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COMMUNITY COMPOSITION, STRUCTURE, AREAL AND TROPHIC RELATIONSHIPS OF DECAPODS ASSOCIATED WITH SHALLOW- AND DEEP-WATER *OCULINA VARICOSA* CORAL REEFS:

STUDIES ON DECAPOD CRUSTACEA FROM THE INDIAN RIVER REGION OF FLORIDA, XXIV

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COMMUNITY COMPOSITION, STRUCTURE, AREAL AND TROPHIC RELATIONSHIPS OF DECAPODS ASSOCIATED WITH SHALLOW- AND DEEP-WATER *OCULINA VARICOSA* CORAL REEFS:

STUDIES ON DECAPOD CRUSTACEA FROM THE INDIAN RIVER REGION OF FLORIDA, XXIV

John K. Reed, Robert H. Gore, Liberta E. Scotto, and Kim A. Wilson

ABSTRACT

Decapod crustaceans associated with living colonies of the scleractinian coral *Oculina varicosa* were sampled quantitatively for 1 year at 4 reef stations encompassing depths of 6, 27, 42, and 80 m off the central eastern Florida coast. A total of 42 samples of individual colonies yielded over 2,300 decapods in 15 families, 35 genera and 50 species, and was species-rich in xanthid and majid crabs (10, 6 spp., respectively), and alpheid shrimp (9 spp.). The community was predominantly anomuran with two species of hermit crabs (*Pagurus carolinensis, P. piercei*), a porcellanid crab (*Megalobrachium soriatum*) and a galatheid crab (*Galathea rostrata*) comprising four of the six most abundant species which accounted for 70% of all collected individuals.

Similarity between stations was low (8%) with only four species present at all stations. A gradient of species assemblages from shallow to deep stations corresponded with a similar gradient in environmental factors, with mean temperatures of 24.6, 18.4, and 16.2°C recorded at 6, 42, and 80 m, respectively. These temperatures and periodic cold-water summer upwelling affected species composition, with several species being lost at 6 m and never occurring at deeper stations. Wave surge and sedimentation, greatest at 6 m, affected trophic partitioning, with a filter feeder (*M. soriatum*) numerically dominant here, whereas a detritivore (*P. carolinensis*) dominated deeper, less disturbed stations. The biotope also differed topographically among stations. At 6 m *Oculina* grew as thick-branched, wave-resistant colonies with encrusting bases and were widely scattered among a cover of algae and sponges on limestone ledges. At 80 m massive coral thickets formed banks composed solely of *O. varicosa*. Greater heterogeneity of the habitat surrounding the 6-m corals may be one reason this station had the highest species numbers (30) and species distribution (32% occurred nowhere but here).

Analyses of the effects of coral age on numbers of decapod species (S) and individuals (N) showed no significant correlation, whereas 48.8% of the variance in S and 42.9% in N were related to the percentage of dead dry weight of the coral colony ($r = .709$, $P < .001$; $r = .667$, $P < .001$, respectively). Mean densities of individuals decreased with depth (44.4–7.5 N/100 g dead coral wt) and densities of most dominant species were positively correlated with size of the dead, rather than the live portion of the coral. Densities of the obligate commensals *Domecia acanthophora* and *Troglocarcinus corallicola*, however, were independent of coral size.

Oculina varicosa Lesueur, 1820, is a branching scleractinian coral found from the shallow subtidal region to depths of 152 m from the West Indies northward to North Carolina and Bermuda. Along the central eastern Florida coast the species occurs either in semi-isolated, low-growing colonies patchily distributed on shallow (2–40 m) coquinoid limestone reefs, or in larger, massive, coalescing aggregates of substantial topographical relief and complexity in deeper waters (70–100 m; Reed, 1980). Coincident to either growth form occur various fish and invertebrate assemblages (Avent et al., 1977), some of which appear to be facultative, and others which may be obligate associates of the coralline biotope.

Few studies have quantitatively analyzed the invertebrate fauna associated with any scleractinian coral. McCloskey (1970) studied *Oculina arbuscula* Verrill in shallow water (5–18 m) off North Carolina and reported that the associated fauna formed a community that was structured in terms of individuals and species in predictable, repeatable and recurring populations. Most other studies on coral-associated fauna have dealt primarily with single groups of organisms such as barnacles (Ross and Newman, 1973), polychaete worms (Peyrot-Clausade, 1974; Hutchings, 1974; Vittor and Johnson, 1977), and fishes (Sale and Dybdahl, 1975; Smith and Tyler, 1975).

Decapod crustaceans often form numerically important and speciose assemblages with scleractinian corals. Several studies have considered the decapod crustaceans living symbiotically with Pacific corals (Hiro, 1937; Garth, 1964; 1974; Patton, 1966; 1974; Knudsen, 1967; Castro, 1976; McCain and Coles, 1979; Takeda and Tamura, 1979). Other studies made by Shaw and Hopkins (1977) investigated commensals of Atlantic corals, and Abele (1976a; 1979) examined the effects of environmental variables on coral-associated decapod populations. Abele and Patton (1976) correlated living coral colony size with numbers of individuals and species of associated decapods. Austin et al. (1980) examined total infauna with coral size, and Coles (1980) compared the effects of both living and dead coral colonies on community structure of decapods.

Several studies determined that mucus produced by corals may be an important food source for associated animals (Hiro, 1937; Utinomi, 1944; Knudsen, 1967; Coles and Strathmann, 1973; Benson and Muscatine, 1974; Richman et al., 1975; Ducklow and Mitchell, 1979). Moreover, the coral polyps themselves are fed upon by various animals including molluscs, echinoderms, polychaete worms, crustaceans (including decapods), and fishes (Robertson, 1970; Ott and Lewis, 1972; Glynn et al., 1972; Sammarco et al., 1974). As a consequence some decapods exhibit mutualistic behavior with corals by defending the coral from predators; e.g., *Trapezia* and *Alpheus* can repulse attacks by the asteroid *Acanthaster* (Glynn, 1976).

It is apparent that the coralline biotope not only offers refuge from predation for the associated epibionts, but also may provide both a place to feed and be a source of food. Thus, the associated decapod crustaceans might provide additional evidence for a hypothesis advanced by Abele (1974; 1976b) which suggested that substrata are important in determining species composition within various habitats, and that marine decapods can use such substrata as shelter, feeding sites, and source of nutrition (Gore et al., 1978).

This paper provides an analysis of the decapod crustacean community associated with the *Oculina varicosa* biotope occurring from depths of 6 m to 80 m on the eastern Floridian continental shelf. We examine species dominance, density, faunal similarity, species richness, numerical distribution and community seasonality within and among the sampled areas. We also discuss the effects of habitat age, coral colony size and the percentage of living and dead coral in a colony on decapod crustacean community structure.

METHODS AND MATERIALS

Four permanent reef stations were established at depths of 6, 27, 42, and 80 m (Fig. 1). SCUBA was employed on the 6-m reef, whereas the three deeper stations were marked with pressure resistant floats, sonar targets, and 37 kHz pingers, and were sampled utilizing lockout diver-scientists from the research submersibles JOHNSON-SEA-LINK I and II. Current meters and thermographs continuously monitored the environment at the 6-, 42-, and 80-m stations. Temperatures were also periodically measured with mercury thermometers. Salinities at all stations were determined using a refractometer

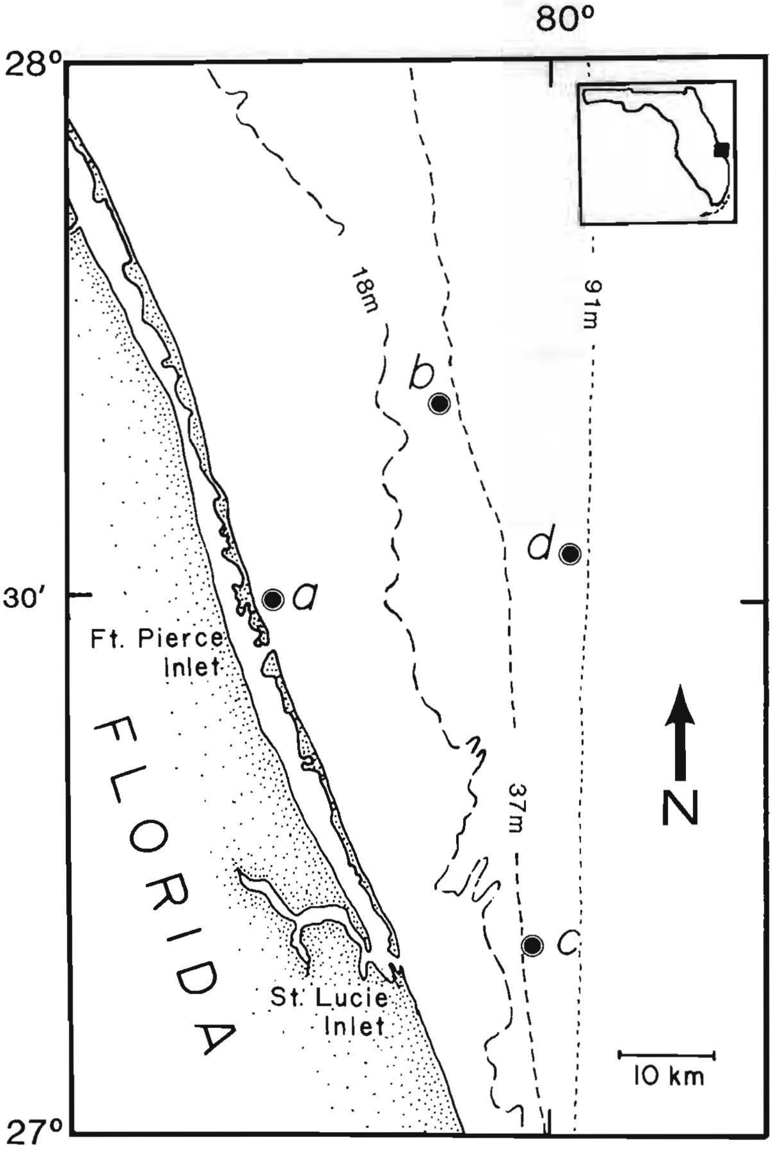

Figure 1. Map of the Indian River region of central eastern Florida with dots indicating reef stations for collections of *Oculina varicosa* coral with associated decapod crustaceans. Station a = 6 m, b = 27 m, c = 42 m, d = 80 m.

or a salinometer. Sedimentation samples were collected only at the 6- and 80-m stations, using sediment traps consisting of three 1-gal jugs with 3.95-cm diameter apertures.

Two to four colonies of *Oculina varicosa* were collected at the 6-, 42-, and 80-m stations every 2–3 months from September 1976 through September 1977. Because of logistical problems only two collections were made at the 27-m site. A 0.5-mm mesh Nytex bag was placed over each coral colony which was then broken at its base from the substrata with a hammer and chisel. All the mobile, attached, and rock-boring fauna associated with each colony were captured. The bag and its contents were immersed in 0.15% propylene phenoxytol (a relaxant) for 60–90 min and then transferred to 70% ethanol until the associated fauna could be sorted.

