Vol. 306: 223–231, 2006 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published January 11

Influence of biogenic habitat on the recruitment and distribution of a subtidal xanthid crab

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ABSTRACT: Biogenic habitat can structure marine communities by serving as both a complex substrate and food source for adult and recruiting organisms. We investigated the role played by biogenic habitats (*Mytilus edulis* and *Crepidula* spp. beds) in influencing the subtidal distribution (kilometers scale) of the mud crab *Dyspanopeus sayi* in Narragansett Bay, New England (USA). In field surveys, *D. sayi* were 1 to 2 orders of magnitude more abundant on *M. edulis* and *Crepidula* spp. beds than at sites lacking these habitats, and a laboratory experiment confirmed that *D. sayi* will consume both of these species. In a field-based, substrate-choice experiment, modules containing rocks had higher *D. sayi* recruit densities than those containing *M. edulis* or *Crepidula* spp. This indicates that structural complexity of those biogenic substrates, rather than their availability as prey, is the primary factor influencing patterns of *D. sayi* recruitment. Densities of recruit and adult *D. sayi* on recruitment modules were higher at bare sites than at sites with biogenic habitat, where modules represented islands of structure in otherwise simple habitat. This suggests small-scale habitat selection by *D. sayi*. Adult *D. sayi* occupied modules indiscriminately at bare sites, but exhibited a preference for modules containing mussels at sites with biogenic habitats. The importance of structure for adult and recruit *D. sayi*, reinforced by adults' response to prey presence, likely explains this organism's association with hard, biogenic habitats in the studied system.

KEY WORDS: Biogenic habitat · Structural complexity · Bottom-up control · Recruitment · *Mytilus edulis* · *Dyspanopeus sayi* · *Crepidula* spp. · Narragansett Bay

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INTRODUCTION

Biogenic substrates, such as bivalve reefs, worm tubes, sea grass, coral, and algae, are thought to play a major role in structuring subtidal benthic marine communities for 2 primary reasons. First, the organisms composing these substrates frequently serve as a food source for predators and grazers, making them an important factor in bottom-up trophic control of ecosystems (Menge 1992, Witman et al. 2003). Biogenic components can affect species composition in a community by attracting adult consumers from surrounding areas (Bologna & Heck 1999, Witman et al. 2003), increasing growth and reproduction of local species (Inglis & Gust 2003, Witman et al. 2003), and influencing recruitment of organisms that settle in response to food cues (Crisp 1974). Second, biogenic habitats can modify the local environment in ways that have profound effects on organisms living in, on, and around their structures, and appropriately have been termed foundation species (sensu Dayton 1972, Bruno & Bertness 2001) and ecosystem engineers (sensu Jones et al. 1997). Biogenic components can stabilize underlying substrates against erosion, can influence flow, local sedimentary composition, and infaunal community structure, and in many cases can provide a hard substrate in an otherwise soft-sediment environment, facilitating the presence of sessile, encrusting, or epifaunal organisms (see Reise 2002 for review). Furthermore, the structural complexity afforded by these habitats can serve as a refuge for many small and young vagile organisms against predation (Witman 1985), disturbance (Woodin 1978), and environmental stresses (Bertness et al. 1999). Biogenic substrates

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thereby serve as a nursery habitat for many marine species (e.g. Carr 1994, Heck et al. 1997). In addition, biomass (de Montaudouin & Sauriau 1999), species richness (see Reise 2002 for review), and density (Woodin 1978, Orth et al. 1984, Witman 1985) of marine fauna tend to be much greater in biogenic habitats than on adjacent bare substrate. For example, Witman (1985) found densities of infauna inside *Modiolus* mussel beds to be 150 to 850% greater than on substratum outside the beds, and similar values have been reported for seagrass beds vs. unvegetated habitats (see Orth et al. 1984 for review). Although the roles of both structure and prey availability in influencing the recruitment and success of many benthic organisms are well documented, the relative importance of these 2 factors is often undifferentiated in studies of biogenic habitats (Heck et al. 1997).

