

Comparative Patterns of Occupancy by Decapod Crustaceans in Seagrass, Oyster, and Marsh-edge Habitats in a Northeast Gulf of Mexico Estuary

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ABSTRACT: Decapod crustaceans occupying seagrass, salt marsh edge, and oyster habitats within the St. Martins Aquatic Preserve along the central Gulf coast of Florida were quantitatively sampled using a 1-m² throw trap during July–August 1999 and March–April 2000. Relative abundance and biomass were used as the primary measures to compare patterns of occupancy among the three habitat types. Representative assemblages of abundant and common species from each habitat were compared using Schoener's Percent Similarity Index (PSI). In all, 17,985 decapods were sampled, representing 14 families and 28 species. In the summer sampling period, mean decapod density did not differ between oyster and seagrass habitats, which both held greater densities of decapods than marsh-edge. In the spring sampling period oyster reef habitat supported greater mean decapod density than both seagrass and marsh-edge, which had similar densities of decapods. Habitat-specific comparisons of decapod density between the two sampling periods indicated no clear seasonal effect. In summer 1999, when seagrasses were well established, decapod biomass among the three habitats was not significantly different. During spring 2000, decapod biomass in oyster (41.40 g m⁻²) was greater than in marsh-edge (4.20 g m⁻²), but did not differ from that of seagrass (9.73 g m⁻²). There was no significant difference in decapod biomass between seagrass and marsh-edge habitats during the spring 2000 sampling period. The assemblage analysis using Schoener's PSI indicated that decapod assemblages associated with oyster were distinct from seagrass and marsh-edge habitats (which were similar). The results of this study suggest that in comparison to seagrass and marsh-edge habitats, oyster reef habitats and the distinct assemblage of decapod crustaceans that they support represent an ecologically important component of this estuarine system.

Introduction

Estuaries along the Atlantic and Gulf Coasts of the United States are comprised of various distinct habitat types that are populated by a variety of fishes and invertebrates. In Florida, common estuarine invertebrate species include commercially and recreationally important decapods such as the blue crab (*Callinectes sapidus*), and pink shrimp (*Penaeus [Farfantepenaeus] duorarum*). Other decapods such as xanthid crabs and caridean shrimps are ecologically important as both predators and prey in estuarine systems (Welch 1975; Coen et al. 1981; Leber 1985; Posey and Hines 1991; Tupper and Able 2000). Structurally complex and highly productive habitats such as seagrass meadows, salt marshes, and oyster reefs provide numerous benefits to estuarine species (Minello 1999). Seagrasses, for example, provide important habitat for numerous resident species, temporary nursery habitat for juveniles, forage areas, and refuge from predation

(see review by Jackson et al. 2001). Inundated salt marshes and their channels and edges also provide valuable habitat (Minello and Rozas 2002), refuge (Giles and Zamora 1973; Minello and Zimmerman 1983), forage (Bell 1980; Boesch and Turner 1984), and nursery functions (Weinstein 1979; Wenner and Beatty 1993; Rozas and Minello 1998). Several recent studies have also shown that oyster reefs provide some of these same benefits (Coen et al. 1997, 1999a,b; Luckenbach et al. 2000; Meyer and Townsend 2000).

Many investigators have described or attempted to quantify the inhabitants of oyster reefs through various means (e.g., Wells 1961; Dame 1979; Wenner et al. 1996; Coen et al. 1997). There are fewer published comparisons of the species composition and abundance of oyster associated fauna relative to other habitat types (e.g., seagrass, marsh-edge) especially in areas where the natural habitats occur in direct proximity to one another. However, the study by Zimmerman (1989) and recent works by Eggleston et al. (1998, 1999), Posey et al. (2001), and Stunz et al. (2002) suggest some interchangeability of habitats, depending on location, season, and species of interest, and several long-term stud-

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ies are in progress that further address these equivalency issues (Coen personal communication). Considering the seasonal variability of some vegetated habitats in many locations, i.e. seagrass and macroalgae (Sand-Jensen 1975; Larkum et al. 1984; Halliday 1995), and the occurrence of oyster reefs in many areas devoid of seagrasses (see Posey et al. 1999, 2001), the ecological functions of oyster reefs in estuarine systems deserve further attention.

We characterize the species composition, relative abundance, and biomass of decapod crustaceans occupying seagrass, marsh-edge, and oyster habitats in a relatively undisturbed shallow water estuary along Florida's central Gulf coast. The study was designed specifically to determine if the different habitat types supported unique and identifiable assemblages of decapods and whether the observed patterns might potentially vary seasonally. Although many comparative habitat studies have focused on the potential value of the habitats to the estuarine species that occupy them (e.g., Zimmerman and Minello 1984; Bell and Westoby 1986; Sogard and Able 1991; Peterson and Turner 1994; Rozas and Minello 1998), conservation and management of estuaries also requires consideration of habitat value on a larger scale. If most decapod species use available habitats fairly interchangeably, then the relative importance of any single habitat is lessened. If a habitat supports a relatively distinct set of species that rely upon it exclusively, that habitat becomes a much more important component of the ecosystem (e.g., maintenance of biodiversity). The similarity between decapod assemblages found in the various habitats is examined in this context.

