Penicillus capitatus: an algal island for macrocrustaceans

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ABSTRACT: Abundance and species richness of crustaceans associated with the calcareous green alga Penicillus capitatus in Puerto Rico increased with algal size. Faunal abundance was higher in the dry season than in the wet season, but species-area regressions were identical for the 2 periods. Faunal abundance rather than algal size, however, proved to be the best predictor of crustacean species richness on P. capitatus. Although there were no negative associations among species pairs, qualitative and quantitative changes in the crustacean assemblages during recolonization of defaunated P. capitatus and increasing dominance with animal density suggest the potential significance of differential immigration rates, displacement of certain taxa, and positive associations in explaining variation in species composition and species richness. Higher abundances of crustaceans (particularly amphipods and tanaidaceans) were found on P. capitatus than in the surrounding seagrass (Halodule wrightii) habitat; this is probably a function of protection from fish predators and habitat selectivity.

INTRODUCTION

Island land masses have long been used to study colonization processes, coexistence of similar species, density dependent phenomena, and species-area effects. Recently, small habitat islands in marine habitats have been examined for some of the same reasons (Abele & Patton 1976, Gotelli & Abele 1982, Gunnill 1982a, Lewis 1982, Abele 1984, Stoner & Greening 1984). The calcareous green alga Penicillus capitatus Lamarck, found in shallow subtidal waters throughout the Caribbean Sea, the Bahamas, Florida and Bermuda (Taylor 1960), provides a convenient model for testing hypotheses related to island biogeographic processes. The alga is composed of interwoven coenocytic filaments forming a rhizoidal base, a thin, rigid stripe, and a brush-like capitulum of free and dichotomously branched filaments (Friedman & Roth 1977). The capitula of P. capitatus support large communities of macrofauna dominated numerically by small Crustacea, mostly amphipods, tanaidaceans and large harpacticoid copepods. Small (late juvenile) and large P. capitatus (to 15 cm tall) are identical in basic structure, except size, and represent an ideal model for examining species-area relations where habitat heterogeneity is constant. In this study, I examine numbers of individuals, numbers of species, and species composition of crustaceans with respect to P.

capitatus size during the dry and wet seasons in Puerto Rico. Further, because interspecific interactions may influence the composition of a species assemblage, tests of interspecific association were employed and recolonizations of defaunated P. capitatus were examined.

MATERIALS AND METHODS

Site description. All collections and experiments were conducted near Punta Ostiones, 7 miles south of Mayaguez on the west coast of Puerto Rico (18°05.5′ N, 67°12.0′ W). The study site is a sublittoral band of coarse calcareous sand, averaging 80 m in width, protected by a fringing coral reef front. Water depths within the study area are less than 60 cm with a tidal range of ca 30 cm. The shallow area is subject to relatively constant high salinities (> 32 ‰). Temperatures during the collecting period ranged from 27 to 32 °C with diurnal temperature excursions of as much as 4 C°. The primary set of collections and recolonization experiment were made in a bed of the seagrass Halodule wrightii (40 to 170 g dry wt m^{-2}), where Penicillus capitatus is abundant (ca 25 to 30 ind. m^{-2}). At this seagrass site, mean depth was 25 cm and wave energy was low, but sufficient to prevent accumulation of fine sediment. 'Reef collections' of P. capitatus were made in the coral rubble zone of the backreef where

the alga is abundant in sandy patches 25 to 50 cm deep. Wave surge is greater in this area than in the *H. wrightii* area, and water temperatures show less diurnal fluctuation.

Collections. Individual *Penicillus capitatus* were covered, *in situ*, with 18 oz. (510 ml) plastic bags, removing the rhizoid before sealing so that infauna were not included in the sample. Forty individual algae were collected in April 1984 (dry season) and 38 were collected in July 1984 (wet season), all of these from the seagrass area. Samples were collected nonrandomly in an attempt to include an even distribution of *P. capitatus* sizes from late juveniles through to the largest available. Fifteen *P. capitatus* were collected in a similar manner from the backreef area in July 1984.

Concurrent with *Penicillus capitatus* collections, epifauna of the seagrass area were sampled with a 15 by 15 cm steel box covered with 0.5 mm mesh. The seagrass cutter is equipped with a serrated steel blade designed to take macrophytes and 1 cm of sediment. Four replicates were collected in haphazard fashion (but avoiding *P. capitatus*) in the sparse stand of *Halodule wrightii* for comparison of the seagrass epifauna with that of *P. capitatus*. Seagrass samples were sieved in the field on a 0.50 mm screen. All samples, *P. capitatus* and *H. wrightii*, were preserved in a 10 % formaldehyde solution. (*P. capitatus* was rare in beds of other seagrass species; these beds were not sampled for this study.)

In the laboratory, individual *Penicillus capitatus* capitula and *Halodula wrightii* blades were vigorously rinsed with fresh water and the faunal associates were collected on a 0.50 mm mesh screen. The macrophytes were measured for dry weight after being held in an oven at 80 °C until constant mass was observed. All crustaceans were sorted from remaining sediment and detritus by hand, using a dissecting microscope. All were identified to the lowest possible taxonomic unit and measured for total length. Other macrofauna, such as polychaetes and gastropods, made up less than 4 % of the total fauna and are not considered here.

