

SEASONAL COMPOSITION AND ABUNDANCE OF DECAPOD AND STOMATOPOD CRUSTACEANS FROM COASTAL HABITATS, SOUTHEASTERN UNITED STATES¹

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ABSTRACT

Decapod and stomatopod crustaceans were collected by trawl during seasonal cruises from Cape Fear, North Carolina to Cape Canaveral, Florida at depths from 4 to 20 m. A total of 60 species of decapod and 3 species of stomatopod crustaceans were collected. Fifteen species accounted for 95% of the total number of individuals and 96% of the total biomass; the portunid crabs *Portunus gibbesii*, *P. spinimanus*, *Ovalipes stephensoni*, *O. ocellatus*, *Callinectes similis*, *C. sapidus*, and *Arenaeus cribrarius*; the calappid crab *Hepatus ephelitus*; the majid crab *Libinia emarginata*; the penaeid shrimps *Penaeus setiferus*, *P. aztecus*, *P. duorarum*, and *Trachypenaeus constrictus*; and the squillid stomatopods *Squilla empusa* and *S. neglecta*.

Season was an important factor affecting the number of individuals and species collected during the study. No consistent changes in number of species, total number of individuals, and mean total weight occurred with latitude. Cluster analysis indicated season and latitude were important factors determining species assemblages in the coastal zone. Although changes in species composition occur seasonally, most species groups delineated by cluster analysis were not consistently collected nor restricted to particular site groups. A seasonally ubiquitous faunal assemblage in the coastal zone was composed of numerically dominant species. Those assemblages which were characterized as being restricted to site groups consisted of relatively rare species or those which were associated with hard-bottom habitat.

Integrated community analyses of the decapod Crustacea of the Carolinian shelf province, extending from Cape Fear, NC to Cape Canaveral, FL were completed by Wenner and Read (1981, 1982). Their studies, which encompassed a broad latitudinal and bathymetric range, described assemblages of decapod Crustacea from the continental shelf of the southeastern United States in terms of depth, season, and latitude and provided estimates of decapod abundance relative to certain biological and physical factors. Although Wenner and Read (1981, 1982) sampled the continental shelf habitats described by Struhsaker (1969), their effort in coastal habitats was limited to depths of 9–18 m.

The coastal zone, defined by Struhsaker (1969) as extending from the sounds and estuaries out to depths of 18 m, has been extensively surveyed since the 1930's (Keiser 1977); however, most of the resulting reports described the composition and magnitude of the incidental catch of finfishes by shrimp trawlers (see Keiser 1977 for literature sur-

vey). Information on invertebrates, and more specifically the noncommercially important species of decapod and stomatopod crustaceans, has been limited. Hoese (1973) reported on the seasonal distribution of decapod and stomatopod species collected on the central Georgia coastal zone and Doboy Sound. Keiser (1977) identified 20 species of decapod and stomatopod crustaceans in a study of the incidental catch of the South Carolina shrimp fishery. Anderson et al. (1977) provided seasonal information on 12 species of decapod and stomatopod crustaceans collected during a survey of the macrofauna in the surf zone off Folly Beach, SC. The present paper describes the assemblages of decapod and stomatopod crustaceans in coastal habitats off the southeastern United States in terms of seasonal and latitudinal variations and characterizes the important species in terms of their abundance, biomass, size composition, and distribution.

METHODS AND MATERIALS

Data Collection

Samples of decapod and stomatopod Crustacea were collected during seasonal cruises from Cape Fear, NC (lat. 33.9°N) to Cape Canaveral, FL (lat.

¹Contribution No. 259 from the South Carolina Marine Resources Center.

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28.5°N) at depths ranging from 4 to 20 m. Dates of the four seasonal cruises were as follows: summer, 15 July–20 September 1980; spring, 28 April–6 June 1981; winter, 7–29 January 1982; fall, 14 October–7 December 1982. Sampling locations were selected by means of a stratified random sampling design (Grosslein 1969). Thirteen strata were established at depths of 4–12 m from Cape Fear to the mouth of the St. John's River, FL (lat. 30.4°N), while south of this point to Cape Canaveral, an additional five strata were delineated in depths ranging from 8 to 20 m with the 5.6 km territorial sea line as the offshore boundary. A change in definition of strata off Florida was necessary because of the steepness of the nearshore continental shelf in the area south of the St. John's River. Areal extent of strata ranged from 7,486 to 31,661 ha (\bar{x} = 17,323 ha).

At each randomly selected site within a stratum, paired tows were made for 20 minutes at a speed of 4.4 km/h using four-seam Gulf of Mexico shrimp trawl nets. Outriggers enabled two nets to be fished simultaneously from the same vessel. The trawl nets, which were attached to 1.5 × 0.8 m wood and chain doors, had headrope lengths of 12.8 m, footrope lengths of 15.8 m and stretch-mesh sizes of 5.1 cm in the wings, 4.4 cm in the body, and 4.1 cm in the cod end. Tickler chains were attached to each door and adjusted to drag at a distance of 0.6 m in front of the nets. Tows were confined to daylight hours (1 hour after sunrise to 1 hour before sunset) to eliminate day-night changes in availability and vulnerability of organisms to the gear. Sampling effort changed from cruise to cruise owing to constraints of funding and vessel availability (Fig. 1). Collections of decapod and stomatopod crustaceans taken during tows in which a net was damaged, failed to reach bottom, or became twisted were considered unsuccessful and were not included in analyses. Bottom temperature was measured following each tow with a stem thermometer mounted within a Van Dohrn bottle.

Decapod and stomatopod crustaceans collected by each net during a tow were identified to species, counted, and weighed to the nearest gram, and either the entire catch or a random subsample of at least 30 individuals was measured to the nearest mm. Measurements included total length (tip of rostrum to tip of telson) for shrimp [carapace length (tip of rostrum to posterior margin of carapace) for majid crabs, and carapace width (measured between the posteriormost lateral spines) for other crabs]. Sex was recorded for brachyuran species. Although the contents of each net were processed indepen-

dently, the catch per standard tow is defined as the combined catch from both trawl nets fished simultaneously at each randomly chosen site within a stratum.

Data Analysis

The stratified mean catch per tow and its standard error were calculated by the expressions (Poole 1974):

$$\bar{y}_{ST} = \sum_{h=1}^L \frac{N_h \bar{y}_h}{N}$$

$$SE_{\bar{y}_{ST}} = \left[\sum W_h^2 \cdot \frac{s_h^2}{n_h} \left(1 - \frac{n_h}{N_h} \right) \right]^{1/2}$$

where \bar{y}_{ST} = stratified mean catch/tow
 \bar{y}_h = mean catch/tow in numbers or weight in the h stratum
 N_h = number of possible sampling units in the h stratum
 N = total number of possible sampling units over all strata
 $SE_{\bar{y}_{ST}}$ = standard error of the stratified mean catch/tow
 W_h = N_h/N
 S_h^2 = sample variance of the h stratum
 n_h = number of trawl tows made in the h stratum.

The effective degrees of freedom for the calculation of confidence limits follows the methodology of Cochran (1977).

Minimum biomass and density estimates for trawl-caught groundfish were calculated from computations of the area swept by the trawl gear. The approximation of the area swept (a) was derived from the following equation (Roe 1969):

$$a = \frac{K \times M \times (0.6 H)}{10,000 \text{ m}^2/\text{ha}}$$

where a = swept area in hectares
 K = speed in meters per hour
 M = time in hours fished
 H = headrope length in meters.

The result (1.12 ha) was multiplied by two since the standard unit of effort was two nets fished simultaneously. Thus, a standard trawl station sampled 2.24 ha.

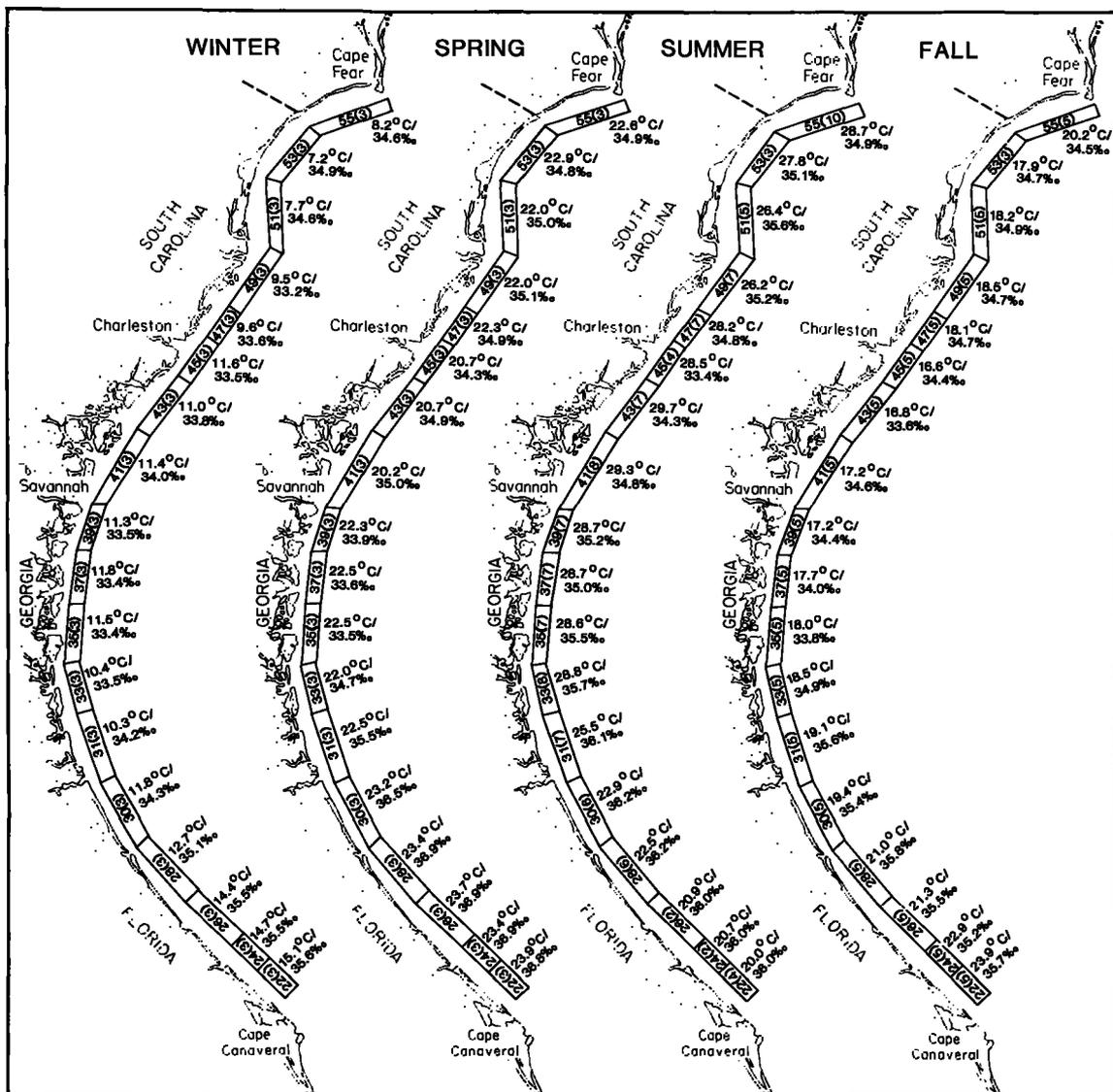


FIGURE 1.—Location and number of collections (in parentheses) from each stratum during seasonal sampling periods. Average temperature and salinity conditions during sampling are noted for each stratum.

