Comparative Species Richness, Composition, and Abundance of Invertebrates in Caribbean Seagrass *(Thalassia testudinum)* Meadows (Panamá)

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Abstract

The results of a year-long study in which epibenthic invertebrates were collected monthly from seagrass (*Thalassia testudinum*) meadows along the Caribbean coast of Panamá and the Panamá Canal Zone are described in this paper. Differences in species composition and abundance among sites were primarily due to the proximity of surrounding habitats, especially coral reefs, which contain a number of species that utilize the seagrass meadows. In contrast to many previous characterizations of tropical marine habitats, important seasonal fluctuations in both species number and abundance took place at each of the sites. Data on breeding activity among several species of decapod crustaceans indicate year-round reproduction, although considerable seasonal differences occur in the percentage of ovigerous females. These interspecific differences in observed reproductive output may be explained by differences in life-cycle length, a factor not often considered in discussions of seasonal breeding patterns in tropical marine invertebrates. Overall species composition was qualitatively similar to that reported in comparable studies of tropical and subtropical seagrass meadows elsewhere, although caridean shrimp and xanthid crab species were reduced in number and total abundance were much lower than in previous studies.

Introduction

Tropical communities are generally thought to contain a large number of species, many of which are rare, and to exhibit a more uniform distribution of relative abundances among these species than temperate communities. These characteristics are hypothesized to result from the relatively low levels of physical stress and the small amount of seasonal variation that are said to characterize tropical environments (MacArthur, 1969). Reasoning along these lines, Copeland (1970) and Odum (1974) describe tropical seagrass (*Thalassia testudinum*) meadows as species-rich habitats which contain complexly organized communities that are subject to fewer stresses and less seasonal variation than temperate seagrass communities. Yet it has been found that organisms associated with seagrasses growing on back-reefs in Jamaica (Jackson, 1972), Puerto Rico (Glynn, 1968), and Panamá (Meyer and Birkeland, 1974) may be seasonally subject to heavy mortality from desiccation and heat stress during periods of extreme low tides. Additionally, Tabb *et al.* (1962) described large seasonal changes in species composition and abundance in subtropical seagrass meadows along the coast of south Florida (USA). These studies indicate that tropical seagrass communities are not unstressed, and make it seem premature to speak in generalities about complex and stable communities and low levels of stress in this habitat.

Part of the difficulty in characterizing tropical seagrass communities is due to the paucity of long-term detailed studies on their biota. As a contribution to the understanding of tropical seagrass communities, and tropical communities in general, the results of a year-long study on epibenthic invertebrates inhabiting seagrass meadows in the Caribbean Sea are discussed in this paper. The effects of both physical and biological factors in shaping species composition throughout the year are considered, and observations on microhabitat preferences among the species are discussed. Additionally, the data presented here are compared and contrasted with previ-

ously studied tropical and subtropical seagrass environments.

Study Areas

Littoral environments on the Caribbean coast of Panamá are subject to pronounced seasonal changes in climatic regimes (Glynn, 1972), with two generally distinct seasons: a rainy and a dry period. The rainy season usually begins in April or May and reaches a first peak in June followed by decreasing rainfall in July. Beginning in August, rainfall begins increasing to a monthly maximum in November, which is followed by a nearly complete cessation of rainfall in December. In shallow Caribbean waters, salinities decrease substantially during this rainy period (Glynn, 1972) and bottom salinities may drop by 15% (from ≅ 34 to 19 %) in a few hours at depths of 1 to 2 m during heavy downpours (personal observation). Temperatures decrease slightly during the rainy season, but there is no upwelling on the Caribbean coast and hence no marked change in water temperature as there is on the Pacific coast of Panamá. During the dry season there is almost no rainfall, salinities are high (≅ 34 %), and the Trade Winds generate strong waves which buffet the Caribbean shores and bring about increased turbidity. This strong wave action during the dry season sometimes dislodges motile species and uproots sessile species (Glynn, 1972). Tidal ranges in this part of the Caribbean are only about 0.5 m (U.S. Department of Commerce Tide Tables).

Four sampling stations were established along the Caribbean coast of Panamá and the Panamá Canal Zone (Fig. 1). The study sites were thickly vegetated subtidal areas, chosen to represent the different conditions in which the seagrass habitat occurs in open subtidal waters (i.e., not on back-reefs) in this part of the Caribbean. One relatively unprotected site (Station 2) and one nearby protected site (Station 3) were chosen to assess the effects of wave shock on the invertebrate biota. A site seaward of a thick growth of red mangroves was also selected (Station 1) as well as a site surrounded by a well developed coral-reef system (Station 4), in order to determine the influence of surrounding habitats on the fauna of seagrass meadows. All sites were located 15 to 30 m offshore.

Dominant plants at the sites in terms of biomass regularly included the marine angiosperms *Thalassia testudinum* and *Syringodium filiforme*, and the calcareous green algae *Halimeda opuntia*, *H. incrassata*, *Penicil-*

lus capitatus, and *Udotea flabellum*, the filamentous green alga *Cladophora jamaicensis*, and periodically the brown alga *Dictyota divaricata*. In general, however, brown algae were relatively scarce and red algae almost entirely absent during the study period. The importance of the lack of these algae will be considered in "Results and Discussion". Water depth at the 4 sites was approximately 1 to 2 m, depending on tidal condition, and the areas were never exposed at low tide. The sites are described in more detail below:

Site 1. The vegetation was composed primarily of thick growths of *Thalassia testudinum* and *Halimeda opuntia*. Less abundant were *Syringodium filiforme*, *Penicillus capitatus*, and *Udotea flabellum*. Sediments were mostly fine muds, derived from deposition by a nearby small stream and from runoff among the mangroves that lined the shore. Water was most turbid here, and this site was relatively protected from wave shock by a patch reef which separated it from Site 2.

Site 2. Dominant plants included *Thalassia testudinum* and *Syringodium filiforme*, with lesser amounts of calcareous green algae. Sediments were calcareous sand with some coral fragments, and parts of *Halimeda* spp. segments. Wave shock was most severe at this site.

Site 3. This site was the most protected and received the least wave shock. *Thalassia testudinum* was the most abundant plant, but some thick patches of *Halimeda opuntia* and *H. incrassata* were present. Sediments were coarse and consisted of *Halimeda* spp. fragments and coral debris which was derived from the reef that sheltered this site from wave action.

Site 4. Well developed coral growths surround this site, which was located on the leeward side of two small islands. *Thalassia testudinum* was the dominant plant, although there were some small patches of *Syringodium filiforme*. Sediments were coarse, consisting of calcareous sand and coral fragments. Wave shock was slight.