In 2001 and 2002 we conducted a series of surveys and experiments to investigate the effect of biogenic habitats on the recruitment and distribution of *Dyspanopeus sayi* across sites at a scale of kilometers. *D. sayi* is a common mud crab in estuaries of the northwest Atlantic, and is frequently associated with biogenic habitats, such as bivalve beds (McDermott & Flower 1952, Ryan 1956), gastropod beds (Stickney & Stringer 1957), eelgrass beds (Strieb et al. 1995), worm tubes (Heck & Hambrook 1991), and sponges (McDermott & Flower 1952). This crab consumes organisms composing, or associated with, these habitats, such as oysters (Ryan 1956), scallops (Strieb et al. 1995), barnacles (McDermott & Flower 1952), and polychaetes (Sagasti et al. 2001), and is small enough that both juveniles and adults of this species may find shelter in these substrates from predators, including fish (McDermott & Flower 1952) and crabs (Heck & Hambrook 1991). In this study, we document the association of *D. sayi* with biogenic habitats formed by mussel and gastropod beds in a shallow New England estuary, and investigate the potential role of those mollusks as complex habitat and prey resource in generating that association.

MATERIALS AND METHODS

Study organisms. *Dyspanopeus sayi* (Smith, 1869) is a xanthid crab that occurs subtidally along the Atlantic coast of North America between Prince Edward Island, Canada, and eastern Florida, USA, and is the most common mud crab from Delaware Bay north (McDermot & Flower 1952, Gosner 1978). *D. sayi* is thought to be important to commercial fisheries, as predation by this species may significantly impact young oyster, clam, and scallop populations important to the shellfishing industry (Landers 1954, Day & Lawton 1988, Streib et al. 1995), and because the crab may serve as an alternate host for the sporozoan oyster parasite *Nematopsis legeri* (Ryan 1956). Understanding the factors influencing *D. sayi* distribution is currently important, because in recent decades this crab has appeared as a highly successful invasive on the coast of Wales, UK (Naylor 1960) and in the Venetian Lagoon, Italy (Mizzan 1993).

Blue mussels *Mytilus edulis* are lamellibranch mollusks that inhabit littoral and shallow sublittoral zones worldwide (Gosling 1992), where they can form large, dense beds with attributes typical of a foundation species. *M. edulis* are a primary food source for many benthic organisms including sea stars, snails, fishes, and crabs (see Suchanek 1986 for review). *M. edulis* beds are also habitat for a variety of infauna for which they serve as an attachment surface and as a refuge against predation, disturbance, and environmental stress (Suchanek 1986). *M. edulis* beds occur on both rocky and soft substrates, making them an important habitat and food supply in a range of marine ecosystems.

Crepidula fornicata are calyptraeid gastropods that occur naturally along the Atlantic coast of the United States and Canada, and are now a common invasive throughout Europe, along the Pacific coast of the United States, and in South America and Japan (Walne 1956, Blanchard 1997). *C. fornicata* are sedentary suspension feeders that have a stacked, protrandrous mating system, which causes them to occur in chains of many individuals and, in some areas, to form extensive, dense beds (e.g. de Montaudouin & Sauriau 1999). The shells of living and deceased individuals provide a hard surface for other sessile marine organisms to settle upon (Stickney & Stringer 1957), including a related species, *C. plana*. Less attention has been paid to the ecological role of *Crepidula* spp. beds than to that of other subtidal biogenic habitats such as kelp forests, coral reefs, and bivalve beds. However, we have observed sea stars feeding on *Crepidula* snails, and *Crepidula* spp. beds tend to occur in soft-bottom areas devoid of other biogenic structures, where the beds can support rich faunal assemblages and high relative biomass (Stickney & Stringer 1957, de Montaudouin & Sauriau 1999).

Study sites. Narragansett Bay is a shallow estuary (average depth 8.3 m) located in Massachusetts and Rhode Island, USA (Pilson 1985). We quantified *Dyspanopeus sayi* abundances at 16 shallow subtidal (4 to 5 m below mean low water) sites in central Narragansett Bay, 10 of which consisted of biogenic substrate (*Mytilus edulis* or *Crepidula* spp. beds) overlying soft-sediment, and 6 of which were bare soft-sediment sites (Fig. 1). The 10 biogenic substrate sites were all that occurred in the study area of central Narragansett Bay within our predetermined depth range, and we chose bare sites that were interspersed among bio-

