

Mussels in seagrass meadows: their influence on macroinvertebrate abundance and secondary production in the northern Gulf of Mexico*

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ABSTRACT: From 1989 to 1990, we studied a previously undescribed mussel *Modiolus americanus* (Leach) habitat (with densities as high as 2000 ind. m⁻²) within the seagrass meadows of St. Joseph Bay, Florida, USA. Using suction sampling, we compared macroinvertebrate abundance, biomass, and annual production estimates in mussel habitat with 3 other habitats: monotypic stands of *Thalassia testudinum* (Banks ex König), *Halodule wrightii* Aschers and unvegetated sand flats. Previous studies have positively correlated macrofaunal densities and species number with measures of vegetation abundance or architecture. This relationship was not found to be strong in our study. Macroinvertebrate abundance, biomass, and annual production were usually equivalent or higher in mussel than in the other 3 habitats despite aboveground seagrass biomass usually being intermediate between pure stands of *T. testudinum* and *H. wrightii*, and leaf surface area lowest. Of particular interest was annual macroinvertebrate production which ranged from 228.77 to 428.59 g ash-free dry mass (AFDW) m⁻² in mussel habitat, followed in descending order by pure stands of *T. testudinum* (144.90 to 245.44 g AFDW m⁻²), *H. wrightii* (83.98 to 180.44 g AFDW m⁻²), and sand flats (19.83 to 42.47 g AFDW m⁻²). These production estimates illustrate the positive effect that mussels can have in elevating already high levels of macroinvertebrate production in seagrass meadows.

INTRODUCTION

It is well documented that seagrass habitats serve as nursery grounds for many macroinvertebrate and fish species (Stoner 1980a, b, c, Coen et al. 1981, Nelson 1981a, b, Stoner 1982, Heck & Thoman 1984, Summerson & Peterson 1984) as well as foraging areas for the adults of many taxa (Thayer et al. 1975, Robertson 1977, Thayer & Phillips 1977, Bell et al. 1978a, b, Weinstein & Heck 1979, Robertson 1984). As a result, seagrass habitats support an abundant and diverse fauna (see reviews by Zieman 1982, Thayer et al. 1984, Zieman & Zieman 1989). Several studies have found positive correlations between faunal abundance, diversity patterns and measures of vegetation abundance, such as aboveground biomass, shoot density, or leaf surface area (Heck & Wetstone 1977,

Orth & Heck 1980, Stoner 1980a, b, c, Lewis 1984, Williams et al. 1990). However, others have found inconsistent relationships between these seagrass attributes and faunal community characteristics (Brook 1978, Stoner 1983, Pihl-Baden & Pihl 1984, Stoner & Lewis 1985, Bell & Westoby 1986, Schneider & Mann 1991a, Worthington et al. 1992), suggesting that other factors also influence macrofaunal distributions within seagrass meadows.

Mussels attached to rocks, both intertidal and subtidal, also support a diverse and abundant fauna by providing refuge from predation for small individuals (Suchanek 1978, Sebens 1985, Witman 1985), food for molluscivores (Paine 1966, 1974, Menge 1976, Lubchenco & Menge 1978, Briscoe & Sebens 1988, Robles et al. 1990), protection from wave induced physical forces (Suchanek 1978, Tsuchiya & Nishihira 1986, Jacobi 1987), and substrate for sessile invertebrate and algal attachment (Witman 1987, Young 1989, Dittman & Robles 1991).

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Recently, we encountered dense concentrations of the semi-infaunal mussel *Modiolus americanus* (Leach) as high as 2000 ind. m⁻². These mussels form clusters within turtlegrass *Thalassia testudinum* (Banks ex Konig) meadows in St. Joseph Bay, Florida, USA. Information on mussel abundance within seagrass habitats elsewhere in the Gulf of Mexico is lacking, possibly due to sampling dominated by otter trawls (e.g. Livingston 1975, Thorhaug & Roessler 1977). However, a literature review indicates that these mussels and turtlegrass co-occur throughout much of their geographic range (Rodriguez 1959, Jackson 1973, Abbott 1974, Roessler et al. 1975, Stromgren 1976, Andrews 1977, Lyons 1989, Young 1989).

Using quantitative sampling, we addressed the following question: does the combination of turtlegrass and mussels support higher macroinvertebrate abundance and biomass than other vegetated habitats without mussels? In addition, we hypothesized that if mussels enhance the nursery function of seagrass habitats, similar to that reported for hard substrates (Witman 1985), higher annual macroinvertebrate production would be detected in seagrass with mussels than in pure stands of seagrass. Comparisons with unvegetated habitat were used to estimate macroinvertebrate abundance, biomass and productivity in St. Joseph Bay in the absence of epibenthic structure.

METHODS AND MATERIALS

Study site. The study site, St. Joseph Bay, Florida, is located in the northeastern Gulf of Mexico (30°N, 85.5°W). St. Joseph Bay is a protected, shallow coastal embayment with no significant source of freshwater input. Salinities range from 30 to 36 ‰ annually (Stewart & Gorsline 1962, Folger 1972, pers. obs.). Temperatures vary annually from approximately 8 to 30 °C (pers. obs.) and the mean tidal range is 0.5 m (Rudloe 1985).

Field and laboratory processing. Monthly collections quantified macroinvertebrate and macrophyte abundance and biomass in 4 visually determined shallow-water (≤ 1.5 m) habitats. The 4 habitats were (1) *Thalassia testudinum* with mussels (hereafter referred to as 'mussel habitat'), (2) *T. testudinum* without mussels ('*Thalassia* habitat'), (3) *Halodule wrightii* where mussels were seldom observed ('*Halodule* habitat'), and (4) unvegetated sand flats ('sand' or 'unvegetated habitat').

