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SEASONAL COMPOSITION AND ABUNDANCE OF DECAPOD CRUSTACEAN ASSEMBLAGES FROM THE SOUTH ATLANTIC BIGHT, USA

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ABSTRACT

Samples of decapod Crustacea were collected by trawl during seasonal cruises at 496 randomly located stations in the South Atlantic Bight between Cape Fear, North Carolina and Cape Canaveral, Florida. Stations were located within depth zones of 9–18 m, 19–27 m, 28–55 m, 56–110 m, 111–183 m and 184–366 m. A total of 184 species of decapod Crustacea, comprising 12,943 individuals from 38 families, was collected. Families with the most species were Majidae and Xanthidae, while the Penaeidae comprised about 42% of the total number of individuals. The ten most abundant species were: the shrimps, *Sicyonia brevirostris, Mesopenaeus tropicalis, Trachypenaeus constrictus, Metapenaeopsis goodei,* and *Solenocera atlantidis*; the portunid crab, *Portunus spinicarpus* and *Ovalipes stephensoni*; the scyllarid lobster *Scyllarus chacei*; the majid crab, *Stenorhynchus seticornis*; and the crangonid shrimp *Pontophilus brevirostris.* These ten species comprised about 77% of all individuals collected. Normal and inverse cluster analyses indicated that site and species groups were related to depth. There was no latitudinal separation of site groups, and depth related changes in groups were altered very little seasonally. Species groups consisted of an inner shelf assemblage, an open shelf assemblage and an upper slope assemblage. Both cluster analysis and reciprocal averaging ordination showed the site groups and faunal assemblages of the upper slope (>145 m) were distinct from those located at shallower depths. Diversity values of H′, species richness and evenness for open shelf, sand bottom stations remained uniform from the inner continental shelf to the upper continental slope; however, stations characterized by hard or rocky substrates and attached sessile invertebrates, such as octocorals, sponges, tunicates and bryozoans, tended to have greater diversity than the open shelf stations at the same depth.

The decapod Crustacea of the Carolinian shelf province, extending from Cape Hatteras to Cape Canaveral, Florida (Briggs, 1974), have been the subject of numerous systematic accounts since the last century (Williams, 1965). Although the number of ecological papers on the decapod Carolinian fauna of the Atlantic has increased, few species have been studied in detail, and information on the spatial and temporal distributional patterns of multi-species assemblages of Decapoda from this area is lacking.

This lack of information is not surprising in view of the extensive collecting efforts needed to reveal latitudinal as well as bathymetric patterns of distribution on a seasonal basis within such a large geographic area. Consequently, one approach of ecological studies to date has been to consider the faunal composition of specific habitats, such as the nearshore "blackrock" reefs (Pearse and Williams, 1951) and the lithothamnion reef on the shelf-slope break off North Carolina (Cain, 1972; Menzies et al., 1966). Others have attempted to synthesize information on the macro- and megafauna collected from a wider geographic area. Cerame-Vivas and Gray (1966) examined distributional patterns of benthic macroinvertebrate assemblages on the continental shelf off North Carolina with regard to biogeographic provinces; Day, Field and Montgomery (1971) examined distribution of the benthic invertebrate fauna across the continental shelf of North Carolina; and George and Staiger (1978) discussed seasonal changes in benthic invertebrate and demersal fish populations in the South Atlantic Bight. Although

Day et al. (1971) included the Decapoda in their study, their sampling was done with benthic grabs and dredges which do not effectively sample the large mobile decapod fauna. In addition, they sampled a transect which was confined to homogeneous terrain, so that depth and temperature were the varying physical parameters with no sudden changes in substrate. This avoids many of the problems associated with sampling of heterogeneous environments, but it does not provide any biological information on the specialized fauna associated with reefs found in the study area. The study by George and Staiger (1978) more effectively described community assemblages of decapods and other invertebrates because they sampled not only the sand bottom areas of the continental shelf but also the "live" or hard bottom, reef areas (Struhsaker, 1969), which are defined as those areas which contain a rich epifaunal community of sessile sponges, bryozoans, tunicates, hydrozoans and anthozoans living upon hard or rocky formations. Their study, however, does not provide much in-depth information on any one taxocene.

The purposes of the present paper are to: (1) describe the assemblages of decapod Crustacea collected within the South Atlantic Bight from both the open shelf and live bottom habitats; (2) examine changes in these assemblages with depth, season and latitude; (3) provide estimates of the relative abundance of the Decapoda; and (4) relate their abundance to biological and physical factors where possible.

METHODS AND MATERIALS

Data Collection and Study Area.—Samples of decapod Crustacea were collected during seasonal cruises at 496 randomly located stations in the South Atlantic Bight between Cape Fear, North Carolina, and Cape Canaveral, Florida. All collections were made with a ¾ scale version of a Yankee No. 36 trawl (Wilk and Silverman, 1976), which has a 16.5-m footrope, an 11.9-m headrope and a 1.3-cm stretch mesh codend liner. Tows were made from the 32.6-m R/V DOLPHIN at a speed of 6.5 km/h and were 0.5-h in duration.

Stations were selected by means of a stratified random sampling design with proportional allocation of stations by area within strata. The strata were southward extensions of the Marine Resources Monitoring, Assessment and Prediction (MARMAP) strata utilized by the National Marine Fisheries Service for sampling groundfish off the Middle Atlantic and New England states (Grosslein, 1969). These strata were originally designed as subdivisions of six depth zones: 9–18 m, 19–27 m, 28–55 m, 56–110 m, 111–183 m and 184–366 m which were chosen by subjective evaluation of physicochemical parameters and practical limitations on vessel operations. Because too few trawl tows were made within strata to warrant inter-strata analysis, strata boundaries were collapsed within the six described depth zones (Wenner et al., 1979).

The dates of the cruises and the allocation of randomly located stations within the six depth zones are found in Table 1. Proportional sampling effort per depth zone changed from cruise to cruise due to constraints of weather, vessel schedules, and unsuccessful sampling. Samples of decapod crustaceans taken during tows in which the net was damaged, failed to reach bottom or became twisted during the tow were considered unsuccessful and were not included in analyses. Although no special attempts were made to intensely sample the hard bottom, reef habitats, we have included decapod crustaceans collected from these reef stations in our analyses because we feel they are an important component of the shelf fauna. At reef stations no attempt was made to collect all Decapoda from microhabitats, such as sponges, due to time constraints. A station was considered to be in the hard bottom, reef habitat when the catch contained large amounts of sponges and/or corals and associated fish species (Wenner et al., 1979).

All decapod Crustacea collected were preserved in 10% seawater-formalin and returned to the laboratory where they were transferred to 40% isopropanol, identified to species or the lowest possible taxon and counted. Bottom temperatures were recorded at all stations by reversing thermometers.

Wenner et al. (1979) indicated that the depth zones sampled during our survey may be defined in terms of the continental shelf habitats described by Struhsaker (1969); i.e., the 9–18 m depth zone is equivalent to the coastal habitat, the 19–27 m and 28–55 m depth zones are equivalent to the open shelf habitat and the 56–110 m and 111–183 m depth zones coincide with the shelf edge and lower shelf or upper slope habitats. The sea bottom within the coastal and open shelf areas of the continental shelf is mostly homogeneous, with more than 90% of the shelf's surface area composed of a fora-

Table 1. Monthly designation of seasonal cruises and number of trawl stations occupied per depth zone for each cruise

			Depth Zones (m)					
Season	Cruise	Dates	9–18	19–27	28–55	56–110	111–183	184–366
Winter	D1-1975	Jan. 16–April 10	13	11	16	6	5	5
Winter	D1-1976	Jan. 12–Feb. 7	12	12	16	13	6	5
Winter	D1-1977	Jan. 17–March 9	10	12	18	12	8	9
Spring	D2-1974	April 1–April 26	15	17	18	11	5	4
Summer	D3-1974	August 13–Sept. 19	4	11	8	8	8	4
Summer	D3-1975	August 30–Sept. 19	11	10	16	12	6	6
Summer	D3-1976	August 28–Sept. 21	12	15	21	12	4	7
Fall	D5-1973	Oct. 23–Nov. 16	12	8	11	13	9	6

miniferan sand-mud matrix (George and Staiger, 1978). However, interspersed throughout depth zones bounded by the 19- and 55-m isobaths are ledges, rocky outcrops and reefs covered with epifaunal growths; these constitute the "live" bottom habitat of Struhsaker (1969). Although the "live" bottom or reef habitat supports extensive faunal communities of invertebrates and fishes, its extent in terms of surface area is limited, and its distribution in the area between Cape Fear and Cape Canaveral is localized and patchy (George and Staiger, 1978). Other reef formations which occur within the study area include the "blackrock" formations off North Carolina at depths of 5 to 15 m (Pearse and Williams, 1951), the ancient lithothamnion reefs that border the shelf break between Cape Hatteras and Miami (Menzies et al., 1966; Emery and Uchupi, 1972); and the rocky outcrops of the shelf-edge which support encrustations of coral, sponge and miscellaneous other invertebrates (Struhsaker, 1969).

Mathews and Pashuk (1977), Atkinson (1978), and Atkinson et al. (1978) concur that the waters overlying the continental shelf in the South Atlantic Bight are most affected by freshwater runoff into the coastal area and intrusions of the Gulf Stream onto the shelf. Increased run-off in winter and spring contribute to the presence of a southwesterly flowing current near shore (Mathews and Pashuk, 1977). Gulf Stream intrusions are a major influence on upwelling and both horizontal and vertical thermal gradients.

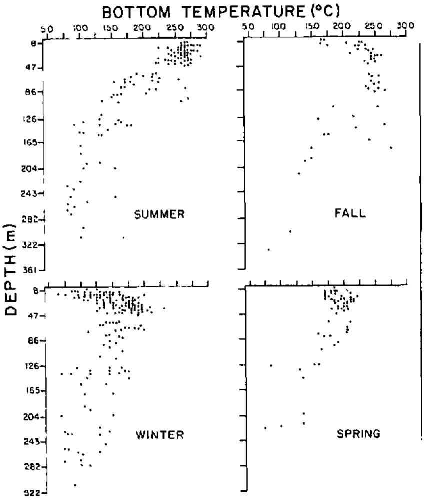
Upwelling has been found to be particularly strong and continuous in the area east of Charleston (Mathews and Pashuk, 1977). The intrusion of the Gulf Stream and its subsequent deflection is the probable cause of the upwelling which renews water in this area of the shelf and provides a fresh source of nutrients (Blanton, 1971; Stefansson et al., 1971). Throughout the South Atlantic Bight, upwelling is most noticeable during the summer months of August and September. During this period, offshore movement of the Gulf Stream in the surface layer is accompanied by intrusion of colder, deeper water at depths up to about 36 m. During December and January, however, the Gulf Stream moves toward shore in the surface layer. This onshore movement is accompanied by cascading of cold shelf water at depths from approximately 36 to 90 m (O. Pashuk, pers. comm.).

