Estuarine Vegetated Habitats as Corridors for Predator Movements

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FIORENZA MICHELI* AND CHARLES H. PETERSON

University of North Carolina at Chapel Hill, Institute of Marine Sciences, 3431 Arendell Street, Morehead City, NC 28557, U.S.A.

Abstract: *The spatial proximity of one habitat to another can strongly influence population and community dynamics. We investigated whether the proximity of intertidal oyster reefs to vegetated estuarine habitats, salt marshes, and seagrass beds, affects the abundance and community structure of benthic macroinvertebrates on reefs and predator-prey interactions between mobile predators and bivalves living on reefs. Benthic macroinvertebrate abundance was highest on reefs spatially separated from salt marshes. Macroinvertebrate species richness was highest on reefs separated from both salt marshes and seagrass beds. Comparisons of predation on juvenile bivalves transplanted to reefs for 7–12 days indicated that survivorship of clams was greatest on reefs spatially separated from both salt marshes and seagrass beds, whereas reef proximity to vegetated habitats did not affect the survivorship of oysters. The foraging behavior of blue crabs may explain patterns of macroinvertebrate abundance and clam survivorship among reefs with different proximity to vegetated habitats. In experiments conducted in 30-m² field enclosures, blue crabs had higher predation rates on hard clams transplanted onto artificial reefs adjacent to salt marshes or seagrass beds than on reefs separated from both habitats by unvegetated sand bottom. Thus, vegetated habitats appeared to act as corridors by facilitating the access of blue crabs to oyster reefs and enhancing the intensity of blue crab predation. Such an understanding of the effects of landscape characteristics of estuarine habitats on their value as habitats for estuarine organisms can be used to predict the consequences of habitat fragmentation on ecosystem function and to improve strategies for habitat and species conservation and restoration.*

Hábitats Estuarinos Vegetados como Corredores para Movimientos de Depredadores

Resumen: *La proximidad espacial de un hábitat con otro puede influenciar fuertemente las dinámicas poblacionales y de comunidades. Investigamos si la proximidad de arrecífes intermareas de ostiones con respecto a hábitats estuarinos con vegetación, ciénegas y pastizales marinos afecta la abundancia y la estructura comunitaria de macroinvertebrados bénticos en los arrecífes y las interacciones depredador-presa entre depredadores móbiles y bivalbos que habitan los arrecífes. La abundancia de macroinvertebrados bénticos fue mayor en arrecífes espacialmente separados de las ciénegas. La riqueza de especies de macroinvertebrados fue mayor en arrecífes separados tanto de las ciénegas como de los pastizales marinos. Las comparaciones de depredación sobre bivalbos juveniles transplantados a los arrecífes por 7–12 días, indican que la supervivencia de almejas fué mayor en arrecifes espacialmente separados tanto de los ciénegas, como de las camas de pastos marinos, mientras que los arrecífes cercanos a hábitats con vegetación no afectó la supervivencia de ostiones. La conducta de forrajeo de el cangrejo azul podría explicar los patrones de abundancia de macroinvertebrados y la supervivencia de almejas entre arrecifes con diferente cercanía a los hábitats con vegetación. En experimentos conducidos en encierros de campo de 30 m², los cangrejos azules tuvieron la tasa de depredación más alta en almejas transplantadas hacia arrecefes adyacentes a ciénegas o pastos marinos que en los arrecifes separados de ambios tipos de vegetación por fondos arenosos. Por lo tanto, los hábitats con vegetación aparentemente actúan como corredores facilitando el acceso de los cangrejos azules a los arrecifes de ostiones e incrementando la intensidad depredadora del cangrejo azul. El entendimiento de los*

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efectos sobre las características del paisaje en hábitats estuarinos y sobre el valor de los hábitats para los organismos estuarinos puede ser utilizado para predecir las consecuencias de la fragmentación del hábitat en la función del ecosistema y para mejorar estrategias para la conservación y restauración de hábitats y especies.

Introduction

Some of the most important theoretical contributions in ecology have implicitly (island biogeography: MacArthur & Wilson 1967; metapopulation theory: Hanski & Gilpin 1997) or explicitly (landscape ecology: Forman & Godron 1986) involved effects of the spatial configuration of habitat patches on population and community dynamics. Despite ongoing debate over the generality and usefulness of concepts generated by these theories in an applied context, they have been widely applied in terrestrial systems to developing species-recovery plans, designing nature reserves, and predicting the consequences of habitat fragmentation (Simberloff 1988; Hanski & Gilpin 1997). For example, vegetated corridors connecting habitat patches and favoring organism dispersal are commonly used in species conservation plans and in the design of nature reserves (Harrison 1992; Hobbs 1992; Simberloff et al. 1992).

Less attention has been paid to how linkages among habitats may affect the structure and dynamics of marine communities (Robbins & Bell 1994; Irlandi & Crawford 1997; Ruckelshaus & Hays 1998). Habitat destruction and fragmentation are especially widespread in coastal marine systems, where trawling for fish, dredging, and eutrophication kills seagrasses, kelps, corals, and other biogenic habitat engineers, such as oysters and polychaetes (Thayer 1992; Hallock et al. 1993; Schroeter et al. 1993; Lenihan & Peterson 1998). Scientists and natural resource managers worldwide are faced with the challenge of predicting the consequences of habitat loss and fragmentation for the function of marine ecosystems and of adopting appropriate strategies for protecting and restoring marine habitats. To date, however, the traditional approach of natural resource managers has been to focus on each estuarine habitat separately (Thayer 1992).

Because of the prevalence among marine animals of larval reproductive stages that are broadly dispersed by currents and tides, maintaining connectivity among habitat patches is generally assumed to be relatively unimportant in managing marine systems (Hedgecock 1986; Palumbi 1992). This assumption has been challenged by studies showing that several species of marine invertebrates and fishes have limited larval dispersal and thus are as vulnerable to habitat fragmentation as many terrestrial species (reviewed by Ruckelshaus & Hays 1998).

Furthermore, dispersal of juveniles and adults among separated habitat patches may also be limited for even large, mobile animals if elevated risk of predation or physical stress forces them to avoid the unstructured, flat bottoms isolating patches of structured habitat such as reefs, seagrass meadows, or kelp beds. For example, sea urchin grazing intensity on seagrass decreases with distance from Caribbean patch reefs because reefs offer refuges from fish predation and thus act as sources of grazers—the "halo effect" (Ogden et al. 1973). The halo effects of predatory impacts around structures have been found in other systems, including soft-sediment macrofauna around temperate rocky outcrops (Posey & Ambrose 1994) and fish around coral patch reefs (Shulman 1985).

