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Macrobenthos of Sandy Beach and Nearshore Environments at Murrells Inlet, South Carolina, U.S.A.[a]

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Quantitative samples of benthic macrofauna were collected seasonally from sandy beaches and adjacent nearshore areas bordering the entrance of a high salinity inlet in South Carolina. Intertidal stations were numerically dominated by the polychaete *Scolelepis squamata*, the amphipod *Neohaustorius schmitzi* and the bivalve *Donax variabilis*. Abundant subtidal species included the polychaetes *Spiophanes bombyx* and *Scolelepis squamata*, the amphipods *Protohaustorius deichmannae* and *Acanthohaustorius millsi*, and the bivalve *Tellina* sp. Species composition, faunal density and species diversity varied along three transects extending from mean high water to depths of about 5 m. Although some species groups were habitat-restricted, the numerically dominant species were widely distributed throughout the subtidal and intertidal zones. Polychaetes dominated the fauna of subtidal and intertidal habitats, both in terms of numbers of species and numbers of individuals. This dominance was attributed to the moderate wave energy in this area, as well as to the sheltering effect of a jetty that was constructed during the course of the study. Jetty construction also resulted in faunal enrichment at intertidal stations on a sheltered transect.

Introduction

Sandy shores provide an environment of high stress and continual change for intertidal marine infauna. As a result, relatively few macroinvertebrate species inhabit the intertidal zone as compared with more stable subtidal areas. On beaches of the south-eastern United States, important intertidal species include several haustoriid amphipods, the polychaete *Scolelepis squamata*, the coquina clam *Donax variabilis*, and the decapod crustaceans *Emerita talpoida* and *Ocypode quadrata* (Pearse *et al.*, 1942; Croker, 1967, 1968; Dexter, 1967, 1969; Dörjes, 1972, 1977; Howard & Dörjes, 1972; Roberts, 1974; Matta, 1977). Although these organisms are common on front beaches of South Carolina, quantitative studies on the intertidal beach communities between North Carolina and Georgia are lacking. Similarly,

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subtidal nearshore benthic communities have been examined off North Carolina and Georgia (e.g. Pearse *et al.*, 1942; Day *et al.*, 1971; Frankenberg, 1971; Frankenberg & Leiper, 1977), but not off South Carolina, with the exception of one investigation in a dredge disposal area near Charleston (South Carolina Wildlife and Marine Resources Department, 1979).

The coast of South Carolina consists of numerous sea islands separated by inlets, which often shoal through the interaction of longshore and tidal currents. To alleviate navigational hazards associated with these shoals, long jetties have been constructed at the entrance to major ports in the state. Additionally, smaller jetties were recently constructed at the mouth of Murrells Inlet. Although the fauna associated with rock jetties in South Carolina has been described (Stephenson & Stephenson, 1952; McCloskey, 1970), few studies have quantitatively investigated the biological impact of these structures on nearby areas (Mulvihill *et al.*, 1980). Thus, construction of the Murrells Inlet jetties offered an excellent opportunity to characterize intertidal and subtidal infaunal assemblages of a coastal area in South Carolina, and also to assess changes in those assemblages after placement of quarrystone jetties.

Description of study area

Murrells Inlet is a biologically productive, marshy lagoon on the northern third of the South Carolina coastline. Waters of the inlet are less turbid than those of most estuarine areas in South Carolina because no river system flows into the inlet. Salinity near the mouth of the inlet is generally high, ranging from 31·8–35·4‰ during the course of this study. Water temperature in this area is more variable, and ranged from 6·0–28·7 °C over the study period. Depths in and adjacent to the inlet are generally less than 6 m.

At its entrance, Murrells Inlet is flanked by Garden City Beach to the north-east and Huntington Beach to the south-west (Figure 1). The sediments of these beaches and adjacent nearshore areas consist primarily of medium to fine quartz sand with varying amounts of sand-size shell fragments (Calder & Knott, 1978). The intertidal zone, with a mean tidal range of 1·4 m (National Ocean Survey, 1979), covers a horizontal distance of approximately 30–40 m on Garden City Beach and 55 m on Huntington Beach in the areas investigated. Although exposed to the open ocean, wave energy is moderate on these beaches because waters are shallow for a considerable distance offshore.

Construction of the quarrystone jetties was initiated in 1977 on the north side of the inlet entrance to provide a stabilized channel to the ocean (Figure 1). At the beginning of our study, construction of the north jetty was restricted to an area landward of the beach. By the end of sampling, this jetty extended seaward about 80% of its projected total length of 1050 m. Construction did not commence on the south jetty until January 1979, several months after field sampling had been completed.

Materials and methods

Three transects were established at the entrance of Murrells Inlet (Figure 1). Transects I (NI01–NS03) and II (SI101–SS03) extended offshore from Garden City Beach along both sides of the proposed north jetty. Transect III (HI01–HS03) extended offshore from Huntington Beach. Three intertidal and three subtidal stations were chosen on each transect. Intertidal stations were located near mean high water (MHW), mean tide level (MTL) and mean low water (MLW) on each transect. These stations were located with reference to permanent landmarks. Subtidal stations on each transect included one adjacent to the beach