In the lab each colony was photographed, wet weight determined, and the height, maximum diameter and diameter at right angles to maximum diameter were measured. Total volume displacement was determined by placing the colony in a plastic bag that was drawn tight and sealed over the colony and then submerged it in water. Available living space was calculated by subtracting the volume of water displaced by the corallum from the total volume displacement. Outer colony surface area was calculated by tightly wrapping the corallum in aluminum foil, then removing, weighing, and converting it to an area measurement based on a previously determined mean foil weight of 0.291 g/64.5 cm^2. Branch surface area was estimated by indiscriminately selecting by eye 8–10 branch segments and removing them from the colony. These were weighed, their area calculated based on the area of a cylinder, and by extrapolating from these values, the total colony branch area was determined by linear regression. Age of selected samples was determined by counting the annual growth rings present in a cross section of the largest diameter branch in any given colony. Finally, coral colonies were broken into pieces separating the live and dead fractions. The percent alive or dead of each coral was determined from dry weights of each fraction. The colonies were washed twice with water, before and after fragmentation, and the fauna retained by a 0.5-mm mesh screen was sorted and enumerated.

Statistical Analyses

Decapod species were ranked by relative abundance and percent occurrence. Sanders' (1960) index of affinity was used to assess the degree of faunal similarity between and within stations. For each pair of samples an index value was derived by summing the smaller percentage compositions for each species present in both samples. Thus, a within station value was derived by averaging the values of all pairs of samples at that station. Similarly, a mean index value for each station pair was derived by averaging the values of all pairs of samples between the stations. Dominance (D_1) was determined by calculating the percent of the total number of individuals for the most abundant species. D_2 is the percent of the total number for the sum of the first and second most abundant species and is equivalent to "DI" utilized by McNaughton (1967).

Similarity of samples within and between stations over the year, and similarity of species between stations, was further analyzed by reciprocal averaging (Hill, 1973), an ordination technique.[1] This statistic shows natural groupings of species and stations that may result from environmental gradients. The actual scores are relative; for example, in a floristic gradient a score of 0 could indicate a "dry" species whereas 100 a "wet" species, and the site score could indicate degree of wetness or some combination of environmental factors.

To determine the effects of coral colony size and structure on numbers of species (S) and individuals (N), regression coefficients were calculated for various colony parameters on samples at the 6-, 42-, and 80-m stations.[1] Total colony volume (height × width × length in cm^3), skeletal displacement volume (ml), available living space (ml), outer surface area (cm^2), total branch surface area (cm^2), dry weight (g), the portion of a colony both living and dead in relation to each of the above factors, as well as the colony age, were all considered as independent variables. The effects of various coral size and structural parameters and age on S and N was calculated by stepwise regression and F-test (significance at $P < .05$). The relationship of S and N with temperature was analyzed by regression correlation and Student's t-test (significance at $P < .05$).

Description of Study Sites

Populations of *Oculina varicosa* occur in densities up to 288 colonies/100 m^2 off central eastern Florida on nearshore coquinoid limestone ledges (4–7-m depth), paralleling the coast. *Oculina* grows on these ledges as low (up to 15 cm in height), compact, wave-resistant colonies with encrusting bases (Fig. 2A). The forereef of this ledge system, approximately 0.6 km off the coast at Ft. Pierce, was selected as the 6-m station. The larger colonies near the forereef are widely interspersed among a plant and animal cover consisting of the algae *Eucheuma isiforme* (C. Agardh) J. Agardh, 1847, *Solieria tenera* (J. Agardh) Wynne and Taylor, 1973, and *Vaucheria* sp.; the keratose sponges *Ircinia campana* (Lamarck, 1813) and *I. strobilina* (Lamarck, 1816); the scleractinian corals *Phyllangia americana* Milne-Edwards and Haime, 1849 and *Siderastria radians* (Pallas, 1766); and the octocorallians *Lophogorgia hebes* (Verrill, 1869) and *Leptogorgia virgulata* (Lamarck, 1815).

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[1] Reciprocal averaging is computationally an eigenanalysis problem and is similar to weighted averages except that both species and sample scores are ordinated simultaneously by a direct iteration algorithm. The ordination or grouping of stations achieved by this technique is very similar to what would have been obtained from principal components analysis; however, the species ordination is more meaningful with reciprocal averaging because species scores are corrected for species abundance.

The Cornell Ecology Programs (Cornell Univ., 1975) and Biomedical Computer Programs (Univ. Calif., 1977) were used with the PDP-11/34 computer (Digital Equip. Co.) for the reciprocal averaging and regression analyses, respectively.

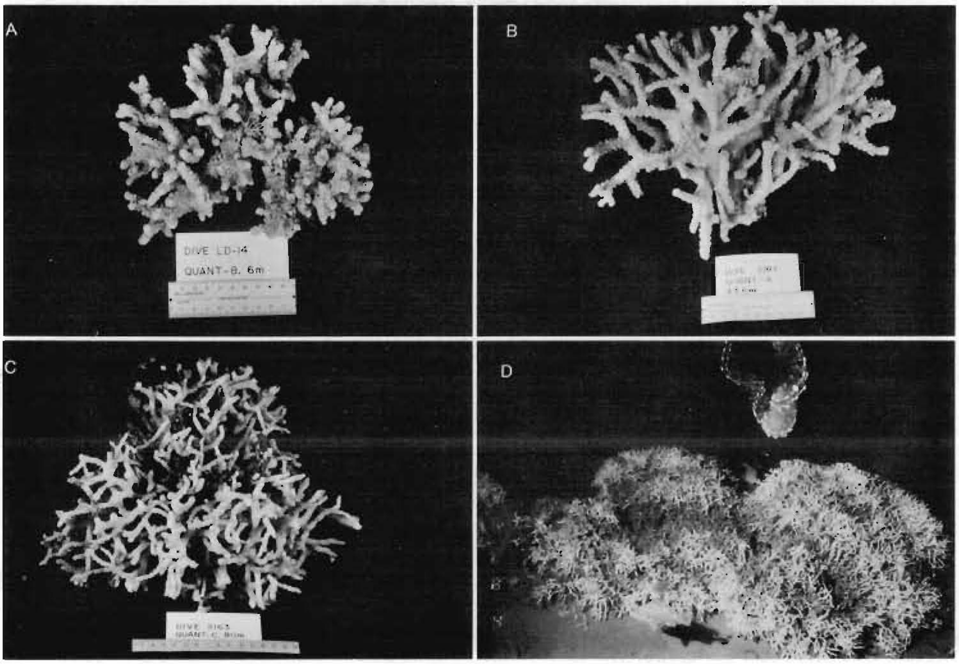


Figure 2. Colonies of *Oculina varicosa*: (A) specimen from 6-m station; (B) specimen from 42-m station; (C) specimen from 80-m station; (D) south slope of the 80-m reef.

Near Bethel Shoal (27-m depth) another ledge system with up to 5-m relief occurs and supports a very small population of *O. varicosa*. These colonies, usually less than 10 cm high, are less compact than the nearshore form. Dominant floral and faunal cover is similar to the 6-m site.

Seven miles east of St. Lucie Inlet (42–44 m depth) numerous patch reefs consisting almost entirely of *O. varicosa* occur on 0.5-m high knolls of sand-covered limestone. On these reefs *Oculina* grows as discrete, spherical colonies (up to 25 cm in height) with widely spaced, thick branches (Fig. 2B), forming dense populations with colonies separated from each other by distances of a meter or less. Plant cover consists primarily of sparsely scattered red algae in the families Rhodymeniaceae and Delesseriaceae.

Paralleling the continental shelf-slope break (70–100 m) from Palm Beach, Florida, to North Carolina is a relict ridge system of discontinuous prominences with 10–25-m relief, composed of algal, oolitic, and coquinoid limestone (Macintyre and Milliman, 1970; Avent et al., 1977). Seventeen miles east of Ft. Pierce this system forms an isolated series of three E-W oriented ridges covered with living *O. varicosa* (Reed, 1980). This reef, locally termed Jeff's Reef, occurs to a maximum depth of 80.8 m and is approximately 1,000 m in circumference at the base, with a relief of 16.8 m. The slopes and top are covered with contiguous, massive thickets of *Oculina* reaching 1–2 m in height (Fig. 2C, D). The fourth station in our study was located at the base of the northeast edge of this reef where scattered colonies up to 1 m in diameter lie unattached on a matrix of green mud and coral debris. At 80 m, because of reduced light levels, *Oculina* is white in color and lacks zooxanthellae. At the other stations *Oculina* is usually various shades of brown from the presence of this dinoflagellate symbiont.

Physical Parameters

Physical parameters at the four stations showed substantial variability (Table 1). Few data are available for the 27-m station, but it appeared to be similar to the deeper stations in physical characteristics. Salinity at 6 m usually ranged between 32 and 36‰ but values as low as 28.17‰ were recorded. Salinity at the 27-, 42- and 80-m sites was relatively more constant and ranged from 35.74 to 36.35‰.

Table 1. Physical parameters measured between 1976 and 1979 at 6-, 42-, and 80-m *Oculina varicosa* coral reef stations. Range (mean and ± 1 standard deviation)

Parameters	6 m	42 m	80 m
Salinity (‰)	28.2–36.4 (32.5 ± 3.4)	35.9–36.2 (only 2 values)	35.7–36.4 (36.0 ± 0.2)
Temperature (°C)	13.7–31.0 (24.6 ± 3.1)	8.0–27.8 (18.4 ± 2.7)	7.4–26.7 (16.2 ± 3.7)
Current (cm/sec)	0–70.5 (8.9 ± 2.1)	0–49.5 (8.7 ± 2.4)	0–58.5 (8.6 ± 1.7)
Visibility (m)	0–9 (3 ± 2)	0–21 (9 ± 5)	0–25 (9 ± 5)
Sedimentation (mg/cm²/day)	137–1,640 (846 ± 593)	No data available	15–78 (53 ± 34)

Between 1976 and 1979 bottom temperatures ranged from a high of 31.0°C at the 6-m station to a low of 7.4°C at 80 m. Temperatures became cooler as depth increased, with mean annual temperatures of 24.6, 18.4, and 16.2°C at the 6-, 42- and 80-m stations, respectively. At the 6-m site mean highest temperature occurred in August–September and lowest in January–February. However, at the 42- and 80-m stations the lowest mean temperature occurred during July–August while October–November had the highest. This anomaly is explained by the fact that the deeper stations are influenced both by cooler deep-water masses and the western edge of the Florida Current which often meanders over them. The summer low temperatures are caused by upwelling which occurs annually off the central eastern coast of Florida (Taylor and Stewart, 1958; Smith, 1981). Although the upwelling may impinge on all stations producing a 4–8°C drop in temperature, the greatest changes occurred at the 42- and 80-m stations where fluctuations of 13.4°C within 48 h were recorded.

Mean current velocity was similar at all stations, ranging from 8.6 to 8.9 cm/sec (Table 1). Maximum velocities (up to 70.5 cm/sec) occurred at the inshore 6-m station, which is also influenced by strong wave surge and 2- to 3-m swells from strong northeast winds in the winter. This wave surge causes reduced visibility and high turbidity (primarily from resuspended sediments) at the 6-m site (Table 1). In the summer when sea conditions are calm, 29.8% of available light is transmitted to the bottom at 6 m, whereas in the winter only 4.2% or less is transmitted. Sedimentation rates are over 10 times greater at the 6-m site than at 80 m. Although wave surge is not an appreciable factor at the deeper sites, personal observation (J.K.R.) has shown that highly turbid, bottom nepheloid layers occasionally occur, especially in the winter.