Estuarine landscapes, or "seascapes," are composed of a patchwork of different habitat types: seagrass meadows, salt marshes or mangroves, biogenic structures produced by reef-building animals such as corals and oysters, and unvegetated sandy and muddy bottoms. Marine ecologists have recently begun to ask whether the landscape characteristics of estuarine vegetated habitats (e.g., the size, shape, and relative proximity of patches of vegetation) influence the mobility of animals and the structure and dynamics of resident sea floor communities (Irlandi 1994; Robbins & Bell 1994; Irlandi & Crawford 1997). To date, little attention has been given to how another key habitat of temperate estuaries, the oyster reef, fits into the landscape-scale function of estuaries. Oysters are managed as a fishery to exploit rather than as a biogenic habitat to conserve (Lenihan & Peterson 1998). Oyster reefs are important habitats not only because they produce harvestable oysters and clams but also because of the ecosystem functions they perform, including improving water quality by filtering out particulates, decreasing erosion by stabilizing sediments and serving as natural breakwaters, enhancing diversity by offering a hard substratum for use of epibiotic invertebrates, and providing structured habitat for mobile fish and crustaceans in an otherwise monotonous sedimentary environment (Bahr & Lanier 1981; Officer et al. 1982; Dame et al. 1984; Newell 1988; Coen 1995; Luckenbach et al. 1997; Eggleston et al. 1998).

Intertidal oyster reefs occur in three distinguishable settings: (1) fringing reefs bordering the edge of salt marshes; (2) reefs extending outward from a point of marsh; or (3) isolated patches (Bahr & Lanier 1981). Fur-

thermore, intertidal oyster reefs may be surrounded by intertidal and subtidal seagrass beds or by unvegetated sand or mud bottom. The position of the oyster reef relative to salt marshes and seagrass meadows seems likely to be an important factor in determining its use by mobile estuarine organisms. Micheli (1997*a*) showed that blue crabs (*Callinectes sapidus*) spend more time and prey more on their bivalve prey at the edges of intertidal salt marshes than in adjacent unvegetated habitats and that this pattern of habitat use is driven largely by risk of predation by birds. Intertidal oyster reefs connected to vegetation are expected to be preferred by crabs, and possibly by other mobile consumers, because they can be reached without transiting unvegetated flats, where they would be exposed to detection and predation by predatory birds (Micheli 1997*a*) and fishes (Moody 1994). Therefore, we predicted that predation on benthic invertebrates should be greater on oyster reefs connected to vegetated habitats than on reefs surrounded by unvegetated bottom.

We tested whether oyster reef proximity to salt marshes affects (1) the benthic macroinvertebrate community on the reef; (2) survivorship of juvenile bivalves of commercial importance, the hard clam (*Mercenaria mercenaria*) and the American oyster (*Crassostrea virginica*); and (3) predation rates by the blue crab (*Callinectes sapidus*) and the stone crab (*Menippe mercenaria*) on juvenile hard clams. In addition, we asked whether another vegetated estuarine habitat, the seagrass meadow, facilitates dispersal of mobile consumers and thus acts as a corridor habitat. To address this question, we conducted sampling and experiments on reefs that were either connected to salt marshes by seagrass meadows or isolated by the presence of unvegetated flats.

Methods

Physical Characteristics and the Benthic Macroinvertebrate Community

To determine whether proximity of intertidal oyster reefs to salt marsh habitat influences benthic communities on reefs, we sampled benthic macroinvertebrates on natural intertidal reefs in three different settings: (1) fringing oyster reefs bordering intertidal *Spartina alterniflora* salt marshes, (2) oyster reefs connected as points to salt marshes at one end, (3) oyster reefs separated from adjacent salt marshes by 8.5–17.5 m of sedimentary bottom (marsh, point, and isolated reefs, respectively). We assigned reefs to these categories based on the proportion of their perimeter in direct contact with salt marsh vegetation: 42–50%, 14–25%, and 0% for marsh, point, and isolated reefs, respectively. Reefs were located at four separate sites within Middle Marsh,

a group of salt marsh islands in Back Sound, North Carolina, U.S.A. (See Peterson and Beal [1989] and Micheli [1997*a*] for maps and descriptions of the physical and sedimentological characteristics of the study area.) Each site contained one reef of every type. To allow us to test the effects of adjoining subtidal seagrasses on reef macroinvertebrate communities, at two of the four sites all three reefs were located adjacent to seagrass beds (<1 m separation), whereas at the remaining two sites the reefs were surrounded by intertidal and subtidal sedimentary flats. Seagrass beds were composed of a mixture of eelgrass (*Zostera marina*) and shoalgrass (*Halodule wrightii*). Reef areas, estimated by assuming that reefs were elliptical in shape, ranged from 59 m^2 to 636 m^2 (Table 1). All reefs had similar tidal elevation and were at least partially exposed at most low tides and covered by about 1 m of water at high tides.

Although reefs were selected solely on the basis of their proximity to other habitats, characteristics other than landscape setting might have also varied. In particular, isolated reefs appeared to be subject to faster water flows than reefs adjacent to salt marshes, possibly because of the baffling effects of salt marsh plants on water currents (Leonard & Luther 1995). To determine whether isolated reefs were located in higher-energy environments than other types of reefs, we compared the organic content of sediments among the different reefs. Organic content of sediments is an indirect measure of an energy regime, greater at low-energy sites where deposition of particles from the water column to the seafloor is higher (Ginsburg & Lowenstam 1958; Scoffin 1970). Two replicate sediment samples were taken on 27 August 1996 from each reef for determination of percent organic matter. Samples were cylindrical cores, 5.2 cm in diameter and 3 cm deep, taken haphazardly along the edges of reefs. Sediments were oven-dried at 60° C for 48 hours, weighed to the nearest 0.0001 g, transferred to a furnace for combustion of organic matter at 550° C, and reweighed after 32 hours.

Benthic sampling of reefs was conducted between 8 November and 15 December 1995. Late-fall sampling reveals the benthic community following the seasons of most intense recruitment (spring–summer: Ortega & Sutherland 1992; F. M., unpublished data) and predation (summer: Micheli 1997*a*). We sampled oysters on each reef by using a 0.25-m^2 circular steel frame. All oysters within six plots haphazardly located along the perimeter of each reef, 1–2 m inside its edges, were collected by hand, counted, and returned to their original location on the reef after shell heights of 20 randomly selected oysters per plot were measured to the nearest 0.01 cm with Vernier calipers. We sampled the benthic macroinvertebrate community by using an hydraulic suction dredge to excavate sediments and oyster shells within six haphazardly chosen plots per reef to a depth of 15 cm. Sampling was conducted along the reef edges to minimize

Table 1.   Characteristics of intertidal oyster reefs within Middle Marsh in Back Sound, North Carolina.

