



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

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ABSTRACT

Structured habitats in estuaries provided by seagrass beds are valued as nurseries for economically valuable and ecologically important fish and crustacean species, explaining why much effort has been expended to restore and protect these habitats. Data on ecological dynamics in seagrass beds are necessary for assessing natural variability and understanding potential impacts from future anthropogenic disturbances. We quantified benthic communities in marine mud flat and seagrass bed habitats throughout Casco Bay, Maine, USA to examine nursery functions. We hypothesized that mobile fish and crustaceans are more abundant in seagrass habitat because this habitat provides refuge, and that mobile predators that use eelgrass beds reduce populations of infaunal prey in adjacent mud flats. Our results indicate seagrass beds are important nursery habitat, and that seagrass presence in an embayment affects the abundance and diversity of local fish and invertebrate communities. Specifically, fish and native mobile crustacean populations were generally most abundant in and adjacent to seagrass beds among habitats studied. Our results also suggest that the proximity of seagrass to mudflats potentially influences community structure within mudflats by affecting predator access. Human activities that result in the degradation of seagrass beds and other biogenic habitats will likely influence community structure and impair ecosystem function in estuaries.

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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 mud flats (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 mud flats 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

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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

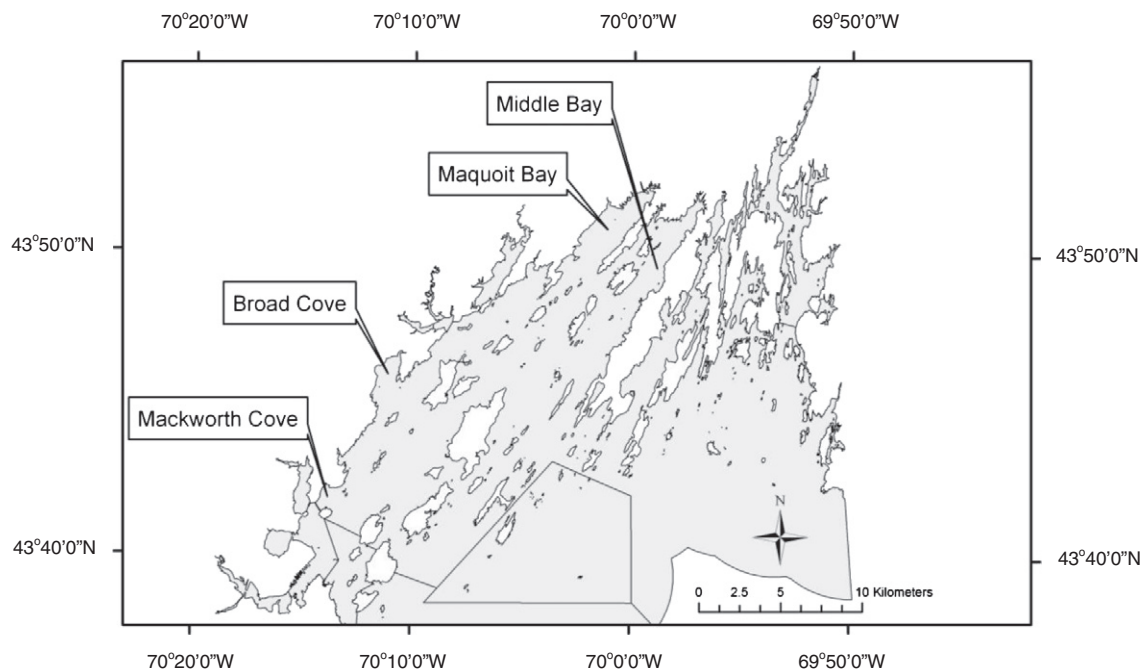


Fig. 1. Location of research sites across Casco Bay, Maine, USA. Sites compared include: Maquoit Bay, Middle Bay, Broad Cove, and Mackworth Cove.

(Underwood, 1981). Fisher's PLSD post-hoc tests were conducted for significant main effects and when the interaction between site and habitat was significant.