RESULTS

Community Structure

The 42 samples of *Oculina* coral from the 4 sites yielded over 2,300 specimens of decapod crustaceans in 15 families, 35 genera, and 50 species. These represented 92% of individuals sufficiently mature or undamaged to be identified to species. Figure 3 shows that by the end of the first month of sampling over 50% of all species (S) were obtained, and that by June of the following year over 90% of all S had been collected. The approach to asymptoticity of the cumulative-percent species curve indicates that only one or two species were being added with additional sampling, so that the community was essentially sampled completely by August. The decapod fauna of the *Oculina* biotope was species-rich in xanthid (7 genera, 10 species) and majid crabs (5 genera, 6 species), and alpheid shrimp (3 genera, 9 species). However, the individual stations differed, often substantially, in faunal dominants from that seen within the biotope as a whole (Table 2).

A dominance-diversity plot of data from the 42 samples (Fig. 4) showed that the decapod community within the *Oculina* biotope may be characterized as being predominantly anomuran with two hermit crab species, a porcellanid crab, and a galatheid crab comprising four of the six most abundant species. An alpheid shrimp and a xanthid crab were also among the most abundant species when all stations were considered. These six species accounted for 70% of all collected individuals. The next 15 (common) species made up 20% whereas the 29 rare

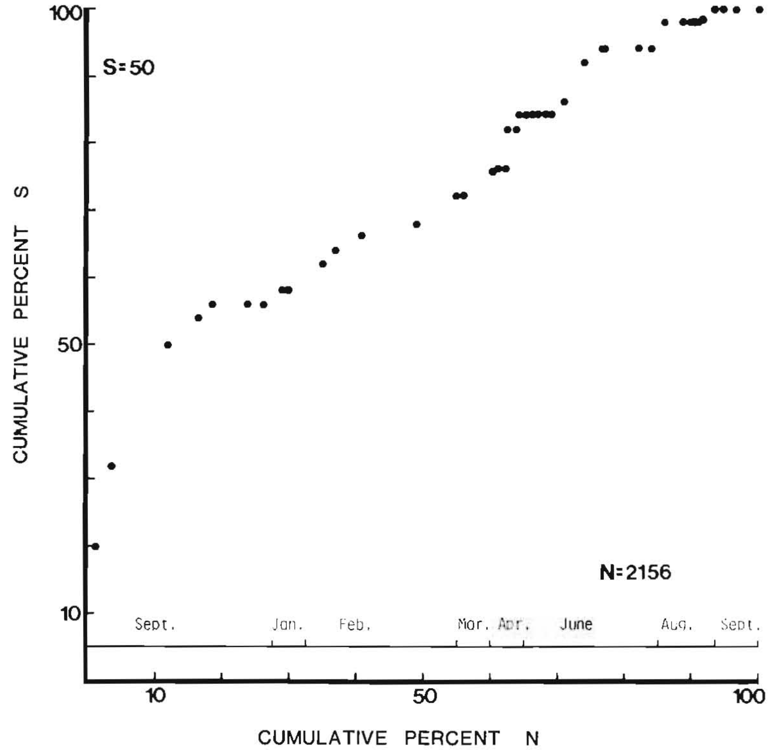


Figure 3. Cumulative percent of number of decapod crustacean species (S) versus cumulative percent of number of individuals (N) collected at all stations from September 1976 to September 1977.

species comprised less than 10% of all collected crustaceans. We arbitrarily designated species of 100 or more individuals as abundant, 10 or more as common, and the remainder as rare. Thus, while xanthid and majid crabs, and alpheid shrimp were important within the biotope in terms of species richness, the anomuran crustaceans exhibited numerical dominance, and perhaps are a better indicator of the overall decapod community structure.

A comparison of the species rankings based on percent occurrence in coral samples within the overall biotope (Fig. 5) and that based on numbers of individuals (N, compare Fig. 4), shows the top 10 species are similar although slightly different in rank. For example, the most abundant species by N was the hermit crab *Pagurus carolinensis* whereas the species that occurred on the majority of coral samples was a porcellanid crab *Megalobrachium soriatum*. Similar variability was seen in the other abundant and common species when ranked according to N as compared to occurrence. The percent occurrence of these same species also showed substantial between-station variation (Fig. 6) with the only similarity being that at any station, two to five species occupied 80% or more of all the samples collected. These results suggested a patchy distribution of dominant species throughout the biotope (i.e., between stations). In fact, a coefficient of dispersion (variance/mean) was calculated for each dominant species, and values ranged from 5.4 to 45.8 which indicates that all have clumped distributions within the *Oculina* biotope.

Table 2. Decapod crustacean community composition and total number of individuals per species on east Floridan *Oculina* coral reefs

	6 m	27 m	42 m	80 m
Families	11	9	10	10
Genera	21	13	13	20
Species	30	14	16	24
Endemic Species	16	1	3	9
Mean Species	7.9	6.8	5.9	10.9
Mean Individuals	39.8	18.5	47.0	87.6
Mean Coral Size (g)	521.8	131.4	1,193.5	1,613.6
Percent Dead Coral	23.3	18.3	21.9	69.9
Number Samples	15	4	13	10
Dominance (D_1)	40	32	72	18
Dominance (D_2)	55	45	79	34
Species				
1. *Pagurus carolinensis*	6	24	439	160
2. *Megalobrachium soriatum*	238	9	41	22
3. *Pagurus piercei*	0	0	37	142
4. *Synalpheus townsendi*	1	8	31	112
5. *Galathea rostrata*	0	1	5	142
6. *Micropanope scuptipes*	1	1	0	137
7. *Pachycheles monilifer*	89	0	0	2
8. *Mithrax forceps*	81	8	0	0
9. *Thor manningi*	49	3	0	29
10. *Pseudomedaeus distinctus*	0	0	11	33
11. *Synalpheus fritzmuelleri*	30	0	0	0
12. *Pseudomedaeus agassizii*	0	0	10	19
13. *Nematopaguroides pusillus*	0	0	0	29
14. *Periclimenes iridescens*	2	1	25	0
15. *Synalpheus minus*	19	0	0	0
16. *Micropanope barbadensis*	0	0	0	17
17. *Synalpheus* cf. *townsendi*	15	0	1	0
18. *Pelia mutica*	4	9	1	1
19. *Euchirograpsus americanus*	1	0	0	10
20. *Stenorhynchus seticornis*	0	3	3	5
21. *Pilumnus dasypodus*	10	0	0	0
22. *Petrolisthes galathinus*	9	0	0	0
23. *Periclimenes rathbunae*	8	0	0	0
24. *Troglocarcinus corallicola*	6	0	1	0
25. *Periclimenaeus atlanticus*	6	0	0	0
26. *Domecia acanthophora*	5	0	0	0
27. *Micropanope nuttingi*	0	3	0	2
28. *Mithrax acuticornis*	0	0	1	3
29. *Paguristes tortugae*	2	2	0	0
30. *Nanoplax xanthiformis*	0	0	0	4
31. *Lobopilumnus agassizii*	2	1	0	0
32. *Synalpheus* cf. *fritzmuelleri*	3	0	0	0
33. *Alpheus cristulifrons*	2	0	0	0
34. *Gonodactylus bredini*	2	0	0	0
35. *Scyllarus depressus*	0	0	2	0
36. *Pinnixa retinens*	0	0	2	0
37. *Parapinnixa hendersoni*	0	0	0	2
38. *Porcellana sigsbeiana*	1	0	0	0
39. *Periclimenes americanus*	1	0	0	0
40. *Epialtus* sp.	1	0	0	0
41. *Alpheus formosus*	1	0	0	0
42. *Eucratopsis crassimanus*	1	0	0	0
43. *Thor dobkini*	1	0	0	0
44. *Paractaea rufopunctata nodosa*	0	1	0	0
45. *Stenocionops furcata*	0	0	1	0

Table 2. Continued

	6 m	27 m	42 m	80 m
46. *Periclimenes longicaudatus*	0	0	0	1
47. *Solenopagurus lineatus*	0	0	0	1
48. *Automate evermanni*	0	0	0	1
49. *Alpheus* cf. *amblyonyx*	0	0	0	1
50. *Pinnotheres* sp.	0	0	0	1

At the 6-m station diversity was relatively high and a total of 597 individuals (N) in 22 genera and 30 species (S) were identified from 15 coral samples. Of these, 4 species were abundant, 9 common and 17 rare. Also 16 of the 17 rare species (32% of the total community of 50 species) were "endemic" to this station, i.e., occurring here and nowhere else in this study. The high number of species solely associated with this station consisted mostly of the caridean shrimp families Alpheidae (S = 5) and Palaemonidae (S = 3). Also included at this station were the only representatives of the brachyuran crab family Goneplacidae and the stomatopod family Gonodactylidae. Twelve of the 15 families occurring

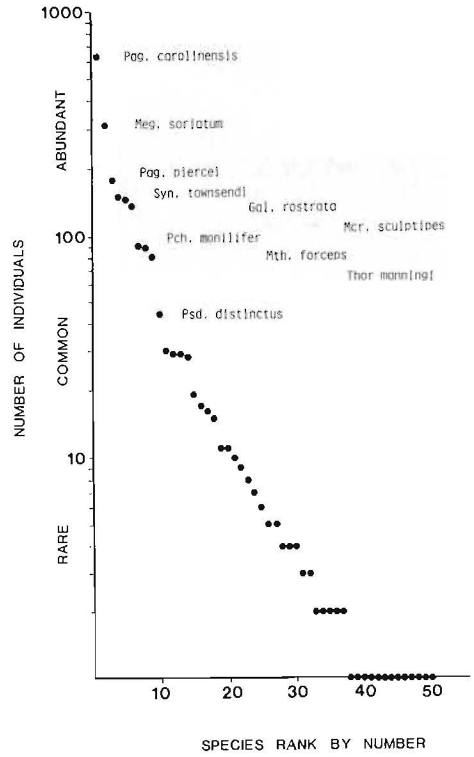


Figure 4. (Left) Dominance-diversity plot of decapod crustacean species ranked by numerical abundance for all stations.

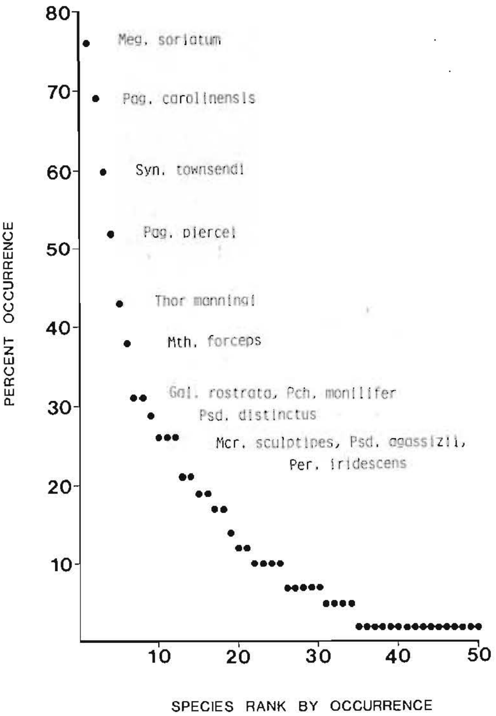


Figure 5. (Right) Decapod crustacean species ranked by percent occurrence in 42 *Oculina* coral samples for all stations.