Statistically significant differences in biomass, number of species, and number of individuals between seasons were determined by the Kruskal-Wallis analysis of variance by ranks (Zar 1984). This nonparametric equivalent of analysis of variance was used because a logarithmic transformation failed to normalize the data. The nonparametric analog of the Tukey multiple comparison test (Zar 1984) was used following rejection of the null hypothesis to determine between which of the samples signifi-

cant differences occurred. The rejection level for the null hypothesis in all statistical tests was $\alpha = 0.05$.

Cluster analysis was used to determine seasonal patterns of similarity among strata and to define assemblages of decapod and stomatopod crustaceans. Prior to analysis, data from standard tows during a season were pooled within each stratum. Data were reduced to eliminate species which occurred in only one stratum during all seasons. The rationale to exclude these species was that they did

not appear to be habitat-restricted, nor did they exhibit a meaningful distribution pattern (Clifford and Stephenson 1975), as indicated by the tendency of the entities to chain rather than form new groups.

Species and pooled collections from a stratum were classified using flexible sorting (Lance and Williams 1967) with a cluster intensity coefficient (β) of -0.25 . The similarity coefficient used was the Bray-Curtis measure (Clifford and Stephenson 1975) on percent standardized data (Boesch 1977).

The postclustering technique of nodal analysis (Williams and Lambert 1961; Lambert and Williams 1962) was used 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). Mathematical definitions of constancy and fidelity and a more detailed explanation of cluster and nodal analysis are found in Boesch (1977).

RESULTS AND DISCUSSION

Hydrographic Measurements and Description of the Study Area

The coastal zone as defined by Struhsaker (1969) ranges from the beaches to 16–24 km offshore where the water depth is 9–18 m. The sea bottom within this depth zone is mostly homogeneous in composition, consisting predominantly of sandy mud with varying amounts of ground-shell. The bottom is ripple-marked by wave action to a depth of 20 m (Sandifer et al. 1980). Hard or "live" bottom reefs are interspersed throughout the coastal zone (Buchanan 1973) and are distinguished from the surrounding sand biotope by supporting a diverse assemblage of sessile invertebrates as well as numerous motile species which are inhabitants of the complex microhabitats (e.g., rock crevices, bare rock, ledges with sand veneer, sand patches between rocks, and sessile organisms) of the reefs (Wenner et al. 1983).

The hydrography of the coastal zone has not been studied as thoroughly as other areas of the continental shelf. The interacting forces of river runoff, wind direction and force, seasonal air temperatures, and proximity of the Gulf Stream produce complicated patterns of circulation (Bumpus 1973) that determine the distribution of sediments, nutrients, oxygen, temperature, salinity, food, and

planktonic forms of larval and adult organisms (Johnson et al. 1974). Bumpus (1973) observed that the southerly flowing coastal current is very transient and restricted to a narrow band along the coast.

Nearshore surface and bottom waters off the southeastern United States have large seasonal variations in temperature. Because of the shallowness of the coastal zone, cooling and warming can occur rapidly when appropriate atmospheric conditions exist; when the amount of cold, fresh, runoff is variable; or when the movement of the Gulf Stream is variable (Mathews and Pashuk 1984). A well-defined recurrent seasonal upwelling exists off the coast of Florida near Cape Canaveral, which occurs in late July with anomalously low multiyear monthly mean surface temperatures (Smith 1983; Lee and Pietrafesa 1987). Warming of bottom waters usually occurs in late August.

Mean bottom water temperatures for each stratum during the present study increased with decreasing latitude for every sampling period except summer (Fig. 1). During that time, temperatures ranging from 20.0° to 23.1°C were noted off the coast of Florida, while the extremes recorded for strata off North Carolina, South Carolina, and Georgia were 25.5°–29.7°C. Temperature extremes during the other sampling periods varied predictably with latitude. During winter sampling, temperatures ranged from a low of 7.2°C off North Carolina to 15.1°C at the southernmost stratum off Florida. Temperatures in spring were the least variable with regional extremes of 20.2°–23.9°C noted. The lowest temperatures were recorded in strata between Charleston, SC and Savannah, GA. Temperatures during the fall sampling ranged from 16.6° to 23.9°C, with the lowest temperatures again occurring for strata between Charleston and Savannah.

Salinity of nearshore waters is generally lower than that of the open shelf because of runoff from rivers. Blanton and Atkinson (1978) noted that runoff into the coastal zone is bimodal with a major peak in spring and a minor peak in late summer. Because most of the freshwater on the open shelf is confined to depths <20 m, salinity regimes 10 or 20 km off the Georgia coast are similar to those of a partially mixed estuary. Rapid mixing occurs due to large tidal fluxes (Blanton and Atkinson 1978). Salinities of bottom waters measured during the present study were fairly uniform seasonally. Highest values were noted for coastal waters off the coast of Florida, while lowest salinities occurred off South Carolina and Georgia (Fig. 1).

Species Composition

A total of 60 species of decapod and 3 species of stomatopod crustaceans comprising 59,966 individuals and 11,000 individuals, respectively, was collected during the study (Table 1). Fifteen species accounted for 95% of the total number and 96% of the total biomass: the portunid crabs *Portunus gibbesii*, *P. spinimanus*, *Ovalipes stephensoni*, *O. ocellatus*, *Callinectes similis*, *C. sapidus*, and *Arenaeus cribrarius*; the calappid crab *Hepatus epheliticus*; the majid crab *Libinia emarginata*; the penaeid shrimps *Penaeus setiferus*, *P. aztecus*, *P. duorarum*, and *Trachypenaeus constrictus*; and the squillid stomatopods *Squilla empusa* and *S. neglecta*. The ranking of these species in terms of numbers of individuals and biomass changed seasonally; however, *Portunus gibbesii* was the most abundant species collected during all seasons except spring, when *Ovalipes stephensoni* dominated catches (Table 1). Previous faunal surveys in the Carolinian Province have shown that *P. gibbesii* is a common and abundant inhabitant of the coastal zone (Hay and Shore 1918; Wass 1955; Rouse 1970). Published information on *O. stephensoni* is limited, but it has previously been reported (as *O. quadulpensis*) by Hoese (1973) not to be common in trawl catches off Georgia. Biomass of catches was dominated by *Callinectes sapidus* during all seasons except fall when *Penaeus setiferus* ranked first. Keiser (1976) likewise noted that *C. sapidus* comprised a large portion by weight of the incidental invertebrate catch of the shrimp fishery off South Carolina. The importance of *P. setiferus* in catches during the fall is not unexpected since the species forms the basis of a major commercial fishery in the South Atlantic Bight during that time (Keiser 1976, 1977).

Community, Biomass, and Density Estimates

Season was an important factor affecting the number of individuals and species collected during the study (Table 2). The median number of individuals was significantly less during winter sampling than at other seasons ($\chi^2 = 29.83$, $P < 0.001$), while the median number of species was significantly less during winter and spring ($\chi^2 = 45.60$, $P < 0.001$). Stratified mean catch per tow values also reflected seasonal differences with considerably fewer individuals and lower biomass in catches during winter (Table 3). Similarly, mean total biomass (kg/ha) and density (no./ha) estimates were lowest for winter. No consistent changes in number of species or num-

ber of individuals occurred with latitude (Table 2); however, the number of individuals was consistently low at stratum 22 off Cape Canaveral.

Our results suggest that the community structure of decapod and stomatopod crustaceans from the coastal zone is influenced primarily by seasonality and not latitude. Other investigators have likewise noted the influence of seasonality on the number of motile invertebrate species in inshore habitats. Van Dolah et al. (1984) found that the median number of invertebrate species collected by trawl off the mouth of Winyah Bay, SC was greater in summer than winter. Anderson et al. (1977) collected more species of fishes and invertebrates in the surf zone in summer than any other season, with diversity being least in winter. These results are not surprising since the coastal region of the southwestern Atlantic is prone to great seasonal changes in water temperature. The occurrence of more species, more individuals, and greater biomass in summer may result from more uniform temperatures across the entire shelf allowing intrusion into the coastal zone by middle- and outer-shelf species which represent a northern extension of the tropical Gulf of Mexico and Caribbean fauna (Cerame-Vivas and Grey 1966), as well as offshore movement by euryhaline estuarine species. The modifying influence of currents, river runoff, and air temperature tend to obscure any latitudinal gradients in community structure. Briggs (1974) considered Cape Canaveral as a zoogeographic boundary for inner-shelf fauna since many species terminated their range there; however, he hastened to point out that Cape Canaveral is an intermediate point in a lengthy geographic area of change. Depending on water temperature, eurythermic tropical species can extend far north in the Carolinian Province. During winter under strong northeasterly winds, an inshore zone of cold Virginian coastal current extends south of Cape Hatteras enabling intrusion by northern temperate species (Cerame-Vivas and Grey 1966). Latitudinal trends in community structure are further obscured by using quarterly data to show relationships and the tendency of many species which inhabit the inner shelf on a regular basis to have broad latitudinal ranges.

The coastal zone along the southeastern United States has previously been reported to contain few species of decapod crustaceans with high abundance (Wenner and Read 1981, 1982). The low number of species in the coastal zone was attributed to the more rigorous and variable hydrographic conditions coupled with a relatively homogeneous substrate compared with other areas of the continental shelf.

TABLE 1.—Decapod and stomatopod crustaceans collected in the coastal zone between Cape Fear, NC and Cape Canaveral, FL. Species are ranked according to numerical abundance. Numbers listed under seasons show rank by number and biomass (in parentheses) during each season, while (+) indicates occurrence.