Study Site

The study was conducted within the 9,357-ha St. Martins Aquatic Preserve, located along the Gulf coast in Citrus County, Florida (28°53'N, 82°41'W). This tidally dominated estuary exists as a mosaic of salt marsh and shell islands, extensive shallow creeks, bays, tidal channels, sandy flats, oyster bars, and seagrass beds. Tides are diurnal with a range of approximately one meter.

Seagrass beds are abundant within the study area (Frazer and Hale 2001) and are predominately comprised of turtle grass (*Thalassia testudinum*), and to a lesser extent shoal grass (*Halodule wrightii*) and manatee grass (*Syringodium filiforme*). Star grass (*Halophila engelmanni*) and widgeon grass (*Ruppia maritima*) are also present in the study area. *T. testudinum*, which was the dominant species at each of our three study sites, typically exhibits increased coverage (i.e., percent areal cover, shoot density, leaf length, and above-ground biomass) in summer

than in spring (Blitch unpublished data). During this investigation, seagrass cover and density at each of the three sites, was markedly reduced in spring 2000 relative to summer 1999 (Glancy personal observation).

The eastern oyster, *Crassostrea virginica*, dominates the intertidal oyster habitat, and the low relief (< 1 m) bars typically have a substrate of sand, mud, and shell fragments overlying a limestone base. The shallow intertidal oyster reef fringe (where the sampling was conducted) ordinarily transitioned from large clumps and dense shell near the interior of the bar to progressively smaller clumps of live and dead oyster, followed by single shells and finer fragments scattered on a sandy shelf. The physical makeup of this habitat (size and frequency of clumps) was qualitatively similar among sites and between the two sampling seasons. Although not as widespread as seagrass and marsh-edge habitats, oyster habitat is common within the St. Martins Aquatic Preserve.

Black needle rush (*Juncus roemarianus*) and cordgrass (*Spartina alterniflora*) dominate the low relief (< 1 m) salt marsh islands typical of the area. No sampling was carried out within the emergent vegetation. Sampling in the designated marsh-edge areas was restricted to the channel and edge habitats directly adjacent (< 1 m) to the emergent marsh vegetation. Substrates within these relatively bare areas of the marsh edge were comprised primarily of fine mud, sand, and decaying vegetation. The width of this interface between the salt marsh and the adjoining habitats was generally in the range of 2–5 m.

Materials and Methods

Three sites (all within 1 km of 28°53'N, 82°41'W) were chosen for study based on their similarities in size, water flow, wave exposure, depth, and the close association of seagrass, oyster reef and salt marsh habitats within each site. Two time periods were sampled which corresponded to times of expected high and low water temperatures (Frazer et al. 1998, 2001), and relative differences in seagrass cover characteristics (Blitch unpublished data). During the summer sampling period (July 19–August 19, 1999) and the spring sampling period (March 20–April 20, 2000), four to five days were spent at each of the three sites, yielding 40 throw-trap samples per habitat during the summer sampling period and 36 samples per habitat during the spring period, respectively.

Throw-trap sampling was conducted during daylight hours, approximately 2 h before to 2 h after low tide, when water depths were between 20 and 90 cm. This allowed time for approximately three samples to be taken from each habitat at a given

site on a single day. The sampling order of the habitats was rotated daily and sample sizes per habitat were balanced within sites and sampling periods. Samples were taken at 3–4 m intervals along the oyster fringe and the bare marsh-edge and across random transects of the seagrass bed at similar spacings. Multiple samples were taken within habitats to more accurately describe the species assemblages of each habitat. An attempt to minimize disturbance was made by moving through each habitat in a linear fashion and avoiding areas that were yet to be sampled. Within each sampled habitat, water temperature, salinity, and dissolved oxygen were recorded daily, and the resultant data averaged for each season-habitat combination.

A 1-m² (100 cm × 100 cm × 90 cm) aluminum throw-trap was used to capture decapods during this study. The size and weight of this trap, combined with the sharp leading edges of the lower panels, allowed the trap to quickly cut through vegetation and attain a tight seal (Chick et al. 1992), especially in the soft sediments of the seagrass and marsh-edge habitats. In order to ensure a tight seal in the coarser substrates of the oyster fringe, the trap was worked into the bottom with a vigorous shaking motion immediately after it was thrown, or was sealed by pouring fine shell hash along the outside perimeter of the trap.