Materials and Methods

Ten replicate samples per month were taken at each of Sites 1, 2, and 3 from July 1974 - May 1975. At Site 4 no samples could be obtained in January,
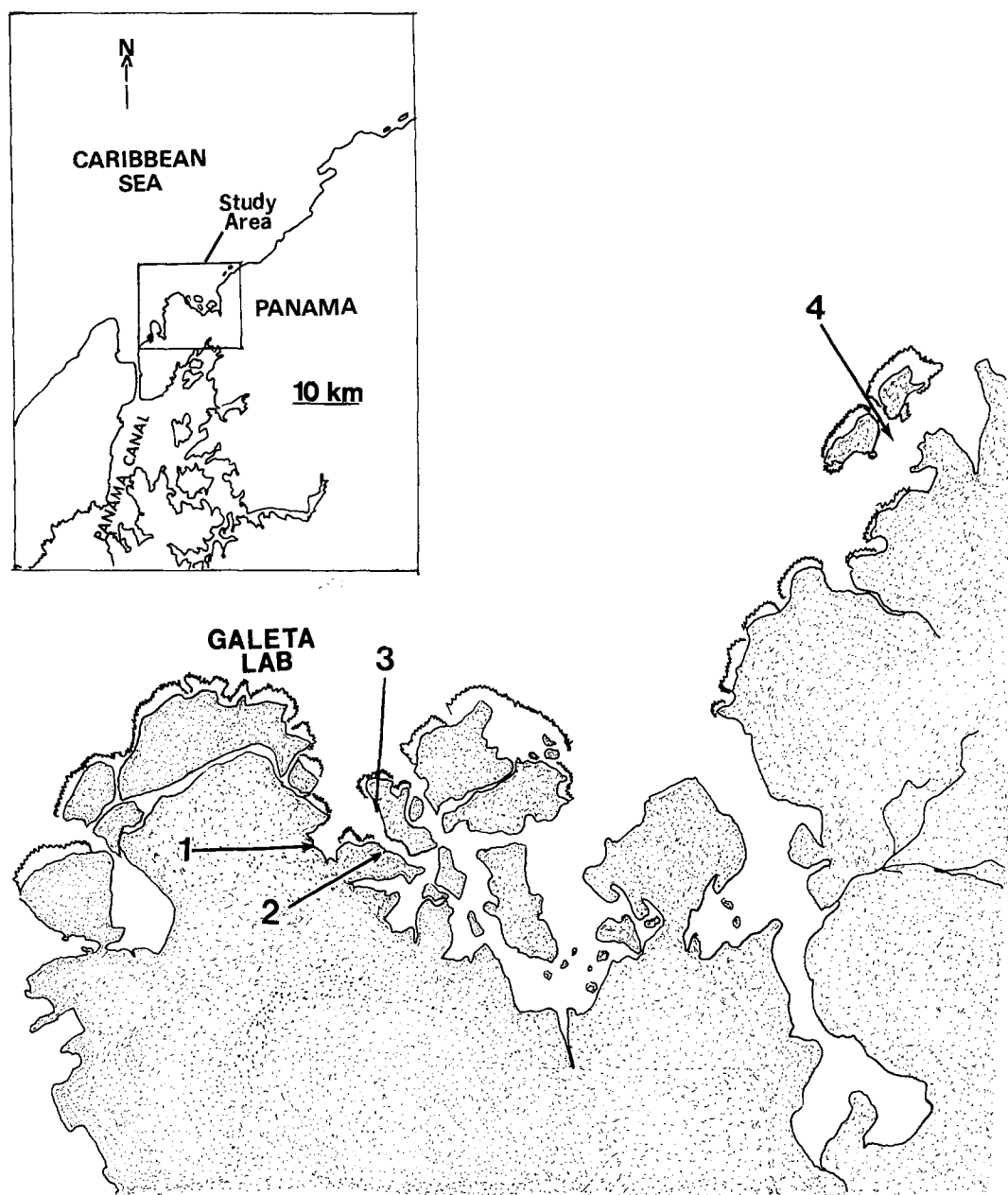
Fig. 1. Map of Panamá and location of study sites. Locations of coral reefs are indicated by scalloped lines seaward of the land boundaries

February, or March because rough seas prevented travel to this station, but in other months 10 replicate samples were taken. Each sample consisted of the catch obtained from a 2 min tow of a 4.87 m (16 ft) otter trawl, pulled at a speed of 2 to 3 knots. The wings of the trawl were of 19 mm (3/4") mesh and the liner of 6.3 mm (1/4") mesh. The contents of each sample were placed in plastic bags and sorted in the laboratory. Only macroscopic epifaunal and semi-infaunal motile species are considered in this study. The smallest animals in the collections were several

species of caridean shrimps with minimum body lengths of approximately 5 mm. Fish species taken in these samples are analyzed in detail elsewhere (Weinstein and Heck, in preparation), although some relevant comments on the identity of important fish predators are provided here. Samples were taken diurnally, except for one set of night samples which was taken in May 1975 and which will be discussed separately.

The sampling limits of the otter trawl are well known (Taylor, 1953), and its catch efficiency is not high. It has previously been shown, however, that

Table 1. Invertebrate species taken at each of study sites along Caribbean coast of Panamá; ranked by abundance (n)