Site	Reef type	Length (m)	Width (m)	Surface area[a] (m²)	Shell volume[b,c] (cm³)	Organic matter (%)[c,d]
With seagrass						
1	marsh	90.0	9.0	636	4220 (450)A	1.4 (0.1) B
	point	28.0	8.5	187	4370 (1000) A	4.7 (0.2) A
	isolated	32.0	15.0	377	5560 (790) A	5.1 (0.3) A
3	marsh	22.5	5.0	88	3500 (260) A	3.2 (1.0) A
	point	30.0	8.5	200	1270 (190) B	2.5 (0.2) A
	isolated	13.0	7.0	71	2500 (440) A,B	4.0 (0.1) A
Without seagrass						
2	marsh	45.0	7.0	247	4240 (200) A	3.1 (0.2) A
	point	22.0	9.0	155	1600 (330) B	2.1 (0.2) A,B
	isolated	27.5	7.0	151	4090 (450) A	1.7 (0.5) B
4	marsh	25.0	5.0	98	1660 (220) B	4.1 (0.3) A
	point	15.0	5.0	59	1070 (190) B	1.2 (0.1) B
	isolated	22.0	4.0	69	3300 (310) A	1.5 (0.04) B

[a]*Estimated from reef lengths and widths, assuming an elliptical shape.*
[b]*Determined by water displacement for each 0.25-m² (15-cm deep) plot sampled (mean + SE).*
[c]*Different letters (A, B) indicate that means were significantly different at $\alpha = 0.05$ in post-hoc Student-Neuman-Keuls comparisons among reef types within each site. For shell volume and percent organic matter, separate comparisons were conducted within each site because of significant interaction terms in analyses of variance (Table 2).*
[d]*Determined for two replicate sediment samples (3-cm deep) collected on each reef (mean + SE).*

structural damage to the reef. Animals and shell materials retained by a 3-mm mesh bag were sorted in the field, and the animals were taken to the laboratory to be measured and identified to species. We quantified shell materials in the mesh bag by measuring shell volume using water displacement and then returned them to their original location. Volumes of shell per plot provide a measure of the amount of structure potentially protecting benthic invertebrates from their predators (Arnold 1984; Sponaugle & Lawton 1990). Both samplings were conducted when reefs were covered by water.

We tested the effects of reef proximity to vegetation on benthic macroinvertebrate communities using a hierarchical experimental design in which four sites (or embayments) were assigned to one of two categories (site type): with or without seagrass around reefs. Within each site, reefs were assigned to one of three reef types: marsh, point, or isolated reefs. Finally, within-reef variability was estimated by sampling benthic invertebrates within six replicate 0.25-m² plots. We compared macroinvertebrate densities and species richness, oyster and hard clam densities, volumes of shell material per plot, and percent organic matter in sediments among reef types with separate three-way nested analyses of variance (ANOVAs), with site type and reef type as fixed factors and site as a random factor, nested within site type. A preliminary analysis of covariance model containing reef surface area (Table 1) as a covariate indicated that reef area did not have a significant effect on any response variable ($p = 0.15$–0.95). Because reef area did not appear to have an important effect on reef macrofaunal communities, at least within the range considered in this study, we did not include this variable in our analyses. We tested the assumption of homoscedasticity with

Cochran's test at $\alpha = 0.05$, and we transformed data when necessary using $\log(x + 1)$. Post-hoc comparisons of means were carried out with the Student-Neuman-Keuls (SNK) procedure at $\alpha = 0.05$ (Day & Quinn 1989).

Survivorship of Transplanted Juvenile Oysters and Hard Clams

We compared the intensity of predation on juvenile bivalves among intertidal oyster reefs with differing proximity to aquatic vegetation with mark-recapture experiments conducted on the same reefs described above. Juvenile oysters and hard clams in size ranges most susceptible to crab predation (oysters < 30 mm in height [Eggleston 1990]; clams < 25 mm in length [Arnold 1984; Peterson 1990]) were purchased at a local hatchery. Individual oysters (20–40 mm in shell height, mean = 27.1 mm ± 0.5 SE, $n = 100$) were deployed in the field in open cages made of 1.3-cm plastic Vexar mesh, with a bottom 20 × 20 cm, 5-cm tall sides, and no top. Cages were used to minimize loss of oysters due to sampling error or transport by currents and waves. Ten large oyster-shell valves were placed within each of six open cages per reef, and 12 live juvenile oysters were wedged among the shells. Open cages were placed haphazardly about 1–2 m inside reef edges, nestled among oysters and shells, and secured to the reef surface with two steel stakes at opposite corners. Because the cage sides did not protrude from the reef surface, any artifact associated with cage structure is likely to be minimal.

Hard clams (12.1–19.7 mm in length; mean = 16.0 mm ± 0.2 SE, $n = 100$) were tethered to 15–cm-long steel gardening staples by 15-cm pieces of transparent monofilament line (10-lb test) attached to the shells with

superglue and a small piece of electrical tape. Tethered clams were deployed onto each of the 12 intertidal oyster reefs within six 1-m² plots placed haphazardly 1–2 m from the reef edges. Twelve clams were introduced to each plot with a removable monofilament grid to achieve regular spacing and to facilitate recovery. Clams were buried just below the surface of sediments or were nestled between oyster shells when no exposed sediments were found at grid positions. Clam densities of 12/m² were within the range of densities observed in intertidal oyster reefs in the study area (F. M., unpublished data). Because artifacts associated with tethering can bias comparisons of relative predation intensity among habitats (Micheli 1996), we also used enclosure experiments to confirm predation patterns described with tethering experiments.

This experiment was conducted both in the fall of 1995 (25 October–6 November with oysters; 16–24 October with clams) and the summer of 1996 (28 July–4 August with oysters; 16–23 August with clams), to compare bivalve survivorship among reefs at times of the year characterized by low and high blue crab abundances respectively (Micheli 1997*a*). After 7–12 days, the bivalves were retrieved and the numbers of live and dead oysters or clams were recorded for each plot. We used three-way nested ANOVAs, Cochran's test (after angular transformation), and SNK contrasts to compare proportional survivorship of clams and oysters among reef types.

Effects of a Seagrass Corridor on Clam Predation Rates by Crabs

We conducted short-term experiments designed to test the hypotheses that blue crabs and stone crabs, two common bivalve consumers in the study area, prey more intensely on isolated reefs when they are connected to a fringing marsh reef by a seagrass corridor and thus that seagrass might act as a corridor connecting oyster reefs and facilitating movement of crabs among them. We chose to conduct controlled prey-patch choice experiments in field enclosures instead of sampling crab abundances on reefs of different proximity to vegetation because patterns of predator abundance and distribution are not necessarily correlated with patterns of predation, as predators may move through a particular habitat without foraging.

