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BIODIVERSITY OF SESSILE AND MOTILE MACROFAUNA ON INTERTIDAL OYSTER REEFS IN MOSQUITO LAGOON, FLORIDA

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ABSTRACT Our research focused on determining the diversity and abundance of sessile and motile macrofauna that use intertidal reefs of the eastern oyster *Crassostrea virginica* for feeding, settlement space or refuge in Mosquito Lagoon, Florida. Five replicate lift nets were deployed at six sites (three impacted reefs with seaward margins of disarticulated shells, three reference reefs without dead margins) to determine the species composition and numbers present on these reef types. All nets were deployed intertidally on backreef areas on living oyster reefs, just above mean low water. One and a half liters of live oysters and oyster shells were placed in each net ($1m^2$) on deployment. Nets were surveyed for all fauna monthly for one year. Metrics used to evaluate habitat use were species richness (total number of different species found) and density (total number of organisms per net). Comparisons were also made between community assemblages found on the two different types of reefs in the area (with and without dead margins) and for sessile species, recruitment on living oysters versus disarticulated shells. Forty sessile and 64 motile species of macroorganisms were found utilizing the oyster reefs in Mosquito Lagoon. However, recruitment on live oysters was twice that on disarticulated shells. Significant temporal variations were documented. When the two reef types were compared, however, no differences were found.

KEY WORDS: oysters, *Crassostrea virginica,* habitat use, fishes, decapods, barnacles, invertebrates, lift nets

INTRODUCTION

Human activities threaten the productivity, diversity, and survival of coastal resources, leading to a growing need to understand and manage all coastal zones (e.g., Jackson et al. 2001). The Indian River Lagoon system (IRL) on the east central Florida coast is one such place. This estuary extends 251 km, from Ponce de Leon Inlet to Jupiter Inlet. The Lagoon system is a series of three distinct, but connected, estuaries: the Indian River, the Banana River and Mosquito Lagoon. This lagoon system may contain the richest biota of any estuary in North America (Provancha et al. 1992). It supports over 3,000 animal and plant species, 50 of which are listed as threatened or endangered. Commercially important intertidal reefs of the eastern oyster *Crassostrea virginica* are common in this estuarine system.

Diversity is extremely high in the IRL because of its location within a zoogeographic transition zone (e.g., Walters et al. 2001, Smithsonian Institution 2006). Researchers have documented the substantial species diversity of many habitats and taxa in IRL waters: seagrass and its associated organisms (e.g., Virnstein et al. 1983, Dawes et al. 1995); finfish (Gilmore 1977, Gilmore 1995, Tremain & Adams 1995); elasmobranchs (Snelson & Williams 1981) and decapods (Smithsonian Institution 2006). To date, there have been no studies of the biodiversity on intertidal oyster reefs in the IRL.

Three-dimensional reef structures of *Crassostrea virginica* are created by years of successive settlement of larvae on adult shells (Dame 1996). Through its structural complexity, these ecosystem engineers create heterogeneity that is rare in marine systems dominated by soft-bottom habitats (e.g., Bartol et al. 1999, Micheli & Peterson 1999). Organisms use oyster reefs for many different reasons; mobile species may: (1) feed directly on live oysters, (2) use shell surfaces for spawning and (3) seek refuge from predation within oyster clusters (e.g., Tolley & Volety 2005), whereas sessile species use oyster reefs for attachment space.

Previous studies on intertidal oyster reef biodiversity include: Wells 1961 (North Carolina), Dame 1979 (South Carolina), Bahr and Lanier 1981 (south Atlantic coast), Crabtree and Dean 1982 (South Carolina), Wenner et al. 1996 (South Carolina), Coen et al. 1999a (South Carolina), Posey et al. 1999 (North Carolina), O'Beirn et al. 2004 (Virginia) and Tolley et al. 2005 (Florida, Gulf of Mexico). In most of these studies, the primary focus was on motile species (fish and crustaceans). Our study adds to this database by investigating the recruitment of motile macrofauna on backreef regions of intertidal oyster reefs of *Crassostrea virginica* in the IRL system along the Atlantic Coast of Florida. In addition, this is the first study in Florida to quantify diversity and abundance of all sessile macrofauna on oyster reefs.

METHODS

Study Site

All research was conducted in Mosquito Lagoon, within the boundaries of Canaveral National Seashore (28°90.68W; 80°82.06N) (Fig. 1). Except where dredged, the average depth of the Lagoon is less than 1 m and the current is primarily wind-driven (Walters et al. 2001). Annual salinity ranges between 18 and 45 ppt, depending on rainfall (Grizzle 1990, Walters et al. 2001).

Within a 5-y period (1998–2003), the number of recreational boat registrations within the counties that border Mosquito Lagoon increased by 43% (Wall et al. 2005). This increasing intensity of year-round boating has helped create piles of disarticulated shells (dead margins) on the seaward edges of oyster reefs along major navigational channels in these shallow waters (Grizzle et al. 2002, Wall et al. 2005). We compared back-reef areas on reefs with and without dead margins to determine if recreational boating pressures influenced biodiversity.

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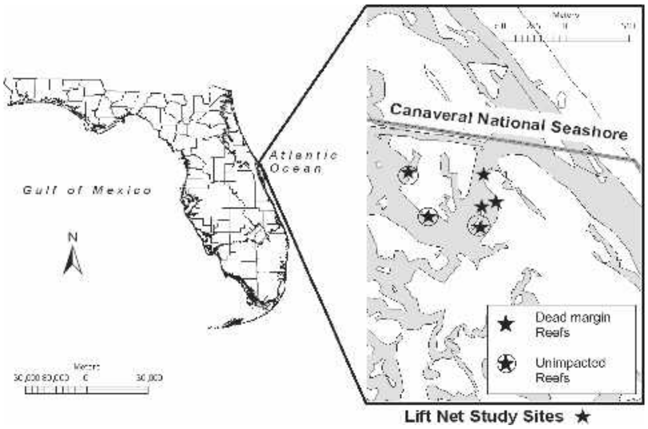

Figure 1. Lift nets study sites in Mosquito Lagoon, Florida.

Lift Net Field Sampling

Six oyster reefs were selected for this study, three impacted reefs (with dead margins) and three reference reefs (without dead margins). All were within a 5-km radius (Fig. 1). Five replicate lift nets were placed on the back-reef area of each reef. The protected back-reef areas were chosen to minimize the loss of nets caused by water motion.