Rank	Species	Abundance	Rank	Species	Abundance
Site 1			Site 2		
(1)	Tozeuma carolinense	268	(1)	Tozeuma carolinense	383
(2)	Penaeus durorum notialis	238	(2)	Cerithium eburneum	338
(3)	Cerithium eburneum	211	(3)	Microphrys bicornutus	95
(4)	Holothuria mexicana	108	(4)	Clibinarius antillensis	53
(5)	Microphrys bicornutus	75	(5)	Paguristes limonensis	42
(6)	Panopeus occidentalis	53	(6)	Modulus modulus	36
(7)	Aplysia dactylomelia	42	(7)	Holothuria mexicana	34
(8)	Paguristes limonensis	38	(8)	Mithrax forceps	18
(9)	Modulus modulus	28	(9)	Lytechinus variegatus	17
(10)	Mithrax forceps	24	(10)	Aplysia dactylomelia	16
(11)	Pitho ilhermani	19	(11)	Synalpheus pandionis	16
(12)	Callinectes danae	17	(12)	Panopeus occidentalis	14
(13)	Pagurus bonairensis	16	(13)	Petrolisthes armatus	14
(14)	Petrolisthes armatus	15	(14)	Cerithium litteratum	9
(15)	Panulirus argus	12	(15)	Pagurus brevidactylus	8
(16)	Macrocoeloma diplacanthus	11	(16)	Penaeus durorum notialis	8
(17)	Alpheus floridanus	10	(17)	Petrolisthes galathinus	8
(18)	Clibinarius antillensis	10	(18)	Synalpheus fritzmulleri	8
(19)	Periclimenes americanus	10	(19)	Callinectes danae	7
(20)	Lytechinus variegatus	8	(20)	Macrocoeloma diplacanthum	5
(21)	Pitho anisodon	8	(21)	Panulirus argus	4
(22)	Cerithium litteratum	7	(22)	Leander tenuicornis	4
(23)	Podochela riisei	7	(23)	Pagurus bonairensis	3
(24)	Periclimenes longicaudatus	6	(24)	Processa fimbriata	2
(25)	Cronius ruber	4	(25)	Pilumnus dasypodus	2
(26)	Pilumnus pannosus	4	(26)	Alpheus normanni	2
(27)	Pitho quadridentata	4	(27)	Alpheus floridanus	2
(28)	Gonodactylus sp.	4	(28)	Ambidexter symmetricus	2
(29)	Alpheus heterochaelis	4	(29)	Calcinus tibicen	1
(30)	Leander tenuicornis	3	(30)	Calappa angusta	1
(31)	Calappa angusta	3	(31)	Dardanus venosus	1
(32)	Bursatella leachi	2	(32)	Diopatra sp.	1
(33)	Cyrtoplax spinidentata	2	(33)	Latreutes fucorum	1
(34)	Hepatus pudibundus	2	(34)	Ophiothrix angulata	1
(35)	Oreaster reticulatus	2	(35)	Oreaster reticulatus	1
(36)	Processa fimbriata	2	(36)	Synalpheus goodei	1
(37)	Sicyonia laevigata	2	(37)	Synalpheus townsendi	1
(38)	Squilla prasolineata	2	(38)	Thor floridanus	1
(39)	Pilumnus reticulata	2			
(40)	Unidentified holothurian	2		Total	1160
(41)	Podochela gracilipes	1			
(42)	Unidentified opisthobranch	1			
(43)	Unidentified nereid	1			
(44)	Nikoides schmitti	1			
(45)	Cronius tumidulus	1			
(46)	Trachycaris restrictus	1			
(47)	Thor floridanus	1			
(48)	Synalpheus pandionis	1			
(49)	Synalpheus fritzmulleri	1			
(50)	Portunus sp.	1			
(51)	Pilumnus dasypodus	1			
(52)	Ophiotrix angulata	1			
(53)	Ophioderma sp.	1			
(54)	Latreutes fucorum	1			
(55)	Hippolyte zostericola	1			
(56)	Conus sp.	1			
(57)	Calappa ocellata	1			
(58)	Alpheus normanni	1			
(59)	Alpheus formosus	1			
	Total	1304			

Table 1 (continued)

| Rank	Species	Abundance	Rank	Species	Abundance
Site 3			Site 4		
(1)	*Tozeuma carolinense*	237	(1)	*Modulus modulus*	269
(2)	*Cerithium eburneum*	91	(2)	*Hermodice carunculata*	139
(3)	*Modulus modulus*	85	(3)	*Tozeuma carolinense*	116
(4)	*Holothuria mexicana*	82	(4)	*Pagurus bonairensis*	101
(5)	*Lytechinus variegatus*	48	(5)	*Lytechinus variegatus*	98
(6)	*Petrolisthes galathinus*	35	(6)	*Cerithium eburneum*	75
(7)	*Paguristes limonensis*	29	(7)	*Cerithium litteratum*	64
(8)	*Cerithium litteratum*	23	(8)	*Pagurus brevidactylus*	34
(9)	*Pagurus bonairensis*	20	(9)	*Callinectes danae*	29
(10)	*Aplysia dactylomelia*	20	(10)	*Mithrax forceps*	23
(11)	*Mithrax forceps*	12	(11)	*Tripneustes ventricosus*	20
(12)	*Penaeus duororum*	12	(12)	*Holothuria mexicana*	17
(13)	*Ophiothrix angulata*	11	(13)	*Astropecten duplicatus*	16
(14)	*Callinectes danae*	11	(14)	*Penaeus duororum*	14
(15)	*Microphrys bicornutus*	9	(15)	*Diadema antillarum*	13
(16)	*Petrolisthes armatus*	9	(16)	*Paguristes limonensis*	12
(17)	*Panopeus occidentalis*	8	(17)	*Ophiactis savignyi*	11
(18)	*Clibinarius antillensis*	8	(18)	*Panopeus occidentalis*	9
(19)	*Oreaster reticulatus*	7	(19)	*Macrocoeloma diplacanthum*	9
(20)	*Pagurus brevidactylus*	7	(20)	*Stenorhynchus seticornis*	8
(21)	*Trachycaris restrictus*	7	(21)	*Conus* sp.	6
(22)	*Macrocoeloma diplacanthum*	6	(22)	*Hemipholus elongata*	5
(23)	Unidentified holothurian	5	(23)	*Eucidaris tribuloides*	5
(24)	*Periclimenes americanus*	4	(24)	*Pilumnus pannosus*	4
(25)	*Alpheus floridanus*	3	(25)	*Pitho quadridentata*	4
(26)	*Conus* sp.	3	(26)	*Murex recurvirostris*	3
(27)	*Pitho anisodon*	3	(27)	*Murex* sp.	3
(28)	*Thor floridanus*	3	(28)	*Microphrys bicornutus*	3
(29)	Unidentified nereid	2	(29)	*Dardanus venosus*	3
(30)	*Nikoides schmitti*	2	(30)	*Clibinarius antillensis*	3
(31)	*Podochela riisei*	2	(31)	*Cronius ruber*	2
(32)	*Periclimenes longicaudatus*	2	(32)	*Oliva* sp.	2
(33)	*Hippolyte zostericola*	2	(33)	*Ophiothrix angulata*	2
(34)	*Dromidia antillensis*	2	(34)	*Panulirus argus*	2
(35)	*Batillaria minima*	1	(35)	*Pilumnus dasypodus*	2
(36)	*Cyrtoplax spinidentata*	1	(36)	*Pitho ilhermani*	2
(37)	*Gonodactylus* sp.	1	(37)	*Podochela gracilipes*	2
(38)	*Leander tenuicornis*	1	(38)	*Gonodactylus* sp.	2
(39)	*Lupella forceps*	1	(39)	Unidentified opistobranch	1
(40)	*Pilumnus dasypodus*	1	(40)	*Murex* sp.	1
(41)	*Pilumnus pannosus*	1	(41)	Unidentified nereid	1
(42)	*Pitho quadridentata*	1	(42)	*Trachypenaeus similis*	1
(43)	*Pitho ilhermani*	1	(43)	*Trachycaris restrictus*	1
(44)	*Podochela sidneyi*	1	(44)	*Sepiateuthis* sp.	1
(45)	*Portunus ordwayi*	1	(45)	*Podochela riisei*	1
(46)	*Stenorhynchus seticornis*	1	(46)	*Pitho anisodon*	1
(47)	*Trachypenaeus similis*	1	(47)	*Pitho aculeata*	1
(48)	*Scylarrus* sp.	1	(48)	*Oreaster reticulatus*	1
(49)	*Tegula* sp.	1	(49)	*Mithrax ruber*	1
			(50)	*Diopatra* sp.	1
	Total	825	(51)	*Alpheus normanni*	1
				Total	1145
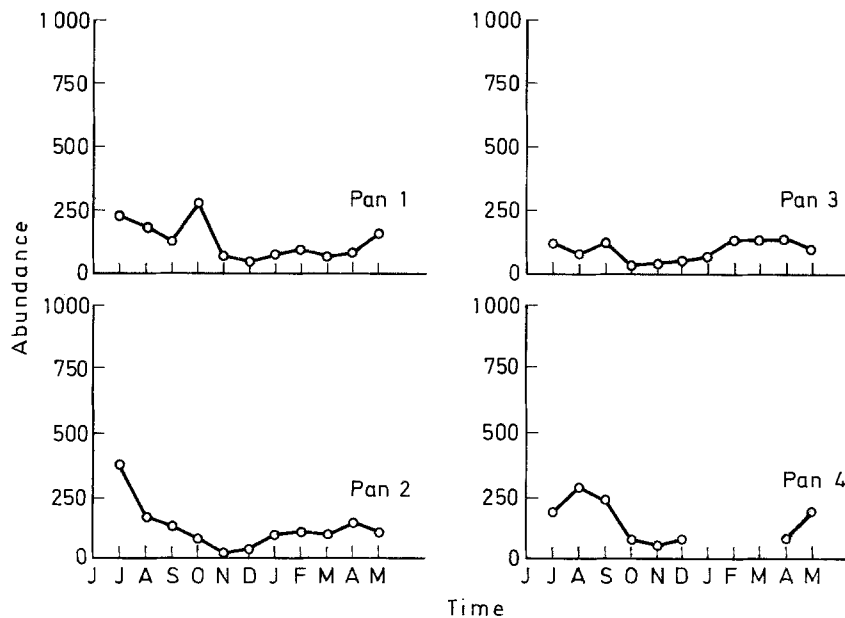
Fig. 2. Monthly abundances at each of the 4 sites during the study period