Species	Number station occurrences	Total number specimens	Total biomass (kg)	Seasonal ranking			
				W	Sp	Su	Fa
<i>Portunus gibbesii</i>	273	17,250	115.2	1(5)	2(3)	1(9)	1(3)
<i>Squilla empusa</i>	237	9,112	137.5	2(4)	3(4)	3(4)	4(4)
<i>Ovalipes stephensoni</i>	155	8,641	56.7	6(7)	1(2)	6(11)	11(13)
<i>Callinectes similis</i>	194	6,470	125.4	14(10)	11(12)	4(3)	2(2)
<i>Penaeus setiferus</i>	192	5,516	133.7	3(3)	15(14)	5(5)	3(1)
<i>Penaeus aztecus</i>	155	4,622	74.4	+	+	2(2)	(15)
<i>Portunus spinimanus</i>	221	2,913	52.1	8(6)	5(7)	7(10)	6(8)
<i>Ovalipes ocellatus</i>	163	2,523	73.9	11(8)	4(5)	9(6)	10(9)
<i>Hepatus epheliticus</i>	197	2,332	77.8	15(14)	10(8)	8(7)	5(5)
<i>Squilla neglecta</i>	150	1,887	21.7	+	6(10)	12(13)	9(12)
<i>Callinectes sapidus</i>	173	1,577	253.3	7(1)	9(1)	10(1)	(6)
<i>Arenaeus cribrarius</i>	130	1,510	57.8	(13)	13(11)	11(8)	8(7)
<i>Trachypenaeus constrictus</i>	118	1,025	3.1	4(9)	14	+	7
<i>Libinia emarginata</i>	170	1,008	50.7	5(2)	8(6)	(12)	(10)
<i>Penaeus duorarum</i>	101	858	12.2	+	7(9)	+	+
<i>Pagurus pollicaris</i>	159	795	1.3	13	+	14	15
<i>Callinectes ornatus</i>	90	788	10.8	+	+	13(14)	13(14)
<i>Libinia dubia</i>	151	575	10.3	9(12)	+	+	12(11)
<i>Persephona mediterranea</i>	149	567	8.2	+	12(15)	15(15)	+
<i>Xiphopenaeus kroyeri</i>	20	346	1.7	10	+	+	14
<i>Porcellana sigsbeiana</i>	25	99	0.1	+	+	+	+
<i>Cancer irroratus</i>	25	81	0.9	12(11)	+	+	+
<i>Neopanope sayi</i>	30	66	0.1	+	+	+	+
<i>Menippe mercenaria</i>	42	60	8.2	(15)	+	+	+
<i>Sicyonia brevirostris</i>	33	53	0.3	+	+	+	+
<i>Pagurus annulipes</i>	2	36	—	+	+	+	+
<i>Pilumnus sayi</i>	19	36	0.1	+	+	+	+
<i>Calappa flammea</i>	21	30	4.3	+	(13)	+	+
<i>Exhippolysmata oplophoroides</i>	9	25	<0.1	+	+	+	+
<i>Pagurus longicarpus</i>	20	25	—	+	+	+	+
<i>Porcellana sayana</i>	16	21	<0.1	+	+	+	+
<i>Hexapanopeus angustifrons</i>	8	11	<0.1	+	+	+	+
<i>Podochela riisei</i>	10	10	<0.1	+	+	+	+
<i>Pagurus hendersoni</i>	1	10	—	+	+	+	+
<i>Portunus sayi</i>	3	9	<0.1	+	+	+	+
<i>Albunea paretii</i>	5	8	<0.1	+	+	+	+
<i>Panopeus occidentalis</i>	5	7	<0.1	+	+	+	+
<i>Pagurus impressus</i>	5	6	—	+	+	+	+
<i>Podochela sidneyi</i>	3	6	<0.1	+	+	+	+
<i>Petrochirus diogenes</i>	4	5	<0.1	+	+	+	+
<i>Speocarcinus carolinensis</i>	5	5	0.2	+	+	+	+
<i>Sicyonia dorsalis</i>	1	4	<0.1	+	+	+	+
<i>Synalpheus townsendi</i>	1	4	—	+	+	+	+
<i>Lysmata wurdemanni</i>	3	4	<0.1	+	+	+	+
<i>Hypoconcha sabulosa</i>	2	3	<0.1	+	+	+	+
<i>Calappa sulcata</i>	3	3	0.3	+	+	+	+
<i>Metoporphaphis calcarata</i>	3	3	<0.1	+	+	+	+
<i>Dromidia antillensis</i>	2	2	<0.1	+	+	+	+
<i>Pilumnus dasypodus</i>	2	2	<0.1	+	+	+	+
<i>Euryplax nitida</i>	1	2	<0.1	+	+	+	+
<i>Pinnixa chaetoptera</i>	1	2	<0.1	+	+	+	+
<i>Hepatus pudibundus</i>	2	2	<0.1	+	+	+	+
<i>Sicyonia typica</i>	1	1	<0.1	+	+	+	+
<i>Polyonyx gibbesi</i>	1	1	<0.1	+	+	+	+
<i>Calappa angusta</i>	1	1	<0.1	+	+	+	+
<i>Calappa ocellata</i>	1	1	<0.1	+	+	+	+
<i>Pinnotheres maculatus</i>	1	1	—	+	+	+	+
<i>Pinnixa cylindrica</i>	1	1	<0.1	+	+	+	+
<i>Pelia mutica</i>	1	1	<0.1	+	+	+	+
<i>Mithrax pleuracanthus</i>	1	1	<0.1	+	+	+	+
<i>Parthenope serrata</i>	1	1	<0.1	+	+	+	+
<i>Dardanus fucosus</i>	1	1	—	+	+	+	+
<i>Lysiosquilla scabricauda</i>	1	1	<0.1	+	+	+	+

TABLE 2.—Number of individuals (N) and number of species (S) for pooled replicate samples of invertebrates at each station.

Strata	Winter		Spring		Summer		Fall	
	N	S	N	S	N	S	N	S
22	43	13	207	18	319	26	238	21
24	78	13	553	17	425	19	1,608	25
26	72	11	526	15	787	20	1,376	27
28	1,707	19	1,074	15	1,301	23	1,823	22
30	172	13	373	17	2,199	25	1,609	22
31	370	21	1,580	20	2,037	24	1,849	23
33	900	15	1,961	17	1,313	20	513	17
35	9	3	609	17	2,688	26	3,071	24
37	399	12	592	15	1,648	26	458	21
39	196	17	1,207	18	1,178	23	592	19
41	51	15	934	15	399	24	232	16
43	264	14	349	15	791	18	2,082	23
45	149	15	1,506	21	1,780	16	1,843	22
47	71	16	214	14	1,269	24	1,053	23
49	213	18	1,658	19	3,235	25	1,417	24
51	70	11	266	15	1,308	25	804	21
53	22	11	1,673	16	1,534	21	616	22
55	177	16	1,927	16	2,906	22	892	22

TABLE 3.—Seasonal stratified mean catch per tow for total number and weight of decapod and stomatopod crustaceans, and density estimates based on a swept area of 2.24 hectares during a standard station.

Season	Stratified mean catch/tow		Mean density No./ha	Mean biomass kg/ha
	No. of individuals	Biomass		
Winter	99	1.969	44	0.879
Spring	298	4.491	133	2.005
Summer	277	5.666	124	2.529
Fall	248	4.283	111	1.912

Hoese (1973) attributed a higher density and biomass of invertebrates in Doboy Sound than in inshore and offshore areas of Georgia to a proximity to productive salt marsh. Comparisons of study results with biomass and density estimates obtained for decapod crustaceans from high salinity areas sampled in Charleston Harbor, SC (Wenner et al. 1984) support Hoese's findings of a decrease in biomass and density from estuarine to nearshore habitats.

Species Assemblages and Distributional Patterns

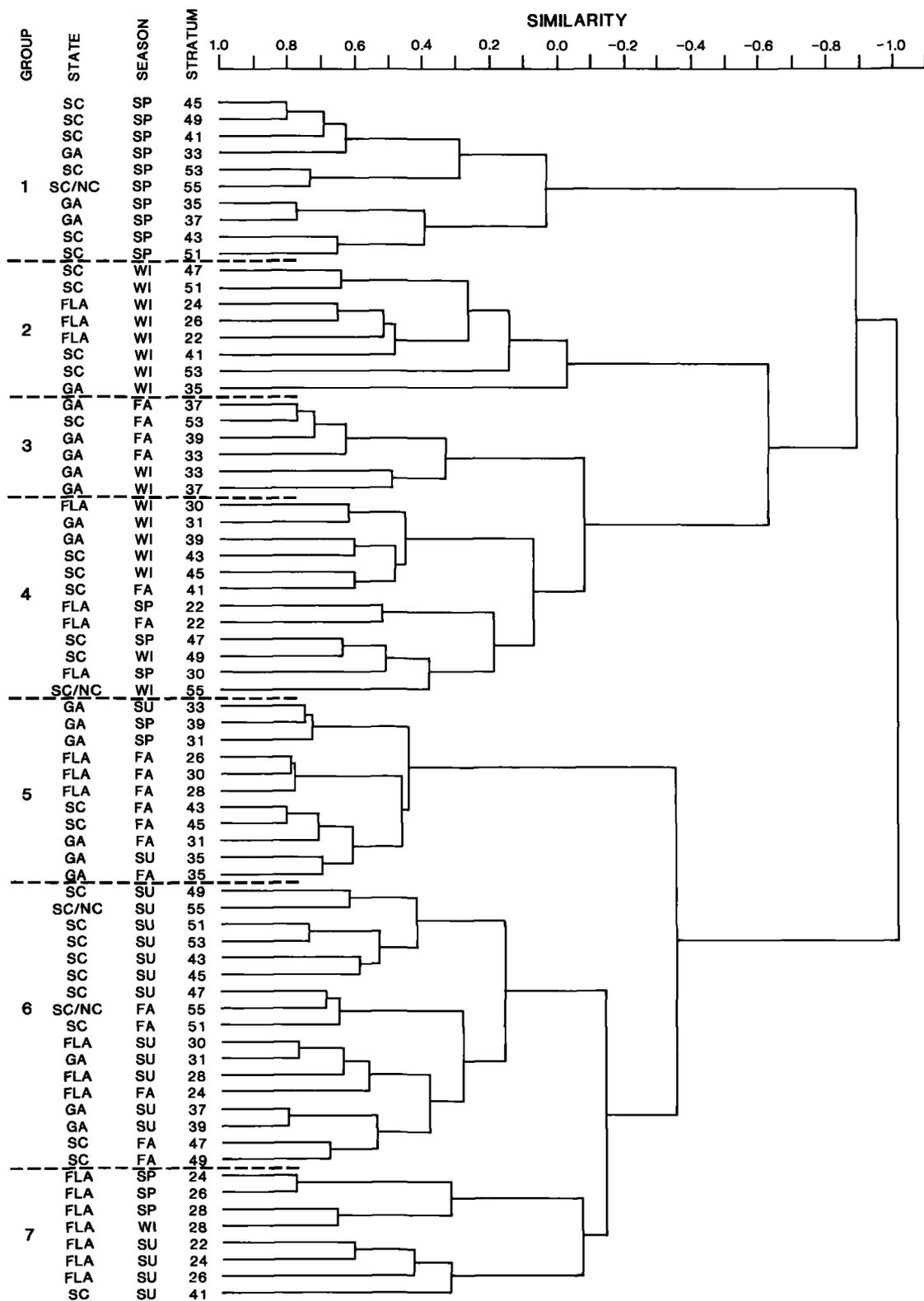
Normal cluster analysis classified pooled collections from each stratum into seven groups which corresponded to season of collection and latitudinal location (Fig. 2). Within each of two major groupings of the dendrogram (Groups 1–4 and Groups 5–7), latitudinal-related groups occurred seasonal-