Lift net methods were adapted from Crabtree and Dean (1982), Coen et al. (1996a), and later modified by Tolley et al. (2005) for use in Florida systems. We further modified the protocol to include the enumeration of sessile species recruiting to oyster reefs. Lift net frames were 1 m^2 and created from 3.8 cm diameter PVC. The nets were 0.5 m deep. The sides of the nets were made from 3.2 cm diameter opening mesh and the bottom was made from a 1-m square of 0.2-cm diameter opening mesh. The two mesh sizes were machine-sewed together using extra strength cloth thread. The sewn mesh was attached to the PVC frame with cable ties (tensile strength: 11 kg).

Lift nets were deployed intertidally, just above mean low water, on living oyster reefs. Volume normalized oysters and oyster shells in good condition (1.5 L) were placed in the lift nets. Half (0.75 L) were single, disarticulated shells from adults (Mean ± SE length: 77.5 ± 1.4 mm; weight: 21.5 ± 1.1 g) and half were similar-sized live clusters collected from the oyster reef. All were mechanically scraped clean of epiflora and epifauna. New shells and clusters were placed into the nets each month. Additionally, at the time of net retrieval, all nets were cleaned to remove organisms that had settled on the mesh or PVC frames.

Lift nets were retrieved by swiftly picking up the nets on two sides and collecting all recruited motile and sessile organisms. In the laboratory, we identified all organisms within 24 h and returned them alive to Mosquito Lagoon. Only sessile organisms attached to oyster shells within the lift nets were counted. Nets were collected monthly for 12 mo (June 2004 to July 2005). No data was collected for September 2004 because Hurricanes Charley, Jeanne and Frances required removal of nets and prevented data collection. Specimens of each species were preserved in 70% isopropanol to create a species archive for the University of Central Florida.

Environmental Variables

Permanent temperature monitors (Onset Stowaway Tidbit Temperature Loggers) were attached to cinder blocks and deployed at each site in water at the same depth as the lift nets. Temperature data were collected once each hour. Salinity was measured on net retrieval using a portable refractometer. Three sediment traps were deployed at each site at the same depth as the lift nets to determine sediment load accumulations during the 4-wk intervals between sampling. Each replicate, cylindrical PVC pipe sediment trap (10-cm diameter × 25 cm deep) was submerged flush with the substrate (Lenihan 1999). We capped traps underwater at the time of retrieval. The sediment traps were retrieved concurrently with the lift nets and new traps were immediately deployed to replace them. Total sediment mass was determined by drying samples at 60°C for 48 h in a drying oven (Econotherm Model Number 51,221,126) and weighing contents on a top-loading balance (O'Haus Scout 2-Model Number SC6010). Relative grain size was determined by grinding the dried sediment and sorting samples with a sieve (0.062 mm) to separate the silt/clay from the sand/gravel fractions.

Analyses

For all cases where analysis of variance (ANOVA) tests were run, prior to running the ANOVAs, homogeneity of variance and normality were tested using Levene and Kolmagorov-Smirnov tests. If significant differences were found with ANOVA, *post-hoc* Tukey-Kramer tests were run. Data assumptions of variance and normality were met for all ANOVAs at the $P = 0.05$ level, thus the data were not transformed.

Sessile Macrofauna

Response variables of species richness (total number of different species) and density (total number of individuals) were analyzed using a 4-way, nested. ANOVA. The factors in the nested ANOVAs were: (1) reef type (reefs with dead margins or reference reefs), (2) month, (3) site and (4) shell type (disarticulated shells or live oysters in clusters). Reef type, month and shell type were fixed factors, whereas site was random. Shell type was nested within site, and site was nested within reef type.

Motile Macrofauna

Community metrics of motile species were similarly examined with a 3-way ANOVA. Response variables of species richness and density were examined as in sessile species. For each ANOVA, the factors were reef type (fixed), site nested within reef type (random), and month (fixed).

Sediment Loads

A 3-way ANOVA was conducted to test whether sediment loads on oyster reefs varied as a function of the following fixed factors: reef type (reference or dead margins) and month. The third factor, site, was random and nested within reef type.

RESULTS

Biodiversity and Composition

Sessile Macrofauna

Twenty-five species of sessile invertebrates recruited to oysters and oyster shells in the lift nets during our study (Table 1). Barnacles in the genus *Balanus* (Arthropoda) dominated all samples numerically. Tube worms in the genus *Hydroides*, the jingle shell *Anomia simplex*, the eastern slipper shell *Crepidula astrasolea*,

TABLE 1.

Total numbers of sessile species collected in lift nets on intertidal oyster reefs in Mosquito Lagoon, Florida.

Phylum	Species	Common Name	Total	6/04	7/04	8/04	10/04	11/04	12/04	1/05	2/05	3/05	4/05	5/05	6/05
Porifera	*Hymeniacidon heliophila*	Sun sponge	28	2	2	1	0	11	0	3	0	1	2	4	2
	Halichondria melandocia	Black volcano sponge	66	1	0	0	0	0	5	0	0	0	0	3	57
	Cliona spp.	Boring sponge	13	0	1	0	0	0	0	9	1	2	0	0	0
Cnidaria	*Aiptasia pallida*	Sea anemone	2	0	0	0	0	0	0	2	0	0	0	0	0
	Haliplanella luciae	Striped anemone	2	0	0	0	0	0	0	0	0	1	1	0	0
Annelida	*Hydroides spp.*	Tube worms	2842	658	491	760	250	134	111	66	33	65	55	42	177
	Sabella spp.	Feather duster worm	46	2	1	9	6	4	6	7	0	0	1	9	1
Arthropoda	*Balanus eburneus*	Ivory barnacle	8782	2070	2447	1380	720	430	210	145	87	132	99	251	811
	Balanus amphitrite	Purple striped barnacle	1524	438	461	450	46	16	13	9	1	5	6	8	71
Mollusca	*Crassostrea virginica* recruits	Eastern oyster	722	173	92	54	69	104	91	7	3	18	4	12	95
	Anomia simplex	Jingle shell	1120	186	178	184	151	93	83	41	4	43	45	80	32
	Crepidula astrasolea	Eastern slipper shell	1178	287	154	207	149	69	59	31	4	25	44	73	76
	Crepidula fornicata	Atlantic slipper shell	40	12	0	3	4	4	0	9	0	1	1	0	6
	Diodora cayensis	Keyhole limpet	3	1	1	1	0	0	0	0	0	0	0	0	00
	Atrina rigida	Pen shell	1	0	0	0	0	0	1	0	0	0	0	0	0
	Tagelus divisus	Jacknife clam	1	0	0	0	0	0	0	0	1	0	0	0	0
	Brachidonetes exuctus	Scorched mussel	4	0	0	2	0	0	1	0	1	0	0	0	0
	Geukensia demissa	Ribbed mussel	128	21	20	19	7	6	4	7	0	2	4	19	18
	Mytella charruana	Charru mussel	3	0	0	0	3	0	0	0	0	0	0	0	0
	Lithophaga bisulcata	Mahogany date mussel	1	0	0	0	0	0	0	0	0	0	0	0	1
Ectoprocta	*Bugula neritina*	Common bryozoan	195	1	1	0	0	2	0	16	0	18	82	48	27
	Hippoporina verrilli	Lacy bryozoan	40	0	0	1	28	11	0	0	0	0	0	0	0
	Zoobotryon verticillatum	Spaghetti bryozoan	2	0	0	0	0	0	0	0	0	0	0	0	2
	Perophera viridis	Encrusting ascidian	16	0	2	0	1	5	3	3	0	2	0	0	0
Chordata	*Styela plicata*	Rough sea squirt	87	0	0	0	26	17	2	1	0	1	15	6	19