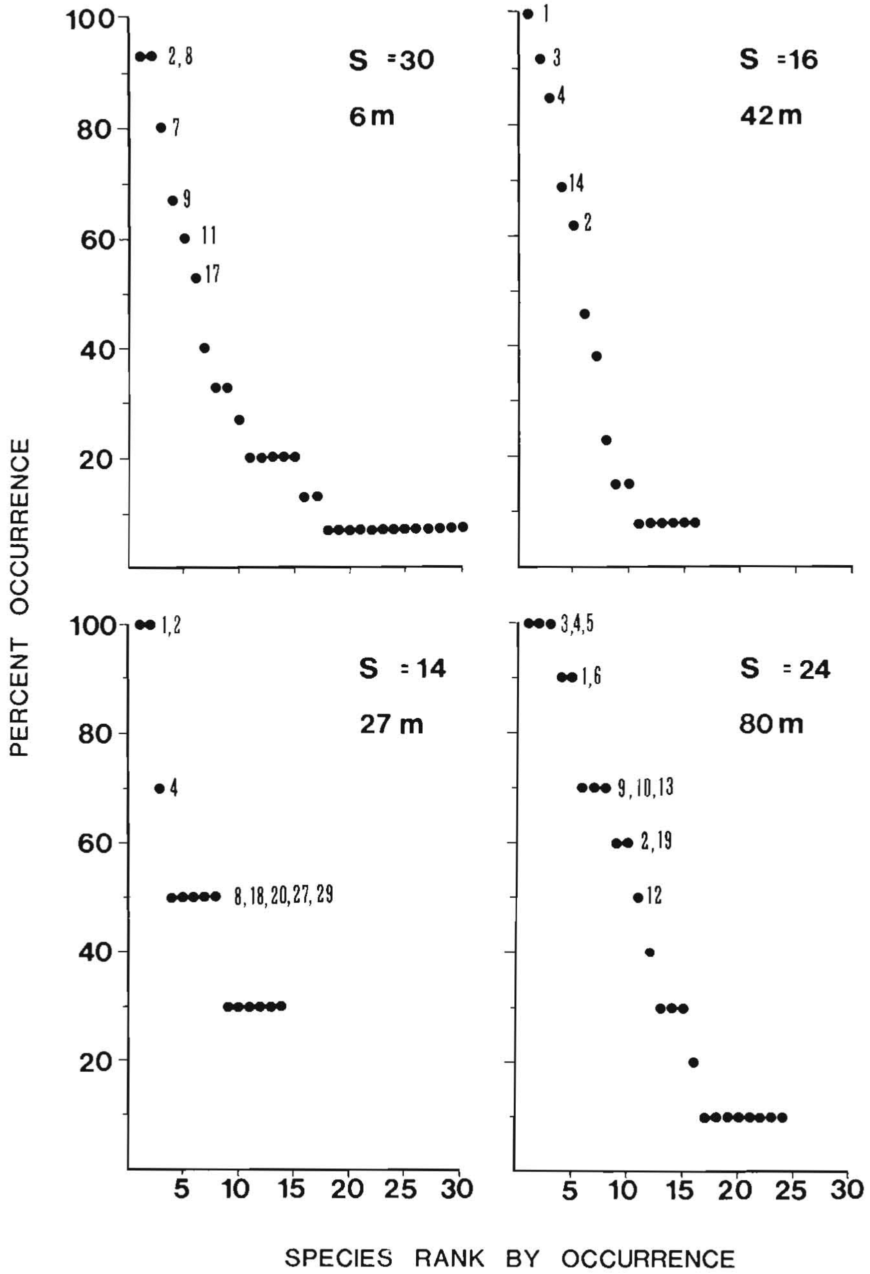


Figure 6. Decapod crustacean species ranked by percent occurrence in *Oculina* coral samples for each station. Numbers by dots indicate species rank by numerical abundance (see Table 2).

throughout the biotope had representative species at this station, the highest of all the stations in our survey.

At the 27-m station, 74 N in 13 genera and 14 S representing 9 families were identified from 4 coral samples. Five species were classified as abundant, five common and four rare. Only one species (2% of the total community) occurred solely at this station. The diversity of the crustacean fauna is somewhat surprising in view of the low number of samples taken.

At the 42-m station, 611 N in 13 genera and 16 S were identified from 13 coral samples. These included five abundant, six common and five rare species. This station had the greatest species dominance (D_1 = 72, D_2 = 79) owing to large populations of *Pagurus carolinensis*. Only three species (6% of the total available community) were solely associated with this station, and of the 10 families represented here only the Scyllaridae (Spanish lobsters) was not found elsewhere during the study. We suspect this to be a sampling artifact because these small lobsters are otherwise abundant on shell hash plains on the nearshore Florida continental shelf (Gore, unpubl. data).

At the 80-m station diversity was also quite high with 20 genera, 24 species and 876 individuals representing 10 families comprising 6 abundant, 9 common and 9 rare forms. This station had the lowest species dominance (D_1 = 18, D_2 = 34) and thus had the most equitable distribution of individuals among species. Only nine species were solely associated with this station, but these included two species of sufficiently high relative within-station abundances to be classified as common forms within the context of the total community.

Relatively low percentages of species were shared among the stations, especially those at intermediate depths. Within the entire community of 50 species in 15 families, only 4 species in 4 different families were collected at every station. These data along with the previously noted high degree of "endemism" exhibited by the species found at the 6-m and 80-m stations suggest that we were dealing with two substantially different communities occurring within the overall *Oculina* biotope.

To test the validity of this concept, S and N occurring in coral samples at each station were examined using reciprocal averaging. Ordination of S and N by species (Fig. 7) showed several distinct species' clusters although some species were common to all stations. Clusters of taxa occurred at the 6- and 80-m stations so these areas were relatively distinct in their respective assemblages. Overall, more species' clusters occurred for adjacent stations (6 and 27 m, 42 and 80 m) than for distant station pairs (6 and 80 m). Moreover, ordination of S and N by samples (Fig. 8) showed strong clustering by station with a gradation from shallow to deep. Samples at the 6-m site were very discrete with considerable separation from the other stations whereas the 42- and 80-m stations had relatively little separation. In addition, faunal similarity values (Fig. 8, inset) between stations decreased with an increase in station separation; for example, the 6- and 80-m stations were least similar at 5.7%. This gradient of species assemblages from shallow to deep apparently reflects a gradient of environmental factors.

Faunal similarity values for samples within station (Fig. 8, inset) indicated the greatest community homogeneity (that is, the least amount of change in both S and N among the coral samples collected from that station) occurred at the 42-m station (68.5% similarity), followed by the 80-m station (57.3%), the 6-m station (47%), and the 27-m station (37.3%). These data suggest that for the time period studied the decapod communities within station were relatively stable in species composition and apparently showed no drastic seasonal overturn of assemblages.

Seasonality

To determine whether temporal fluctuations of decapods occurred at the sample sites, regression correlations for both S and N were plotted against the mean

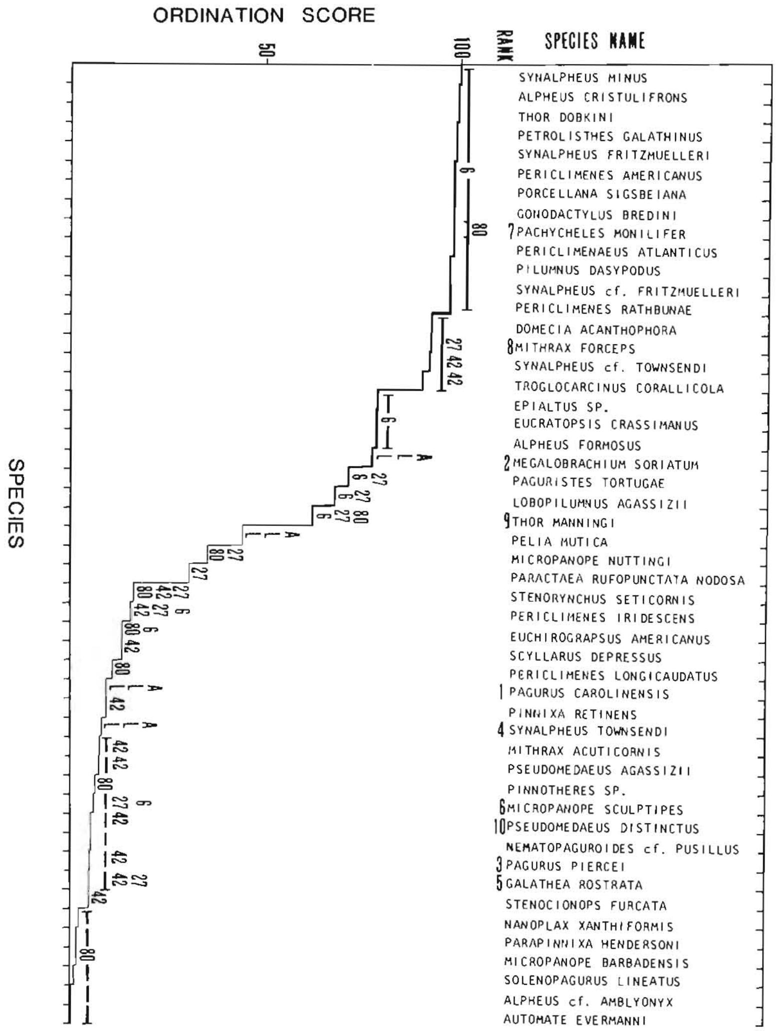
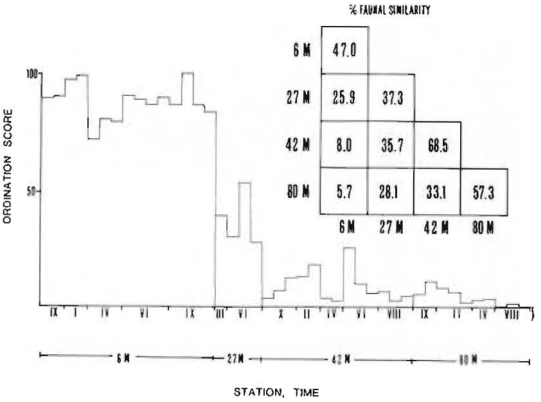


Figure 7. Ordination of decapod crustacean species assemblages using reciprocal averaging (Hill, 1973). Numbered species indicate rank by numerical relative abundance for all stations. Numbers over the curve indicate the station at which the species occurs.

temperature for each collection period. No relationship existed between N and temperature at the 6-m station although S showed a slight but not significant correlation (r = .589; t-test, $P < .4$). In September 1977 both S and N were reduced (Fig. 9) even though temperature at this time was similar to that in June when N was largest, and also the samples were similar in size and percentage of live coral. The S and N reductions in September followed an upwelling event and apparently were caused by the loss of some of the less common species, including three species of alpheid shrimp, a palaemonid shrimp, and a porcellanid crab. Similar reductions in S and N were not seen at the 42- and 80-m stations in post-upwelling collections made in August; however, none of the five species noted above occurred at the deeper stations during any time of the year. The reduced numbers at the 6-m site in January was partially a collection artifact. Only two samples were taken and one was a very small colony which was composed of 97% live coral.