Four Vexar-mesh enclosures (10 × 3 m; mesh diameter 1.3 cm) were constructed at site 1, with the longest side perpendicular to the edge of a salt marsh so that each enclosure contained a narrow strip of marsh vegetation (0.5–1 m wide). Enclosure walls (1.3 m tall) were dug 15 cm into the sediments to prevent crabs from escaping. Water depth within the enclosures was approximately 1 m at most high tides and varied less than 1 cm,

on average, between opposite sides of the enclosures. Two enclosures contained an intertidal sand flat adjacent to the salt marsh, whereas the other two contained an intertidal seagrass bed. The seagrass was mostly *Halodule wrightii*, with some sparse *Zostera marina*. Within each enclosure, two artificial oyster reefs (elliptical in shape, 2-m long on the axis parallel to the marsh edge, and 1-m wide) were constructed with oyster shells approximately 4 weeks before experiments were begun. One reef was placed at the edge of the salt marsh just outside the vegetation, and the other approximately 8 m away from the marsh edge. Prior to experiments, we removed crabs and fishes within enclosures with baited traps and by searching each enclosure at low tides, when the seafloor was exposed. Juvenile hard clams (14.0–21.5 mm, mean = 16.3 mm ± 0.2 SE, *n* = 50) were placed on each reef within one, 1-m² plot at densities of 16/m². To facilitate recovery, clams were deployed at the intersections of a removable monofilament grid.

Experiments using blue crabs as predators were conducted between 28 July and 20 August 1996. Because only four enclosures were available, replicate trials were repeated on six different dates, with all treatment combinations applied on each date. At the beginning of each experimental trial, one blue crab (105–129 mm in carapace width, mean = 115 mm ± 2.4 SE, *n* = 12) was added to two of the enclosures, whereas the remaining two did not receive crabs and served as controls for bivalve mortality due to causes other than blue crab predation. This experiment had four treatments: (1) reefs connected by seagrass and crab added, (2) reefs connected by seagrass and no crab added, (3) reefs not connected by seagrass and crab added, and (4) reefs not connected by seagrass and no crab added. After 2 days, we searched all enclosures at low tide for surviving clams by removing oyster shells and digging sediments by hand at the intersections of the monofilament grid. The blue crabs were captured and released, and a new trial was started with different crabs. This experiment was repeated with stone crabs (82–107 mm in carapace width, mean = 92.4 mm ± 3.0 SE, *n* = 8) following an identical protocol between 14 and 27 August 1996. Four experimental trials were conducted with stone crabs.

We quantified predation rates on clams as the sum of clams crushed by crabs or missing from reefs (Micheli 1997*a*). Predation rates were compared among treatments with two-way ANOVAs, with predator (with or without crab) and seagrass treatment (present or absent) as crossed fixed factors and date as a blocking factor. Because predation rates on clams on the two reefs within each enclosure were not independent, analyses were conducted on the difference between predation rates on the two reefs within each enclosure (Peterson & Renaud 1989). Two-way ANOVAs were also conducted on the total numbers of clams lost from each enclosure to determine whether addition of a predator to the enclo-

sures and the presence of seagrass had significant effects on overall clam mortality. Separate ANOVAs were conducted on the blue crab and stone crab data sets. Data were not transformed because Cochran's test indicated homogeneous variances at $\alpha = 0.05$.

Results

Physical Characteristics and Benthic Macroinvertebrate Community

Patterns in shell volume per plot and percent organic matter in sediments among reef types (R) varied significantly with site (S) (Table 2: R × site (S) interaction). Shell volume per plot, a measure of the proportion of the reef made of bivalve shell, varied significantly among marsh, point, and isolated reefs at all sites except site 1 (Table 1). At the other three sites, shell volumes were lower for point reefs than for marsh and isolated reefs, but both contrasts were simultaneously significant only at site 2 (Table 1). Organic matter in sediments tended to be higher in isolated than marsh reefs at sites with seagrass, although significantly so at only one of two sites, whereas the opposite was observed at sites without seagrass (Table 1). Percent organic matter in point reefs varied among sites, with no consistent trend (Table 1).

Table 3 lists forty-seven macroinvertebrate species collected on intertidal oyster reefs. Because of the coarse 3-mm mesh, this list excludes many species from some invertebrate groups also commonly found on intertidal oyster reefs, such as small polychaetes, amphipods, isopods, and tanaids, and the juveniles of some of the species on this list. Nevertheless, this faunal grouping represents the size classes most likely to be included in the diets of predatory crabs.

The effects of reef type on patterns of abundance of benthic macroinvertebrates varied significantly among sites (Table 2: R × site (S) interaction). Reefs spatially isolated from salt marshes had benthic macroinverte-

brate abundances that were approximately 1.5–2.5 times greater than those of reefs adjacent to salt marshes at all four sites, although not significantly so at site 3 (Fig. 1a). There was a trend for isolated reefs to have greater abundances of benthic macroinvertebrates than point reefs, although significantly so only at the two sites without seagrass (Fig. 1a).

Patterns of macroinvertebrate abundance among reefs differed between infauna and epifauna (Fig. 1b, 1c). For infaunal abundance, there was a significant interaction between site and reef type (Table 2). At sites with seagrass, infaunal abundances were similar among marsh, point, and isolated reefs (Fig. 1b). At sites without seagrass, infauna was six or seven times denser on isolated reefs than on marsh reefs (Fig. 1b). At sites without seagrass, infauna on isolated reefs tended to be denser than on point reefs, but this pattern was significant at only one site (Fig. 1b). Patterns of epifaunal abundance differed between sites with and without seagrass (Table 2). Although at all sites there was a trend for epifaunal abundance to be greater on isolated than on point and marsh reefs, this trend was significant only for point reefs at the sites without seagrass (Fig. 1c). In the absence of seagrass, epifauna was also denser on marsh reefs than on point reefs (Fig. 1c).

Patterns of species richness among marsh, point, and isolated reefs differed between sites with and without seagrass around reefs (Table 2). At both sites without seagrass, significantly more macroinvertebrate species were found on isolated than on point reefs or marsh reefs, with no significant difference between these two reef types (Fig. 1d). At both sites with seagrass, significantly more species were found on point reefs than on marsh reefs (Fig. 1d). Species richness was not significantly different between point and isolated reefs at site 1 and between marsh and isolated reefs at site 3 (Fig. 1d).

The abundance of oysters was highly variable and showed a significant interaction between site and reef type, although with no consistent trends (Table 2; Fig. 2a). Oysters were significantly more abundant on iso-

Table 2. Results of three-way analyses of variance comparing shell volume, percent organic matter in sediments, and abundance and number of species of benthic invertebrates among marsh, point, and isolated oyster reefs, and between sites with or without seagrass around reefs.

Source[b]	df	F ratios and significance levels[a]							
		Shell volume	Organic matter (%)	Total invertebrates	Infauna	Epifauna	Number of species	Oysters	Hard clams
R	2	4.4	0.2	5.3	4.0	11.5*	8.7*	1.0	0.2
S	1	0.5	25.5*	0.04	4.7	0.1	0.04	1.2	57.8*
R × S	2	0.4	3.7	2.0	4.8	7.3*	9.2*	0.3	0.01
Site (S)[c]	2	23.5***	1.2	49.8***	3.5*	33.3***	23.0***	8.8***	0.1
R × site (S)[c]	4	3.5**	9.7***	3.8***	2.7*	0.9	0.2	13.0***	1.5
Residual	60								

[a]*p < 0.05; **p < 0.01; ***p < 0.001.
[b]R, reef type; S, site type.
[c]Site is a nested factor within site type (two sites with seagrass and two sites without seagrass).

