

measured as the accumulation of  $\text{NH}_4^+$  in KCl extracts of the sediments through the incubation period (6,7). Rates for both DIN flux and mineralization were calculated from regression fit to the time courses, with standard error included.

The rates of  $\text{NH}_4^+$  increase were higher in the sediments from Childs River than in those from Sage Lot Pond (Fig. 1, top). In contrast, no  $\text{NO}_3^-$  was released (Fig. 1, top). The lack of nitrate flux indicates either low rates of nitrification or close coupling of nitrification and denitrification. The rate of DIN flux was about twice as high in the two Childs River cores ( $520 \pm 47$  and  $692 \pm 33 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ) as in the two Sage Lot Pond cores ( $298 \pm 20$  and  $226 \pm 16 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ) (Fig. 1, top, bottom). These values fall within previously measured ranges (8).

Production of ammonium occurred largely in the top layers of sediment (Fig. 1, middle), as found in other studies (7). The rates of mineralization, calculated from the regression line fit to the time course, were not different from the rates of flux in one core from each estuary (Fig. 1, bottom). However, rates of mineralization were higher than flux rates in the other core taken from each estuary. This difference represents a maximum rate of denitrification. We found denitrification rates of  $269 \pm 120$  and  $-48 \pm 146 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (an average of  $111 \pm 94 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ) in the Childs River cores, with rates of  $-148 \pm 149$  and  $227 \pm 119 \mu\text{mol N m}^{-2} \text{h}^{-1}$  (an average of  $79 \pm 95 \mu\text{mol N m}^{-2} \text{h}^{-1}$ ) for Sage Lot Pond.

These results suggest that N loading causes higher rates of N flux and mineralization. This would seem to imply that N

loading causes faster N cycling in estuary sediments. On average, however, denitrification does not appear to be occurring at a high enough rate in these sediments, during the season we sampled, to create differences measurable by this method. The rates of land-derived N loading seem relatively uncorrelated to rates of denitrification in estuary sediments.

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### Literature Cited

1. Vitousek, P. M. 1975. *Ecology* 75: 1861-1876.
2. Vitousek, P. M., and R. W. Howarth. 1991. *Biogeochemistry* 13: 87-115.
3. Fenchel, T., and T. H. Blackburn. 1979. Pp. 101-126 in *Bacteria and Mineral Cycling*. Academic Press, London.
4. Banta, G. T. 1992. *Decomposition and Nitrogen Cycling in Coastal Marine Sediments—Controls by Temperature, Organic Matter Inputs, and Benthic Macrofauna*. Ph.D. Thesis, Boston University. 278 pp.
5. Parsons, T. R., Y. Maita, and C. M. Lalli. 1984. Pp. 14-17 in *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford.
6. Rosenfeld, J. K. 1979. *Limnol. Oceanogr.* 24: 356-364.
7. Rosenfeld, J. K. 1981. *Am. J. Sci.* 281: 436-462.
8. LaMontagne, M. G. 1996. *Denitrification and the Stoichiometry of Organic Matter Degradation in Temperate Estuarine Sediments—Seasonal Pattern and Significance as a Nitrogen Sink*. Ph.D. Thesis, Boston University. 172 pp.

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## Effect of Eelgrass (*Zostera marina*) Density on the Feeding Efficiency of Mummichog (*Fundulus heteroclitus*)

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Eelgrass (*Zostera marina*) beds are important coastal nursery habitats for a variety of fishes. Eelgrass beds also provide food for many fish species by supporting an abundant and diverse benthic community (1). Nitrogen loading from anthropogenic sources alters eelgrass shoot density and may, in turn, affect the feeding efficiency of benthivorous fishes (2). For instance, decreases in eelgrass shoot densities significantly enhance the feeding efficiency of predators as well as the vulnerability of prey to predation (3). However, the dynamic response of fish feeding efficiency to varying eelgrass densities is not well known. This study examined the functional relationship between eelgrass shoot density and the feeding efficiency of the mummichog (*Fundulus heteroclitus*), a benthivorous fish. Natural eelgrass densities were studied in the field and, in the laboratory, eelgrass densities were manipulated.

Specimens of second-year (55-70 mm total length) *F. heteroclitus* were obtained by seining in subestuaries of Waquoit Bay, Massachusetts. All fish were starved for 24 h to ensure that the gut was completely empty and were given 30 min to acclimate to environmental conditions prior to use in experiments.