Recolonization experiment. In April, on the day following routine *Penicillus capitatus* collections, a field experiment was begun to examine patterns of colonization of the alga by motile Crustacea. In a large, uniform area of sparse *Halodule wrightii*, three 90 by 90 cm string quadrats were fixed to the bottom and all *P. capitatus* were removed. *P. capitatus* of the appropriate size for the experiment were gently pulled from the area in and around the quadrats, being careful to retain as much of the rhizoid as possible. The capitula were then washed in 3 changes of fresh water to remove the animals, and held in a tray of seawater until replanting. Preliminary experiments examining *P. capitatus* handled in this manner showed that the defaunation

method was 100 % effective in removing taxa retained on a 0.5 mm screen. The quadrats were then each planted with 20 defaunated *P. capitatus* of ca equal and average size (0.29 ± 0.10 g dry wt) on 15 cm centers. After placement in the quadrats, the capitula of the alga quickly accumulated a light dusting of silt, and the transplants appeared green and healthy until Day 6 of the recolonization when the experiment was terminated.

In a manner similar to that described for routine collections, 2 *Penicillus capitatus* were randomly removed from each grid on a schedule of: 1 h 20 min, 3 h, 6 h, 10 h, 21 h, 2 d, 3 d, 4 d and 6 d. (Time zero was at 0940 h.) Because some of the alga showed signs of deterioration, such as loss of filaments and color, on Day 6, this last collection was not included in the analysis. Collections were processed as previously described. During the experiment, water temperatures were recorded between 26.9 and 31 °C, and depth at the site ranged from 12 to 26 cm.

RESULTS

Collections

The number of macrofaunal individuals found on *Penicillus capitatus* was significantly correlated with *P. capitatus* weight. Log_{10}-transformations provided normal distribution of residuals and highly significant correlation coefficients (Fig. 1, Table 1), not found for untransformed data. Analysis of covariance with weight as the covariate showed that linear regressions for the wet and dry seasons were not significantly different in slope, but July collections yielded signifi-

Table 1. *Penicillus capitatus*. Summary statistics for linear regressions of number of individuals and species richness of macrofauna found on capitula. N: number of individuals; S: number of species; W: *P. capitatus* dry weight

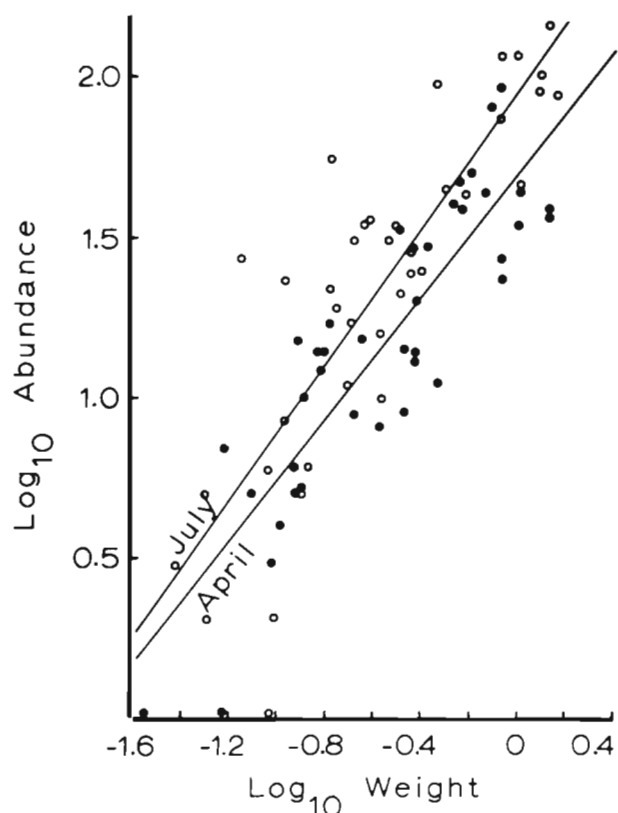| Month	Slope	Y-intercept	n	r	F
		Log N *vs* Log W			
Apr	0.947	1.689	40	0.864	114.92**
Jul	1.060	1.948	38	0.837	82.72**
		Log S *vs* Log W			
Apr	0.440	0.885	40	0.735	47.74**
Jul	0.471	0.924	38	0.647	102.91**
		Log S *vs* Log N			
Apr	0.423	0.157	40	0.825	81.03**
Jul	0.380	0.141	38	0.812	66.04**
Significance: ** $p < 0.01$					