Table 3. Macroinvertebrate species collected on intertidal oyster reefs.

Species*	No. collected	Species	No. collected
Bivalves		Crustaceans	
Chione cancellata (I)	111	*Panopeus herbstii* (E)	830
Mercenaria mercenaria (I)	73	*Eurypanopeus depressus* (E)	458
Geukensia demissa (E)	35	*Alpheus* sp. (E)	131
Nucula proxima (I)	21	*Palaemonetes* sp. (E)	15
Lima pellucida (E)	12	*Upogebia affinis* (E)	9
Cumingia tellinoides (I)	11	*Pinnotheres ôstreum* (E)	8
Semele proficua (I)	9	*Pagurus longicarpus* (E)	4
Lithophaga bisulcata (I)	9	*Callinectes sapidus* (E)	4
Chione grus (I)	9	*Menippe mercenaria* (E)	2
Tellina versicolor (I)	7	*Heterocrypta granulata* (E)	1
Tellina equistriata (I)	5		
Tagelus divisus (I)	4	Other	
Parvilucina multilineata (I)	3	*Ophioderma brevispinum* (E)	16
Argopecten irradians (E)	3	*Arbacia punctulata* (E)	3
Anadara ovalis (E)	2	*Styela plicata* (E)	2
Corbula barattiana (I)	2	*Chaetopleura apiculata* (E)	1
Solemya velum (I)	2		
Mactra fragilis (I)	1		
Gouldia cerina (I)	1		
Petricola pholadiformis (I)	1		
Rupellaria typica (I)	1		
Pitar fulminatus (I)	1		
Atrina rigida (I)	1		
Gastropods			
Cerithium atratum (E)	245		
Urosalpinx cinerea (E)	147		
Boonia impressa (E)	31		
Fasciolaria hunteria (E)	25		
Anachis avara (E)	10		
Pyramidella crenulata (E)	5		
Diodora cayenensis (E)	1		
Turbonilla interrupta (E)	1		
Mangelia plicata (E)	1		

*Oysters not included. Species assigned to one of two categories: infaunal (I) or epifaunal (E).

lated than on point or marsh reefs at site 1 (with seagrass), less abundant on point reefs than on the other two reef types at site 4 (without seagrass), and invariant among all reef types at the remaining two sites (Fig. 2a).

Hard clam abundance was significantly greater at sites without seagrass than at sites with seagrass around reefs (Table 2; Fig. 2b). Clam abundance did not vary significantly with reef proximity to salt marsh habitat (Fig. 2b).

Survivorship of Transplanted Juvenile Oysters and Hard Clams

Survivorship of juvenile oysters transplanted to intertidal oyster reefs ranged between 51% and 85% in fall and between 58% and 89% in summer (Fig. 3a, 3b). In summer, there were no significant differences in oyster survivorship among marsh, point, and isolated reefs or between sites with or without seagrass (Table 4; Fig. 3a). In fall, patterns of oyster survivorship among reef types varied with site (Table 4: R × site (S) interaction). Survivorship was significantly greater on the marsh than on the point

or isolated reefs at site 4, whereas it did not differ among reef types at the other three sites (Fig. 3b).

Survivorship of juvenile clams transplanted to intertidal oyster reefs ranged between 47% and 90% in fall and between 13% and 58% in summer (Fig. 3c, 3d). In summer, patterns in clam survivorship among reef types varied with site (Table 4: R × site (S) interaction). Proportions of live clams retrieved from isolated reefs were 1.5–3.5 times higher than from point or marsh reefs at both sites without seagrass, with no significant difference between marsh and point reefs (Fig. 3c). Clam survivorship was significantly lower on the marsh than on the point or isolated reefs at one of the two sites with seagrass, whereas survivorship was similar among reef types at the other site (Fig. 4c). In fall, patterns in clam survivorship among reef types differed significantly between sites with and without seagrass (Table 4: R × S interaction). Clam survivorship tended to increase with increasing distance from salt marshes at the two sites without seagrass, whereas the opposite trend was observed at the two sites with seagrass (Fig. 3d). Post-hoc
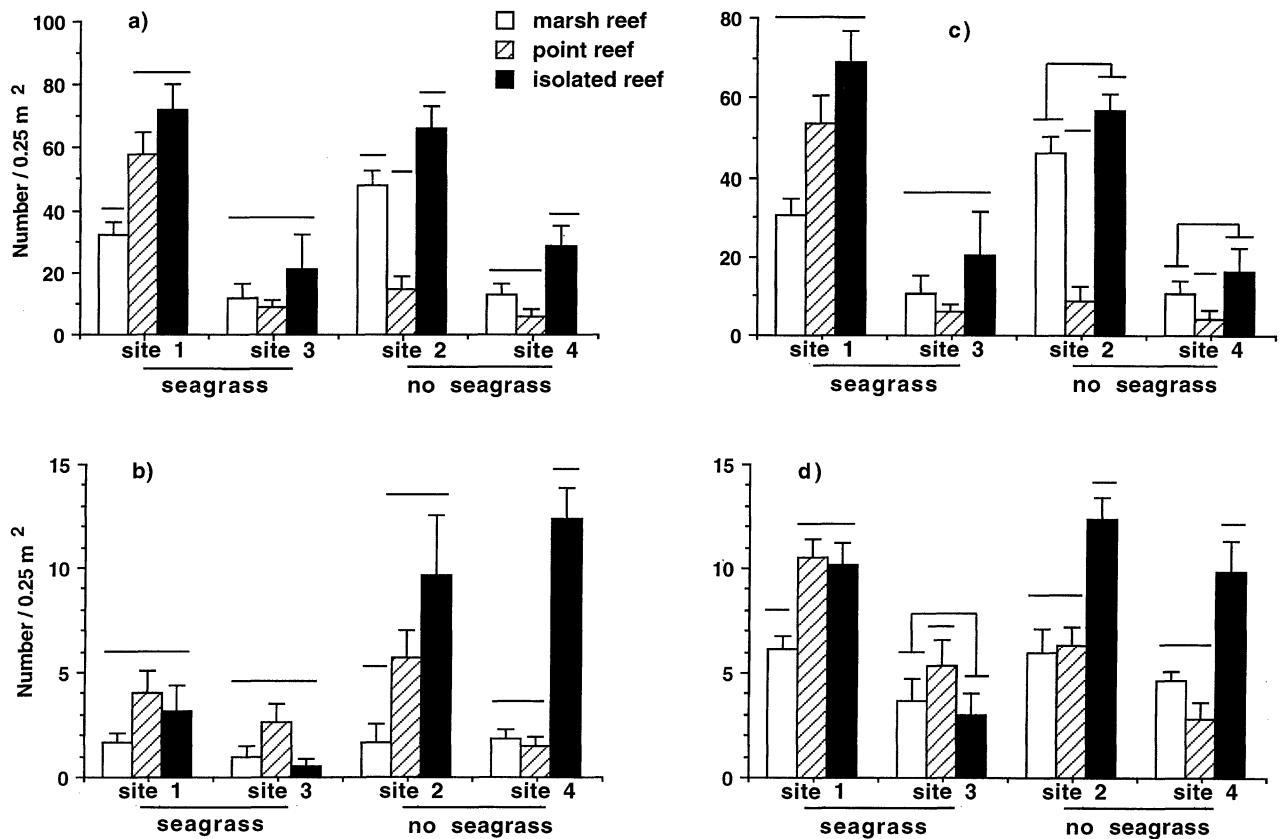
Figure 1. Patterns of total abundance (a), total infaunal abundance (b), total epifaunal abundance (c), and species richness (d) of benthic macroinvertebrates on intertidal oyster reefs with differing proximity to salt marsh habitat (marsh, point, and isolated reefs). All reefs were adjacent to seagrass beds at sites 1 and 3, and they were surrounded by unvegetated sand or mud flats at sites 2 and 4. Bars represent averages + 1 SE (n = 6). Bars underlying the same line are not significantly different at α = 0.05 (Student-Neuman-Keuls test).

