Studies on Decapod Crustacea from the Indian River Region of Florida

XI. Community Composition, Structure, Biomass and Species–Areal Relationships of Seagrass and Drift Algae-associated Macrocrustaceans

Robert H. Gore[a], Edward E. Gallaher[b,c], Liberta E. Scotto[a] and Kim A. Wilson[a]

[a]*Smithsonian Institution, Fort Pierce Bureau, Fort Pierce, Florida 33450 and* [b]*Harbor Branch Foundation, Inc., Link Port, Fort Pierce, Florida 33450, U.S.A.*

A 1-year study, using six 10 m² drop nets at monthly stations, was conducted on the seagrass and drift algae-associated macrocrustaceans (primarily Decapoda) in the Indian River lagoon on the central eastern Florida coast. The macrocrustacean community consisted of 38 species, in 28 genera and 17 families, the majority of which were caridean (grass) shrimp and brachyuran crabs.

Two caridean shrimp, a pagurid crab, and a penaeid shrimp were numerically dominant species which, together with 10 less numerous species, were considered to be characteristic representatives of the macrocrustacean community. Both a species–area and individuals–area relationship were demonstrated using a combinatorial statistical method, and a modification of the Fisher species–individuals relationship. The community as a whole responded in numbers of individuals, and in total crustacean biomass, to increases in seagrass and drift algae (as plant biomass g^{-1} m^{-2}). Macrocrustacean community diversity appeared to be regulated by above-ground plant abundance, and is thus a function of habitat complexity. The consistency of decapod species composition indicated that the community is both predictable and resilient, with resultant stability due, in some measure, to habitat diversity produced by the periodic trimonthly increases in drift algae abundances. Competitive exclusion may be more important than predation on this seagrass bed in regulating the within-habitat diversity of the macrocrustacean community.

Introduction

Tropical and subtropical estuaries in Florida have long been recognized as important physiographic and biological regions in which the ecological interplay of maritime, paludal and marine flora with the associated vertebrate and invertebrate faunal communities has resulted in complex ecosystems of substantial species richness and diversity. Many of the studies conducted specifically on Floridan estuarine systems (e.g. McNulty *et al.*, 1962; Tabb & Manning, 1962; Dragovich & Kelly, 1964; O'Gower & Wacasey, 1967; Moore

[c]Present address: Division of Limnology and Ecology, Academy of Natural Sciences, Philadelphia, Pennsylvania 19103, U.S.A.

et al., 1968; Odum & Heald, 1972; Hooks *et al.*, 1976; Young *et al.*, 1976; Weinstein *et al.*, 1977; and a synopsized series of investigations published in 1974 by Livingston *et al.*; Roessler & Beardsley; Simon and Taylor) have recognized the importance of benthic macroinvertebrate communities associated with seagrasses in such estuaries. More recent investigations have discovered, in addition to the traditionally acknowledged contribution of seagrasses and mangroves, that drift algae ean also be valuable in such systems (Phillips, 1963; Roessler, 1971; Roessler *et al.*, 1972; Thorhaug, 1974; Thorhaug & Roessler, 1977; Turner, 1977).

Decapod crustaceans comprise a notable component of seagrass and drift algae-associated macroinvertebrates, and form a community both numerically and trophically important to estuarine food webs (Heck, 1976; Hooks *et al.*, 1976). However, it is only recently that consideration of this community has gone beyond simple species listings and annotated check lists, and the composition and structure of the decapod community associated with seagrass-drift algae remains little investigated. Moreover, the role of decapod crustaceans as predators in the seagrass has assumed new importance based on recent studies conducted by Young *et al.* (1976), Virnstein (1977) and Young & Young (1977). The latter studies were among the first to quantitatively assess the decapod crustacean seagrass community, but emphasized only selected species in regard to their predation on microcrustacean or infaunal taxa. There are no data on whether a decapod community in this biotope is controlled by predation, competitive exclusion, or other factors, although the similarity in modes of nutrition in, for example, grass shrimp implies an important role for competitive exclusion.

Because of temporal and spatial variability in members of the seagrass and drift algae-associated decapod community, it is necessary to obtain relatively large, repetitive, consistently quantitative samples. A portable drop net, recently developed for ichthyofaunal studies (e.g. Hoese & Jones, 1963; Kjelson & Johnson, 1973) provides such samples both from the benthos and the entire water column above it (Kjelson *et al.*, 1975). Although the net design does not adequately sample deeper infauna, shallower-burrowing species can usually be isolated and then collected by rigid-framed seine nets during the cleaning sweep of the drop net.

Such a device was employed in a 1-year program during April 1976 to March 1977 to quantitatively sample both the epibenthic and shallow infaunal deeapod crustaceans, as well as the suprabenthic assemblages found in the floating algae superstory above a tidal seagrass flat in the Indian River lagoon on the central eastern Florida coast. The objective was to determine species composition and community structure of seagrass-drift algae decapods, and to ascertain whether a quantitative relationship existed between this community and seagrass or drift algae abundances. This study is the first to quantitatively assess such a macrocrustacean community in a subtropical area. It is of added interest that the species investigated inhabit a zoogeographical transitional zone (the central eastern Florida coast) lying between the tropical Antillean–West Indian faunal provinces to the south and the warm-temperate Carolinian province to the north. The data which were obtained are discussed with aspects of equilibrium theory (e.g. MacArthur & Wilson, 1967) and presently accepted concepts of species– and individuals–area relationships.

Materials and methods

Description of the area

The study area was a shallow intertidal to subtidal seagrass flat located adjacent to the north peninsula of Link Port, St. Lucie Co., along the western shore of the Indian River
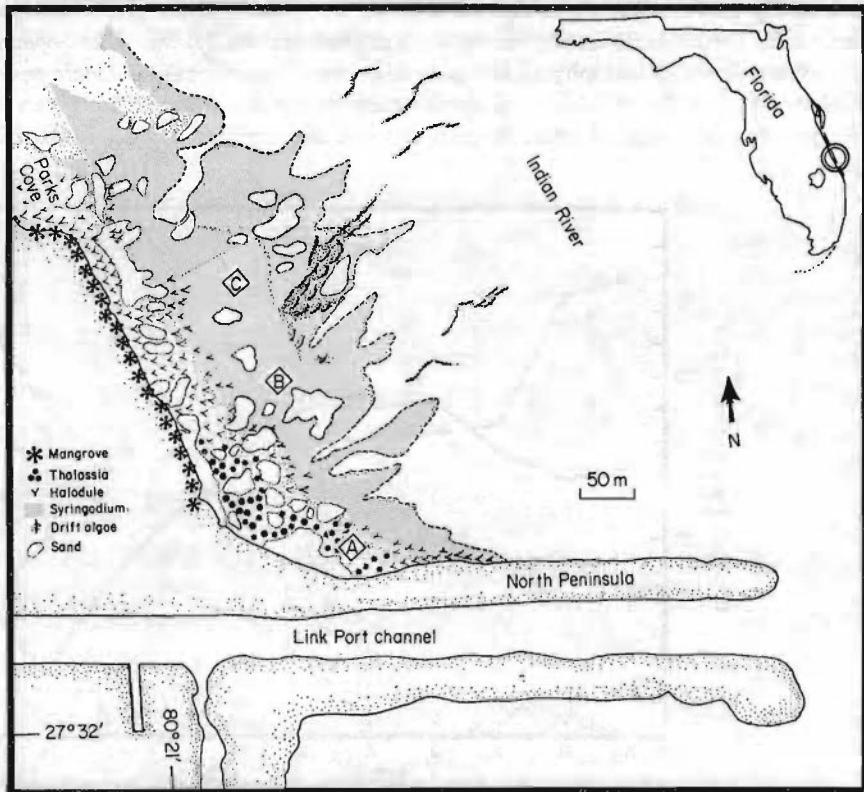
Figure 1. Map of the sampling site in the Indian River lagoon, Florida. Geographical position of Link Port circled on inset. Squares A, B and C on seagrass area show general location of each drop net station per month. Seagrasses represented in the figure are a composite of the three most abundant species over the sampling year.

lagoon (27°32′N, 80°21′W) (Figure 1). The Indian River is a subtropical, positive, bar-built lagoonal estuary [see Gilmore (1977) for a more complete physiographic description]. The juncture of the north peninsula and the western shore of the lagoon forms a small, open embayment usually covered by seawater to approximately 0·5–2 m, over a sandy or muddy-sand substratum. Salinity fluctuated from 24‰ to 37‰ and water temperatures ranged from 11·5 to 28 °C based on data taken monthly at each station for the 12 months of the study (Figure 2). The tidal flat was subject to astronomical and meteorological tides; the latter are often of greater import in the long, narrow, relatively shallow barrier island-enclosed lagoon (Von Zweck, unpublished data).

The western shore of the sampled area is fringed with red [*Rhizophora mangle* (L.)], black [*Avicennia germinans* (L.)] and white (*Laguncularia racemosa* Gaertner f.) mangroves. Four species of spermatophytic seagrasses grow on the flat, three in abundance. Manatee Grass (*Syringodium filiforme* Kutzing) and Cuban Shoal Grass (*Halodule wrightii* Ascherson) were, respectively, the most abundant during the study. A smaller, patch-like strand of Turtle Grass (*Thalassia testudinum* (Banks ex-Konig and Sims) was also present along the north-west shore (Figure 1). At least 30 species of red, brown and green algae occurred interspersed among, or growing epiphytically on, the seagrass blades. These algae, hereafter

collectively termed drift algae, formed a major component of the plant biomass from the study area. Predominant among these (albeit at times seasonally) was *Acanthophora spicifera*, *Hypnea cervicornis* (Rhodophyta), *Dictyota dichotoma* (Phaeophyta) and *Caulerpa sertulariodes* (Chlorophyta). A list of other algal species occurring in the study area is given in Table 1. Many of the drift algae themselves were covered with epiphytic algae, but the latter were
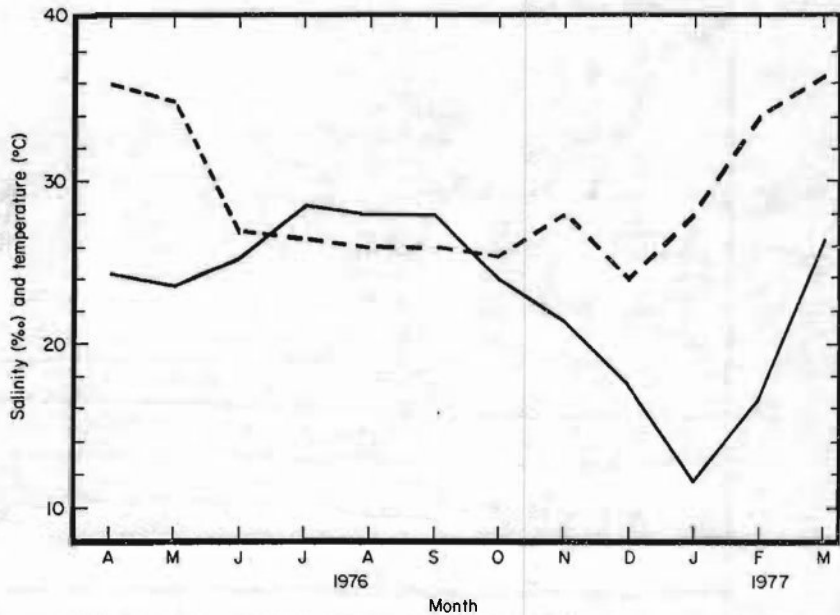

Figure 2. Salinity (dashed line) and temperature (solid line) on the sampling site during the year, as recorded during sampling each month.