valid comparisons among sites can be made, if sampling methodology is standardized and the limitations of the gear are acknowledged (cf. Livingston, 1975; Heck, 1976b).

Salinity was measured whenever biological samples were taken, using a Beckman salinometer or a temperature compensated refractometer. Temperature data were obtained from the Smithsonian Tropical Research Institute's constant recording thermograph at Galeta Island (Fig. 1).

The following similarity indices were used in determining affinities among sites: Simpson's (1949) coefficient; the Jaccard coefficient (see Clifford and Stephenson, 1974); and the $c\lambda$ measure of affinity (Morisita, 1959; Horn, 1966). Data sets were reduced before computing similarities by eliminating from consideration those species which were represented by only one individual among all the samples (singletons), and hence could not, by definition of these indices, contribute to similarity among sites. The reduced data matrix contained 70 species.

Results and Discussion

A total of 90 species and 4,435 individuals were taken in the diurnal collections. The majority of animals, 55% of the individuals and 68% of the species, were decapod crustaceans (Table 1). The most abundant species was the caridean

shrimp *Tozeuma carolinense*, which accounted for about 22.6% of all animals collected. Only 10 other species were collected in abundances greater than 100 individuals. These were the gastropods *Cerithium eburneum*, *C. litteratum* and *Modulus modulus*, the shrimp *Penaeus duororum notialis*, the majid crab *Microphrys bicornutus*, the sea urchin *Lytechinus variegatus*, the hermit crabs *Pagurus bonairensis* and *Paguristes limonensis*, the sea cucumber *Holothuria mexicana*, and the polychaete *Hermodice carunculata*. *H. carunculata* is predaceous, while all the rest of these species are grazers or detritivores. This group of the 11 most abundant species accounts for about 78.6% of all animals collected.

Monthly total abundances at each site are shown in Fig. 2, and monthly species totals in Fig. 3. Drops in both abundance and species number during November and December occurred during periods of large salinity decreases (Fig. 4). Drops in temperature also tended to occur during periods of heavy rainfall and reduced salinities, but since annual subtidal temperature varies only from about 27° to 31°C annually in the vicinity of the study sites (Glynn, 1972; Meyer and Birkeland, 1974), it is not likely that temperature change influences the abundances of the resident species.