comparison of means, however, failed to detect any significant difference in percent clam survivorship among pairs of reef types in the fall experiment (Fig. 3d).

Effects of a Seagrass Corridor on Clam Predation Rates by Crabs

Differences between the numbers of clams eaten by blue crabs on reefs located at the edge of a salt marsh and approximately 8 m from the marsh edge varied significantly depending on whether the two reefs were connected by seagrass or by unvegetated sand bottom (Table 5: P (predator) × S interaction). When reefs were connected by seagrass, similar numbers of clams had been crushed by crabs or were missing from the two reefs (Fig. 4a). In contrast, twice as many clams were crushed or missing on reefs adjacent to salt marsh than on isolated reefs when they were separated by unvegetated bottom (Fig. 4a). Clam losses in control enclosures with no crabs added were similar between the two reef types and were not significantly different between en-

closures with and without seagrass (Fig. 4a). Total clam losses within the enclosures were significantly affected by both the predator and seagrass treatments, with no significant interaction between these two factors (Table 5). Total clam losses were significantly greater in enclosures containing one blue crab than in control enclosures (Fig. 4a). Total clam losses were also significantly greater for enclosures containing seagrass than for enclosures containing unvegetated bottom (Fig. 4a).

There were no significant effects of either the predator or seagrass treatment on patterns of clam losses between artificial oyster reefs adjacent to a salt marsh and isolated reefs in the stone crab experiment (Table 5). Clam losses were similar between reefs adjacent to salt marsh and isolated reefs in enclosures both with and without seagrass (Fig. 4b). In contrast to experiments using blue crabs, in our study total clam losses to predation were not significantly different between enclosures with and without stone crabs (Table 5), suggesting that stone crabs were not a significant source of mortality of juvenile hard clams in the enclosures on this time scale
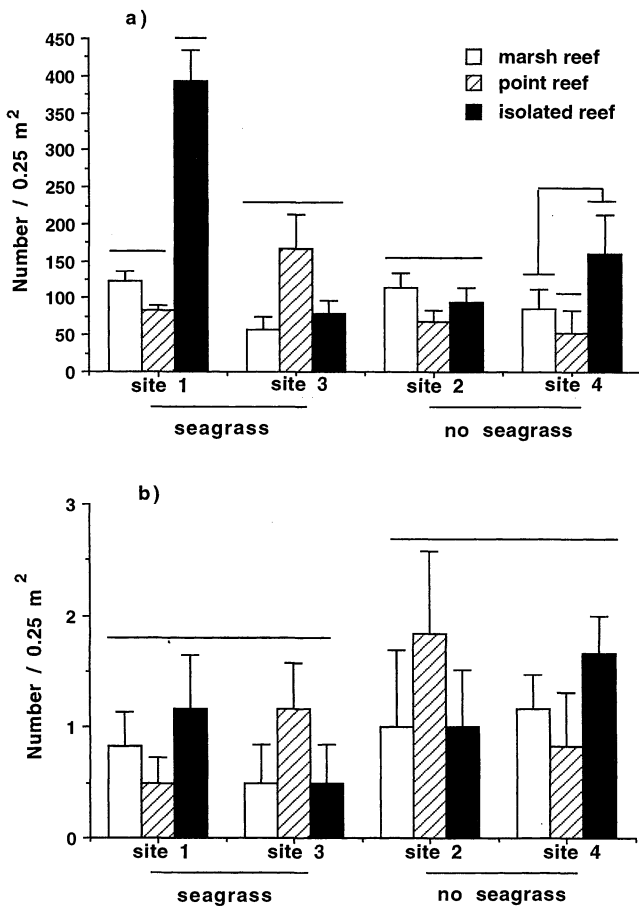
Figure 2. Patterns of abundance of oysters (a) and hard clams (b) on intertidal oyster reefs. See Fig. 1 legend for site description. Bars represent averages + 1 SE (n = 6). Bars underlying the same line are not significantly different at α = 0.05 (Student-Neuman-Keuls test).

(2 days). There was, however, a significant effect of seagrass treatment on total clam predation losses (Table 5). As in the blue crab experiment, total clam losses were significantly greater in enclosures containing seagrass than in enclosures containing unvegetated bottom (Fig. 4b).

Discussion

The spatial relationship of intertidal oyster reefs to salt marshes and seagrass beds had significant effects on both abundance and diversity of benthic macroinvertebrates and on predator-prey interactions between predatory crabs and bivalves living on reefs. In particular, the presence of seagrass connecting reefs to salt marshes modified patterns of macroinvertebrate abundance and species richness among reefs, and patterns of predation on juvenile hard clams transplanted to reefs. Behavioral

modification of blue crab predation can explain observed patterns of predation among reefs with different proximity to vegetated habitats. Our results indicate that seagrasses may act as corridors to facilitate the movement of blue crabs and possibly other predators between salt marshes and oyster reefs. To our knowledge, this is the first test of a corridor function for vegetated habitats in the marine environment.

Our study is also novel in that it investigates the effects of the landscape characteristics of estuarine habitats by focusing on how landscape patterns affect ecological processes, such as predator-prey interactions. A mechanistic understanding of the consequences of landscape pattern increases our predictive ability under different conditions and allows for both stronger generalizations about the effects of spatial structure on communities and more informed management decisions (Turner 1989).