TABLE 1. Drift algae collected during the drop-net study April 1975–March 1976

Chlorophyta
    Caulerpa sertularioides (Gmelin) Howe
    Chaetomorpha brachygona Harvey
    Chaetomorpha gracilis Kutzing
    Cladophoropsis membranacea (C. Agardh) Børgesen
    Enteromorpha lingulata J. Agardh

Phaeophyta
    Cladosiphon occidentalis Kylin
    Dictyota dichotoma (Hudson) Lamouroux
    Giffordia mitchellae (Harvey) Hamel
    Rosenvingia intracata (J. Agardh) Børgesen

Rhodophyta
    Acanthophora spicifera (Vahl) Børgesen
    Chondria sp.
    Gracilaria spp.
    Hypnea cervicornis J. Agardh
    Hypnea musciformis (Wulfen) Lamouroux
    Jania adherens Lamouroux
    Jania capillacea Harvey
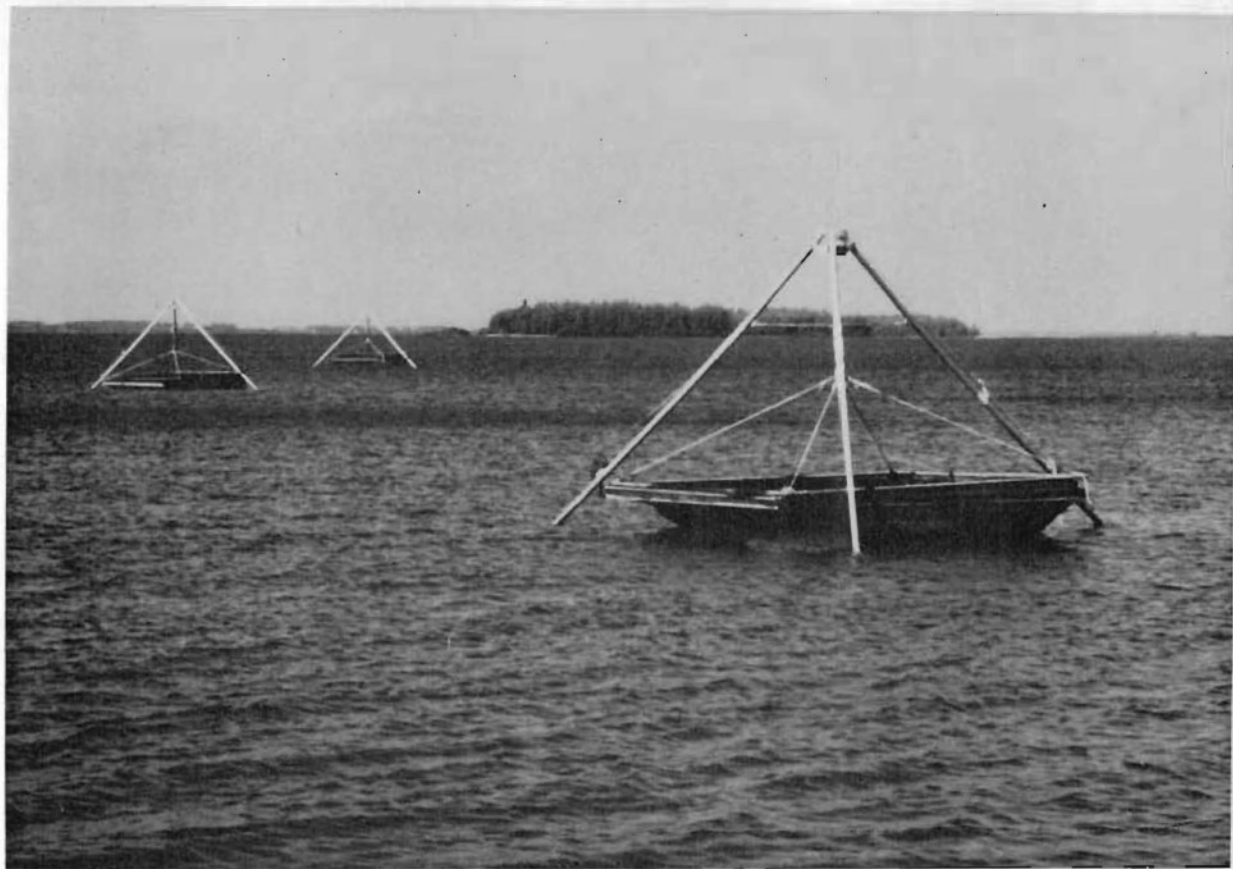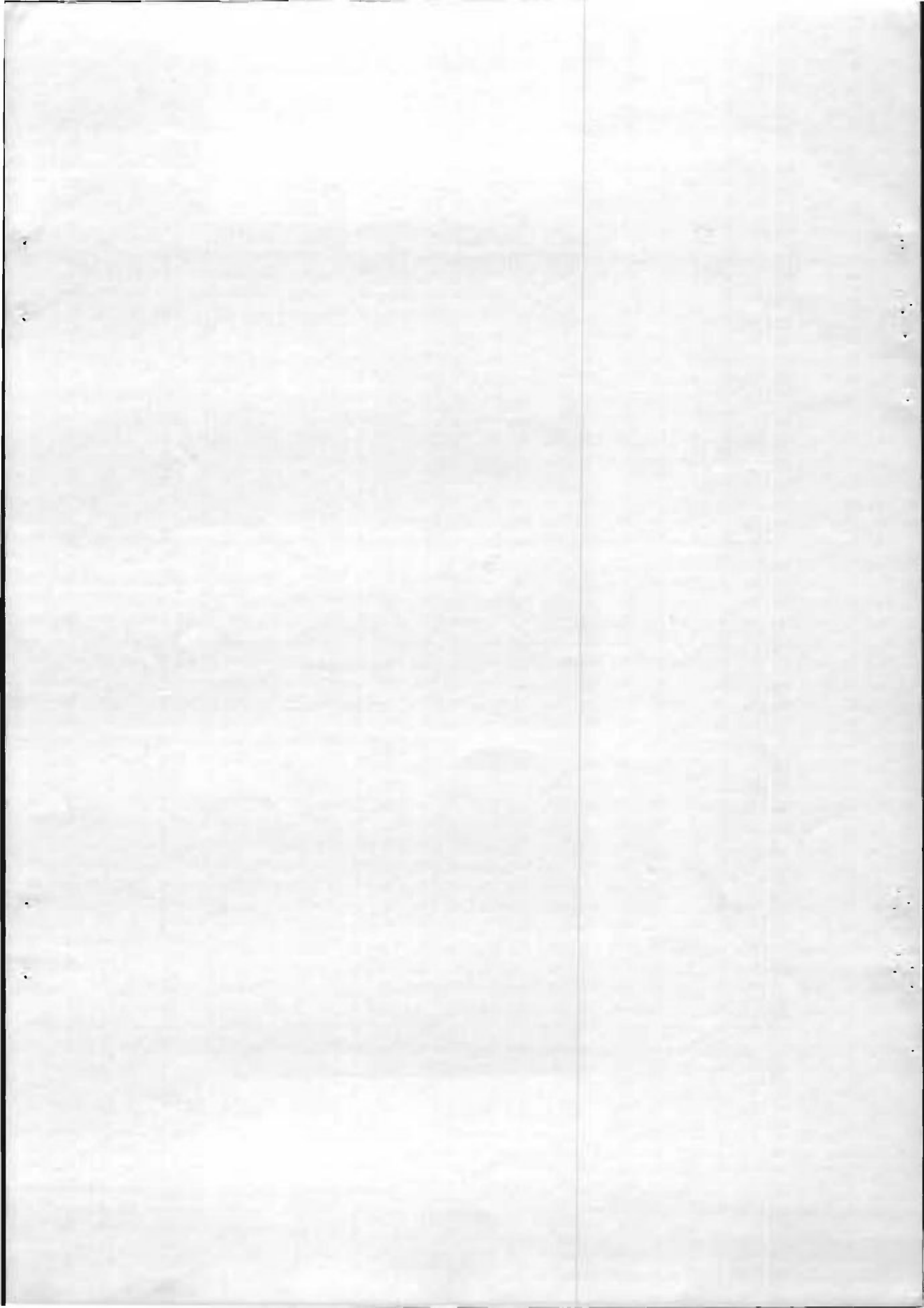   *Spyridia filimentosa* (Wulfen) Harvey

Plate 1. A typical array of three drop nets before triggering. Water depth at each net, progressing offshore, about 0·5, 0·8 and 1 m, respectively. General direction of photograph faces north-east, with observer standing on shore of Link Port north peninsula.

not identified because of constraints in time. A complete listing of Indian River algae is given in Eiseman & Benz (1975).

Drop net and laboratory methods

Three portable drop nets of 3·2 mm mesh, each capable of sampling 10 m² (see Gilmore *et al.*, 1978) were erected from 60–70 m apart proceeding offshore in a line approximately perpendicular to the north peninsula and oblique to the western shore at Link Port (Figure 1, boxes A, B, C; Plate 1). Six stations (three in the morning and three in the evening) sampling 60 m² were occupied 1 day each month, producing 72 stations (720 m²) for the year. The nets were left undisturbed after initial erection for about 1 h prior to triggering, in order to allow the tidal flat to return to pre-sampling 'equilibrium'. The three nets were then triggered simultaneously, between 10.00–11.00 h in the morning and 1 h after sunset in the evening, by using a 20–30 m line attached to a trigger pin on the pyramidal frame of the gear. After triggering, five repetitive hauls were made within each net, using a rigid frame 3·2 mm mesh seine net which spanned the drop net interior. The frame seine was pressed firmly into the substratum with each sweep in order to collect as much plant material and associated fauna as possible. All plant materials and invertebrates were placed in 10 gallon (42 l) 'Liquipak' containers and returned to the laboratory for preliminary sorting. Drop nets were either repositioned in the same general area and reset for the subsequent evening sample, or retrieved for the next monthly series.

It was not possible to collect the total rooted plant material at each station, but all drift algae in the water column, most spermatophyte blade (and much rhizome) biomass was obtained during the cleaning sweeps. The plant biomass figures (P_B) given in Table 4 are therefore conservative, but reflect well the abundances as we subjectively observed them throughout the year.