Qualitative and quantitative changes in species composition also occurred during the sampling period. This can be shown by presence-absence (Jaccard) and meristic ($c\lambda$) similarity indices which compare the initial collections (July)
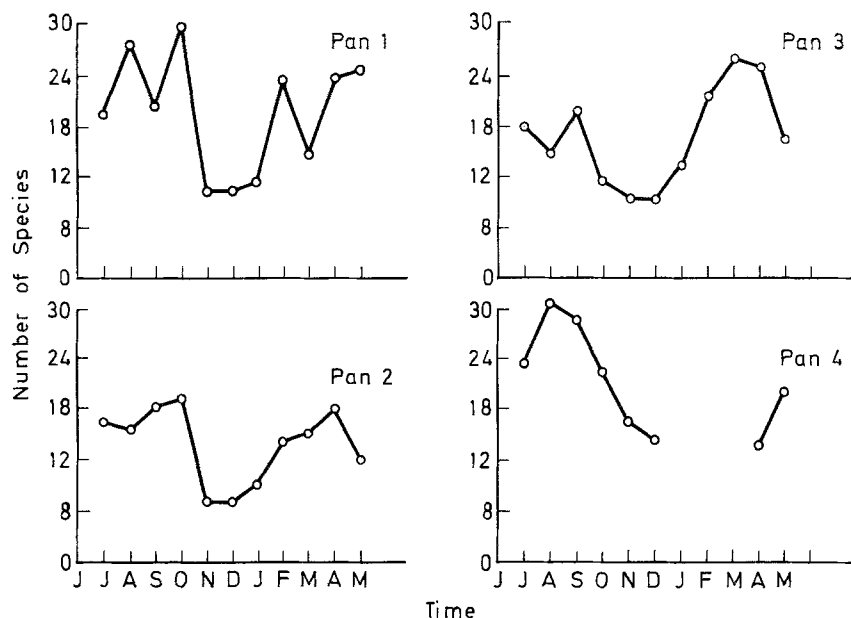
Fig. 3. Number of species taken monthly at each site during the study period
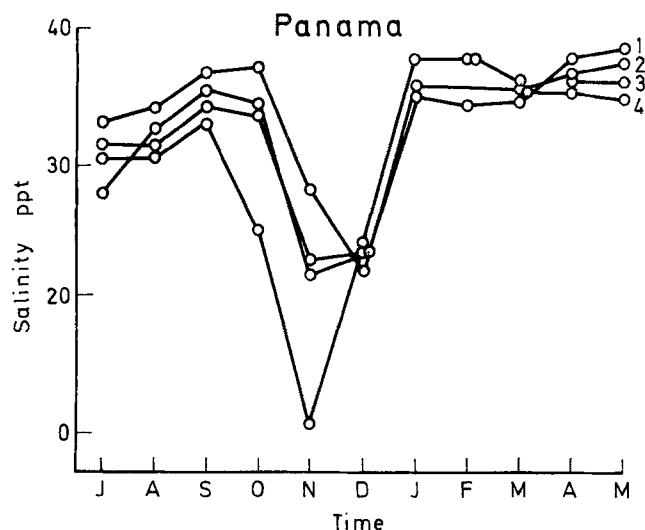
Fig. 4. Monthly salinity readings at each of the study sites (1-4)
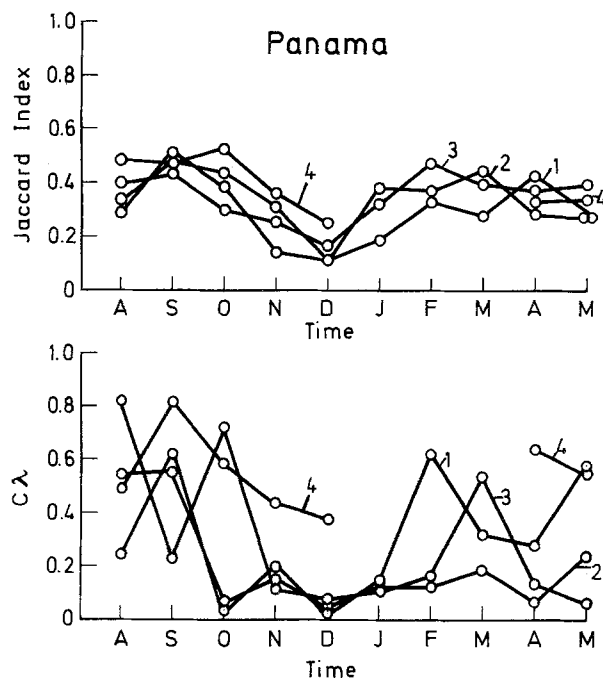
Fig. 5. Values of Jaccard and $C\lambda$ similarity indices computed among initial collections (July) and the collections of each succeeding month of the sampling period. 1-4: Sampling sites

with those taken in succeeding months. The resulting similarity values are then plotted against time as has been done in Fig. 5. It can be seen that there is considerable variation in both number and relative abundances of species from month to month, although variation in relative abundance is much greater than that of overall species composition.

Inter-Site Comparisons

Sites 1, 2, and 3 were generally similar in overall faunal composition and proportional species composition (Table 2). At each of these sites, *Tozeuma carolinense* was the most abundant species, and 8 of the 10 most abundant species were shared between Stations 1 and 2, 6 of 10 be-

Table 2. Values of similarity indices computed among all combinations of sites (S_{1-4}). Simpson and Jaccard indices only consider presence or absence of species, while $C\lambda$ index uses meristic data

Index	S_1-S_2	S_1-S_3	S_1-S_4	S_2-S_3	S_2-S_4	S_3-S_4
Simpson	.713	.750	.596	.631	.578	.596
Jaccard	.420	.527	.383	.363	.323	.430
$C\lambda$	.786	.778	.389	.832	.406	.600

tween Stations 1 and 3, and 7 of 10 between Stations 2 and 3. There are, however, some interesting differences in composition among these sites, some of which can be interpreted in terms of microhabitat differences and corresponding habitat preferences of individual species.

For example, at Site 1 Penaeus duororum notialis was the second most abundant species taken. This reflects the fact that the muddy substrates at this site provide a suitable habitat for this burrowing species. Incidentally, P. duororum notialis was one of the few species in which a seasonal pattern of abundance could be discerned, since 197 of the 238 individuals collected at Station 1 were taken in October and November. Most of these were juveniles (<50 mm in length) which indicates that the spawning season of this species probably occurs in early fall in deeper waters. At least two other species, Panopeus occidentalis and Alpheus floridanus were predominantly taken at Site 1 owing to the presence of muddy substrates at this site. Juveniles of the lobster Panulirus argus were also taken primarily at Station 1, probably because of the presence of nearby red mangrove trees which provide shelter for this species among their prop roots during periods of inactivity (personal observation). A correlation between the abundance of Tozeuma carolinense and Syringodium filiforme has been observed by Ewald (1969), and T. carolinense was most abundant at Site 2, probably because the seagrass S. filiforme was most abundant there. It seems likely that T. carolinense is less conspicuous to predators on the round blades of S. filiforme than on other plant species, and hence more abundant in stands of this marine angiosperm.

Site 4 was unique among the areas studied (Table 1). Several species (Diadema antillarum, Hermodice carunculata, Eucidaris tribuloides, and Tripneustes ventricosus) occurred only at this site, and 8 of the 9 individuals of Stenorhynchus seticornis were collected here. These species are usually associated with coral reefs, and their presence reflects the proximity of well developed reefs. Several other species taken at Site 4, namely Murex recurvirostris, Murex sp., Astropecten duplicatus, Oliva sp. and Conus sp. are usually found on sandy bottoms which surround reef facies, and their presence is probably due to the open sandy areas which surround the grass beds at this site. In summary, the reef habitat is an important factor influencing species composition at Site 4 because of the rather large number of reef-associated species that "spill over" into the grass-bed habitat. Other areas that I have sampled in the nearby San Blas Islands, where coral reefs and seagrass beds are interspersed over relatively large areas, possess a faunal composition similar to that found at Site 4.

Two other groups of species were recognized and found from time to time at each of the four sites. One group, composed of the brittle stars Ophiactis savignyi, Hemipholus elongata and the snapping shrimps Synalpheus fritzmulleri and S. townsendi, were usually associated with sponges, and the occurrence of these species is due to the collection of their sponge host at the time of sampling. The other group, composed of the porcelain crabs Petrolisthes armatus and P. galathinus and the snapping shrimp S. apiocerus, often occurred in dense clumps of Halimeda opuntia where they were afforded a hiding place among the foliose branches of this alga.