Organisms were removed from the throw-trap with a 1-m × 1-m bar seine (1-mm mesh), and after three consecutive empty pulls, a narrow (20-cm) rake was used to agitate the substrate and uncover any animals that had attempted to burrow. The trap was then cleared with a dip net (20 cm × 25-cm opening and 1.5-mm bar mesh) until three consecutive empty sweeps were made. In the oyster habitat, shell clusters were removed from the trap (so as not obstruct the bar seine or tear the mesh) and forceps were used to remove crabs from the small recesses of the shells. The bar seine, rake and dip net were then used as in the other habitats.

The 1-m² throw-trap was chosen based on reports of its high accuracy and precision in a variety of habitats (e.g., Kushlan 1981; Chick et al. 1992; Jordan et al. 1997; Rozas and Minello 1997). Throw traps have been used extensively in marsh (Kushlan 1981; Rozas and Odum 1987; Jordan et al. 2000; Castellanos and Rozas 2001; Raposa and Roman 2001) and seagrass habitats (Sogard 1989; Sogard and Able 1991, 1994; Sheridan and Minello 1999), but have not previously been used to sample decapods in oyster reef areas. In spite of its unknown efficiency in the latter habitat, the 1-m² throw-trap effectively sampled the decapod assemblages of the three habitats with the least risk of noise from method-treatment interactions (see Peterson and Black 1994). The greatest risk for bias

among the habitats would be escape of animals during the lengthy removal process in oyster habitat, resulting in a subsequent underestimation of density and biomass. A preliminary study was conducted that showed that two species of mud crabs common to oyster habitat could be introduced and then removed in the standard manner with a recapture efficiency (ca. 75%) that was within the range of removal efficiencies reported by Wenner and Beatty (1993, 44–66%), Rozas and Reed (1994, 85–100%), and Rozas and Odum (1987, 93–100%) in vegetated habitats.

Samples were frozen prior to processing in the laboratory, and then thawed, rinsed, and blotted dry. All decapods were then identified to the lowest possible taxon according to Williams (1984) and Abele and Kim (1986) and their total weight was recorded for each sample.

Data Analysis

ABUNDANCE AND BIOMASS

The effects of season, site, and habitat (including site-by-season and habitat-by-season interactions) on total decapod density and biomass were analyzed using a mixed model ANOVA (Proc Mixed; SAS Institute 1996) after assumptions of normality (Proc Univariate) and homogeneity of variances were verified (Levene's test). Significant effects ($p < 0.05$) were then further delineated with a post-hoc least-squared means test (LSMeans; SAS Institute 1996). To guard against possible error that can result from making multiple comparisons on the same data set, adjusted p-values for the least-squared means comparisons were also calculated using the Bonferroni procedure. As the Bonferroni correction has been criticized for being overly conservative (Perneger 1998) the unadjusted p-values are provided along with the adjusted values (Bp) for the readers' benefit.

SPECIES ASSEMBLAGES

A species assemblage was described for each sampling period-habitat combination. Assemblages included species with > 1% numerical abundance that also occurred in > 5% of the samples within each habitat during a specific sampling season. Species that occurred in at least 25% of the samples from a habitat were also included regardless of numerical abundance. These criteria were chosen to identify assemblages of common and abundant species from each habitat. Species included in these assemblages accounted for 98 to 99% of the total abundance within each habitat.

Similarities and overlap between assemblage pairs (e.g., summer seagrass versus summer oyster) were compared using Schoener's overlap index (Schoener 1970; Hurlbert 1978). This index, also

TABLE 1. Mean (SE; range) water temperature (°C), salinity (‰), dissolved oxygen (mg l⁻¹), and water depth (cm) by season and habitat for all sampling sites within the St. Martins Aquatic Preserve, 1999–2000.

Parameter	Seagrass	Oyster Reef	Marsh-edge	Grand Mean
Summer 1999				
Water temperature	30.96 (0.63; 28.2–37.0)	30.53 (0.33; 27.5–32.4)	31.51 (0.61; 28.0–36.1)	30.99
Salinity	13.75 (2.86; 5.5–21.0)	13.62 (3.39; 76.5–20.0)	17.91 (2.13; 7.5–21.0)	15.28
Dissolved oxygen	5.94 (0.50; 3.1–8.95)	6.11 (0.36; 3.0–7.8)	6.59 (0.83; 1.7–12.7)	6.21
Water depth	63.80 (1.6; 40.0–80.0)	39.60 (2.9; 15.0–80.0)	37.30 (4.0; 5.0–80.0)	46.90
Spring 2000				
Water temperature	22.34 (0.91; 17.5–25.8)	21.40 (0.60; 16.5–23.6)	22.89 (1.07; 16.4–28.0)	22.21
Salinity	17.53 (2.06; 13.0–25.0)	20.50 (1.77; 12.0–25.0)	16.18 (1.95; 9.5–25.0)	18.00
Dissolved oxygen	8.70 (0.54; 6.7–12.1)	7.45 (0.44; 5.10–9.60)	8.37 (0.41; 6.70–10.57)	8.15
Water depth	55.8 (3.8; 15.0–90.0)	21.70 (2.7; 5.0–50.0)	44.70 (4.8; 5.0–90.0)	40.71