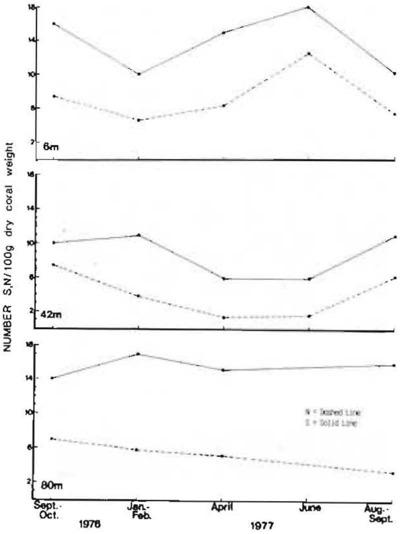


Figure 8. (Left) Similarity of samples over time within and between stations by relative ordination of decapod crustacean species and numbers using reciprocal averaging (Hill, 1973). Each bar represents one sample, and Roman numerals indicate month of collection. Inset shows matrix of relative percent faunal similarity (Sanders, 1960) for all samples compared within and between stations.

Figure 9. (Right) Number of decapod crustacean species (S) and density of individuals (N/100 g dry coral wt) collected during each sampling period at the 6-, 42-, and 80-m *Oculina* reef stations.

At the 42-m site both S and N showed negative but not significant correlation with mean temperature throughout all collections ($r = -.539$, $P < .4$; $r = -.606$, $P < .4$, respectively). Reduction in S and N was noted in the April and June samples (Fig. 9) although the coral colonies were similar in size to the preceding samples in February. Although the temperature in April was similar to February ($\bar{x} = 16.2$°C), the highest temperature for the collections occurred in June. The reduction of individuals was largely due to lower numbers of the dominant hermit crabs, *Pagurus carolinensis* and *P. piercei,* in April and June samples.

At the 80-m site, S showed no relationship with mean temperature ($r = .312$, $P < .9$) and was almost constant over the year (Fig. 9) with the largest number found in February when water temperature ($\bar{x} = 15.0$°C) was intermediate to the yearly range for that station. Numbers of individuals showed a slight but not significant correlation ($r = .788$, $P < .4$), gradually decreasing over the year even though sample size was relatively constant. Numbers of *Pagurus carolinensis,* a summer breeder (Gore et al., 1978), were reduced in the August samples after the temperature had dropped to a low of 8°C in July owing to the previously mentioned upwelling. Populations of *P. piercei, Galathea rostrata,* and *Micropanope sculptipes* were highest from September to February at the 80-m site.

Areal Effects on S and N

Previous analyses showed that coral dry weight, skeletal volume, branch surface area, and age were each significantly correlated with coral volume ($r = .867$, $.837$, $.732$, $.558$, respectively; F-test, $P < .05$) so that any of these parameters, if equated to colonizable area, could prove applicable in the S-N/areal relationship. Moreover, as colony size (or area) increased, the percentage of live coral (g dry weight) decreased ($r = -.472$, $t = -3.171$, $P < .01$, where % live coral was transformed by arcsine $\sqrt{p}$). In addition, the average percent of dead coral

Table 3. Correlation, regression and probability of correlation coefficient (Student's t-test) of number of species and individuals for each station with dead coral volume, dead branch area, and dead coral weight

	Number of Species			Number of Individuals		
	6 m	42 m	80 m	6 m	42 m	80 m
Dead Volume (cm^3)						
Correlation coefficient (r)	0.458	0.550	0.917	0.462	0.672	0.842
y-intercept (a)	7.101	4.612	6.775	32.258	7.185	−5.927
Slope (b)	0.002	0.001	0.001	0.017	0.014	0.011
Probability of t-value (p)	<.1	<.1	<.001	<.1	<.02	<.01
Dead Branch Area (cm^2)						
r	0.446	0.662	0.772	0.492	0.758	0.613
a	7.010	4.859	8.312	30.339	14.860	35.200
b	0.005	0.006	0.002	0.052	0.120	0.037
p	<.2	<.05	<.02	<.1	<.01	<.1
Dead Dry Weight (g)						
r	0.473	0.656	0.795	0.431	0.697	0.878
a	6.969	4.616	7.716	32.211	12.954	−4.098
b	0.009	0.008	0.004	0.077	0.145	0.087
p	<.1	<.05	<.02	<.2	<.02	<.01
Degrees of freedom	12	11	8	12	11	8

per colony was greater at 80 m (69.9%) than at 6 or 42 m (23.3, 21.9%, respectively). On the other hand, age of coral, *per se,* showed no significant correlation with either S or N at any of the stations. Because the general precept in the S-N/areal relationship hypothesizes a potential increase in S or N with increasing area, we suspected that S or N might also prove dependent on the relative abundance of dead or living coral (i.e., as an areal effect) in any given *Oculina* colony.

When correlation coefficients were calculated for the stations, the best predictor of S or N as a function of coral size was the dead portion of the coral colony, regardless of whether volume (cm^3), branch area (cm^2) or weight (g) was used to measure the amount of dead coral (Table 3). For all stations, 48.8% of the variance in S could be related to percentage of dead coral by dry weight ($r = .709$, $F = 35.33$, $P < .001$) and 42.9% for N ($r = .667$, $F = 28.03$, $P < .001$). Total colony size, viz. total volume, skeletal displacement volume, available living space, or dry weight, seemed less important with only the corals from the 80-m station showing significant relationship between S or N and total colony size. At the 6-m station, although no significant relationship existed among any of the considered factors, the best correlation was seen with dead dry weight, and this coefficient increased progressing from 6 to 80 m. We therefore equated area with dead dry weight (g) as the most logical parameter with which to assess decapod community response.

Densities

Decapod crustacean densities (N/100 g dry wt coral) were compared with colony size within- and between station groups. No significant relationship existed between densities and the total dry weight of a colony ($r = -.257$). Although

Table 4. Correlation coefficient (r) and probability value from Student's t-test (*P*) of population densities of dominant species by rank with size of living and dead portions of *Oculina* coral

	Live Dry Weight		Dead Dry Weight	
	r	*P*	r	*P*
6 m				
1) *M. soriatum*	−.063	<.9	.316	<.4
2) *P. monilifer*	.376	<.2	.316	<.4
3) *M. forceps*	.372	<.2	.561	<.05
4) *T. manningi*	−.393	<.2	.142	<.9
42 m				
1) *P. carolinensis*	−.117	<.9	.632	<.05
2) *M. soriatum*	.374	<.4	.790	<.01
3) *P. piercei*	−.179	<.9	.379	<.4
4) *S. townsendi*	.283	<.4	.526	<.1
80 m				
1) *P. carolinensis*	−.236	<.9	.452	<.2
2) *P. piercei*	.852	<.01	.553	<.1
2) *G. rostrata*	.564	<.1	.703	<.05
3) *M. sculptipes*	.106	<.9	.755	<.02
4) *S. townsendi*	.158	<.9	.765	<.01

(Degrees of freedom = 12 at 6 m; 11 at 42 m; 8 at 80 m).

mean densities for the 6-, 42-, and 80-m stations ranged from 4.3 to 8.8 N/100 g total coral wt, they were not significantly different among any pair of stations (t-test, $P > .05$). However, when densities were compared with the dry weight of the dead portion of the corals for all stations, a reasonably strong negative correlation could be demonstrated ($r = -.539$, $t = -3.784$, $P < .001$). Mean densities for the 6-, 42-, and 80-m stations also decreased with increasing depth (44.4, 21.7, and 7.5 N/100 g dead coral wt, respectively) and these differed significantly among themselves (t-test, $P < .05$). These data support the earlier contention that N is dependent on dead, rather than living coral. They also show that in deeper water a greater percentage of the coral colony is dead, even though the reefs themselves are more massive than their shallow water counterparts.

To determine the relationship of coral size on individual species populations, regression coefficients and t-tests were calculated for each dominant species against the size of living and dead portions of each coral (Table 4). Again, population densities for the majority of dominant species were positively correlated with the size of the dead portion of coral. For example, populations of *Pagurus carolinensis, Megalobrachium soriatum, Synalpheus townsendi,* and *Galathea rostrata* all showed a significant relationship with dead coral weight. The only species showing a significant relationship to the size of the living portion of the colony was *Pagurus piercei,* and this was seen only at the 80-m station ($r = .852$, $P < .01$). At the 6-m station population size of *Domecia acanthophora, Synalpheus* cf. *townsendi,* and *Troglocarcinus corallicola* appeared to be independent of coral size, with the latter two species tending to occur in pairs. As discussed below, both *D. acanthophora* and *T. corallicola* are obligate commensals; if *S.* cf. *townsendi* is also a coral specialist, densities for these species may be a function of some parameter other than plain area, or percent live or dead coral.

DISCUSSION

Species Composition

Zoogeographical trends of decapod communities associated with corals can be compared from the studies on *Oculina arbuscula* in warm temperate waters off North Carolina (McCloskey, 1970), *O. varicosa* from subtropical waters off central eastern Florida (this study), *Pocillopora damicornis* from the tropical eastern Pacific off Panama (Abele and Patton, 1976) and the Great Barrier Reef (Austin et al., 1980), and *P. meandrina* from the tropical central Pacific off Hawaii (Barry, 1965; Coles, 1980). The corals in these studies all form branching compact colonies and appear to be similar in both size range, topographical complexity, and in general habitat heterogeneity.

Species composition of the macroinvertebrate communities show greater similarity between temperate and subtropical oculinids than with the tropical pocilloporid corals. However, percent composition of the associated decapod communities is variable. The *Oculina varicosa* decapods represent only 11.5% of the total number of individuals of all macroinvertebrates whereas amphipods, molluscs, polychaete worms, and tanaid crustaceans represent 20, 19, 15, and 12%, respectively. McCloskey (1970) found these same groups dominant on colonies of *Oculina arbuscula* but with polychaetes, tanaids, amphipods, and molluscs comprising 29, 19, 17, and 8% of all individuals, and decapod crustaceans accounting for only 1% of the total N. Of the 35 genera and 50 decapod species found on *O. varicosa,* 13 genera and 12 species co-occurred on *O. arbuscula* (Table 5). The latter coral supported only 16 genera and 19 species of decapods, so that 34% of the genera and 21% of the species were shared among the two coral species. Numerically dominant decapods shared by both oculinid species include *Megalobrachium soriatum* (Porcellanidae), *Pagurus carolinensis* [=*P. brevidactylus,* Paguridae], *Mithrax forceps* (Majidae), and *Synalpheus fritzmuelleri* (Alpheidae). The decapod crustaceans (although exhibiting generic and species similarity) are clearly numerically less important in the more northern biotope off the Carolinas.

On the other hand, the macroinvertebrate community associated with living *Pocillopora* coral in the Pacific is totally dominated by decapods which can represent from 80–96% of all individuals (Abele, 1976a; Austin et al., 1980). The Atlantic oculinid corals shared 13 genera and one species (*Petrolisthes galathinus*) out of a total of 55 species found on living *Pocillopora damicornis* off Panama, at least 9 genera out of 64 species from living *P. damicornis* on the Great Barrier Reef, and 10 genera out of 127 species from living and dead *P. meandrina* off Hawaii (Table 5). The porcellanid crab *Pachycheles,* the spider crab *Mithrax,* and the pistol shrimp *Synalpheus* were common in both oculinid and pocilloporid corals. The Pacific coral communities as a whole are obviously more species-rich than those of the Atlantic oculinid corals.

