.73 \pm 0.15
	<i>pugnator</i>	539 \pm 116	270 \pm 3	3.38 \pm 2.92	2.54 \pm 3.95	0.05 \pm 0.005
HM-RS	<i>pugnax</i>	305 \pm 20.2	82.1 \pm 7.6	2.5 \pm 0.33	3.74 \pm 0.3	0.73 \pm 0.19
	<i>pugnator</i>	567 \pm 12.5	277 \pm 32	1.34 \pm 0.2	0.15 \pm 0.22	0.06 \pm 0.07
HM-P	<i>pugnax</i>	303 \pm 19.2	80.1 \pm 8.02	2.5 \pm 0.09	4.43 \pm 1.25	0.71 \pm 0.03
	<i>pugnator</i>	365 \pm 87	235 \pm 111	1.15 \pm 0.42	0.57 \pm 0.52	0.02 \pm 0.019
AC-NS	<i>pugnax</i>	262 \pm 46.4	73.1 \pm 10.78	2.34 \pm 0.03	5.59 \pm 0.89	0.63 \pm 0.24
	<i>pugnator</i>	366 \pm 94	253 \pm 27	1.48 \pm 0.25	0.25 \pm 0.11	0.08 \pm 0.015
AC-RS	<i>pugnax</i>	287 \pm 59.6	85.6 \pm 6.15	2.07 \pm 0.25	4.41 \pm 2.01	0.80 \pm 0.39
	<i>pugnator</i>	422 \pm 104	228 \pm 6	1.40 \pm 0.73	0.48 \pm 0.31	0.07 \pm 0.04
AC-P	<i>pugnax</i>	292 \pm 42.4	81.1 \pm 10.16	2.19 \pm 0.15	3.65 \pm 2.73	0.64 \pm 0.30
	<i>pugnator</i>	483 \pm 249	307 \pm 119	1.24 \pm 0.19	1.26 \pm 0.57	0.12 \pm 0.11
SRM		29.0 \pm 1.1	94.2 \pm 3.4	0.46 \pm 0.14	0.36 \pm 0.39	1.88 \pm 0.18
(expected)		25.8 \pm 1.1	85.8 \pm 2.5	0.37 \pm 0.08	0.22 \pm 0.02	1.99 \pm 0.10

occurred again. In this trial, both groups eating P appeared to survive somewhat better than the other groups (except controls eating flake food), and on day 14, those eating HM-P had statistically less mortality than the other groups, except controls (Figure 7). Total mortality occurred somewhat faster in this trial than in the first one, probably because in the first trial some shrimp got nutrition from the ones they had cannibalized.

In the experiment in which shrimp were given HM sediment (trial 3), which contained additional nutrition (microflora and meiofauna) beyond the plant detritus, survival was much better. After six weeks, the con-

trol group fed flake food (C) had 20% mortality, the NS group 33% mortality, the RS group 0% mortality, and the P group 20% mortality. Growth occurred in all groups, and by week four (Figures 8 and 9) there were significant differences in both length and weight among the groups ($F = 4.92$, $p < 0.003$ for length, $F = 6.24$, $p < 0.001$ for weight). Bonferroni post-hoc comparisons indicated two homogeneous groups (RS, C > C, NS, P) for both length and weight. Thus, those fed the RS sediment and the flake food grew better than those fed the NS or P mud. By six weeks, these differences persisted for both length ($F = 4.60$, $p < 0.005$) and weight ($F = 7.15$, $p < 0.005$). Bonfer-

Table 3. Results of two-way ANOVAs for metal concentrations (Cr, Cu, Hg, Pb, Zn) in detritus of *Phragmites*, natural *Spartina* and restored *Spartina* populations.