Total abundance was lowest at Site 3 and monthly totals were significantly lower than those at Site 4 (Kruskal-Wallis multiple comparisons test P <0.05 – see Hollander and Wolfe, 1973, p. 124), but no other comparisons of monthly totals were significantly different. (The non-parametric Kruskal-Wallis test is a conservative test which requires fewer assumptions than comparable parametric tests. I consider this type of statistic appropriate in attempting to test for differences among data that are extremely high in variability, as are those considered here.) Qualitatively, benthic vegetation appeared to be less dense at Site 3 than at the other sites, and since plant biomass has been found to be positively correlated with invertebrate abundance at nearby sampling sites (Heck, 1976a; Heck and Wetstone, 1977), this may partially explain the lower abundances at this site. The increased abundances at Site 4 are due primarily to the additional presence of the reef-associated invertebrates that are an important part of the fauna at this station.

The total number of species collected over the sampling period was much lower at Site 2 than the other three sites. Using a modification of the rarefaction diversity measure described by Heck *et al.* (1975), a sample size-independent means of comparing species richness among sites has been performed. This procedure "scales down" the larger sample sizes among sites to that of the smallest (in this case an abundance of 825 at Site 3; cf. Table 1) and generates an expected number of species at each site for the sample size of 825 individuals. The results of this analysis showed that Site 2 contained a significantly lower species number (>10 standard deviations away from the means of the other 3 sites) while Sites 1, 3, and 4 did not significantly differ in total number of species. However, only Sites 2 and 4 showed significant differences (P <0.05) in monthly species totals (Kruskal-Wallis multiple comparisons test).

Since Station 2 was originally chosen to represent an area exposed to heavy wave shock, it is logical to propose that wave action is the factor responsible for the low species number at this site. This is probably not so, however, since many of the "missing" species were either very rare at the other sites (see Table 1) or were taken during the night sampling, thereby indicating that they were present at Site 2. Rather, the overall effect of wave shock seems to be simply to prevent the establishment of seagrasses themselves and thereby preclude the development of an associated invertebrate fauna, instead of directly affecting the invertebrate species. Several unvegetated areas surrounding Site 2 in the zones of heaviest wave action bear out this explanation. There is at present no satisfactory explanation which accounts for the low species number taken at Site 2.

Night Collections

The night collections (Table 3) provided some interesting data, even though they were few in number and only taken at Sites 1, 2, and 3. First, the number of individuals taken at night was significantly larger than that taken diurnally, as determined by the Wilcoxon Rank Sum Test (P <0.003 at Station 1; P <0.009 at Station 2; P <0.01 at Station 3). The increases at night came both from greater abundances of species that had been collected diurnally and from newly collected species. Those species taken exclusively at night were *Alpheus armillatus, Pitho sexdentata, Metapenaeopsis* sp., and *Chorinus heros*. In general, caridean

shrimps were more abundant at night, especially *Processa fimbriata* which was only rarely taken diurnally. Also present in greatly increased numbers at night were spider crabs of the genus *Pitho*, as well as the portunid crabs *Cronius ruber* and *Portunus ordwayi*, and the penaeid shrimps *Penaeus duororum, Sicyonia laevigata* and the previously mentioned *Metapenaeopsis* sp.

Portunid crabs and penaeid shrimp burrow during the day, and it is well known that they are more active at night. The increased abundance of *Pitho* spp. and the caridean shrimps was more surprising, since these animals (excluding alpheid shrimps) are not known for their burrowing habits. The carideans may rest at the sediment-water interface diurnally, thereby escaping the trawl for the most part, and become more susceptible to capture if they actively swim in the water column at night. The whereabouts of *Pitho* spp. during the day is unknown, since their morphology is not well suited to burrowing and they probably do not spend the day in the sediments. They most likely migrate to deeper sandy channels and spend the daylight hours on unvegetated bottoms.

Fish Predators

There are a number of fish species that routinely forage in the seagrass meadows and prey on the invertebrate species considered here. Since a detailed treatment of these fish species is now in progress, only a few appropriate observations will be made at this time.

Probably the most important predators of epibenthic species of seagrass-associated invertebrates are several species of snappers, *Lutjanus analis, L. synagris, L. griseus,* and *Ocyurus chrysurus*; two species of scorpion fishes, *Scorpaena grandicornis* and *S. brasiliensis*; two species of nojarras, *Eucinostomus argenteus* and *E. gula*; the puffers *Sphoeroides spengleri* and *S. testudineus*; and the groupers *Epinenephelus afer* and juveniles of *E. striatus*. There is an additional important group of predators that shelters on coral reefs but forages over the grass beds at night; included in this group are the grunts *Haemulon plumieri, H. sciurus, H. bonairensis,* the snapper *Lutjanus apodus,* and the moray eel *Gymnothorax funebris*. (Several of the previously mentioned snappers might well be included in this reef-associated group.) The work of Randall (1967) and Starck (1971) as well as unpublished results (Weinstein and Heck, in preparation) show that all these piscine predators feed on the invertebrates taken in this study, with crustaceans being the most commonly taken prey.

Table 3. Species taken at sites sampled at night during May 1975. Three 2-min trawl samples were taken at Site 1, 5 samples at Site 2, and 4 samples at Site 3