Preliminary sorting consisted of separation and preservation in 70% ethanol of every specimen of decapod and stomatopod crustacean associated with the plant materials. Collections from stations which could not be immediately sorted, because of a large volume of plant material, were either frozen or preserved in their entirety in 70% ethanol depending on sample bulk and capacity of the freezer. In general, preliminary sorting was finished less than a week after collection.

In final sorting, all macrocrustaceans (defined here as decapods and stomatopods) were identified, sex determined, and measured (if undamaged) with dial calipers to the nearest 0·1 mm for rostral carapace length in shrimps, shield length in pagurid crabs, and along the longest and across the widest parts of the carapace in brachyuran and porcellanid crabs. Data on species composition, numbers of individuals, relative abundances and densities per m² for both day and night stations were pooled into monthly composites. Total yearly values for these parameters, monthly maxima and minima in numbers, and species rankings and percentages were also compiled and appear in Tables 2, 3 and 4.

To determine macrocrustacean biomass (C_B) all specimens were segregated by species for each station, blotted dry of ethanol, and wet-weighed before being oven-dried at 100 °C for 72 h. Dry weights to the nearest 0·1 g were obtained from this material.

Plant material from each station was defrosted and/or blotted dry of preservative and divided into suitable smaller increments for wet-weighing. Drift algae and seagrasses from 58 of 72 stations were air-dried for 72 h on screened tables outdoors, in order to remove most of the water, and then oven-dried at 100 °C for another 72 h to arrive at final dry weight. However, in 14 stations the volume of plant material was too large to fit into the

TABLE 2. Species composition, relative abundance and density of the macrocrustacean community on the Link Port grassbed

Species	Rank	Total number	% Relative abundance	Mean number per month[a]	Density $(N\,m^{-2})$[a]	Monthly maxima and minima[b]			
1. *Hippolyte pleuracanthus*	1	35 824	57·9	2985	49·8	Apr	(10 598)–Feb	(261)
2. *Palaemonetes intermedius*	2	11 344	18·3	945	15·8	Jul	(3646)–Feb	(7)
3. *Pagurus bonairensis*	3	7297	11·8	608	10·1	Sep	(1323)–May	(106)
4. *Penaeus duorarum*	4	4026	6·5	336	5·6	Jul	(845)–Feb	(47)
5. *Periclimenes americanus*	5	1018	1·6	85	1·4	Sep	(398)–Feb	(1)
6. *Neopanope packardii*	6	748	1·2	62	1·0	Jul	(185)–Jun	(13)
7. *Alpheus heterochaelis*	7	523	0·8	44	0·7	Sep	(128)–Dec	(2)
8. *Callinectes sapidus*	8	314	0·5	26	0·4	Jan	(81)–Apr	(3)
9. *Alpheus normanni*	9	196	0·3	16	0·3	Jul	(56)–Dec	(1)
10. *Periclimenes longicaudatus*	10	154	0·25	13	0·2	Nov	(47)–Mar	(4)
11. *Tozeuma carolinense*	11	125	0·20	10	0·2	Apr	(33)–Jan	(1)
12. *Callinectes ornatus*	12	110	0·18	9	0·2	May	(22)–Aug	(1)
13. *Libinia dubia*	13	98	0·16	8	0·1	Jul	(19)–Feb	(1)
14. *Ambidexter symmetricus*	14	38	0·06	3	0·05	May	(13)–Dec	(1)
15. *Neopanope sayi*	15	33	0·05	3	0·04	Aug	(10)–Oct	(1)
16. *Alpheus armillatus*	16	24	0·04	2	0·03	Jul	(11)–Feb	(1)
17. *Latreutes fucorum*	17	8	0·01	0·7	0·01	May	(7)–Apr	(1)
18. *Paguristes tortugae*	17 (18)	8	0·01	0·7	0·01	Jul	(6)–Dec	(1)
19. *Alpheus viridari*	19	4	<0·01	0·3	<0·01	Data not applicable			
20. *Thor dobkini*	20	3	<0·01	0·3	<0·01	Data not applicable			
21. *Penaeus aztecus*	20 (21)	3	<0·01	0·3	<0·01	Data not applicable			
22. *Portunus ordwayi*	22	2	<0·01	0·2	<0·01	Data not applicable			
23. *Petrolisthes armatus*	22 (23)	2	<0·01	0·2	<0·01	Data not applicable			
24. *Pelia mutica*	22 (24)	2	<0·01	0·2	<0·01	Data not applicable			
25. *Portunus gibbesi*	25	1	<0·01	<0·1	<0·01	Data not applicable			
26. *Pachygrapsus transversus*	25	1	<0·01	<0·1	<0·01	Data not applicable			
27. *Pachygrapsus gracilis*	25	1	<0·00	<0·1	<0·01	Data not applicable			
28. *Pinnixa chaetopterana*	25	1	<0·01	<0·1	<0·01	Data not applicable			
29. *Mithrax forceps*	25	1	<0·01	<0·1	<0·01	Data not applicable			
30. *Pitho anisodon*	25	1	<0·01	<0·1	<0·01	Data not applicable			
31. *Processa hemphilli*	25	1	<0·01	<0·1	<0·01	Data not applicable			
32. *Menippe mercenaria*	25	1	<0·01	<0·1	<0·01	Data not applicable			
33. *Panulirus argus*	25	1	<0·01	<0·1	<0·01	Data not applicable			
34. *Callinectes similis*	25	1	<0·01	<0·1	<0·01	Data not applicable			
35. *Metapenaeopsis* sp.	25	1	<0·01	<0·1	<0·01	Data not applicable			
36. Trachypenaeus sp.	25	1	<0·01	<0·1	<0·01	Data not applicable			
37. *Gonodactylus oerstedii*	25	1	<0·01	<0·1	<0·01	Data not applicable			
38. *Pseudoquilla ciliata*	25	1	<0·01	<0·1	<0·01	Data not applicable			

[a]Values rounded.
[b]Includes months only in which species was collected; months without species not listed.

TABLE 3. Monthly species rank and relative percentage/month of the major macrocrustacean groups occurring on the Link Port seagrass flat

Species rank	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	
Hippolyte pleuracanthus	1	1	1	1	1	1	2	1	2	3	1	1	
Palaemonetes intermedius	2	3	2	2	3	3	1	4	3	1	7	3	
Pagurus bonairensis	3	4	4	3	2	2	3	2	1	2	2	2	
Penaeus duorarum	4	2	3	4	4	4	4	3	4	6	4	4	
Neopanope packardii	5	6	8	5	7	7	6	8	6	4	5	6	
Periclimenes americanus	6	7	6	8	5	5	5	7	9	9	12	10	
Alpheus heterochaelis	7	5	5	6	6	6	8	9	12	8	8	7	
Alpheus normanni	8	6	10	7	9	9	11	11	13	11	10	9	
Tozeuma carolinense	9	8	7	14	11	12	10	12	8	13	11	7	
Libinia dubia	10	10	9	9	10	8	12	13	12	10	12	—	
Callinectes ornatus	11	8	—	10	12	—	13	10	7	10	9	8	
Ambidexter symmetricus	12	9	9	12	11	—	14	—	13	—	12	10	
Callinectes sapidus	13	—	—	—	—	—	9	5	5	5	3	5	
Neopanope sayi	—	—	—	—	8	10	16	—	10	12	—	8	
Alpheus armillatus	—	—	—	11	—	11	14	—	—	—	12	—	
Periclimenes longicaudatus	—	—	—	—	—	—	7	6	11	7	—	8	
Paguristes tortugae	—	—	—	13	—	—	—	—	13	13	—	—	
Group percentage													Mean %
Caridean shrimp	96	76	83	85	64	74	84	60	42	60	46	71	70
Penaeid shrimp	1	19	10	6	11	6	5	14	6	2	8	3	8
Anomuran crabs	1	3	7	7	24	18	10	21	47	28	31	23	18
Brachyuran crabs	2	2	<1	2	1	2	1	5	5	10	15	3	4
Macrura and Stomatopoda													<1

TABLE 4. Monthly values of Indian River drift algae and macrocrustacean community parameters

Species	Total biomass year^{-1a}	Mean biomass month^{-1b}	Species rank by weight	by N
Libinia dubia	232·78	19·4	1	13
Penaeus duorarum	128·14	10·7	2	4
Palaemonetes intermedius	112·98	9·4	3	2
Hippolyte pleuracanthus	69·42	5·8	4	1
Pagurus bonairensis	59·55	4·9	5	3
Neopanope packardii	57·83	4·8	6	6
Alpheus heterochaelis	39·96	3·3	7	7
Callinectes sapidus	30·34	2·5	8	8
Periclimenes americanus	17·53	1·5	9	5
Callinectes ornatus	15·82	1·3	10	12
Alpheus normanni	6·34	0·5	11	9
Neopanope sayi	3·55	0·3	12	15
Alpheus armillatus	2·65	0·2	13	16
Tozeuma carolinense	1·35	0·1	14	11
Periclimenes longicaudatus	0·74	0·1	15	10
Portunus ordwayi	0·72	0·1	16	22
Ambidexter symmetricus	0·55	0·1	17	14
Alpheus viridari	0·20	0·1	18	19
Portunus gibbesi	0·1	0·1	19	25
Petrolisthes armatus	0·1	0·1	20	22
All remaining species	0·1	0·1	—	—

Month	S	N ($\times$1000)	$C_B(g)$†	$P_B(g)$†
April	17	12·24	87·1	5713
May	20	3·72	59·8	946
June	11	4·06	40·3	2107
July	17	12·65	141·6	3851
August	14	4·58	141·0	1056
September	14	7·35	107·6	2652
October	20	8·08	80·3	1805
November	15	1·98	40·6	792
December	17	1·47	13·0	616
January	16	2·58	79·2	9059
February	15	0·64	17·2	1992
March	15	2·55	30·1 = 838 g	1702 = 32291 g

^{a}Based on 720 m² sampled year^{-1}.
^{b}Based on 60 m² sampled month^{-1}.

drying oven in use at the time. The total volume of material from these 14 stations was air-dried for 72 h as above, and a 10% aliquot of air-dried weight was then further dried as before at 100 °C in the oven. Dry weights obtained from these subsamples were multiplied by 10 to give an extrapolated dry weight for the entire station sample. The pooled biomass data (dry wt, g 60 m^{-2}) for both macrocrustaceans and plants are presented in Table 4.