Vertical gradients in temperature also change seasonally due to Gulf Stream influence. In general, little vertical thermal stratification occurs on the shelf in winter and spring; however, a strong thermocline caused by intrusion of cold, deep water onto the shelf occurs during the fall and summer.

An examination of bottom temperature with depth indicates that a horizontal temperature gradient up to 47 m is most pronounced in the study area during winter (Fig. 1). Bottom temperatures were lowest at the shallowest depths, whereas temperatures were warmer at depths approaching 47 m, due to the intruding Gulf Stream water. Beyond 47 m, bottom temperatures slowly decreased with increasing depth. In summer, horizontal bottom temperatures decreased toward deeper water. Atkinson et al. (1978) noted that temperature ranges tend to be much greater in winter than in summer because of the cooling influence of meteorological cold fronts from the continent or the warming influence of Gulf Stream intrusions. Spring and fall are hydrographic transitional periods, although in fall there was a tendency for bottom temperatures to increase from the shallowest depths to approximately 86 m, beyond which they began to decrease. In spring, there was a slow decrease in bottom temperature with increasing depth.

Data Analysis.—An index of abundance (Musick and McEachran, 1972; Elliott, 1973) was used to assess relative abundance of numerically dominant species within depth zones and is calculated by the following expression:

$$\text{Index of Abundance} = 1/n \sum_{1}^{n} \log(x + 1)$$



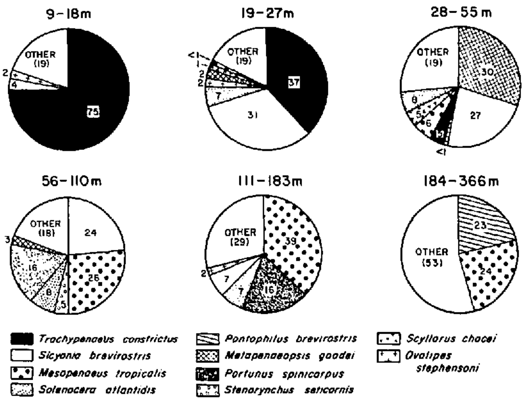


Figure 1. (Left) Bottom temperatures as a function of depth for otter trawl stations made in the South Atlantic Bight between Cape Fear and Cape Canaveral from 1973–1977.

Figure 2. (Right) Percent total abundance of 10 numerically dominant decapod Crustacea in six depth zones sampled with otter trawls. Numbers inside pie diagrams indicate percent of total decapod fauna within each depth zone contributed by individuals of the 10 dominant species.

where x = number of individuals of a given species within a depth zone and n = number of collections in a depth zone.

Statistically significant differences in abundance by depth zone were determined by one-way analysis of variance (Model I) and Duncan's multiple mean comparison test (Steel and Torrie, 1960).

Numerical classification (cluster analysis) and reciprocal averaging ordination were used to determine species associations and distributional patterns. Prior to analysis, the data were reduced by elimination of species which occurred at only one or two stations occupied during a sampling season. Similarly, stations were eliminated from analysis if they contained only one species prior to or after data reduction. These data reductions were necessary because species which occur at only one or two stations generally lack a perceivable distribution pattern (Boesch, 1973). Further, inclusion of stations which contain only one species may lead to confusion in interpreting the site cluster analysis and do not give a representative catch of the decapod fauna.

After data reduction, numerical classification analysis was performed on quantitative collections from each season using the program COMPAH. Algorithms used included a combination of square root transformation ($\sqrt{\pi}$), the Canberra metric similarity measure and flexible sorting with $\beta = -0.25$ (Clifford and Stephenson, 1975; Boesch, 1977). The Canberra metric similarity coefficient (Lance and Williams, 1967) was chosen because it is effective when organisms are contagiously distributed (and benthic organisms generally are) and because it gives rare species as much weight in determining similarity as abundant species (Boesch, 1977). Therefore, with the use of the Canberra metric similarity coefficient, an outstandingly abundant species does not dominate the index (Clifford and Stephenson, 1975). Because the Canberra metric measure is insensitive to large values and can be used with data which contain abundant as well as rare species, it may be used with a mild transformation, such as square root (Clifford and Stephenson, 1975).

Post-clustering techniques of nodal analysis (Williams and Lambert, 1961; Lambert and Williams, 1962) were employed to examine species and site group coincidences, to identify misclassifications, and to describe site groups in terms of their characteristic species and species groups in terms of their occurrence within site groups. Nodal analysis interpretations were made by using patterns of constancy (a measure of how consistently a species is found in a site group) and fidelity (a measure of how restricted a species group is to a site group). Both constancy and fidelity are qualitative measures and imply nothing about the abundance of species. Constancy has a value of 1 when all species occur in all collections in a site group and 0 when none of the species occur in the collections in the group. The fidelity index ranges from values greater than 2, suggesting strong association of species with a site group, to less than 1, which suggests "negative" association of species with a site group (Boesch, 1977).

After the species and site assemblages were determined by cluster analysis, reciprocal averaging ordination (Hill, 1973) was used to determine where major changes in faunal composition occurred along the depth gradient. This technique is useful in revealing correspondences between species and samples by simultaneous ordinations of these components in the same space (Gauch, et al., 1977) and in relating the coenocline modeled in the sample ordination to the depth gradient (Wenner and Boesch, 1979). A summary of the underlying mathematics of ordination is found in Hill (1973). Ordinations were produced by Cornell Ecology Program CEP-25A, ORDIFLEX (Gauch, 1977).

Prior to ordination, a logarithmic transformation, log (x + 1) where x is number of individuals for a given species, was used to reduce scalar differences in the inverse ordination (of species) and to reduce the weight of abundant species relative to those less abundant in the normal ordination (of collections) (Fasham, 1977). After transformation and data reduction, reciprocal averaging ordination was performed on quantitative collections from each season individually.

Species diversity was measured by H′ (Pielou, 1977) and the components of diversity, species richness (the number of species in a community) and evenness (how evenly the individuals are distributed among the species). The index H′ is expressed by:

$$H' = -\sum_{i=1}^{s} P_i \log_2 P_i$$

where s = number of species in the sample
P_i = proportion of the i^{th} species in the sample

The components of diversity were estimated by the following equations:

$$\text{Species Richness} = (s - 1)/\log_e N \text{ (Margalef, 1958)}$$
$$\text{Evenness} = H'/\log_2 s \text{ (Pielou, 1966)}$$

where N = number of individuals
s = number of species in the collection

RESULTS

Species Composition

A total of 184 species of decapod Crustacea comprising 12,943 individuals from 38 families was collected during seasonal cruises. The number of individuals of species collected and the minimum and maximum depth and temperature where they occurred are shown in Table 2. The total number of species collected was much less than the 291 species of Decapoda reported from shelf waters of the Carolinas (Herbst et al., 1978). This under-estimation is probably due to invulnerability of the Decapoda to the ¾ scale Yankee 36 trawl. This trawl, designed for capture of groundfishes, is equipped with 6-in rubber discs on the footrope which facilitate movement of the trawl over and slightly off the bottom, thus minimizing snags of the net. It is probable that the ¾ Yankee trawl under-estimates the decapod fauna both in terms of total number and species.

The total number of species and individuals collected varied both seasonally and annually (Table 3). The greatest number of species was usually collected in the fall and summer, whereas fewer species were generally represented in collections from winter and spring. The variability in species number with season does not appear to be an artifact of sampling because increased total sampling effort in winter and summer, which extended over several years, did not bias collection efforts toward an increased number of species during both those seasons.

Families with the most species were Majidae and Xanthidae with 27 and 16 species, respectively, while the Penaeidae comprised about 42% of the total number of individuals of all species. The Portunidae were the second most abundant family represented and made up about 11% of the total number of Decapoda collected.

Table 2. Decapod Crustacea collected on the continental shelf between Cape Fear and Cape Canaveral for all seasons and cruises combined. Decapoda with questionable identification are not included. Species are ranked according to abundance