During the field experiment, the fish were allowed to feed on naturally occurring prey in habitats with different eelgrass shoot densities. Four experimental sites with contrasting shoot densities ( $0, 40 \pm 11.31, 80 \pm 14.79, \text{ and } 375 \pm 9.24$  shoots/ $\text{m}^2$ , mean  $\pm$  SE) were established in subestuaries of Waquoit Bay. Ten exclusion cages, each containing three *F. heteroclitus*, were placed on the substrate at random locations within each site. A cage consisted of a 500- $\mu\text{m}$ -mesh bag sealed to a 30-cm-diameter ring ( $0.07 \text{ m}^2$ ). After 2 h, the fish were retrieved from the cages and preserved with 95% ethanol in preparation for gut analysis. Preliminary experiments had indicated that prey were completely digested approximately 3 h after ingestion. Stomach contents were identified and enumerated under a dissecting microscope (50 $\times$ ). The average density of invertebrate prey was determined by collecting three random samples

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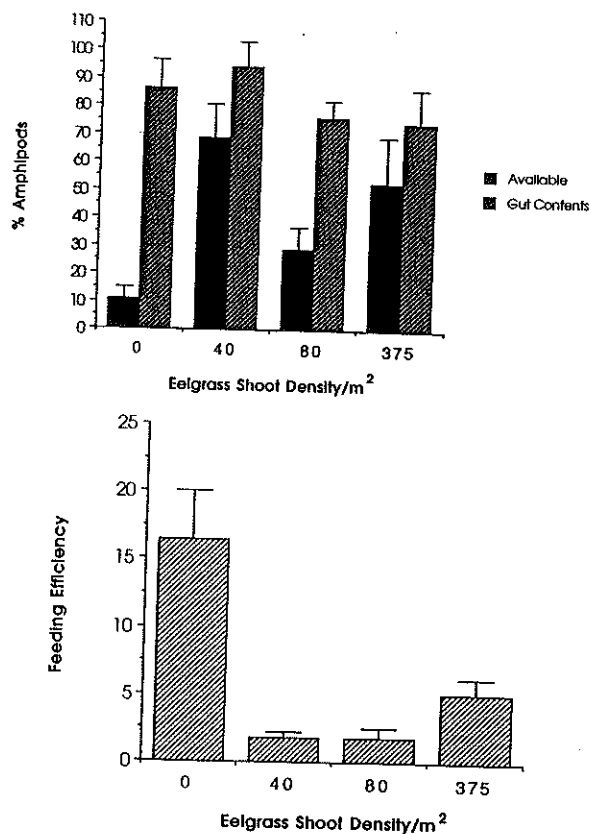
<sup>2</sup> Roger Williams University, Bristol, RI.

<sup>3</sup> Boston University Marine Program, MBL.

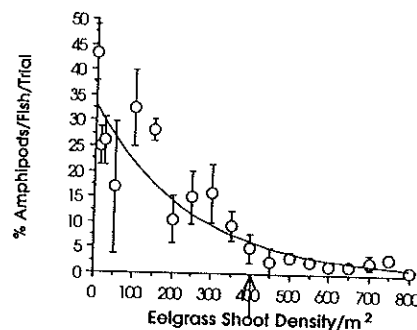
from each site with an Ekman grab (0.02 m<sup>2</sup>), and enumerating the organisms retained on a 250- $\mu$ m-mesh screen.

The parallel laboratory experiment was conducted using 33-l tanks with 19 densities (0-800 shoots per m<sup>2</sup>) of artificial eelgrass clusters ( $n = 3$ ). Artificial eelgrass was designed from green polypropylene and consisted of four blades per shoot. Eelgrass shoots were randomly attached to a 1-cm-mesh grid within each tank. The grids were covered with washed beach sand, and the tanks were filled with running seawater at ambient temperature ( $\sim 20^{\circ}\text{C}$ ). Prey were a mixture of amphipods (*Amphipoe* sp., *Cyanea* sp., *Microdeutopus* sp., and *Gammarus* sp.) that are commonly associated with eelgrass beds in Waquoit Bay. Two *F. heteroclitus* and 20 amphipods were placed in each tank. After 2 h, the fish were removed and preserved in 95% ethanol for gut analysis.