Definite distinctions also exist between the oculinid and pocilloporid decapod communities both in species composition and trophic structure. These distinctions may be a result of historical differences between the ages of the Atlantic and Pacific faunas. The historically long and diverse development of corals in the Indo-Pacific Ocean (Wells, 1956) probably enabled a parallel expansion of obligate commensal decapod genera such as the xanthid crab genus *Trapezia,* a dominant decapod associated with living Indo-West Pacific, central and eastern Pacific *Pocillopora.* But whether they were either blocked from the western Atlantic or became extinct in the Atlantic after the closing of the Central American seaway

Table 5. Genera and species of decapod crustaceans occurring on branching corals and shared with *Oculina varicosa*

*Oculina arbuscula** (North Carolina)	*Pocillopora damicornis*† (Perlas Island)	(Uva Island)	*Pocillopora meandrina*‡ (Hawaii)
Megalobrachium soriatum	*Megalobrachium (smithii)*	----------	----------
Pilumnus dasypodus	*Pilumnus* (sp. *1*)	*Pilumnus (reticulatus)*	*Pilumnus (longicornis)*
Synalpheus fritzmuelleri	*Synalpheus (digueti)*	*Synalpheus* (cf. *mexicanus*)	*Synalpheus* (sp.)
Synalpheus minus	*Synalpheus* (sp. *1*)	*Synalpheus (digueti)*	*Synalpheus (biungulatus)*
Mithrax forceps	*Mithrax (pygmaeus)*	*Mithrax (pygmaeus)*	----------
Pagurus carolinensis	*Pagurus* (cf. *lepidus*)	*Pagurus (lepidus)*	*Pagurus* (sp.)
Pelia mutica	*Pelia (pacifica)*	*Pelia (pacifica)*	----------
Petrolisthes galathinus	*Petrolisthes galathinus*	----------	----------
----------	*Petrolisthes (haigae)*	*Petrolisthes (haigae)*	----------
Thor (floridanus)	*Thor (amboinensis)*	*Thor (maldivensis)*	*Thor (maldivensis)*
Pseudomedaeus agassizzi	----------	----------	----------
Domecia acanthophora	----------	*Domecia (hispida)*	*Domecia (hispida)*
Periclimenes longicaudatus	----------	----------	*Periclimenes (grandis)*
Stenorhynchus seticornis	*Stenorhynchus (debilis)*	*Stenorhynchus (debilis)*	----------
Micropanope (sp.)	----------	*Micropanope (xanthusii)*	----------
----------	*Alpheus (lottini)*	*Alpheus (lottini)*	*Alpheus (clypeatus)*
----------	*Pachycheles (biocellatus)*	*Pachycheles (biocellatus)*	----------
----------	----------	----------	*Galathea (spinosirostris)*
----------	----------	----------	*Periclimenaeus (quadridentatus)*
----------	----------	----------	*Gonodactylus* (cf. *chiraga*)

* Data from McCloskey, 1970; † Abele and Patton, 1976; Abele, 1979; ‡ Coles, 1980 and unpublished data.

by the late Miocene or Pliocene cannot be ascertained (Patton, 1967). At present, no fossil evidence exists for these decapod genera in either the Pacific or Atlantic Oceans, even though the Indo-Pacific coral genus *Pocillopora* did occur in the western Atlantic until possibly the late Pleistocene (Frost, 1977).

Additional, albeit circumstantial, evidence for this association is seen when one considers that the commensal decapods associated with corals are confined primarily to the brachyuran crab families Xanthidae (e.g., *Trapezia* with 23 known species), and Hapalocarcinidae (several genera and at least 27 species; Fize and Serène, 1957; Castro, 1976). In the western Atlantic, however, the only known obligate commensal decapods on any scleractinian coral are the hapalocarcinid coral-gall crabs, *Troglocarcinus* (Verrill, 1908) and *Pseudocryptochirus* (Shaw and Hopkins, 1977), and the xanthid *Domecia acanthophora* (Patton, 1967). Of these, only *D. acanthophora* has been found on both *Oculina varicosa* and *O. arbuscula.*

Trophic Partitioning

Differences in species composition suggest different trophic structuring for the Atlantic oculinid and Pacific pocilloporid coral communities. Within the western Atlantic oculinid biotope the aforementioned hapalocarcinid and xanthid crabs are obligate commensals on the coral by virtue of their nutritional requirements (i.e., feeding on coral mucus; see Potts, 1915; Patton, 1967). This does not mean that the other decapod species do not feed, albeit facultatively, on coral mucus or detritus entrapped in that secretion because several species are known to utilize this nutritional mode (Patton, 1967). But with many of the species not characterized as mucus-feeders but as omnivores, it seems reasonable to suppose that absence of living mucus-producing coral polyps in a colony might prove a more attractive habitat for such species. These forms would then utilize the coral colony primarily as a refuge and would not be metabolically dependent on the living polyps (as is, for example, *T. corallicola*). Included in this grouping would be porcellanid crabs (filter feeders), and pagurid crabs and alpheid shrimp (deposit feeders) which are numerically important on Floridian and Carolinian oculinids, and tend to stay near the non-living center or bases of the corals. Also included would be xanthid crabs (predators on some omnivores and detritivores) and majid crabs (herbivores or facultative carnivores). In the Pacific, however, the commensal species (xanthid and hapalocarcinid crabs and alpheid shrimp) dominant on live *Pocillopora* obtain food from the living areas of the colony by eating coral mucus containing entrapped detritus, rather than feeding at the dead bases. As Coles (1980) has demonstrated, a comparison of decapod communities on both living and dead *Pocillopora* showed that the dead coral was dominated by non-symbiotic xanthid and pagurid crabs and alpheid shrimp, all of which were considered deposit feeders that randomly colonized the dead coral from within the general reef environment. Thus the decapod communities of the Atlantic oculinid corals parallel more closely those of dead, rather than the living Pacific *Pocillopora.* The most noteworthy exception is that no filter-feeding porcellanids were numerically dominant on dead coral (contrary to that seen in the Atlantic), although at least three species were numerically abundant (including one ranked first overall) on living *Pocillopora* in Panama (Abele and Patton, 1976), and one ranked third on *Pocillipora* from the Great Barrier Reef (Austin et al., 1980).

Within the *Oculina varicosa* biotope itself there is also apparent trophic partitioning between stations. Characterizing the shallowest versus the deeper water sites by a single species, based on numerical dominance as an indicator of trophic relationships, the porcellanid crab, *Megalobrachium soriatum* (a filter feeder), delineates the former and *Pagurus carolinensis* (an omnivorous detritivore) the latter. The reasons for these delineations will be explained below.

Environmental Effects on Community Structure

Although long-term environmental stability has been considered a primary factor for high species richness in tropical environments (Sanders, 1968; also review by Holling, 1973), recent studies have suggested the alternative importance of periodic physical perturbations in maintaining high numbers of species (Loya, 1976; review by Levandowsky and White, 1977; Connell, 1978; Gore et al., 1978; Coles, 1980). According to the intermediate disturbance hypothesis (Connell, 1978), periodic disturbances tend to eliminate highly competitive dominant species thereby opening habitat space for either recovery of suppressed associated species or invasion of new species. For example, species richness increased in the decapod communities of *Pocillopora* after either perturbations caused by siltation (Coles, 1980) or after severe temperature fluctuations caused by upwelling (Abele, 1976a; 1979). The question that arises, however, is to define just what is considered "long-term" versus "short-term" and how either concept depends upon, or is associated with, periodicity and/or predictability (Holling, 1973).

Based on data from our study we cannot determine whether Floridian oculinid reefs experience either long-term environmental stability or fluctuations, regardless as to any periodicity in either. Our data do show the occurrence of short-term perturbations, and at least one of these, that of seasonal upwelling, is periodic. Might this affect species composition?

The environment of the 6-m station varied more in terms of salinity, wave surge, and sedimentation, but less in terms of temperature fluctuations than did the other more offshore stations. The 6-m station had both the highest S and highest number of uniquely-associated species (which we term "endemicity"), as well as relatively high numerical dominance in these species. The 42-m station, with the greatest temperature fluctuations owing to upwelling but with less variable salinity changes or sedimentation rates, had relatively low S and "endemicity" while exhibiting the highest numerical dominance in species of all the stations. The 80-m station, which was similar to the 42-m site in physical parameters, nevertheless exhibited both high S and "endemicity" while showing the lowest numerical dominance. These data suggest to us that fluctuating temperature, especially the periodic fluctuation caused by upwelling, is an important factor controlling community structure on these reefs. Although the upwelling events affect the 80-m reefs just as they do the 42-m reefs, the associated fauna on the deeper reefs appears to be more tolerant to already existing cold-water conditions, so that any upwelling event is less perturbing than it would be to the shallower, warmer-water community at 42 m (Fig. 10). The inshore community at 6 m apparently is far enough removed from the primary temperature effects of such upwelling (being approximately 20 miles westward) that sudden influxes of cold water are considerably dampened by both horizontal and vertical mixing as the upwelling moves toward shore.

These results conflict with those found by Abele (1976a; 1979) for *Pocillopora*-associated decapods. In that community greater species richness but lower dominance occurred in a fluctuating environment subjected to cold-water upwelling

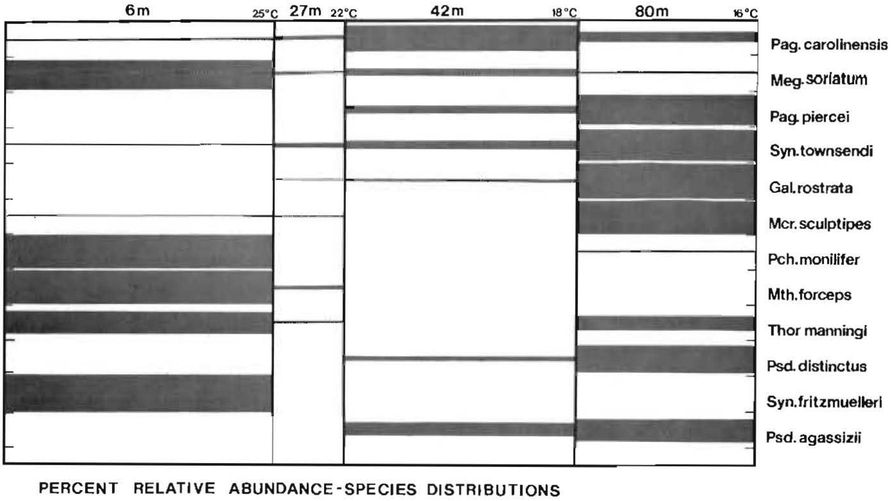


Figure 10. Comparison of mean station temperature and percent relative numerical abundance of the common decapod crustacean species for each station. Total width of each species increment equals 100%, with relative abundance shaded proportionately.

events than that seen in a more constant environment. Abele postulated that upwelling reduced or prevented coral growth with a loss of soft parts on coral branch tips thereby reducing mucus production. This, in turn, could reduce the attractiveness of the habitat for the various obligate symbiotic decapods that utilized coral mucus for food. As a consequence, colonization by a variety of generalist species occurred, but in lower numbers.