Macrophyte sampling consisted of 5 haphazardly located 0.01 m² clippings of aboveground seagrass from each vegetated habitat. Aboveground seagrass biomass samples were initially frozen. In the laboratory, macrophyte samples were thawed, sorted into seagrass and algal components, and dried to constant

weights in an oven set at 90 °C. Dried samples were weighed to the nearest milligram.

Macrofaunal samples were collected using a gasoline-powered pump (cf. Orth & van Montfrans 1987) which suctioned epibenthic macroinvertebrates from a 0.56 m diameter cylinder whose lower edge was embedded into the substratum (cf. Williams et al. 1990). A 1.0 mm mesh sample bag was used to collect individuals from the pump outflow for 1 min. Ten haphazardly assigned suction samples were collected from each vegetated habitat and 7 from the unvegetated habitat. Fewer replicates were collected from the unvegetated habitat since these habitats support significantly lower epibenthic densities and diversities than do vegetated habitats (see Orth et al. 1984 for summary). Care was taken not to sample in areas previously disturbed by the collection team. Prior to suctioning in mussel habitat, a 0.01 m² quadrat was dropped into the cylinder and mussel density recorded.

Suction samples were frozen then transported to the laboratory for preservation (in 40 % isopropyl alcohol), sorting and identification to species and/or major taxonomic group. Major taxonomic groups included amphipods, chitons, crabs, gastropods, hermit crabs, isopods, shrimps and sea urchins. Such groupings were sufficient to characterize the fauna in each habitat. For the increased effort required to identify organisms to lower taxonomic levels little information would be added (Warwick 1988). Other taxa, such as scallops, sea hares and juvenile horseshoe crabs were collected only once and are not included in our results due to their low abundance. Since the sampling method did not allow the collection of representative fish abundances, fishes are also excluded.

Dry biomass (DW) was determined, to the nearest 1 mg, for each major taxonomic group after drying to constant weights at 90 °C. Hermit crabs were removed from shells prior to drying and weighing. Following dry weighing, the ash weight (AW) of organisms with high inorganic fractions (i.e. gastropods, crabs and sea urchins) was determined by ashing these organisms at 550 °C for 2 h after which samples were placed in desiccators to cool again before reweighing. Ash-free dry mass (AFDW) of these organisms was calculated as DW – AW. The AFDW of the remaining organisms (shrimp, amphipods, isopods and chitons) was calculated as DW × 0.9 (Waters 1977).

Estimates of annual macroinvertebrate production were used to compare the relative contribution of these 4 habitats to energy flow in St. Joseph Bay. Annual secondary production was determined using the regression equation:

$$P = \text{antilog} (0.66 - 0.726 \log_{10} L + \log_{10} \bar{B})$$

where P = annual secondary production; \bar{B} = mean annual biomass; and L = lifespan in years.

This was derived from the regression equation:

$$\log_{10} P/\bar{B} = 0.66 - 0.726 \log_{10} L$$

This equation was provided by Robertson (1979) in an effort to simplify estimating annual secondary production. This method requires reliable estimates of organism life spans, which are difficult to obtain from the literature. Therefore, we used both the upper and lower estimates of organism lifespan, which in some cases are only rough estimates, to calculate a range for estimated annual production of the major taxonomic groups within the 4 habitats.

Comparisons of macroinvertebrate abundance and biomass, and aboveground seagrass biomass were conducted in a similar manner to Williams et al. (1990). For comparative purposes, data were standardized to 1 m^2 and are reported as $\bar{x} \pm 1 \text{ SE}$. Analyses were conducted using 1-way analysis of variance (ANOVA) following transformation $[(n+0.5)^{1/2}]$, where n = the major taxonomic group density or biomass] since homogeneity of variance was violated in many cases (cf. Williams et al. 1990). If ANOVA was significant, *a posteriori* comparisons were conducted using Scheffe's multiple comparison procedure (Day & Quinn 1989). Results from all statistical comparisons were considered significant at the preselected 5% level of significance.

RESULTS

Suction samples

Distributional patterns

Total macroinvertebrate abundance was similar in the 3 vegetated habitats (Fig. 1a). The average densities of sea urchins *Lytechinus variegatus*, chitons *Ischnochiton striolatus* (Gray), *Acanthochitona pygmaea* (Pilsbry) and *Acanthopleura granulatum* (Gmelin), and crabs (primarily xanthids) were generally higher in mussel habitat, but were seldom significantly higher than in the other habitats (Table 1). Of the macroinvertebrates collected, only sea urchins and chitons consistently occurred in significantly higher densities in mussel habitat. Crabs were found in significantly higher densities in mussel habitat than all of the other habitats in 6 of the months. Pairwise comparisons between mussel and *Thalassia* habitats found higher crab densities in mussel habitat in mo, but only 7 times were these differences significant. Crabs densities were usually also higher in mussel than *Halodule* habitat (8 mo).

Amphipods, gastropods, hermit crabs, isopods and shrimps (primarily carideans) were more patchily dis-

tributed within the vegetated habitats. Each of these taxonomic groups was found to be significantly more abundant in vegetated than unvegetated habitats but pairwise differences between vegetated habitats were seldom found. For example, gastropods (dominated by *Diastoma varium* Pfeiffer which is usually found on leaf blades) were most abundant in *Halodule* habitat but significant differences among the vegetated habitats were few (4 mo). Amphipods were significantly more abundant in habitats with *Thalassia* sp. than in *Halodule* habitat (9 mo) but differences between the habitats with *Thalassia* sp. were seldom detected. Isopods were usually more abundant in *Halodule* habitat but few times were these densities significantly higher than in the other vegetated habitats. Shrimp were also more abundant in vegetated habitats than in bare sand but again significant differences between the vegetated habitats were seldom detected. When taken together, these data indicate that faunal abundances among vegetated habitats were highly variable but significant differences between the habitats were few.

