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Benthic community composition and faunal stable isotopic signatures differ across small spatial scales in a temperate estuary

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ABSTRACT

Anthropogenically induced changes to estuaries, including shifts from seagrass to macroalgae-dominated habitats, have led to concerns about the ability of estuaries to support fish and invertebrates. To assess differences in habitat quality of seagrass and macroalgae, we examined faunal community structure and consumer carbon assimilation in adjacent areas of seagrass, macroalgae, and bare sediments in Sage Lot Pond, Waquoit Bay, MA. Vegetation was an important factor controlling abundances, and both seagrass and macroalgae provided suitable habitat for a range of benthic fauna. Differences in consumption and assimilation of carbon of seagrass and macroalgal origin were demonstrated by shifts in $\delta^{13}C$ values of consumers between the seagrass meadow and adjacent macroalgal mats. Overall, consumers generally reflected incorporation of carbon from the dominant producers in the habitat where they were collected although macroalgae was an important carbon source for organisms in this study. These results revealed differences in carbon flow from producers to consumers across very small spatial scales (<10 m) within an estuary.

1. Introduction

The estuarine benthos is heterogeneous and may be made up of a mosaic of different habitats including bare sediment, macroalgal mats and seagrass meadows. Human activities on land have drastically altered this subtidal landscape. Eutrophication has fuelled proliferation of macroalgae, which limits light availability for seagrasses, and can ultimately lead to shifts from seagrass meadows to macroalgae-dominated habitats (McGlathery, 2001; Hauxwell et al., 2003). Changes to subtidal habitats have led to concerns about the ability of estuaries to support fish and invertebrates that are both ecologically and economically important (Valiela et al., 1992; Hauxwell et al., 1998; Hughes et al., 2002). Macrophytes typically support higher densities of fish and invertebrates, and have enhanced diversity and higher rates of survival compared to adjacent unvegetated habitats (Orth et al., 1984; Sogard and Able, 1991; Orth, 1992; Lee et al., 2001). Submerged vegetation plays important roles in providing structured and complex habitat as refugia against predation (Heck and Thoman, 1981; Heck and Wilson, 1987) and food (Orth et al., 1984; Connolly, 1997; Mattila et al., 1999; Heck et al., 2003). Macroalgae are a nutritious food source for many invertebrates and fish, whereas seagrass tends to be less palatable and enter the food web mainly as detritus (Cebrián, 1999). Seagrasses, however, support a diverse epiphyte community that is heavily grazed by small invertebrates (Orth and Van Montfrans, 1984; Neckles et al., 1993). Benthic producers differ in their abilities to support faunal communities. For example, in a temperate estuary, epibenthic fish and some crustaceans were more abundant in eelgrass (*Zostera marina*) meadows compared to sites where the macroalga *Ulva lactuca* was the dominant vegetation type, suggesting that macroalgal cover was not an equivalent substitute for eelgrass (Sogard and Able, 1991). Changes in benthic habitat structure and the availability of food and shelter can therefore alter the faunal community in both abundance and taxonomic composition.

Changes in the relative abundances and composition of benthic producers and consumers have implications for trophic relationships and benthic food webs (Fox et al., 2009; Olsen et al., 2011). To examine trophic relationships among organisms and the origins of organic matter incorporated into food webs, we can use stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) (Peterson and Fry,

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1987). Producer δ^{13}C depends largely on the degree of fractionation during carbon assimilation, which results in different ranges of δ^{13}C values for different marine macrophytes (Fry and Sherr, 1984; Hemminga and Mateo, 1996). In systems where the δ^{13}C values of macroalgae and seagrasses do not overlap, carbon isotopic analysis can establish their relative contribution to the benthic food web (Olsen et al., 2011). Nitrogen stable isotopes can be used to determine trophic levels of consumers (Peterson and Fry, 1987; McClelland et al., 1997) because of predictable trophic enrichment of ^{15}N (Minagawa and Wada, 1984). They can also be used to trace sources of N entering coastal and estuarine waters owing to heavier δ^{15}N values of producers and consumers after incorporation of N from human-derived wastewater (McClelland and Valiela, 1998a; Cole et al., 2004; Olsen et al., 2011).

Spatial differences in δ^{13}C and δ^{15}N of benthic fauna have been studied at different scales from 100s or 1000s of m (Jennings et al., 1997; Kanaya et al., 2007) to 10s of km (Thomas and Cahoon, 1993). Differences may reflect site-specificity in consumer diets or represent spatial variability in the stable isotopic signatures of the same food source. By establishing spatial patterns of stable isotope values in organic matter, producers, and consumers, we can examine carbon transport between habitats.

Guest et al. (2004) suggested that carbon movement in estuaries would fit one of three models. The coarsest model (>30 m) predicted large-scale movement of carbon and no pattern in C isotopic signatures across habitat boundaries. The intermediate-scale model (2–30 m) would have limited movement and assimilation of C among habitats, and isotopic signatures would follow a gradient as organic material of different origins were mixed across habitat boundaries. The third and finest scale (<2 m) would have almost no movement of C between habitats resulting in fauna with stable isotopic signatures characteristic of the habitat in which they live. In some aquatic systems, carbon sources appear to be distributed homogeneously, primarily through the movement of particulate organic matter (Connolly et al., 2005), and therefore fit the coarse model. Despite the fact that movement of carbon in aquatic systems is facilitated by water acting as a vector for particulate and dissolved organic matter (Carr et al., 2003), some studies have shown that carbon sources differ across relatively short distances and that animals assimilate carbon from local sources. Therefore, distinct isotopic signatures in consumers across short distances are produced, as described in the two finer-scale models (e.g. Marguillier et al., 1997; Deegan and Garritt, 1997; Bouillon et al., 2004; Guest et al., 2004; Richoux and Froneman, 2007).