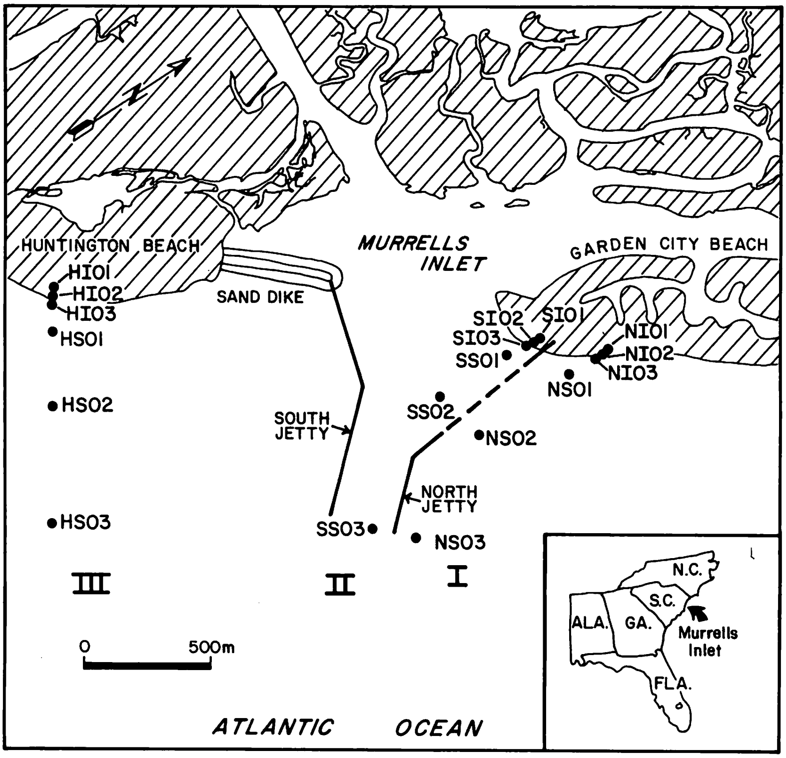

Figure 1. Map of Murrells Inlet, South Carolina, U.S.A., showing the location of the jetties. The three transects of benthic sampling stations are indicated by roman numerals.

in depths of 1–2 m (nearshore), one 0·5 km from shore at a depth of approximately 2 m (midshore) and one 0·9–1·1 km from shore in depths of 4–5 m (offshore). All subtidal stations were located using triangulation on fixed landmarks ashore.

Three replicate samples were collected at every station during November 1977 and February, May and August 1978. Intertidal samples of 0·05 m^2 and 11 cm deep were taken using a quadrat and shovel. Subtidal samples were collected using a 0·10 m^2 modified Van Veen grab. All samples were gently washed on a 0·5 mm mesh sieve to remove excess sediment and preserved in a 10% formaldehyde–seawater solution with rose bengal stain. In the laboratory, macrofaunal organisms sorted from the samples were preserved in 70% isopropanol, identified to the lowest taxon possible and counted.

Community structure was evaluated through numerical classification and comparison of species numbers, number of individuals, and Pielou's (1977) indices of species diversity (H'), evenness (J') and richness (SR). Similarity was computed on log-transformed abundance values of pooled seasonal data from each station, using the Bray-Curtis coefficient (Clifford & Stephenson, 1975). Clustering was done using flexible sorting with $\beta = -0{\cdot}25$ (Lance & Williams, 1967). Both normal (site group) and inverse (species group) analyses were performed. The resulting dendrograms were evaluated using a variable 'stopping rule' (Boesch, 1977) in order to form groups of stations and species. Those groups were then subjected to nodal analysis (Lambert & Williams, 1962) and their coincidence was expressed by graded constancy and fidelity. Constancy expresses the frequency with which species of a particular group are found in a given collection group and fidelity measures the degree to which species are restricted to a particular collection group.

To avoid confusion in interpreting the cluster analysis, rare species occurring at fewer than three stations were deleted from the data set. Specimens of indeterminate identity were also deleted, except in those cases where they could be consistently recognized as being unique species.

Results

Species composition

We identified 223 species of benthic macroinvertebrates in samples from the 18 stations. Collections from subtidal stations contained 205 species, whereas those from intertidal stations yielded 88 species. Polychaetes dominated the fauna, both in terms of species (Table 1) and numbers of individuals (Table 2). Together with amphipods and pelecypods, they accounted for more than 95% of the individuals and 70% of the species. The 10 most abundant species, comprising nearly 82% of the fauna, were *Spiophanes bombyx*, *Scolelepis squamata*, *Protohaustorius deichmannae*, *Donax variabilis*, *Acanthohaustorius millsi*, *Neohaustorius schmitzi*, *Tellina* sp., *Ensis directus*, Platyischnopidae (n. gen., n. sp.) and *Parahaustorius longimerus*. A complete listing of all organisms collected, in ranked order of overall abundance, is available upon request.

TABLE 1. Number of species representing each of the major macroinvertebrate taxa in intertidal and subtidal samples from Murrells Inlet

Taxon	No. species intertidally	No. species subtidally	No. species both areas combined	Percent of total	Cumulative percent
Polychaeta	25	83	89	39·91	39·91
Amphipoda	25	31	38	17·04	56·95
Pelecypoda	13	27	30	13·45	70·40
Decapoda	4	17	17	7·62	78·02
Gastropoda	2	12	12	5·38	83·40
Isopoda	5	8	10	4·48	87·88
Echinodermata	3	6	6	2·69	90·57
Cumacea	5	5	5	2·24	92·81
Mysidacea	1	4	4	1·79	94·60
Anthozoa		2	2	0·90	95·50
Hydroida	1	1	1	0·45	95·95
Turbellaria	1	1	1	0·45	96·40
Rhynchocoela	1	1	1	0·45	96·85
Brachiopoda	1	1	1	0·45	97·30
Oligochaeta		1	1	0·45	97·75
Tanaidacea		1	1	0·45	98·20
Hemichordata	1	1	1	0·45	98·65
Ascidiacea		1	1	0·45	99·10
Cephalochordata		1	1	0·45	99·55
Unidentified taxon		1	1	0·45	100·00

Intertidal. The spionid *Scolelepis squamata* accounted for 80% of all polychaetes at the intertidal stations and was present throughout the year. This species was especially abundant at the middle and lower intertidal stations in winter and spring on all three transects (Figure 2). The only other polychaete represented by substantial numbers in the intertidal zone was

TABLE 2. Numbers of individuals of each of the major macroinvertebrate taxa in intertidal and subtidal samples from Murrells Inlet