ly. Group 1 contained collections having similar faunal composition which were primarily off South Carolina and Georgia during spring. Collections in this group were least similar faunistically to those in groups 2–4. Collections in group 2 were also faunistically distinct and were mainly taken off Florida and South Carolina in fall. Group 3 represented a highly similar latitudinal grouping of collections with most taken off Georgia during fall and winter. This group contained collections that were similar in species composition to those in group 4. Group 5 was least similar to groups 5–6 and contained collections from Georgia, Florida, and South Carolina from fall, spring, and summer. Collections in group 6 were from all locations but were taken only in summer and fall. Some latitudinal grouping of collections was evident in group 7 which mostly contained those off Florida.

The species assemblages identified by inverse cluster analysis (Table 4) displayed generally low constancy for site groups, except for Groups A and B which contained the numerically dominant decapod species. Species in these groups had moderate to high constancy for all site groups and, consequently, were not restricted to any group (Fig. 3).

TABLE 4.—Species groups resulting from inverse cluster analysis using the Bray-Curtis similarity coefficient and flexible sorting.

Group A	Group D
<i>Portunus gibbesii</i>	<i>Dromidia antillensis</i>
<i>Squilla empusa</i>	<i>Panopeus occidentalis</i>
<i>Penaeus setiferus</i>	<i>Hypoconcha sabulosa</i>
<i>Penaeus duorarum</i>	<i>Podocheila sidneyi</i>
<i>Trachypenaeus constrictus</i>	
<i>Ovalipes stephensoni</i>	Group E
<i>Ovalipes ocellatus</i>	<i>Pilumnus dasypodus</i>
<i>Squilla neglecta</i>	<i>Metoporphaphis calcarata</i>
<i>Callinectes sapidus</i>	<i>Pilumnus sayi</i>
<i>Pagurus pollicaris</i>	<i>Neopanope sayi</i>
<i>Persephona mediterranea</i>	<i>Podocheila riisei</i>
<i>Hepatus epheliticus</i>	<i>Pagurus longicarpus</i>
<i>Portunus spinimanus</i>	<i>Hexapanopeus angustifrons</i>
<i>Libinia emarginata</i>	<i>Cancer irroratus</i>
<i>Libinia dubia</i>	<i>Sicyonia brevirostris</i>
<i>Penaeus aztecus</i>	<i>Menippe mercenaria</i>
<i>Callinectes similis</i>	<i>Porcellana sigsbeiana</i>
<i>Arenaeus cribrarius</i>	<i>Calappa flammaea</i>
<i>Callinectes ornatus</i>	<i>Lysmata wurdemanni</i>
Group B	
<i>Exhippolysmata oplophoroides</i>	
<i>Porcellana sayana</i>	
<i>Xiphopenaeus kroyeri</i>	
Group C	
<i>Albunea paretii</i>	
<i>Hepatus pudibundus</i>	
<i>Petrochirus diogenes</i>	
<i>Speocarcinus carolinensis</i>	
<i>Portunus sayi</i>	
<i>Pagurus impressus</i>	
<i>Calappa sulcata</i>	



Wenner and Read (1982) found that *Trachypenaeus constrictus*, *Portunus spinimanus*, *P. gibbesii*, and *Ovalipes stephensoni* form a frequently co-occurring assemblage on the inner shelf. Although their importance in terms of abundance and biomass changed seasonally, all species in groups A and B, except *Callinectes ornatus*, were collected during every sampling period, indicating that these species are a core-assemblage of the coastal zone. Several species in these groups (*O. ocellatus*, *P. gibbesii*, and *P. spinimanus*) are common inhabitants of high-salinity estuarine waters in South Carolina (Wenner et al. 1984) and Georgia (Hoese 1973), while others, such as *C. sapidus*, *Penaeus setiferus*, and *P. aztecus*, are migratory and seasonally dominant inhabitants of estuarine systems in the southeastern United States (Weinstein 1979; Wenner et al. 1983, 1984). Another member of this assemblage, *Arenaeus cribrarius*, is a common member of the sandy beach community along the southeastern United States (Pearse et al. 1942; Williams 1984; Anderson et al. 1977; Leber 1982; DeLancey 1984).

Species from groups C and D were restricted to sites as indicated by moderate to high fidelity values and have previously been reported as nearshore inhabitants of the southwestern Atlantic (Williams 1984). Most species in these groups are found on sand or mud bottom and occur throughout the latitudinal extent of the study area (Williams 1984). Exceptions include *Portunus sayi* which is commonly associated with *Sargassum* (Williams 1984), and *Hepatus pudibundus* which has not been reported north of Georgia (Coelho and Ramos 1972). Species in Group E are generally associated with hard-bottom areas (Wenner and Read 1982; Williams 1984) and were neither abundant or commonly encountered in the coastal habitat. These species were most restricted in their distribution to collections from site group 7.

Group E contained species which were not constant or faithful to any site groups. In addition, there was no consistency in their occurrence with regard to season, latitude, or substrate preference. Most of the species in this group have broad bathymetric ranges on the continental shelf and none were abundant in our collections from the coastal zone.

Seasonality and latitude are important factors determining species assemblages in coastal habitats.

The grouping of strata by season suggests that the decapod and stomatopod fauna of the coastal zone changes throughout the year and may also change with latitude. Although changes in species composition occur seasonally, most species groups delineated by cluster analysis were not consistently collected nor restricted to particular site groups. A seasonally ubiquitous faunal assemblage in the coastal zone was composed of numerically dominant species. The species assemblages which were characterized as being restricted to site groups consisted of relatively rare species or those which were associated with hard-bottom habitat.

Temporal and Spatial Distributions of Numerically Dominant Species

Portunus gibbesii

Although its known range extends from southern Massachusetts through the Gulf of Mexico, this portunid crab is more common and abundant in shallow shelf waters of the Carolinian Province and Caribbean Sea (Williams 1984). *Portunus gibbesii* has been reported on mud, sand, and shell substrates (Park 1969, 1978).

This species far outranked other decapod and stomatopod crustaceans in total number (24% of the total catch) and was present in 273 of the 303 collections made during all seasons (Table 1). In terms of biomass, *P. gibbesii* was the fifth most important species collected, constituting 9% of the total catch by weight. Abundance differed seasonally, with the stratified mean catch per tow being highest in fall (79 individuals/tow) and lowest in winter (26 individuals/tow) (Table 5). The number of individuals per tow differed between areas with more *P. gibbesii* collected in strata off Georgia during every season (Fig. 4).

The mean size of *P. gibbesii* differed between areas with largest crabs (\bar{x} CW = 50 mm, n = 1,484) caught off Florida. Crabs off Georgia averaged 44 mm CW (n = 2,347), while those from strata off South Carolina/North Carolina averaged 41 mm CW (n = 3,158), suggesting decreased size with increasing latitude. Mean size of *P. gibbesii* differed between seasons, with smallest individuals collected in summer (\bar{x} CW = 37.5 mm, n = 1,985). Mean carapace width of individuals was similar during other seasons (winter: \bar{x} = 46.9 mm, n = 609; spring; \bar{x} = 48.2 mm, n = 1,305; fall; \bar{x} = 45.9 mm, n = 3,090). Seasonal size differences may reflect influx of crabs from a spring hatch. Oviparous females occur off Beaufort Inlet, NC from

FIGURE 2.—Normal cluster dendrogram of site groups formed using percent standardization and flexible sorting. Data from standard tows during a season were pooled within each stratum.

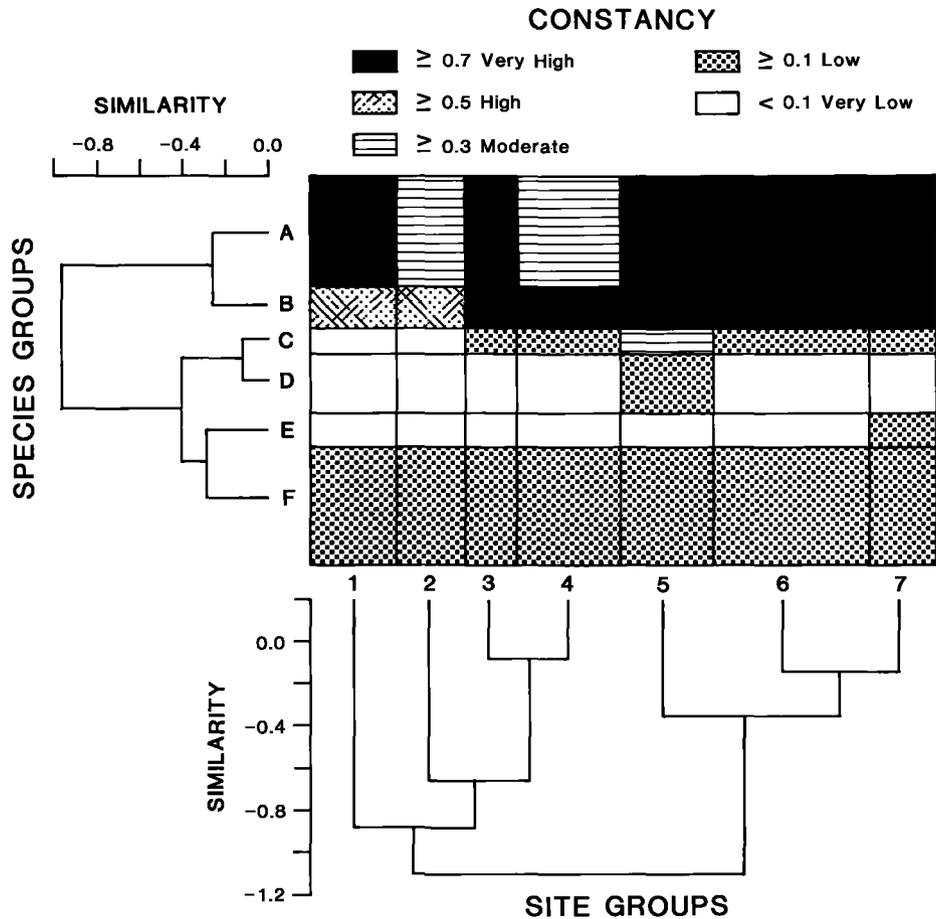


FIGURE 3.—Inverse and normal classification hierarchies and nodal diagram showing constancy and fidelity of site—species group

May to August but are known to occur from February to November in other portions of its range (Dudley and Judy 1961). In the present study, 185 of the 187 ovigerous females collected were taken in spring.