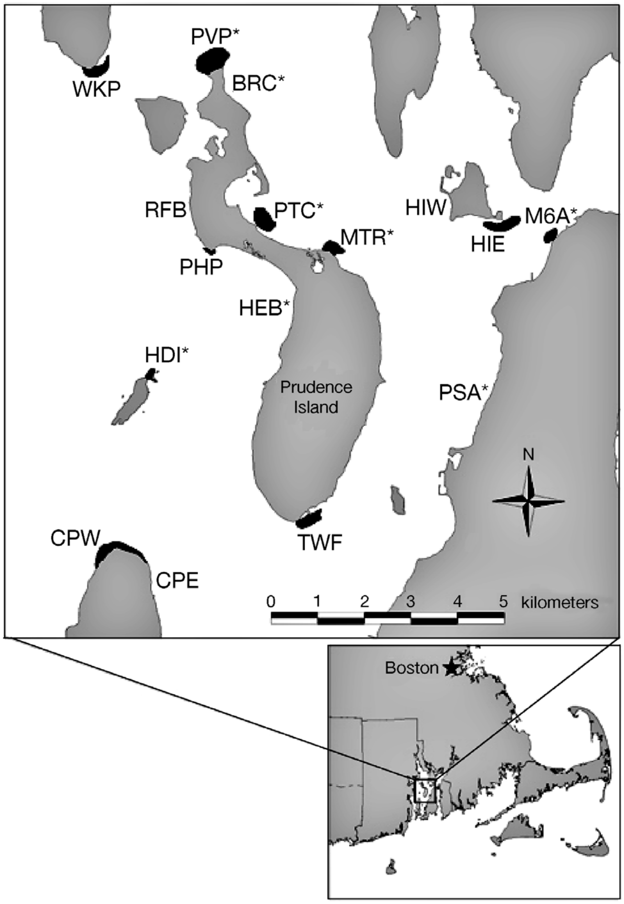

Fig. 1. Map of study sites in Narragansett Bay, New England, USA (41.2° N, 71.2° W) (white: water; gray: land; black: biogenic substrate [*Mytilus edulis* beds with the exception of PTC where black represents a *Crepidula* spp. bed]). Surveys were conducted at all 16 sites, and recruitment experiments were conducted at the 8 sites indicated by asterisks (BRC: Bear Cove; CPE: Conanicut Point East; CPW: Conanicut Point West; HDI: Hope and Despair Islands; HEB: Home Beach; HIE: Hog Island East; HIW: Hog Island West; M6A: Marker 6A; MTR: Mount Tom Rock; PHP: Pine Hill Point; PSA: Portsmouth Abbey; PTC: Potter's Cove; PVP: Providence Pt.; RFB: Rossi Farm Backside; TWF: T-Wharf; WKP: Warwick Point)

genic sites to avoid bias from large-scale factors. The 8 most accessible sites were used for recruitment experiments, of which 5 had biogenic substrate and 3 did not. Because sites were selected according to the above criteria, they were treated as fixed factors in analyses of variance (ANOVA) (below). We strived for generality by working at a large number of sites.

Surveys. Visual surveys to assess adult *Dyspanopeus sayi* abundances were conducted with SCUBA in spring 2001, fall 2001, and fall 2002. At each site and in each sampling period, all *D. sayi* along each of 5 replicate randomly placed, 15 × 2 m transects were counted by 2 divers swimming side by side, each covering one-half of the transect width. Differences in *D. sayi* densities between types of habitat (biogenic vs. bare substrate) were analyzed by 2-factor nested ANOVAs (site nested within habitat) performed on log-transformed [$\log_{10}(x + 1)$] data using JMP Version 4.0.4 analytical software. Each sampling period was analyzed separately, because we were not interested in detecting changes in *D. sayi* abundance through time, only whether the difference between biogenic and bare substrate was qualitatively similar.

Laboratory predation experiment. Neither the consumption of mytilids nor gastropods has been reported for *Dyspanopeus sayi*. Therefore, to test whether the species composing the biogenic habitats in our study were potential prey items of *D. sayi*, we conducted a laboratory-based predation experiment using *Mytilus edulis* and 2 species of *Crepidula* snails (*C. fornicata* and *C. plana*). *M. edulis* and *Crepidula* spp. individuals measuring <10 mm in length were collected from 3 sites in Narragansett Bay in April 2002. *D. sayi* measuring between 5 and 18 mm were collected from these same locations. *M. edulis* and *Crepidula* spp. were sorted into six 1 mm size classes between 3 and 9 mm, and each *M. edulis* was paired with a *Crepidula* spp. individual from its same size class. The smallest pair was presented to the smallest *D. sayi*, the second smallest pair to the second smallest *D. sayi*, and so on. One *D. sayi* (starved for the previous 24 h), and a pair of prey items were placed in a 15 cm diameter bowl with 250 ml of seawater from the collection sites. Thirty replicates were run simultaneously in the laboratory for 7 d, and the prey item(s) consumed in each replicate within each 24 h period were recorded. Consumed prey were not replaced. The cumulative proportion of *D. sayi* that had consumed *M. edulis*, *Crepidula* spp., or both, was calculated at the end of the experiment.