Taxon	No. individuals intertidally	No. individuals subtidally	Total numbers	Percent of total fauna	Cumulative percent
Polychaeta	4899	18 253	23 152	61·00	61·00
Amphipoda	2239	6166	8405	22·15	83·15
Pelecypoda	1546	3082	4628	12·19	95·34
Decapoda	60	237	297	0·78	96·12
Cumacea	31	243	274	0·72	96·84
Isopoda	64	161	225	0·59	97·43
Rhynchocoela	21	169	190	0·50	97·93
Tanaidacea		146	146	0·39	98·32
Echinodermata	5	135	140	0·37	98·69
Hydroida	62	33	95	0·25	98·94
Oligochaeta		89	89	0·23	99·17
Anthozoa		81	81	0·21	99·38
Mysidacea	2	77	79	0·21	99·59
Gastropoda	3	73	76	0·20	99·79
Unidentified taxon		52	52	0·14	99·93
Turbellaria	1	10	11	0·03	99·96
Ascidiacea		5	5	0·01	99·97
Hemichordata	2	1	3	0·01	99·98
Brachiopoda	1	1	2	0·01	99·99
Cephalochordata		2	2	0·01	100·00

another spionid, *Spiophanes bombyx*. This species was absent from intertidal samples during November, but was present in February (Figure 2) and numerically codominant with *S. squamata* at stations SI02 and SI03. During May and August, *S. bombyx* was present only at SI03.

Haustoriid amphipods were well-represented in the intertidal zone. *Neohaustorius schmitzi* was the most abundant, accounting for 77% of the total number of amphipods collected at beach sites. Densities of *N. schmitzi* were lowest in November and highest during February and May (Figure 2). This species was most prevalent at middle and lower intertidal stations. Two other haustoriids that were found in substantial numbers in the low intertidal zone on Transects I and II were *Acanthohaustorius millsi* and *Parahaustorius longimerus*.

Thirteen species of pelecypods were collected intertidally, but only the coquina clam *Donax variabilis* was numerically abundant (Table 3). This species was generally more prevalent in samples from Transect III than from Transects I and II (Figure 2). Specimens were collected intertidally throughout the year, but largest numbers were present in May samples. Maximum densities were found at HI03 in May, and densities declined on all three transects between May and August.

Subtidal. Spiophanes bombyx was numerically dominant at subtidal stations, accounting for about 45% of the total subtidal fauna (Table 4) and more than 36% of the macroinvertebrates from all intertidal and subtidal stations combined. This spionid underwent large seasonal fluctuations in abundance due to juvenile recruitment (Figure 3). Densities at most stations increased substantially between November and February, with most of the specimens collected being quite small. Furthermore, the average size of *S. bombyx* increased over subsequent sampling periods. Numbers of *S. bombyx* were typically highest at the outermost stations on Transects I and II and at all three Huntington Beach stations (Figure 3), where sediments were mostly fine sand (Calder & Knott, 1978).