Our results indicate that connectivity between habitat patches can have important consequences for habitat use and the ecological impacts of mobile marine predators due to behavioral constraints. Blue crabs are highly mobile and can cover distances of kilometers in a few days (Hines & Wolcott 1990). Thus, the spatial scales considered in this study (<20-m distances between oyster reefs and vegetated habitats) are well within the range of blue crab movements in the field. The discovery that even a few meters of unvegetated bottom can modify habitat use by blue crabs indicates that behavioral and not mobility constraints underlie patterns of predation by blue crabs (Micheli 1997*a*).
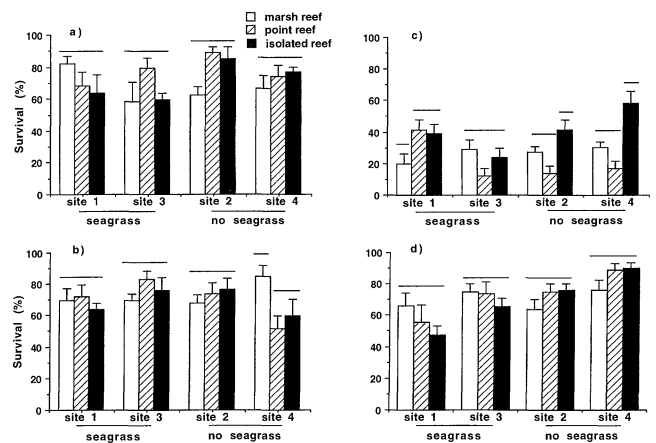

Figure 3. Patterns of survivorship of juvenile oysters (a,b) and hard clams (c,d) transplanted to intertidal oyster reefs over 7-12 days. This experiment was conducted following the same protocol in summer 1996 (a,c) and fall 1995 (b,d). See Fig. 1 legend for site description. Bars represent averages + 1 SE (n = 6). Bars underlying the same line are not significantly different at α = 0.05 (Student-Neuman-Keuls test).

Table 4. Results of three-way analyses of variance comparing percent survivorship of juvenile oysters and hard clams transplanted to intertidal oyster reefs with different proximity to salt marshes and at sites with or without seagrass around reefs.

| | | Oysters | | | | Hard clams | | | |
| | | Summer | | Fall | | Summer | | Fall | |
Source[a]	df	MS	F[b]	MS	F[b]	MS	F[b]	MS	F[b]
R	2	0.06	1.0	0.01	0.1	0.24	3.6	0.01	1.8
S	1	0.09	2.7	0.02	0.4	0.03	0.3	0.37	2.1
R × S	2	0.09	1.5	0.08	1.0	0.14	2.1	0.12	26.4**
Site (S)[c]	2	0.03	0.9	0.05	1.8	0.09	4.6**	0.18	7.4***
R × site (S)[c]	4	0.06	1.8	0.07	2.5*	0.07	3.6**	0.01	0.19
Residual	60	0.03		0.03		0.02		0.02	

[a] R, reef type (marsh, point, or isolated); S, site type.
[b] *p < 0.05; **p < 0.01; ***p < 0.001.
[c] Site is a nested factor within site type (two sites with seagrass and two sites without seagrass).

The abundance and species richness of benthic macroinvertebrates in a size class likely to be targeted by blue crabs and other larger consumers tended to be greater along the edge of reefs spatially separated from salt marshes than adjacent to salt marshes (Fig. 1). The presence of seagrass around reefs, however, had different effects on epifauna and infauna. Epifaunal macroinvertebrates, mostly small crabs and gastropods (Table 3), tended to be more abundant on isolated reefs than on reefs adjacent to salt marshes, regardless of the presence of seagrass around reefs (Fig. 1c), whereas infaunal macroinvertebrates (several species of infaunal bivalves; Table 3) tended to be most abundant on reefs spatially separated from both salt marsh and seagrass (Fig. 1b).

The patterns of abundance and species richness of benthic macroinvertebrates on reefs may reflect lower predation intensity, particularly on infaunal bivalves, on reefs spatially separated from both salt marshes and seagrass beds. This interpretation is supported by the result that survivorship of juvenile clams transplanted onto oyster reefs tended to be greater on reefs separated from both salt marshes and seagrass beds than on reefs adja-

cent to vegetation (Fig. 3). Blue crabs exert greater predation rates along the vegetated edges of salt marshes and seagrass beds than in unvegetated intertidal flats (Micheli 1997a; this study). Preference for vegetated habitats by blue crabs (Micheli 1997a) and possibly other predators may explain the lower abundance and species richness of infauna on reefs adjacent to vegetation.

That seagrass habitat may act as a corridor facilitating movement of blue crabs among oyster reefs and salt marshes, and thus possibly enhancing predation intensity on clams, is also supported by the greater abundance of hard clams on reefs separated from seagrass meadows than on reefs surrounded by seagrasses (Fig. 2b). Mortality of hard clams due to predation may be generally greater on reefs surrounded by seagrass than on reefs without adjacent seagrass.

Patterns of oyster abundance and survivorship of juvenile oysters transplanted to reefs with differing proximity to vegetation varied among sites, with no apparent overall trend (Fig. 3). One possible explanation for the different responses of clams and oysters, and possibly of

Table 5. Results of two-way analyses of variance comparing predation rates (i.e., numbers of clams crushed and missing) of blue crabs and stone crabs at clam patches set up on artificial reefs in the enclosure experiments.

| | | Blue crabs | | | | | Stone crabs | | | |
| | | Difference[b] | | Total[c] | | | Difference[b] | | Total[c] | |
Source[a]	df	MS	F[d]	MS	F[d]	df	MS	F[d]	MS	F[d]
P	1	7.04	2.6	210.04	18.1***	1	1.0	0.24	16.0	2.43
S	1	35.04	13.1**	57.04	4.9*	1	0.25	0.06	110.3	16.8**
P × S	1	22.04	8.2**	9.4	0.8	1	1.0	0.24	1.0	0.15
Date[e]	5	8.07	3.0*	12.1	1.05	3	1.75	0.41	8.4	1.3
Residual	15	2.68		11.59		9	4.25		6.58	

[a] The fixed factors in the ANOVAs are predator treatment (P, enclosures with or without one crab added) and seagrass treatment (S, enclosures with or without seagrass).
[b] Difference between predation rates on reefs constructed at the edge of a salt marsh and 8 m away from the marsh edge within each enclosure.
[c] Total predation rates in each enclosure.
[d] *p < 0.05; **p < 0.01; ***p < 0.001.
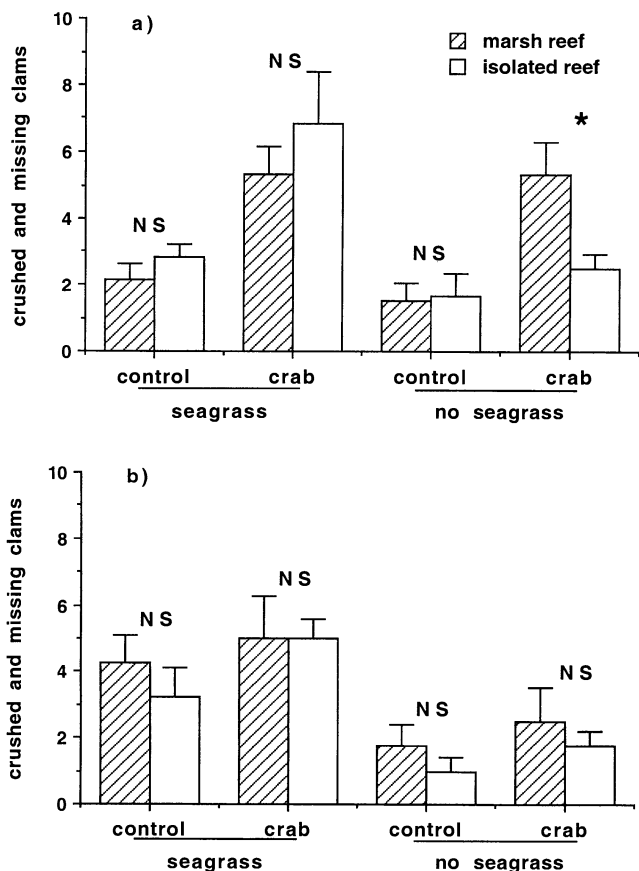[e] Date is a blocking factor in the ANOVAs.