Metal	Source	Df	SS	MS	F	P
Chromium (Cr)	Site	1	29659.1	9.659.1	226.23	<0.0001
	Vegetation	2	6668.68	3334.34	25.43	<0.0001
	Site * Veg.	2	7412.62	3706.31	28.27	<0.0001
	Residual	12	1573.20	131.100		
Copper (Cu)	Site	1	16616.6	16616.6	254.96	<0.0001
	Vegetation	2	3713.81	856.91	28.49	<0.0001
	Site * Veg.	2	2932.29	1466.15	22.50	<0.0001
	Residual	12	782.093	65.1744		
Mercury (Hg)	Site	1	7.26186	7.26186	18.89	0.0010
	Vegetation	2	2.38068	1.19034	3.10	0.0823
	Site * Veg.	2	2.68332	1.34166	3.49	0.0638
	Residual	12	4.61202	0.38434		
Lead (Pb)	Site	1	50.0000	50.0000	42.95	<0.0001
	Vegetation	2	42.7122	21.3561	18.34	0.0002
	Site * Veg.	2	29.1679	14.5840	12.53	0.0012
	Residual	12	13.9711	1.16426		
Zinc (Zn)	Site	1	627.761	627.761	2.88	0.1154
	Vegetation	2	7980.1	3990.11	18.31	0.0002
	Site * Veg.	2	7641.77	3820.89	17.53	0.0003
	Residual	12	2615.53	217.961		

Table 4. Carbon and nitrogen contents (mean \pm SD) in detritus of *Phragmites*, natural *Spartina*, and restored *Spartina* populations from HM. Super-script characters denote differences between diets from Bonferroni multiple comparison tests.

Vegetation type	Nitrogen	Carbon	Carbon:Nitrogen
Natural <i>Spartina</i>	1.63 \pm 0.21 ^a	32.70 \pm 2.25 ^a	20.16 \pm 1.10 ^a
Restored <i>Spartina</i>	1.52 \pm 0.18 ^a	33.21 \pm 5.72 ^a	21.82 \pm 1.94 ^a
<i>Phragmites</i>	2.35 \pm 0.28 ^b	36.28 \pm 2.38 ^a	15.55 \pm 1.02 ^b
'Fly Chow'	2.77 \pm 0.25 ^b	39.32 \pm 0.57 ^a	14.25 \pm 1.30 ^b

roni post-hoc comparisons showed that there were two homogeneous groups for length: RS (25.1 mm \pm 3.1 SD), C (24.8 mm \pm 1.9), and NS (23.5 mm \pm 1.7) were larger than C, NS, and P (23.0 mm \pm 1.7). There were three groups for weight: RS and C weighing the most at 133 \pm 50 (SD) and 126 \pm 30 mg, respectively, and NS and P weighing the least, at 100 \pm 20 and 95 \pm 20 mg, respectively. The overall increase in length was 3% for NS, 5% for P, 11% for RS, and 15% for C. As seen in Figure 9, the P group did not gain weight, the NS group lost weight, and the RS group and controls gained weight.

Discussion

In general, the data obtained in this study do not support the general assumption that *Phragmites* detritus is inferior to *Spartina* detritus as a food for invertebrate detritus feeders. In the case of the sand fiddler, *Uca pugilator*, detritus from both species of plants from both sites provided adequate nutrition to support regeneration and completion of the molt cycle within a normal time period. It was interesting to find that the larger individuals of *U. pugnax* were not supported adequately by any of the diets, and many ceased regeneration about midway through the process. This

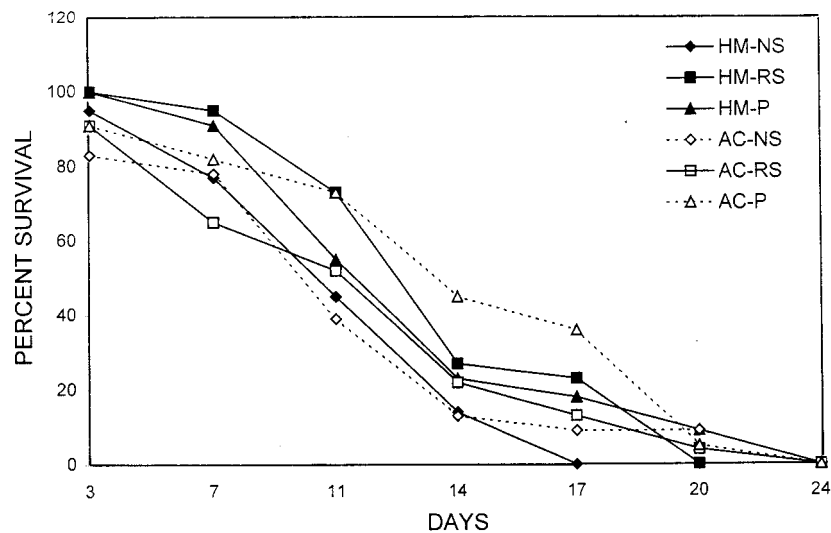


Figure 6. Survival of *Palaemonetes pugio* on the different detritus diets, experiment 1, in group containers (see Figure 1 for legend).