Analyses of species– and individuals–area relationships

The monthly changes in relative abundances of both plant materials and contained macro-crustacean fauna occurred primarily as a result of wind-drifting of drift algae into the sampled area, and not to an *in situ* increase in plants. Much algae grew attached elsewhere in the Indian River lagoon, and became 'drift' algae after breaking from their holdfasts. In a similar sense, macrocrustacean numbers were probably not so much an effect of post-larval recruitment (although unpublished size–frequency data indicate that some recruit-

ment did occur) as they were a result of immigration via the floating algal clumps into the sampled area each month. Consequently, monthly drift algae fluctuations affected both the areal extent (in the water column), and the habitat diversity (foliose complexity) available to the macrocrustacean community. The number of species (S) and individuals (N) distributed within each 10 m² 'island' was thus not so much dependent on the benthic area sampled as on the combination of benthic and water column area ($1 \times w \times$ depth, d) contained within the drop net. The average water depth over the grassflats during our sampling was 1 m. By pooling the three day and three night samples we thus treated each monthly station as a volume sample with a water surface area of 60 m². The mathematical effect of this thereby integrates the biota found in this volume of water into (i.e. beneath) the 60 m² sampled by the drop nets.

The water column, however, was never completely saturated with drift algae during any of our sampling periods. Indeed, it would be difficult to determine just how much drift algae was necessary for water column saturation, because a typical floating clump was so compressible that in any given 10 m² area additional drift algae could always be accommodated, resulting in both increased areal extent and topographical complexity within the water column. Nonetheless, if a species– or individuals–area relationship existed, we suspected that it could be more easily demonstrated using the plant value associated with the area (instead of just area alone) as the independent variable. Because the animals were distributed within the seagrass–drift algae material, which varied in area and conformational complexity as noted above, we chose dry weight plant biomass (pooled to give monthly dry wt g 60 m⁻²) as the easiest factor expressing plant abundance per sampled area. This factor varied from month to month and gave us 12 variable-sized 'islands' from which we could draw our analyses concerning S, N and crustacean biomass (C_B).

Statistical methodology

In examination of the species– or individuals–area relationship, data from areas of various sizes have usually been compared to S or N that occur in these areas, with a suitable regression line derived from which a predicted S or N per areal increment may be extrapolated. However, because all samples in this study were collected from areas of uniform size (i.e. 10 m², or 60 m² month⁻¹) it was necessary to generate artificial sample areas of variable sizes in order to examine the accumulation of S, N, and C_B and any relation of these parameters to plant biomass (P_B). A method was employed which generated sums of all combinations of data taken from multiples of 60 m². The monthly counts were used in this procedure; however, they were first tested for randomness by von Neuman's successive difference test (von Neuman *et al.*, 1941; Hart, 1942), and Spearman's rank correlation coefficient. The hypothesis of no trend over the months of February through December was accepted, but January was not included in the analysis for reasons that will be discussed later. Although some shorter term seasonality effects were apparent, they were not considered relevant to this analysis, but will be discussed later.

Acceptance of the randomness hypothesis enabled us to make the following assertions. First, successive samples were uncorrelated; that is, a value obtained in one month did not depend on previous values. Second, we assumed *a posteriori*, that no value was more probable than any other. Therefore, samples of arbitrary size ($m \leqslant 12$) were created by random selection from among the original samples. Sums of all combinations were then generated, and exactly $p = m + 1$ were selected and averaged. Choice of the p m-combinations was accomplished by an algorithm of form (1).

$$\delta = 0, \ (_nC_m - t)U \geqslant (p-k) \tag{1}$$
$$= 1, \text{ otherwise}$$

where: δ=decision parameter, $_nC_m$=number of combinations of n things taken m at a time' n=number of original samples taken (12), m=number of samples to be extracted, t=record count not to exceed $_nC_m$, k=selected record count not to exceed p, p=number of m-combinations to be selected from $_nC_m$, U is a random number, uniformly distributed in the interval [0, 1], and was generated according to methodology given by MacLaren & Marsaglia (1965).

In the use of (1), the tth combinatorial sum is selected if δ is 1, or is otherwise rejected; counts t, k are incremented appropriately after each decision. This algorithm guarantees that exactly p sums will be selected from a set of $_nC_m$. Furthermore, repetitions are not possible.

From the sample sets generated it was possible to simulate and examine the accumulation of species, individuals and biomass as the sample area increased. In order to derive a relationship of area (which in this instance was a function of the habitat complexity which obtained in each 60 m² area) the combinatorial data was used in the following general form for P_B:

$$P_B = k_1 A^z \tag{2}$$

where A=area in m², k=a constant dependent on the geographical area and the taxocene, and z=slope of the regression line.

Macrocrustacean abundance (N) as a function of P_B was:

$$N(P_B) = k_2 \, P_B{}^z. \tag{3}$$

These are traditional power curve equations employed in our regression analyses. Both exponentional and linear regressions were also calculated but were not considered further because the correlation coefficients obtained using these equations were either very close to, or were exceeded by, those generated for the power curve equations. For a thorough discussion of the rationale of the various formulae used in species/individuals–area relationships the reader is referred to Connor & McCoy (1979).

The combinatorial data formed the basis of our statistical analysis. We examined the relationship between S and N in a random sample using a concept developed by Fisher *et al.* (1943) wherein:

$$S = a \ln\!\left(1 + \frac{N}{a}\right). \tag{4}$$

Parameter a is proportional to the number of species in the collection, such that when a is large, rare species are more common than abundant species. Conversely, when a is small, abundant species are relatively more common. Following this method, an a was computed from each abundance–species pair (N, S). However, we were unable to find any single a from among the 12 values which would yield species values close to those observed in the field. Regression of a against N provided a simple means to modify a to estimate S from each observed N. When the $a(N)$ relationship was incorporated in (4) above, the species–estimate curves improved but were still frequently unacceptable.

In our study, the critical factor in the distribution of decapod species abundances was apparently P_B. Parameter a was found to covary with P_B; hence we modified Fisher's formulation to incorporate this dependency as:

$$S'a = a(P_B) + \ln\left[1 + \frac{N}{a(P_B)}\right]. \tag{5}$$

TABLE 5. Relationships of the number of individuals (N) and species (S) to plant biomass (P_B) using field and combinatorial data with the Fisher species/individuals equations and its modification (Sa^*)

Area	Cumulative field data[a]			Combinatorial (COMBO)			Predicted (Fisher S/N)			
	P_B	N	S	P_B	N	S	P_B	N	Sa	Sa^*
1	1702	2553	15	1799·0	3306	13	2495	4270	22	14
2	7415	14 798	20	8056·7	10 143	17	5130	9235	25	19
3	8361	18 517	26	7299·0	13 042	24	7821	14 501	26	22
4	10 468	22 576	26	11 297·6	22 890	24	10 549	19 974	27	25
5	14 319	35 230	29	13 078·5	26 881	26	13 304	25 603	28	27
6	15 375	39 812	30	18 962·0	31 945	22	16 082	31 363	28	28
7	18 027	47 162	32	18 549·3	39 719	30	18 878	37 231	29	30
8	19 832	55 245	35	18 985·0	44 352	26	21 691	43 197	29	32
9	20 624	57 225	37	23 069·0	48 100	27	24 517	49 245	30	33
10	21 240	58 692	38	25 464·4	52 709	27	27 357	55 373	30	34
11	30 299	61 276	38	29 600·0	57 026	31	30 207	61 567	30	36
12	32 291	61 911	38	32 291·0	61 911	38	33 068	67 826	31	37

[a]Field data accumulated beginning with March, 1977 followed by April, 1976 and sequentially thereafter.

From this expression it was possible to obtain accurate estimates of S which would be expected to occur in an area of size 60 m², or any multiple thereof. The results of these analyses are presented in Table 5, and will be discussed below.

Results

A total of 61 911 specimens of decapod and stomatopod crustaceans, apportioned among 17 families, 28 genera and 38 species (Table 2) were collected. This fauna consisted primarily of caridean shrimp (13 species, 6 of which are commonly known as grass shrimp), brachyuran crabs (15 species and all previously known associates with seagrass beds), and anomuran crabs (3 species, with the hermit crab *Pagurus bonairensis* being most numerous). Four species of penaeid shrimp were taken, but only one was collected in sufficient numbers to allow analysis.[a] Two species of stomatopod mantis shrimps and one palinurid lobster juvenile completed the community list.

As seen in the steeply-sloped dominance–diversity curve (Figure 3) and Tables 2 and 3, 14 species dominated in the distribution of individuals among the 38 species. Abundant species (4) were represented by more than 4000 individuals each; common species (9) comprised 100–1000 individuals; uncommon species (3) consisted of 24–38 individuals. The fourth and largest group (rare species) contained 22 species, of which none totalled more than 10 individuals and 14 were known from a single specimen.

[a]Because all of the penaeids examined in this study were juveniles, the important morphological characters of the petasma and thelycum were often poorly developed. Consequently, identification was made only to the specific level, although it is known that two subspecies of the four species of *Penaeus* recorded from the east coast of Florida have ranges encompassing the Indian River region (Farfante, 1969).

All decapod crustaceans in this study were identified using standard authoritative texts, including the monographs on American Brachyura by Mary Jane Rathbun, the caridean shrimp faunal listing by Chace (1972), and the zoogeographical species listing of Carolinian Decapoda by Williams (1965).
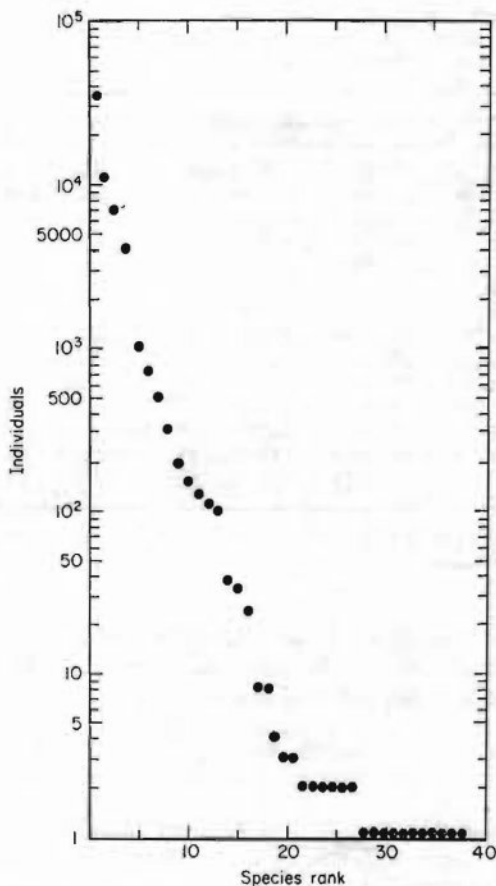
Figure 3. Dominance–diversity curve showing species rank, based on a semi-log plot of the total number of individuals collected from the sampling site over one year.

The 14 numerically dominant species were considered characteristic of the seagrass and drift algae macrocrustacean community. The first nine in Table 3 occurred consistently at every station during the year, and accounted for 98% of all specimens. The next three species were absent from one, two or three non-consecutive monthly stations, respectively. Two other characteristic species were temporally disjunct; the palaemonid grass shrimp *Periclimenes longicaudatus* did not appear in our stations until halfway through the program in October, and the blue crab *Callinectes sapidus* (only juveniles were collected) was absent from May through September. Seven of the characteristic species (97% of all N) demonstrated a marked graphic relationship to changes in P_B (see Figure 7), and, by their great numbers influenced the apparent response of the entire macrocrustacean community to changes in plant abundances (Figure 4).