known as the PSI, is one of the simplest and most attractive measures of niche overlap because it yields an accurate (Linton et al. 1981) and easily interpreted measure (i.e., percentage) of the actual area of overlap of the resource utilization curves (Krebs 1999). Abundances within the designated assemblages were standardized to percentages so that the relative abundances summed to 100% in each habitat. The index was then calculated as:

$$P = \sum_i \text{minimum} (p_{1i}, p_{2i})$$

where P = percentage similarity between assemblage 1 and 2, p_{1i} = percentage of species i in as-

semblage 1, and p_{2i} = percentage of species i in assemblage 2.

Results

As expected, due to the close proximity of the habitats within and among the three sites, physical and chemical variables were similar among habitats within each sampling period (Table 1). Between sampling periods, only water temperature was markedly different, i.e., 31°C and 22°C in summer and spring respectively.

A total of 17,985 decapods were collected, representing 14 families, 21 genera, and 28 species (Table 2). The mixed model ANOVA indicated significant (p < 0.05) habitat and season effects on

TABLE 2. Abundance of decapods by sampling period and habitat type for all sampling sites within the St. Martins Aquatic Preserve, Florida, 1999–2000. Species are listed in rank order of overall abundance. Italics indicates inclusion in designated assemblage for that season-habitat. Numerals in parentheses indicate the rank order of a species within the season-habitat assemblage, and the number of samples in which the species occurred in that season-habitat. (N = 40 for each habitat in Summer 1999, N = 36 for each habitat in Spring 2000).

Species	Summer 1999				Spring 2000				Overall
	Seagrass	Oyster Reef	Marsh-edge	Total	Seagrass	Oyster Reef	Marsh-edge	Total	
<i>Eurypanopeus depressus</i>	8	<i>4,105</i> _(1,40)	<i>9</i> _(9,5)	4,122	0	<i>3,184</i> _(1,36)	0	3,184	7,306
<i>Panopeus herbstii</i>	0	<i>618</i> _(3,40)	<i>9</i> _(10,6)	627	0	<i>1,514</i> _(2,36)	20	1,534	2,161
<i>Hippolyte zostericola</i>	<i>1,522</i> _(1,38)	11	<i>11</i> _(8,4)	1,544	<i>172</i> _(3,24)	1	0	173	1,717
<i>Petrolisthes armatus</i>	1	<i>1,184</i> _(2,36)	0	1,185	0	<i>395</i> _(3,36)	<i>8</i> _(7,3)	403	1,588
<i>Palaemonetes intermedius</i>	<i>1,122</i> _(2,40)	3	<i>111</i> _(2,9)	1,236	<i>273</i> _(2,30)	1	<i>2</i> _(11,2)	276	1,512
<i>Neopanope texana</i>	<i>282</i> _(9,34)	<i>44</i> _(5,11)	<i>106</i> _(3,11)	432	<i>742</i> _(1,35)	3	<i>6</i> _(8,6)	751	1,183
<i>Alpheus heterochaelis</i>	<i>260</i> _(5,34)	<i>95</i> _(4,25)	<i>17</i> _(7,8)	372	<i>88</i> _(5,21)	<i>270</i> _(4,3)	<i>6</i> _(9,4)	364	736
<i>Rhithropanopeus harrisi</i>	<i>254</i> _(6,27)	7	<i>141</i> _(1,19)	402	<i>157</i> _(4,21)	0	<i>12</i> _(5,8)	169	571
<i>Penaeus duorarum</i>	<i>394</i> _(3,40)	<i>24</i> _(6,15)	<i>44</i> _(6,15)	462	<i>24</i> _(10,14)	3	<i>3</i> _(10,3)	30	492
<i>Palaemonetes pugio</i>	<i>132</i> _(7,16)	1	<i>67</i> _(4,11)	200	<i>44</i> _(7,5)	0	<i>9</i> _(6,4)	53	253
<i>Callinectes sapidus</i>	<i>74</i> _(8,25)	1	<i>63</i> _(5,27)	138	<i>35</i> _(8,20)	<i>9</i> _(6,9)	<i>26</i> _(2,4)	70	208
<i>Processa bermudensis</i>	1	0	1	2	<i>50</i> _(6,16)	1	1	52	54
<i>Uca speciosa</i>	0	0	10	10	0	0	<i>41</i> _(1,6)	41	51
<i>Upogebia affinis</i>	1	9	1	11	1	<i>25</i> _(5,10)	0	26	37
<i>Periclimenes americanus</i>	2	0	0	2	<i>28</i> _(9,12)	1	0	29	31
<i>Macrocoeloma trispinosum</i>	3	0	0	3	<i>13</i> _(11,11)	2	1	16	19
<i>Erytium limosum</i>	1	0	2	3	0	0	<i>13</i> _(4,3)	13	16
Total	4,061	6,134	593	10,788	1,32	5,13	152	7,197	17,985