Fig. 1. Abundance of macrofauna on the capitula of *Penicillus capitatus* as a function of alga weight. Closed circles = April collections; open circles = July. Least squares regression lines shown
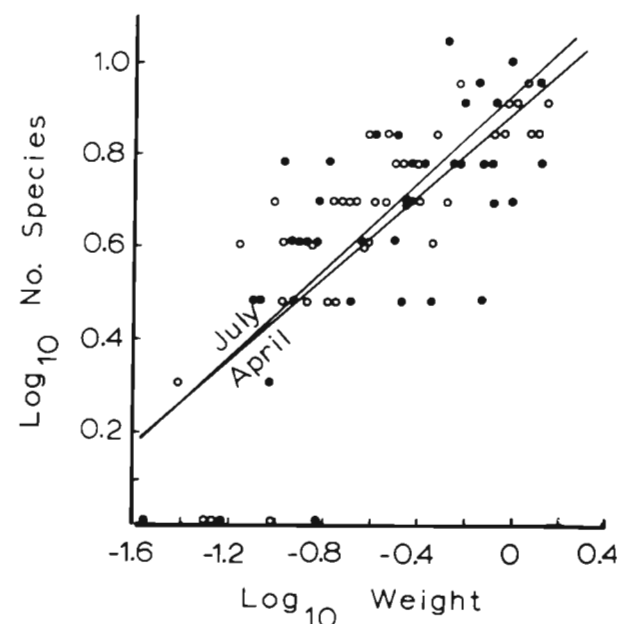

Fig. 2. Species richness of macrofauna on the capitula of *Penicillus capitatus* as a function of alga weight. Closed circles = April collections; open circles = July. Least squares regression lines shown

cantly higher numbers of individuals than April collections (Table 2).

Species richness was significantly correlated with both *Penicillus capitatus* weight and abundance of individuals when the data were $\log_{10}$-transformed (Fig. 2 & 3, Table 1). Animal abundance was the best predictor of species richness, explaining 68 % of the variation in April, and 66 % in July. Multiple linear regression models, using both numbers of individuals and *P. capitatus* weight as independent variables,

improved the correlation coefficients to 0.911 and 0.915 for April and July collections, respectively. Consequently, approximately 82 % of the variation in species richness is explained by the 2 predictors examined. Analysis of covariance revealed no significant seasonal effects on species richness with *P. capitatus* weight ($p > 0.10$) and a weak seasonal effect with faunal abundance ($p < 0.10$) (Table 2).

For comparative purposes, abundance of macrofauna may be expressed in terms of numbers of individuals per unit dry weight and per unit surface area of different macrophytes. *Penicillus capitatus* has 634 $cm^2\,g^{-1}$ ash-free dry wt (Lewis unpubl.), (or 199 $cm^2\,g^{-1}$ dry wt) and *Halodule wrightii* has 715 $cm^2\,g^{-1}$ dry wt (Stoner 1980). Despite considerable variation in the abundance of fauna in samples of *P. capitatus* and *H.*

Table 2. *Penicillus capitatus*. Results of analyses of covariance for seasonal effects on abundance and species richness of macrofauna on capitula

Y-variable	Covariate	Factor	n	F values Test for differences among	
				Slopes	Intercepts
Abundance	*P. capitatus* weight	Season	78	$0.553_{(1,74)}$	$10.622^{***}{}_{(1,75)}$
Species richness	*P. capitatus* weight	Season	78	$0.487_{(1,74)}$	$0.396_{(1,75)}$
Species	Abundance	Season	78	$1.248_{(1,74)}$	$3.782^{+}{}_{(1,75)}$

Significance: $^{+}$ $p < 0.10$; *** $p < 0.005$

Fig. 3. Species richness of macrofauna on the capitula of *Penicillus capitatus* as a function of animal abundance. Closed circles = April collections; open circles = July. Least squares regression lines shown
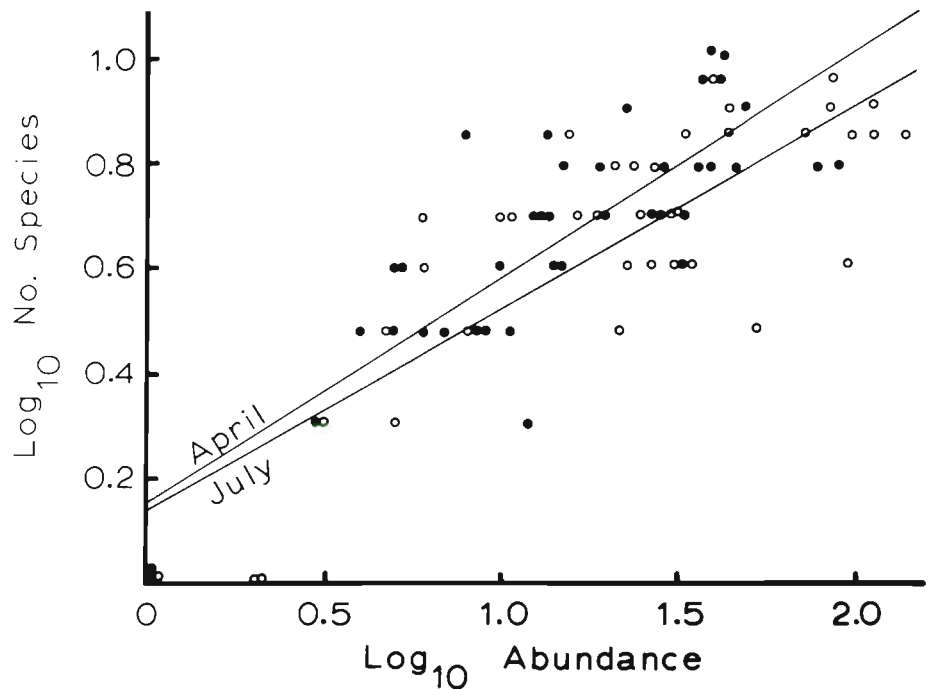
Table 3. Abundance of macrofauna on *Halodule wrightii* and *Penicillus capitatus* standardized to numbers per unit macrophyte dry weight and surface area. Values are means ± SD