Male *P. gibbesii* were slightly larger (\bar{x} CW = 45.2 mm) than females (\bar{x} CW = 43.2 mm) but were less numerous. Analysis of sex ratios indicated significantly more female crabs than males were collected each season (Table 6).

Squilla empusa

This stomatopod is widely distributed in the western Atlantic, occurring from Maine to South America as far south as Surinam (Manning 1969; Gore and

Becker 1976). Camp (1973) found *S. empusa* to be most abundant at 18 m depths on the central west Florida shelf.

This species was the most abundant stomatopod collected and ranked second among the total catch of decapod and stomatopod species. It was frequently collected throughout the study area, occurring in 78% of the 303 trawl tows made. In terms of biomass, *S. empusa* constituted 11% of the total catch, being outranked only by the blue crab, *Callinectes sapidus* (Table 1). The stratified mean catch per tow was highest in spring (40 individuals/tow) and summer (42 individuals/tow) (Table 5). The number of individuals per tow differed between the areas with more *S. empusa* collected off Florida during every season (Fig. 4).

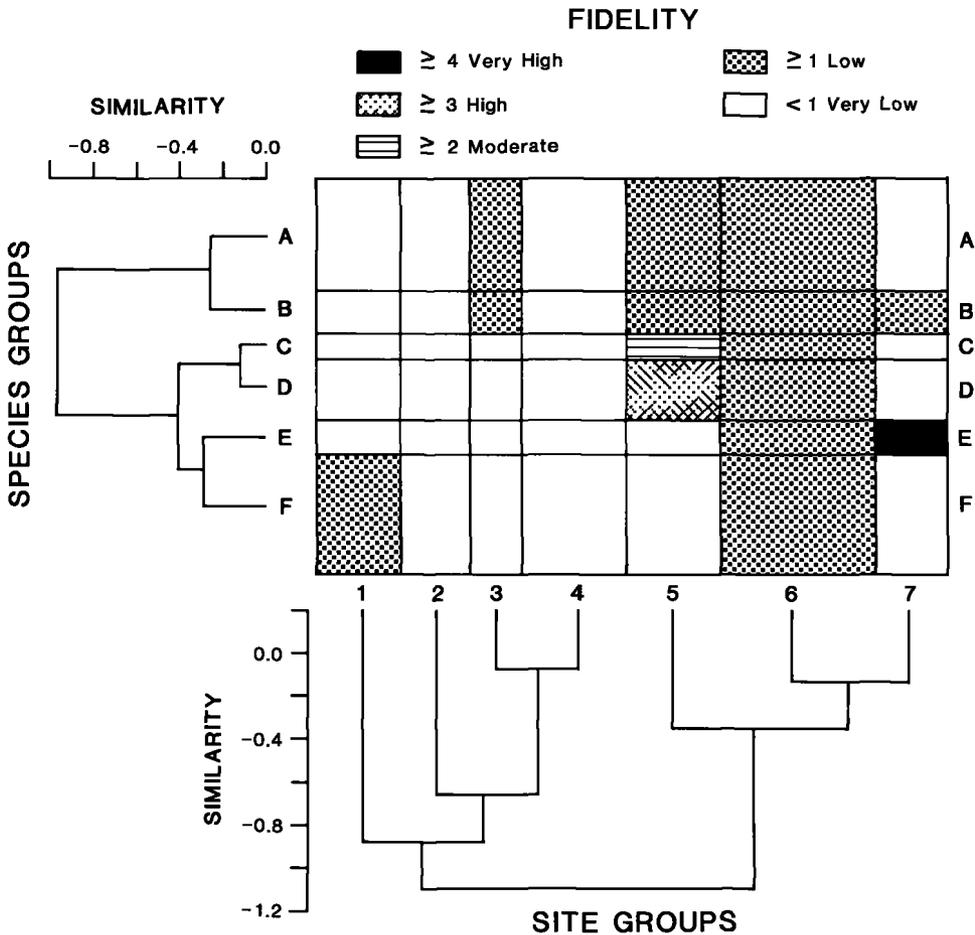


FIGURE 3.—Continued—coincidence from pooling collections during a season within each stratum.

Ovalipes stephensoni

This portunid crab, which was the third most abundant species collected in this study (12% of total catch), occurs off Virginia (Musick and McEachran 1972) to near Biscayne Bay, FL (Park 1969). Adult *O. stephensoni* are found farther from shore than adults of its congener *O. ocellatus*; however, young of both species occur nearshore (Williams 1984). Wenner and Read (1982) found *O. stephensoni* to reach maximum abundance from 9 to 18 m between Cape Fear, NC and Cape Canaveral, FL. In the study area, *O. stephensoni* was most numerous in strata off South Carolina and North Carolina where 43 individuals/tow were collected. Catches decreased off Georgia to 29 individuals/tow and were lowest

in strata off Florida (<1 individual/tow). Stratified mean catch per tow was highest in spring (120 individuals/tow) and declined markedly during other seasons (Table 5, Fig. 4).

Analysis of size composition indicated mean carapace width differed between strata and season. Largest crabs were found off Florida (\bar{x} CW = 45 mm, $n = 63$), while average sizes off Georgia ($n = 713$) and South Carolina/North Carolina ($n = 2,349$) were 30 mm and 34 mm, respectively. *Ovalipes stephensoni* collected in fall were larger (\bar{x} CW = 42 mm, $n = 273$) than those collected during other seasons (winter: \bar{x} CW = 38 mm, $n = 199$; spring: \bar{x} CW = 30 mm, $n = 1,591$; summer: \bar{x} CW = 36 mm, $n = 1,062$).

Analysis of sex ratios by season indicated signif-

icantly more female than male *O. stephensoni* were collected (Table 6). Male crabs (\bar{x} CW = 34 mm, $n = 1,278$) were comparable in size to females (\bar{x} CW = 33 mm, $n = 1,840$); however, most of the crabs collected were immature, being smaller than sizes (short carapace width) at full sexual maturity of 61 mm for males and 51 mm for females given by Haefner (1985). This supports previous observations (Williams 1984) that there is a positive size-depth relationship for the species.

Callinectes similis

The lesser blue crab occurs in the oceanic littoral

zone where it is commonly associated with the blue crab. Along the east coast of the United States, *C. similis* ranges from Delaware Bay to Key West, but is primarily a Carolinian species. Northern occurrence of the species occurs seasonally during years with favorable annual temperature (Williams 1984).

Callinectes similis ranked fourth in terms of number of individuals among all species collected in this study and occurred in 64% of the trawl tows made. The species constituted 10% of the total biomass, which was considerably less than *C. sapidus* (Table 1). The stratified mean catch per tow for numbers and weight was highest in summer and fall (Table 5). Tagatz (1967), who did not distinguish between

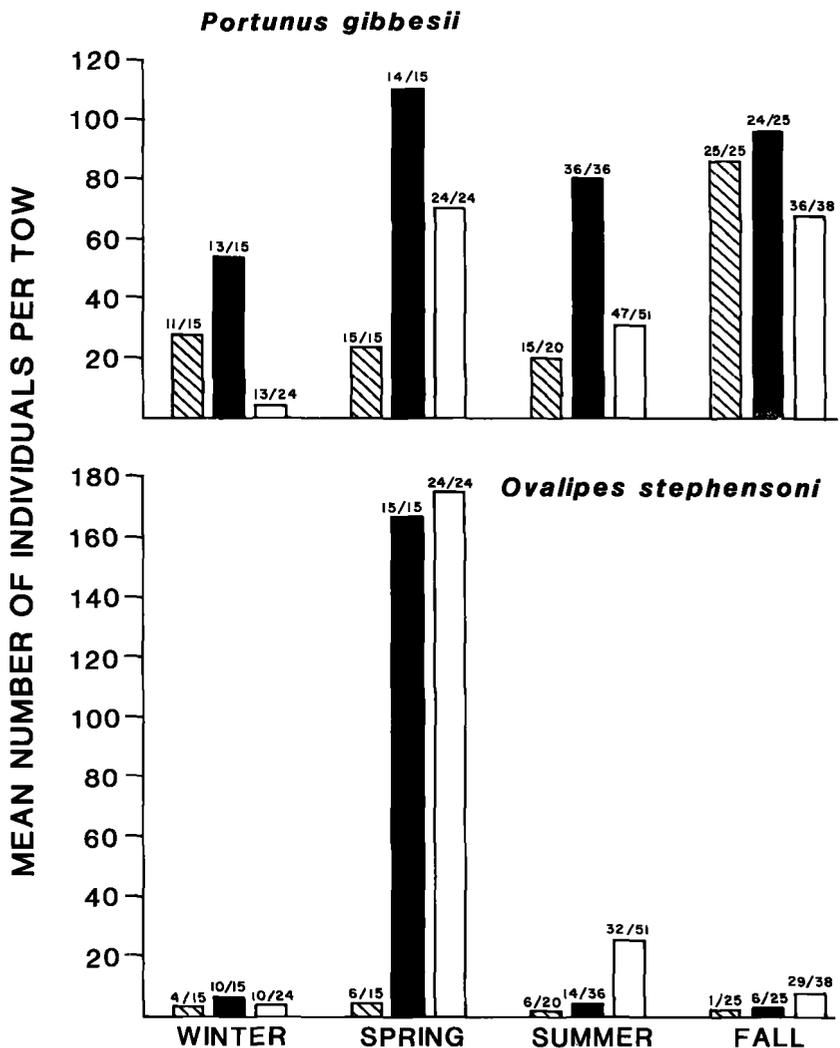


FIGURE 4.—Seasonal catch rates of the dominant decapod and stomatopod species.

TABLE 5.—Stratified mean catch per tow of 15 most numerous species caught during the coastal study.