and the eastern oyster *Crassostrea virginica* were also very abundant (Table 1). Mollusca represented the most abundant phyla, with nine species found. Other phyla represented included Annelida, Cnidara, Porifera, Ectoprocta and Chordata (Table 1). Outside of the lift nets, 15 additional species of sessile organisms were found in small numbers on the intertidal oyster reefs and nearby subtidal areas throughout the course of our study in Mosquito Lagoon, although they do not represent any additional phyla (Table 2).

Measures of oyster community metrics with sessile invertebrates exhibited clear trends in Mosquito Lagoon. Species richness and the density differed temporally, because of the month of sampling (ANOVA: $P < 0.001$; Fig. 2, 3; Table 3, Table 4). Richness was significantly higher during June, July, August and October ($P < 0.001$; Fig. 2). Additionally, February had the lowest richness (Fig. 2). Density, the number of organisms per net, was significantly higher in June, July and August of 2004 than all other sampling periods (ANOVA; $P < 0.001$; Fig. 3). Furthermore, species richness and density were higher on living oysters in clusters than on single disarticulated oyster shells (ANOVA for both: $P < 0.001$; Tables 3, 4; Fig 4). Species found only on live oysters included mussel *Lithophaga bisulcata*, acsidian *Perophera virdis* and bryozoan *Hippoprina verrilli*. Reef type (reefs with dead margins or reference reefs) did not have a significant influence on the community metrics, species richness ($P = 0.098$) or density ($P = 0.207$) (Tables 3, 4). Site did not have a significant effect on species richness (ANOVA: $P = 0.964$) or density ($P = 0.644$) (Tables 3, 4).

Motile Macrofauna

During this study, 64 motile species were found on oyster reefs in Mosquito Lagoon. Fifty-one species were collected using lift nets (Table 5) and an additional 13 species were observed by researchers elsewhere on reefs and in nearby subtidal waters (Table 2). Chordata was the most abundant phyla found to be

TABLE 2.

Additional macrofauna observed on oyster reefs within Mosquito Lagoon. These species were not collected in the lift nets.

Sessile Species Phylum	Species Name	Common Name
Annelida	*Polydora websteri*	Oyster mud worm
Mollusca	*Modiolus americans*	Tulip mussel
	Mercenaria mercenaria	Hard shelled clam
	Anadara transversa	Tranverse ark
	Anadara ovalis	Blood ark
	Martesia cuneiformis	Striated wood paddock
	Crepidula convexa	Convex slipper shell
Ectoprocta	*Conopeum spp.*	Lacy crust bryozoan
	Zoobotryon verticillatum	Moss bryozoan
	Hippoporina verrilli	
Chordata	*Mogula manhattensis*	Sea grape
	Botrylloides nigrum	Black tunicate
	Botryllus planus	Royal tunicate
	Botrylloides schlosseri	Goldenstar tunicate
	Didemnum sp.	
Motile species		
Phylum	**Species Name**	**Common Name**
Arthropoda	*Hexapanopeus angustifrons*	Narrow mud crab
	Limulus polyphemus	Horseshoe crab
	Neopanope sayi	Say's mud crab
	Pinnotheres ostreum	Oyster pea crab
Mollusca	*Aplysia brasiliana*	Sooty sea hare
	Busycon contrarium	Lightening whelk
	Busycon spiratum	Pear whelk
	Fasciolaria hunteria	Banded tulip
	Fasciolaria tulipa	True tulip
	Melongena corona	Crown conch
	Pleuroploca gigantean	Florida horse conch
	Polinices duplicatus	Atlantic moon snail
Chordata	*Symphurus plagiusa*	Blackcheek tonguefish

utilizing the oyster reefs, with 23 fish species found. Mollusca were the second most prevalent phyla, with 20 different species found (Tables 2, 5). Other phyla that were represented in the collections included: Arthropoda (18 species), Echinodermata (2 species) and Annelida (1 species) (Tables 2, 5). The bigclaw snapping shrimp *Alpheus heterochaelis* and the flat mud crab *Eurypanopeus depressus*, dominated the collections numerically year-round (Table 5).

Species richness and density differed because of the month of

TABLE 3.

Four-factor nested ANOVA comparing species richness of sessile organisms in lift nets. Factors were reef type (dead margin or reference; fixed), shell type (live clusters or disarticulated shells) nested within site nested within reef type (random), and month (fixed).

Source	df	Mean Square	F	Significance
Reef type	1	64.201	4.625	0.098
Site (Reef type)	4	13.881	0.133	0.964
Shell type (Site (Reef type))	6	104.321	42.236	<0.001
Month	11	85.401	34.576	<0.001
Residual	697			

TABLE 4.

Four-factor nested ANOVA comparing density of sessile organisms in lift nets. Factors were reef type (dead margin or reference; fixed), shell type (live clusters or disarticulated shells) nested within site nested within reef type (random), and month (fixed).