Month	*Halodule wrightii*	*Penicillus capitatus* Seagrass site	Reef site
	No. g⁻¹ dry wt		
Apr	12.0 ± 4.4	59.4 ± 30.0	–
Jul	15.2 ± 13.4	102.4 ± 76.7	181.6 ± 95.4
	No. 100 cm⁻²		
Apr	1.67 ± 0.61	29.1 ± 15.8	–
Jul	2.13 ± 1.88	51.4 ± 38.6	91.3 ± 47.9

wrightii the capitula of *P. capitatus* represent islands of very high animal density compared to the surrounding *H. wrightii* habitat, regardless of the standardization used (Table 3). The concentration of macrofauna on *P. capitatus* tops is even more pronounced in the reef habitat where few alternative microhabitats exist.

The macrofauna of *Penicillus capitatus* was dominated numerically by members of the tanaidacean genus *Leptochelia* (Table 4). Two species were collected in approximately equal numbers, *L. dubia* and *L. forresti*. Other abundant fauna were the isopod *Bagatus stylodactylus*, 2 undescribed amphipods in the genus *Maera*, and a large, unidentified harpacticoid copepod. Species composition varied little with *P. capitatus* size (Fig. 4), except that *Leptochelia* species decreased in relative abundance with increasing *P. capitatus* weight in July, while *B. stylodactylus*

increased in abundance. Again, numbers of species collected were largely a function of faunal abundance and did not increase with alga size when abundance was similar within the different *P. capitatus* size classes. Because of considerable variation in lengths, *L. forresti*, *L. dubia*, *Maera* sp. A, *Maera* sp. C, and *B. stylodactylus* showed no significant change in size with *P. capitatus* size class (ANOVA, p > 0.10).

Penicillus capitatus differed distinctively from *Halodule wrightii* in species composition and relative abundances (Table 4). Although *Leptochelia* species dominated the fauna on both macrophytes, only 1 *Maera* individual was collected on *H. wrightii*, and isopods were relatively rare on the seagrass. Cumaceans and the large harpacticoid were found only on *P. capitatus*. On the other hand, the amphipod *Melita* sp. and shrimp were found only on *H. wrightii*, and the amphipods *Cymadusa filosa* and *Lembos unicornis* were of greatest relative abundance on *H. wrightii*. Cluster analysis (Fig. 5) indicated that the fauna of *P. capitatus* collected in reef and seagrass habitats were very similar, but were dissimilar to those associated with *H. wrightii*. Seasonal effects on species composition appeared to be greater in the *H. wrightii* fauna than that associated with *P. capitatus*.

On the basis of numbers of species collected, *Penicillus capitatus* collected in April appeared to support the most diverse assemblage of crustaceans (Table 4); however, the relation was largely a function of the number of individuals collected. When the rarefaction method of Heck et al. (1975) and Simberloff (1978) was used to compensate for numbers of individuals in the

Table 4. Composition of macrofauna associated with the seagrass *Halodule wrightii* and *Penicillus capitatus* in 2 different locations. Numbers of individuals collected and percent of total collection (in parentheses)

Species taxa	April Seagrass-associated Penicillus	Halodule	July Seagrass-associated Penicillus	Reef-associated Penicillus	Halodule
TANAIDACEA					
Leptochelia dubia	201 (22.6)	18 (17.3)	313 (21.5)	235 (19.7)	28 (28.3)
Leptochelia forresti	226 (25.4)	15 (14.4)	401 (27.6)	256 (21.4)	12 (12.1)
AMPHIPODA					
Cymadusa filosa	8 (0.9)	13 (12.5)			31 (31.3)
Elasmopus pocillimanus	3 (0.3)		8 (0.5)	9 (0.7)	
Ericthonius brasiliensis				29 (2.4)	
Hemiaegina minuta	1 (0.1)				
Hyale periperi				19 (1.6)	
Lembos unicornis	1 (0.1)	10 (9.6)	21 (1.4)	4 (0.3)	22 (22.3)
Leucothoe spinicarpa		7 (6.7)			
Maera sp. A	114 (12.8)		53 (3.7)	146 (12.2)	
Maera sp. C	160 (18.0)	1 (1.0)	28 (1.9)	22 (19.1)	
Melita sp. A		3 (2.9)			2 (2.0)
Pontogeneia bartchi	2 (0.2)	11 (10.6)			
Unident. amphipod	3 (0.3)				
ISOPODA					
Bagatus stylodactylus	105 (11.8)	9 (8.7)	416 (28.6)	191 (16.0)	
Cirolana parva	2 (0.2)		7 (0.5)	1 (0.1)	
Gnathia puertoricensis			1 (0.1)	1 (0.1)	
Mesanthura decorata				1 (0.1)	
Paracerceis caudata	3 (0.3)			21 (1.7)	
DECAPODA					
Alpheus sp.		7 (6.7)			1 (1.0)
Majidae	1 (0.1)				
Paguridae	5 (0.6)	1 (1.0)	4 (0.3)		
Palaemonetes sp.		2 (1.9)			
Periclimenes sp.		4 (3.8)			1 (1.0)
Xanthidae	1 (0.1)	3 (2.9)			2 (2.0)
Unident. crab juvenile			1 (0.1)		
MISCELLANEOUS					
Cumacea	2 (0.2)		5 (0.3)	8 (0.7)	
Harpacticoida	51 (5.7)		197 (13.5)	47 (3.9)	
Pycnogonida	2 (0.2)				
TOTAL N	891	104	1455	1196	99
TOTAL S	19	14	13	15	8
E.N.S.$_{(100)}$	9.1	12.8	8.1	10.1	7.0