Substrate experiment. *Mytilus edulis* and *Crepidula* spp. can form complex habitats and are also potential prey for *Dyspanopeus sayi*. The relative influence of these roles on the recruitment and distribution of *D. sayi* was assessed by comparing rates of recruitment to, and affinity of adults for, recruitment modules containing different substrates. Enclosed plastic mesh modules (laterally flattened cylinders 23 × 12 × 5 cm; 7 × 7 mm mesh size), containing 0.5 l of either biogenic substrate (*M. edulis* or *Crepidula* spp.), which represented both food and structure, or geologic substrate (rocks), which represented structure only, were deployed on the bay floor at each site (n = 5 treatment^{-1} site^{-1}). Substrates were checked to be free of crabs and macrofauna before placing in modules. The mesh size was found to allow recruitment to substrate within modules, and to prevent adults from entering (adults were never found inside modules). *D. sayi* spawns throughout the summer, and recruitment occurs throughout the late summer and fall (Swartz 1972), so modules were deployed at the experimental sites for 6 wk starting in early September 2002. At the end of the deployment period, modules were carefully collected, placed directly in re-sealable plastic bags while underwater, and frozen until laboratory analysis. Care was taken to eliminate loss of recruits from within modules, and loss of adults clinging to the outside. Since modules were sampled at the end of the 6 wk experimental period, recruitment into the modules (minus early post-settlement mortality) was measured.

Thawed samples were examined in the laboratory. Crabs were removed with forceps, and all associated material was strained through 75 µm mesh and examined under a microscope for smaller individuals. All xanthid crabs in and on modules were identified as *Dyspanopeus sayi* (Williams 1984, Weiss 1995). *D. sayi* carapace width was measured between the bases of the 5th anterolateral spines, and carapace measurements were used to construct a size-frequency distribution for *D. sayi* in order to distinguish crabs that had recruited directly into the modules ('recruits'), from older crabs that had walked onto the modules ('adults'). These distributions tended to be bi- or polymodal, indicating distinct cohorts of crabs at each site, and size divisions between presumed cohorts (~5.5 mm carapace width) coincided with evidence of sexual differentiation (recorded during laboratory analysis) and life-history descriptions for this organism (Ryan 1956, Swartz 1972). We therefore defined individuals with carapace width <5.5 mm as 'recruits' and those with carapace width >5.5 mm as 'adults'. Total *D. sayi* recruit and adult densities from modules were analyzed for differences between habitat (biogenic vs. bare site) and experimental treatment (*Mytilus edulis* vs. *Crepidula* spp. vs. rocks) by 3-factor ANOVAs (substrate treatment, habitat type, and site nested within habitat) performed on log-transformed $[\log_{10}(x + 1)]$ data using JMP Version 4.0.4 software. Post-hoc analyses were performed using Tukey's tests of honestly significant difference (HSD).

RESULTS

Surveys

Average *Dyspanopeus sayi* densities were significantly higher, by a factor of 24 to 47, at sites with biogenic substrates than at bare sites in all 3 sampling periods ($p < 0.0001$; Fig. 2, Table 1). *D. sayi* densities varied temporally, with lowest densities observed in the spring, and higher densities in fall 2001 than in fall 2002. There was also variation in *D. sayi* densities among sites of a given habitat regime (biogenic or bare) within a given season. Two or three sites with biogenic substrate typically had significantly more crabs than all other sites, and these high-density sites were not necessarily the same season to season (Table 2).