Species	Number Station Occurrences	Total Number Specimens	Depth (m)		Temperature (C)	
			Min.	Max.	Min.	Max.
1. *Sicyonia brevirostris*	154	2,355	10	155	10.4	29.0
2. *Mesopenaeus tropicalis*	72	2,090	11	223	10.0	27.8
3. *Trachypenaeus constrictus*	76	1,892	9	44	10.4	29.0
4. *Metapenaeopsis goodei*	63	1,065	15	232	8.6	29.0
5. *Portunus spinicarpus*	58	869	38	188	6.8	29.0
6. *Solenocera atlantidis*	69	766	16	232	8.0	29.0
7. *Pontophilus brevirostris*	17	368	48	329	6.8	27.7
8. *Stenorhynchus seticornis*	46	223	17	188	13.0	28.6
9. *Ovalipes stephensoni*	69	164	10	227	6.7	29.0
10. *Scyllarus chacei*	40	158	20	66	14.0	29.0
11. *Portunus gibbesii*	42	153	9	60	6.7	28.6
12. *Catapagurus sharreri*	21	—[a]	20	311	6.8	18.4
13. *Parapenaeus longirostris*	17	151	102	229	8.6	24.0
14. *Portunus spinimanus*	58	145	12	82	11.1	28.6
15. *Cancer irroratus*	19	122	13	311	6.8	27.4
16. *Penaeopsis serrata*	7	117	221	329	7.3	27.7
17. *Rochinia crassa*	27	112	66	329	6.8	21.6
18. *Cancer borealis*	23	93	48	329	7.4	27.7
19. *Plesionika tenuipes*	10	76	159	274	7.3	24.0
20. *Calappa flammea*	40	75	9	262	9.2	28.6
21. *Parapandalus willisi*	5	66	256	329	7.3	27.7
22. *Portunus ordwayi*	14	63	15	72	16.8	28.6
23. *Sicyonia typica*	23	55	9	82	7.7	28.6
24. *Pilumnus sayi*	31	48	9	48	9.1	29.0
25. *Calappa angusta*	17	45	17	188	12.8	29.0
26. *Nephropsis aculeata*	7	41	137	260	7.4	14.0
27. *Parthenope fraterculus*	13	41	31	128	13.0	26.8
28. *Anasimus latus*	14	40	27	188	13.1	25.7
29. *Penaeus duorarum*	14	38	12	31	12.7	28.6
30. *Processa vicina*	15	38	24	223	10.0	29.0
31. *Tozeuma serratum*	11	35	15	188	12.8	26.4
32. *Porcellana sayana*	16	33	18	110	15.5	27.5
33. *Stenocionops furcata coelata*	18	32	13	91	9.1	27.5
34. *Processa tenuipes*	10	32	44	110	13.1	26.4
35. *Pseudomedaeus agassizii*	11	30	11	221	9.2	27.5
36. *Iliacantha subglobosa*	11	28	16	232	8.0	26.5
37. *Scyllarus depressus*	6	28	31	72	16.8	24.8
38. *Petrochirus diogenes*	25	27	16	128	13.0	27.6
39. *Podochela sidneyi*	18	26	11	72	13.1	27.3
40. *Synalpheus townsendi*	11	25	11	72	6.7	26.2
41. *Munida iris iris*	10	24	43	254	11.0	27.5
42. *Parthenope agona*	11	24	70	124	13.5	26.4
43. *Parthenope serrata*	19	23	15	66	12.8	29.0
44. *Processa* nr. *tenuipes*[b]	5	23	64	82	13.1	23.8
45. *Collodes trispinosus*	16	23	22	247	8.6	26.8
46. *Dardanus insignis*	16	23	22	192	11.3	25.1
47. *Pachycheles rugimanus*	13	22	11	75	9.2	27.5
48. *Munida irrasa*	12	22	44	203	10.4	26.8
49. *Osachila semilevis*	5	21	66	91	15.5	23.8
50. *Podochela gracilipes*	12	20	25	137	8.5	16.4
51. *Pyromaia cuspidata*	9	18	124	210	8.5	17.6
52. *Stenocionops spinimana*	15	18	60	170	8.9	21.3
53. *Mithrax pleuracanthus*	7	16	11	43	9.2	27.5
54. *Mithrax forceps*	5	16	20	40	9.2	18.9
55. *Processa profunda*	6	16	159	232	8.0	24.0

Table 2. Continued

Species	Number Station Occurrences	Total Number Specimens	Depth (m)		Temperature (C)	
			Min.	Max.	Min.	Max.
56. *Dromidia antillensis*	15	16	13	82	10.5	27.5
57. *Porcellana sigsbeiana*	7	15	16	203	10.4	27.6
58. *Sicyonia stimpsoni*	7	15	66	210	12.8	20.7
59. *Dardanus fucosus*	9	13	20	73	17.2	26.7
60. *Libinia dubia*	9	12	10	31	15.0	27.6
61. *Pilumnus lacteus*	4	11	11	32	16.7	26.8
62. *Galathea rostrata*	3	10	43	66	13.1	27.5
63. *Myropsis quinquespinosa*	9	10	102	155	8.5	17.7
64. *Bathynectes longispina*	6	9	137	311	7.8	13.4
65. *Megalobrachium soriatum*	3	8	11	24	9.2	27.9
66. *Pantomus parvulus*	3	8	139	247	8.0	17.9
67. *Nibilia antilocapra*	3	7	66	159	16.8	24.0
68. *Iliacantha intermedia*	7	7	18	84	16.3	29.0
69. *Hepatus epheliticus*	6	7	10	22	13.5	27.6
70. *Parthenope pourtalesii*	4	7	24	101	15.8	26.4
71. *Clythrocerus nitidus*	2	7	278	329	8.0	27.7
72. *Bythocaris nana*	2	6	247	247	8.4	14.0
73. *Solenocera necopina*	4	6	174	232	8.0	15.2
74. *Palicus sica*	4	6	82	159	13.0	26.4
75. *Pylopagurus corallinus*	5	6	42	91	15.5	27.5
76. *Homola barbata*	2	6	70	72	15.5	16.8
77. *Metoporhaphis calcarata*	5	6	16	44	6.7	26.2
78. *Batrachonotus fragosus*	5	6	22	247	8.4	26.1
79. *Callinectes sapidus*	5	6	11	24	9.6	27.9
80. *Micropanope sculptipes*	4	6	11	128	13.0	17.0
81. *Carpoporus papulosus*	6	6	59	97	14.0	26.8
82. *Synalpheus fritzmuelleri*	3	6	11	43	16.7	27.9
83. *Scyllarides nodifer*	3	5	38	59	18.4	27.3
84. *Penaeus aztecus*	4	5	15	24	15.0	27.9
85. *Palicus faxoni*	3	5	72	82	16.8	26.4
86. *Pelia mutica*	1	5	11	11	16.7	16.7
87. *Podochela riisei*	5	5	11	139	11.9	22.2
88. *Pagurus impressus*	4	5	12	20	17.2	27.6
89. *Portunus sayi*	3	5	13	40	19.1	22.9
90. *Pagurus politus*	4	5	35	260	7.8	26.3
91. *Munida longipes*	4	5	40	311	8.6	19.6
92. *Munida pusilla*	1	5	66	66	20.7	20.7
93. *Coelocerus spinosus*	5	5	26	38	18.9	26.3
94. *Merhippolyte americana*	1	5	232	232	8.0	8.0
95. *Mithrax spinosissimus*	3	4	25	43	13.4	27.5
96. *Lysmata rathbunae*	3	4	35	64	13.1	27.5
97. *Hadropenaeus affinis*	2	4	232	329	8.0	8.6
98. *Latreillia elegans*	2	4	168	214	13.4	16.7
99. *Geryon quinquedens*	3	4	247	278	7.9	14.0
100. *Acanthocarpus alexandri*	2	4	137	139	16.0	17.6
101. *Pylopagurus discoidalis*	2	4	214	278	13.4	27.7
102. *Palicus alternatus*	2	4	44	278	22.2	27.7
103. *Euchirograpsus americanus*	3	4	40	75	18.0	20.7
104. *Nanoplax xanthiformis*	2	4	11	43	16.7	27.5
105. *Pilumnus pannosus*	1	4	11	11	16.7	16.7
106. *Pilumnus floridanus*	2	4	11	43	16.7	27.5
107. *Sicyonia dorsalis*	3	4	12	15	13.2	25.8
108. *Petrolisthes galathinus*	1	3	11	11	16.7	16.7
109. *Albunea gibbesii*	3	3	37	38	15.1	26.7
110. *Ranilia muricata*	3	3	16	101	15.9	21.1
111. *Osachila tuberosa*	3	3	44	91	20.5	26.4
112. *Marocoeloma trispinosum*	3	3	15	27	27.0	27.6

Table 2. Continued

Species	Number Station Occurrences	Total Number Specimens	Depth (m)		Temperature (C)	
			Min.	Max.	Min.	Max.
113. *Cycloes bairdii*	1	3	59	59	21.9	21.9
114. *Thalassoplax angusta*	2	3	203	232	8.0	10.4
115. *Tetraxanthus rathbunae*	2	3	232	247	8.0	8.4
116. *Leptochela carinata*	3	3	37	66	18.1	20.7
117. *Portunus floridanus*	1	3	81	81	22.1	22.1
118. *Plesionika edwardsi*	1	3	232	232	8.0	8.0
119. *Plesionika martia*	1	3	232	232	8.0	8.0
120. *Leptochela papulata*	1	2	20	20	12.3	12.3
121. *Palicus* nr. *cursor*[c]	1	2	221	221	13.1	13.1
122. *Hardopenaeus modestus*	2	2	232	329	8.0	8.6
123. *Stenopus scutellatus*	1	2	43	43	27.5	27.5
124. *Pylopagurus holthusisi*	1	2	66	66	20.7	20.7
125. *Gastroptychus affinis*	1	2	260	260	9.5	9.5
126. *Collodes robustus*	2	2	101	137	14.5	26.0
127. *Ethusa mascarone americana*	2	2	35	66	25.4	26.7
128. *Pinnaxodes floridensis*	2	2	22	38	18.0	27.7
129. *Eumunida picta*	2	2	278	239	8.0	9.9
130. *Calocaris jenneri*	1	2	232	232	8.0	8.0
131. *Periclimenes* nr. *yucatanicus*[d]	1	2	72	72	16.8	16.8
132. *Calappa sulcata*	2	2	124	128	15.9	16.0
133. *Hypoconcha sabulosa*	2	2	17	79	16.1	27.6
134. *Iridopagurus dispar*	2	2	62	82	19.5	26.4
135. *Pilumnus dasypodus*	2	2	11	16	6.7	16.7
136. *Lobopilumnus agassizii*	2	2	38	40	23.5	24.4
137. *Frevillea hirsuta*	2	2	137	137	16.0	16.0
138. *Synalpheus minus*	1	2	11	11	16.7	16.7
139. *Alpheus formosus*	1	2	43	43	27.5	27.5
140. *Mithrax acuticornis*	1	1	66	66	17.0	17.0
141. *Gnathophyllum modestum*	1	1	66	66	17.0	17.0
142. *Pontonia margarita*	1	1	24	24	24.3	24.3
143. *Synalpheus longicarpus*	1	1	72	72	16.8	16.8
144. *Alpheus normanni*	1	1	82	82	26.4	26.4
145. *Leptochela serratorbita*	1	1	20	20	23.3	23.3
146. *Acetes americanus carolinae*	1	1	16	16	26.5	26.5
147. *Paguristes sericeus*	1	1	20	20	13.8	13.8
148. *Ogyrides alphaerosteis*	1	1	16	16	27.4	27.4
149. *Periclimens iridescens*	1	1	42	42	26.1	26.1
150. *Dissodactylus mellitae*	1	1	124	124	16.0	16.0
151. *Glyptoxanthus erosus*	1	1	43	43	27.5	27.5
152. *Hexapanopeus angustifrons*	1	1	12	12	25.8	25.8
153. *Pagurus defensus*	1	1	44	44	22.2	22.2
154. *Paguristes spinipes*	1	1	72	72	16.8	16.8
155. *Hypoconcha arcuata*	1	1	66	66	17.0	17.0
156. *Albunea paretii*	1	1	13	13	14.4	14.4
157. *Persephona mediterranea*	1	1	16	16	16.3	16.3
158. *Plesionika longipes*	1	1	234	234	8.8	8.8
160. *Cryptopodia concava*	1	1	44	44	22.2	22.2
161. *Aepinus septemspinosus*	1	1	44	44	22.2	22.2
162. *Axiopsis hirsutimana*	1	1	137	137	16.0	16.0
163. *Munidopsis polita*	1	1	247	247	14.0	14.0
164. *Hypoconcha spinosissima*	1	1	42	42	19.1	19.1
165. *Ethusa microphthalma*	1	1	201	201	13.6	13.6
166. *Goneplax barbata*	1	1	278	278	27.7	27.7
167. *Munida simplex*	1	1	278	278	9.9	9.9
168. *Pseudomedaeus distinctus*	1	1	72	72	16.8	16.8
169. *Pagurus carolinensis*	1	1	11	11	16.7	16.7
170. *Benthopagurus cokeri*	1	1	260	260	9.5	9.5