Monthly variations in S and N (and by interpolation, densities as N 60 m^{-2}) are given in Figure 5. Monthly S varied between 11 and 20 ($\bar{X}=16$). Highest S were seen in May, July, October and December–January, but nearly half of all species in the study, including 13 of the 14 characteristic species, were taken in April during the first month's collection. A cumulative plot of previously unrecorded species ($S+$) showed that species number

gradually and consistently increased over the wet season months (April–October). A comparison with monthly species-inventory data indicated that the cumulative increase during this period was caused chiefly by the recording of 17 of the 22 rare species. During the dry season (November–March) the nearly asymptotic $S+$ curve reflected the collection of only four previously unrecorded species, all rare forms represented by a single individual. Two of these (*Metapenaeopsis* sp., *Trachypenaeus* sp.) taken in November, are not known associates with seagrass beds in the Indian River lagoon (Gore, unpublished data) and are therefore vagrants. The diogenid hermit crab *Paguristes tortugae* was the only rare species taken during both wet and dry seasons. While it can be argued that continued sampling might have provided additional unrecorded species we suspect that these would be numerically unimportant forms (e.g. vagrants), represented by one or two individuals at best.

Monthly N varied from 635 in February to 12 654 in July ($\bar{X}=5159$ month^{-1}). High N were also recorded in April (12 245), September–October (7350, 8083), and a relative peak of 2584 in January. Except for April, these peaks were coincident with those noted above for greatest S (Figure 5). As before, greatest N was associated with the 14 characteristic species, and seven were predominant. This fauna, dominated by caridean shrimp, accounted for a mean percentage of 79% of the highest monthly N listed quarterly, above.

Mean densities per month were calculated from 720 m^2, the total area sampled in 1 year. These ranged from nearly 50 m^{-2} for the grass shrimp *Hippolyte pleuracanthus*,[a] the most abundant decapod in the study area, to fewer than 0·01 m^{-2} for 20 of the 22 rare species (Table 2). The characteristic species thus remained dominant in both N, and N m^{-2} from month to month.

Preliminary analyses suggested that the events taking place during the study could be viewed in better perspective if the N (2553) for March 1977 (the last month of the program) was transposed in sequence as if it were the beginning of the sampling period (April 1976), thus making February 1977 (the month of lowest N) the end of the sample year. Cumulative arithmetic values of N ($N+$), plotted against cumulative area and graphed by eye, appeared as four parabolic arcs. These corresponded to a trimonthly period centered on each of the N maxima previously noted for April, July, October and January [Figure 6(a), dots]. Except for December–February ($N+=4686$), the $N+$ for each trimonthly period was of the same order of magnitude, with highest values occurring during June–August (21 295), March–May (18 517), and September–November (17 413). The trimonthly increases in $N+$ indicated that N increased throughout the year, but in gradually decreasing increments, corresponding to the waning of the wet season and the approach of the dry season. Comparatively,

[a]According to Chace (1972) *Hippolyte pleuracanthus* and *H. zostericola* (Smith, 1873) are extremely closely related, and the latter may yet prove to be a junior synonym of the former. Both species, as presently characterized, can be identified from isolated individuals in the Indian River system, but the morphological features used to distinguish them taxonomically are subject to a rather high degree of variability in this area and tend to become obscure when large populations such as were collected for this study, are examined. In anticipation of future nomenclatural stability we called all *Hippolyte* examined by us *H. pleurocanthus*, thereby referring the taxon to the older name. A recent paper by Shield (1978) reported on some minor morphological differences between the larvae of *H. pleuracanthus* from North Carolina, and '*H. zostericola*' from Bermuda. The latter species was originally described by Gurney (1936) as *H. pleuracanthus bermudensis* but was subsequently synonymized with *H. zostericola* by Chace (1972). In view of the relatively minor differences between the larvae of the two forms, and the fact that Shield noted additional variability in adults of *H. pleuracanthus* (*sensu lato*), we believe the question of the status of *H. zostericola* remains unsettled, and the referral of our specimens to *H. pleuracanthus* to have sufficient validity at this time.
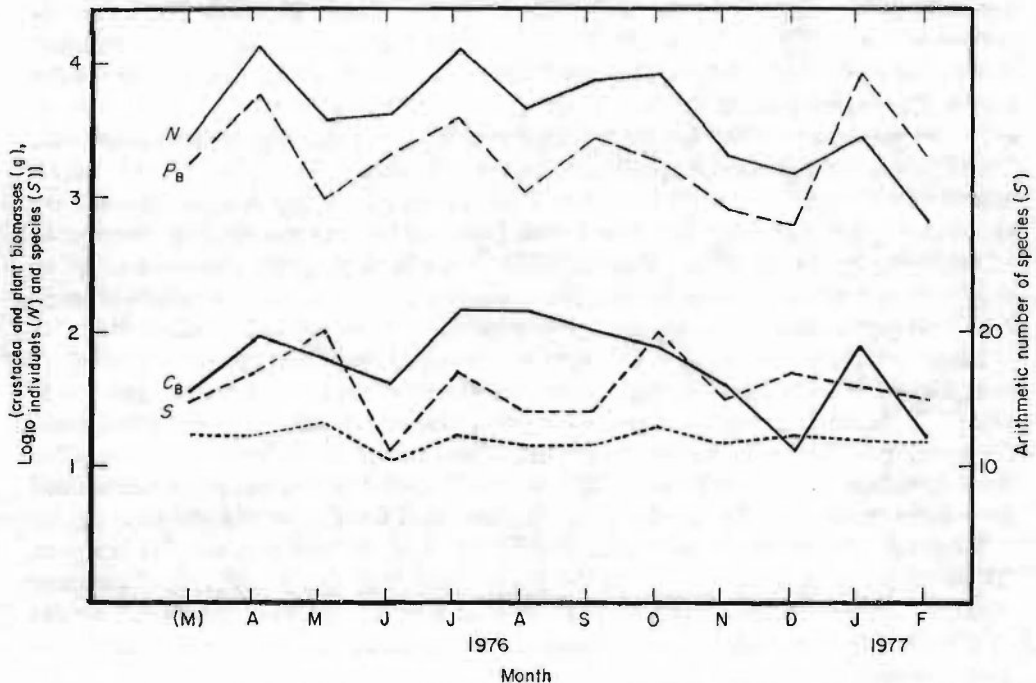
Figure 4. Variation of $\log_{10}$ values for plant biomass (P_B, g 60 m^{-2}), crustacean numbers of individuals (N), biomass (C_B, g 60 m^{-2}) and numbers of species (S) with month. $\log_{10} S$=short dashed line; arithmetic S=long dashed line. Data for March 1977 transposed in sequence to 1976 (see text).

these values from month to month exhibited a five-fold increase during March–May, three-fold during June–August, slightly more than one-fold in September–November, and nearly two-fold in December–February.

Relationship of S, N, and C_B with P_B

We suspected, from the consistency in the relative monthly abundances of the characteristic species, and in overall species composition to a lesser extent, that an individual– or species–areal relationship existed. Although variations in S, N and C_B were noted, all exhibited some relationship to P_B, but N showed the best agreement (Figure 4). In fact, except for an anomalous inversion occurring in January 1977 and persisting through February, the differences between the graphs of N and P_B are virtually constant throughout the year. We believe that the January variation can be explained by the severe meteorological conditions that obtained at that time. From 16–19 January, weather, unseasonably cold even for January, prevailed, with snow flurries recorded on 19 January not only along the subtropical Indian River region but throughout south Florida to Miami and even in the Bahamas Islands. The drop net station was occupied on 24 January and water temperatures of 11·5 °C were recorded at both day and night stations. Onshore winds caused an extreme accumulation of drift algae and seagrass blades in the study area, and in conjunction with cold air and water temperatures, produced hypothermal shock and subsequent mortality of resident crustaceans and fishes [see Gilmore *et al.* (1979) for a more complete description].

Statistical tests against the January data indicated that P_B and, thus its correlates, should be rejected as an outlier [see Beyer (1969: 329) for details]. However, February N (and P_B)
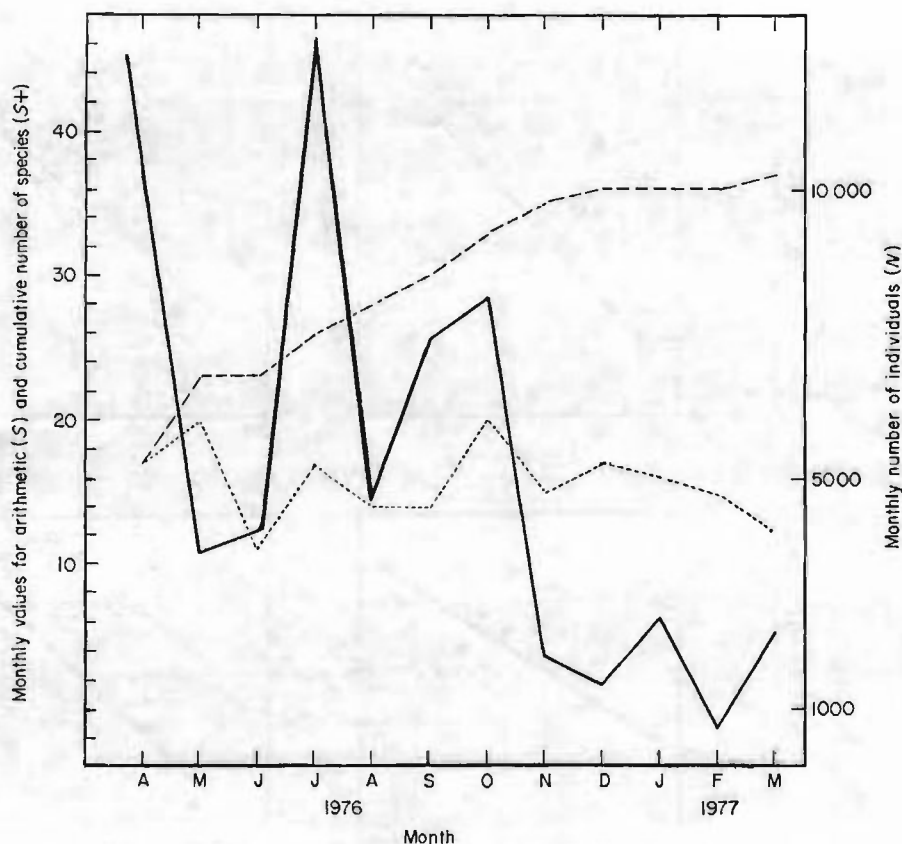
Figure 5. Total monthly number of individuals (N; solid line), cumulative number of species ($S+$; large dashed line) and arithmetic number of species (S; small dashed line) from the sampling site. S, $S+$ values <40 (thin lines), N values >500 (thick lines) on abcissa.

should be retained even though small, and presumably a consequence of the aforementioned hypothermal effects. In the following analysis, the data from Table 4 (with the exception of January) for N, C_B, and P_B were therefore used. These data were tested for independence using Spearman's rank correlation coefficient, which confirmed two significant relationships. Firstly (and perhaps not unexpectedly), C_B was not independent of N; i.e. as N increased, so did the total weight of N [Figure 6(c)]. Secondly, and more importantly, N was not independent of P_B [Figure 6(d)], thereby substantiating the trend suggested by the graphical similarity in Figure 4. That is, the number of individuals living in the drift algae is dependent on the amount of plant matter available. The parameters of N and C_B appear to respond more or less trimonthly to some factor associated with plant materials (as biomass). This factor could presumably be either habitat area, or habitat complexity, or perhaps both.