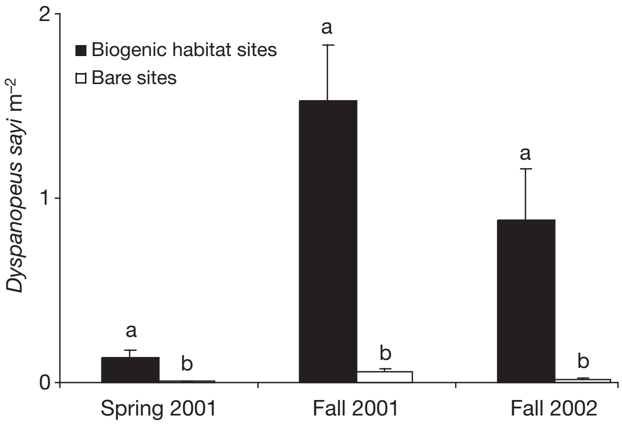

Fig. 2. *Dyspanopeus sayi*. Densities quantified in surveys at sites with and without biogenic substrate (*Mytilus edulis* or *Crepidula* spp. beds) in Narragansett Bay over 3 sampling periods. Error bars represent 1 standard error from the mean derived from pooled data. Bars with different letters above them are significantly different from one another (within sampling periods). ANOVA summary statistics are presented in Table 1

Table 1. *Dyspanopeus sayi*. Summary of ANOVA analyses

Source	df	*F*	p
Densities in surveys			
Spring 2001			
Habitat	1, 64	53.20	<0.0001
Site (habitat)	14, 64	42.26	<0.0001
Fall 2001			
Habitat	1, 64	153.53	<0.0001
Site (habitat)	14, 64	28.56	<0.0001
Fall 2002			
Habitat	1, 64	102.35	<0.0001
Site (habitat)	14, 64	43.87	<0.0001
Recruitment in substrate experiment			
Substrate treatment	2	39.77	<0.0001
Habitat	1	246.56	<0.0001
Site (habitat)	6	65.55	<0.0001
Habitat × substrate	2	2.45	0.09
Adults in substrate experiment			
Substrate treatment	2	5.62	<0.01
Habitat	1	20.21	<0.0001
Site (habitat)	6	3.72	<0.01
Habitat × substrate	2	2.24	0.11

Laboratory predation experiment

Dyspanopeus sayi consumed both *Mytilus edulis* and *Crepidula* spp. (Table 3). *D. sayi* paired with prey items that were proportionally much smaller than themselves generally consumed both prey items. Only very large crabs (>16 mm) consumed *M. edulis* or *Crepidula* spp. larger than about 7 mm. This size is consistent with that reported in the literature for bivalve prey of *D. sayi* (Landers 1954, Swartz 1972), and this size limitation probably explains why a high proportion of crabs in the experiment consumed neither prey item.

Substrate experiment

Habitat type (biogenic vs. bare site) had a significant effect on densities of *Dyspanopeus sayi* recruits in modules ($p < 0.0001$; Fig. 3A, Table 1). For a given treatment (*Mytilus edulis*, *Crepidula* spp., or rocks), modules at bare sites had approximately twice as many *D. sayi* recruits as did modules at sites with biogenic habitats (Fig. 3A). Recruit densities were also significantly affected by module treatment (*M. edulis*, *Crepidula* spp., or rocks) ($p < 0.0001$; Fig. 3A, Table 1). Post-hoc analysis revealed that in both habitat types (biogenic and bare sites), *D. sayi* recruitment was as high or higher in modules containing rocks than in those containing *M. edulis.* Modules with *M. edulis*, in turn, had higher recruitment than *Crepidula* spp. (Fig. 3A).

Densities of adult *Dyspanopeus sayi* present on modules were significantly affected by habitat type ($p < 0.0001$; Fig. 3B, Table 1), but this pattern varied across substrate treatments (Fig. 3B). Modules containing *Crepidula* spp. and rocks had approximately twice as many adult *D. sayi* at bare sites as did their counterparts at sites with biogenic habitat, but adult densities on modules containing *Mytilus edulis* were similar in both habitats. Substrate treatment (*M. edulis*, *Crepidula* spp., or rocks) had a significant effect on the densities of adult *D. sayi* present on modules ($p < 0.01$), but this trend varied by habitat type — post-hoc analysis revealed a difference among treatments only at bare sites where modules with *Mytilus* had approximately double the number of adults as the modules with either *Crepidula* spp. or rocks (Fig. 3B).

For all modules pooled across site habitat types and substrate treatments ($n = 120$), there was no correlation detected between the number of recruits and number of adults per module ($R^2 = 0.0065$, $p = 0.38$).