Biomass patterns

Macroinvertebrate biomass patterns were noticeably different from the abundance patterns in that total biomass in mussel habitat was nearly twice that in the other habitats (Fig. 1b). In each month, total biomass was significantly higher in mussel habitat than in any

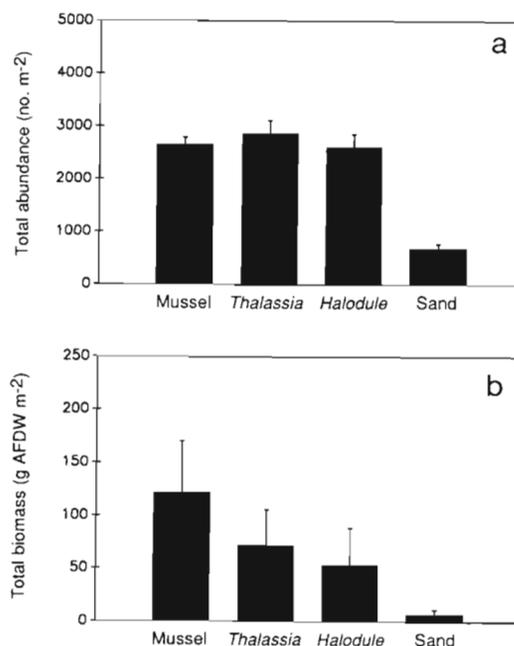


Fig. 1 Total macroinvertebrate (a) abundance and (b) biomass in St. Joseph Bay, Florida. Error bars indicate 1 SE

Table 1. Mean abundance (no. m⁻²) of the major taxonomic groups in the 4 habitats in St. Joseph Bay, Florida, in 1986 and 1987. M: *Thalassia testudinum* with mussels; T: *T. testudinum* without mussels; H: *Halodule wrightii* where mussels were seldom observed; S: unvegetated sand flats. Bold print indicates those densities that were statistically significantly higher than other densities within the same month

Group Habitat	1989									1990			
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	
Amphipods													
M	19.2	145.5	113.2	117.3	44.1	55.4	35.7	69.3	94.7	11.9	144.3	101.7	
T	11.2	69.7	209.9	22.1	40.1	44.7	52.4	65.6	141.9	183.9	255.8	99.2	
H	57.0	63.1	101.7	26.2	54.1	33.2	67.3	65.7	96.8	170.6	98.0	42.2	
S	2.2	108.7	12.3	2.5	8.2	20.5	5.7	8.2	7.8	25.8	11.5	4.9	
Isopods													
M	2.0	10.3	17.9	27.9	17.2	29.9	13.9	27.1	15.2	0.0	23.8	1.2	
T	3.5	7.4	15.2	0.8	17.8	0.8	9.4	11.1	4.5	3.3	12.7	6.2	
H	55.0	34.9	13.5	32.8	14.1	5.7	16.0	24.6	18.9	11.1	43.1	9.8	
S	1.2	5.6	4.1	1.2	4.1	0.4	14.4	0.4	0.4	1.2	5.6	4.0	
Shrimp													
M	2.2	3.3	20.1	6.7	10.0	83.2	13.5	24.6	7.0	2.9	80.8	86.1	
T	2.4	5.2	8.6	0.6	2.0	22.5	52.9	34.0	8.2	2.1	91.8	25.0	
H	4.5	0.0	66.9	2.1	6.4	44.7	2.5	14.4	7.4	25.9	87.8	3.7	
S	0.0	0.0	0.6	0.4	0.0	0.0	0.0	0.0	3.5	0.0	2.5	0.6	
Hermit crabs													
M	18.0	32.8	43.5	22.6	13.5	8.6	25.4	73.8	60.3	16.0	35.7	22.6	
T	52.9	53.7	36.9	50.2	21.9	16.4	21.3	31.6	20.1	24.6	28.7	27.9	
H	55.0	34.9	13.5	32.8	14.1	5.7	16.0	24.6	19.3	11.1	43.1	9.8	
S	54.9	8.2	5.3	4.1	1.7	3.7	1.6	7.8	5.9	4.1	0.2	0.0	
Crabs													
M	5.8	32.9	53.3	25.8	24.2	31.9	29.1	27.1	29.9	12.3	20.9	20.8	
T	8.2	5.7	23.8	29.1	6.6	4.1	13.1	17.6	23.1	16.8	2.1	3.7	
H	16.8	9.8	16.9	22.3	9.8	1.6	7.0	9.8	13.5	10.7	23.8	6.9	
S	2.1	0.8	0.0	1.17	2.3	0.0	0.8	0.9	1.2	0.0	1.6	1.6	
Gastropods													
M	35.0	117.7	37.3	38.5	32.4	31.6	90.2	87.7	61.9	34.4	30.3	58.2	
T	426.6	25.4	150.9	66.0	85.2	13.1	85.7	157.1	116.9	159.9	34.9	68.8	
H	120.1	88.2	102.1	100.0	132.1	42.2	77.9	150.9	95.7	223.9	154.6	134.1	
S	42.2	57.4	25.8	74.4	79.7	30.5	25.4	60.8	37.5	223.9	18.8	60.3	
Chitons													
M	5.6	16.4	10.7	4.1	6.6	14.8	9.0	23.0	32.4	33.2	21.3	41.9	
T	3.7	4.5	12.7	3.3	1.4	0.0	0.0	8.7	1.6	9.8	4.5	12.3	
H	0.6	0.0	1.2	2.5	0.5	0.0	0.4	0.0	0.0	3.7	3.3	1.6	
S	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Sea urchins													
M	0.8	0.4	9.8	29.5	22.0	19.3	11.5	17.6	0.6	0.0	31.6	0.4	
T	0.0	4.9	0.0	0.0	12.3	0.4	0.0	0.0	0.0	0.0	7.8	0.0	
H	0.0	0.4	0.0	0.0	2.3	1.6	0.0	0.0	0.0	0.0	0.4	0.0	
S	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	