Figure 4. Numbers of crushed and missing hard clams out of patches of equal clam density (16/m²) on artificial oyster reefs constructed within field enclosures at the edge of a salt marsh (marsh) or approximately 8 m away from the salt marsh edge (isolated). Reefs were separated by a seagrass bed in two of the enclosures (seagrass) and by a sand flat in the remaining two enclosures (no seagrass). On each trial, one blue crab (a) or stone crab (b) was added to one of the enclosures containing seagrass and to one of the enclosures with no seagrass, whereas the other two enclosures did not receive any crabs and served as controls. Bars (+1 SE) represent averages of six trials in the blue crab experiment and four trials in the stone crab experiment. NS, not significant; asterisk indicates a significant difference at α = 0.05 in Student-Neuman-Keuls post-hoc comparisons.

infaunal and epifaunal macroinvertebrates in general, could be that clams and oysters are most affected by different predators. Juvenile hard clams appear to suffer greatest mortality from blue crab predation (Peterson 1990; Micheli 1997a), but juvenile oysters may suffer higher predation from xanthid crabs, such as the stone crab and the mud crab (*Panopeus herbstii*) (Micheli 1997b). Results of the enclosure experiments indicate that the proximity of oyster reefs to salt marshes and sea-

grass meadows has a significant effect on clam predation rates by blue crabs but not by stone crabs (Table 5; Fig. 4). Differences in foraging behavior and habitat use between these two crabs may explain why reef proximity to vegetation affects clam but not oyster survivorship. The result of an overall greater clam mortality in enclosures containing seagrass (Table 5), however, suggests that we did not remove all potential clam predators from enclosures with seagrass prior to experiments and that at least part of the clam mortality in our experiments was caused by predators other than the blue crabs and stone crabs we added to the enclosures.

We focused on predator-prey interactions and predator behavior as mechanisms that explain patterns of abundance and community structure of benthic invertebrates based on the results of previous studies indicating that predation is the dominant process structuring benthic communities in estuarine soft bottoms of the southeastern United States (Virnstein 1977; Summerson & Peterson 1984; Hines et al. 1990; Eggleston et al. 1992; Micheli 1997a). A variety of abiotic factors and biotic interactions other than predation may have differed among reefs and may help explain patterns in bivalve survivorship and in macrobenthic abundance and community structure. For example, isolated reefs at sites without seagrass had a lower percentage of organic matter in sediments (Tables 1 & 3), and thus possibly faster water flows than reefs adjacent to vegetation.

Water current speeds and the amount of water turbulence have significant effects on the rates of recruitment, growth, and survival of oysters (Lenihan 1999; Lenihan & Peterson 1998) and benthic fishes (Breitburg et al. 1995) on subtidal oyster reefs and are likely to have important effects on other organisms living on oyster reefs. In particular, faster water flows on isolated reefs cause greater rates of larval delivery than on reefs located in lower-energy environments, which may explain the greater abundance and species richness of infaunal macroinvertebrates along the edge of reefs separated from both salt marshes and seagrass beds than on reefs adjacent to vegetated habitats. In addition to water current speeds, a whole suite of variables is likely to differ among the four sites in our study, including sediment characteristics other than percent organic matter and the actual proportions and configurations of different habitat types. The significant effect of site on most of the variables in these analyses (Tables 2 & 4) suggests that multiple characteristics of each site may be important in determining overall patterns of abundance and mortality of reef benthic invertebrates.

Our results have important management and conservation implications. Oyster reefs along the east and Gulf coasts of southeast North America have value both for the natural ecosystem functions they provide as filters, shoreline stabilizers, and unique habitat and also for the production of shellfish commodities for human markets

and consumption. Depending upon which of these two values one is managing for, our results suggest a different optimal landscape setting. To mitigate the extensive damage done to oyster reefs by shellfish harvesting, many programs are now actively rebuilding reefs by constructing shell mounds (e.g., Marshall 1993; Luckenbach et al. 1997; Lenihan & Peterson 1998; Lenihan 1999). In addition, hard clam production is being enhanced by programs that introduce seed clams to natural bottom, the yields from which are vastly improved by planting the seed in oyster shell bottom (Peterson et al. 1995).

Reef restoration and clam plantings are presently done without specific landscape-scale siting criteria because no systematic understanding exists of the effects of location on oyster reef habitat value and shellfish production. Proximity between salt marsh, seagrass, and oyster reef habitat favors movements of crabs and fishes between these habitat types and increases predation intensity on infaunal bivalves on reefs (Irlandi & Crawford 1997; E. A. Irlandi, unpublished data; this study). In particular, reefs separated from salt marshes by 10–15 m of unvegetated bottom or seagrass meadows tend to host a denser macroinvertebrate community than reefs adjacent to salt marshes, and reefs spatially separated from both salt marshes and seagrass beds host more species of benthic macroinvertebrates and have higher survivorship of juvenile clams. Thus, restoring reefs near salt marshes and seagrass beds can be expected to enhance the transfer of secondary production of restored reefs to higher trophic levels and possibly to lead to greater production of fish and crustaceans feeding on reefs. In contrast, restored and natural reefs spatially separated from aquatic vegetation provide refuges from predation for clams and infaunal bivalves in general and may be targeted as sites for maintaining higher abundance and species richness of bivalves and restocking natural populations with hatchery-raised seed clams. Conservation efforts should consider not only how much oyster reef habitat is lost but also its landscape setting.

The importance of ecological interactions among species and linkages between habitats for the structure and function of ecosystems calls for a more integrated approach to management that aims to preserve ecological processes as well as species or habitats (Christensen et al. 1996; Botsford et al. 1997). Effective management and restoration of estuarine and coastal marine habitats must view each habitat type as an integral part of an ecosystem and take into account its interconnections with other ecosystem components mediated through animal movements and fluxes of matter and nutrients.

Acknowledgments

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