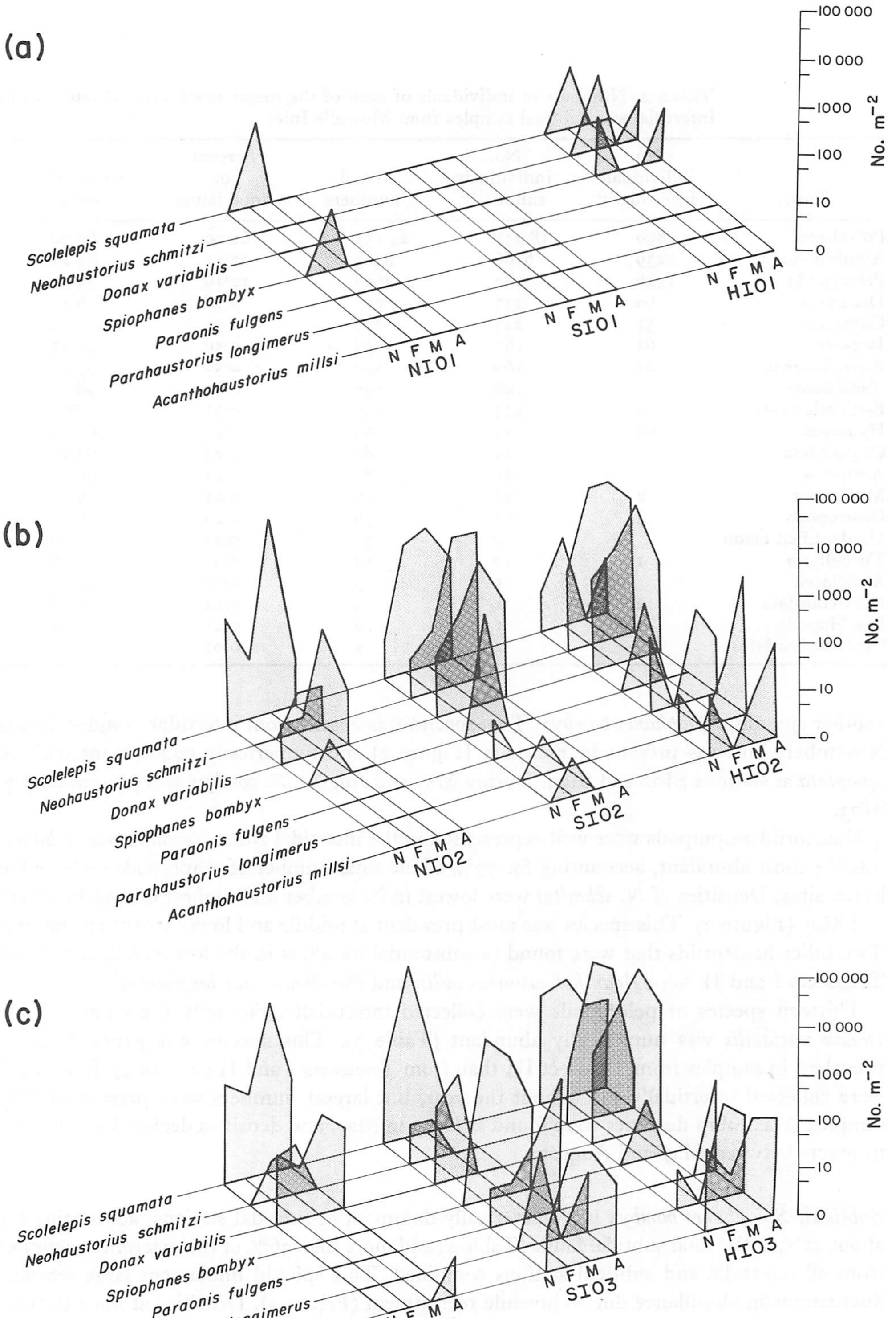

Figure 2. Seasonal abundance of dominant macroinvertebrates at (a) MHW, (b) MTL and (c) MLW intertidal stations along the three transects. Vertical scales are logarithmic and sampling periods are labelled as: N = November; F = February; M = May; A = August.

TABLE 3. Numbers of individuals and ranked abundance of dominant macroinvertebrate species collected at nine intertidal stations at Murrells Inlet. (Only species comprising $\geq 1\%$ of the total number collected are presented)

	MHW	MTL	MLW	Total	Percent of fauna	Cumulative percent	Rank by number
Scolelepis squamata	11	2223	1680	3914	43·8	43·8	1
Neohaustorius schmitzi	7	1201	520	1728	19·3	63·1	2
Donax variabilis	5	623	733	1361	15·2	78·3	3
Spiophanes bombyx	3	69	657	729	8·2	86·5	4
Paraonis fulgens	0	24	144	168	1·9	88·4	5
Parahaustorius longimerus	0	40	125	165	1·8	90·2	6
Acanthohaustorius millsi	0	21	137	158	1·8	92·0	7
Others (81 species)	18	343	352	713	8·0	100·0	—

The polychaete *S. squamata* was also abundant subtidally, especially during the winter. This species was moderately numerous in May, and infrequent in samples taken during August and November (Figure 3). Maximum densities of *S. squamata* occurred at the shallow subtidal stations, and few specimens were collected at the deepest stations of each transect.

Six species of amphipods (*Protohaustorius deichmannae*, *Acanthohaustorius millsi*, Platyischnopidae (n. gen., n. sp.), *Bathyporeia parkeri*, *Parahaustorius longimerus* and *Trichophoxus epistomus*) were common throughout the year at subtidal stations (Figure 3). *Protohaustorius deichmannae* was most abundant, and frequently dominant, at two of the subtidal stations nearest the beach (NS01, HS01). Maximum numbers of this species were observed in spring samples at HS01. *Parahaustorius longimerus* was also common at nearshore stations, particularly on Transects I and II, but was absent at the outermost station on each transect. *Acanthohaustorius millsi* and *Bathyporeia parkeri* were most prevalent at midshore stations on each subtidal transect, and *A. millsi* was the numerically dominant macroinvertebrate at all subtidal stations of Transect III during November. *Bathyporeia parkeri* was frequently observed in winter and spring samples but was scarce in August samples.

The new platyischnopid species (Thomas & Barnard, in press) occurred in greatest numbers at midshore and offshore stations. More specimens of this species were collected during February than any other sampling interval. The phoxocephalid *Trichophoxus epistomus* was also more frequent at midshore and offshore stations than elsewhere.

Three species of pelecypods were also common subtidally. *Donax variabilis* was present almost exclusively at nearshore and midshore sites. Large numbers of juveniles were present in samples from February, but this species was scarce in subtidal samples by May. This decline may reflect a migration into the intertidal zone, since substantial increases in density were observed between February and May at most middle and lower intertidal stations (Figure 2). In contrast to *D. variabilis*, the razor clam *Ensis directus* was collected primarily in fine sands offshore. Length–frequency relationships indicated that a single spawning of *E. directus* occurred during the study, with the first recruits collected in high densities during February. A third pelecypod, *Tellina* sp., appeared to spawn at approximately the same time as *E. directus* and was also prevalent at offshore stations.

Community structure

Differences in species numbers and overall faunal density occurred along the length of each transect (Table 5). The fauna was scarce at all high intertidal stations, with maximum number of species at this level being five, and overall densities never exceeding 107 individuals m^{-2}.

TABLE 4. Numbers of individuals and ranked abundance of dominant macroinvertebrate species collected at nine subtidal stations at Murrells Inlet. (Only species comprising ≥1% of the total number collected are presented)

	Nearshore	Midshore	Offshore	Total	Percent of fauna	Cumulative percent	Rank by number
Spiophanes bombyx	436	935	11 828	13 199	45·5	45·5	1
Protohaustorius deichmannae	1851	378	105	2334	8·0	53·5	2
Scolelepis squamata	1552	403	15	1970	6·8	60·3	3
Acanthohaustorius millsi	542	1069	19	1630	5·6	65·9	4
Tellina sp.	285	102	1028	1415	4·9	70·8	5
Donax variabilis	399	311	3	713	2·5	73·3	6
Ensis directus	1	16	607	624	2·2	75·5	7
Platyischnopidae (n. gen., n. sp.)	34	299	229	562	1·9	77·4	8
Maldanidae (undet.)	0	0	412	412	1·4	78·8	9
Bathyporeia parkeri	57	349	4	410	1·4	80·2	10
Parahaustorius longimerus	171	201	0	372	1·3	81·5	11
Trichophoxus epistomus	40	145	112	297	1·0	82·5	12
Others (193 species)	969	1477	2632	5078	17·5	100·0	—