Site 1			Site 2			Site 3		
Rank	Species	Abundance (*n*)	Rank	Species	Abundance (*n*)	Rank	Species	Abundance (*n*)
(1)	*Cerithium eburneum*	33	(1)	*Cerithium eburneum*	186	(1)	*Pitho anisodon*	37
(2)	*Cronius ruber*	32	(2)	*Tozeuma carolinense*	32	(2)	*Pagurus bonairensis*	36
(3)	*Penaeus duororum*	18	(3)	*Paguristes limonensis*	24	(3)	*Cronius ruber*	31
(4)	*Tozeuma carolinense*	16	(4)	*Cronius ruber*	22	(4)	*Pitho ilhermani*	25
(5)	*Thor floridanus*	12	(5)	*Processa fimbriata*	21	(5)	*Cerithium eburneum*	24
(6)	*Paguristes limonensis*	12	(6)	*Clibinarius antillensis*	14	(6)	*Processa fimbriata*	22
(7)	*Leander tenuicornis*	11	(7)	*Pagurus bonairensis*	12	(7)	*Lytechinus variegatus*	17
(8)	*Pitho quadridentata*	11	(8)	*Pitho ilhermani*	11	(8)	*Tozeuma carolinense*	16
(9)	*Pitho anisodon*	9	(9)	*Holothuria mexicana*	8	(9)	*Holothuria mexicana*	14
(10)	*Panopeus occidentalis*	9	(10)	*Sicyonia laevigata*	7	(10)	*Paguristes limonensis*	9
(11)	*Aplysia dactylomelia*	9	(11)	*Thor floridanus*	7	(11)	*Modulus modulus*	7
(12)	*Processa fimbriata*	8	(12)	*Latreutes fucorum*	6	(12)	*Microphrys bicornutus*	7
(13)	*Portunus ordwayi*	8	(13)	*Modulus modulus*	6	(13)	*Thor floridanus*	6
(14)	*Panulirus argus*	7	(14)	*Penaeus duororum*	6	(14)	*Trachypenaeus similis*	5
(15)	*Latreutes fucorum*	7	(15)	*Trachypenaeus similis*	6	(15)	*Mithrax forceps*	5
(16)	*Sicyonia laevigata*	5	(16)	*Pitho quadridentata*	4	(16)	*Penaeus duororum*	4
(17)	*Periclimenes americanus*	5	(17)	*Pitho anisodon*	4	(17)	*Portunus ordwayi*	3
(18)	*Podochela gracilipes*	3	(18)	*Leander tenuicornis*	4	(18)	*Chorinus heros*	3
(19)	*Mithrax forceps*	3	(19)	*Microphrys bicornutus*	3	(19)	*Bulla striata*	3
(20)	*Microphrys bicornutus*	3	(20)	*Mithrax forceps*	3	(20)	*Panulirus argus*	2
(21)	*Holothuria mexicana*	3	(21)	*Panopeus occidentalis*	3	(21)	*Sicyonia laevigata*	2
(22)	*Clibinarius antillensis*	3	(22)	*Trachycaris restrictus*	2	(22)	*Tripneustes ventricosus*	1
(23)	*Ambidexter symmetricus*	3	(23)	*Portunus ordwayi*	2	(23)	*Trachycaris restrictus*	1
(24)	*Alpheus armillatus*	2	(24)	*Lytechinus variegatus*	2	(24)	*Stenorhynchus seticornis*	1
(25)	*Pagurus bonairensis*	2	(25)	*Aplysia dactylomelia*	2	(25)	*Stenopus hispidus*	1
(26)	*Synalpheus apiocerus*	2	(26)	*Alpheus armillatus*	2	(26)	*Podochela gracilipes*	1
(27)	*Pitho sexdentata*	2	(27)	*Calappa ocellata*	1	(27)	*Leander tenuicornis*	1
(28)	*Trachycaris restrictus*	1	(28)	*Chorinus heros*	1	(28)	*Hippolyte zostericola*	1
(29)	*Squilla prasolineata*	1	(29)	*Ophiothrix angulata*	1	(29)	*Callinectes danae*	1
(30)	*Podochela riisei*	1	(30)	*Pagurus brevidactylus*	1	(30)	*Calcinus tibicen*	1
(31)	*Pitho ilhermani*	1	(31)	*Petrolisthes galathinus*	1	(31)	*Petrolisthes galathinus*	1
(32)	*Modulus modulus*	1	(32)	*Podochela gracilipes*	1		Total	288
(33)	*Chorinus heros*	1		Total	405			
(34)	*Callinectes danae*	1						
(35)	*Alpheus heterochaelis*	1						
	Total	246						

Table 4. Seasonal reproductive activity of several species of decapod crustaceans taken during sampling period. +: ovigerous females present; -: no ovigerous females present; O: no females collected

Species	Month											No. of individuals
	J	A	S	O	N	D	J	F	M	A	M	
Tozeuma carolinense	+	+	+	+	+	+	+	+	+	+	+	1004
Microphrys bicornutus	+	+	+	+	+	+	+	+	-	+	+	182
Pagurus bonairensis	+	+	+	-	+	-	-	-	+	-	+	140
Paguristes limonensis	+	+	+	-	+	O	+	O	+	+	+	121
Panopeus occidentalis	+	O	+	+	O	O	O	-	O	O	O	84
Mithrax forceps	+	+	+	+	O	O	+	O	+	+	+	79
Clibinarius antillensis	-	+	+	-	O	-	-	-	-	-	75
Petrolisthes galathinus	+	+	-	-	O	O	O	+	+	O	O	43
Pagurus brevidactylus	-	+	+	O	O	O	-	+	+	+	+	49
Macrocoeloma diplacanthum	+	-	O	-	+	O	O	O	O	+	-	32

Since fishes may forage at considerable distances from the reefs on which they shelter (Starck, 1971) their influence may extend to seagrass meadows well removed from the reef structure.

Seasonality

There are several evident trends in species number and abundance at each of the 4 sites. Most obvious are the decreases in both these variables that occur in November and December (Figs. 2 and 3). Those species which showed the greatest reductions during this period were the usually abundant molluscs *Cerithium eburneum* and *Modulus modulus*; lesser reductions occurred among the caridean shrimp *Tozeuma carolinense*, some of the hermit crabs, and the spider crabs *Microphrys bicornutus* and *Mithrax forceps*. These decreases coincide with low salinities (caused by heavy rainfall during this time of the year; Fig. 4), and it is possible that there may be a causal relationship (but see next paragraph).

In January species richness and abundance began to increase, and continued to rise in succeeding months to levels that were generally similar to the summer and early fall months. These increases coincide with increasing salinities that accompany the changeover from wet to dry seasons, again suggesting that salinity may be important in determining fluctuations in faunal composition and abundance at the study sites. However, at Stations 2 and 4 the drops in species number and abundance began to take place in October when salinities were still high. In addition, the abundance of echinoderms (e.g. *Lytechinus variegatus* and *Holothuria mexicana*), which are poor ion regulators and not often found in low-salinity waters (Kinne, 1967) did not drop appreciably during the periods of reduced salinity. Thus, there may well be other as yet unknown factors involved.

There is also seasonal variability in species composition at each of the study sites. This can be shown by calculating the similarity between the initial (July) collections and the collections in each of the succeeding months; the resulting similarity values are then plotted against time as a measure of the constancy of community composition throughout the year. This has been done using two different similarity indices in Fig. 5. The Jaccard index, which reflects qualitative (presence-absence) similarity in species composition, shows drops in similarity beginning in October and further decreases in November and December. These decreases coincide with the

overall decreases in catch during these months. Beginning in January, similarity begins to increase to former levels. At no time however is similarity high. Using the $c\lambda$ index of affinity, which measures the total similarity in proportional species composition between two samples, the November-December lows are present, but the behavior of this index is much more erratic than the Jaccard index, and no trends are readily apparent. This implies that changes in relative abundances among individual species are quite variable from month to month. Thus, there appears to be little constancy in either proportional abundances or overall species composition throughout the year. Underlying these low similarity values from month to month is, however, another pattern in which a group of "core" or dominant species are present in the great majority of samples taken at each site. For example, the 10 most abundant species at each site occur about 78% of all the times that they could potentially be present in the samples (321 out of 410 possibilities; 410 because at Sites 1, 2, and 3 there were 10 species x 11 months and at Site 4 there were 10 species x 8 months). Hence, the dominant species are almost always present at each of the stations.