Note: Seven crab species and four shrimp species collected during the two seasons were not included in the statistical analysis due to their lower numerical abundance (45 individuals total, <10 per species); their numbers are included in the above totals.

density, but no significant site ($p > 0.05$), site-by-season, or habitat-by-season interaction effects. During the summer sampling period, mean decapod density did not differ between oyster and seagrass habitats, though both habitat types supported greater densities of decapods than the marsh-edge. During the spring sampling period oyster reef habitat supported a greater mean decapod density than both seagrass and marsh-edge, which supported similar densities of decapods. Although the mixed model ANOVA initially detected a seasonal effect on density within habitats, the LSM means post-hoc analysis (combined with the conservative Bonferroni correction) provided no additional statistical support for the nature of the effect.

The mixed model ANOVA for decapod biomass showed a significant ($p < 0.05$) effect only for habitat. In the summer, decapod biomass was not statistically different among the three habitats (Table 4). In the spring sampling period, decapod biomass in oyster (41.40 g m^{-2}) was greater than marsh-edge (4.20 g m^{-2}), but did not differ from that of seagrass (9.73 g m^{-2}). Decapod biomass within seagrass and marsh-edge was not significantly different.

Six species made up the oyster decapod assemblage in both seasons (Table 2), although two species of mud crabs, *Eurypanopeus depressus* and *Panopeus herbstii*, and the green porcelain crab, *Petrolisthes armatus*, accounted for approximately 95% of the abundance in both sampling periods. *Alpheus heterochaelis* was the fourth most abundant species in the assemblages during both sampling periods, and although it never comprised more than 5% of the total abundance, it occurred in a high number of samples (~62%) in both seasons.

The summer seagrass assemblage was comprised of eight species (Table 2). The assemblage was dominated by two species of caridean shrimp (*Hippolyte zostericola* and *Palaemonetes intermedius*) and the pink shrimp (*P. [F.] duorarum*) that accounted for 37.7%, 27.8%, and 9.8% of the abundance, and occurred in 95%, 100%, and 100% of the samples, respectively. During summer, the remaining five species each accounted for 1.8–7.0% of the total abundance and occurred in a minimum of 40% of the samples. The spring seagrass assemblage was comprised of 11 species (Table 2) and was dominated by the Texas mud crab, (*Neopanope texana*), which accounted for 45.6% of the total abundance and occurred in 97.2% of the samples. *P. intermedius* and *H. zostericola* followed with 16.8% and 10.6% abundance, and 83.3% and 66.6% percent occurrence, respectively. The remaining members of the assemblage represented 0.8–9.7% of the total abundance, and occurred in a minimum of 13.9% of the samples.

The marsh-edge assemblage for the summer period was comprised of 10 species (Table 2). Harris' mud crab, *Rhithropanopeus harrisi*, exhibited the highest total abundance (24.4%) and occurred in 47.5% of the samples. *Palaemonetes intermedius*, *N. texana*, *C. sapidus*, and the marsh grass shrimp (*Palaemonetes pugio*), each accounted for at least 10% of the total abundance and occurred in at least 22% of the samples. Although only fifth most abundant, *C. sapidus* was the most frequently occurring species and was present in 67.5% of the samples. The spring marsh-edge assemblage was comprised of 11 species (Table 2). The fiddler crab, *Uca speciosa*, was the most abundant member of this assemblage, followed by *C. sapidus* and *P. herbstii*. These species accounted for 28.1%, 17.8%, and 13.7% of the total abundance, but occurred in only 16.6%, 11.1%, and 19.4% of the samples, respectively. *R. harrisi* was the fifth most abundant species in the assemblage, but exhibited the highest percent occurrence (22.2%).

Irrespective of season, seagrass and oyster assemblages were the least similar (summer 3.7%; spring 5.6%). Oyster and marsh-edge assemblages also exhibited little overlap within seasons (summer 7.2%; spring 23.5%). Decapod assemblages in seagrass and marsh-edge habitats exhibited the most overlap (summer 50%; spring 24.2%). Within-habitat comparisons between-seasons revealed that the assemblages from oyster habitat remained the most similar (78.1%), followed by decapod assemblages in seagrass (52.1%) and marsh-edge (35.8%) habitats.