Table 3. *Dyspanopeus sayi.* Proportion of individuals consuming *Mytilus edulis* and *Crepidula* spp. in a laboratory-based binary prey choice experiment

Prey consumed	Proportion of crabs
Mytilus edulis only	0.17
Crepidula spp. only	0.07
Both	0.33
Neither	0.43

Table 2. *Dyspanopeus sayi.* Abundance of *D. sayi* by site and habitat type for each of 3 surveys. Data presented as individuals m^{-2} (mean ± 1 SE) (for site abbreviations, see Fig. 1)

Site	Substrate	Spring 2001	Fall 2001	Fall 2002
BRC	Bare	0.01 ± 0.01	0.15 ± 0.08	0.01 ± 0.01
CPE	Bare	0	0	0.01 ± 0.01
HEB	Bare	0	0.04 ± 0.03	0.03 ± 0.02
HIW	Bare	0.01 ± 0.01	0.01 ± 0.01	0
PSA	Bare	0.01 ± 0.01	0.15 ± 0.06	0.07 ± 0.05
RFB	Bare	0	0	0
CPW	Mussel bed	0	0	0.01 ± 0.01
HDI	Mussel bed	0	2.70 ± 0.94	4.66 ± 1.73
HIE	Mussel bed	0.01 ± 0.01	1.49 ± 0.53	0
M6A	Mussel bed	0.91 ± 0.12	6.75 ± 0.47	0.15 ± 0.06
MTR	Mussel bed	0	0.48 ± 0.31	0.03 ± 0.02
PHP	Mussel bed	0	1.94 ± 0.12	0
PTC	*Crepidula* bed	0.4 ± 0.14	1.75 ± 0.16	3.12 ± 0.17
PVP	Mussel bed	0.04 ± 0.02	0.16 ± 0.10	0.01 ± 0.01
TWF	Mussel bed	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
WKP	Mussel bed	0	0.02 ± 0.01	0.01 ± 0.01

DISCUSSION

Both adult and recruit *Dyspanopeus sayi* were present at all experimental sites in this study, demonstrating both that competent larvae of this species arrive and settle at all sites in our study and that adult *D. sayi* are capable of surviving in these areas. However, the high densities of *D. sayi* on *Mytilus edulis* and *Crepidula* spp. beds, as observed in our surveys, indicate that these habitats represent an advantage for this species, resulting in differential recruitment, survival, or migration of *D. sayi* at sites with different substrate regimes. Though greater larval supply to sites with biogenic habitat could also explain the distribution pattern (i.e. larval limitation at bare sites), this seems unlikely given the high rates of recruitment to experimental modules at bare sites.

The biogenic habitats in this study had the potential to influence *Dyspanopeus sayi* distribution through both trophic and structural processes. First, our labo-

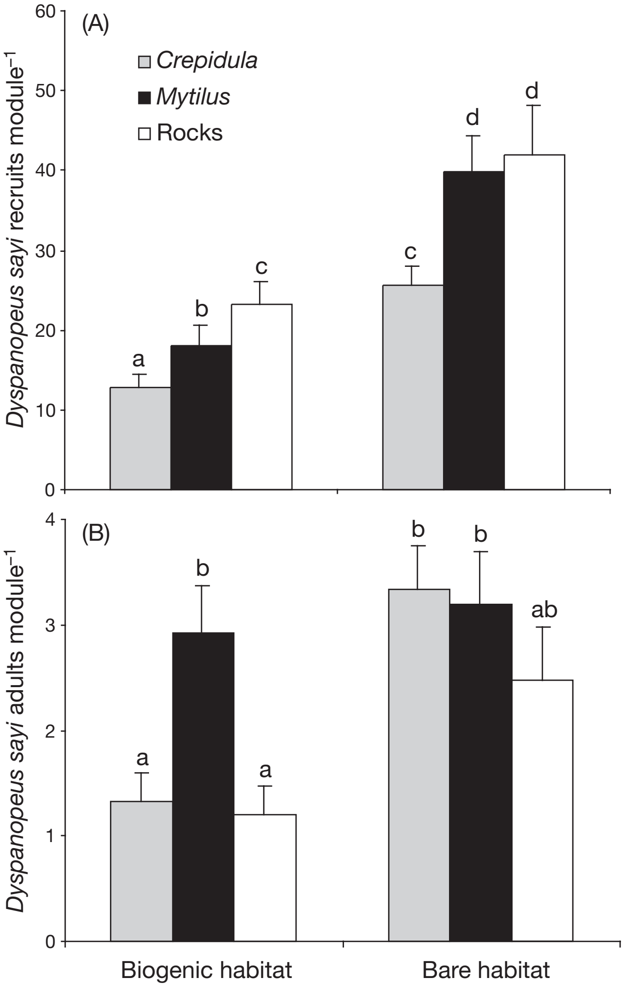

Fig. 3. *Dyspanopeus sayi*. Densities of: (A) recruits in and (B) adults on recruitment modules containing either *Mytilus edulis*, *Crepidula* spp., or rocks after a 6-wk deployment in fall 2002. Error bars represent 1 standard error from the mean derived from pooled data. Bars with different letters above them are significantly different from one another. ANOVA summary statistics are presented in Table 1