The quantity of organisms in each taxa group identified in both trawls collected at each site during each season was averaged. The effects of site (all 4) and habitat (seagrass, near intertidal, near subtidal, and far intertidal) on the density of nursery fish (four-bearded rockling, cunner, sculpins, winter flounder, white hake, and tom cod) and crustaceans (lobsters and crabs) were analyzed using separate two-way ANOVAs. The effects of site and habitat on the density of prey species including alewives, mummichogs, pipefish, hermit crabs, *Crangon* shrimp, gastropods, and sticklebacks were also analyzed

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 benthos 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%; *Edotea triloba* and *Idotea balthica*), and decapods (17.3%; largely the grass shrimp *Crangon septemspinosa*, hermit crabs, and the green crab *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: $F_{9,14} = 25.6$, $p < 0.0001$). 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, *Macoma balthica* (45.2%), Tellinids (18.1%), *Mya arenaria* (13.3%), *Gemma gemma* (9.3%) and *Mercenaria mercenaria* (5.2%) accounted for 91% of bivalves found in cores. *M. balthica* was extremely abundant in the northern portions of Casco Bay at the far and near intertidal habitats. *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 *Nassarius obsoletus* (56.8%) and the slipper shells *Crepidula* spp. (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

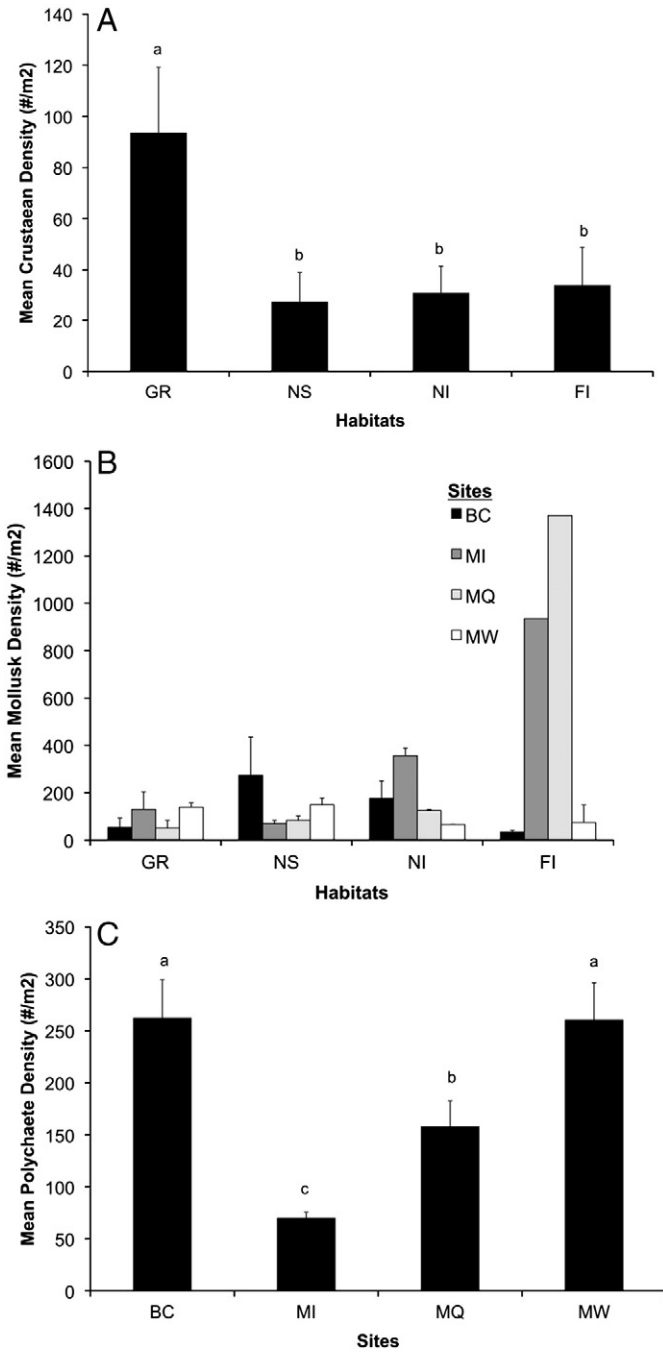


Fig. 2. Mean density of crustaceans (A), mollusks (B), and polychaetes (C) from core sampling across habitats and sites. Seagrass beds (GR) had higher density of crustaceans than other habitats; mollusks were most abundant in the far intertidal (FI) habitat at Middle (MI) and Maquoit (MQ) Bays; and, polychaete densities were highest at Broad (BC) and Mackworth (MW) Coves.

Table 1

Invertebrates caught in trawls conducted in Casco Bay during 2005. Catch (#/100 m trawl) is presented by habitat (GR: Seagrass habitat; NS: Subtidal mud near seagrass; NI: 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).