The field experiment revealed that amphipods were the preferred prey of mummichogs (74%–94% of total contents, mean = 85%) (Fig. 1 top). Other prey items were polychaetes (7%), snails (5%), and other crustaceans (3%). However, amphipods represented a lower percentage of total prey abundance (10%–65%, mean = 39.3%) in field collections than in the gut contents at all field sites. These data indicate that mummichogs selected amphipods regardless of total prey abundance. Feeding efficiency (*i.e.*, average number of amphipods consumed per fish



**Figure 1.** (Top) Percent occurrence of amphipods in total invertebrate sample and percent of amphipods found in *Fundulus heteroclitus* guts at sites with different eelgrass shoot densities. (bottom) Mean feeding efficiency of *F. heteroclitus* ( $\pm$ SE) (% amphipods consumed per fish per hour).



**Figure 2.** Mean feeding efficiency ( $\pm$ SE) as a function of eelgrass shoot density in laboratory experiments. Regression line shown is an exponential curve fit relating consumption rate ( $y$ ) to eelgrass density ( $D$ ): ( $y = 79.2 (\pm 1.6)e^{-0.0043(\pm 0.0004)D}$ ,  $r^2 = 0.880$ ,  $D =$  density constant). The arrow indicates an intermediate density beyond which consumption rate is largely unchanged. Trial duration = 2 h.

per h) was normalized to the number of amphipods available and was reported as a percentage of those available.

Mummichogs consumed virtually all (96%) the amphipods in the zero eelgrass treatment and might have consumed even larger quantities had more been available, since fish in other treatments were observed to have eaten up to 16 amphipods/h. An expected maximal consumption rate can be derived for the other treatments by multiplying the rate observed in the zero eelgrass treatment by the relative difference in prey availability between the zero eelgrass and other treatments. These expected values (expressed as number of amphipods consumed in 2 hours by three fish) are as follows: 96 consumed at 40 shoots, 40 consumed at 80 shoots, 67 consumed at 375 shoots. In each instance, fish consumed far fewer amphipods than expected: actual values were 12 amphipods consumed at 40 shoots, 4 consumed at 80 shoots, 18 consumed at 375 shoots. The discrepancy between expected and actual values implies that prey accessibility was diminished in treatments with eelgrass.

Feeding efficiency of *F. heteroclitus* was significantly higher (16.4% fish<sup>-1</sup> h<sup>-1</sup>) in the site with no eelgrass (Fig. 1 bottom) than in the sites with eelgrass ( $\sim 3\%$  fish<sup>-1</sup> h<sup>-1</sup>) (Tukey HSD,  $P < 0.01$ ). Feeding efficiency did not differ significantly among the three sites with eelgrass.

Laboratory experiments revealed that eelgrass shoot density had a significant effect on fish feeding efficiency ( $P < 0.0001$ , one-factor ANOVA) (Fig. 2). Feeding efficiency decreased sharply at lower densities (0 to  $\sim 400$  shoots/m<sup>2</sup>) and approached a constant value for densities higher than 400 shoots/m<sup>2</sup> (Fig. 2). The relationship between feeding efficiency and shoot density can be described as a decreasing exponential function ( $P < 0.0001$ , Fig. 2). This finding contrasts with that of Nelson (2), who found that the feeding efficiency of perch (*Perca fluviatilis*) was linearly related to habitat complexity.

Field and laboratory results both suggest that a simple linear relationship between feeding efficiency and habitat complexity does not exist for mummichog and its amphipod prey. Laboratory data show that there is a critical level of habitat complexity ( $\sim 400$  shoots/m<sup>2</sup>) beyond which feeding efficiency is low but unaffected by further increases in structural density. The feeding

response observed in the field experiment suggests that this critical density is lower. These differences could be due to other structural elements of the habitat that are not mimicked in the experimental tanks. At the field sites, the presence of macroalgae and a canopy of dead eelgrass leaves may have provided additional refuge for amphipods.

In laboratory trials at zero eelgrass density, mean amphipod consumption approached the maximum amount of prey available, possibly explaining the low amphipod abundance found in field sites with no eelgrass. Laboratory trials at 12 shoots/m<sup>2</sup> revealed a 42% decrease in the amphipod consumption rate from that at 0 shoots/m<sup>2</sup>. Field experiments indicated a 89% decrease in the amphipod consumption rate from the zero eelgrass habitat to that with 37 shoots/m<sup>2</sup>. These results suggest that relatively low habitat complexity provides refuge for amphipod prey.