Source	df	Mean Square	F	Significance
Reef type	1	68406.006	2.265	0.207
Site (Reef type)	4	30195.728	0.657	0.644
Shell type (Site (Reef type))	6	45976.603	16.335	<0.001
Month	11	35020.837	12.443	<0.001
Residual	697			

sampling (ANOVA: both $P < 0.001$; Table 6, Table 7). Richness was higher in November December, January and May (Fig. 2). Density was significantly higher in June, November and December 2004 than any of the other sampling dates (Fig. 3). Reef type (reefs with dead margins or reference reefs) did not have a significant influence on species richness (ANOVA: $P = 0.985$) or density ($P = 0.624$) (Tables 6, 7). Site did not significantly affect species richness (ANOVA: $P = 0.181$), however it did significantly affect density ($P = 0.002$) (Tables 6, 7).

Environmental Variables

During the 13-mo study, the monthly mean temperatures in Mosquito Lagoon ranged from 16°C to 31°C (Fig. 5a). Salinity ranged from 25–35 ppt (Fig. 5b), falling within the typical average range of 25–45 ppt for the monthly mean in Mosquito Lagoon (Walters et al. 2001). The lowest salinity (25 ppt) occurred immediately after the 2004 hurricane season (Fig. 5b). Total sediment loads differed significantly between sites (ANOVA: $P = 0.011$), but not reef type ($P = 0.234$) (Table 8; Fig. 5c). After sediment loads were separated into fractions, percent silt/clay still did not differ significantly between reef type (ANOVA: $P = 0.454$) or sites ($P = 0.482$) (Table 9; Fig. 5d). During the months of June 2004 and June 2005, both sediment load and percent silt/clay differed temporally (ANOVA: $P = 0.004$ and <0.001, respectively). Tukey results showed sediment loads to peak in June 2004,

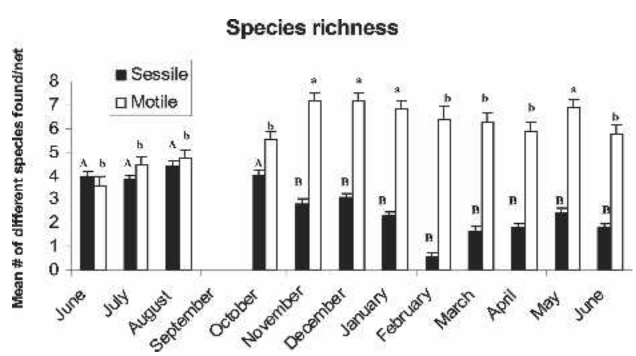

Figure 2. Monthly mean richness (total number of species) ±SE per net per month from June 2004 to June 2005. September data are missing because of 2004 hurricane activity. When compared with ANOVA and a Tukey-Kramer *post-hoc* test, significantly higher months are depicted by A versus B for sessile species and a versus b for motile species.

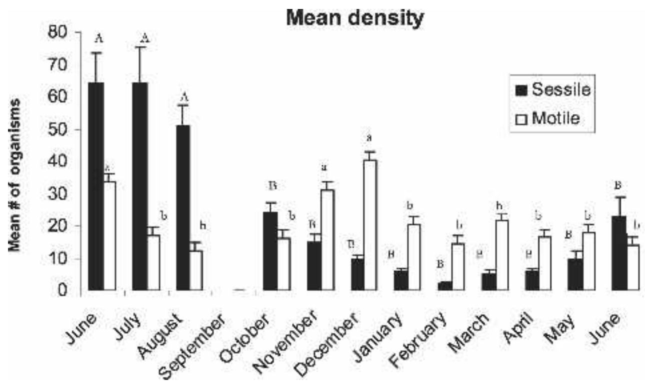

Figure 3. Monthly mean density (number of individuals) ±SE per net per month from June 2004 to June 2005. September data missing because of 2004 hurricane activity. When compared with ANOVA and a Tukey-Kramer *post-hoc* test, significant higher months are depicted by A versus B for sessile species and a versus b for motile species.

whereas percent silt/clay fractions were highest in June and July 2004, and January 2005 (Fig. 5c, 5d).

DISCUSSION

The assemblage of marcofauna associated with the intertidal oyster reefs during our lift net study was similar to those previously reported on oyster reefs in the southeastern United States (sessile species: Wells 1961; motile species: Meyer 1994, Breitburg 1999, Coen et al. 1999, Posey et al. 1999, Glancy et al. 2003,

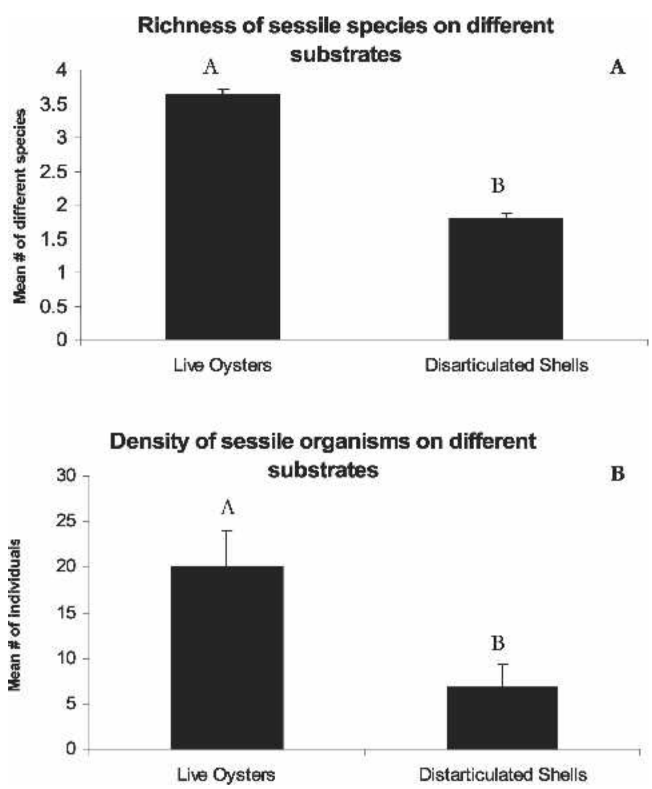

Figure 4. (a) Mean richness (±SE) of sessile organisms on live oysters compared with disarticulated shells. (b) Mean density (±SE) of sessile organisms on live oysters compared with disarticulated shells. Significant differences are depicted by A versus B.

TABLE 6.

Three-factor nested ANOVA comparing species richness of motile species in lift nets. Factors were reef type (dead margin or reference; fixed), site nested within reef type (random), and month (fixed).