sample, values for expected numbers of species drawn with sample sizes of 100 individuals (E.N.S.$_{100}$) were similar. Highest expected number of species was found on *Halodule wrightii* in April (12.8) and lowest E.N.S. was associated with *H. wrightii* in July (7.0). E.N.S. values for *P. capitatus* all ranged between 8.1 and 10.1, once again indicating that species richness was a function of numbers of individuals, not alga size.

To test for potential interspecific interactions among animals living on the capitula of *Penicillus capitatus,* Hurlbert's (1969) coefficient of interspecific association (C_8) was calculated for all pairwise combinations of the 5 most abundant taxa from the seagrass site (Table 5).

Positive values indicate that 2 species tend to co-occur. Most of the associations did not vary significantly from zero indicating no interactions; none of the associations were negative. Significant positive relations occurred between the 2 *Maera* species during both collections and between *Leptochelia forresti* and *L. dubia* in July.

Recolonization experiment

In less than 1.5 h, 6 crustacean species colonized defaunated *Penicillus capitatus* (Fig. 6), and species
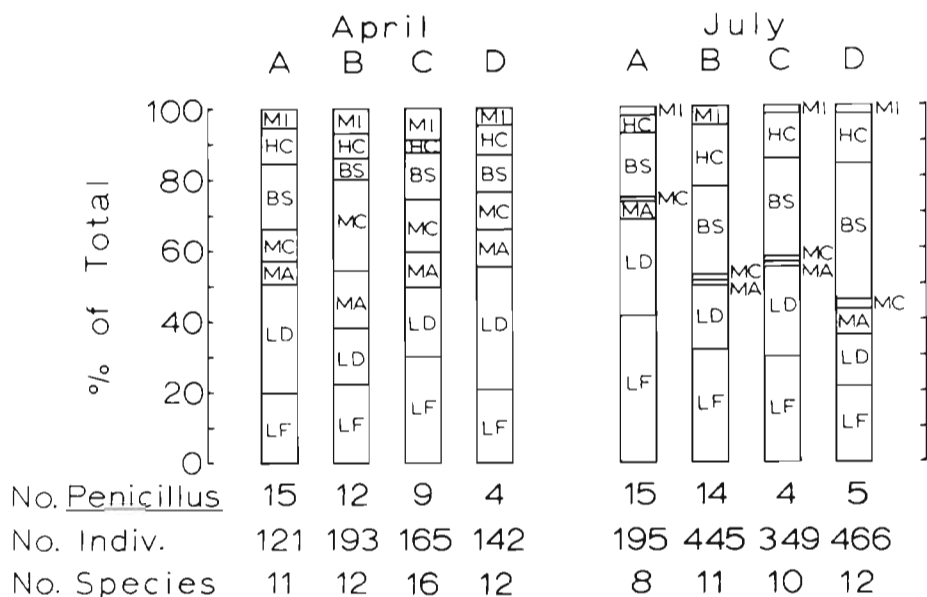
Fig. 4. Relative abundance of the most numerous taxa on *Penicillus capitatus* by alga size class. A = < 0.2 g dry wt, B = 0.2 to 0.5 g, C = 0.5 to 1.0 g, D = > 1.0 g. LF *Leptochelia forresti*; LD *Leptochelia dubia*; MA *Maera* sp. A; MC *Maera* sp. C; BS *Bagatus stylodactylus*; HC harpacticoid copepod; MI miscellaneous other taxa
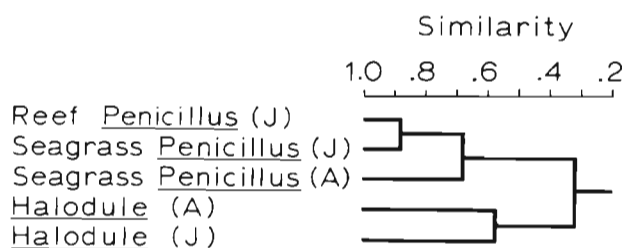