other habitat. Sea urchin biomass was highest in mussel habitat from June through November 1989 and again in February 1990 (Table 2). Chiton biomass was also highest in mussel habitat in 7 of the months. Shrimp and crab biomass were significantly higher in mussel habitat in only 2 and 5 months respectively. Despite being more abundant in the seagrass habitats with *Thalassia* sp., amphipod biomass was most often highest in *Halodule* habitat. Isopod biomass was higher in the vegetated habitats than the unvegetated

habitat but consistent differences between vegetated habitats were not apparent. Gastropods, despite being more abundant in *Halodule* habitat, usually had higher biomass in habitats with *Thalassia testudinum*.

Aboveground seagrass biomass

Aboveground seagrass biomass in the 3 vegetated habitats was highest during August and from October

Table 2. Mean biomass (g AFDW m⁻²) of the major taxonomic groups in the 4 habitats in St. Joseph Bay, Florida, in 1986 and 1987. Abbreviations as in Table 1. Bold print indicates weights that were statistically significantly higher than others in the same month

Group Habitat	1989								1990			
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Amphipods												
M	0.093	0.069	0.103	0.004	0.023	0.027	0.008	0.074	0.275	0.025	0.115	0.247
T	0.020	0.107	0.007	0.000	0.016	0.014	0.021	0.146	0.143	0.089	0.159	0.040
H	0.123	0.091	0.013	0.007	0.025	0.009	0.033	0.077	0.053	0.182	0.139	0.022
S	0.000	0.029	<0.0001	<0.0001	<0.0002	<0.0001	0.026	0.000	<0.001	0.070	0.004	0.015
Isopods												
M	0.084	0.025	0.001	0.001	0.001	0.003	0.001	0.062	0.007	0.006	0.017	0.031
T	0.008	0.048	0.000	0.000	0.001	0.004	0.000	0.430	0.000	0.006	0.037	0.007
H	0.006	0.009	0.001	0.001	0.009	0.003	0.008	0.022	0.017	0.106	0.187	0.002
S	0.000	0.001	0.0001	0.000	0.0001	0.0001	0.001	0.000	0.00001	0.010	0.001	0.0004
Shrimp												
M	0.185	0.197	0.221	0.705	0.615	0.275	0.414	0.720	0.517	0.029	1.484	0.570
T	0.045	0.057	0.148	0.000	0.050	0.234	0.742	0.992	0.492	0.033	0.578	0.135
H	0.045	0.125	0.381	0.424	0.097	0.381	0.242	0.241	0.127	0.205	0.406	0.041
S	0.000	0.000	0.230	0.006	0.000	0.000	0.000	0.000	0.455	0.000	0.008	<0.0001
Hermit crabs												
M	0.203	0.258	0.631	0.066	0.127	0.033	0.096	0.543	0.199	0.991	0.270	0.122
T	0.218	0.321	0.122	0.170	0.096	0.081	0.130	0.071	0.122	0.085	0.225	0.417
H	0.194	0.107	0.033	0.099	0.070	0.041	0.114	0.355	0.088	0.048	0.436	0.513
S	0.646	0.074	0.063	0.011	0.085	0.023	0.151	0.048	0.0001	0.007	0.001	0.000
Crabs												
M	0.34	0.964	0.422	0.226	0.553	0.090	0.220	3.570	0.155	1.149	0.537	0.660
T	6.355	0.053	0.279	0.709	0.213	0.152	0.492	0.715	0.139	0.195	2.239	0.189
H	1.029	0.033	0.181	0.344	0.189	0.123	0.059	0.189	0.148	0.094	0.451	0.718
S	<0.0001	<0.0001	0.000	0.012	<0.0001	0.000	0.055	0.185	0.000	0.000	0.066	0.045
Gastropods												
M	0.529	0.611	7.704	0.357	1.048	0.037	0.926	2.948	1.521	0.562	2.202	2.722
T	1.656	0.602	1.095	0.406	0.496	0.091	0.98	2.144	1.681	2.565	1.427	2.239
H	1.320	0.230	1.562	1.426	0.549	0.046	0.672	2.612	0.918	1.209	1.689	4.818
S	0.353	0.291	0.211	0.164	0.589	0.023	0.792	0.233	0.374	0.177	0.484	0.879
Chitons												
M	0.562	0.886	0.201	0.037	0.013	0.053	0.041	0.077	0.435	0.381	0.238	0.652
T	0.07	0.115	0.355	0.082	0.012	0.000	0.000	0.062	0.021	0.549	0.029	0.131
H	0.086	0.000	0.120	0.004	0.000	0.000	0.004	0.000	0.000	0.004	0.004	0.029
S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sea urchins												
M	0.402	0.000	2.435	16.531	4.540	5.006	9.651	8.815	0.090	0.000	15.629	0.008
T	0.000	0.001	0.000	0.000	0.995	0.0001	0.000	0.000	0.000	0.000	11.845	0.000
H	0.000	0.000	0.000	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.357	0.000
S	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

through December (Fig. 2). Among vegetated habitats, aboveground seagrass biomass was usually highest in *Thalassia* habitat, followed by mussel and then *Halodule* habitats. Based on ANOVA and subsequent Scheffe's comparisons, aboveground seagrass biomass was significantly higher in *Thalassia* habitat than in mussel habitat in 5 of the months. *Halodule* habitat biomass tended to be lower than the other vegetated habitats. Algae were collected in measurable quantities only during June and July in *Thalassia* habitat (Fig. 2).