Source	df	Mean Square	F	Significance
Reef type	1	0.003	0.000	0.985
Site (Reef type)	4	8.019	1.574	0.181
Month	11	37.699	9.340	<0.001
Residual	343			

Tolley et al. 2005, Tolley & Volety 2005). Our data also support earlier research conducted in the Indian River Lagoon system that looked at the sessile species diversity on hard substrata, although not specifically associated with *Crassostrea virginica* (Mook 1976, 1980, 1981 and 1983). As is typical for shellfish assemblages (O'Beirn et al. 2004), the oyster reef community within Mosquito Lagoon was dominated (in terms of abundance) by only a few taxa (i.e., Annelida, Arthropoda and Chordata) (Table 1 and 5).

Sessile Macrofauna

The most abundant sessile species in the nets were in the genus *Balanus*. These organisms were present year-round on oyster reefs and numerically dominant in all nets. *Balanus eberneus*, the native ivory barnacle recruited to shells placed in lift nets during each month of our survey (Table 1). Monthly recruitment ranged from 87 recruits in February 2005 to 2,447 in July 2004. In fact, every net always had at least one *B. eberneus*. *Balanus amphitrite*, the purple striped barnacle, invaded the IRL approximately 100 y ago (J. Carlton pers. comm.). It was common but not as abundant as its conger (Table 1). Numbers of *B. amphitrite* decreased dramatically during the colder months of the year (Table 1). The abundance of these barnacles in this system outcompeting *C. virginica* for space may be associated with declines in oyster populations in Mosquito Lagoon (Boudreaux 2005). Dense sets of *Balanus* spp. monopolizing all free space on oyster reefs suggest intense spatial competition between oysters and barnacles in the IRL during summer and fall months (Boudreaux 2005).

The nonnative bivalve mussel, *Mytella charruana*, was found during this study (Boudreaux & Walters 2006). This South American bivalve was first found in lift nets in August 2004 and has since rapidly spread within northern Mosquito Lagoon (Boudreaux & Walters 2006). Although low numbers of this species may have predated our study, no individuals were recorded in a 3-y study in these waters between 1998 to 2001 (L. Walters unpublished data).

TABLE 7.

Three-factor nested ANOVA comparing density of motile species in lift nets. Factors were reef type (dead margin or reference; fixed), site nested within reef type (random), and month (fixed).

Source	df	Mean Square	F	Significance
Reef type	1	356.001	0.281	0.624
Site (Reef type)	4	1267.778	4.430	0.002
Month	11	2379.484	10.278	<0.001
Residual	343			

TABLE 5.

Total numbers of motile species collected in lift nets on intertidal oyster reefs in Mosquito Lagoon, Florida.

Phylum	Species	Common Name	Total	Mean Length (cm) (range)	Mean Weight (g) (range)	6/04	7/04	8/04	10/04	11/04	12/04	1/05	2/05	3/05	4/05	5/05	6/05
Echinodermata	*Axiognathus squamatus*	Brooding brittle star	1	0.3	0.1	0	0	0	0	0	0	0	0	0	0	1	0
	Ophionereis reticulata	Reticulated brittle star	3	0.2 ± 0.1 (0.1–0.3)	0.1	0	0	0	1	1	0	0	0	1	0	0	0
Annelida	*Phyllodoce fragilis*	Green oyster worm	3	0.5 ± 0.1 (0.4–0.6)	0.1	0	0	0	1	2	0	0	0	0	0	0	0
Mollusca	*Boonea impressa*	Oyster mosquito	1	0.3	0.1	0	0	0	1	0	0	0	0	0	0	0	0
	Cerithiopsis emersoni	Awl miniature cerith	26	1.2 ± 0.1 (1.0–1.6)	0.2 ± 0.1 (0.1–0.6)	3	3	0	7	1	5	0	2	1	2	2	0
	Cerithiopsis greeni	Green's miniature cerith	1	0.4	0.1	0	0	0	0	0	0	0	0	1	0	0	0
	Cerithium atratum	Florida cerith	5	2.2 ± 0.1 (2.1–2.4)	0.8 ± 0.1 (0.7–1.0)	0	0	0	0	0	0	0	0	0	0	0	5
	Doriopsilla pharpa	Lemon drop sea slug	18	1.2 ± 0.3 (0.7–2.0)	0.1	0	0	0	2	0	0	2	0	7	3	2	2
	Eupleura caudata	Thick-lipped drill	2	2.1 ± 0.4 (1.7–2.5)	0.8 ± 0.5 (0.3–1.3)	0	0	0	1	0	0	0	1	0	0	0	1
	Littorina irrorata	Marsh periwinkle	2	0.8 ± 0.1 (0.8–0.9)	0.3 ± 0.1 (0.2–0.3)	0	0	0	0	0	2	0	0	0	0	0	0
	Nassarius vibex	Mottled dog whelk	78	1.1 ± 0.1 (1.0–1.3)	0.4 ± 0.1 (0.3–0.5)	2	4	12	11	5	10	8	1	8	5	8	4
	Pyrgocythara plicosa	Plicate mangelia	48	0.5 ± 0.1 (0.5–0.8)	0.1 ± 0.01 (0.1–0.2)	4	4	0	6	0	6	6	4	13	4	0	1
	Terebra salleana	Salle's auger snail	1	0.4	0.1	0	0	0	0	0	1	0	0	0	0	0	0
	Thais haemastoma floridana	Florida rock snail	2	0.8 ± 0.1 (0.7–0.8)	0.2 ± 0.1 (0.1–0.3)	0	0	0	2	0	0	0	0	0	0	0	0
	Urosalpinx cinerea	Atlantic oyster drill	19	1.5 ± 0.1 (1.2–1.9)	0.4 ± 0.2 (0.2–0.9)	1	3	2	3	2	2	0	1	3	2	0	0
Arthropoda	*Alpheus heterochaelis*	Bigclaw snapping shrimp	2489	2.0 ± 0.2 (1.6–2.5)	0.4 ± 0.1 (0.3–0.5)	54	79	98	180	299	370	278	210	302	247	214	158
	Callinectes sapidus	Blue crab	75	3.0 ± 0.3 (2.3–4.3)	3.4 ± 0.8 (1.5–6.6)	2	0	0	9	30	9	11	4	6	3	1	0
	Clibanarius vittatus	Striped hermit crab	2	5.0 ± 0.1 (4.0–5.0)	2.5 ± 0.1 (2.0–3.0)	0	0	0	0	0	0	0	0	0	1	1	0
	Eurypanopeus depressus	Flat mud crab	1217	1.1 ± 0.1 (0.8–1.3)	0.6 ± 0.1 (0.5–0.8)	461	257	100	71	78	112	45	14	34	19	11	15
	Eurytium limosum	Broad-backed mud crab	4	1.0 ± 0.1 (1.0–1.1)	0.3 ± 0.1 (0.2–0.4)	0	0	0	1	1	0	0	0	1	0	1	0
	Heterocrypta granulate	Pentagon crab	1	1.5	0.5	0	0	0	0	0	0	0	0	0	0	1	0
	Libnia dubia	Doubtful spider crab	2	3.8 ± 0.2 (3.5–4.0)	24.3 ± 0.3 (23.5–25)	0	0	0	0	0	0	0	0	0	0	1	1