In the present study, we examined differences in benthic faunal community structure and benthic food web relationships across small spatial scales (<10 m) within an estuary. We carried out this study in Sage Lot Pond, a shallow, temperate estuary located in Waquoit Bay, MA, USA. The benthos of the estuary is made up of a mosaic of eelgrass meadows, macroalgal canopies, and bare, unvegetated sediments. First, to assess how the presence of vegetation and macrophyte identity affected the structure of benthic faunal communities, we surveyed benthic organisms in areas of dense seagrass, macroalgal mats, and bare sediments. Second, to establish if food web linkages and carbon flows differed between macroalgal mats and adjacent seagrass habitats, we examined producer and consumer δ^{13}C and δ^{15}N values in each of these habitats.

2. Methods

2.1. Site description

Sage Lot Pond is a shallow (<2 m), temperate estuary located in Waquoit Bay on the south coast of Cape Cod, MA, USA (Fig. 1). The estuary has a relatively undeveloped watershed, mainly covered by a forested state park, and receives a low nitrogen load (11 kg N ha^{-1} y^{-1}). The estuary has low annual concentrations of dissolved inorganic nitrogen (0.3 ± 0.1 μM NO_3 and 2.1 ± 0.5 μM NH_4) (Holmes, 2008). Surrounding the estuary is a fringing salt marsh dominated by *Spartina alterniflora*. The benthic macrophyte community is characterized by *Z. marina* and macroalgae (Fox et al., 2008; Olsen et al., 2011). The average biomass of *Z. marina* within the seagrass meadow has been estimated to around 70–80 g dw m^{-2} (Hauxwell et al., 2003; Olsen unpublished data), but can reach up to 104 g dw m^{-2} within dense meadows (Olsen et al., 2011). Macroalgae are found interspersed within the seagrass meadow and in dense, mixed species mats adjacent to seagrass beds. The mean macroalgal biomass is relatively low (50 g dw m^{-2}), and the maximum biomass recorded was 430 g dw m^{-2} (Fox et al., 2008).

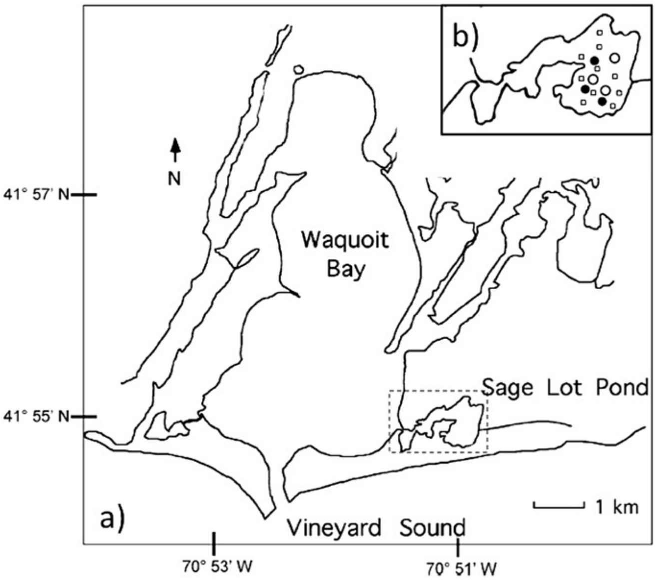

Fig. 1. a) Location of study site, Sage Lot Pond. Dashed line indicates area shown in insert top right corner. b) Detail of Sage Lot Pond showing locations of sampling stations for macroalgae (squares), bare sediment (black circles) and seagrass (open circles).

2.2. Sampling benthic faunal communities

To evaluate differences in benthic invertebrate communities among seagrass, macroalgal, and bare, unvegetated habitats, we collected benthic fauna from each of the three habitats in July–August 2006. Four sites were sampled within the seagrass meadow in areas without macroalgal aggregations. At each site, a 0.073 m^2 pvc-ring with an attached mesh bag (500 μm mesh) was lowered over the seagrass canopy, pushed into the sediment and a thin plate was inserted underneath (Deegan et al., 2002). The apparatus was then inverted and the sample, including the seagrass canopy and the top 3 cm of sediment, was captured inside the mesh bag. Four samples were collected from bare sediment using the same technique. Ten benthic samples were collected from within macroalgal canopies distributed throughout the estuary. Samples were collected approximately 10 m from the seagrass meadow using a 15 × 15 cm Ekman benthic grab. The collected material was rinsed through a 1 mm sieve to remove mud and brought back to the laboratory to be sorted. In a qualitative analysis, we determined that a 1 mm sieve sufficiently sampled the macrofauna in this system, since few additional macroorganisms were retained on a