Table 2. Continued

Species	Number Station Occurrences	Total Number Specimens	Depth (m)		Temperature (C)	
			Min.	Max.	Min.	Max.
171. *Libinia emarginata*	1	1	73	73	11.1	11.1
172. *Rochinia umbonata*	1	1	329	329	8.0	8.0
173. *Rochinia tanneri*	1	1	278	278	27.7	27.7
174. *Robertsella* nr. *mystica*[e]	1	1	247	247	14.0	14.0
175. *Lyreidus bairdii*	1	1	260	260	9.6	9.6
176. *Periclimenaeus wilsoni*	1	1	11	11	16.7	16.7
177. *Anomalothir furcillata*	1	1	139	139	17.9	17.9
178. *Hemus cristulipes*	1	1	16	16	27.4	27.4
179. *Goneplax sigsbei*	1	1	137	137	8.5	8.5
180. *Hepatus pudibundus*	1	1	24	24	24.3	24.3
181. *Synalpheus fritzmuelleri elongatus*	1	1	11	11	16.7	16.7
182. *Pontophilus gracilis*	1	1	274	274	7.3	7.3
183. *Processa hemphilli*	1	1	24	24	27.3	27.3
184. *Arenaeus cribrarius*	1	1	9	9	18.6	18.6

[a] Total number not available.
[b] Variation of *Processa tenuipes* (A. B. Williams, pers. comm.).
[c] Variation of *Palicus cursor* (A. B. Williams, pers. comm.).
[d] Variation of *Periclimenes yucatanicus* (A. B. Williams, pers. comm.).
[e] Variation of *Robertsella mystica* (A. B. Williams, pers. comm.).

The 10 most abundant species were: the penaeoid shrimps *Sicyonia brevirostris, Mesopenaeus tropicalis, Trachypenaeus constrictus, Metapenaeopsis goodei,* and *Solenocera atlantidis*; the portunid crabs *Portunus spinicarpus* and *Ovalipes stephensoni*; the scyllarid lobster *Scyllarus chacei*; the majid crab, *Stenorhynchus seticornis*; and the crangonid shrimp *Pontophilus brevirostris*. These 10 species comprised about 77% of all individuals collected (Table 2). Although many of the remaining 173 species of Decapoda were regularly collected, they were not abundant.

The abundance of the ten numerically dominant species for each depth zone is shown in Figure 2. *Trachypenaeus constrictus* was the most abundant species in the 9–18 m and 19–27 m depth zones. At 28–55 m, *Metapenaeopsis goodei* predominated, while in depth zones of 56–110 m and 111–183 m, *Mesopenaeus tropicalis* was the most abundant species collected. At the deepest depths sampled (184–366 m), most of the catch (53%) consisted of species other than the top ten Decapoda, although *Pontophilus brevirostris* and *Mesopenaeus tropicalis* made up 23% and 24% of the total catch, respectively.

Relative Abundance of Numerically Dominant Species.—The relative abundance of the dominant Penaeidea by depth zone and for each season is shown in Figure 3. *Sicyonia brevirostris* was the most abundant decapod collected ($\Sigma Y = 2{,}355$, where Y is number of individuals per station) and occurred at 31% of the 496 stations. Rock shrimp occurred between depths of 10 and 155 m, but analysis of variance showed a significant difference in abundance among depth zones ($F = 11.67$, $P < 0.01$, df 5/490). Duncan's multiple range test indicated that maximum abundance was within the 56–110 m depth zone, where *S. brevirostris* occurred in 40 of 87 trawl tows. Rock shrimp were most abundant in fall and least abundant in winter. The greater abundance of rock shrimp in fall has been noted by Kennedy et al. (1977) and Cobb et al. (1973) for the continental shelf off Florida. Lunz (1957) noted that rock shrimp abundance off South Carolina was greatest from September through December and in May. Increased abundance of *S. bre-*

Table 3. The total number of species and number of individuals collected by season from 1973–1977

	Year	Fall	Winter	Spring	Summer
Number of species	1973	96			
	1974			79	71
	1975		51		106
	1976		87		91
	1977		57		
Number of individuals	1973	2,912			
	1974			1,094	875
	1975		979		2,940
	1976		1,505		2,114
	1977		527		

virostris during fall has been attributed to recruitment of juvenile shrimp which reach adult size during late summer and fall (Kennedy et al., 1977).

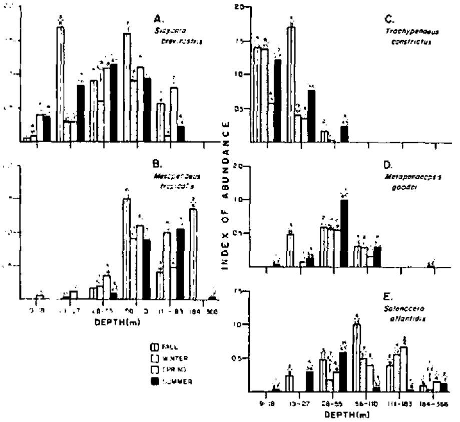
Mesopenaeus tropicalis, which ranked second in abundance of Decapoda ($\Sigma Y = 2{,}090$), occurred in 14.5% of all collections. It was found in all depth zones but was collected at depths shallower than 28 m only during winter and spring. Abundance of *M. tropicalis* was significantly different among depth zones ($F = 19.16$, $P < 0.01$, df 5/490), with catch rates highest between 56 and 183 m, where it occurred in 37% of the 138 collections. This species usually occurred in greatest numbers during fall. Perez Farfante (1977) states that *M. tropicalis* is infrequently encountered in shallow waters of the continental shelf and does not appear to undergo seasonal migration from shelf waters to upper slope depths.

Trachypenaeus constrictus was the third most abundant decapod collected ($\Sigma Y = 1{,}892$). It was found only in depths shallower than 55 m, where there was a significant difference in abundance among depth zones ($F = 25.91$, $P < 0.01$, df 5/490). *Trachypenaeus constrictus* was most abundant at depths of 9–18 m, where it occurred in 12 of 31 trawl tows. Catches were highest in fall and lowest in spring. Chace (1972) indicates that the depth range of *T. constrictus* extends from shallow water to 59 m throughout its geographic distribution.

Metapenaeopsis goodei was collected at depths between 15 and 232 m, but its abundance differed significantly among depth zones ($F = 15.88$, $P < 0.01$, df 5/490). Depths of greatest occurrence for *M. goodei* were from 28–55 m. Perez Farfante (1971) indicates that most specimens have been taken from depths less than 60 m; however, the known depth range does extend to 329 m. Catches in our study area were greatest in summer, which agrees with Wheeler's (1937) results on *M. goodei* from the Bermudas.

Solenocera atlantidis was the least abundant shrimp collected ($\Sigma Y = 766$) and ranked sixth in total number among all Decapoda. Specimens were taken at depths from 16–232 m, and there was a significant difference in catch rates among depth zones ($F = 4.65$, $P < 0.01$, df 5/490). Most individuals occurred in depth zones of 28–55 m and 56–110 m. Catches were highest during fall. Most specimens of *S. atlantidis* have been previously taken at depths <75 m, and only a few shrimp have been collected in water >125 m (Perez Farfante and Bullis, 1973).

Pontophilus brevirostris was the only caridean shrimp included among the ten most abundant Decapoda. This species was found from 48 to 329 m but occurred at only one station at depths <111 m (Fig. 4). Within its bathymetric range, catches of *P. brevirostris* were significantly different among depth zones ($F = 25.25$, $P < 0.01$, df 5/490), with largest catches occurring at depths of 184–366 m and in summer.



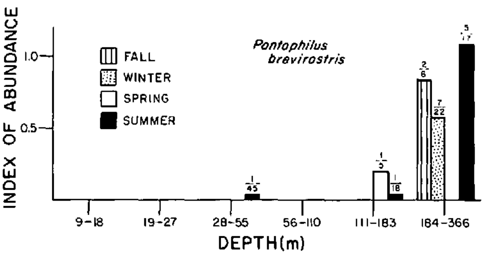
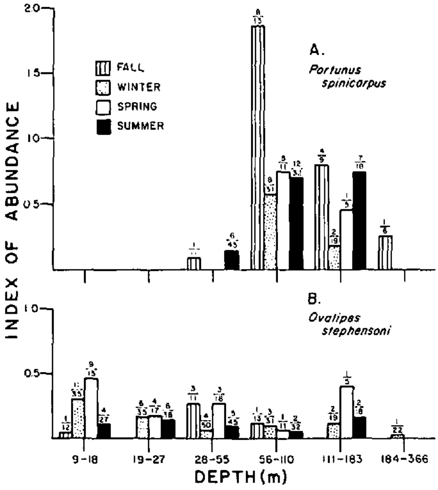


Figure 3. (Left) Index of relative abundance (see text for explanation) by depth zone and season for numerically dominant Penaeoidea: A, *Sicyonia brevirostris*; B, *Mesopenaeus tropicalis*; C, *Trachypenaeus constrictus*; D, *Metapenaeopsis goodei*; E, *Solenocera atlantidis*. Fraction above each depth zone is the ratio of successful trawls in which individuals were collected to total number of trawls made in that depth zone.