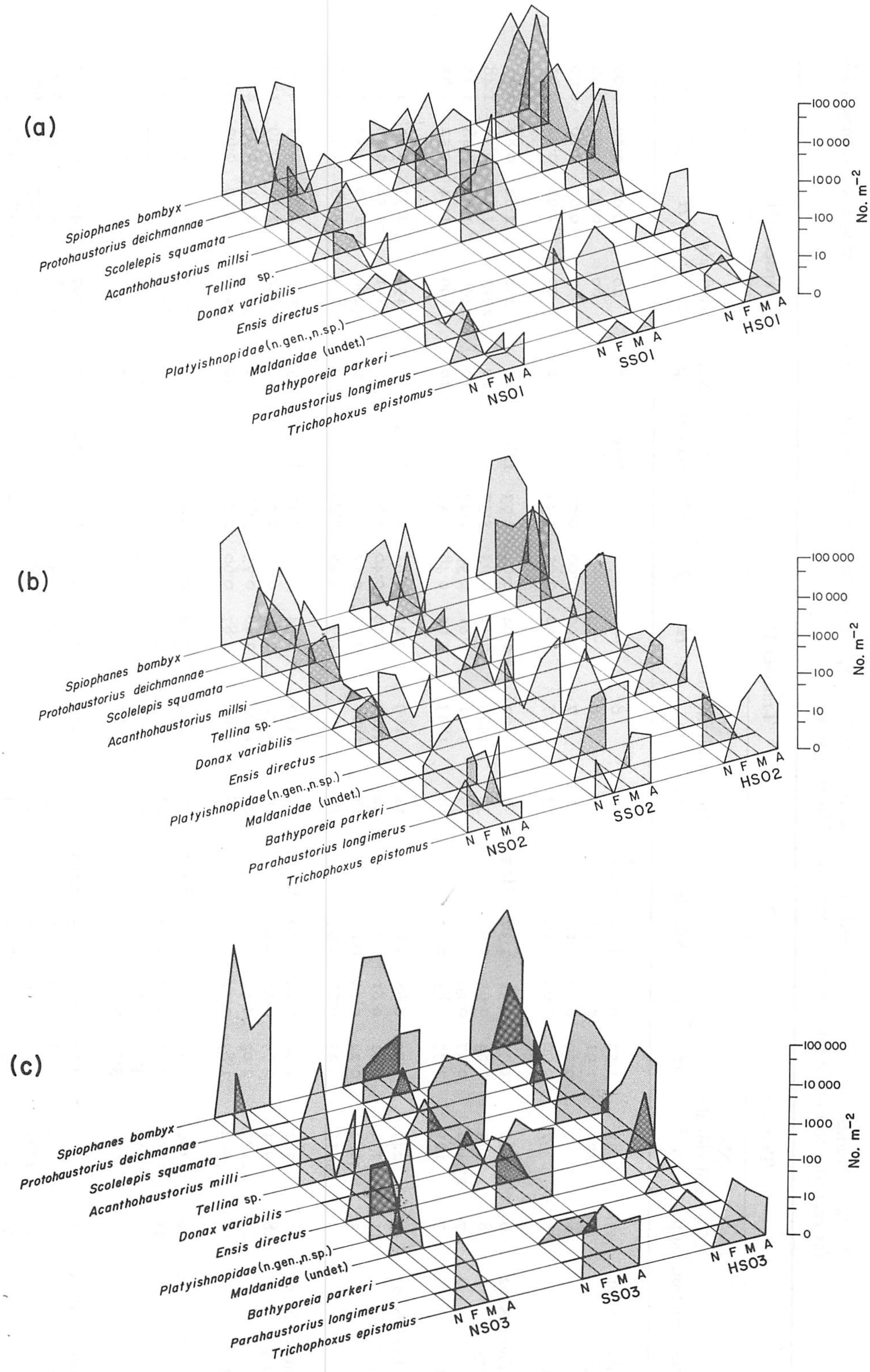

Figure 3. Seasonal abundance of dominant macroinvertebrates at (a) nearshore, (b) midshore and (c) offshore subtidal stations along the three transects. Vertical scales are logarithmic and sampling periods are labelled as in Figure 2.

TABLE 5. Number of species, estimated numbers of individuals m^{-2}, species diversity (H') in bits, evenness (J') and species richness (SR) for each station during four sampling periods at Murrells Inlet

	Transect I						Transect II						Transect III					
Month	Station	No. spp.	No. individuals m^{-2}	H'	J'	SR	Station	No. spp.	No. individuals m^{-2}	H'	J'	SR	Station	No. spp.	No. individuals m^{-2}	H'	J'	SR
November	NI01	3	33	1·52	0·96	1·24	SI01	0	0	—	—	—	HI01	1	20	0·00	0·00	0·00
February		5	107	1·91	0·82	1·44		0	0	—	—	—		2	60	0·92	0·92	0·46
May		1	7	0·00	0·00	0·00		1	7	0·00	0·00	0·00		1	7	0·00	0·00	0·00
August		1	7	0·00	0·00	0·00		3	27	1·50	0·95	1·44		2	20	0·92	0·92	0·91
November	NI02	6	262	1·33	0·51	1·36	SI02	7	62	2·64	0·94	2·73	HI02	11	262	2·82	0·82	2·73
February		8	75	2·84	0·95	2·92		30	1475	3·11	0·63	5·37		10	2957	1·12	0·34	1·48
May		7	13 408	0·27	0·10	0·79		9	3591	1·81	0·57	1·27		10	4496	1·60	0·48	1·38
August		7	101	2·33	0·83	2·22		10	1893	1·61	0·48	1·59		10	1699	1·74	0·52	1·62
November	NI03	7	247	1·92	0·68	1·66	SI03	14	269	3·25	0·85	3·52	HI03	8	455	2·33	0·78	1·66
February		11	236	2·81	0·81	2·81		42	9921	2·14	0·40	5·61		11	3451	1·58	0·46	1·60
May		5	5082	0·24	0·10	0·60		18	1661	2·17	0·52	2·98		9	5090	1·60	0·50	1·21
August		9	415	2·45	0·77	1·94		16	1007	1·91	0·48	2·99		9	814	2·23	0·70	1·67
November	NS01	20	1562	1·84	0·42	3·09	SS01	19	578	2·54	0·60	3·47	HS01	23	559	2·86	0·63	4·29
February		28	994	2·79	0·58	4·47		16	772	2·12	0·53	2·75		16	6342	1·58	0·39	1·99
May		25	2173	2·03	0·44	3·70		24	1264	3·46	0·75	3·87		34	3643	2·71	0·53	4·72
August		18	962	1·83	0·44	3·00		28	869	2·87	0·60	4·85		30	1343	3·06	0·62	4·83
November	NS02	22	1170	2·53	0·57	3·58	SS02	23	434	3·66	0·81	4·51	HS02	17	2768	1·20	0·29	2·38
February		33	2759	3·08	0·61	4·76		22	871	3·20	0·70	3·76		35	2989	3·27	0·64	5·00
May		35	484	4·32	0·84	6·82		22	2240	2·85	0·64	3·22		52	2526	3·81	0·67	7·69
August		22	665	3·32	0·74	3·96		34	965	3·85	0·76	5·82		43	924	4·31	0·79	7·46
November	NS03	27	570	3·78	0·79	5·05	SS03	33	415	4·41	0·87	6·62	HS03	25	297	4·01	0·86	5·33
February		65	35 162	1·37	0·23	6·91		53	3306	2·36	0·41	7·53		35	3008	2·76	0·54	5·00
May		49	1767	4·42	0·79	7·65		48	2631	2·19	0·39	7·04		52	6624	2·17	0·38	6·71
August		50	1725	3·36	0·60	7·84		34	473	4·37	0·86	6·64		30	651	3·68	0·75	5·49