Although not directly measured, it is possible to estimate relative leaf surface area in each vegetated habitat

using conversions based on ratios of leaf surface area:leaf biomass (715 cm² g⁻¹ DW for *Halodule wrightii* leaf surface and 515 cm² g⁻¹ DW for *Thalassia testudinum* leaf surface area) provided by Stoner (1983). Using our aboveground seagrass biomass determinations, we find that *Thalassia* habitat usually had the greatest leaf surface area (8 months), followed by *Halodule* habitat (4 months) and then mussel habitat. Leaf surface area was higher in mussel than *Thalassia* habitat in only 1 month and was never higher than *Halodule* habitat. Despite less leaf surface area and/or aboveground seagrass biomass, macroinvertebrate densities

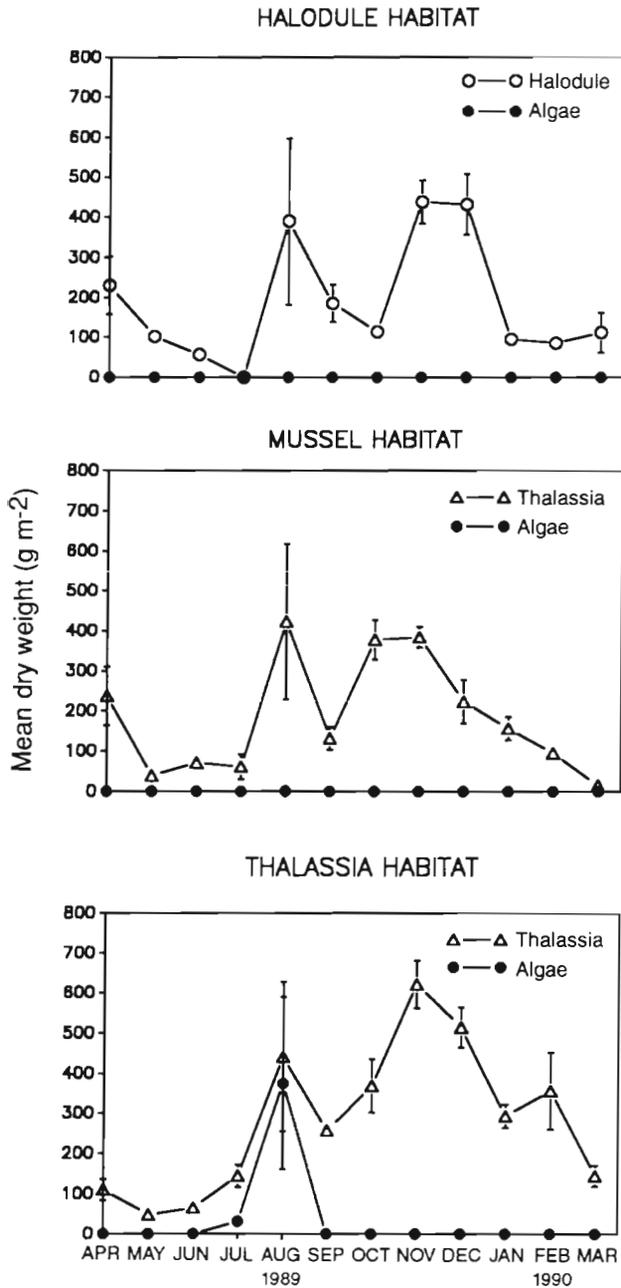


Fig. 2. Mean aboveground seagrass biomass in the 3 vegetated habitats in St. Joseph Bay, Florida, from 1989 through 1990

and biomass were often equivalent or higher in mussel habitat than the other vegetated habitats.

Annual secondary production

Estimated annual macroinvertebrate (all major taxonomic groups excluding *Modiolus americanus*) production ranged from 20 to 430 g AFDW m⁻² yr⁻¹ depending

Table 3. Annual secondary production of major epifaunal taxonomic groups (g AFDW m⁻²) from the 3 vegetated and 1 unvegetated habitats of St. Joseph Bay, Florida. Numbers in parentheses indicate the low and high estimates of life span in years

Group	Habitat			
	Mussel	<i>Thalassia</i>	<i>Halodule</i>	Unvegetated
Amphipods ^{a,b}				
(0.08)	29.51	19.07	19.34	3.63
(0.25)	11.96	8.58	8.71	1.64
Crabs ^c				
(1)	40.58	53.58	16.25	1.66
(3)	18.29	21.33	7.33	0.75
Gastropods				
(1)	96.68	70.26	77.88	20.84
(3)	43.57	31.67	34.96	9.41
Hermit crabs ^d				
(1)	16.17	9.39	9.58	5.06
(3)	7.29	4.23	4.31	2.28
Isopods ^b				
(0.08)	10.3	6.66	14.99	0.36
(0.25)	4.66	2.99	6.75	0.16
Shrimp ^d				
(0.17)	89.60	52.96	41.00	10.56
(0.42)	46.35	27.23	21.09	5.43
Chitons				
(1)	16.63	6.78	0.61	0.36
(3)	7.50	0.48	0.28	0.16
Sea urchins ^e				
(3)	129.12	26.64	0.79	0.0
(5)	89.15	18.39	0.55	0.0
Total (without sea urchins)				
Low	299.47	218.80	179.65	42.47
High	139.62	96.51	83.43	19.83
Total (with sea urchins)				
Low	428.59	245.44	180.44	42.47
High	228.77	144.90	83.98	19.83