Figure 4. (Right) Index of relative abundance for the crangonid shrimp, *Pontophilus brevirostris*. See legend of Figure 3 for explanation.

The portunid crabs *Portunus spinicarpus* and *Ovalipes stephensoni,* were the fifth ($\Sigma Y = 869$) and ninth ($\Sigma Y = 164$) most abundant decapods. *Portunus spinicarpus* was not collected in depths <28 m. Catch rates of this crab were significantly different among depth zones (F = 22.99, $P < 0.01$, df 5/490) and were greatest at depths of 56–110 m. *Portunus spinicarpus* was most abundant during the fall (Fig. 5). *Ovalipes stephensoni* was collected in all depth zones, although it was taken in only one trawl tow at depths >183 m. There was a significant



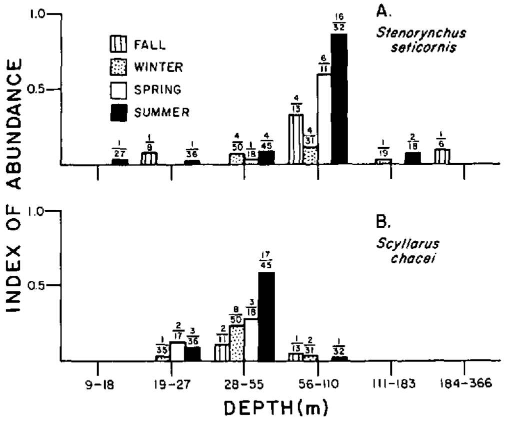


Figure 5. (Left) Index of relative abundance for dominant Portunidae: A, *Portunus spinicarpus*; B, *Ovalipes stephensoni*. See legend of Figure 3 for explanation.

Figure 6. (Right) Index of relative abundance for A, *Stenorynchus seticornis*; B, *Scyllarus chacei*. See legend of Figure 3 for explanation.

Table 4. Site groups represented by numerical classification of Decapoda during four seasons of sampling. (Depths in parentheses indicate depth of misclassified stations.) Areas of the shelf under distribution refer to generalized affinity of site group

Site Group		Number of Stations	Depth (m)	Distribution
Fall	1	6	13–16 (75)	coastal shelf
	2	9	20–40	open shelf
	3	3	35–44	open shelf
	4	3	(38) 128–174	outer shelf
	5	11	40–188	outer shelf
	6	3	159–210	upper slope
Winter	1	18	9–44	coastal shelf
	2	11	10–37	coastal shelf
	3	17	20–79	open shelf
	4	17	31–115	open shelf
	5	10	30–110 (232)	outer shelf
	6	10	(24) 68–170	outer shelf
	7	16	137–311	upper slope
Spring	1	8	9–26	coastal shelf
	2	8	13–60 (124)	coastal shelf
	3	6	22–93	open shelf, outer shelf
	4	14	27–144	open shelf, outer shelf
	5	4	126–219	upper slope
Summer	1	19	12–38	coastal shelf
	2	14	20–44	open shelf
	3	22	13–75 (104)	open shelf
	4	25	11–128 (247)	open shelf
	5	15	(16) 95–260	upper slope
	6	24	(17) 48–155	outer shelf

difference in abundance by depth zone (F = 2.60, $P < 0.05$, df 5/490) with the crabs being most abundant between 9 and 18 m. Catches were highest during spring (Fig. 5).

The reptantians *Stenorhynchus seticornis* and *Scyllarus chacei* ranked eighth ($\Sigma Y = 223$) and tenth ($\Sigma Y = 158$), respectively, among all Decapoda collected. *Stenorhynchus seticornis* occurred from 17–188 m. Catch rates were significantly different among depth zones (F = 18.89, $P < 0.01$, df 5/490) with greatest abundance at depths of 56–110 m (Fig. 6). Williams (1965) states that this crab is most often collected at depths <180 m. Most captures of *S. seticornis* were made in summer, but it was relatively uncommon during all seasons, being caught at only 9% of the 496 trawl collections made. *Scyllarus chacei* occurred between 20 and 66 m, and analysis of variance indicated a significant difference in abundance among depth zones (F = 14.28, $P < 0.01$, df 5/490). Most individuals were collected at 28–55 m in summer.

Species Assemblages and Distributional Patterns.—The dendrograms resulting from both normal and inverse cluster analyses are found in Wenner and Read (1979). Because of limitations in existing computer programs, we were unable to formulate dendrograms which included station and species data combined for all seasons. Therefore, we have focused our analysis on data for each of the four seasons with emphasis on broad spatial and temporal distributional patterns.

Examination of normal cluster analyses indicated that site groups could be categorized according to habitat types described by Struhsaker (1969): an inner shelf or coastal habitat, a mid or open shelf habitat, an outer shelf habitat, and

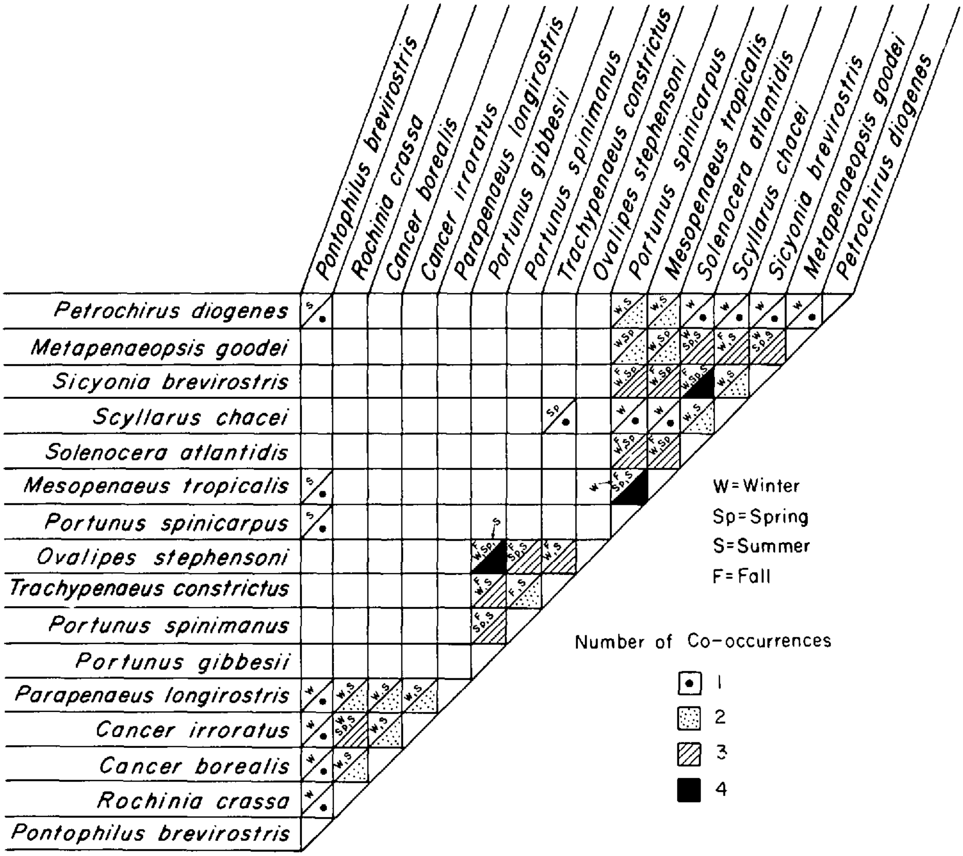


Figure 7. Trellis diagram showing co-occurrences of major species within the same species cluster.

an upper slope habitat. Although the number and bathymetric range of site groups varied seasonally according to habitat type, the depths of these site groups overlapped considerably within each season (Table 4). There was no latitudinal separation of site groups, and major depth-related changes in groups were altered very little seasonally. Greatest similarity occurred among stations located on the upper slope during winter and spring when coastal, open shelf and outer shelf stations in site groups were least similar in species composition to stations in the upper slope site group. In summer and fall, however, this deeper site group was more similar to the open and/or outer shelf site groups which indicates that upper slope and open shelf stations contained many of the same species.

Inverse cluster anlayses indicated that species groups (Table 5), regardless of season, clustered together according to their distribution on the continental shelf. Examination of a trellis diagram, which displays the number of times dominant species occurred within the same species group as determined by four seasonal inverse cluster analyses, showed that three cohesive species groups were present (Fig. 7): an inner or coastal shelf assemblage, an open shelf assemblage which includes species that occur at mid to outer shelf depths, and an upper slope assemblage.

Nodal analyses aided in our interpretation of the relation of species groups to site groups through concepts of constancy and fidelity. *Trachypenaeus constric-*

Table 5. Species groups of decapod Crustacea resulting from numerical classification of trawl-collected data for four seasons