In summary, based on data for one year it seems that there are important seasonal changes in composition and abundance at the study sites. This is contrary to the idea that tropical habitats in general, and seagrass meadows in particular, are stable areas with little seasonal variability. However, as more long-term studies are carried out in tropical habitats, earlier notions that there is no seasonality, or that no physico-chemical stresses occur in the tropics, are being discarded (e.g. Moore, 1972; Fleming and Hooker, 1975). These ideas are clearly no more applicable to several other littoral environments in the tropical Caribbean (Glynn, 1968, 1972), than to the seagrass habitat being considered here.

Reproductive Biology

It is difficult to generalize from the data gathered on reproductive activity because of the rarity of invertebrate species on which adequate data could be obtained. In several months no females of some species were taken, and it is only safe to speak of the presence and not the absence of breeding in any given month. Among those species for which I have the best data on reproductive activities are several species of decapod crustaceans (Table 4). The species col-

lected in greatest numbers, the caridean shrimp *Tozeuma carolinense*, breeds throughout the year with the percentage of ovigerous individuals never dropping lower than 60% in any month. Based on sporadic collections of *Alpheus floridanus*, *Leander tenuicornis*, *Trachycaris restrictus*, *Periclimenes longicaudatus* and other related species, it appears that all species of caridean shrimps collected in the samples breed continuously in these areas. At a nearby locality (Galeta Reef) several caridean shrimps of the genus *Alpheus* have been found to contain nearly 100% ovigerous females in every month of the year (L.G. Abele, personal communication), and it is not surprising that most caridean shrimps, which have very similar life histories, should show similar breeding periodicities.

This does not mean that the percentage of ovigerous females does not vary seasonally among decapod species. For example, Meyer and Birkeland (1974) found periods of both high and low reproductive activity in the spider crab *Microphrys bicornutus* at the Galeta Reef, even though some females were reproductively active at all times of the year. Over a two-year span they found that these two periods of annual low points in reproductive output did not occur during the same months in each year.

There may be a simple explanation for the differences in the seasonality of reproductive output between a crab such as *Microphrys bicornutus* and a small shrimp such as *Tozeuma carolinense*. In general, in an environment in which year-round breeding takes place it would not be surprising to observe greater seasonality in reproductive activity among longer than shorter-lived organisms. This could occur because, compared to rapidly maturing organisms, a greater amount of time is required by more slowly maturing organisms to produce enough overlapping generations so that breeding effort appears continuous. A slowly maturing species would show much more obviously and for a greater period of time, the effects of a very good or bad year-class, the local effects of a disastrous physical disturbance, or heavy rates of predation or parasitism over a short time-period. Also, a fluctuation in the intensity of observable reproductive output over a several-year span, such as that observed in *M. bicornutus* by Meyer and Birkeland (1974), would be expected if differential survivorship of generations occurred frequently. Among those species that mature and reproduce in a period of a few months, the effects of poor recruitment or unfavorable local events would be much more quickly "covered up" and be

less readily observed, since many generations of reproductively active females would constantly be producing offspring. In longer-lived species unpredictable survival of year classes would lead to yearly changes in the time when breeding activity was most intense. Of course, in an environment in which no severe disturbances occurred for a sufficient period of time differences in reproductive activity between long- and short-lived species would not be observable.

This explanation may account for the apparent differences in reproductive activity found in the relatively long-lived crab *Microphrys bicornutus* and the shorter-lived *Tozeuma carolinense*. In fact, it may account for some of the confusion that exists in the literature regarding whether breeding is or is not continuous in tropical invertebrates and which factors are responsible for the differences in reproductive activity that exist among species.

Comparison with Previous Studies

The overall species composition observed here generally agrees with that reported in the few studies in tropical and subtropical seagrass meadows that have employed comparable sampling techniques (Tabb *et al.*, 1962; Murina *et al.*, 1974; Roessler *et al.*, 1974). However, it is necessary to recognize that a dichotomy exists between subtidal open-water seagrass meadows of the type considered here, and the seagrass beds that often occur among hermatypic corals of back-reefs. The fauna in these two types of seagrass habitats is substantially different, primarily due to the presence of living and dead corals and other coelenterates on the back-reef, which provide a much more heterogeneous habitat and support a more diverse biota than areas without these faunal components (compare for example the species lists given here with those of Glynn, 1964). The back-reef flat seagrass environment is also subject to the most severe physical stresses as a result of very low tides which can cause mass mortalities from heat stress and desiccation (Glynn, 1968; Meyer and Birkeland, 1974). Any future generalizations about seagrass habitats should probably be restricted to only one or the other of these types of seagrass environments, since they differ so markedly.

While the qualitative species composition was found to be similar to that of other tropical and subtropical seagrass meadows, the total abundances were much

lower at these sites and the relative abundances were also quite different among taxa (cf. Roessler *et al.*, 1974; Heck, 1976b; Hooks *et al.*, 1976). Perhaps one of the most striking differences between this study and those cited above is the much lower abundances of caridean shrimps found here. Previously the abundance of carideans, xanthid crabs, and many other species has been found to be great whenever large biomasses of red algae are present in the seagrass meadows (Tabb *et al.*, 1962; Roessler *et al.*, 1974; Hooks *et al.*, 1976). Presumably the algae provide the invertebrates with a refuge from predators (Tabb *et al.*, 1962; Roessler *et al.*, 1974). Since red algae were so scarce at the Panamá sites, the abundance of caridean shrimp may be low because tropical fish predators are more successful in obtaining these invertebrates in the absence of thick algal growths.

In conclusion, the seagrass meadows studied here are closely linked to surrounding habitats, and a number of invertebrate species divide their time among these habitats. Coral reefs are especially important because a relatively large number of reef-associated species of invertebrates utilize the surrounding seagrass environment and also because they may indirectly exert an influence on seagrass communities through the feeding activities of far-ranging foraging fishes even when reef structures are not in close proximity. It also seems that there are important seasonal changes in composition and abundance among the invertebrate species considered here, and that some of these changes are correlated with drops in salinity at the sampling sites. Finally, even though the qualitative species composition is similar to comparable studies in tropical and subtropical seagrass meadows, the total abundance of invertebrates is much lower at the sites in the present study, possibly due to the reduced biomasses of large red algal species.

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