	Menippe mercenaria	Stone crab	3	1.6 ± 0.5 (1.0–2.1)	2.5 ± 0.8 (1.7–3.3)	0	1	0	0	1	0	0	0	0	2	0	0
	Palaemonetes vulgaris	Grass shrimp	610	2.9 ± 0.2 (2.5–3.8)	0.4 ± 0.1 (0.3–0.6)	1	0	2	14	28	261	52	92	66	18	44	32
	Panopeus herbstii	Atlantic mud crab	534	1.8 ± 0.1 (1.4–2.1)	3.3 ± 0.3 (1.5–4.3)	70	72	51	24	28	59	47	21	48	38	33	43
	Penaeus duorarum	Pink shrimp	145	4.6 ± 0.5 (2.8–6.5)	1.3 ± 0.3 (0.3–2.4)	0	3	9	5	3	6	5	0	0	40	56	18
	Petrolisthes armatus	Green porcelain crab	584	0.7 ± 0.1 (0.6–0.8)	0.5 ± 0.1 (0.3–0.6)	383	54	29	9	15	36	16	6	14	9	4	9
	Rhithropanopeus harrisii	Harris's mud crab	243	0.9 ± 0.1 (0.5–1.4)	0.6 ± 0.1 (0.2–1.0)	0	6	17	26	17	46	11	12	50	15	13	30
	Squilla empusa	Common mantis shrimp	1	10.0	18.0	0	0	0	0	0	0	0	0	0	0	0	1
Chordata	*Archosargus probate-cephalus*	Sheepshead	21	7.2 ± 0.1 (4.4–9.7)	12.7 ± 1.9 (8.5–19.8)	3	1	1	7	0	0	4	0	0	0	3	2
	Bairdiella chrysoura	Silver perch	7	4.6 ± 0.2 (4.0–5.0)	1.5 ± 0.2 (1.0–2.0)	3	0	0	3	0	0	0	0	0	0	0	1
	Bathygobius soporator	Frillfin goby	1	4.0	0.8	0	0	0	0	0	1	0	0	0	0	0	0
	Chasmodes saburrae	Florida blenny	6	4.3 ± 0.2 (4.0–4.8)	1.2 ± 0.4 (0.6–1.8)	0	0	0	1	3	1	0	0	0	0	0	1
	Cyprinidon variegatus	Sheepshead minnow	3	5.5 ± 0.7 (4.1–6.5)	3.1 ± 1.1 (1.1–4.8)	1	0	0	0	1	1	0	0	0	0	0	0
	Diapterus auratus	Irish pompano	1	7.3	10.9	0	0	1	0	0	0	0	0	0	0	0	0
	Floridichthys carpio	Goldspotted killifish	1	6.8	7.8	0	1	0	0	0	0	0	0	0	0	0	0
	Fundulus grandis	Gulf killifish	2	8.8 ± 1.7 (7.1–10.5)	11.1 ± 6.9 (4.2–17.9)	0	0	0	0	1	0	0	1	0	0	0	0
	Gobionellus boleosoma	Darter goby	54	3.5 ± 0.3 (2.2–5.0)	0.5 ± 0.2 (0.2–1.2)	0	0	1	18	19	3	3	0	1	2	0	7
	Gobiosoma bosc	Naked goby	736	3.1 ± 0.2 (2.6–3.8)	0.6 ± 0.1 (0.3–1.0)	13	23	24	31	165	228	62	47	54	28	32	29
	Gobiosoma robustum	Code goby	267	2.9 ± 0.2 (2.3–4.5)	0.5 ± 0.2 (0.1–1.5)	1	3	12	49	139	27	6	3	4	12	3	8
	Haemulon flavolineatum	French grunt	34	3.7 ± 0.3 (2.1–5.5)	1.1 ± 0.2 (0.1–3.0)	0	0	0	0	0	0	0	0	0	6	25	3
	Lagodon rhomboides	Pinfish	148	3.8 ± 1.0 (2.3–7.7)	1.8 ± 1.1 (0.1–8.3)	3	1	2	0	1	0	34	19	20	29	20	19
	Lucania parva	Rainwater killifish	84	2.5 ± 0.3 (2.0–3.3)	0.3 ± 0.1 (0.1–0.5)	0	0	0	0	5	1	11	0	5	4	47	11
	Lutjanus griseus	Gray snapper	25	5.9 ± 1.1 (3.0–11.2)	6.5 ± 3.0 (0.6–21.3)	1	0	1	1	10	2	4	0	2	1	3	0
	Mugil cephalus	Striped mullet	2	22.0 ± 1.0 (21.0–23.0)	13.4 ± 0.6 (12.8–14.0)	0	0	1	0	0	1	0	0	0	0	0	0
	Mugil curema	White mullet	1	11.5	16.0	0	0	0	0	0	1	0	0	0	0	0	0
	Opsanus tau	Oyster toadfish	40	6.9 ± 1.2 (2.3–9.0)	7.8 ± 2.3 (0.2–13.3)	4	1	5	0	5	0	1	0	3	5	8	8
	Paralichthys albigutta	Gulf flounder	1	4.9	1.1	0	0	0	0	0	0	0	0	0	1	0	0
	Paralichthys lethostigma	Souther flounder	1	3.6	0.4	0	0	0	0	0	0	0	0	1	0	0	0
	Poecilia latipinna	Sailfin molly	109	4.8 ± 0.4 (4.3–5.6)	2.1 ± 0.4 (1.6–3.0)	1	0	2	0	75	23	6	2	0	0	0	0
	Sygnathus scovelli	Gulf pipefish	16	6.6 ± 0.4 (5.6–8.6)	0.2 ± 0.1 (0.1–0.4)	0	0	0	0	0	0	0	0	0	0	3	13