This was not the case in the oculinid communities we studied. In contrast, the linear growth rates of *O. varicosa* were greater at 80 m (even though mean annual temperature was 8°C cooler than at 6 m), leading us to believe that mucus production was not much curtailed by upwelling events. The deep *Oculina* habitat, even though located in a fluctuating environment, probably retains whatever attractibility it had for mucus-feeding decapods. However, as discussed below, we suspect that very few species are totally dependent, and most are only partially dependent (if at all) on coral mucus production for food. If this is true, it further suggests that the differences we have observed between the stations in our studies, as well as those among the different oculinid and pocilloporid species, are due to some other factor. Among these would be within-reef habitat heterogeneity (including size and topographical complexity of the coral), or the heterogeneity of the surrounding-reef habitat (including the available associated decapod species within this habitat which would be colonizers of the coral colonies as well).

Colonization Effects on Community Structure

Total S was greater at the 6-m station than at 42 or 80 m. This perhaps reflects some measure of habitat complexity. The 6-m site was characterized by small, more or less isolated, widely scattered coral colonies interspersed among extensive algal and sponge cover, and was substantially more heterogeneous than the relatively monotonous sites at 42 and 80 m. The 6-m site yielded 22 rare species (i.e., those represented by less than 10 N at the station), or 73% of the 30 species found there, and 16 (53%) endemic species (i.e., those not found at the other stations). The 42-m site had 9 rare (56% of 16 S) and 3 (19%) endemic, and the 80-m site had 11 rare (46% of 24 S) and 9 (38%) endemic. The numbers differ, but it is clear that rare species comprise a major component, nearly half or greater, of the communities among the three stations.

At the shallow station we suspect colonization by these species from two directions: first, from the surrounding algal-sponge habitat, and second, possibly from the adjacent sabellariid worm reefs near shore and in the surfzone. Many of the species found on the 6-m oculinid corals have also been collected from sponges, or are known associates of either sponges or algae (e.g., *Epialtus* spp., *Pagurus* spp., *Synalpheus* spp.). Furthermore, 14 species in 12 genera and 7 families are shared between the oculinid and sabellariid worm reef biotopes (Gore et al., 1978). Six of these species are considered common or abundant on the oculinid reefs; two of these six (*Pachycheles monilifer, Synalpheus fritzmuelleri*) were abundant, one (*Pagurus carolinensis*) was common, and three (*Synalpheus minus, S. townsendi, Megalobrachium soriatum*) were rare on sabellariid worm reefs. The eight remaining shared species are all listed as rare on the oculinid reefs, but in decided contrast, five of these (*Pilumnus dasypodus, Petrolisthes galathinus, Epialtus* sp., *Alpheus formosus, Synalpheus* cf. *fritzmuelleri*) were considered common on the sabellariid worm reefs.

There is, of course, no way to be certain that these species are colonizing from inshore to offshore, or vice versa. However, the possibility of the former happening cannot be dismissed, especially when one considers that *Pachycheles monilifer,* the dominant sabellariid reef species, was almost completely restricted to the 6-m oculinid station, whereas *Megalobrachium soriatum,* the second most abundant oculinid associate was found at every oculinid station, yet was known from but a single individual on the sabellariid worm reefs (Gore et al., 1978). A similar situation was seen with *Synalpheus fritzmuelleri, Pilumnus dasypodus, Petrolisthes galathinus, Alpheus formosus* and *Epialtus* sp., all of which occurred in some numbers on sabellariid reefs and the 6-m oculinid reefs but were nearly or completely absent from all deeper oculinid stations.

A third alternative, that the above named species are recruited from the plankton and settle out on all the oculinid reefs, from 80 m shoreward, and eventually onto the sabellariid worm reefs, may also be considered. This hypothesis, however, requires subsequent selective elimination (perhaps by colder waters during upwelling) of these species from all the deeper reefs and their ultimate restriction to 6-m oculinid reefs and surfzone sabellariid reefs. But this seems not to be occurring, for the general distribution of many of the supposedly cold-tolerant species proceeds shoreward but stops in the vicinity of either the 27- or 42-m oculinid stations (Fig. 10). *Pagurus carolinensis* and *Synalpheus townsendi* are the two most notable exceptions, both having relatively high populations on the deeper reefs, and both with ranges extending further inshore than 27 m. The former species ranked first in overall abundance in our study and the latter ranked eleventh.

Density of S and N

Cumulative number of species was plotted against total colony size for all stations (Fig. 11). The curves show that once a critical size (i.e., in area equated to weight) is reached the rate of increase in species density slows, and with further increase in coral size actual density decreases. Although the species-area concept states that the availability of additional area should allow still more species, especially rare forms, to become established, the data do not support this prediction. A similar relationship was found by Abele and Patton (1976) for the *Pocillopora*-associated decapod community in the eastern Pacific. In both their study and ours it appears that N increases in previously established species, rather than new S, and these apparently pre-empt available space thereby preventing further increases in the number of rare species in the community.

Densities of individuals also decreased with increasing colony size in both the *Pocillopora* and *Oculina* communities. In the pocilloporid community this was partially because some of the dominant obligate commensal species, e.g., *Alpheus lottini,* were area-independent and tended to occur only in single pairs on each colony, regardless of colony size. In the oculinid corals only two rare species, *Troglocarcinus corallicola* and *Synalpheus* cf. *townsendi,* showed this tendency to pair and neither species was restricted to single mated pairs per colony. One might expect other alpheid shrimp species to act accordingly because many form pairs (Hendrix, 1971), but we have no observations supporting this for the oculinid associates. Furthermore, as noted earlier, most of the numerically dominant species associated with *Oculina* appeared to be dependent on the size of the dead, not the living, portion of coral. Strict interpretation of the species-area hypothesis means that a larger coral should always be able to support more individuals as a simple consequence of an increase in the topographical complexity. In our study, however, species and individual densities tended to decrease with increasing coral size, perhaps because with an increase in coral volume there is a concomitant decrease in outer surface area available for colonization per unit volume. A direct consequence would then be a reduced flow of immigrants onto the colony. In addition, because of the reduced amount of surface area per unit volume, the availability of detrital rain as a food source would be reduced. Still another important factor is that *Oculina* coral colonies eventually reach a critical size dependent on the general colony structure. At this point seawater circulation around the inner branches is severely reduced or stopped altogether, causing varying degrees of stagnation (Chamberlain and Graus, 1975). This often results in death of the inner branches, thereby opening up more space for those decapods responding to dead branch area. Of course, these species must then contend with reduced supplies of oxygenated water, but based on the observed S and N in our study this seems not to be a major problem.

Areal Effects on S and N

As noted above, at the three deeper stations (27, 42, and 80 m) both S and N were positively correlated with percent available dead coral, and negatively correlated with percent living coral. The negative correlation of S and N with living *Oculina* is in decided contrast to results reported by Abele (1976a; 1979) and Abele and Patton (1976) who found a strong positive correlation between S and N and living coral colony size in eastern Pacific *Pocillopora* coral. On the other hand, our results agree very well with a similar study by Coles (1980) on living and dead *Pocillopora* in Hawaii. In Coles' study nonsymbiotic decapods were best correlated with dead coral area while symbiotic species were positively correlated with size of live portions of coral. As noted earlier, the only known obligate commensal decapods from Atlantic oculinid corals are *Domecia acanthophora* and *Troglocarcinus corallicola,* both of which were rare species in our study and the former was rare in McCloskey's (1970) study. Thus the dominant

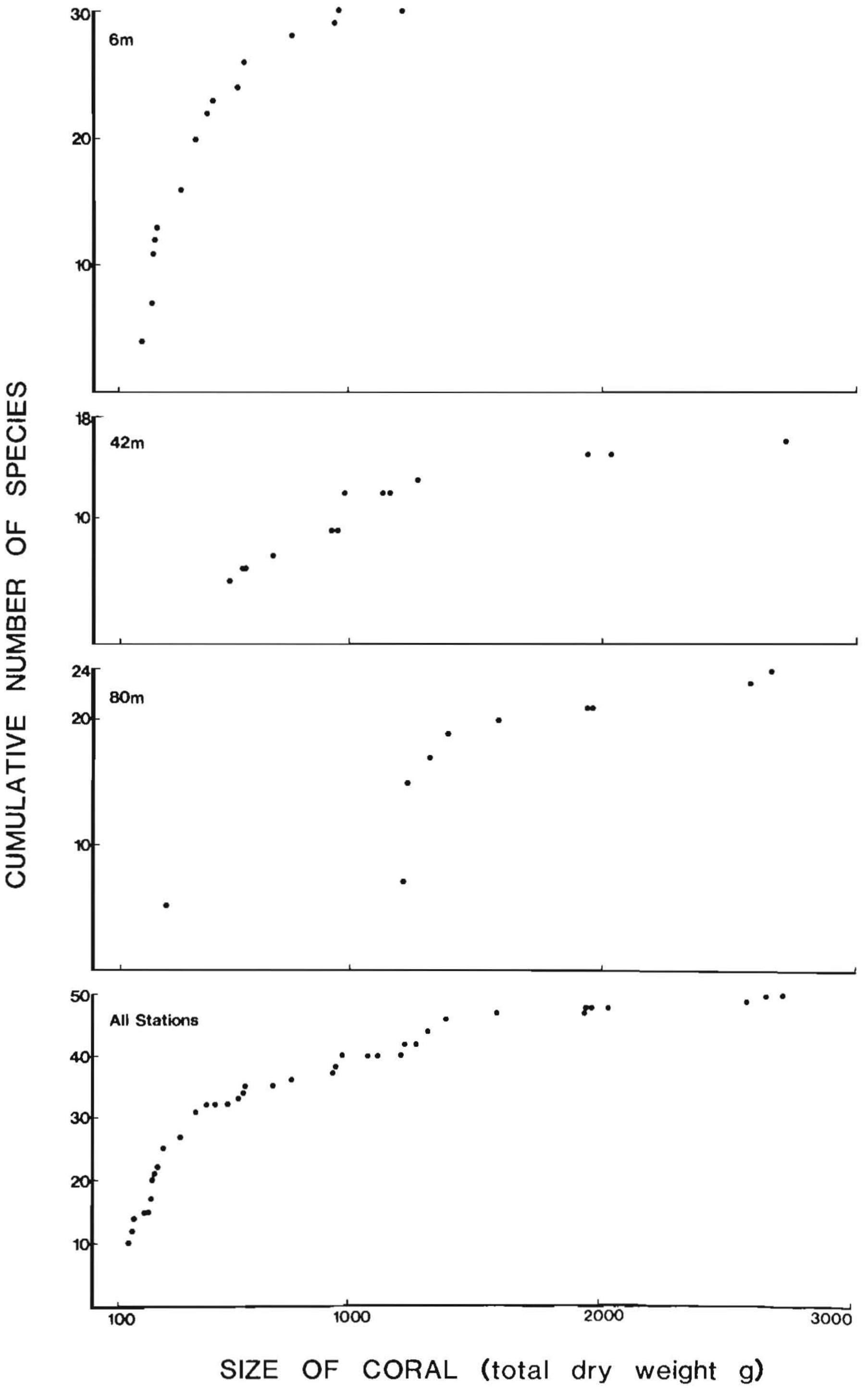


Figure 11. Comparison of cumulative number of decapod crustacean species and size of all *Oculina* coral colonies.

decapods found in the Atlantic oculinids as well as in the dead portions of Pacific pocilloporid corals are nonsymbiotic omnivores which utilize the coral as a refuge, not as a source of food (i.e., mucus). Included in this grouping would be xanthid and majid crabs, both species-rich in *Oculina varicosa,* as well as the numerically dominant procellanid, pagurid and galatheid anomuran crabs.