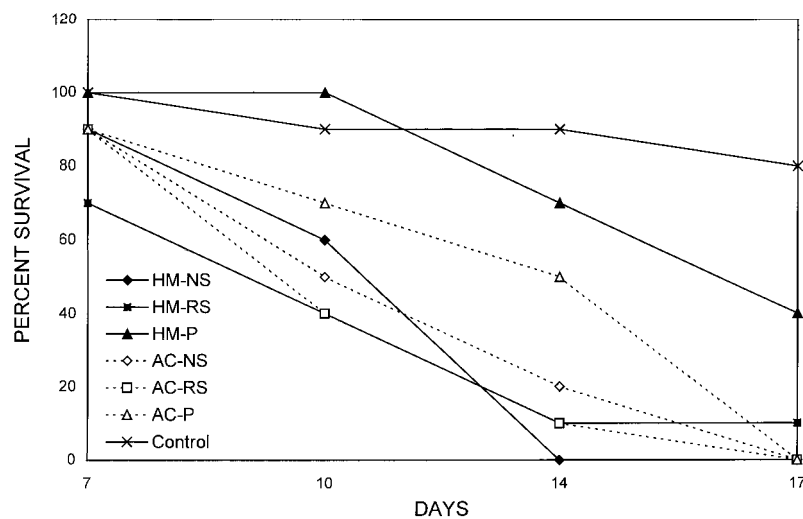


Figure 7. Survival of *P. pugio* on the different detritus diets, experiment 2, in individual containers (see Figure 1 for legend).

did not appear to be due to an inadequate quantity of food, since all detritus was not consumed between feedings, and the crabs did gain weight comparable to *U. pugilator*. Survival was very high on all diets in both trials, and in trial 2 the small *U. pugnax* did complete regeneration and molt on all diets, at a rate comparable to that previously noted with this species fed a control ('Fly Chow') diet (Callahan and Weis, 1983). Both species of fiddler crabs are considered detritus feeders, but *U. pugnax*, which inhabits muddy areas, is likely to have a richer diet than *U. pugilator*, which is generally found in sandy habitats. None of

the detritus diets were adequate for larger *U. pugnax* to regenerate completely and molt, but AC detritus seemed to foster greater weight gain than HM detritus (although data are not statistically significant). If this difference were meaningful, it might be due to higher toxicant levels in the HM detritus.

Although crab growth was not influenced by the different detritus diets, leaf detritus from *Phragmites* has a greater nitrogen content and lower carbon:nitrogen ratio, suggesting that it may be more nutritious than leaf detritus from *Spartina*. The lack of effect of nitrogen concentrations on growth is sim-

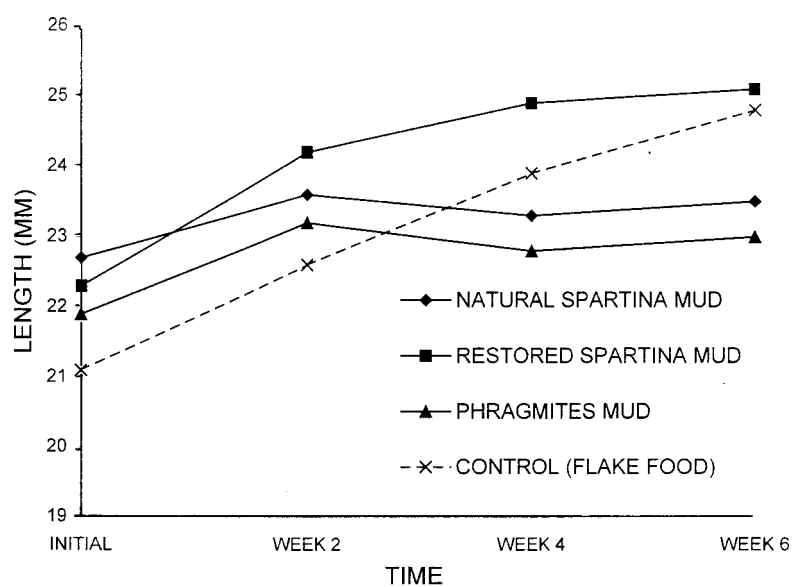


Figure 8. Growth (length) of *P. pugio* on the different sediment diets.