Discussion

With twice the overall decapod abundance of seagrass, and more than 15 times that of marsh-edge habitat, oyster reefs certainly appear to be an ecologically important habitat within the shallow estuarine waters of the St. Martins Aquatic Preserve. Many previous studies have shown that greater densities of organisms occur in structural habitats such as seagrass relative to non-structural habitats (e.g., Orth and Van Montfrans 1987; Heck et al. 1989, 1995; Rozas and Minello 1998). Consistent with these studies, we found that structurally complex habitats (i.e., oyster and seagrass) generally supported greater densities of decapod crustaceans than bare marsh-edge habitats. During the summer, when seagrasses were well developed, decapod densities were similar to those in the oyster habitat, and both seagrass and oyster supported much greater densities of decapods than the sparsely vegetated marsh-edges. In the spring, when seagrass structural characteristics (i.e., shoot density, leaf length, and areal coverage) were at a minimum (Glancy personal observation), decapod

TABLE 3. Results of LSMeans comparisons for total decapod density within season-habitat combinations for all sites combined within the St. Martins Aquatic Refuge, Florida, 1999–2000. Only relevant comparisons, as indicated by the mixed-effects model, are shown. Mean densities (individuals m^{-2}) for each season-habitat combination are shown in parentheses. (Bp = Bonferroni adjusted p-values)

Habitat	Seasonal Comparisons					
	Summer 1999	Spring 2000	df	T	p	Bp
Oyster	(153.90)	(150.88)	4	-0.23	0.8312	1.0000
Seagrass	(101.61)	(45.44)	4	-4.24	0.0133	0.1990
Marsh-edge	(15.29)	(4.33)	4	-0.83	0.4544	1.0000
Comparison						
	df	T	p	Bp		
Summer 1999						
Oyster (153.90) versus Seagrass (101.90)	4	3.93	0.0171	0.257		
Oyster (153.90) versus Marsh-edge (15.29)	4	-10.41	0.0005	0.0072		
Seagrass (101.90) versus Marsh-edge (15.29)	4	-6.49	0.0029	0.0437		
Spring 2000						
Oyster (150.88) versus Seagrass (45.44)	4	7.66	0.0016	0.0234		
Oyster (150.88) versus Marsh-edge (4.33)	4	-10.65	0.0004	0.0066		
Seagrass (45.44) versus Marsh-edge (4.33)	4	-2.99	0.0405	0.6068		

densities within seagrass more closely resembled those found in the marsh-edge. During the spring sampling period, the difference in decapod density between the structurally complex oyster habitat and the two comparatively bare habitats was most evident. It is important to recognize that our sampling of the marsh channel and edge habitats during low tide may not reflect the temporal patterns of occupancy exhibited by decapods that exploit the marsh and its associated resources. Although the results of the pairwise seasonal comparisons within habitats were not statistically significant, it is noteworthy that in comparison to the summer sampling period, decapod densities in the spring were lower by more than 55% in seagrass, and 71% along the marsh edge, yet remained virtually unchanged in oyster habitat. The unadjusted p-values suggest that the significant seasonal effect found in the mixed-model ANOVA might be attributed to the reduction in density within seagrass in the spring (see Table 3).

Biomass measures also suggest the importance

of oyster habitat in this system. Overall decapod biomass averaged $34.7 g m^{-2}$ in oyster, $11.6 g m^{-2}$ in seagrass, and $6.9 g m^{-2}$ in marsh-edge over the course of this study. During the summer, when seagrass beds were relatively dense (Glancy personal observation), the interstitial spaces and three-dimensional structure afforded by the oyster shell matrix supported more than twice the mean biomass of that observed in seagrass ($27.98 g m^{-2}$ and $13.44 g m^{-2}$, respectively) and almost three times that in the marsh-edge habitat ($9.65 g m^{-2}$). The difference in biomass measures among the three habitats during the summer sampling period was not statistically significant (see Table 4), most likely due to the greater variability of biomass data that resulted from the occasional presence of very large specimens (i.e., blue crabs) in the marsh-edge. During the spring, when seagrass cover was noticeably reduced (see above), oyster habitat supported nearly 4.5 times the biomass of seagrass, and roughly 11.5 times that of marsh-edge habitat. In spite of this, the only statistically significant differ-

TABLE 4. Results of LSMeans comparisons for total decapod biomass within season-habitat combinations for all sites combined within the St. Martins Aquatic Refuge, Florida, 1999–2000. Only relevant comparisons, as indicated by the mixed-effects model, are shown. Mean biomass measures (gm^{-2}) for each season-habitat combination are shown in parentheses. (Bp = Bonferroni adjusted p-values).