The correlation coefficient of oculinid decapod S and N to dead coral size increased with increasing station depth (Table 3). We suspect that this is more of a function of two totally different communities present at the shallowest and deepest stations (Fig. 8) which in turn are responding to different environmental processes. The 42- and 80-m stations are dominated numerically by detritus and deposit feeding species which may exhibit a high correlation to dead coral size. On the other hand, at the inshore station (6 m) where wave surge and water turbidity are higher, an abundance of filter-feeding species is noted. These species are not as dependent on areas of dead coral as possible detrital-collection and feeding sites.

In summary, the species composition of the decapod community associated with the Floridian *Oculina varicosa* coral biotope seems regulated by several factors, including areal parameters derived from the amount of dead coral habitat available, associated habitat heterogeneity in the sense of adjacent non-coralline assemblages as a source of recruitment, periodic perturbations of temperature owing to seasonal upwelling events, and trophic restrictions within the species themselves. In considering the relative complexity of the oculinid-associated decapods with that of the sabellariid worm reef associated fauna, we have deliberately ignored categorizing the former in terms of "control" by predator-prey, or competitive relationships. These terms, while obviously of value in some ecosystems, are admittedly simplistic, and we feel are of limited value in understanding the oculinid fauna. Instead, we have shown that the oculinid decapod crustacean fauna, even though associated with a biotope which can be simplistically categorized in regard to the general uniformity of its morphological parameters, areal, and geographical extent, is, nevertheless, exceedingly complex and appears to respond to several, closely intertwined factors in order to maintain its existence.

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LITERATURE CITED

Abele, L. G. 1974. Species diversity of decapod crustaceans in marine habitats. Ecology 55: 156–161.

———. 1976a. Comparative species richness in fluctuating and constant environments: coral associated decapod crustaceans. Science 192: 461–463.

———. 1976b. Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panama. Mar. Biol. 38: 263–278.

———. 1979. The community structure of coral-associated decapod crustaceans in variable environments. Pages 265–287 *in* R. J. Livingston, ed. Ecological processes in coastal and marine systems. Plenum Press, N.Y. and London.

and the polychaete *Hermodice carunculata* (Pallas) as coral reef predators. Canad. J. Zool. 50: 1651–1656.

Patton, W. K. 1966. Decapod crustacea commensal with Queensland branching corals. Crustaceana 10: 271–295.

———. 1967. Studies on *Domecia acanthophora*, a commensal crab from Puerto Rico, with particular reference to modifications of the coral host and feeding habits. Biol. Bull. 132: 56–67.

———. 1974. Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. Pages 219–243 *in* W. Vernberg, ed. Symbiosis in the sea. Univ. of S. Carolina Press, S. Carol.

Peyrot-Clausade, M. 1974. Ecological study of coral reef cryptobiotic communities: an analysis of the polychaete cryptofauna. Proc. 2nd Int. Coral Reef Symp. 1: 269–284.

Potts, F. A. 1915. *Hapalocarcinus*, the gall-forming crab, with some notes on the related genus *Cryptochirus*. Publs. Carnegie Instn. Pap. Tortugas Lab. 8: 35–71.

Reed, J. K. 1980. Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida. Bull. Mar. Sci. 30: 667–677.

Richman, S., Y. Loya, and L. B. Slobodkin. 1975. The rate of mucus production by corals and its assimilation by the coral reef copepod *Acartia negligens*. Limnol. Oceanogr. 20: 918–923.

Robertson, R. 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. Pac. Sci. 24: 43–54.

Ross, A., and W. A. Newman. 1973. Revision of the coral-inhabiting barnacles (Cirripedia: Balanidae). San Diego Soc. Nat. Hist. Trans. 17: 137–173.

Sale, P. F., and R. Dybdahl. 1975. Determinants of community structure for coral reef fishes in an experimental habitat. Ecology 56: 1343–1355.

Sammarco, P. W., J. S. Levinton, and J. C. Ogden. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. J. Mar. Res. 32: 47–53.

Sanders, H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. Limnol. Oceanogr. 5: 138–153.

———. 1968. Marine benthic diversity: a comparative study. Am. Nat. 102: 243–282.

Shaw, J. K., and T. S. Hopkins. 1977. The distribution of the family Hapalocarcinidae (Decapoda, Brachyura) on the Florida Middle Ground with a description of *Pseudocryptochirus hypostegus* n. sp. Proc. 3rd Int. Coral Reef Symp. 1: 177–183.

Smith, C. L., and J. C. Tyler. 1975. Succession and stability in fish communities of dome shaped patch reefs in the West Indies. Amer. Mus. Nat. Hist. 2572: 1–18.

Smith, N. P. In Press. An investigation of seasonal upwelling along the Atlantic coast of Florida. Proc. 12th Int. Liege Colloq. Ocean Hydrodynamics.

Takeda, M., and Y. Tamura. 1979. Coral-inhabiting crabs of the family Hapalocarcinidae from Japan. I. Three species obtained from mushroom coral, *Fungia*. Bull. Natn. Sci. Mus., Ser. A (Zool.) 5: 161–172.

Taylor, C. B., and H. B. Stewart, Jr. 1958. Summer upwelling along the east coast of Florida. J. Geophysical Res. 64: 33–40.

Utinomi, H. 1944. Studies on the animals inhabiting reef corals. III. A revision of the family Hapalocarinidae (Brachyura) with some remarks on their morphological peculiarities. Palao Trop. Stud. 2: 687–731.

Verrill, A. E. 1908. Decapod crustacea of Bermuda. Pt. 1. Brachyura and Anomura, their distribution, variations, and habits. Trans. Acad. Arts Sci. 3: 299–474.

Vittor, B. A., and P. G. Johnson. 1977. Polychaete abundance, diversity and trophic role in coral reef communities at Grand Bahama Island and the Florida Middle Ground. Proc. 3rd Int. Coral Reef Symp. 1: 163–168.

Wells, J. W. 1956. Scleractinia. Pages 329–479 *in* R. C. Moore, ed. Treatise on invertebrate paleontology. Part F. Coelenterata. Geol. Soc. Amer. and Univ. Kansas Press, Kansas.

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———, and W. K. Patton. 1976. The size of coral heads and the community biology of associated decapod crustaceans. J. Biogeog. 3: 35–47.

Austin, A. D., S. A. Austin, and P. F. Sale. 1980. Community structure of the fauna associated with the coral *Pocillopora damicornis* (L.) on the Great Barrier Reef. Aust. J. Mar. Freshwater Res. 31: 163–174.

Avent, R. M., M. E. King, and R. H. Gore. 1977. Topographic and faunal studies of shelf-edge prominences off the central eastern Florida coast. Int. Revue ges. Hydrobiol. 62: 185–208.

Barry, C. K. 1965. Ecological study of the decapod crustaceans commensal with the branching coral *Pocillopora meandrina* var. *nobilis* Verrill. M.S. Thesis, Univ. of Hawaii. 64 pp.

Benson, A. A., and L. Muscatine. 1974. Wax in coral mucus: Energy transfer from corals to reef fishes. Limnol. Oceanogr. 19: 810–814.

Castro, P. 1976. Brachyuran crabs symbiotic with scleractinian corals: A review of their biology. Micronesia 12: 99–110.

Chamberlain, J. A., Jr., and R. R. Graus. 1975. Water flow and hydromechanical adaptations of branched reef corals. Bull. Mar. Sci. 25: 112–125.

Coles, S. L. 1980. Species diversity of decapods associated with living and dead reef coral *Pocillopora meandrina*. Mar. Ecol. Prog. Ser. 2: 281–291.

———, and R. Strathmann. 1973. Observations on coral mucus "flocs" and their potential trophic significance. Limnol. Oceanogr. 18: 673–678.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Ducklow, H. W., and R. Mitchell. 1979. Composition of mucus released by coral reef coelenterates. Limnol. Oceanogr. 24: 706–714.

Fize, A., and R. Serène. 1957. Les Hapalocarlinidés du Viet-Nam. Mem. Inst. Oceanogr. Nhatrang. 10: 1–202.

Frost, S. H. 1977. Miocene to Holocene evolution of Caribbean Province reef-building corals. Proc. 3rd Int. Coral Reef Symp. 2: 353–359.

Garth, J. S. 1964. The crustacea decapoda of Eniwetak Atoll, Marshall Islands, with special reference to the obligate commensals of branching corals. Micronesica 1: 137–144.

———. 1974. On the occurrence in the eastern tropical Pacific of Indo-west Pacific decapod crustaceans commensal with reef-building corals. Proc. 2nd Int. Coral Reef Symp. 1: 397–404.

Glynn, P. W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol. Monog. 46: 431–456.

———, R. H. Stewart, and J. E. McCosker. 1972. Pacific reef corals of Panama: structure distribution and predators. Sond. Geol. Rund. Band 61: 483–519.

Gore, R. H., L. E. Scotto, and L. J. Becker. 1978. Community composition, stability and trophic partitioning in decapod crustaceans inhabiting some subtropical sabellariid worm reefs. Studies on decapod crustacea from the Indian River Lagoon region of Florida. IV. Bull. Mar. Sci. 28: 221–248.

Hendrix, G. Y. 1971. A systematic study of the genus *Alpheus* (Crustacea: Decapoda: Alpheidae) in south Florida. Ph.D. Dissertation, University of Miami, Florida. 184 pp.

Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61: 237–247.

Hiro, F. 1937. Notes on some of the animals inhabiting reef corals. Palao trop. biol. Stn. Stud. 1: 137–154.

Holling, C. S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4: 1–23.

Hutchings, P. A. 1974. A priliminary report on the density and distribution of invertebrates living in coral reefs. Proc. 2nd Int. Coral Reef Symp. 1: 285–296.

Knudsen, J. W. 1967. *Trapezia* and *Tetralia* (Decapoda, Brachyura, Xanthidae) as obligate ectoparasites of pocilloporid and acroporid corals. Pacif. Sci. 21: 51–57.

Levandowsky, M., and B. S. White. 1977. 2. Randomness, time scales, and the evolution of biological communities. Pages 69–161 *in* K. Hecht, C. Steere and B. Wallace, eds. Evolutionary biology, Vol. 10. Plenum Press, N.Y. and London.

Loya, Y. 1976. Recolonization of Red Sea corals affected by natural catastrophies and man-made perturbations. Ecology 57: 278–289.

Macintyre, I. G., and J. D. Milliman. 1970. Physiographic features on the outer shelf and upper continental slope, Atlantic continental margin, southeastern United States. Bull. Amer. Geol. Soc. 81: 2577–2598.

McCain, J. C., and S. L. Coles. 1979. A new species of crab (Brachyura, Hapalocarcinidae) inhabiting pocilloporid corals in Hawaii. Crustaceana 36: 81–90.

McCloskey, L. R. 1970. The dynamics of the community associated with a marine scleractinian coral. Int. Revue ges. Hydrobiol. 55: 13–81.

McNaughton, S. J. 1967. Relationships among functional properties of California grasslands. Nature, Lond. 216: 168–169.

Ott, B., and J. B. Lewis. 1972. The importance of the gastropod *Coralliophila abbreviata* (Lamarck)