Species numbers and species richness increased seaward along each transect, with abrupt changes occurring between MHW and MTL. A substantial increase in faunal richness was also noted between intertidal and subtidal stations on Transects I and III; however, this difference was less marked on Transect II (Table 5). Midshore and offshore stations typically had the greatest number of species on each transect.

Species diversity (*H′*), evenness (*J′*) and species richness (*SR*) varied considerably from season to season at a given station (Table 5), probably reflecting the different reproductive periodicity of several dominant species. Diversity was generally lowest in samples from the high intertidal stations and in samples with unusually high faunal densities (i.e. May samples at NI02 and NI03, February sample at NS03) which were dominated by a single species. The highest diversity was noted at offshore sites on Transects I and II, and at the midshore site on Transect III. Despite the temporal differences observed in species diversity, consistent seasonal patterns were not clearly reflected by these indices.

Four station groups were chosen from the normal cluster analysis (Figure 4). Group 1 consisted of the three MHW intertidal stations, all of which lacked a characteristic and persistent suite of macroinvertebrate species, and which were generally represented by very few species and individuals. The internal similarity of this group was lower than other groups, with SI01 being least similar to all other intertidal stations. Samples from two seasons at this station contained no organisms (Table 5), and only five animals were collected there during the entire study. Three of those five specimens were *Talorchestia megalophthalma*, a talitrid amphipod that is generally restricted to the higher intertidal level of sandy beaches (Bousfield, 1973). Although this species was deleted prior to computation of similarity (see Methods), its presence illustrates an affinity to the high intertidal level, and for this reason SI01 was included with the other higher intertidal stations to form Group 1.

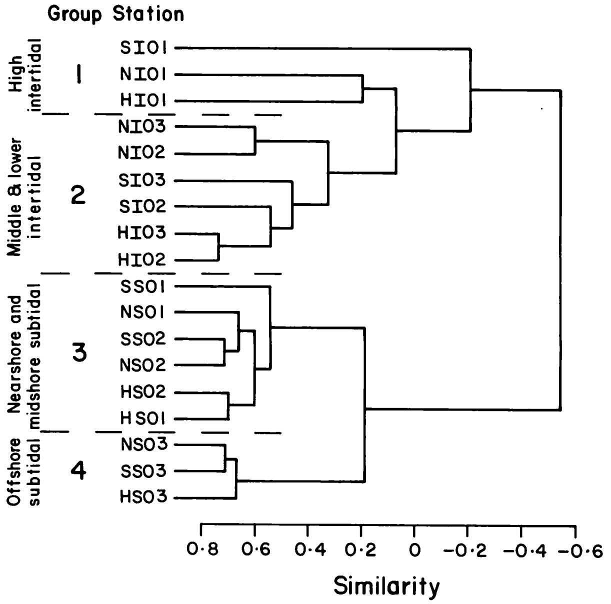

Figure 4. Normal cluster dendrogram of benthic samples showing the four station groups.

The remaining intertidal stations formed Group 2 (Figure 4). This group had closer resemblance to the high intertidal stations than to the subtidal stations. Inspection of the matrix of similarity values revealed that resemblance between middle and lower intertidal levels on Transects I and III (i.e. between NI02 and NI03, and between HI02 and HI03) was greater than between equivalent levels on different transects. However, such a strong resemblance was not apparent between the middle and lower intertidal stations on Transect II (SI02 and SI03), which were largely sheltered from wave exposure by the jetty.

Subtidal stations formed two groups, both dissimilar to intertidal stations. These groups differed from one another primarily as a function of their distance from shore. Group 3 was composed of midshore and nearshore stations, and offshore stations comprised Group 4 (Figure 4).

Inverse cluster analysis of the 92 species remaining after data reduction resulted in the selection of 11 species groups (Table 6), whose hierarchical arrangement is illustrated in Figure 5. Nodal diagrams of constancy and fidelity (Figure 5) indicate distinct distribution patterns for most of these species groups.

Species Groups A, B, C, and D had high to very high constancy at offshore stations (Group 4) and were also moderately to highly faithful to those stations (Figure 5). Group E was moderately constant in both subtidal station groups, but was not particularly faithful to either group. While the species comprising Groups A through E were characteristic of the deeper subtidal stations, they were not especially abundant there, and none contributed as much as 1% of the total number of individuals collected subtidally.