Categories	Habitats				Sites			
	GR	NS	NI	FI	MW	BC	MQ	MI
Asteroidae	2.09	1.06	0.03	0.09	1.40	0.58	0.59	0.28
Bivalve	214.91	0.31	0.22	0.66	0.73	171.85	0.00	0.38
Decapod	86.34	89.90	2.50	3.81	5.13	4.95	133.23	37.70
Gastropod	247.84	297.48	10.66	19.59	4.23	3.50	76.60	490.16
Peracarida	1.66	0.13	0.00	0.00	1.33	0.00	0.06	0.06
Invertebrate total	552.85	388.88	13.41	24.16	12.80	180.88	210.49	528.57
Invertebrate richness	5	5	4	4	5	4	4	5

Sample size: all habitats n = 8.

Casco Bay at Broad and Mackworth Coves. Polychaetes from 16 different families that grouped into 6 orders were identified in cores. The Order Scolecida were most abundant (44.1%), followed by the following orders: Phyllodocida (28.5%), Spionida (10.3), Terebellida (7.8%), Eunicida (3.2%), and (Sabellida 0.7%).

Sixteen species of fish were captured in trawl surveys conducted in shallow subtidal and intertidal habitats throughout Casco Bay in 2005 (Table 2). The biomass of fish was typically greatest in seagrass and near subtidal habitats. Exceptions to this pattern were largely driven by the occasional capture of larger fish. For instance, in the early summer, 2 juvenile striped bass were captured in the far intertidal habitat at Maquoit Bay, explaining why this site contained the greatest biomass. Fish biomass was lowest in the early summer. Surprisingly, Atlantic cod (*Gadus morhua*) were not present in any of the seagrass beds sampled in this study.

Nursery fish caught in trawls differed as a function of both site and habitat (Fig. 3A, site x habitat interaction: $F_{9,48} = 2.0$, $p = 0.058$). Nursery fish were largely absent from the northern 2 sites, and were most abundant in Mackworth Cove, where they were mostly found in seagrass and near subtidal habitats. Meanwhile, nursery crustaceans varied with site (Fig. 3B, $F_{3,48} = 21.1$, $p < 0.0001$) and marginally with habitat ($F_{3,48} = 2.4$, $p = 0.071$) independently. Crustaceans were more abundant in the southern sites, and were slightly more abundant in the seagrass and near subtidal habitats.

Tomcod, lobsters and crab species were three common nursery species that utilize habitats differently in Casco Bay (Tables 1 and 2). In particular, lobsters and tomcod were present only in seagrass and the adjacent mudflat, whereas crabs were found in all four habitats and were most abundant in the far intertidal mudflats. Green crabs were common in all habitats, but were most abundant at the near subtidal mudflats adjacent to seagrass patches and at far intertidal mudflats.

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: $F_{9,48} = 3.9$, $p = 0.001$). 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

Table 2

Fish caught in trawls conducted in Casco Bay during 2005. Catch (g/100 m trawl) is presented by habitat (GR: seagrass habitat; NS: subtidal mud near seagrass; NI: 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).

Species	Mean biomass (g/100 m trawl)							
	Habitats				Sites			
	GR	NS	NI	FI	MW	BC	MQ	MI
Three-spine stickleback	0.42	0.06	0.05	0.00	0.08	0.04	0.37	0.05
Four-spine stickleback	2.11	6.05	0.08	1.04	0.12	0.04	7.87	1.21
Nine-spine stickleback	0.14	0.04	0.01	0.29	0.00	0.00	0.43	0.04
Four-bearded rockling	0.07	0.00	0.00	0.00	0.06	0.00	0.00	0.00
Atlantic alewife	0.21	0.00	0.00	0.00	0.00	0.00	0.21	0.00
Atlantic silverside	0.12	3.51	0.16	0.03	0.14	0.00	0.03	3.62
Cunner	0.00	0.05	0.00	0.00	0.00	0.04	0.00	0.00
Lumpfish	0.14	1.16	0.07	0.00	1.00	0.10	0.00	0.00
Grubby	1.02	0.39	0.08	0.00	0.71	0.16	0.42	0.00
Shorthorn sculpin	0.65	0.00	0.00	0.00	0.00	0.00	0.65	0.00
Striped bass	0.00	0.00	0.00	21.25	0.00	0.00	21.25	0.00
Mummichog	0.03	2.07	0.00	0.30	0.00	0.00	0.27	2.12
Pipefish	0.72	0.11	0.05	0.00	0.09	0.06	0.50	0.26
Tomcod	0.00	0.47	0.00	0.00	0.38	0.00	0.00	0.00
White hake	0.81	0.00	0.00	0.00	0.65	0.00	0.00	0.00
Winter flounder	1.69	0.76	2.41	1.55	0.70	5.34	1.09	0.78
Fish total	8.12	14.66	2.91	24.46	3.91	5.78	33.08	8.09
Fish richness	13	11	8	6	10	7	11	7