Comparison	df	T	p	Bp
Summer 1999				
Oyster (27.98) versus Seagrass (13.44)	4	2.62	0.0591	0.8858
Oyster (27.98) versus Marsh-edge (9.65)	4	-3.06	0.0376	0.5640
Seagrass (13.44) versus Marsh-edge (9.65)	4	-0.62	0.5664	1.0000
Spring 2000				
Oyster (41.40) versus Seagrass (9.73)	4	5.81	0.0044	0.0657
Oyster (41.40) versus Marsh-edge (4.20)	4	-6.75	0.0025	0.0377
Seagrass (9.73) versus Marsh-edge (4.20)	4	-0.99	0.3763	1.0000

ence in decapod biomass was between oyster and marsh-edge habitats. The temporal stability in biomass and abundance within the oyster habitat further accentuates its potential significance within this estuary. In addition, the consistent habitat effects on abundance and biomass among sites suggest that the localized patterns of habitat use may hold over a larger landscape-scale within the broader study region. The lack of significant site effects may also be attributable to the deliberate choice of sampling sites with very similar physical characteristics. Documenting these larger-scale spatial patterns of habitat use by decapods is essential to a fuller understanding of the ecology of this area and others with similar habitat characteristics.

In spite of their dominance in terms of decapod abundance and biomass, the oyster reefs in this study harbored the least diverse of the three assemblages. While the oyster assemblage had six members in both seasons, the high numerical abundance was due primarily to three resident species. During both seasons, *E. depressus*, *P. armatus*, and *P. herbstii* accounted for roughly 95% of the total abundance and occurred together in at least 95% of all the samples. PSI analysis showed this highly predictable assemblage to be quite distinct from the seagrass and marsh-edge assemblages. Overlap averaged only 4.6% between oyster and seagrass for the two seasons, and the two habitats had only three of eight species in common in the summer and only two of eleven in spring. Assemblage overlap between oyster and marsh-edge assemblages was slightly higher (mean = 15.3%), as nearly all of the species found in oyster during this study were sampled from the marsh edge as well (Table 2). They were found in far fewer numbers (e.g., *E. depressus*; $n = 7,289$ in oyster, $n = 9$ in marsh-edge) in the latter habitat. In spite of the low within-habitat decapod diversity in oyster, the low overlap with seagrass and marsh-edge assemblages suggests a unique and important contribution to overall species diversity of this estuarine area.

The low within-habitat diversity in oyster appears to be related to the types of species utilizing the habitat. In oyster, the dominant species were primarily residents specially suited to the unique structure and forage offered by this harsh intertidal habitat. *E. depressus* and *P. herbstii* were two of the most habitat-dependent (specialist) species sampled in this study, based on their predominance in oyster. *Panopeus herbstii* is a predator on oysters and other mollusks (Dame and Patten 1981; McDonald 1982) and *E. depressus* is an omnivore that feeds primarily on algae and detritus (Bahr 1974; McDonald 1977), along with amphipods, polychaetes, sponges, and other crabs (Bahr 1974; McDonald 1982). Other investigators have also documented

the dominance of these xanthid crabs in oyster habitat (e.g., Wells 1961; Zimmerman 1989; Micheli and Peterson 1999). Meyer (1994) and McDonald (1977, 1982) found that where they co-occurred, *E. depressus* utilized the crevasses within oyster clumps, while *P. herbstii* utilized the area under the clumps and single shells of the rubble zone. In addition to the benefits of refuge from predation, Grant and McDonald (1979) point out that such associations also provide protection against the harsh environment of the intertidal zone. The behavior of these species allows them to avoid desiccation during the tidal exposure of the reefs, which may force other decapods out of the habitat and thereby expose them to increased predation. With the high densities of resident crabs remaining on the reef during ebb tides, non-resident species that return with the flood tide likely find most of the available refuge occupied.

In contrast to oyster reefs, seagrass and marsh-edge harbored richer and more evenly represented species assemblages during both sampling periods. Between eight and 11 species comprised these assemblages, and there was a substantial 37.1% average overlap between them. Eight of the 11 members of the seagrass assemblage also used marsh-edge habitat during this study. Other studies have also found that salt marshes and seagrass support quite similar species assemblages, although the degree of usage varies between habitats and among species (Zimmerman and Minello 1984; Rozas and Minello 1998). Rozas and Minello (1998) found that marsh-edge assemblages were highly influenced by adjacent habitat types. These investigators concluded that where salt marshes and seagrasses co-occurred, most decapods preferred salt marsh or showed no preference. In this study, seagrass beds were adjacent to much of the sampled marsh edges, and this may help to explain the high overlap between the respective assemblages. Marsh-edge offered the most interchangeable of the habitats (and thus most diverse), sharing many species from both oyster and seagrass habitats, although at significantly lower densities in most cases.