^a Fredette & Diaz (1986); ^b Fredette et al. (1990);

^c Warner (1977); ^d Bauer (1989); ^e Moore et al. (1963)

on the estimated life expectancy and habitat (Table 3). Annual production was highest in mussel habitat (229 to 429 g AFDW m⁻² yr⁻¹) followed by *Thalassia* habitat (145 to 245 g AFDW m⁻² yr⁻¹), *Halodule* habitat (84 to 180 g AFDW m⁻² yr⁻¹), and unvegetated habitat (20 to 43 g AFDW m⁻² yr⁻¹).

Crustacean (amphipods, crabs, hermit crabs, isopods and shrimp combined) production was the highest of any group and was comparable in mussel (89 to 186 g AFDW m⁻² yr⁻¹) and *Thalassia* (64 to 141 g AFDW m⁻² yr⁻¹) habitats, followed by *Halodule* (48 to 98 g AFDW m⁻² yr⁻¹) then unvegetated habitat (10 to 20 g AFDW m⁻² yr⁻¹). Sea urchin production was the next highest and was greatest in mussel habitat (90 to 130 g AFDW

$\text{m}^{-2} \text{yr}^{-1}$) followed in descending order by *Thalassia* (18 to 27 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) and *Halodule* (<1 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) habitats. Gastropod annual production was similar in mussel (44 to 97 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) and *Thalassia* (32 to 70 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) habitats, followed by *Halodule* (35 to 78 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) and unvegetated (9 to 21 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) habitats. The annual production of chitons was highest in mussel habitat (8 to 17 g AFDW $\text{m}^{-2} \text{yr}^{-1}$), followed by *Thalassia* (<1 to 7 g AFDW $\text{m}^{-2} \text{yr}^{-1}$), *Halodule* (<1 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) and unvegetated (<1 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) habitats.

Since sea urchins were abundant only in mussel habitat and contributed over 30% of the annual secondary production of this habitat, a second calculation, excluding sea urchins, was performed. Estimated annual secondary production was still highest in mussel habitat (140 to 299 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) but was more closely followed by *Thalassia* (97 to 219 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) and *Halodule* (85 to 180 g AFDW $\text{m}^{-2} \text{yr}^{-1}$). Annual secondary production in unvegetated habitats remained the same (20 to 43 g AFDW $\text{m}^{-2} \text{yr}^{-1}$) since sea urchins were not collected there (Table 3).

DISCUSSION

Vegetation abundance, expressed as macrophyte biomass or leaf surface area, is the most commonly used estimate of seagrass habitat complexity. Typically, vegetation biomass is positively correlated with increased macrofaunal survivorship, density and species diversity (see Heck & Orth 1980, Heck & Crowder 1991 for summaries, and Stoner 1980a, b, c, Lewis 1984). As a result, the higher macroinvertebrate densities and biomass collected in the vegetated habitats of St. Joseph Bay were not unexpected. Mussel habitat generally supported equivalent or higher macroinvertebrate densities and greater biomass than *Thalassia* habitat, despite having lower aboveground seagrass biomass and leaf surface area.

Several investigators have hypothesized that habitat heterogeneity [i.e., the patchy distribution of microhabitat types (Sebens 1991)], in addition to vegetation abundance, is important in influencing macrofaunal distributions within seagrass systems (see Heck & Orth 1980 for a summary, Pihl-Baden & Pihl 1984, Stoner & Lewis 1985, Schneider & Mann 1991b). Seagrass habitat heterogeneity usually manifests itself in the form of biogenic substrates, both plant and animal. For example, Stoner & Lewis (1985) found that combinations of the calcareous green alga *Hali-medea opuntia* (Linnaeus), which can form dense understories beneath seagrass canopies, and lower aboveground *Thalassia testudinum* biomass supported higher macrofaunal densities and species richness

than monotypic stands of *T. testudinum* with higher aboveground biomass. Stoner & Lewis (1985) hypothesized that habitat architecture or combinations of different substrate types are important in determining local epifaunal abundance and diversity in seagrass meadows. Drift algae within seagrass habitats are also known to support higher epifaunal abundances and species abundance than similar stands of seagrass without drift algae (Hooks et al. 1976, Gore et al. 1981, Pihl-Baden & Pihl 1984, Schneider & Mann 1991a). Sponges (Westinga & Hoetjes 1981), corals and coral rubble (Heck & Wetstone 1977, Heck 1979), bryozoans (Heck & Orth 1980), polychaete tubes (Bell & Coen 1982) and calcareous worm tubes (Heck & Hambrook 1991), all of which occur within seagrass habitats, have been documented to elevate macrofaunal abundance and species diversity as well. Semi-infaunal mussels, which form structurally complex habitats beneath seagrass canopies, are also associated with increased macroinvertebrate biomass and secondary production.