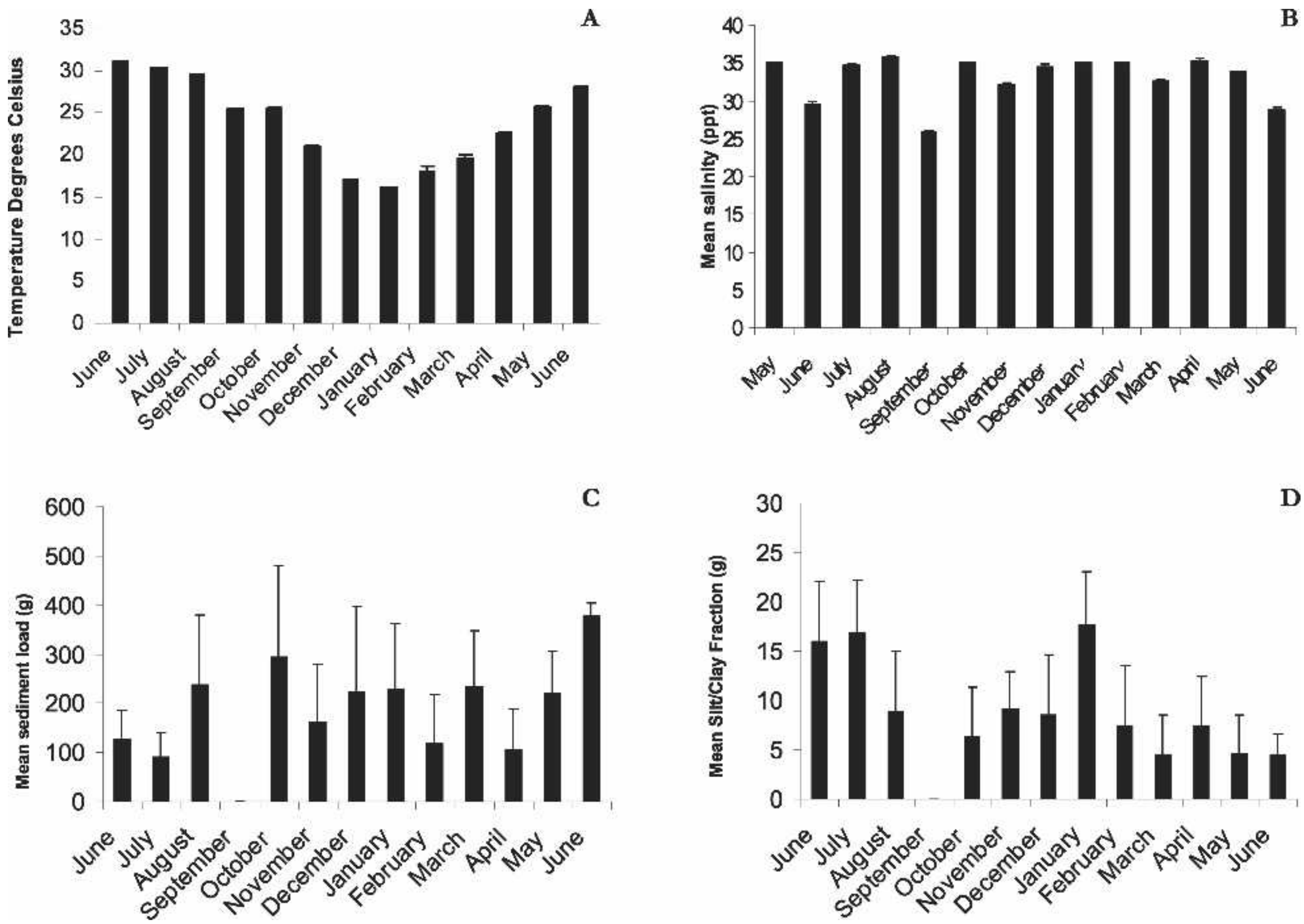

Figure 5. Abiotic variables (a). Mean monthly temperatures (± SE) at lift net sampling dates in Mosquito Lagoon. (b) Mean salinities (±SE) of Mosquito Lagoon on lift net sampling dates. (c) Mean sediment load (±SE) per month from June 2004 to June 2005. (d) Mean silt/clay percentage (±SE) per month from June 2004 to June 2005.

One individual of the invasive Asian green mussel *Perna viridis,* which has devastated some oyster reefs in Tampa Bay, Florida (Baker et al. 2003), was also recently found on a piling in Mosquito Lagoon (MB pers. obs.). It has not been found on Mosquito Lagoon oyster reefs to date. Both nonnative bivalves continue to be monitored within the IRL.

Motile Macrofauna

The two most abundant motile species sampled within the lift nets were the bigclaw snapping shrimp *Alpheus heterochaelis* (2,489 individuals) and the flat mud crab *Eurypanopeus depressus* (1,217 individuals) (Table 5). Previous studies found these two species to be present in temperate waters on both the Atlantic coast of North Carolina (132 individuals of *E. depressus*; Glancy et al. 2003) and the gulf coast of Florida (3,184 individuals of *E. depressus*, 364 individuals of *A. heterochaelis*; Meyer 1994). Similar to Tolley et al. (2005), we found the replacement of temperate species by tropical cogeners, including the replacement of the striped blenny *Chasmodes bosquianus* in the Northern Atlantic (Breitburg 1999, Coen et al. 1999) by the Florida blenny *Chasmodes saburrae*.

TABLE 8.

Three-factor nested ANOVA comparing total sediment loads collected per month at lift net sites. Factors were reef type (dead margin or reference; fixed), site nested within reef type (random), and month (fixed).

Source	df	Mean Square	F	Significance
Reef type	1	317305.223	1.961	0.234
Site (Reef type)	4	161861.650	3.357	0.011
Month	11	124938.063	2.624	0.004
Residual	199			

TABLE 9.

Three-factor nested ANOVA comparing silt/clay fractions collected per month at lift net sites. Factors were reef type (dead margin or reference; fixed), site nested within reef type (random), and month (fixed).