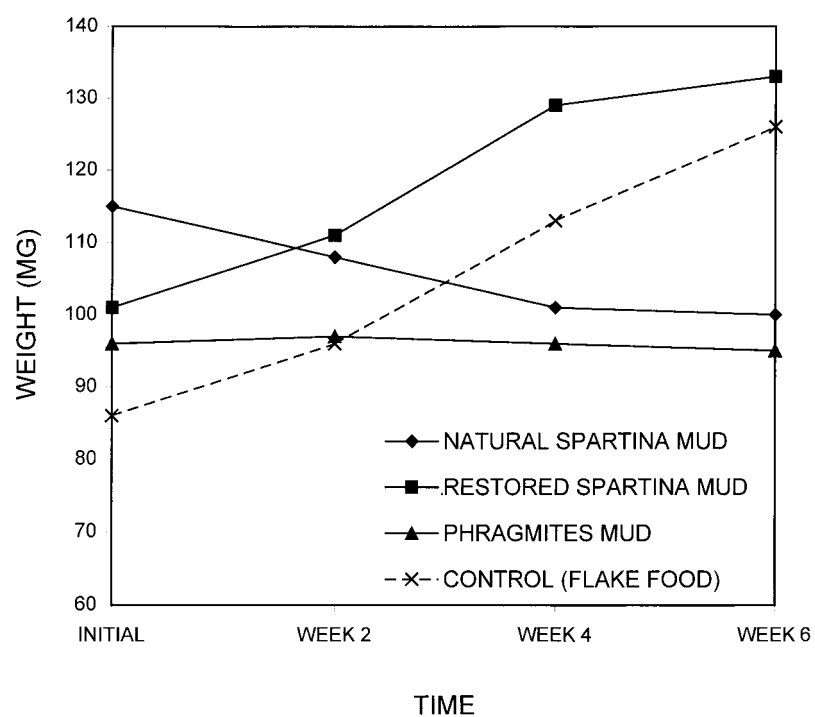


Figure 9. Growth (wet weight) of *P. pugio* on the different sediment diets.

ilar to the results of Rietsma et al. (1988) who found that growth of the snail *Melampus bidentatus* was not affected by nitrogen concentrations in different *Spartina* detritus diets. A possible explanation for this is the finding of Rice (1982) that the percent nitrogen is of limited use in assessing the nutritional value of detritus since the increased nitrogen is due to unavailable humic substances. However, Rietsma et al. (1988) also found no association of growth with available amino-nitrogen. Other differences may exist in the detrital chemistry of these plant species (e.g. phenolics, proteins), but the lack of effect of diet in these multiple experiments indicates that these potential differences do not affect short-term growth and survival of these animals.

Metal analyses indicate that all plants from the AC site had lower concentrations of Cu, Cr, Hg, and Pb. Zn concentrations were similar between sites, although they were highest in the HM-NS samples. The AC samples all had more Cr than expected, but the blender used for pureeing could have contributed to all samples from its stainless steel blades. Further, the elevated Pb concentrations in the AC samples may represent road runoff.

Plant species also affected metal concentrations in leaf detritus. For all metals except Zn, RS and P detritus at HM had metal concentrations 2–3 times the concentrations in NS. Zn concentrations in NS detritus were 3–4 times those of RS and P detritus. High levels of the toxic contaminants Cr, Pb, and Hg in the HM-RS samples (from Mill Creek) are in keeping with unpublished data (Weis) on bulk sediment metal concentrations. Mill Creek sediments had about twice as much Cu (about 130 vs 70 ppm), Zn (about 340 vs 140 ppm), and Pb (about 135 vs 85 ppm), and 3–4 times as much Cr (about 200 vs 70 ppm) and Hg (about 4 vs 1.2 ppm) as Saw Mill Creek. Thus, the plant metal concentrations are related to sediment metal concentrations.