ratory predation experiment revealed that adult *D. sayi* will consume small individuals of both *Mytilus edulis* and *Crepidula* spp. Both *M. edulis* (Peterson 1984) and *Crepidula* spp. (McGee & Targett 1989) preferentially recruit to conspecifics, and therefore established *M. edulis* and *Crepidula* spp. beds should represent a predictable seasonal supply of young individuals of their respective species, and thus a predictable food source for *D. sayi*. Second, the *M. edulis* and *Crepidula* spp. beds in our study constituted distinct, highly complex structures on the otherwise soft, flat bottom of Narragansett Bay, and thus could serve as a prey refuge from potential predators of *D. sayi*, including fish and crabs, that were present in the study areas (A. Altieri unpubl. data).

Dyspanopeus sayi recruited in much higher densities to modules at bare sites than to those at sites comprising biogenic habitat. However, survey results suggest that recruit densities on modules are not representative of naturally occurring recruitment levels. When placed at bare sites, modules acted as islands of complex substrate, and *D. sayi* larvae may have selected for this heterogeneity within sites, settling disproportionately often in modules at bare sites and more evenly over the bay floor at sites with biogenic habitat. This indicates that structure is highly important in determining recruitment in this species, and suggests a capacity for active habitat selection over small scales (meters) by settling *D. sayi* larvae. The possibility that relative recruitment rates to structurally complex collectors varies as a function of surrounding habitat complexity could confound interpretation of benthic settlement and recruitment studies of organisms for whom habitat structure is a determining factor of recruitment, as these studies frequently use such collectors as a way to standardize substrate between sites (e.g. Rabalais et al. 1995, Palma et al. 1999).

The primacy of structure over food cues produced by *Mytilus edulis* and *Crepidula* spp. in influencing recruitment of *Dyspanopeus sayi* was supported by results from the substrate experiment. In both habitat types (biogenic and bare sites), overall *D. sayi* recruitment was as high or higher in modules containing rocks than in those containing *M. edulis* and *Crepidula* spp. Modules with *M. edulis*, in turn, had higher recruitment than *Crepidula* spp. These relative differences in recruitment rates may have been due to differences in degrees of complexity between the substrate types. Though all modules started with the same volume of similar-sized substrate units, *Crepidula* spp., which experienced the lowest levels of *D. sayi* recruitment, stacked to form large masses, leaving little interstitial space. Rocks remained unconsolidated, and mussels clumped to an intermediate extent, by attaching to one another at their anterior end by byssal threads. This potential explanation is supported by the findings of Dittel et al. (1996), who found predation risk for megalopae of the xanthid *Panopeus herbstii* to correlate negatively with increasing habitat complexity, and suggest higher recruitment into a predation refuge, as has been demonstrated in other decapod species including crabs (Moksnes 2002) and lobsters (Wahle & Steneck 1992).

Adult *Dyspanopeus sayi*, like recruits, were present in greater overall densities on modules at bare sites than on modules at sites with biogenic habitat. Although they were too large to pass through the mesh, adults at these sites may have been attracted to modules because they represented a structure on the otherwise featureless substrate, and therefore a potential refuge. At bare sites, modules of all treatments had similar densities of adult *D. sayi*, which suggests that in these areas the structure of the module, rather than its contents, was of primary importance. At sites with biogenic habitat, however, adult *D. sayi* displayed a strong preference for modules containing *Mytilus edulis* over those containing either *Crepidula* spp. or rocks, demonstrating that, in structurally complex environments, adult *D. sayi* can exhibit a preference based on potential prey items. Since many crab species are cannibalistic, it is possible that the abundance of adult *D. sayi* (potential predators) on modules and recruits (potential prey) within modules had an effect on one another. However, we did not detect a correlation between the 2 factors, indicating that the experimental substrate within modules and the habitat type of a given site were the primary determinants of abundance.

