Examining how landscapes influence benthic community assemblages in seagrass and mudflat habitats in southern Maine

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1. Introduction

Seagrass habitats provide important ecosystem functions such as producing and exporting organic carbon, cycling nutrients, stabilizing sediments and enhancing biodiversity (Orth et al., 2006). Seagrass beds provide nursery habitat for ecologically and economically important predatory crustacean and fish species, yet the seagrass beds also support higher densities of benthic invertebrate prey than adjacent mudflats (Mosknes, 2002; Orth, 1977; Rooker et al., 1998; Spanier and Almog-Shtayer, 1992; Summerson and Peterson, 1984; Thayer et al., 1978). The paradoxical overlap in these predators and their prey is partly explained by the refuge that seagrass beds afford both trophic levels. In particular, the root structure and grass blades reduce crustacean and fish consumption of benthic invertebrate prey inside the seagrass bed.

The spatial arrangement of habitats or landscape setting can largely influence ecological processes such as predation, competition and recruitment (Turner, 1989). In estuarine ecosystems, juvenile crustaceans and fish utilize seagrass beds during the day to avoid large-fish predators that are visually oriented, but forage in unvegetated mud adjacent to the seagrass bed at night (Summerson and Peterson, 1984). Thus the proximity of a mudflat to a seagrass bed likely influences the survival of infaunal invertebrates and community structure within the mudflat. Structured habitats such as seagrass beds provide refuge for intermediate predators and allow them to move more freely around estuaries, which can increase their foraging efficiency and reduce competitive interactions. For instance, Micheli and Peterson (1999) demonstrated that blue crabs, an important intermediate predator species in mid-Atlantic estuaries, use seagrass habitat as a corridor to move away from salt marshes and access prey on oyster reefs and the edge of mudflats while avoiding being consumed by fish and bird predators. In New England, seagrass beds have been noted as important lobster and juvenile cod habitat (Short et al., 2001), but the degree to which these predatory species affect prey community structure in adjacent mud flats is unclear.

The location of a seagrass bed within an estuary invariably will influence local physical conditions such as salinity, temperature, and flow regimes (Ward et al., 1984). These factors all can influence the extent to which species utilize different portions of the estuary. Thus, while seagrass beds are valued for serving as nursery habitat, the degree to which seagrass beds provide this function is ultimately influenced by the location of a bed within the greater context of the estuary (Fonseca and Bell, 1998). In coastal Maine, it is currently unclear whether seagrass beds located further up the estuary function as habitat for economically valuable marine fish and crustaceans (Jackson et al., 2001). Efforts to quantify natural variation in the
nursery function of seagrass habitat along such estuarine gradients will be valuable for coastal managers attempting to restore and protect seagrass habitat to maximize their value as nursery habitat.

We quantified the benthic communities in seagrass beds and mud flats in Casco Bay, Maine to better understand if seagrass in this region functions as nursery habitat and influences nearby prey. We hypothesized that seagrass beds support higher densities of juvenile fish and crustaceans because the beds provide refuge from their predators. Also, since the nursery function of seagrass beds is influenced by their location within the estuary, we hypothesized that seagrass beds near shore have higher fish and crustacean abundances because their predator populations increase further offshore. Last, we hypothesized that infaunal prey species are less abundant in mud flats close to seagrass beds than in mud flats further from seagrass beds because the juvenile fish and crustaceans would be more likely to forage closer to their nursery habitat. By quantifying the nursery function of pristine estuarine habitats in coastal Maine, this study provides necessary baseline information in the unfortunate event of a significant coastal disturbance. Efforts to quantify these functions are extremely important given that seagrass beds globally have been significantly reduced from anthropogenic activities over the past century (Orth et al., 2006; Waycott et al., 2009).