Species in Groups H through K, on the other hand, were abundant in the subtidal zone, and Group J was comprised of the most dominant species. These included *S. squamata*, *D. variabilis*, *S. bombyx*, *A. millsi*, *P. fulgens* and *P. longimerus*, all of which were fairly ubiquitous at all but the highest intertidal level. Numerically dominant species which clustered into Group H included *P. deichmannae*, *T. epistomus* and Platyischnopidae, and the dominant subtidal species *E. directus* and *B. parkeri* were found in Groups I and K, respectively.

Species Groups H, I, J, and K were highly constant at subtidal stations (Figure 5), and Group J was highly constant at lower and middle intertidal stations as well. Unlike species in previously mentioned subtidal groups (A through E), those of Groups H through K were ubiquitous throughout the subtidal zone. As a consequence, their fidelity was generally low for subtidal station groups, with the exception of Group I, a large assemblage which was more restricted to the deeper offshore stations (Figure 5).

Group F consisted of species which were frequently collected at middle and lower intertidal stations and which were largely restricted to those stations (Figure 5). This group was the only assemblage which exhibited a distinct intertidal preference, and consisted of one isopod species, one decapod species and four haustoriid amphipod species, including *N. schmitzi*, which ranked second in abundance among intertidal species (Table 4).

Three species comprised Group G, and none were abundant or frequently collected. Constancy and fidelity for this group were low in station Groups 2 and 3, and no specimens were collected at station Groups 1 or 4. No apparent ecological factors or habitat preferences were observed that would characterize this species group.

Discussion

Many previous studies of the benthic macroinvertebrate fauna inhabiting sandy beaches have been limited to the intertidal zone (Croker, 1967, 1968, 1970, 1977; Dexter, 1967, 1969, 1979; Croker *et al.*, 1975; Holland & Dean, 1977; Saloman & Naughton, 1977, 1978; Simon &

TABLE 6. Species groups resulting from inverse numerical classification of data

Group A
Ogyrides limicola (D)
Travisia sp. (P)
Trachypenaeus constrictus (D)
Apanthura magnifica (I)
Phyllodoce arenae (P)
Olivella mutica (Mo)
Nassarius trivittatus (Mo)
Magelona phyllisae (P)
Polynices duplicatus (Mo)
Turbonilla sp. (Mo)
Podarke obscura (P)
Paraprionospio pinnata (P)

Group B
Hemipholis elongata (E)
Unknown Pelecypoda no. 3 (Mo)
Unciola serrata (Am)
Eulalia sanguinea (P)
Chione cancellata (Mo)
Unknown Pelecypoda no. 9 (Mo)
Unknown Polychaeta no. 26
Crassinella lunulata (Mo)
Unknown Polychaeta no. 31

Group C
Terebra dislocata (Mo)
Unknown Cumacea no. 2
Mulinia lateralis (Mo)
Magelona rosea (P)
Erichthonius brasiliensis (Am)

Group D
Heteromastus filiformis (P)
Edotea montosa (I)
Corophium tuberculatum (Am)
Mysidopsis bigelowi (My)
Sabellaria vulgaris (P)
Euceramus praelongus (D)
Onuphis eremita (P)
Scoloplos rubra (P)
Tiron tropakis (Am)
Brania clavata (P)

Group E
Nucula sp. (Mo)
Parapleustes aestuarius (Am)
Metamysidopsis munda (My)
Callianassidae (D)

Group F
Exosphaeroma diminutum (I)
Amphiporeia virginiana (Am)
Emerita talpoida (D)
Haustorius longirostris (Am)
Neohaustorius schmitzi (Am)
Lepidactylus dytiscus (Am)

Group G
Unknown Pelecypoda no. 2 (Mo)
Jassa falcata (Am)
Gammarus sp. (Am)

Group H
Nephtys picta (P)
Haploscoloplos sp. (P)
Protohaustorius deichmannae (Am)
Platyischnopidae (n. gen., n. sp.) (Am)
Trichophoxus epistomus (Am)
Synchelidium americanum (Am)
Magelona papillicornis (P)
Renilla reniformis (Cn)

Group I
Tharyx marioni (P)
Amastigos caperatus (P)
Batea catherinensis (Am)
Owenia fusiformis (P)
Ancinus depressus (I)
Unknown Polychaeta no. 15
Tellina alternata (Mo)
Microprotopus raneyi (Am)
Unknown Pelecypoda no. 1 (Mo)
Ensis directus (Mo)
Spisula solidissima (Mo)
Scolelepis texana (P)
Caulleriella killariensis (P)
Oxyurostylis smithi (Cu)
Glycera dibranchiata (P)
Dissodactylus mellitae (D)
Mellita quinquiesperforata (E)
Pagurus longicarpus (D)

Group J
Scolelepis squamata (P)
Donax variabilis (Mo)
Spiophanes bombyx (P)
Acanthohaustorius millsi (Am)
Paraonis fulgens (P)
Parahaustorius longimerus (Am)
Lovenella gracilis (Cn)

Group K
Bowmaniella sp. (My)
Ogyrides alphaerostris (D)
Chiridotea stenops (I)
Unknown Cumacea no. 3
Eteone heteropoda (P)
Dispio uncinata (P)
Leptognatha caeca (T)
Bathyporeia parkeri (Am)
Acanthohaustorius intermedius (Am)
Unknown Polychaeta no. 11

Am = Amphipoda; Cn = Cnidaria; Cu = Cumacea; D = Decapoda; E = Echinodermata; I = Isopoda; Mo = Mollusca; My = Mysidacea; P = Polychaeta; T = Tanaidacea.