	Fall		Winter		Spring		Summer
Group A	*Portunus gibbesii*	Group A	*Iliacantha subglobosa*	Group A	*Trachypenaeus constrictus*	Group A	*Synalpheus townsendi*
	Ovalipes stephensoni		*Processa* sp.		*Sicyonia typica*		*Pseudomedaeus agassizii*
	Portunus spinimanus		*Sicyonia stimpsoni*		*Scyllarus chacei*		*Parthenope fraterculus*
	Trachypenaeus constrictus		*Processa tenuipes*		*Coelocerus spinosus*		*Munida iris iris*
	Penaeus duorarum		*Calappa angusta*		*Pilumnus sayi*		*Carpoporus papulosus*
	Calappa flammea	Group B	*Libinia dubia*	Group B	*Portunus spinimanus*		*Micropanope sculptipes*
Group B	*Dardanus fucosus*		*Hepatus epheliticus*		*Portunus gibbesii*		*Dardanus insignis*
	Porcellana sayana	Group C	*Metapenaeopsis goodei*		*Ovalipes stephensoni*	Group B	*Iliacantha subglobosa*
Group C	*Metapenaeopsis goodei*		*Sicyonia brevirostris*	Group C	*Parthenope serrata*		*Parthenope agona*
	Dardanus insignis		*Scyllarus chacei*		*Stenocionops furcata coelata*		*Munida irrasa*
	Scyllarus chacei		*Solenocera atlantidis*		*Stenorhynchus seticornis*		*Processa* sp.
Group D	*Anasimus latus*		*Mesopenaeus tropicalis*		*Parthenope agona*		*Podochela gracilipes*
	Stenorhynchus seticornis		*Portunus spinicarpus*		*Petrochirus diogenes*		*Processa tenuipes*
Group E	*Solenocera atlantidis*		*Petrochirus diogenes*		*Collodes trispinosus*		*Osachila tuberosa*
	Mesopenaeus tropicalis		*Porcellana sayana*	Group D	*Anasimus latus*		*Tozeuma serratum*
	Sicyonia brevirostris		*Processa vicina*		*Portunus spinicarpus*	Group C	*Penaeus duorarum*
	Portunus spinicarpus		*Collodes trispinosus*		*Sicyonia brevirostris*		*Calappa flammea*
Group F	*Munida irrasa*		*Parthenope serrata*		*Mesopenaeus tropicalis*		*Trachypenaeus constrictus*
	Calappa angusta		*Sicyonia typica*		*Metapenaeopsis goodei*		*Ovalipes stephensoni*
	Parapenaeus longirostris	Group D	*Stenorhynchus seticornis*		*Solenocera atlantidis*		*Portunus spinimanus*
	Processa profunda		*Parthenope fraterculus*		*Calappa flammea*		*Portunus gibbesii*
			Dromidia antillensis	Group E	*Cancer irroratus*		*Sicyonia typica*
			Stenocionops furcata coelata		*Rochinia crassa*		*Podochela sidneyi*
			Calappa flammea				*Callinectes sapidus*
			Trachypenaeus constrictus			Group D	*Porcellana sigsbeiana*
			Ovalipes stephensoni				*Dromidia antillensis*
			Portunus gibbesii				*Macrocoeloma trispinosum*
			Synalpheus townsendi				*Portunus spinicarpus*
			Podochela sidneyi				*Mesopenaeus tropicalis*
			Pilumnus sayi				*Petrochirus diogenes*
			Podochela gracilipes				

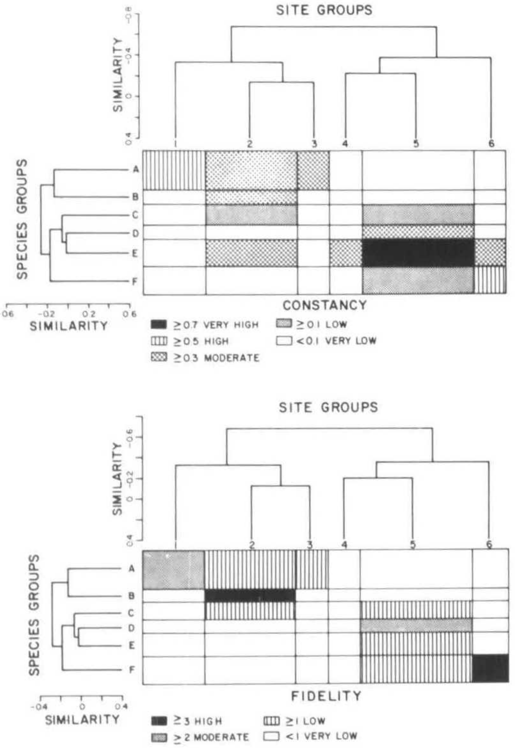
Table 5. Continued

Fall	Winter		Spring	Summer	
	Group E	*Scyllarus depressus*			*Porcellana sayana*
		Dardanus fucosus			*Mithrax pleuracanthus*
		Portunus spinimanus			*Calappa angusta*
		Pachycheles rugimanus			*Libinia dubia*
		Pseudomedaeus agassizii			*Pachycheles rugimanus*
		Mithrax forceps			*Pilumnus sayi*
	Group F	*Parapenaeus longirostris*			*Pontophilus brevirostris*
		Myropsis quinquespinosa			*Pantomus parvulus*
		Pyromaia cuspidata		Group E	*Sicyonia brevirostris*
		Stenocionops spinimana			*Metapenaeopsis goodei*
		Plesionika tenuipes			*Scyllarus chacei*
		Penaeopsis serrata			*Solenocera atlantidis*
		Catapagurus sharreri			*Collodes trispinosus*
		Rochinia crassa			*Processa vicina*
		Cancer irroratus			*Portunus ordwayi*
		Pontophilus brevirostris			*Parthenope serrata*
		Munida longipes			*Iliacantha intermedia*
		Cancer borealis			*Stenorhynchus seticornis*
					Stenocionops furcata coelata
					Batrachonotus fragosus
				Group F	*Cancer irroratus*
					Cancer borealis
					Rochinia crassa
					Processa profunda
					Plesionika tenuipes
					Parapenaeus longirostris
					Bathynectes longispina
					Nephropsis aculeata
					Stenocionops spinimana
					Pyromaia cuspidata

tus, Portunus spinimanus, P. gibbesii and *Ovalipes stephensoni* formed a frequently co-occurring inner shelf assemblage whose constancy and fidelity at inner shelf stations changed seasonally. During the fall, these species formed a group (Group A) which was most consistently encountered at stations in site group 1 on the inner shelf (Fig. 8). These species were not restricted to stations in any particular site group, but they also occurred in collections represented in site groups 2 and 3 on the open shelf. In our winter samples, *T. constrictus, O. stephensoni,* and *P. gibbesii* were grouped with Decapoda which were associated with the rocky reef habitat (Group D). These species were collected at few stations in site groups 1 and 2 on the inner shelf and were not restricted to either site group (Fig. 9). *Portunus spinimanus* formed a separate species assemblage (Group E) which was infrequently encountered but restricted to site group 3 on the open shelf. During the spring, *T. constrictus* formed an assemblage (Group A) which was restricted to site group 1 on the shallow shelf but which was infrequently encountered at stations in that site group (Fig. 10). *Portunus spinimanus, P. gibbesii* and *O. stephensoni* comprised a discrete assemblage (Group B) which was common in collections from site group 2 on the coastal shelf and was also restricted to that site group. During summer, *T. constrictus, O. stephensoni, P. spinimanus* and *P. gibbesii* formed a group (C) which was not consistently collected at stations in any site group and showed only moderate faithfulness to inner shelf stations in site group 1 (Fig. 11).

A recurrent group of species which constituted the open shelf decapod assemblage included *Portunus spinicarpus, Mesopenaeus tropicalis, Sicyonia brevirostris* and *Solenocera atlantidis*. These species occurred together during fall, winter and spring. During fall sampling, they were found at stations in several site groups (2, 4, 5, 6) which encompassed the open to upper slope regions but were consistently collected at stations on the outer shelf (site group 5) only. They were not restricted to any site group (Fig. 8). During winter, these species formed a group (Group C) which was not encountered consistently at any site group (Fig. 9). Although the substrate preferences of these species have not been determined, they seem to occur most frequently on the open shelf's sandy substrate. During spring, *P. spinicarpus, S. brevirostris, M. tropicalis,* and *S. atlantidis* and other members of Group D were most consistently collected at stations in site group 4 which ranged bathymetrically from open shelf to outer shelf, but they were not restricted to any site group (Fig. 10). In summer, *S. brevirostris* and *S. atlantidis* belonged to a group of species (Group E) which was most consistently located at stations in site group 2 and was restricted to this open shelf group of stations (Fig. 11). *Portunus spinicarpus* and *Mesopenaeus tropicalis* formed a separate group of species (Group D) which was not constant and not restricted to any site group. Other species in this group, such as *D. antillensis, M. trispinosum, P. sayana, M. pleuracanthus* and *P. sayi,* are most frequently associated with hard bottom and rocky outcrops (Williams, 1965; Powers, 1977).

Parapenaeus longirostris, Cancer irroratus, Cancer borealis, Rochinia crassa and *Pontophilus brevirostris* formed the core of a third species assemblage found predominantly on the upper continental slope. In the fall, *Parapenaeus longirostris* was representative of a species group (Group F) which was collected at the deepest stations (site group 6) and which was highly faithful to that site group (Fig. 8). Although *Processa profunda* is the only member of this group which is restricted to depths >150 m (Manning and Chace, 1971), species in Group F appeared to be restricted in their bathymetric distribution at this time of year. In winter samples, *Parapenaeus longirostris, Cancer irroratus, C. borealis, Rochi-*



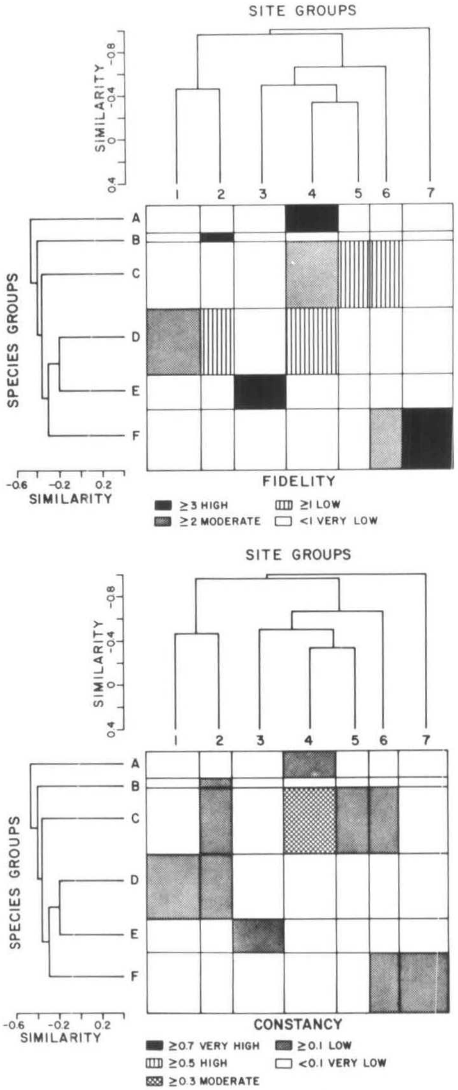
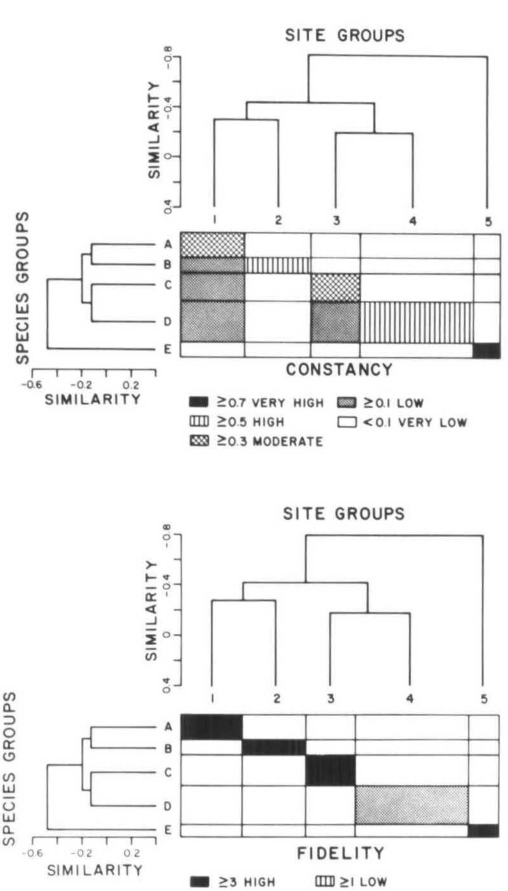


Figure 8. (Left) Normal and inverse classification hierarchies and nodal constancy and fidelity for site-species group coincidence during fall.