2. Materials and methods

2.1. Field survey

In the Gulf of Maine, Casco Bay contains ~146,000 acres of marine habitats, including over 10,000 acres of tidal flats and 7000 acres of seagrass habitat that offer prey resources for juvenile fish, birds, and large crustaceans (Casco Bay Estuary Project, 2003). To determine how habitat influences the distribution and abundance of fish in Casco Bay, ME, four coastal locations with sizable seagrass beds (Zostera marina) and mudflats were sampled (Fig. 1). From south to north, the locations were Mackworth Cove, Broad Cove, Maquoit Bay, and Middle Bay. At each location, samples were collected in four habitats: a subtidal seagrass bed (referred to as 'seagrass', GR), a subtidal mudflat adjacent to the seagrass bed ('near subtidal', NS), an intertidal mudflat near the seagrass bed (i.e., between seagrass bed and shore; 'near intertidal', NI), and an intertidal mudflat distant from the seagrass bed were sampled ('far intertidal', FI). Each site was sampled once every six weeks starting in the spring and ending in the fall of 2005.

Core sampling was conducted to assess the effects of site and habitat on resident infauna and epifauna. During July and September, six 20 cm deep soil cores were collected at each habitat that was sampled. Core sampling was conducted in the far intertidal only in the summer at Maquoit and Middle Bays. Each core was sieved on site and the resulting sample was preserved in formalin. After transfer to ethanol and staining with rose bengal for easier identification, organisms were picked, identified, counted, and weighed.

Trawl surveys were conducted in order to examine the effects of site and habitat on nekton communities. During all four seasons, a 3-m wide otter net lined with 2.5-cm stretch net was used to pull two non-overlapping 100-m long trawl tows through each habitat at each site. Distances were estimated using a handheld GARMIN GPS unit. Collected fish and a select number of crab and lobster guts were preserved for gut content analysis. All other species were identified and quantified before being released.

2.2. Statistical analyses

The quantity of organisms in each taxa group identified in all six cores collected at each site during each season was averaged. Crustaceans, Polychaetes, and Mollusks accounted for 98.8% of all individuals found in cores and were highly uncorrelated ($R^2$ was less than 0.025 for all 3 pairwise comparisons), thus we proceeded with individual ANOVAs for each taxonomic group rather than conducting a MANOVA. The effects of habitat (seagrass, near intertidal, and near subtidal) and site (Mackworth Cove, Broad Cove, Maquoit Bay, and Middle Bay) on the density of crustaceans (largely amphipods and isopods), mollusks (bivalves and gastropods), and polychaetes were analyzed using separate two-way ANOVAs for each taxonomic group. Cochran's test for heterogeneity of variances was performed on each dataset (Underwood, 1981). Those that violated Cochran's test were square-root transformed, and data were reanalyzed.

When the effect site was highly non-significant (i.e., $p > 0.25$), this factor was removed from the model and data were reanalyzed.

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**Fig. 1.** Location of research sites across Casco Bay, Maine, USA. Sites compared include: Maquoit Bay, Middle Bay, Broad Cove, and Mackworth Cove.
using a two-way ANOVA. Finally, the effects of site and habitat on the amount of seagrass and algae were analyzed using separate two-way ANOVAs.

3. Results

To examine patterns in predator and prey communities, we conducted trawl and core sampling in less disturbed sites throughout Casco Bay. Both site and habitat influenced the distribution and abundance of the benthi cs captured in core sampling efforts in 2005. Crustacean densities were 2 to 3 times greater in the seagrass habitat regardless of site, but did not differ in the other habitats (Fig. 2A, \( F_{3,14} = 4.0, p = 0.029 \); Fisher’s PLSD \( p < 0.05 \)). There was also a marginal effect of site on crustacean densities, with densities in Broad and Mackworth Coves greater than twice those in Maquoit and Middle Bays (Table 1, \( F_{3,14} = 2.4, p = 0.112 \)). Examination of isopods and amphipods separately suggested that both of these taxonomic groups were more abundant in seagrass habitat. Amphipods (54.0%; a mixture of ampeliscids, corophids, caprellids, and gammarids), isopods (27.3%; \textit{Edoda triloba} and \textit{Idotea balthica}), and decapods (17.3%; largely the grass shrimp \textit{Cragon septemspinosus}, hermit crabs, and the green crab \textit{Carcinus maenas}) contributed over 98% of total crustaceans counted.