Species	Stratified mean catch per tow							
	Winter		Spring		Summer		Fall	
	No.	Weight	No.	Weight	No.	Weight	No.	Weight
<i>Portunus gibbesii</i>	26	0.240	54	0.473	41	0.156	79	0.588
<i>Squilla empusa</i>	28	0.335	40	0.580	42	0.635	31	0.515
<i>Ovalipes stephensoni</i>	4	0.096	120	0.578	14	0.151	4	0.075
<i>Callinectes similis</i>	<1	0.016	4	0.091	34	0.836	35	0.571
<i>Penaeus setiferus</i>	15	0.289	2	0.063	12	0.260	30	0.791
<i>Penaeus aztecus</i>	<1	—	<1	0.005	44	0.722	2	0.048
<i>Portunus spinimanus</i>	3	0.096	13	0.214	14	0.207	11	0.269
<i>Ovalipes ocellatus</i>	1	0.063	17	0.344	12	0.389	4	0.164
<i>Hepatus epheliticus</i>	<1	0.007	5	0.138	12	0.357	10	0.352
<i>Squilla neglecta</i>	<1	0.002	9	0.120	7	0.065	4	0.059
<i>Callinectes sapidus</i>	2	0.361	6	1.316	8	1.202	1	0.214
<i>Arenaeus cribrarius</i>	<1	0.010	2	0.076	9	0.348	5	0.210
<i>Trachypenaeus constrictus</i>	5	0.014	2	0.005	1	0.001	6	0.019
<i>Libinia emarginata</i>	6	0.390	6	0.203	2	0.085	2	0.145
<i>Penaeus duorarum</i>	<1	0.005	9	0.152	2	0.020	3	0.031

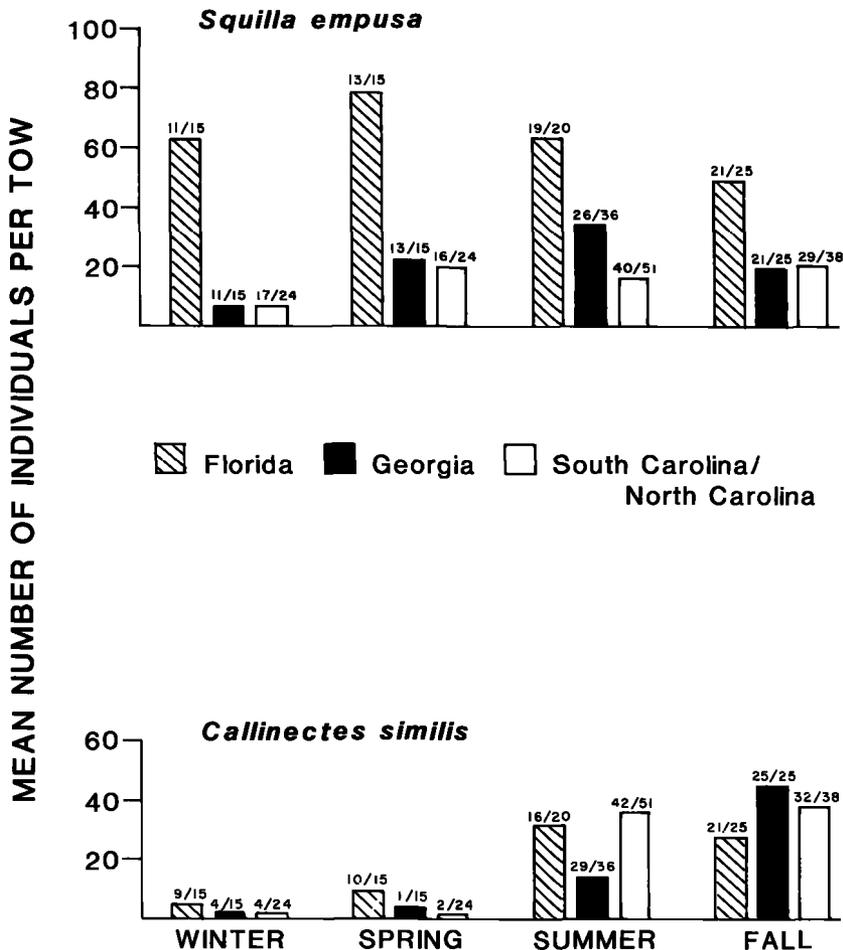


FIGURE 4.—Continued.

C. similis and *C. ornatus*, noted increased abundance from May to November with the largest catches in May, June, and October. Comparison of mean catch per tow between areas showed that *C. similis* was most abundant in strata off Florida and North Carolina/South Carolina during summer and in strata off Georgia during fall (Fig. 4). For all seasons, however, the mean catch per tow was highest for strata off North Carolina/South Carolina where an average of 24 individuals and 0.49 kg were taken per tow.

Size composition of *C. similis* differed between seasons with average size smallest in fall (\bar{x} CW = 61 mm, $n = 1,685$). Average sizes during other seasons were spring (68 mm CW, $n = 167$); summer (67 mm CW, $n = 2,558$); and winter (64 mm CW, $n = 36$). The average size of individuals collected from strata off Florida (\bar{x} CW = 72 mm, $n = 1,025$) was larger than those from Georgia (\bar{x} CW = 59 mm, $n = 1,111$) and South Carolina/North Carolina (\bar{x} CW = 65 mm, $n = 2,310$).

Sex ratios of *C. similis* indicated a significant

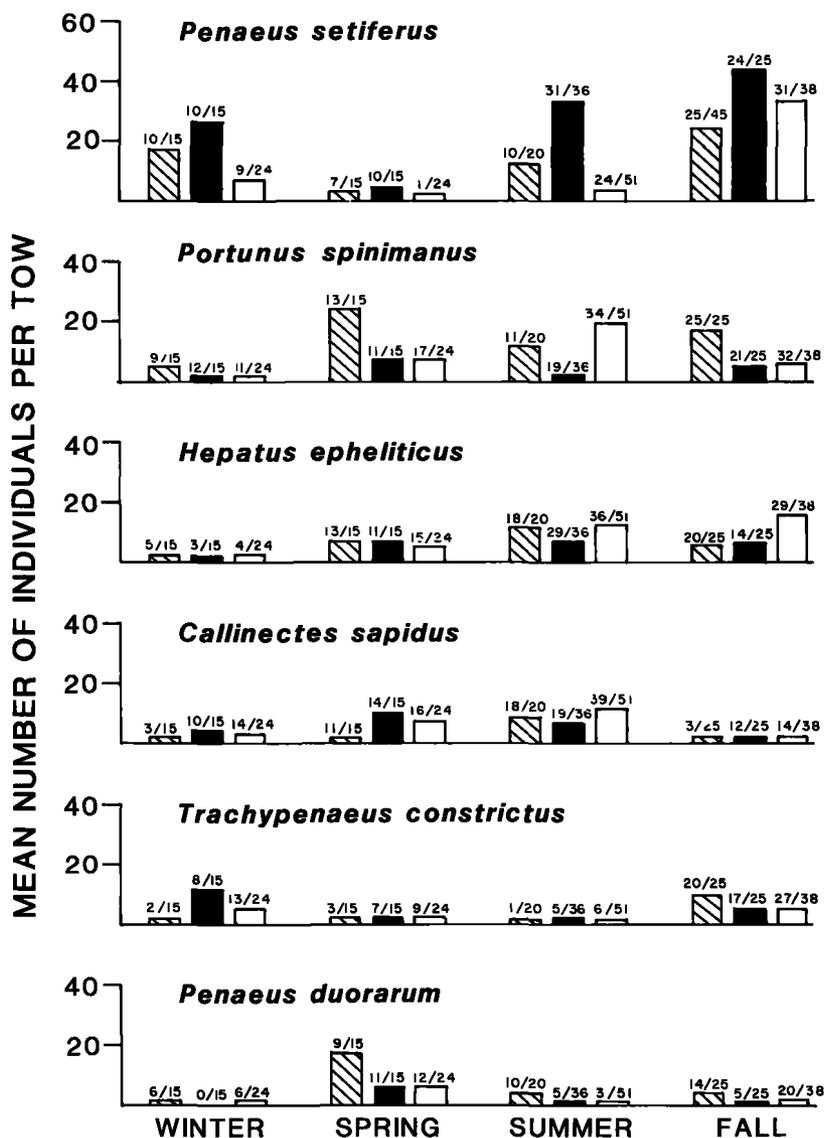


FIGURE 4.—Continued.

deviation from 1:1 during summer only (Table 6). Male *C. similis* were found to have a greater average size (\bar{x} CW = 69 mm, $n = 2,130$) than females (\bar{x} CW = 61 mm, $n = 2,294$). Of the 2,128 female *C. similis* examined for sexual maturity, 466 individuals were mature. Mature females ranged in size from 41 to 114 mm CW, while immature females were from 25 to 92 mm CW.

Penaeus setiferus

The white shrimp ranges from Fire Island, NY

to Saint Lucie Inlet, FL and in the Gulf of Mexico from the Ochlocknee River, FL to Campeche, Mexico (Williams 1984). Along the Atlantic coast of the United States, white shrimp are most abundant in South Carolina, Georgia, and northeast Florida where the species constitutes a substantial commercial fishery (South Atlantic Fishery Management Council 1981). Within the region, white shrimp are concentrated in waters <16.5 m (Anderson 1956), but abundance of *Penaeus* spp. appears to be related to distance from shore with shrimp most abundant within five miles of the coast line

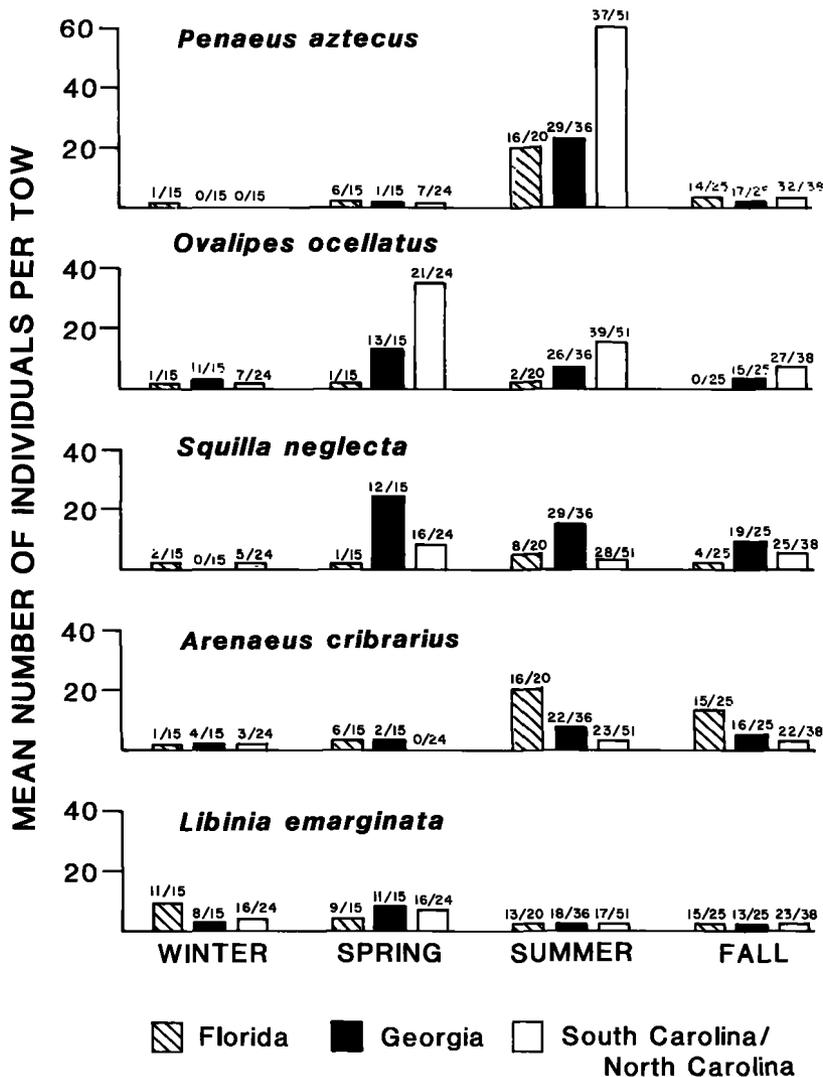


FIGURE 4.—Continued.