Source	df	Mean Square	F	Significance
Reef type	1	39.068	0.687	0.454
Site (Reef type)	4	56.862	0.871	0.482
Month	11	409.454	9.004	<0.001
Residual	199			

The fifth most abundant mobile species was the green porcelain crab, *Petrolisthes armatus* (Table 5). It is considered an invasive exotic along the South Atlantic Bight (Knott et al. 1999, Glancy et al. 2003). Populations of this species can historically be found in the Pacific (i.e., California to Peru) and the Atlantic (i.e., Africa, Ascension Island, Bermuda, Bahamas, Gulf of Mexico, West Indies, Caribbean and South America down to Brazil; Knott et al. 1999). Although the pathway of introduction remains unknown, ballast transport and increasing winter temperatures, which favor its establishment are possibilities (Knott et al. 1999). It was first collected along Florida's east coast in the 1930s in Biscayne Bay and Miami Beach (Knott et al. 1999). Slowly, it spread northward, becoming well established in the Indian River Lagoon system (Knott et al. 1999). Studies have shown abundances to increase dramatically in only a few years after introduction (Knott et al. 1999). The current range of *P. armatus* along the South Atlantic Bight stretches from South Carolina down to the southern tip of Florida (Knott et al. 1999).

Size and biomass data for several crustacean and fish species revealed that both juvenile and adult individuals were present on the reefs (Table 5). For example, large ranges were seen for the big-claw snapping shrimp *Alpheus heterochaelis* (length 1.6–2.5 cm; biomass 0.3–0.5 g), blue crab *Callinectes sapidus* (length 2.3–4.3 cm; biomass 1.5–6.6 g), stone crab *Menippe mercenaria* (length 1.0–2.1 cm; biomass 1.7–3.3 g), grass shrimp *Palaemonetes vulgaris* (length 2.5–3.8 cm, biomass 0.3–0.6 g) and pink shrimp *Penaeus duorarum* (length 2.8–6.5 cm, biomass 0.3–2.4 g) (Table 5). Within the Chordata family, different life stages were seen for the sheepshead *Archosargus probatocephalus* (length 4.4–9.7 cm, biomass 8.5–19.8 g), pinfish *Lagodon rhomboides* (length 2.3–7.7 cm, biomass 0.1–8.3), gray snapper *Lutjanus griseus* (length 3.0–11.2 cm, biomass 0.6–21.3 g), oyster toadfish *Opsanus tau* (length 2.3–9.0 cm; biomass 0.2–13.3 g), and numerous killifish and goby species (Table 5).

The blue crab *Callinectes sapidus*, the pink shrimp *Penaeus duorarum* and juvenile forms of several important finfish species were collected in the lift nets within Mosquito Lagoon (Table 5). Hence, commercially and recreationally valuable species are utilizing oyster reefs within Mosquito Lagoon, confirming the importance of oyster reefs to the economy of this region. These species were also found to be utilizing oyster reefs on the west coast of Florida (Tolley et al. 2005).

Additional comparisons can be made with the motile species found on oyster reefs in Mosquito Lagoon to lift net studies of intertidal reefs on the west coast of Florida (26° 25′56″N, 81°48′34″W) (Tolley et al. 2005, Tolley & Volety 2005). Salinities and temperatures found in Mosquito Lagoon (mean: 33 ppt, 23.8°C) are comparable to the system studied in southwest Florida (mean: 32.5 ppt, 27.1°C). Overall species richness (the total number of species found per net) was found to be similar between the two different Florida locations (Gulf: 4–11 species/month versus Mosquito Lagoon: 4–11 species/month), whereas density was slightly lower in Mosquito Lagoon (Gulf: 20–400 organisms/net versus Mosquito Lagoon: 12–40 organisms/net). In both systems, there were more fishes than decapod crustacean species (Gulf: 16 versus 9, Mosquito Lagoon: 23 versus 18). In both locations, decapod crustaceans dominated all motile samples numerically.

Dead Margins Affect on Oyster Reef Communities

Dead margins, attributed to wakes from recreational boating in Mosquito Lagoon (Grizzle et al. 2002, Wall et al. 2005), did not have a significant effect on the back-reef usage of oysters as substrate by either sessile or motile species (Tables 3, 4, 6 and 7). The back-reef areas of both were also visually very similar. This suggests the back-reef areas on oyster reefs with dead margins function similarly to a reference oyster reef with no dead margin.

Although dead margins did not have an impact on richness or density of organisms found, sessile organisms preferred to settle on living oyster clumps rather than on the disarticulated shells placed within the nets (Fig. 4). The 3-dimensional structure of the two settlement substrates was very different. Disarticulated shells were single and loose, laid flat on the benthos, and were often covered by sediment. These shells were frequently displaced by water motion. Live oysters attached together to form clusters and rarely moved. These 3-dimensional clusters probably provided more protection and refuge from predators for sessile inhabitants than the 2-dimensional, disarticulated shells. Subsequent research has shown that reference reefs contained twice more oyster clumps than reefs with dead margins within Mosquito Lagoon (Stiner 2006). Combined, these results reveal a new negative impact of dead margins on sustaining biodiversity in Mosquito Lagoon.

Wall et al. (2005) found an increase in sediment accumulation on the seaward edges (fore-reef areas) of reefs with dead margins in Mosquito Lagoon and suggested this was caused by sediment resuspension associated with large numbers of boat wakes. Increased sediment has been shown to decrease the settlement of *Crassostrea virginica* (Boudreaux 2005). Thus, any difference in sediment loads between locations would have been predicted to have an effect on species assemblages between the two types of reefs (reference and dead margins). However, this study focused exclusively on the back-reef regions of oyster reefs and did not show any differences in sediment loads between reef types. Dead margins are hypothesized to protect these back-reef areas by preventing sediment accumulation.

During this study we documented the usage of intertidal oyster reefs in Mosquito Lagoon by 105 different species. This included 76 invertebrates and 29 chordates. The richness in diversity found within the reefs of *Crassostrea virginica* is comparable with other systems in the Indian River Lagoon system. A study of decapods associated with seagrass communities in the Indian River Lagoon showed remarkable diversity. In all, 38 decapod species were found in seagrass beds (Gore et al. 1981; Smithsonian Institution 2006) as compared with the 19 decapod species we found using oyster reefs (Tables 2 and 5). These examples demonstrate the extremely high diversity in the IRL that can be attributed to its important habitats, including seagrass beds and oyster reefs. The data from this study are an important step to gaining a better understanding of these oyster reefs and their essential role in the estuary. Additionally, this data provides a baseline from which to evaluate efforts to practice sustainable ecosystem management of *Crassostrea virginica* within Mosquito Lagoon.

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