Mollusk densities in core samples also differed as a function of both habitat and site (Fig. 2B, Table 1, significant interaction: \( F_{3,14} = 25.6, p < 0.0001 \)). In the northern part of Casco Bay at Maquoit and Middle Bays, bivalve densities per core were much higher at the far and near intertidal sites (i.e., \(-17–25\) vs. \(1–2\) per core). Meanwhile, mollusk densities in Broad Cove were 3 to 5 times greater in near subtidal and near intertidal habitats compared to seagrass and far intertidal habitats. Mollusk densities did not differ as a function of habitat in Mackworth Cove. Bivalves accounted for 90.9% of mollusks found in cores. Of the fourteen bivalve species identified, \textit{Macoma balthica} (45.2%), Tellinids (18.1%), \textit{Mya arenaria} (13.3%), \textit{Gemma gemma} (9.3%) and \textit{Mercenaria mercenaria} (5.2%) accounted for 91% of bivalves found in cores. \textit{M. balthica} was extremely abundant in the northern portions of Casco Bay at the far and near intertidal habitats. \textit{Mya arenaria} was also more abundant at the northern sites, whereas Tellinids were more common in the southern portion of Casco Bay. Of the six gastropod species identified, the most abundant were the eastern mudsnail \textit{Nassarius obsoletus} (56.8%) and the slipper shells \textit{Crepidula fornicata} (29.7%). Mudsnails were most common at Maquoit and Middle Bays, whereas slipper shells were randomly distributed throughout our sites in Casco Bay.

Polychaete densities in cores varied largely as a function of site independent of habitat (Fig. 2C, Table 1, \( F_{3,14} = 13.3, p = 0.0002 \)). In particular, densities were much higher in the southern portion of

| Invertebrates caught in trawls conducted in Casco Bay during 2005. Catch (#/100 m trawl) is presented by habitat (GR: Seagrass habitat; NI: Subtidal mud near seagrass; MI: intertidal mud near seagrass; and FI: intertidal mud habitat in isolation (i.e., >100 m) from seagrass habitat) and by sampling site (MW: Mackworth Cove; BC: Broad Cove; MQ: Maquoit Bay; and MI: Middle Bay). |

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Sample size: all habitats \( n = 8 \).
Trawl surveys resulted in the capture of 26,581 animals categorized as prey for nursery species (i.e., small fish, shrimp, and gastropods; Tables 1 and 2). Total prey caught in trawls varied with both site and habitat together (Fig. 3C, site x habitat interaction: $F_{9,48} = 2.0, p = 0.058$). Total prey required fourth root transformation to remove heterogeneity of variances. The density of total prey was greater in the near subtidal and seagrass habitats. This result was more pronounced in the northern portion of Casco Bay. The four most common prey included gastropods (74.2% of catch), hermit crabs (14.3%), Crangon shrimp (8.2%), and sticklebacks (2.6%). Examination of gastropod results revealed that there was no difference among habitats in the south, but gastropods were more abundant in the near subtidal and seagrass habitats in the north at Maquoit and Middle Bays. Hermit crabs were more abundant in the far intertidal at Mackworth Cove, whereas they were more abundant in the near subtidal and seagrass habitats in the other three habitats.
Cragon shrimp and sticklebacks were consistently more abundant in the near subtidal and seagrass habitats across all four habitats. Sticklebacks were also much more abundant in the northern sites.

Both habitat and site affected the amount of seagrass present in trawl surveys in Casco Bay. In particular, seagrass was three times more prevalent in the northern than in the southern sites ($F_{3,48} = 3.5; p = 0.022$). Seagrass was also more prevalent in the near subtidal and seagrass habitats ($F_{3,48} = 5.8; p = 0.002$). Meanwhile, algal biomass did not vary as a function of site, habitat or their interaction ($p > 0.19$ for all effects).