TABLE 6.—Frequency of males and females for species by season. * reflects significant deviation of M:F from 1:1 ($P < 0.05$) as determined by χ^2 analysis.

Species	Winter	Spring	Summer	Fall
<i>Portunus gibbesii</i>	*	*	*	*
Male	239	563	890	1,144
Female	369	739	1,019	1,908
Total	608	1,302	1,909	3,052
<i>Ovalipes stephensoni</i>	*	*	*	*
Male	84	694	398	102
Female	114	895	861	171
Total	198	1,589	1,059	273
<i>Callinectes similis</i>			*	
Male	18	77	1,166	874
Female	18	90	1,378	814
Total	36	167	2,544	1,688
<i>Portunus spinimanus</i>		*		
Male	74	254	450	395
Female	69	335	443	383
Total	143	589	893	778
<i>Ovalipes ocellatus</i>				*
Male	28	289	457	149
Female	30	269	502	208
Total	58	558	959	357
<i>Hepatus opheliticus</i>		*	*	*
Male	14	100	320	231
Female	16	206	718	541
Total	30	306	1,038	772
<i>Callinectes sapidus</i>	*	*	*	*
Male	7	8	23	12
Female	145	306	863	116
Ovigerous	0	214	405	2
Total	152	314	886	128
<i>Arenaeus cribrarius</i>		*	*	*
Male	9	61	446	205
Female	4	36	348	157
Total	13	97	794	362
<i>Libinia emarginata</i>	*			
Male	161	158	92	107
Female	120	153	86	89
Total	281	311	178	196

(South Atlantic Fishery Management Council 1981).

Penaeus setiferus was the most abundant penaeid collected in this survey, and it constituted 9% of the total catch of decapod crustaceans (Table 1). This species accounted for 10% of the total biomass of stomatopods and decapods and occurred in 63% of the 303 collections made. The stratified mean catch per tow differed among seasons, with abundance greatest in fall (30 individuals/tow) and lowest in spring (2 individuals/tow) (Table 5). This seasonal difference in abundance of *P. setiferus* in the near-shore coastal zone is explained by movement of white shrimp from estuaries to offshore waters in fall. This emigration is associated with declining water temperatures (Lindner and Anderson 1956;

Pullen and Trent 1970). White shrimp enter the estuaries as postlarvae in May, grow rapidly in the estuarine nursery grounds, and move seaward through late summer and fall (Weymouth et al. 1933).

Within the three areas sampled, white shrimp were most abundant in strata off Georgia during every season except spring (Fig. 4). This may result from a predominantly southward movement of white shrimp during fall, winter, and summer as discussed by Shipman (1980).

The mean total length of white shrimp differed by season with largest individuals occurring in spring ($\bar{x} = 162$ mm, $n = 93$). The larger average size at this time was probably influenced by occurrence of female roe shrimp that move to nearshore coastal waters from estuaries during the spring (Lindner and Anderson 1956; Joyce and Eldred 1966; Harris 1974; Music 1979; Farmer et al. 1978). The mean size of shrimp collected was largest in strata off North Carolina/South Carolina ($\bar{x} = 152$ mm, $n = 1,439$), while those from strata off Georgia and Florida averaged 145 mm ($n = 2,269$) and 142 mm ($n = 1,121$), respectively.

Penaeus aztecus

Brown shrimp occur from Martha's Vineyard, MA to the Florida Keys and into the Gulf of Mexico where they occur on the Sanibel grounds, in Appalachicola Bay, and to northwestern Yucatan (Williams 1984). Along the Atlantic coast of the United States, *P. aztecus* is most abundant off North and South Carolina (Cook and Lindner 1970).

Brown shrimp were collected in 51% of the trawl tows made during the study and were the second most abundant *Penaeus* collected (Table 1). The stratified mean catch per tow was much greater in summer (44 individuals/tow) than during the other seasons when <2 individuals/tow were collected (Table 5). Brown shrimp usually occupy the estuarine nursery grounds from March through July before emigrating to coastal waters in August. Emigration, however, may be delayed if cooler than normal temperatures occur in spring (South Atlantic Fishery Management Council 1981). The summer cruise occurred from mid-July into September, which overlapped the period when brown shrimp emigrated from the estuary. During the summer sampling period, brown shrimp abundance was greatest in strata sampled off North Carolina/South Carolina (Fig. 4). Abundance during other seasons was too low to assess any difference between areas.

The mean total length of brown shrimp was greatest in summer (\bar{x} = 126 mm, n = 2,718) and fall (\bar{x} = 126 mm, n = 214) following emigration from the estuaries. Size at emigration for brown shrimp has been reported to be 100–105 mm (Joyce 1965) and 60–103 mm (Trent 1967). Off North Carolina, *P. aztecus* enters the commercial fishery in June at a size of 100 mm (South Atlantic Fishery Management Council 1981). Mean size of brown shrimp was largest off Georgia (\bar{x} = 138 mm, n = 871) and Florida (\bar{x} = 127 mm, n = 493), while those from strata off North Carolina and South Carolina averaged 119 mm (n = 1,600). The capture of larger shrimp further south may result from migration of individuals to waters off Georgia and Florida. These shrimp are probably supplied by the sounds and estuaries of North and South Carolina. Tagging studies off North Carolina indicate that brown shrimp move to the south and to deeper, nontrawlable waters once they leave the sounds (Purvis and McCoy 1974). Shipman (1980) noted few recaptures of brown shrimp tagged off Georgia and suggested that lower return rates may indicate offshore movement of brown shrimp, out of the nearshore trawling grounds.

Portunus spinimanus

This common portunid of the inner continental shelf ranges from New Jersey to southern Florida (Powers 1977), often co-occurring with *P. gibbesii*. Camp et al. (1977) found *P. spinimanus* to be one of the commonest decapod crustaceans in samples from nearshore east Florida waters with salinity of 32–39‰ and temperature ranging from 19.2° to 32°C.

In the present study, *P. spinimanus* was the 7th most numerous species (4.1% of the total catch) and the 11th most important by weight (4%) (Table 1). This species occurred at 73% of the trawl stations from all seasons. The stratified mean catch per tow was lowest in winter (3 individuals/tow). Catch per tow values by stratum were higher in spring (13 individuals/tow) and summer (14 individuals/tow), but decreased to 11 individuals/tow in fall (Table 5). Catch of *P. spinimanus* per tow differed among areas with most individuals collected in trawl tows off Florida (15 individuals/tow). Increased abundance in strata off Florida was observed for every season except summer (Fig. 4).

The size composition of *P. spinimanus* in trawl catches differed between strata and seasons. Mean carapace width was largest for individuals collected off Florida (\bar{x} CW = 54 mm, n = 974)

and Georgia (\bar{x} CW = 53 mm, n = 343), while those collected in combined strata off South Carolina and North Carolina averaged 46 mm CW (n = 1,129). Largest individuals were collected in winter (\bar{x} CW = 58 mm, n = 144) and fall (\bar{x} CW = 56 mm, n = 782). The smaller average size of individuals collected in spring (\bar{x} CW = 48 mm, n = 601) and summer (\bar{x} CW = 46 mm, n = 919) may reflect an influx of small crabs from the previous fall hatch.

Analysis of sex ratio by season indicated no significant deviation from unity except during spring when female *P. spinimanus* outnumbered males (Table 6). Average size was similar for males (\bar{x} CW = 51.4 mm, n = 1,172) and females (\bar{x} CW = 49.8 mm, n = 1,230).

Ovalipes ocellatus

This portunid crab has a broad geographic range from Canada to Georgia (Williams 1984). Abundance decreases in southern latitudes, apparently in response to lessened tolerance to warm-water temperatures (Vernberg and Vernberg 1970). In the present study, *O. ocellatus* occurred more frequently than *O. stephensoni*, but was not as numerous (Table 1). Abundance of this crab decreased from the northern to southern area, with most individuals collected in trawl catches off North Carolina/South Carolina (14 individuals/tow) (Fig. 4). Abundance in strata off Georgia was 6 individuals/tow, while <1 individual/tow was caught off Florida. The stratified mean catch per tow differed among season with most individuals collected in spring (Table 5).

Average size of *O. ocellatus* differed among areas. The average size of individuals collected in strata off Florida was larger (\bar{x} CW = 65 mm, n = 11) than that from other areas (Georgia: \bar{x} CW = 53 mm, n = 588; South Carolina/North Carolina: \bar{x} CW = 51 mm, n = 1,340). Seasonal differences in size composition were noted as well, with average carapace width smallest in spring (\bar{x} CW = 48 mm, n = 558). This may reflect occurrence of juveniles from a fall-winter hatch (Dudley and Judy 1971). Average size of individuals during other seasons was winter (\bar{x} CW = 59 mm, n = 58), summer (\bar{x} CW = 52 mm, n = 966), and fall (\bar{x} CW = 57 mm, n = 357).

No significant seasonal difference in sex ratio was noted, with the exception of fall when females were more numerous than males (Table 6). Male *O. ocellatus* (\bar{x} CW = 54 mm, n = 923) were larger than females (\bar{x} CW = 50 mm, n = 1,009).