Figure 9. (Right) Nodal constancy and fidelity for classifications of winter collections.

nia crassa and *Pontophilus brevirostris* co-occurred within a species group (Group F) which was most faithful to site group 7 located on the upper continental slope, although the group was encountered at a few outer shelf stations (Fig. 9). In the spring, *Cancer irroratus* and *Rochinia crassa* formed a species group (Group E) which was restricted to the deepest stations (site group 5) (Fig. 10). In summer, the species group (Group F) containing *Parapenaeus longirostris, Cancer irroratus, C. borealis* and *Rochinia crassa* was entirely associated with the deepest stations (site group 5), although the component species were not collected at many stations in that site group (Fig. 11). These species formed a



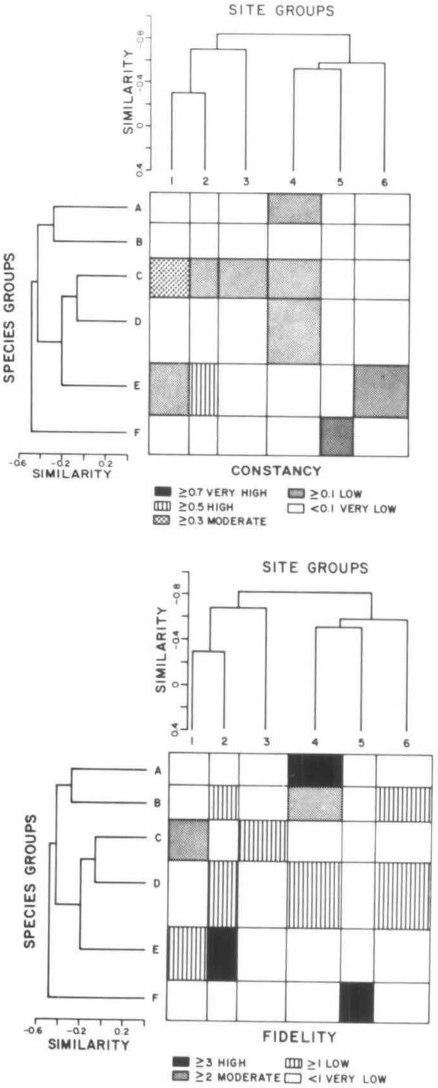


Figure 10. (Left) Nodal constancy and fidelity for classifications of spring collections.

Figure 11. (Right) Nodal constancy and fidelity for classifications of summer collections.

cohesive group which was clearly not very similar to shallower species groups. *Pontophilus brevirostris* was grouped with upper slope species during winter and occurred with open shelf species (Group D) during summer.

Species which were associated with the rocky reef habitat either through our collecting efforts or published accounts by others, occurred in species groups that were generally highly faithful but not constant to stations within site groups. In fall, the group (Group D) of *Anasimus latus* and *Stenorhynchus seticornis* displayed moderate constancy and fidelity to stations in site group 5 on the outer continental shelf (Fig. 8). *Anasimus latus* has been reported from coarse sand, coral, mud and shell bottoms (Williams, 1965) while *Stenorhynchus seticornis* has been reported from similar substrates (Williams, 1965) and sponges (Powers,

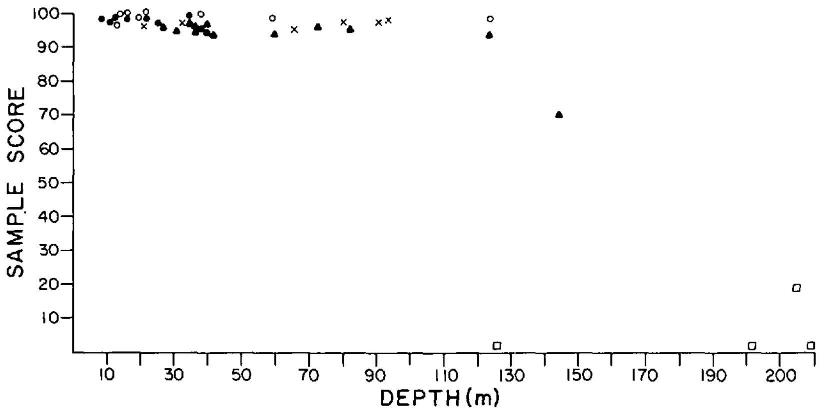
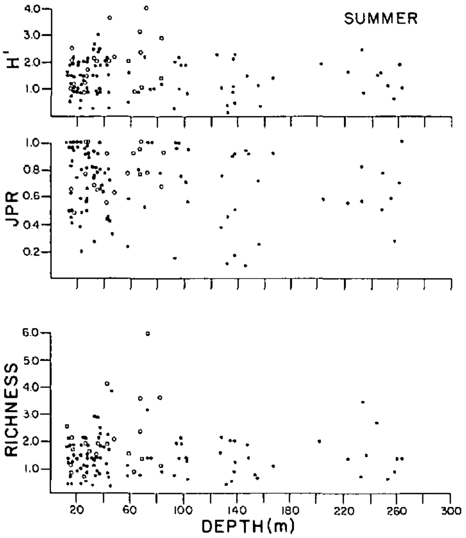


Figure 12. Scaled sample scores of axis 1 resulting from reciprocal averaging ordination plotted against depth for spring collections. Samples are identified according to their site group affinity as determined by results of normal cluster analysis for spring collections (see Table 4). Legend: ○ = site group 1, ● = site group 2, × = site group 3, ▲ = site group 4, □ = site group 5.

1977). In winter, rocky reef species such as *Stenorhynchus seticornis, Parthenope fraterculus, Dromidia antillensis, Stenocionops furcata coelata, Synalpheus townsendi, Pilumnus sayi, Podochela sidneyi* and *Podochela gracilipes* were found at inner shelf stations but were infrequently encountered and unrestricted to these stations (Fig. 9). The rocky reef species collected in spring formed an assemblage (Group C) which was also collected at stations on the coastal or inner shelf (site groups 1 and 3) and was not consistently collected anywhere (Fig. 10). This species group was highly faithful to stations in site group 3, however. Mixed assemblages of rocky reef and eurytopic species were indicated by our analysis of summer data. Species which were associated with the reef included *Synalpheus townsendi, Pseudomedaeus agassizii, Carpoporus papulosus,* and *Micropanope sculptipes,* from Group A; *Dromidia antillensis, Macrocoeloma trispinosum, Mithrax pleuracanthus, Pachycheles rugimanus,* and *Pilumnus sayi* from Group D; *Stenorhynchus seticornis, Stenocionops furcata coelata,* and *Batrachonotus fragosus* from Group E. These species groups were primarily associated with open shelf sites (Fig. 11).

Our general interpretation of the results of the nodal analyses is that the open shelf decapod assemblage is not as restricted in its distribution as the inner shelf and upper slope assemblages. The inner shelf species groups containing the coastal dominants *Trachypenaeus constrictus, Portunus spinimanus, P. gibbesii* and *Ovalipes stephensoni* were mostly found at stations in site groups on the inner shelf, while the upper slope species groups were generally restricted to stations in site groups on the upper slope. There was considerable overlap in the distribution of the open shelf groups, however, such that they were associated with stations in site groups on the open shelf, outer shelf and upper slope, depending on season.

Ordinations of samples and species analyzed separately for each season, produced three axes which accounted for 21–49% of the total variance between samples. The first ordination axes from the seasonal analyses was related to depth, while the second and third axes extracted were involuted and did not relate to any extrinsic factors. When sample scores resulting from ordination were plotted against sample depth, the deepest stations and their associated decapod fauna



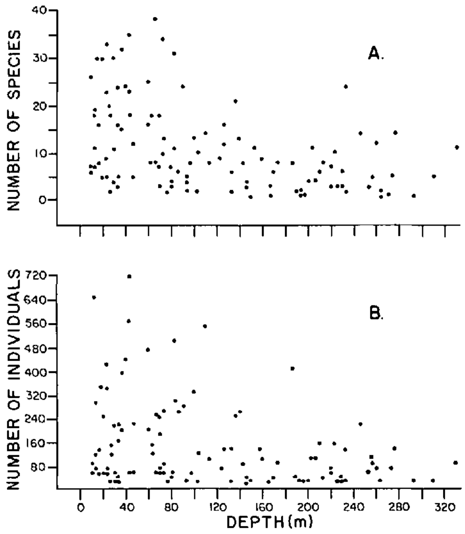


Figure 13. (Left) H' diversity, evenness (JPR) and species richness of Decapoda as a function of depth for summer collections. Legend: ● = open shelf sand bottom stations, ○ = "live" bottom stations.

Figure 14. (Right) Total number of decapod crustacean species (A) and individuals (B) per station as a function of depth for all seasons.

were distinct from those stations and species found at shallower depths (Fig. 12). In our analysis of spring data, only the deep stations containing *Rochinia crassa* and *Cancer irroratus* were distinctly grouped. At depths out to ca. 145 m, there was considerable mixing and overlap of station groups indicating that there was little if any separation among faunal assemblages. Ordination from other seasons reflected the same results as those shown during spring sampling, i.e., stations and assemblages from the coastal, mid-shelf and outer shelf habitats appeared homogeneous with little faunal change, whereas the greatest change occurred between these sites and those on the upper slope.