We determined that the logarithms of N and P_B were approximately normally distributed according to the rankit method for small samples (Sokal & Rohlf, 1969). There was some suggestion of bimodality which we interpreted to be seasonal effects, which are discussed later. Regression analysis yielded the following functional relationship ($r=0.88$):

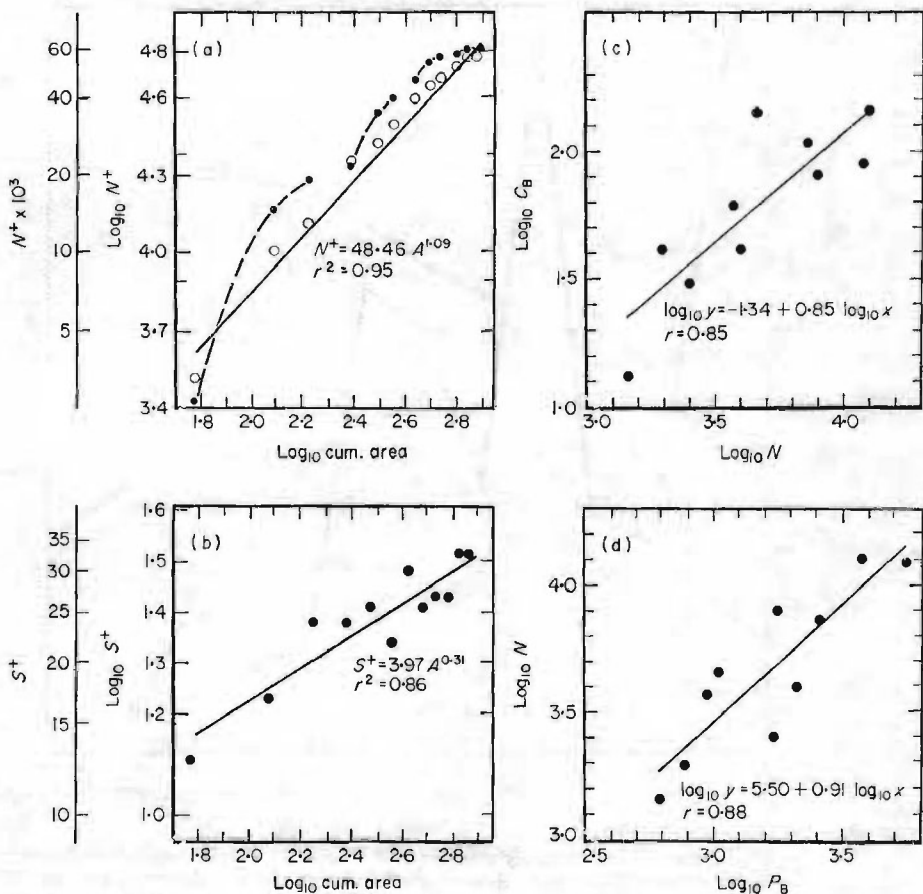$$\log (N) = 0.74 + 0.91 \log (P_B). \qquad (6)$$

Figure 6. Log–log relationships of crustacean individuals (N), species (S) and biomass (C_B) to area, or plant biomass (P_B). (a) cumulative number of individuals to cumulative area; dots denote arithmetic field data, open circles data points generated combinatorially; (b) cumulative number of species to cumulative area, data points generated combinatorially; (c) crustacean biomass to number of individuals; (d) number of individuals to plant biomass. Data in (c) and (d) from field samples, excluding January as noted in text; February N data a negative value and therefore not graphed, but included in analysis.

Similarly, C_B was found to be related to N ($r=0.86$) by the expression:

$$\log (C_B) = -1.34 + 0.85 \log (N). \tag{7}$$

Thus, the number and weight of decapod crustaceans can be related to the amount of plant material available.

Finally, the combinatorial plant biomass data (P_B+) shown in Table 5 was tested for normality and found to agree closely with their rankits. This follows from the normal approximation to a binomial distribution, and the binomiality of randomly generated cumulative sums (Feller, 1967). The areal relationship was developed further by regression, and was given by ($r=0.98$):

$$\log (P_B) = 0.39 + 1.05 \ln (A). \tag{8}$$
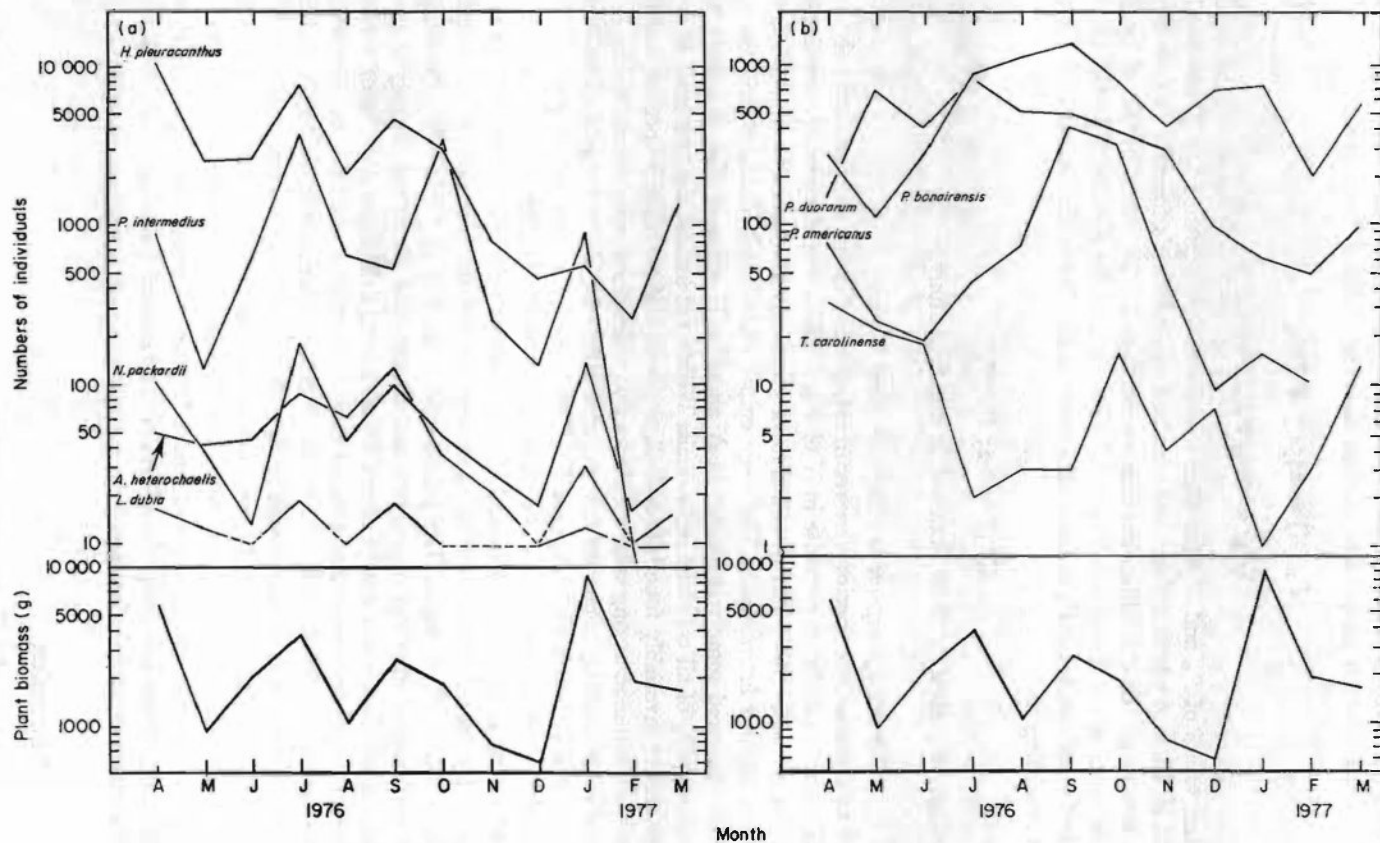
Figure 7. Comparison of monthly plant biomass (P_B, g 60 m^{-2}) with monthly numbers of crustacean individuals for seven consistently recurring decapods. Dotted lines denote months when less than 10 individuals were collected. (a) species with strong associations; (b) species with relatively weaker associations, to plant biomass.

Re-expressing (6) and (8) as power functions yields the following set of equations by which P_B can be estimated from a sample size A, thus allowing N also to be derived:

$$P_B(A) = 2454 \cdot 7\ A^{1.05}; \tag{9}$$

$$N(P_B) = 5495 \cdot 1\ P_B^{0.91}. \tag{10}$$

Appropriate values of P_B and N were then substituted into equation (5). These results are provided in Table 5 where the estimate obtained using Fisher's formula may be compared with that using the a modification that we developed. The values predicted by the combinatorial method are also given. These values show that the relationship of S and N can indeed be formulated using P_B as the spatial component. The modification of the Fisher formulation according to

$$a(P_B) = 0 \cdot 25\ P_B^{0.26}$$

produced values very close to those obtained in our field study.

Community response to changes in plant biomass

Nine of the 14 characteristic species were recurrent monthly in our samples, but only four [Figure 7(a)] showed consistent response in N to P_B. A fifth recurrent species, the alpheid shrimp *Alpheus normanni* (not plotted) tended to vary in a manner similar to its more abundant congener, *Alpheus heterochaelis*. The large spider crab *Libinia dubia*, which was not recurrent, also exhibited some relationship in N and P_B. The five species in Figure 7(a) comprised about 78% of all collected individuals. Within the habitat the two grass shrimp species were almost invariably found in drift algae; both alpheid shrimp species, and the spider crab, were common among seagrass blades and rhizomes during our collecting.

In the four other monthly recurrent species, accounting for about 20% of all collected individuals, only the hermit crab *Pagurus bonairensis*, and the commercial pink shrimp *Penaeus duorarum* showed consistent association in N with P_B [Figure 7(b)]. The pagurid was collected among seagrass rhizomes and blades, whereas the pink shrimp (known only from juveniles) lay buried in the substratum during the day and moved into the seagrass and drift algae superstory at night. The palaemonid grass shrimp *Periclimenes americanus* occurred in about equal numbers in seagrass and among drift algae; the hippolytid grass shrimp *Tozeuma carolinense* was nearly always found among drift algae during our sorting.