Mussel habitats may be associated with increased macroinvertebrate productivity simply by being sites of increased food abundance or survivorship for small macroinvertebrates. We hypothesize that mussel habitats might increase food abundance (1) by providing abundant substrate for sessile algal and invertebrate attachment which in turn provides increased food for herbivores and predators (Witman 1987, Young 1989, Dittman & Robles 1991), (2) by producing feces and pseudofeces which could be an attractive food source for many macroinvertebrates (Frankenberg & Smith 1967, Frankenberg et al. 1967, Stuart et al. 1982), similar to that demonstrated for intertidal mussels (Bayne et al. 1976, Kautsky & Evans 1987), (3) by altering water flow which could allow the passive settlement of suspended particulate matter (Eckman 1983) such as detritus and planktonic larvae, and/or (4) by serving as food themselves for molluscivores, particularly crabs and gastropods.

Macrogazers, such as sea urchins and chitons, which feed on algae and seagrass, were clearly most abundant in mussel habitat. Opportunistic omnivores (xanthid crabs, caridean shrimps and isopods) which feed on a variety of foods including molluscs, small crustaceans, decaying animal material and detritus were also usually found at equivalent or higher densities in mussel habitat. In contrast, amphipods and hermit crabs, which typically feed on seagrass epiphytes and algae, showed less clear distributional patterns among the vegetated habitats, while gastropods, dominated by *Diastoma varium*, and isopods were consistently more abundant in *Halodule* habitat. During our collecting, we noted that epiphyte and macroalgal abundance were low in areas where sea urchins were abundant, possibly explaining

lower epiphytic grazer abundances in mussel habitat. Alternatively, mussel habitats may provide an important refuge for small sea urchins, similar to that reported from the northeastern coast of the United States (Witman 1985).

The relatively high macrofaunal biomass, as well the high estimates of annual secondary production in mussel habitats, indicate that mussels may be significantly influencing energy flow in nearshore seagrass meadows. Comparisons of annual secondary production, even without the inclusion of sea urchins, show that differences between the vegetated habitats were still large.

Our estimates of annual secondary production, although crude, are higher than previously reported estimates for seagrass habitats (Table 4). In Swedish *Zostera marina* habitats, Pihl-Baden & Pihl (1984) estimated annual secondary production to be from 2.5 to 6.6 g AFDW m⁻² yr⁻¹, based on collection of 20 species, 10 of which were fish and 10 which were crustaceans. Fredette et al. (1990) estimated annual macroinvertebrate production to be 37.8 g AFDW m⁻² yr⁻¹ in a mixed *Ruppia maritima* and *Z. marina* seagrass habitat in the lower Chesapeake Bay, USA, based on 13 macroinvertebrate species (10 crustacean, 2 gastropod and 1 bivalve species). These estimates were based on only 20% of the available pool of taxa previously reported from the study site (Orth & van Montfrans 1982) and extrapolations suggest that annual secondary production in this seagrass habitat could be near 180 g AFDW m⁻² yr⁻¹ (Fredette et al. 1990), assuming that production was comparable in the fraction of the fauna that was not used to calculate

these estimates. Robertson (1984) determined that annual macroinvertebrate secondary production varied between 20.7 and 39.4 g AFDW m⁻² yr⁻¹ in sparse *Z. muelleri* and more densely vegetated *Heterozostera tasmanica* habitats, respectively, in western Australia. Organisms used in this estimation included crustaceans and gastropods. Similar results were obtained by Edgar (1990), who determined that annual secondary production in vegetated habitats ranged between 11.7 and 47.2 g AFDW m⁻² yr⁻¹.

Our annual secondary production estimates from St. Joseph Bay, based on the 49 macroinvertebrate species in Appendix 1 and ranging between 83 and 429 g AFDW m⁻² yr⁻¹, are the highest estimates reported from seagrass habitats to date. Multiplying our estimates of secondary production in the vegetated habitats by the estimated 25.6 km² covered by seagrass in the bay (McNulty et al. 1972) indicates that somewhere between 2 and 11 kt of macroinvertebrates are produced annually in the seagrass habitats of St. Joseph Bay. We believe that the high salinity St. Joseph Bay seagrass habitats are likely to function in a manner similar to the nearly 300 000 ha of offshore seagrass habitats which occur along the western coast of Florida. Assuming similar production rates, these offshore seagrass systems could produce 252 to 1285 kt of macroinvertebrates annually and indicate the extremely important role vegetated habitats could play in determining productivity of the entire eastern Gulf of Mexico.

Earlier studies have probably underestimated the annual secondary production of seagrass habitats due to sampling intervals longer than many macroinverte-

Table 4. Reported annual secondary production estimates of epifaunal organisms in seagrass habitats

Location	Seagrass habitat	Annual production (g AFDW m ⁻² yr ⁻¹)	Source
Sweden	<i>Zostera marina</i> mixed with <i>Fucus</i> sp.	2.50–6.60 ^{a,b}	Pihl-Baden & Pihl (1984)
Chesapeake Bay, USA	<i>Zostera marina</i> and <i>Ruppia maritima</i>	41.90–180.00 ^{c,d}	Fredette et al. (1990)
St. Joseph Bay, Florida, USA	<i>Thalassia testudinum</i> and mussel	228.77–428.59 ^{a,d}	This study
	<i>T. testudinum</i> alone	144.90–245.44 ^{a,d}	
	<i>Halodule wrightii</i> alone	83.98–180.44 ^{a,d}	
Western Port, Australia	Bare sand and sparse <i>Zostera muelleri</i>	20.70 ^{d,e}	Robertson (1984)
	<i>Heterozostera tasmanica</i>	39.40 ^{d,e}	
Western Australia	<i>Heterozostera tasmanica</i> and <i>Halophila ovalis</i>	24.30–42.20 ^{d,g}	Edgar (1990)
	<i>Amphipolis antarctica</i>	11.70–47.20 ^{d,e}	