Fig. 5. Comparison of crustacean fauna associated with *Penicillus capitatus* and *Halodule wrightii* near Punta Ostiones. A = April collection; J = July collection. Dendogram: cluster analysis of faunal similarity using Czekanowski's index

accumulation increased slowly to the 3 d point when 10 species were collected in 6 samples. To compensate for variation in the size of individual *P. capitatus*, numbers of individuals collected were standardized to

Table 5. Coefficients of interspecific association (C$_8$) for the 5 most abundant species on seagrass-associated *Penicillus capitatus*

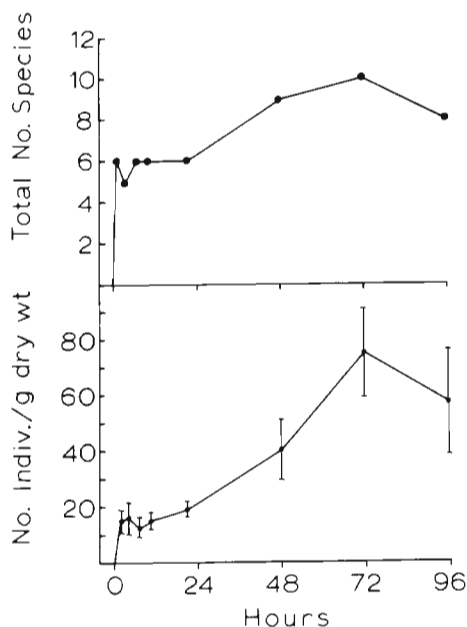| Species	pair		Apr	Jul
L. forresti	×	*L. dubia*	0.000	0.681 *
L. forresti	×	*Maera* sp. A	0.136	0.115
L. forresti	×	*Maera* sp. C	0.398 *	0.100
L. forresti	×	*B. stylodactylus*	0.033	0.000
L. dubia	×	*Maera* sp. A	0.000	0.125
L. dubia	×	*Maera* sp. C	0.140	0.100
L. dubia	×	*B. stylodactylus*	0.189	0.000
Maera sp. A	×	*Maera* sp. C	0.542 *	0.695 *
Maera sp. A	×	*B. stylodactylus*	0.000	0.000
Maera sp. C	×	*B. stylodactylus*	0.029	0.397

Significance: * p < 0.05

Fig. 6. Accumulation of crustacean species (top) and individuals (bottom) on defaunated *Penicillus capitatus* introduced into the field site near Punta Ostiones. Total number of species found on 6 *P. capitatus* shown. Abundance data standardized to number of individual per gram dry weight of *P. capitatus*, where means and standard errors are indicated for 6 samples each

numbers per g dry weight of *P. capitatus*. Abundance started at ca 15 ind. g^{-1} (or 41 ind. on 6 *P. capitatus*), but increased 4-fold by Day 3. A decline in animal abundance on Day 4 was coupled with a decline by 2 in species richness. Generally, variation in animal abundance on the alga increased with time. By Day 4 abundance of crustaceans on experimental alga

Fig. 7. Relative abundance of the most numerous taxa colonizing defaunated *Penicillus capitatus* as a function of time. Species codes same as in Fig. 4
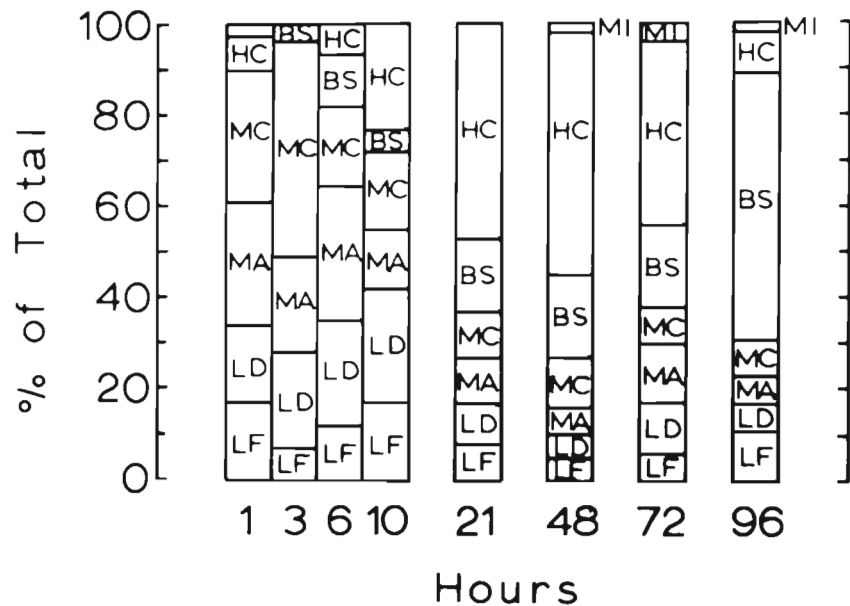
(58 g^{-1} dry wt) was similar to the abundance on unmanipulated *P. capitatus* (59.4 g^{-1} dry wt) (Table 3) and species richness for the 55 individuals collected (E.N.S.$_{100}$ = 8) was compatible with the E.N.S.$_{(100)}$ of 9.1 for unmanipulated *P. capitatus* assemblages.