Alternatively, metal levels were significantly different between P and NS detritus from HM, although both were collected along Saw Mill Creek on either side of a relatively undisturbed tidal creek. P detritus was elevated in Cu, Cr, Hg, and Pb concentrations, whereas NS was elevated in Zn concentrations. In another study of these two species growing in a different area of HM (Jersey City Aqueduct), Burke et al. (2000) found that fresh leaves of *Phragmites* plants had lower tissue metal concentrations than leaves from neighboring natural *Spartina alterniflora* plants. The opposite results found in this study suggest that the

decay process may alter metal concentrations within detrital leaves. Although attached sediment particles could elevate the metal concentration within detritus, the metal-specific enrichments within each species' detritus (high Zn in NS vs. high Cu, Cr, Pb, and Hg in P) suggest that the differences in detritus metal concentrations are not confounded by differences in sediment incorporation between species.

In any case, the different metal concentrations among detritus types had no relationship to the levels of metals seen in the crab consumers and no apparent effects on growth or survival. No differences in concentration of any metal were seen in the different experimental groups of either species of fiddler crabs. This may be because crabs can regulate their metal levels regardless of the uptake from food, particularly at these relatively low concentrations. It must also be considered that these were short-term feeding studies lasting 1–2 months, which is very small compared with the crabs' previous lifetime of a year or two. In contrast, exposure to sublethal levels of waterborne metals for one month produced significant accumulation as well as effects on limb regeneration (Weis, 1976b). Differences between the two crab species in the contaminant metals Cr, Pb, and Hg probably reflect the previous exposure to these contaminants in the different field sites from which they were collected – *U. pugnax* from contaminated Piles Creek, and *U. pugilator* from AC. It was interesting to note that *U. pugilator* had significantly higher levels of Cu and Zn, which are required trace elements. Because Cu and Zn are lower at AC (source of the *U. pugilator*) than Piles Creek (source of the *U. pugnax*) (Khan and Weis, 1993), this pattern is more likely due to species differences.

Detritus alone was an inadequate diet for survival of the grass shrimp. Shrimp on all six of the detritus diets died, while controls eating flake food survived. It has been shown that *P. pugio* does assimilate detritus (Adams and Angelovic, 1970). It has been known for some time that many organisms that consume detritus (plant material and associated microbes) cannot subsist on a diet of detritus alone (Marinucci, 1982). Prinslow et al. (1974) showed that the mummichog, *Fundulus heteroclitus*, did not grow when fed a diet of detritus alone. Although the mummichogs did not grow, they did not die, however, as did all the grass shrimp that were fed detritus alone in the present study. When shrimp were supplied with HM sediments containing additional nutritional material, survival was much better, and those given sediments

from the RS site did better than those with sediments from the NS site or from the P site. The differences are probably not due to the nutritional quality of the plant detritus itself (as demonstrated by experiments 1 and 2), but to other contents of the sediments. The P and NS sediments were both collected from Saw Mill Creek, and the RS mud from Mill Creek. It is possible that there are denser populations of microalgae and/or meiofauna present in the latter creek, which would provide better nutrition for the shrimp. Unpublished data on chlorophyll A (L. Windham) indicate that there are much denser populations of microalgae in Mill Creek sediments than in Saw Mill Creek sediments. Newell and Kreeger (1998) found that microphytobenthos (diatoms and cyanobacteria) are readily consumed and assimilated by *P. pugio*. While the elevated metals in the Mill Creek sediments do not appear to have negative consequences on grass shrimp growth, at least in these short-term experiments, the phytobenthos appears to be quite important.

The detritus we produced in the lab was from leaves collected from the marsh surface and was stored in containers in the refrigerator. Thus it could not have been colonized by significant amounts of microflora or meiofauna, which would happen in the field. It is possible that in the field there may be differential colonization of detritus of the different plants, which might have effects on its nutritional quality for these animals. We do not know if the higher levels of microphytobenthos at Mill Creek are related to the restored *Spartina* at that site, or to other environmental factors.

In short, we have found no evidence that leaf detritus of *Phragmites* is nutritionally inferior to that of *Spartina* for the growth and survival of these estuarine invertebrates. For *U. pugnator*, detritus from natural *Spartina*, restored *Spartina*, and *Phragmites* from both HM and AC were all equally satisfactory in supporting regeneration and completing the molt cycle. Stable isotope data suggest that where *Phragmites* is the dominant marsh plant, it appears in the diets of consumers in the same way as *Spartina* does in sites where it is dominant (Wainright et al., 2000). However, for larger *U. pugnax*, none of the diets were adequate to support complete regeneration, although survival was high in all groups. For *P. pugio*, none of the diets were adequate to even support survival unless detritus was supplemented with other sources of food found in sediments.