^a Reported as g AFDW m⁻² yr⁻¹
^b Macroinvertebrates and fish
^c Reported as g DW m⁻² yr⁻¹, converted to g AFDW m⁻² yr⁻¹ using a correction factor of 0.9 × g DW m⁻² yr⁻¹ (Waters 1977)
^d Macroinvertebrates only
^e Reported as kcal m⁻² yr⁻¹, converted to DW m⁻² yr⁻¹ using a correction factor of kcal/5 (Crisp 1975)

brate species' generation times. Each of these studies, except Fredette et al. (1990), also used 1.0 mm mesh samplers which probably also resulted in the under-sampling of smaller macroinvertebrates, such as amphipods and isopods, that characteristically have high turnover rates and production (Fredette & Diaz 1986, Fredette et al. 1990). The effects of this should be greatest in warmer water habitats where macroinvertebrates, particularly crustaceans (Sastry 1983, Bauer 1989), produce more generations annually than in colder waters. In this work, we probably also under-sampled larger, more mobile invertebrates such as blue crabs and stone crabs as well as nocturnally feeding gastropods, such as whelks, that we commonly encountered while snorkeling. In addition, we did not include estimates of mussel production since mussels were treated as a habitat rather than as a component of the community. Asmus (1987) estimated the annual production of intertidal mussels in the North Sea at 436 g AFDW m⁻² yr⁻¹, suggesting that mussels can contribute significantly to nearshore productivity.

Our results indicate that the presence of mussels within seagrass habitats positively influences the abundance of most macroinvertebrate groups. Our secondary production estimates, which are the first from subtropical seagrass meadows, are among the highest reported to date for seagrass habitats. These results also provide one of the first comparative estimates of the relative secondary production of different seagrass habitats (i.e. *Thalassia* vs *Halodule* habitats). We believe that these estimates are conservative and that true annual macroinvertebrate productions will likely be higher based on (1) our conservative estimates of the life expectancy of these organisms, and (2) our use of 1.0 mm mesh collection bags which probably resulted in lower collections of smaller more productive organisms such as amphipods and isopods. When taken together with the likely high production of fishes, which were not included in this study, the extremely large contribution of seagrass habitats to the secondary productivity of nearshore ecosystems is further underscored.

Appendix 1. Macroinvertebrate species used in estimating the annual secondary production of the 4 habitats in St. Joseph Bay, Florida. M: *Thalassiosira testudinum* with mussels; T: *T. testudinum* without mussels; H: *Halodule wrightii* where mussels were seldom observed; S: unvegetated sand flats

Taxon	Habitat	Taxon	Habitat
Mollusca			
Gastropods		<i>Lysianopsis alba</i>	H, T, M
<i>Anachis obesa</i>	H, T	<i>Melita</i> spp.	H, T, M, S
<i>Balcis arcuata</i>	T	<i>Monoculodes nyei</i>	M, S
<i>Cerithium floridanum</i>	H, T, M, S		
<i>Crepidula</i> spp.	H, T, M, S	Isopoda	
<i>Diastoma varium</i>	H	<i>Aegathoa oculata</i>	T
<i>Epitonium rupicola</i>	H, T, S	<i>Cymodoce faxoni</i>	H, T, M
<i>Haminoea succinea</i>	T	<i>Edotea montosa</i>	T, M
<i>Marginella aureocincta</i>	H, T	<i>Erichsonella filiformis</i>	H, T, S
<i>Mitrella lunata</i>	H, T	<i>Meroceras nitidum</i>	T
<i>Nassarius vibex</i>	H, T, M, S	<i>Paracerceis caudata</i>	M
<i>Odostomia weberi</i>	H, T, M, S	<i>Xenanthura brevitelson</i>	H, S
<i>Olivella pusilla</i>	H, T, M, S		
<i>Prunum apicinium</i>	H, T, M, S	Decapoda	
<i>Stellatoma stelatta</i>	H, M	<i>Alpheus</i> spp.	T, M
<i>Turbo castanea</i>	T	<i>Ambidexter symmetricus</i>	M
<i>Turbonilla</i> spp.	H, T, M	<i>Callinectes sapidus</i>	H, T, M, S
		<i>Hippolyte zostericola</i>	H, T, M, S
Polyplacophora		<i>Lysmata wurdemani</i>	M
<i>Acanthochitona pygmaea</i>	H, T, M	<i>Neopanope texana</i>	H, T, M
<i>Acanthopleura granulatum</i>	M	<i>Paguristes</i> spp.	H, T, M, S
<i>Ischnochiton striolatus</i>	H, T	<i>Palaemonetes vulgaris</i>	H, T
		<i>Penaeus duorarum</i>	H, T, M, S
Crustacea		<i>Pitho anisodon</i>	H, T, M
Amphipoda		<i>Portunus depressifrons</i>	H, S
<i>Acanthoastorius</i> spp.	H	<i>Ogyrides alphaerostris</i>	H, M
<i>Ampelisca</i> spp.	T, M, S	<i>Menippe mercenaria</i> × <i>adina</i>	M
<i>Corophium</i> spp.	M	<i>Tozeuma carolinensis</i>	M
<i>Cymadusa compta</i>	H, T, M		
<i>Erichthonius brasiliensis</i>	H, S	Echinodermata	
<i>Gammarus mucronatus</i>	H	Echinoidea	
		<i>Lytechinus variegatus</i>	H, T, M

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