Patterns of colonization by individual species (Fig. 7) showed that *Maera* and *Leptochelia* species colonized *Penicillus capitatus* very quickly in the daytime. By evening of the first day, harpacticoid copepods appeared along with the isopod *Bagatus stylodactylus*. At 24 h, the large harpacticoid had become the most abundant species; the rapid overnight increase in harpacticoids indicates nocturnal locomotory activity. After the first 24 h, *Leptochelia* and *Maera* populations remained relatively stable, but by Day 4, *B. stylodactylus* became the numerically dominant species.

Mean lengths of the 5 most abundant peracarid crustaceans collected on the manipulated *Penicillus capitatus* showed no significant variation over time indicating that colonization was not related to animal size.

DISCUSSION

The relation between numbers of species and island size has been of interest to biologists since first examined by Preston (1960, 1962) and Williams (1964). MacArthur & Wilson (1967) provided the theoretical framework upon which a multitude of species-area studies have followed in aquatic as well as terrestrial habitats (see review by Connor & McCoy 1978). In some cases, particularly in studies of terrestrial fauna on islands, increasing species richness with island size may be a function of increasing numbers of habitat

types; however, recent studies in the marine field, using smaller 'islands' such as macroalgae (Gunnill 1982b, 1983, Lewis 1982, Stoner & Greening 1984) and individual coral heads (Gotelli & Abele 1982), have indicated the significance of abundance of individuals as a proximate variable affecting species richness. Similarly, in this study, species-area effects on the tops of *Penicillus capitatus* were best explained by animal abundance patterns. Given the essentially identical structure of large and small *P. capitatus*, increasing species richness is independent of habitat heterogeneity and probably results from a simple random sampling effect.

Variation in the species composition of *Penicillus*-associated crustaceans may be related to chance events. Like the lottery system proposed by Sale (1978) for reef fishes, priority of arrival as recruits may determine which species hold space on the alga. Lack of negative interactions among even the congeneric species pairs suggest that a hierarchy of interspecific competition on *P. capitatus* is unlikely. However, changes in species composition over time on defaunated *P. capitatus* and reduced numbers of species with high animal densities in July suggest some non-random effects, such as (1) differential immigration and/or emigration rates; (2) displacement of certain taxa such as harpacticoid copepods; (3) certain positive associations such as those between the 2 *Maera* species and the 2 *Leptochelia* species; (4) differential susceptibility to predation.

First, the largest change in faunal composition occurred during the first night of the recolonization experiment suggesting that certain of the key species were nocturnal immigrants. Nocturnal locomotory

activity is well-known in seagrass-associated peracarids (Robertson & Howard 1978, Stoner 1980) and any differential dispersal characteristics could greatly influence the pattern of recruitment on *Penicillus capitatus*. Second, Nagle (1968) suggested that competitive interactions among peracarid species result in displacement of certain species from macroalgae. Replacement of harpacticoid copepods by the isopod *Bagatus stylodactylus* indicates that such interactions could take place on *P. capitatus*. Manipulative experiments would be most useful in testing for displacement. Third, positive associations and simultaneous recruitment patterns are most likely related to similar habitat or food requirements coupled with similar locomotory characteristics. Many peracarid species have similar food habits (Zimmerman et al. 1979) and requirements for shelter.

Large differences between crustacean assemblages associated with *Penicillus capitatus* and with *Halodule wrightii* are probably related to differential susceptibility to predation and associated habitat choices. Juvenile fishes, many of which consume large numbers of peracarids, are very abundant in seagrass beds (Adams 1976, Heck & Orth 1980, Stoner 1983, Livingston 1984). At the study site, these included small grunts, snappers, damselfishes, and mojarras. There seems little doubt that the extreme density of crustaceans on *P. capitatus* tops is a function of the protection offered to small crustaceans by the densely packed filaments of the alga and fine silt available for tube-building. Comparatively, the sparse blades of *H. wrightii* offer little refuge to peracarids. The islands of refuge would be particularly important in the backreef area where few other similar substrata occur; densities on *P. capitatus* were greatest in that area. Similar to the findings of this study, Lewis (1982, unpubl.), in the Gulf of Mexico, showed that surrounding seagrasses supported relatively few crustaceans compared to a variety of macroalgae including *Penicillus lamourouxii*.

Large differences in species composition between *Penicillus capitatus* and *Halodule wrightii* associates may also be a result of habitat choice. The larger crustaceans such as shrimps and crabs, absent from *P. capitatus*, undoubtedly receive little protection from predation on the alga and select alternative habitats. Although some peracarid species, such as the 2 *Leptochelia* species, were found in all habitats, many species appear to be habitat specialists. *Elasmopus pocillimanus*, *Erichthonius brasiliensis*, *Hyale periperi*, *Maera* sp. A, *Maera* sp. C (except 1 individual), *Cirolana parva*, *Paracerceis caudata*, cumaceans and the large harpacticoid copepod were all abundant and collected exclusively on *P. capitatus*. *Leucothoe spinicarpa* and *Melita* sp. A were collected only on *H.*

wrightii. Given the similar sizes and general behavioral characteristics of the taxa it would seem likely that habitat associations are a function of habitat choice, perhaps ultimately related to the effects of predation.