Hepatus epheliticus

The known range for this crab extends from Chesapeake Bay to southern Florida where it is a common inhabitant of nearshore waters. Evidence suggests it buries in sandy substrate (Williams 1984) and may be nocturnally active (Powers 1977).

Hepatus epheliticus occurred throughout the study area and was present in 65% of the collections made during all seasons (Table 1). Abundance differed among seasons with the stratified mean catch per tow being highest in fall (10 individuals/tow) and summer (12 individuals/tow) (Table 5). Number of individuals per tow also differed between areas with highest catches noted from strata off South Carolina and North Carolina (10 individuals/tow) (Fig. 4). Larger crabs were noted in this region with a mean carapace width (\bar{x} CW) of 58 mm ($n = 1,176$). The mean size of *H. epheliticus* from Georgia coastal waters was 58 mm ($n = 526$), while those from strata off Florida averaged 54 mm ($n = 456$). There was a noticeable decrease in size and number of crabs collected in winter (\bar{x} CW = 38 mm, $n = 30$) compared with sizes noted for other seasons (spring: \bar{x} CW = 52 mm, $n = 306$; summer: \bar{x} CW = 57 mm, $n = 1,050$; fall: \bar{x} CW = 60 mm, $n = 772$). This may reflect movement of larger crabs further offshore during the winter.

Female *H. epheliticus* significantly outnumbered male crabs during every season except winter (Table 6). Carapace width was similar among the sexes (male \bar{x} CW = 58 mm, $n = 663$) (female \bar{x} CW = 57 mm, $n = 1,479$).

Squilla neglecta

This stomatopod species has a more disjunct distribution than its congener, *S. empusa*, and occurs from North Carolina to Florida, the Gulf of Mexico from western Florida to Texas, and southwest to Brazil (Gore and Becker 1976). *Squilla neglecta* was found by Camp (1973) to co-occur with *S. empusa* on the central west Florida Shelf where both were most abundant at 18 m depths.

Squilla neglecta occurred in 49% of the trawl tows and was most abundant in spring (9 individuals/tow) (Table 5). The number of individuals per tow was highest in strata off Georgia during every season except winter when none occurred there (Fig. 4).

Callinectes sapidus

The blue crab occurs along the western Atlantic

coastline from Maine to northern Argentina, with the main commercial fishery in Chesapeake Bay (Williams 1984). Blue crabs occur on a variety of bottom types and are mainly abundant out to depths of 35 m.

Callinectes sapidus ranked first in terms of biomass, making up about 19% of the entire catch of decapods and stomatopods (Table 1). Blue crabs occurred in 173 of the 303 trawl tows made during the survey.

The stratified mean catch per tow for number and weight was greatest in the coastal zone during spring and summer (Table 5). Comparison of catches between areas showed abundance was comparable for strata off Georgia and North Carolina/South Carolina during all seasons (Fig. 4).

Size composition of blue crabs differed between seasons with the average carapace width being greatest in winter and spring (Fig. 5). Mean carapace width was similar between areas, however, with those collected off Florida averaging 137 mm ($n = 164$) and those from strata off Georgia ($n = 485$) and North Carolina/South Carolina ($n = 835$) averaging 139 mm and 138 mm, respectively.

Sex ratios were overwhelmingly dominant in terms of female *C. sapidus* for each season (Table 6). No ovigerous female crabs were collected in winter and only two individuals were found in fall collections. During spring and summer, however, the number of ovigerous females constituted 70% and 47% of the catch of female crabs, respectively. Among non-ovigerous females ($n = 809$), 95% of the blue crabs were mature.

Greater numbers of females in the coastal zone are expected in view of the life history of the blue crab. With the exception of the breeding season, when females migrate into lower salinity waters of the estuary, they are usually found near the mouths of estuaries where the eggs are spawned and hatch. Most spawning occurs in spring and early summer, with the season becoming progressively shorter from Florida to North Carolina (Norse 1977). Males, however, remain in the middle to upper reaches of estuaries as juveniles and adults (Gunter 1950; Hildebrand 1954).

Arenaeus cribrarius

This portunid is a common inhabitant of the shallow coastal zone along beaches (Hoese 1972; Williams 1984). The known geographic range extends from Massachusetts to Brazil. It occurs abundantly in the penaeid shrimp grounds of the Gulf of Mex-

ico (Hildebrand 1954). Anderson et al. (1977) seined 422 specimens in the surf at Folly Beach, SC and *A. cribrarius* was the most abundant macroinvertebrate collected in the same area by DeLancey (1984). In the present study, *A. cribrarius* constituted only 2% of the total catch of decapods and stomatopods but occurred in 43% of the total collections (Table 1). Mean catch per tow increased from northern to southern sampling areas, with highest catches (10 individuals/tow) off Florida. Catches decreased to 5 individuals/tow off Georgia to 2 individuals/tow off North Carolina/South Carolina. The stratified mean catch per tow showed a seasonal trend with highest catch occurring in summer and fall (Table 5). This corresponds with observations reported by Anderson et al. (1977) who found a positive correlation of number of crabs with water temperature.

Average carapace width was greatest for individuals collected off South Carolina/North Carolina (\bar{x} CW = 82 mm, $n = 286$). Those from strata off Georgia ($n = 436$) and Florida ($n = 544$) averaged 78 mm. Size differences were noted between seasons, as well; however, the small number of individuals collected in winter ($n = 13$) did not provide adequate information on size composition for that season. During spring (\bar{x} CW = 81 mm, $n = 97$), summer (\bar{x} CW = 77 mm, $n = 794$), and fall (\bar{x} CW = 83 mm, $n = 362$), the size composition of the catch was similar.

The M:F ratio was significant for every season except winter (Table 6). Male *A. cribrarius* were larger (\bar{x} CW = 82 mm, $n = 721$) than females (\bar{x} CW = 76 mm, $n = 545$).

Trachypenaeus constrictus

This penaeid shrimp is caught incidentally in the commercial shrimp fishery along the southeastern and Gulf coasts. Eldred (1959) reported that *T. constrictus*, along with *T. similis*, constituted 7% of the annual catch in the Tortugas area of Florida. In the South Atlantic Bight, *T. constrictus* was most abundant in the 9–18 m depth zone sampled by Wenner and Read (1981, 1982).

This species was seasonally abundant in collections from the coastal zone, with stratified mean catch per tow highest in fall (6 individuals) and winter (5 individuals) (Table 5). Increased abundance of the species during fall and winter was previously noted by Wenner and Read (1981, 1982) and is probably due to recruitment from spawning in spring and late summer (Williams 1969; Anderson 1970; Subrahmanyam 1971). The number of individuals per tow

did not noticeably differ between the areas sampled (Fig. 4).

Libinia emarginata

The common spider crab ranges from Nova Scotia to south Florida where it occurs mostly on mud and mud-sand bottom in shallow water (Powers 1977). This species was reported by Hildebrand (1954) to be the most common large spider crab on the western Gulf of Mexico shrimp grounds. Winget et al. (1974) found *L. emarginata* seasonally most abundant in spring and summer in Delaware Bay where it was common in mud of sloughs. This species ranked 14th in overall abundance in the current study and occurred in 56% of the trawl collections (Table 1). Abundance of *L. emarginata* was nearly equal between the three areas: 4 individuals/tow off Florida, 3 individuals/tow off Georgia, and 3 individuals/tow off North Carolina/South Carolina. The stratified mean catch per tow differed among seasons with abundance highest in winter and spring (Table 6).

Carapace length was similar between areas, with largest individuals collected off Georgia (\bar{x} CL = 54 mm, $n = 232$), while those from Florida and North Carolina/South Carolina waters averaged 52 mm ($n = 283$) and 50 mm ($n = 451$), respectively. Analysis of size frequencies by season (not shown) indicated a broad range of sizes. Small individuals, reportedly associated with the coelenterate *Stomolophus meleagris* (Hildebrand 1954), occurred in low numbers during every season. Average size of the sampled individuals was lowest in spring (\bar{x} CL = 47 mm, $n = 312$) and summer (\bar{x} CL = 50 mm, $n = 179$), while those collected in fall (\bar{x} CL = 57 mm, $n = 193$) and winter (\bar{x} CL = 54 mm, $n = 282$) were slightly larger.

Sex ratios were significantly different from unity in winter, when males dominated (Table 6). Winget et al. (1974) also noted dominance by male *L. emarginata* in winter. Carapace length differed between the sexes, with males slightly larger (\bar{x} CL = 53 mm, $n = 514$) than females (\bar{x} CL = 50 mm, $n = 447$).

Penaeus duorarum

Pink shrimp occur from southern Chesapeake Bay to the Florida Keys, along the coast of the Gulf of Mexico to the southern Yucatan Peninsula (Williams 1984). In the southern United States, *P. duorarum* occurs in commercial quantities only off North Carolina. Pink shrimp reach maximum abun-

dance in the coastal zone at depths from 11 to 37 m (South Atlantic Fishery Management Council 1981).

Pink shrimp were the least abundant *Penaeus* collected in this study (Table 1). They were collected in 101 of the 303 trawl tows made. The stratified mean catch per tow was highest for collections in spring when 0.15 individuals per tow were collected (Table 5). During spring, catches were highest in strata off Florida (Fig. 4). The average size of pink shrimp was greatest in spring (\bar{x} TL = 121 mm, $n = 502$). Mean sizes during other seasons were winter (\bar{x} TL = 113 mm, $n = 11$), summer (\bar{x} TL = 95 mm, $n = 101$), and fall (\bar{x} TL = 106 mm, $n = 209$). Average total length decreased from northern to southern areas as follows: North Carolina/South Carolina ($\bar{x} = 119$ mm, $n = 256$), Georgia ($\bar{x} = 114$ mm, $n = 108$), Florida ($\bar{x} = 111$ mm, $n = 459$).

The increased abundance and size of shrimp in spring probably relates to their movement to the nearshore zone then. In North Carolina, pink shrimp emigrate from the estuaries in May and June, at which time spawning takes place (Williams 1984). Kennedy and Barber (1981) reported that movement offshore of Cape Canaveral begins in April and May. The larger average size of pink shrimp in spring probably reflects the presence of roe-bearing females in the coastal zone at that time.

ACKNOWLEDGMENTS

We sincerely thank P. Richards, M. Schwarz, and J. LaRoche of the South Carolina Wildlife and Marine Resource Department RV *Lady Lisa* and RV *Atlantic Sun*. Scientific personnel whose assistance was invaluable included K. Thornley, W. Waltz, W. Roumillat, D. Stubbs, C. Barans, and others from the S.C. MARMAP project. Technical assistance was provided by M. J. Clise, K. Swanson, and M. Lentz. This work is a result of research sponsored by the National Marine Fisheries Service (MARMAP program) under contract no. 6-35147.

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