Sample size: all habitats n = 8.

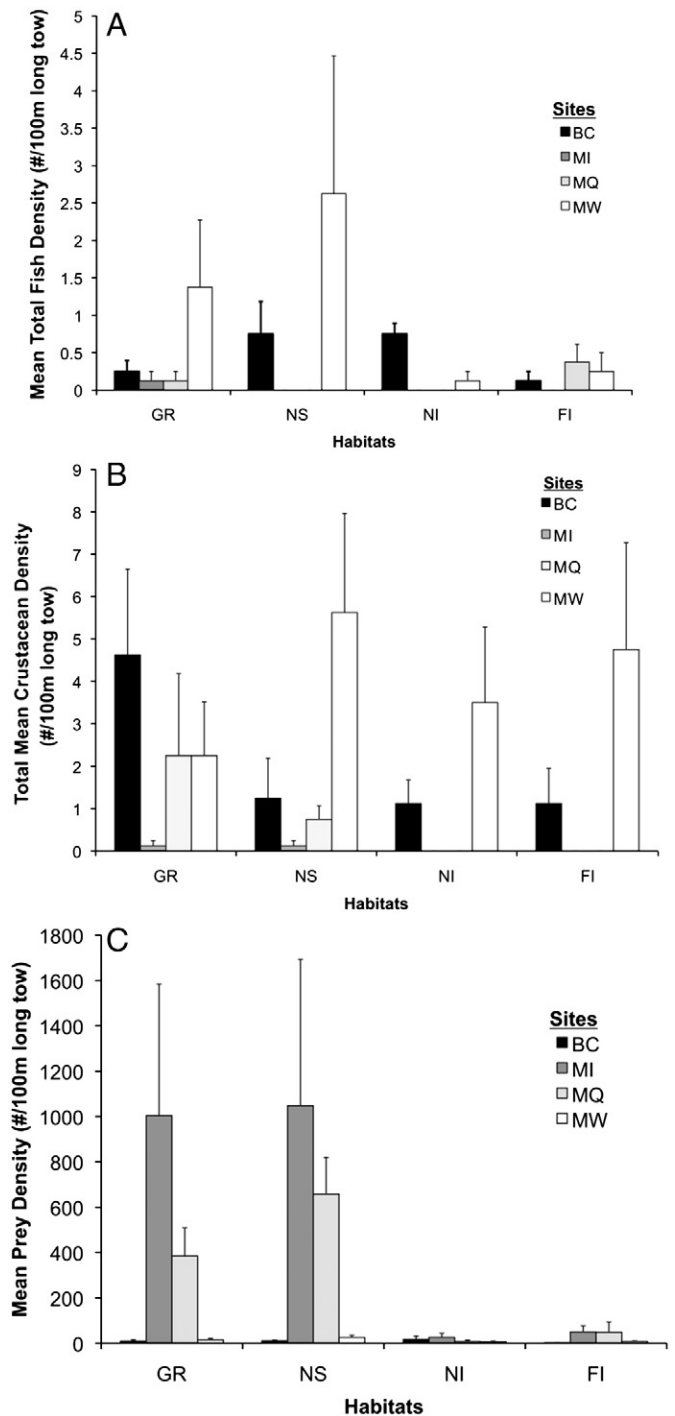


Fig. 3. Mean density of fish (A), crustaceans (B), and combined prey species (C) from trawls across habitats and sites. Fish were most abundant in seagrass (GR) and near subtidal (NS) habitats in Mackworth Cove (MW); crustacean densities were also high in seagrass and at Mackworth Cove; combined prey species were most dense in seagrass and near subtidal habitats.

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, whereas they were more abundant in the near subtidal and seagrass habitats in the other three habitats.

Crangon 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; Gotceitas 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).

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