The present study shows that species-area effects may be an artifact of the number of individuals inhabiting an island habitat. Early colonization is probably stochastic, with the best dispersers arriving first. Colonization patterns, however, suggest that the effects of density-dependent phenomena increase with time, and that the species are not distributed independently. *Penicillus* species, because of their abundance in shallow-water habitats, their unique morphology, and small, island-like characteristics, provide an unusual model system for new experimental research on congeneric use of space, and patterns of immigration, emigration, and species richness.

LITERATURE CITED

Abele, L. G. (1984). Biogeography, colonization and experimental structure of coral-associated crustaceans. In: Strong, D. R., Simberloff, D. S., Abele, L. G., Thistle, A. B. (ed.) Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, Princeton, N. J., p. 123–137

Abele, L. G., Patton, W. K. (1976). The size of coral heads and the community biology of associated decapod crustaceans. J. Biogeogr. 3: 35–47

Adams, S. M. (1976). The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. J. exp. mar. Biol. Ecol. 22: 269–291

Connor, E. F., McCoy, E. D. (1978). The statistics and biology of the species-area relationship. Am. Nat. 113: 791–833

Friedman, E. I., Roth, W. C. (1977). Development of the siphonous green alga *Penicillus* and the *Espera* state. J. Linn. Soc. 74: 189–214

Gotelli, N. J., Abele, L. G. (1982). Community patterns of coral-associated decapods. Mar. Ecol. Prog. Ser 13: 131–139

Gunnill, F. C. (1982a). Macroalgae as habitat patch islands for *Sentillidium lamellipes* (Copepoda: Harpacticoida) and *Ampithoe tea* (Amphipoda: Gammaridae). Mar. Biol. 69: 106–116

Gunnill, F. C. (1982b). Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetia fastigiata*. Mar Biol. 69: 263–280

Gunnill, F. C. (1983). Seasonal variations in the invertebrate faunas of *Pelvetia fastigiata* (Fucaceae): Effects of plant size and distribution. Mar Biol. 73: 115–130

Heck, K. L., Jr., Orth, R. J. (1980). Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy, V S. (ed.) Estuarine perspectives. Academic Press, New York, p. 449–464

Heck, K. L., Belle, G. van, Simberloff, D. S. (1975). Explicit calculation on the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1159–2261

Hurlbert, S. H. (1969). A coefficient of interspecific association. Ecology 50: 1–9

Lewis, F. G., III. (1982). Habitat complexity in a subtropical seagrass meadow: the effects of macrophytes on species composition and abundance in benthic crustacean assemblages. Ph. D. Dissertation, Florida State Univ., Tallahassee

Livingston, R. J. (1984). Trophic response of fishes to habitat variability in coastal seagrass systems. Ecology 65: 1258–1275

MacArthur, R. H., Wilson, E. O. (1967). The theory of island biogeography. Princeton Univ. Press., Princeton, N. J.

Nagle, J. S. (1968). Distribution of the epibiota of macrobenthic plants. Publs. Inst. mar. Sci. Univ. Tex. 13: 105–144

Preston, F. W. (1960). Time and space and the variation of species. Ecology 41: 611–627

Preston, F. W. (1962). The canonical distribution of commonness and rarity. Ecology 43: 185–215, 410–432

Robertson, A. I., Howard, R. K. (1978). Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. Mar. Biol. 48: 207–213

Sale, P. F. (1978). Coexistence of coral reef fishes – a lottery for living space. Environ. Biol. Fish. 3: 85–102

Simberloff, D. (1978). Use of rarefaction and related methods in ecology. In: Dickson, K. L., Cairns, J., Jr., Livingston, R. J. (ed.) Biological data in water pollution assessments: quantitative and statistical analyses. American Society for Testing Materials, ASTM STP 652, p. 150–165

Stoner, A. W. (1980). Perception and choice of substratum by epifaunal amphipods associated with seagrasses. Mar. Ecol. Prog. Ser. 3: 105–111

Stoner, A. W (1983). Distribution of fishes in seagrass meadows: role of macrophyte biomass and species composition. Fish. Bull. U. S. 81: 837–846

Stoner, A. W., Greening, H. S. (1984). Geographic variation in the macrofaunal associates of pelagic *Sargassum* and some biogeographic implications. Mar. Ecol. Prog. Ser. 20: 185–192

Taylor, W. R. (1960). Marine algae of the eastern tropical and subtropical coasts of the Americas. Univ. Michigan Press, Ann Arbor

Williams, C. B. (1964). Patterns of the balance of nature and related problems in quantitative ecology. Academic Press, New York

Zimmerman, R. J., Gibson, R., Harrington, J. (1979). Herbivory and detrivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. 54: 41–47