These results indicate that the relative importance of prey and structure attributes of biogenic habitats may be somewhat different for different life stages of *Dyspanopeus sayi*, with the prey component increasing in importance as crabs age. This shift, from structure being of primary importance for settling larvae to food playing a secondary role in influencing adult behavior, might reflect different cues employed by larvae and adult crabs, or a lower susceptibility of older crabs to predation (Seitz et al. 2003). Many motile aquatic macrofauna spend their juvenile stages sheltering in structurally heterogeneous nursery habitats before venturing out into higher risk but food-rich areas (see Werner & Gilliam 1984 for review), and adult decapods of many species migrate over long distances in search of food, shelter, or mates (Palma et al. 1999). Biogenic habitats, such as the 2 investigated in this study, can fulfill both structural and trophic functions for some species. Association with such a habitat may be particularly advantageous in relatively small organisms, such as *D. sayi*, which do not attain a size refuge from predation and the post-settlement dispersal potential of which is likely limited. It is also possible that structurally complex habitats (regardless of whether they are biogenic or not) may attract or passively collect food such as detritus and microfauna for young organisms.

Aside from their value as a food resource, complex biogenic habitats have other unique attributes relative to geologic substrates. While many of the structural benefits of biogenic habitats, i.e. stability, firmness, and complexity, are also afforded by some hard geologic substrates (e.g. creviced rock faces or cobble beds), the latter constitute a small portion of underwater substrate and are largely limited to the nearshore and intertidal (Woodin 1978). Biogenic structures, on the other hand, can provide complex habitat in areas that would otherwise be devoid of hard surfaces or structural complexity, such as estuaries, lagoons, and the deep sea floor (Bergquist et al. 2003). Moreover, these habitats can change physical location in response to long-term ecological change, and can be introduced into novel systems. For example, invasive biogenic structures such as *Crepidula* beds (de Montaudouin & Sauriau 1999) and polychaete colonies (Luppi & Bas 2002) are now causing profound changes in species composition and community structure in areas that formerly had no analogous habitat.

Conversely, biogenic habitats are susceptible to disturbance and destruction in ways that non-living substrates are not. In our study system of Narragansett Bay, for example, some *Mytilus edulis* beds have been eliminated by episodes of hypoxia (Altieri & Witman in press). Other biogenic habitats, including kelp forests, eelgrass beds, oyster reefs, and coral, are also in jeopardy from anthropogenic impacts around the globe (Jackson et al. 2001). As is suggested by this study, the loss of such biogenic structures, which serve important ecosystem functions as both food and habitat for many organisms, would have concomitant impacts on marine communities.

SUMMARY

Biogenic habitats are particularly important in soft-sediment areas, where both food resources and complex physical structure can be scarce. *Dyspanopeus sayi* in the soft-bottomed, Narragansett Bay subtidal are concentrated in hard, biogenic habitats composed of *Mytilus edulis* and *Crepidula* spp., and the complex structure afforded by these beds appears to be the primary cause of this pattern. Habitat complexity of *M. edulis* and *Crepidula* spp., rather than their availability as a prey resource, appears to be the determining factor of high *D. sayi* recruitment to biogenic structures, and such complexity continues to strongly affect behavior in adults of this species. However, the pattern is likely reinforced by the retention of adult *D. sayi* within the biogenic habitats in response to their potential as a prey resource. This study underscores the dependence of marine populations on biogenic habitats, and reveals in the case of *D. sayi* the mechanisms by which these habitats structure populations on the scale of kilometers within an ecosystem.

Acknowledgements. We thank A. Aver, E. Brazer, C. Lay, M. Parikh, and C. Siddon for field and laboratory assistance. M. Bertness and B. Silliman enabled transportation to and from study sites. K. Bromberg and L. Carlson generated Fig. 1. Earlier versions of this paper were improved through comments by J. Byrnes, J. Palardy, K. Heck, and 3 anonymous reviewers. Lodging during portions of this project was provided by the Narragansett Bay National Estuarine Research Reserve, P. Constantine, J. Resnick-Ault, and D. and E. Morse. Funding for this project was provided by a Brown University Undergraduate Teaching and Research Assistantship (UTRA) grant to E.L.L., a NOAA NERRS Graduate Research Fellowship to A.H.A., a Rhode Island Sea Grant to A.H.A. and J.D.W., and a grant from the Andrew W. Mellon Foundation to J.D.W.

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Editorial responsibility: Kenneth Heck (Contributing Editor), Dauphin Island, Alabama, USA

Submitted: November 4, 2004; Accepted: July 8, 2005
Proofs received from author(s): December 4, 2005