Efforts to restore salt marsh areas by replacing the undesired *Phragmites* with the desired *Spartina* are often justified by the assumption that the productivity

of animal populations will be enhanced. Yet, evidence from this study and others (Fell et al., 1998; Wainright et al., 2000) does not support the general assumption that *Phragmites* leaf detritus is of poorer nutritional quality than that of *Spartina*.

Acknowledgements

This work was supported by NSF grant # DEB 98-13812, the Meadowlands Environmental Research Institute (MERI), and USGS Water Resources Research Institute of Rutgers University. Additional assistance was received from Douglass College's 'Project Super' and Rutgers-Newark's MBRS program. We appreciate the technical assistance of Jennifer Tan, Cassandre Cherilus, Lidia Dounaevskaia, Carla Peterman, Tochi Okwuosa, Craig Woolcott, and Theodore Proctor. We are also grateful to the Hackensack Meadowlands Development Commission for their staff support for field collections.

References

- Adams, S.M. and Angelovic, J.W. 1970. Assimilation of detritus and its associated bacteria by three species of estuarine animals. *Chesapeake Sci.* 11: 249–254.
- Allen, E., Fell, P., Peck, M., Gieg, J., Guthke, C. and Newkirk, M.D. 1994. Gut contents of common mummichogs, *Fundulus heteroclitus* L., in a restored impounded marsh and in natural reference marshes. *Estuaries* 17: 462–471.
- Barlocher, F. and Newell, S.Y. 1994. Phenolics and proteins affecting palatability of *Spartina* leaves to the gastropod *Littoraria irrorata*. *P.S.Z.N. 1: Marine Ecol.* 15: 65–75.
- Bertness, M.D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology* 66: 1042–1055.
- Bliss, D.E. 1956. Neurosecretion and the control of growth in a decapod crustacean. In: Wingstrand, K. (ed.), Bertil Hanström: Biological Papers in honor of his sixty-fifth birthday, Nov 20, 1956. pp. 56–75. Zoological Institute, Lund, Sweden.
- Burke, D.J., Weis, J.S. and Weis, P. 2000. Release of metals by the leaves of the salt marsh grasses *Spartina alterniflora* and *Phragmites australis*. *Estuarine, Coastal and Shelf Sci.* 51: 153–159.
- Buttery, B.R. and Lambert, J.M. 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlington Broad I. The competition mechanism. *J. Ecol.* 53: 163–181.
- Callahan, P. and Weis, J.S. 1983. Methylmercury effects on regeneration and ecdysis in fiddler crabs (*Uca pugnator*, *U. pugnax*) after short-term and chronic pre-exposure. *Arch. Env. Cont. Tox.* 12: 707–714.
- Currin, C.A., Newell, S.Y. and Paerl, H.W. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Marine Ecol. Prog. Ser.* 121: 99–116.