Diversity.—Diversity, expressed as H', and its components, species richness and evenness, showed little change with season or depth. Diversity values of open shelf sand bottom stations remained uniform from the inner continental shelf to the upper continental slope (Fig. 13, only summer data shown). There was, however, a tendency for rocky reef stations to have greater diversity than the open shelf stations at the same depth. We realize the inadequacy of our samples from the reef habitat and are presenting information on the diversity of that fauna with some reservation; but the fact that H' and species richness values were highest for collections from the rocky reef habitat, despite our sampling gear limitations and time constraints for sorting, is indeed worthy of noting. Preliminary results of a survey of the Decapoda from the reef habitat (MS in preparation) show that H' and species richness are higher for the reef than for the surrounding sand bottom.

The maximum total number of species and individuals collected at each depth decreased with increasing depth. The greatest number of species and individuals occurred at depths <100 m (Fig. 14) and specifically within depth zones of 28–55 m and 56–110 m (Table 6). The number of species declined thereafter with depth,

Table 6. Total number of unique species, mean number of species per tow and mean number of individuals per tow for decapod Crustacea by depth zone (Data are pooled from all collections)

Depth Zone (m)	Total Number of Species	Mean Number of Species/Tow	Mean Number of Individuals/Tow
9–18	69	3	19
19–27	64	3	13
28–55	87	3	25
56–110	84	5	46
111–183	54	3	25
184–366	72	4	37

although more species occurred between 184 and 366 m than occurred in either 9–18 m or 19–27 m depth zones. Because of unequal sampling effort in depth zones, we also calculated the mean number of species and mean number of individuals per tow for each depth zone (Table 6). The average number of species per tow ranged from 3 species at the shallowest depths to 5 species at 56–110 m. The mean number of individuals per tow was greatest in the 56–110 m depth zone.

DISCUSSION

Our analysis of the decapod Crustacea collected from the South Atlantic Bight indicated that the geographic area between Cape Hatteras, North Carolina and Cape Canaveral, Florida is divisible into several habitats or depth zones based on faunal content: an inner shelf or coastal habitat; an open or mid-shelf habitat; an outer shelf habitat; and an upper continental slope habitat. The distinctions among these habitats were strongest and most obvious for the inner shelf and upper slope areas which are vastly different in species composition and structure.

The coastal shelf regions of the South Atlantic Bight contained few species with relatively high abundance. *Trachypenaeus constrictus* was the most abundant decapod encountered here. Other Decapoda, such as *Sicyonia brevirostris* and *Ovalipes stephensoni,* occurred in the coastal zone but were not numerically important in this depth zone. The coastal assemblage appears to be composed of physiologically adaptable species which are not stressed by large amounts of river run-off or seasonal changes in bottom temperature but benefit from proximity to the nutrient enriched estuarine habitat. The relatively low number of species found in the coastal habitat is probably related to the more rigorous physical conditions found there. Day et al. (1971) characterized the coastal shelf of North Carolina out to 20 m as a turbulent zone where the benthic fauna is greatly affected by wave action and seasonal temperature changes. They found few benthic species in the turbulent zone but noted that these species may be present in large numbers. Although a probable high extinction rate exists in the inner shelf habitat due to marked seasonal fluctuations in hydrographic factors, areal species richness may not be as great as would be expected in such an unstable environment (Abele, 1976) because of homogeneous substrate (Abele, 1974; 1976; Felder and Chaney, 1979).

The open and outer shelf habitats encompassed depth zones of roughly 19–110 m and were characterized by a very rich and numerically abundant assemblage of Decapoda. The increased number of species observed in the open and outer shelf is probably related to the presence of rocky reefs there. Rocky reef species, such as *Dromidia antillensis, Stenocionops furcata coelata, Synalpheus* *townsendi,* and *Pilumnus sayi,* were not numerically dominant but contributed to the high species richness and diversity observed in open and outer shelf habitats. Because rocky reef habitats are structurally more complex than sand substrates and probably afford more shelter, feeding sites and sources of nutrition (Abele, 1974), species diversity tends to be higher on the reefs. Felder and Chaney (1979) furnished additional evidence of higher diversity on reefs by noting that diversity values were highest on heavily fouled reefs where a variety of resources are conducive to the development of a more diverse assemblage of generalist and specialist decapod species.

The rocky reef species were not sufficiently abundant or constant to be considered a separate faunal assemblage. Although reef species were grouped together by our cluster analysis of winter, spring and summer data, constituent species also frequently occurred with Decapoda collected predominantly on sand substrates. Whereas others (Pearse and Williams, 1951; Struhsaker, 1969; Cain, 1972; Wenner et al., 1979) have indicated that the semi-isolated reef or "live bottom" areas support invertebrate and/or fish faunas which are distinct from the larger more homogeneous sand biotope, we believe that the co-occurrences of reef and sand bottom species resulted from our use of a trawl which frequently traverses both sand and reef habitats during a tow. George and Staiger (1978) also noted that reef-associated and sand bottom-associated fish species frequently co-occurred, and they speculated that co-occurrences could result from such a traverse of habitats by the trawl.

The decapod assemblage of the upper continental slope consisted of fewer species than were found in the open and outer shelf habitats. Although there were several species which occurred both at outer shelf and upper slope depths, such as *Portunus spinicarpus, Solenocera atlantidis* and *Mesopenaeus tropicalis,* the region of greatest faunal change occurred between the outer shelf and upper slope habitats. George and Staiger (1978) also noted the distinctiveness of the upper slope fauna which was composed of species belonging to the archibenthal zone. Off North Carolina, Day et al. (1971) recognized that the faunistic zone on the continental slope was separate from that on the outer shelf but indicated that 37% of the common species spread from one zone to another. They found the upper slope to have a more uniform fauna than the continental shelf and suggested that more stable bottom temperatures of the outer shelf, in conjunction with absence of water movements on the bottom, reduced light and increased distance from land made the outer shelf a faunistically distinct zone. In the Middle Atlantic Bight, Boesch et al. (1977) found that the greatest changes in faunal assemblage similarity occurred at or near the shelf break. They attributed the faunal distinctiveness of the shelf break to the variable temperature conditions of the inner and central shelf which restrict the shoreward distribution of stenothermal macrobenthic invertebrates from the shelf break region. The greater faunal change we observed in the decapod Crustacea near the shelf-slope break, is probably related to both temperature and substrate. We found bottom temperatures to be <16°C during all seasons at depths >165 m but fluctuations as great as 10°C did occur at these depths during summer and winter. Temperature, therefore, appears to be variable, but the variation observed is not as great as that reported for the continental shelf where temperatures are subject to sudden extreme changes caused by impingement of the Gulf Stream. Sediments of the outer shelf are also diverse, consisting of relict coarse sand, shell hash, mud and rock outcrops which support heavy encrustaceans of coral, sponge and other invertebrates (Struhsaker, 1969; Menzies et al., 1973). In contrast, the sediments of the upper slope are homogeneous, consisting of mud (Struhsaker, 1969). Thus, the combination of extremely variable sediments and temperatures on the outer shelf may be sufficient to cause marked zonation between decapod assemblages from the outer continental shelf and upper continental slope habitats.

There is no reported effect of latitude on the distribution of decapod crustaceans (present paper; George and Staiger, 1978) or fishes (Wenner et al., 1979) from the South Atlantic Bight. Any latitudinal effects are apparently masked by strong bathymetric tends which are, in turn, largely determined by currents and thermal properties of the continental shelf and slope water. The study area between Cape Hatteras and Cape Canaveral is historically considered to be part of the Carolinian biogeographic province (Cerame-Vivas and Gray, 1966; Briggs, 1974) and is composed of a mixed fauna consisting of tropical species as well as native temperate and a few boreal species. The fauna of the inner shelf is mixed, consisting of both northern temperate and tropical species. The intrusion of species with northern affinities is seasonal and results from extensions of the cold Virginian Coastal Current around Cape Hatteras, whereas open and outer shelf faunas represent northern extensions of the tropical Gulf of Mexico and Caribbean fauna (Cerame-Vivas and Gray, 1966). The upper continental slope is composed of boreal species, such as *Cancer borealis, C. irroratus,* and *Rochinia crassa,* which submerge in tropical latitudes or species, such as *Parapenaeus longirostris,* which probably originated from the Gulf of Mexico and the Caribbean. Based on affinities of the component fauna, it is evident that any zoogeographic boundaries present in our study area are complicated by the fact that most species have broad latitudinal ranges. Briggs (1974) indicates that an area of latitudinal change does exist in the Carolinian Province but that the boundary which separates warm-temperate species from tropical species is not sharp. We have no evidence that qualitative differences exist in decapod assemblages between Cape Hatteras and Cape Canaveral and therefore must concur that any influence of oceanic circulation (e.g., Florida Current and Virginian Coastal Current) acts to support bathymetric rather than latitudinal stratification.

Current patterns and temperature regimes found in the South Atlantic Bight not only determine zoogeographic distribution but are principal factors affecting temporal stability of faunal assemblages. Our data showed that a few species assemblages of decapod crustaceans occurred at stations of similar depth regardless of season. Any lack of consistency between station and species groups by season may reflect sampling error and patchiness as well as temporal fluctuations in abundance and migrations of species between depth zones. The semi-quantitative nature of trawls as sampling gear probably masks true seasonal distribution patterns. This occurs because temporal stability in communities is largely based on stability in abundance of species (Davis and Van Blaricom, 1978). Thus, if species composition and abundances do not change over a time period, the system is in a biological steady-state (Fager, 1968). Our abundance estimates for several dominant decapod species show that there are definite changes in abundance with season and depth. Furthermore, overlap in faunal composition of station groups from the upper slope, open and outer shelf habitats during summer and fall suggests that decapod community composition at these faunistic zones varies seasonally. Seasonal hydrographic and temperature regimes lend credence to the idea that there are temporal shifts of fauna assemblages in the South Atlantic Bight. In work on benthic communities in the Middle Atlantic Bight, Boesch et al. (1977) found that at any given station, collections from one season to another were very similar, indicating seasonal stability. In another study, George and Staiger (1978) found that epifaunal invertebrate assemblages of the South Atlantic occupied various provinces on the continental shelf as the seasons progressed.

Both of these studies incorporated fixed sampling locations into their survey design which makes the determination of dynamic shifts in community assemblages over time more obvious than it would if random station allocation was used. We, therefore, are cautious in interpretation of our results and hasten to point out that further data need to be collected before a conclusive statement can be made concerning seasonal shifts in decapod assemblages from the South Atlantic.

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