The species that were sampled primarily in seagrass and marsh-edge habitats were less-specialized resident (e.g., *C. sapidus*) and transient species (e.g., *P. [F]. duorarum*) that are able to utilize both habitat types for their forage, refuge, and nursery qualities. The blue crab, *C. sapidus*, for example, is a commercially important generalist that is known to occupy seagrass beds as juveniles (Orth and van Montfrans 1987; Thomas et al. 1990), but shallow marsh channels (Zimmerman and Minello 1984; Orth and van Montfrans 1990; Thomas et al. 1990; Wilson et al. 1990) and other shallow shoreline ar-

eas (Ruiz et al. 1993; Dittel et al. 1995; Hines and Ruiz 1995) may be important habitats especially for larger juveniles. The blue crab was a relatively dominant member of both seagrass and marsh assemblages in this study and their abundance was similar in both habitat types, though larger individuals were sampled in the marsh-edge habitat relative to seagrass. The mean carapace width of *C. sapidus* in the marsh was 43.98 mm during spring and only 19.67 mm in seagrass during the same sampling period. In summer, the mean carapace widths of sampled blue crabs were 26.54 mm and 18.63 mm for marsh and seagrass habitats, respectively (Glancy unpublished data).

The pink shrimp (*P. [F.] duorarum*) is also a commercially important species that occupies estuaries during the juvenile portion of its lifecycle before moving to deeper offshore waters. As in this study, Rozas and Minello (1998) found high abundance of *P. [F.] duorarum* in seagrass habitat, but low densities in non-vegetated bottoms adjacent to salt marshes. During the summer sampling period, similarly sized *P. [F.] duorarum* (ca. 12 mm carapace length [CL]) occupied each of the three habitats, while in the spring, larger shrimp (> 25 mm CL) were found in marsh-edge and oyster habitats than in seagrass (ca. 17 mm CL; Glancy unpublished data).

Although the dominant decapods within oyster habitat in this study are not of commercial importance, they and other oyster reef inhabitants represent a potentially significant food source for predatory fish that migrate onto oyster reefs to feed during flood tides. Many of these fish, such as spotted seatrout (*Cynoscion nebulosus*), redfish (*Sciaenops ocellatus*), sheepshead (*Archosargus probatocephalus*), and assorted flounders (*Paralichthys* spp.), are commercially and recreationally important species that feed on decapods associated with oyster reefs (Coen et al. 1999b; Posey et al. 1999; Luckenbach et al. 2000). Xanthid crabs also make up a significant portion of the diet of large blue crabs (Laughlin 1982). As a stable food source during times when seagrass fauna are greatly reduced, the decapods that dominate oyster reef habitats represent a significant amount of biomass that may serve as a potentially important (though unquantified) food resource in this estuary.

A basic assumption in many field studies is that mobile, epifaunal invertebrates have the ability to choose among habitats with different qualities that lead to enhanced growth and survival and, as such, habitats with higher abundances are assumed to be more valuable (Zimmerman and Minello 1984; Bell and Westoby 1986; Peterson and Turner 1994; Perkins-Visser et al. 1996; Rozas and Minello 1998). Value and quality are highly subjective

terms that should be used cautiously, and to assume selection or preference based solely on patterns of occupancy ignores the many underlying processes and interactions involved. Patterns of occupancy may suggest greater habitat quality or active selection by certain species, but specific, detailed studies are required to verify these assumptions.

Mechanisms that underlie the relatively high abundance of decapods within oyster reef habitat are unclear, but may include factors such as increased survival or greater availability of forage. Refuge from predators has been one of the most touted benefits of vegetated habitats such as seagrasses and marshes. Coen et al. (1981) and others (e.g., Nelson 1979; Heck and Thoman 1981; Stoner 1982) have shown that foraging efficiency of predators is significantly reduced by increases in the structural complexity of aquatic vegetation. Although the three-dimensional nature of seagrasses affords a great deal of refuge from predators for decapods, it seems to do so more by providing opportunities for cryptic avoidance (Heck and Wetstone 1977) rather than through actual physical protection. The still-articulated but dead oyster shells, and the interstitial spaces between the cemented live and dead shells associated with oyster reefs, on the other hand, appear to offer a nearly impenetrable refuge for some of the most abundant resident decapods. The physical protection oyster reefs provide, especially to juvenile decapods, could be a significant factor in explaining the high abundance and biomass within these habitats. There is no information to date on the turnover rates of individuals in oyster habitat that, in turn, would provide insight into the refuge function of this habitat. Similar measurements made concomitantly in the other habitats investigated here could also provide insight into their relative importance as foraging habitats for predators in this system.

The comparatively high measures of abundance and biomass within oyster reef habitat in this study suggest that these areas provide an important refuge and foraging habitat for several estuarine decapods. Assemblage analysis has also shown oyster reefs to support a distinct group of decapods, further underscoring the importance of this habitat as it contributes to the overall biodiversity of this and potentially other estuarine systems. Although we did not attempt to quantify the specific characteristics that underlie habitat quality, the findings suggest that the seasonally stable forage and complex refuge provided from both predators and pressures of the harsh intertidal environment allows oyster reefs to maintain high abundance and

biomass of ecologically important decapod crustaceans.

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