The N curves for *P. americanus* and *Penaeus duorarum* typify a seasonality similar to that seen for these species in south-western Florida estuaries (Weinstein *et al.*, 1977), and the decreasing curve for the pink shrimp undoubtedly reflects the yearly maturational migration of the species from the Indian River lagoon, through the barrier island inlets, and into the open ocean for spawning. The poor association of *T. carolinense* numbers to P_B remains unexplained, because this species is considered a 'typical' seagrass drift algae inhabitant. The general extent of our knowledge for the other seagrass and drift algae associated decapods remains sparse or entirely lacking.

Discussion

Until recently, the effects of drift algae on macroinvertebrate and fish communities had been little examined. Phillips (1963) stated that algal mats screen off light, add weight to seagrass leaves, produce hydrogen sulfide and oxygen, and act as a probable food source or nutrient sink for seagrass-associated animals. Thorhaug & Roessler (1977) found that the highest

catches of animals in Biscayne Bay, Florida were correlated with the abundance of the red, free-floating algae *Laurencia*, and demonstrated that numbers of (e.g.) *Hippolyte pleuracanthus* closely followed changes in vegetation. These authors also stated that the species composition, diversity and seasonal and annual numbers of animal individuals were responsive to changes in epiphytic vegetation, as well as to physical factors of salinity and temperature. Similar results were provided by O'Gower & Wacasey (1967), Hooks *et al.* (1976) and Weinstein *et al.* (1977) for south-eastern, north-western, and south-western Florida *Thalassia* communities, respectively. In all these studies, the greatest numbers of macroinvertebrate individuals were usually collected at stations having the densest vegetation. Moreover, in the study by Hooks *et al.* (1976) the species composition of seagrass-associated macrofauna was highly predictable, and they listed *Palaemonetes intermedius, Periclimenes longicaudatus, Tozeuma carolinense, Hippolyte pleuracanthus, Pagurus bonairensis* and *Libinia dubia* among the most abundant species, but not in the same relative abundances as we found in our study. The latter authors noted that large numbers of several species were often found in drifting clumps of red algae, but provided no quantitative data correlating plant with animal abundances.

In a related study on fauna associated with the floating algae *Sargassum serratifolium*, Mukai (1971) demonstrated a positive correlation between numbers of individuals (especially hippolytid shrimps) and invertebrate species with the standing crop of *Sargassum*. Differences in shape, height and consistency and degree of branching in the algae were postulated to account for the observed variations in animal densities. That is, habitat complexity influenced both S and N of the associated invertebrate community.

Brook (1978), however, found no relationship between numbers of *Thalassia* blades and relative faunal abundances or species composition, even in geographically closely related areas in south Biscayne Bay that he sampled. While not specifically referring to drift algae, Brook noted that other factors in addition to seagrass abundances may affect faunal abundances, and suggested that seagrass communities be more precisely defined than by reference to a single, visually dominant, spermatophyte. Earlier, O'Gower & Wacasey (1967) suggested that oxygenation produced by tidal flow and vegetative cover were among several parameters affecting faunal abundances in north Biscayne Bay *Thalassia* beds, but neglected drift algae altogether.

Few of these studies attempted to quantify species or numbers of individuals with abundances of plant material. Instead, they provided much-needed data on standing crops of either macrofauna or plant material on a monthly or annual basis. It therefore remained unclear whether changes in S or N, or both, in the faunal communities could be directly correlated to changes in vegetation. Habitat complexity was not considered, probably because of a lack of a suitable measure for this parameter.

Recently, Heck & Wetstone (1977) suggested that a reasonable measure of habitat complexity may be above-ground plant biomass, because it is possible to significantly correlate this value with invertebrate S or N. Plant S, according to these authors, shows no such significance. They stated that P_B and macroinvertebrate S correlations were probably based on the addition of 'cryptic' species (i.e. rare, plant-associated forms or non-associated vagrants) which were living among the densely branched plants. But no consideration was given to increases in N of extant species.

We suggest here that both macrocrustacean community composition and diversity are controlled, at least in part, by monthly changes in above-ground plant abundances, *sensu* Heck & Wetstone (1977). We equate increased P_B with increased habitat complexity, and suggest that the correlation between P_B and macrocrustacean N observed in our study is

therefore related to habitat complexity. Such complexity would not only provide a decreased probability of encounter among both predators and prey, but would also decrease intraspecific competition through an increase in available living space for the drift algae inhabitants. Either or both situations could allow large numbers of individuals to co-exist within the algal clumps. That drift algae functions as a renewable energy resource is concomitant with this concept.

Macrocrustacean community stability

Our field observations indicated that the drift algae itself probably undergoes little major physical change other than in areal extent, as long as it remains in the water column. During this time the floating algal clumps are subjected to the wide ranges of salinity, temperature, and other physical factors characteristic of the euryhaline and eurythermic Indian River lagoon (see Gilmore, 1977). However, the relatively consistent composition and numbers of the characteristic species in this habitat show that these members of the community can persist over a biological year that begins in March, just prior to the subtropical wet season, and ends in February of the following year, at the end of the dry season. We noted, furthermore, that the S and N of most rare species were temporally restricted in occurrence to the wet season months having the highest abundances of drift algae. At the same time, S of the characteristic species showed less fluctuation, although N varied directly with high and low abundances of P_B. From this we infer that the drift algae habitat is very nearly, if not completely, species-saturated at all times of the year. If, as seems likely, the stability in species composition and species saturation of this habitat (exhibited primarily by characteristic species) is directly related to habitat complexity, then some degree of resilience in response to changing environmental parameters must also obtain in the community.

Alternatively, the presence of rare species might be a result of interaction with the characteristic species. The latter, with relatively large N could partition the resource of living space (for example) to such a degree that immigration of rare species would only occur with increases in drift algal abundances. This type of interaction may be more important in subtropical seagrass regions such as the Indian River lagoon, than in tropical areas (e.g. Panama). According to Heck & Wetstone (1977) low invertebrate densities and (apparently) large amounts of unused living space are more prevalent in the tropics. We concur, however, with these authors that such partitioning may have even greater importance in temperate seagrass areas, where living space may be at more of a premium because of higher densities of individuals, although species densities may be lower.

Predation vs. *competition*

We agree with several authors (Hooks *et al.*, 1976; Heck & Wetstone, 1977) that drift algae offers protection from predation to at least some of the associated invertebrates. Data on external ichthyofaunal predators from the same area as our study (Kulczycki, unpublished) show that the two dominant fishes associated directly with floating algae clumps, the code goby *Gobiosoma robustum* (Gobiidae) and the Gulf pipefish *Syngnathus scovelli* (Syngnathidae) feed predominantly on copepods and amphipods in the floating clumps, and only rarely on grass shrimps. Our field observations on the large matted algal clumps that we sampled further convince us that the higher order grassflat carnivores such as snappers (Lutjanidae), sea trout and silver perch (Sciaenidae), pinfish (Sparidae) and pigfish (Pomadasyidae) would find feeding difficult in such algal mats, although not necessarily so on the more open (unmatted) seagrass areas, or in sandy spots where, in addition to penaeid shrimp, polychaete worms and pericaridan crustaceans may occur (see Brook, 1977).

On the other hand, if the majority of seagrass or drift algae-associated macrocrustaceans (especially the characteristic decapod species) are correctly classified as either omnivores or detritivores (see e.g. Reid, 1954; Ewald, 1969; Odum & Heald, 1972; Young *et al.*, 1976; and others), then the decapod community would presumably be regulated more by competitive exclusion among its members than by predation from within. None of the characteristic species, for example, are classifiable as strictly predatory, although all are probably facultatively carnivorous at one time or another. The two species of *Callinectes* are probably the only decapods capable of within-community predation on both the benthos and the drift algae inhabitants. The two xanthid crab species, *Neopanope packardii* and *N. sayi* are known benthic carnivores and would be unlikely to feed within the floating algae. Instead, we think it likely that these four species feed predominantly on the polychaete worms and gastropod molluscs associated with the drift algae.

Finally, the proximity of individuals among the various decapod species may also be conducive to community stability in that breeding is facilitated. Our data show that the three most abundant species (listed in Table 3) were ovigerous year around; ovigerous females in other characteristic species occurred from January–March generally through November or occasionally December, usually encompassing a breeding season of 9 or 10 months of the year.

Habitat complexity and community dynamics

'Equilibrium theory' states that the available area will proportionately influence the size of a population in the area (MacArthur & Wilson, 1967). As area increases, both habitat diversity and population size should also increase, because more species, and larger populations of such species, can be supported as a consequence of more habitats and fewer species extinctions. Recent studies (e.g. Abele & Patton, 1976; Simberloff, 1976; among others) have supported these hypotheses by demonstrating positive species–area relationships for a variety of organisms. The two studies cited concluded that area alone can act as a regulating mechanism for population size, independent of habitat diversity. This concept provides one (i.e. non-stochastic) explanation of our results.

To demonstrate any increase of S with area, these (and other) studies have compared sampled areas of various (increasing) sizes with the population census of the contained animals. Our study differs from previous works in that the actual encompassed area sampled from month to month remained constant, while within-sampled-area habitat complexity (equated and measured as plant biomass) changed. In the context of island biogeography, we were (in effect) sampling floating islands that continually conglomerated within a restricted area, consequently increasing both available area (as the vertical component) and complexity of habitat for those species utilizing these 'islands'. The most obvious change in habitat complexity in this case was the increased conformational diversity as a consequence of increases in the highly foliose, often compacted, drift algal clumps in the water column above the seagrass bed. The positive correlation of macrocrustacean species, numbers of individuals and biomass with plant biomass indicates that the community was responding directly to area via habitat complexity, because the effects of P_B and area cannot be separated from one another.

In the context of 'equilibrium theory' the increased habitat complexity apparently allows increased numbers of individuals of the characteristic species to exist in the drift algae clumps, while at the same time allowing the immigration and temporary establishment of rare species into these clumps during periods of greater algal abundance. It is important to note that nine of the characteristic species never went 'extinct', three others

were absent for no more than one to three non-consecutive months, and two others were seasonally abundant for at least half the year (Table 3). The most noteworthy change in all of these species, however, was the fluctuations in numbers of individuals. Even so, the characteristic species composition remained quite predictable, regardless of the individual stations sampled. Although total macrocrustacean community species numbers and numbers of individuals varied, it was still possible, using combinatorial data to show that cumulative S and N increased proportionately to cumulative area.