4. Discussion

Our results indicate that seagrass beds are inhabited by mobile fish and crustacean species, and thus likely serve as important nursery-habitat in Casco Bay. Furthermore, the presence of seagrass habitat affected the abundance and diversity of local fish and invertebrate communities in estuaries. Of the habitats investigated, seagrass beds contained the highest abundance of crustaceans and polychaetes (Fig. 2A and C), suggesting that seagrass beds are important biogenic habitat refuges for intermediate predator and basal prey species. This is consistent with previous findings, which have demonstrated the prominent role seagrass beds play as nurseries for multiple species (Heck and Thoman, 1984), as an important habitat for many infaunal invertebrates (Irlandi, 1994; Micheli, 1997; Summerson and Peterson, 1984), and as a source of prey and refuge for predators such as juvenile fish, crabs, and lobsters (Clark et al., 1999; Gotoeitas et al., 1997; Micheli and Peterson, 1999).

Invertebrate prey (e.g. small fish, shrimp, and mollusk) species collected in trawl surveys were much more abundant in and around (near subtidal habitat) seagrass beds than away from seagrass beds at the sites located in the northern portion of Casco Bay (MI and MQ) where crustacean densities were extremely low. Meanwhile, trawl surveys indicated that prey generally were much lower and differences among habitats were less pronounced at the southern (MW and BC) sites in Casco Bay where predatory crustaceans were more prevalent. Native crustaceans were especially common along the edges of and within seagrass habitat at these sites. Mollusk densities quantified in core sampling efforts were also lower (BC) or did not differ (MW) in seagrass beds relative to other habitats at the southern sites. Collectively, these results are counter to previous seagrass studies that suggest seagrass beds provide refuge for mollusks and other prey species. However, our results align with previous studies indicating that seagrass beds are important habitat for intermediate predators such as crustaceans that likely forage within or around seagrass beds on prey species, but the degree to which they provide this function is positively correlated with their proximity to the coast.

Lobsters were only captured at the southern sites, and 73.9% of all cancer crabs captured were located at the southern two sites. In general, lobster catches were surprisingly low given that these seagrass beds are reported to be important shedding grounds (local lobster fishermen, pers. comm.). Whether predation is high on juvenile lobsters in Casco Bay deserves further attention, especially since native predators such as striped bass and cod (to a lesser extent) have recovered locally. Striped bass have been shown to be important consumers of lobsters elsewhere in New England (Nelson et al., 2003).

In contrast to habitat use patterns of native predators, the green crab was most abundant in the far intertidal mud flat habitat. The green crabs were also the only predator common in all four habitat types, suggesting that the crabs were less reliant on being protected by seagrass beds. One explanation for this could be that as an invasive species, green crabs have fewer natural predators than the codfish and lobster (Grosholz and Ruiz, 1995), which are native to the Gulf of Maine. The generalist habitat and diet capabilities of green crabs may also enable persistence across the broader range of sites (Snyder and Evans, 2006). In general, this pattern of green crab presence across sites corresponds with the phenomenon of increases in the likelihood of invasive species establishment and proliferation post-disturbance (Byers, 2002; Hobbs and Huenneke, 1992).

Our results generally suggest that while the direct habitat connection between mudflats and seagrass beds is important to predator and prey populations, the larger matrix of extended mudflats around seagrass beds also mediates community structures and habitat use. This finding is consistent with other habitat based studies that have shown the importance of habitat connectivity and multi-habitat spaces on ecosystem function and community structure (Grabowski et al., 2005; Micheli and Peterson, 1999). Measures of existing community patterns across vulnerable habitats generate effective preparation through establishing valuable baseline data for assessing future impacts on community dynamics and ecosystem functions (Loreau et al., 2001).

Acknowledgments

We would like to thank Kiersa Benson, Sarah Hauke, Curt Brown, and Julian Gaudette for assistance in the field and lab on this project. Brendan Ready and Rob Bernat provided vessel support in the field. Support for this project was provided by the Maine Oil Spill Advisory Council (grant no. UM-S583).

References