Both field and laboratory experiments suggest that there is a critical habitat complexity at which the feeding efficiency of the fish is strongly affected. Many healthy eelgrass beds have higher shoot densities than the laboratory-determined critical value of 400 shoots/m<sup>2</sup>. Hence, fishes may have a limited feeding efficiency in dense eelgrass beds. However, fish abundance

in healthy eelgrass beds has been observed to be substantially greater than that in adjacent unvegetated habitats (Deegan *et al.*, unpubl. data). The high abundance of invertebrates in eelgrass beds offers greater food availability for fishes despite, and maybe because of, enhanced protection for individual prey (3, 4). Further field investigations should be conducted to clearly define the minimum shoot density necessary to sustain a stable and diverse eelgrass community.

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#### Literature Cited

1. Valiela, I., K. Foreman, M. LaMontagne *et al.* 1992. *Estuaries* 15: 443-457.
2. Nelson, W. G., and E. Bonsdorff. 1990. *J. Exp. Mar. Biol. Ecol.* 141: 183-194.
3. Heck, K. L., and T. A. Thoman. 1981. *J. Exp. Mar. Biol. Ecol.* 53: 125-134.
4. R. J. Orth, K. J. Heck, J. van Montfrans *et al.* 1984. *Estuaries* 7: 339-350.

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### Lead Concentration as an Indicator of Contamination History in Estuarine Sediments

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Exposure to lead has increased over the century, but has not been of concern until recently. Atmospheric lead concentration worldwide has increased 200-fold during the past 3000 years (1). The lead found in estuarine sediment cores comes from regional, large-scale atmospheric sources such as automobile exhaust and industry or from local sources such as gasoline outboard motors or street runoff (2). Thus, local sources, produced by human activities as coastal watersheds urbanize, will add to the more global atmospheric sources. Local urbanization of watersheds could further alter the accumulation of Pb in the sediments of receiving estuaries.

In this study we measured Pb concentrations in vertical sediment profiles of three estuaries of Waquoit Bay, Massachusetts, to (a) document the historical record of concentrations of Pb and (b) compare the effects of different degrees of watershed urbanization on the lead content of sediments in each estuary. Waquoit Bay comprises a series of estuaries with different histories of urbanization (3): Childs River has the most urbanized watershed, Quashnet River is moderately urbanized, and Sage Lot Pond is still in a near-pristine forested state.

We sampled two sediment cores (6.5 cm in diameter and 50 cm deep) from the three estuaries of Waquoit Bay. The cores were sectioned into 1-cm intervals for the first 10 cm and into 5-cm intervals for the remainder of the core. The sections were

oven dried at 60°C for 2-3 days and then ground with a mortar and pestle. For Pb analysis, weighed samples of sediment (0.18-0.22 g) were digested with 8 ml of HNO<sub>3</sub> and shaken overnight. The following day, 2.5 ml of HNO<sub>3</sub> was added to the shaken mixture and centrifuged for 1 min. The supernatant was decanted, and the Pb in the supernatant was measured by flame atomic absorption spectrometry. To learn more about possible biogeochemical controls of Pb in the sediment, we also measured other chemical properties, including % C, on a Perkin-Elmer 2400 CHN elemental analyzer (4). The sediments were also ashed at 490°C overnight.

The Pb profiles of the sediments (Fig. 1, top) show the changing history of Pb in the sediments of the three estuaries of Waquoit Bay. In general, Pb concentrations are low near the bottom of the profile and increase in the upper layers. The Pb depth profiles are similar to others from California (2) and New England (4). <sup>210</sup>Pb-dated cores taken in New England show increases in Pb concentrations around 1900 (4). In our samples, the Pb concentration in sediments of all three estuaries rose between 30 and 37 cm. This initial rise could signal a date of about 1930, determined on the basis of Pb and <sup>210</sup>Pb data from Connecticut lakes (P. Siver, University of Connecticut, pers. comm.). This agrees with the date of 1931-1932 estimated for the 30-37 cm layer in our cores by using the abundance of eelgrass seed coats (5).

We assumed that the rise in Pb concentration from 35-15 cm in the Childs River core (Fig. 1, top left), was of a similar origin, and that the rise continued into the 1970s when Pb concentrations

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