By applying a modification of Fisher *et al.* (1943) formulation it was possible not only to demonstrate a quantifiable relationship between S and N, with P_B as the areal component, but also to produce a descriptive formula which showed very good agreement with actual field data. It is apparent that the numbers of individuals in the drift algae community are related to the number of species, and both depend closely on available area. Indeed, the stability of the community seems intimately tied to the complexity of the habitat, and thus directly to area. While not denigrating the traditionally accepted importance of seagrasses in the biotope, we feel that in the Indian River estuarine system, and perhaps in other subtropical or tropical environments, the contribution toward community stability and dynamics by the drift algae is of equal or greater importance.

Acknowledgements

References

Abele, L. G. & Patton, W. K. 1976 The size of coral heads and the community biology of associated decapod crustaceans. *Journal of Biogeography* **3**, 35–47.

Beyer, W. H. (ed.) 1968 *CRC Handbook of Tables for Probability and Statistics.* The Chemical Rubber Company, Cleveland. 643 pp.

Brook, I. M. 1977 Trophic relationships in a seagrass community (*Thalassia testudinum*) in Card Sound, Florida. Fish diets in relation to macrobenthic and cryptic faunal abundance. *Transactions of the American Fisheries Society* **106**, 219–229.

Brook, I. M. 1978 Comparative macrofaunal abundance in turtlegrass (*Thalassia testudinum*) communities in south Florida characterized by high blade density. *Bulletin of Marine Science* **28**, 212–217.

Chace, F. A., Jr. 1972 The shrimps of the Smithsonian–Bredin Caribbean expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). *Smithsonian Contributions to Zoology* **98**, 1–179.

Connor, E. F. & McCoy, E. D. 1979 The statistics and biology of the species–area relationship. *American Zoologist* **113**, 791–833.

Dragovich, A. & Kelly, J. A., Jr. 1964 Ecological observations of macroinvertebrates in Tampa Bay, Florida 1961–1962. *Bulletin of Marine Science of the Gulf and Caribbean* **14**, 74–102.

Eiseman, N. J. & Benz, M. C. 1975 Marine algae of the Indian River. 1. Species of the algal drift community collected from April 1974 to April 1975. *Technical Report* No. 1, *Harbor Branch Foundation, Inc.* 1–16.

Ewald, J. J. 1969 Observations of the biology of *Tozeuma carolinense* (Decapoda, Hippolytidae) from Florida, with special reference to larval development. *Bulletin of Marine Science* **19**, 510–549.

Farfante, I. P. 1969 Western Atlantic shrimps of the genus *Penaeus. Fishery Bulletin, U. S. Fish & Wildlife Service* **67**, i–x, 461–591.

Feller, W. 1968 *An Introduction to Probability Theory and its Applications* Volume 1, 3rd edition. John Wiley & Sons, New York. 509 pp.

Fisher, R. A., Corbet, A. S. & Williams, C. B. 1943 The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**, 42–58.

Gilmore, R. G., Jr. 1977 Fishes of the Indian River lagoon and adjacent waters, Florida. *Bulletin of the Florida State Museum, Biological Sciences* **22**, 101–147.

Gilmore, R. G., Bullock, L. H. & Berry, F. H. 1979 Hypothermal mortality in marine fishes of south-central Florida, January, 1977. *Northeast Gulf Science* **2**, 77–97.

Gilmore, R. G., Jr., Holt, J. K., Jones, R. S., Kulczycki, G. R., MacDowell, L. G., III & Magley, W. C. 1978 Portable tripod drop net for estuarine fish studies. *Fishery Bulletin, U. S. Fish & Wildlife Service* **76**, 285–289.

Gurney, R. 1936 Notes on some decapod Crustacea of Bermuda. II. The species *Hippolyte* and their larvae. *Proceedings of the Zoological Society of London* **1**, 25–32.

Hart, B. I. 1942 Significance levels for the ratio of the mean square successive difference to the variance. *Annals of Mathematical Statistics* **13**, 445–447

Heck, K. L., Jr. 1976 Community structure and the effects of pollution in sea-grass meadows and adjacent habitats. *Marine Biology* **35**, 345–357.

Heck, K. L., Jr. & Wetstone, G. S. 1977 Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* **4**, 135–142.

Hoese, H. D. & Jones, R. S. 1963 Seasonality of larger animals in a Texas turtle grass community. *Publications of the Institute of Marine Science, University of Texas* **9**, 37–46.

Hooks, T. A., Heck, K. L., Jr. & Livingston, R. J. 1976 An inshore marine invertebrate community: Structure and habitat associations in the north-eastern Gulf of Mexico. *Bulletin of Marine Science* **26**, 99–109.

Kjelson, M. A. & Johnson, G. N. 1973 Description and evaluation of a portable drop-net for sampling nekton populations. *Proceedings of the 27th Annual Conference of the Southeast Association of Game Fish Commission*, 653–662.

Kjelson, M. A., Turner, W. R. & Johnson, G. N. 1975 Description of a stationary drop-net for estimating nekton abundance in shallow waters. *Transactions of the American Fisheries Society* **104**, 46–49.

Livingston, R. J., Iverson, R. L., Estabrook, R. H., Keys, V. E. & Taylor, J., Jr. 1974 Major features of the Apalachicola Bay system: Physiography, biota and resource management. *Quarterly Journal of the Florida Academy of Sciences* **37**, 245–271.

MacArthur, R. A. & Wilson, E. O. 1967 *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey. 203 pp.

McLaren, M. D. & Marsaglia, A. 1965 Uniform random number generators. *Journal of the Association of Computing Machinery* **12**, 83–89.

McNulty, J. K., Work, R. C. & Moore, H. B. 1962 Some relationships between the infauna of the level bottom and the sediment in south Florida. *Bulletin of Marine Science of the Gulf and Caribbean* **12**, 322–332.

Moore, H. B., Davies, L. T., Fraser, T. H., Gore, R. H. & Lopez, N. R. 1968 Some biomass figures from a tidal flat in Biscayne Bay, Florida. *Bulletin of Marine Science* **18**, 261–279.

Mukai, H. 1971 The phytal animals on the thalli of *Sargassum serratifolium* in the *Sargassum* region, with reference to their seasonal fluctuations. *Marine Biology* **8**, 170–182.

Odum, W. E. & Heald, E. J. 1972 Trophic analyses of an estuarine mangrove community. *Bulletin of Marine Science* **22**, 671–738.

O'Gower, A. K. & Wacasey, J. W. 1967 Animal communities associated with *Thalassia, Diplanthera*, and sand belts in Biscayne Bay. 1. Analysis of communities in relation to water movements. *Bulletin of Marine Science* **17**, 175–210.

Peterson, C. H. 1975 Stability of species and of community for the benthos of two lagoons. *Ecology* **56**, 958–965.

Phillips, R. C. 1963 Ecology of floating algal communities in Florida. *Quarterly Journal of the Florida Academy of Sciences* **26**, 329–334.

Rathbun, M. J. 1918 The grapsoid crabs of America. *United States National Museum Bulletin* No. 97, i–xxii, 1–461.

Rathbun, M. J. 1925 The spider crabs of America. *United States National Museum Bulletin* No. 129, i–xx, 1–613.

Rathbun, M. J. 1930 The cancroid crabs of America of the families Euryalidae, Portunidae, Atcle-cyclidae, Cancridae and Xanthidae. *United States National Museum Bulletin* No. 152, i–xvi, 1–609.

Reid, G. K. 1954 An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. *Bulletin of Marine Science of the Gulf and Caribbean* **4**, 1–94.

Roessler, M. A. 1971 Environmental changes associated with the Turkey Point power plant on Biscayne Bay, Florida. *Marine Pollution Bulletin* **2**, 87–90.

Roessler, M. A. & Beardsley, G. L. 1974 Biscayne Bay: Its environment and problems. *Quarterly Journal of the Florida Academy of Sciences* **37**, 186–204.

Roessler, M. A., Moore, H. B., Beardsley, G., Smith, R., Hixon, R., Hoberg, C., Brook, I., Sprogis, J. & Hatfield, N. 1972 V. Benthic ecology. In *An Ecological Study of South Biscayne Bay and Card Sound* (Bader, R. G. & Roessler, M. A., eds). Progress Report to the United States Atomic Energy Commission (AT (40–1)–3801–4) & Florida Power and Light Company, V1–V115.

Shield, P. D. 1978 Larval development of the caridean shrimp, *Hippolyte pleuracanthus* (Stimpson), reared in the laboratory. *Estuaries* **1**, 1–16.

Simberloff, D. 1976 Experimental zoogeography of islands: Effects of island size. *Ecology* **57**, 629–648.

Simon, J. L. 1974 Tampa Bay estuarine system—a synopsis. *Quarterly Journal of the Florida Academy of Sciences* **37**, 217–244.

Sokal, R. R. & Rohlf, F. J. 1969 *Biometry*. W. H. Freeman & Co. San Francisco. 776 pp.

Tabb, D. C. & Manning, R. B. 1962 Aspects of the biology of northern Florida Bay and adjacent estuaries. In *The ecology of Northern Florida Bay and Adjacent Estuaries* (Tabb, D. C., Dubrow, D. L. & Manning, R. B., eds). Florida State Board of Conservation, Technical Series No. 39, 39–79.

Taylor, J. L. 1974. The Charlotte Harbor estuarine system. *Quarterly Journal of the Florida Academy of Sciences* **37**, 205–216.

Thorhaug, A. 1974 Effect of thermal effluents on the marine biology of southeastern Florida. In *Thermal Ecology* (Gibbons, J. W. & Sharitz, R. R., eds). Atomic Energy Commission Symposium Series (Conference 730505), 518–531.

Thorhaug, A. & Roessler, M. A. 1977 Seagrass community dynamics in a subtropical estuarine lagoon. *Aquaculture* **12**, 253–277.

Turner, R. E. 1977 Intertidal vegetation and commercial yields of penaeid shrimp. *Transactions of the American Fisheries Society* **106**, 411–416.

Virnstein, R. W. 1977 The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* **58**, 1199–1217.

von Neuman, J., Kent, R. H., Bellison, H. R. & Hart, B. I. 1941 The mean square successive difference. *Annals of Mathematical Statistics* **12**, 153–162.

Weinstein, M. P., Courtney, C. M., & Kinch, J. C. 1977 The Marco Island estuary: a summary of physicochemical and biological parameters. *Florida Scientist* **40**, 97–124.

Williams, A. B. 1965 Marine decapod crustaceans of the Carolinas. *Fishery Bulletin, U. S. Fish & Wildlife Service* **65**, i–xi, 1–298.

Young, D. K., Buzas, M. A. & Young, M. W. 1976 Species densities of the macrobenthos associated with seagrass: a field experimental study of predation. *Journal of Marine Research* **34**, 577–595.

Young, D. K. & Young, M. W. 1977 Community structure of the macrobenthos associated with seagrass of the Indian River estuary, Florida. In *Ecology of Marine Benthos* (Coull, B. C., ed.).University of South Carolina Press, Colombia, South Carolina **6**, 359–382.