- Fell, P.E., Weissbach, S., Jones, D., Fallon, M., Zeppieri, J., Faison, E., Lennon, K., Newberry, K. and Reddington, L. 1998. Does invasion of oligohaline tidal marshes by reed grass, *Phragmites australis* (Cav.) Trin ex Steud., affect the availability of prey resources for the mummichog, *Fundulus heteroclitus* L.? J. Exp. Marine Biol. Ecol. 222: 59–77.
- Giblin, A.E., Bourg, A., Valiela, I. and Teal, J.M. 1980. Uptake and losses of heavy metals in sewage sludge by a New England salt marsh. Amer. J. Bot. 67: 1059–1068.
- Hatch, W.R. and Ott, W.L. 1968. Determination of sub-microgram quantities of mercury by atomic absorption spectrophotometry. Anal. Chem. 40: 2085–2087.
- Khan, A.T. and Weis, J.S. 1993. Bioaccumulation of heavy metals in two populations of mummichog (*Fundulus heteroclitus*). Bull. Env. Cont. Tox. 51: 1–5.
- Kneib, R.T. 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (L.) and *Fundulus luciae* (Baird). J. Exp. Marine Biol. Ecol. 83: 41–51.
- Levin, L.A., Talley, D. and Thayer, G. 1996. Succession of macrobenthos in a created salt marsh. Marine Ecol. Prog. Ser. 141: 67–82.
- Marinucci, A.C. 1982. Trophic importance of *Spartina alterniflora* production and decomposition to the marsh-estuarine ecosystem. Biol. Cons. 22: 35–58.
- Minello, T.J. and Webb, J. 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. Marine Ecol. Prog. Ser. 151: 65–179.
- Montague, C.L. 1980. A natural history of temperate Western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. Cont. Marine Sci. 23: 25–55.
- Newell, R.I.E. and Kreeger, D.A. 1998. Trophic Links in Salt Marshes: Relative Roles of Angiosperms and Microphytobenthos as Carbon Sources for Invertebrate Consumers. Presented at conference on Concepts and Controversies in Tidal Marsh Ecology, Vineland NJ, April 1998.
- Nomann, B.E. and Pennings, S.C. 1998. Fiddler crab-vegetation interactions in hypersaline habitats. J. Exp. Marine Biol. Ecol. 225: 53–68.
- Odum, E.P. and de la Cruz, A. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine system. In: Lauff, G.H. (ed.), Estuaries. pp. 383–388. AAAS Publication 83, Washington DC.
- Prinslow, T.E., Valiela, I. and Teal, J.M. 1974. The effect of detritus and ration size on the growth of *Fundulus heteroclitus* (L.). J. Exp. Marine Biol. Ecol. 16: 1–10.
- Rao, K.R. 1965. Studies on the influence of environmental factors on growth in the crab *Ocypode macrocera*, H. Milne Edwards. Crustaceana 11: 257–276.
- Rice, D.L. 1982. The detritus nitrogen problem: new observations and perspectives from organic geochemistry. Marine Ecol. Prog. Ser. 9: 153–162.
- Rietsma, C.S., Valiela, I. and Buchsbaum, R. 1988. Detrital chemistry, growth, and food choice in the salt marsh snail (*Melampus bidentatus*). Ecology 69: 261–266.
- Rooth, J. and Stevenson, C. 1998. Vertical Accretion in *Phragmites australis* and *Spartina* spp. Communities in Mid-Atlantic Marshes: Implications for Coastal Areas Threatened by Rising Sea-Level. Presented at conference on Concepts and Controversies in Tidal Marsh Ecology, Vineland NJ April 1998.
- Sacco, J.N., Seneca, E.D. and Wentworth, T.R. 1994. Infaunal community development of artificially established salt marshes in North Carolina. Estuaries 17: 489–500.
- Shisler, J.R. 1990. Creation and restoration of coastal wetlands of the northeastern United States. In: Kusler J. and Kentula, M.E. (eds.), Wetland Creation and Restoration: The Status of the Science. pp. 143–170. Island Press, Washington DC.
- Silberhorn, G.M. 1982. Common Plants of the mid-Atlantic Coast. A Field Guide. Johns Hopkins U. Press, Baltimore. 256 pp.
- Skinner, D.M. and Graham, D.E. 1972. Loss of limbs as a stimulus to ecdysis in Brachyura (true crabs). Biol. Bull. 143: 222–233.
- Wainright, S.C., Weinstein, M.P., Able, K.W. and Currin, C.A. 2000. Relative importance of benthic microalgae, phytoplankton, and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish marsh food webs. Marine Ecol. Prog. Ser. 200: 77–91.
- Weis, J.S. 1976a. The effects of environmental factors on limb regeneration and molting in fiddler crabs. Biol. Bull. 150: 152–162.
- Weis, J.S. 1976b. The effects of mercury, cadmium and lead salts on limb regeneration in the fiddler crab, *Uca pugnator*. Fishery Bull. 74: 464–467.
- Weis, J.S. 1977. Limb regeneration in fiddler crabs: species differences and effects of methylmercury. Biol. Bull. 152: 263–274.
- Weis, J.S., Cristini, A. and Rao, K.R. 1992. Effects of pollutants on molting and regeneration in Crustacea. Amer. Zool. 32: 495–500.
- Welsh, B. 1975. The role of grass shrimp, *Palaemonetes pugio* in a tidal marsh ecosystem. Ecology 56: 513–530.