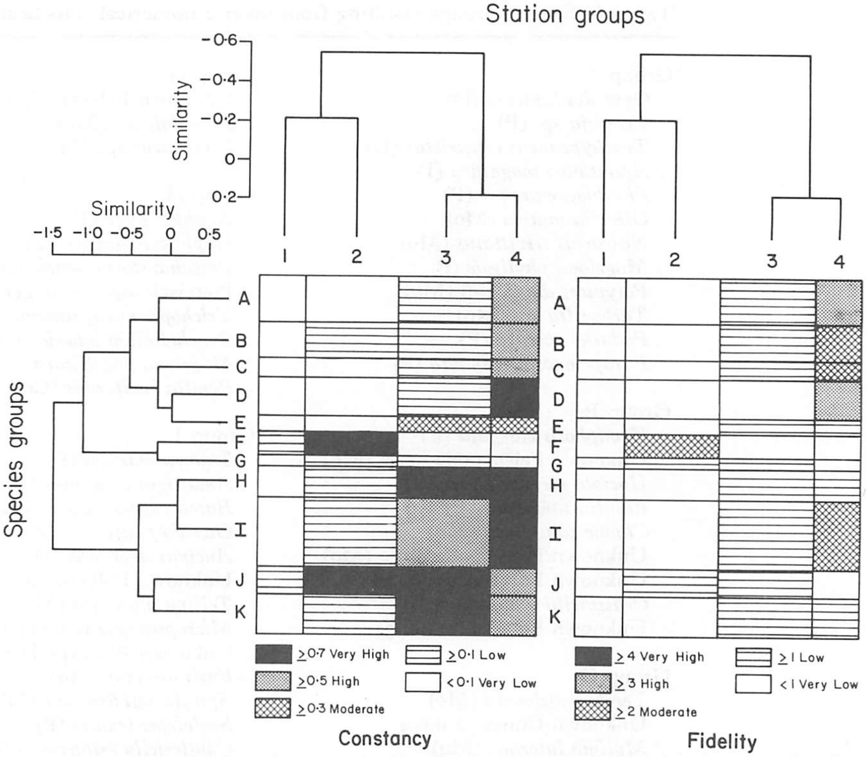

Figure 5. Normal and inverse classification hierarchies, and nodal diagrams showing constancy and fidelity of station-species group coincidence.

Dauer, 1977; Croker & Hatfield, 1980) or to shallow subtidal waters (Frankenberg, 1971; Frankenberg & Leiper, 1977; Maurer *et al.*, 1979*a*; Oliver *et al.*, 1980). Treatment of the intertidal and subtidal zones as distinctly separate habitats is most likely the result of convenience and economy of sampling, with the mean low water mark being traditionally regarded as the transition between intertidal and subtidal communities (Dexter, 1969; Croker, 1977). The results of the present study confirm that a distinct difference in overall community structure exists between the intertidal and subtidal zones (Figure 4), but it is important to note that many of the numerically dominant species are prevalent in both zones (Tables 3 and 4). *Scolelepis squamata*, for example, was the dominant intertidal species at Murrells Inlet, and it was also important subtidally, where it ranked third in abundance. Matta (1977) also noted that this species was dominant in the subtidal areas of a high-energy beach in North Carolina, even though it is typically considered an intertidal species (Croker, 1970, 1977; Foster, 1971; Croker *et al.*, 1975; Saloman & Naughton, 1978).

The coquina clam *D. variabilis* and the polychaete *S. bombyx* are also important in both intertidal and subtidal assemblages (Tables 3 and 4). *Donax variabilis* is a rapidly burrowing bivalve that is common on beaches along the United States Atlantic coast between New York and Texas (Abbott, 1974), where it is frequently seen in large aggregations. Pearse *et al.* (1942), Jacobson (1955) and Turner & Belding (1957) reported that populations of *D. variabilis* move up and down the beach with the tide, and our collections in the nearshore and midshore areas document that it is also common subtidally. *Spiophanes bombyx* was the most abundant species at Murrells Inlet, ranking first in abundance subtidally and fourth in the intertidal zone.

The persistent abundance of *S. squamata*, *D. variabilis* and *S. bombyx*, across the range of beach elevations at Murrells Inlet, illustrates that the intertidal and shallow-water sand regions can be considered an ecological unit, as Fincham (1971) has suggested. These species clustered together into species Group J, which consisted mostly of numerically dominant species that were widely distributed throughout both the intertidal and subtidal zones. However, we are not suggesting that there are no differences between intertidal and subtidal assemblages, since many of the less abundant species were primarily habitat-restricted, with most groups confined to subtidal waters. For example, several species groups (A–D) were specifically restricted to the deepest subtidal stations, while others (E, H, I and K) were more widely distributed in the subtidal zone (Figure 5). Group F, on the other hand, was restricted to the middle and lower intertidal zones. Very few specimens of this group were found at high intertidal stations, and only one specimen occurred in subtidal samples.

The intertidal fauna of U.S. Atlantic coast sandy beaches has typically been characterized as dominated by peracarid crustaceans, especially haustoriid amphipods (Pearse *et al.*, 1942; Croker, 1967, 1977; Dexter, 1969; Sameoto, 1969*a*; Holland, 1974; Holland & Dean, 1977). These fossorial amphipods have been frequently noted to also dominate subtidal assemblages in shallow nearshore waters (Sameoto, 1969*b*; Dörjes, 1972; Maurer *et al.*, 1979*b*). At Murrells Inlet, however, polychaete worms dominated the intertidal and subtidal faunal assemblages, both in terms of the number of species and number of individuals. Similar domination of sandy beach fauna by polychaetes has been correlated to the degree of exposure to wave action by previous investigators. Croker (1977) observed increased dominance by polychaetes (*S. squamata*, *Pygospio elegans*, *Paraonis fulgens*) with increased protection from wave exposure on New England beaches. Oliver *et al.* (1980) defined two distinct faunal zones on a subtidal high-energy beach in California. The first zone was a shallow (<14 m) 'crustacean zone' in which the relatively mobile haustoriid, oedicerotid and phoxocephalid amphipods and ostracod crustaceans were predominant. Deeper waters contained the 'polychaete zone', which consisted primarily of organisms that maintain relatively permanent tubes and burrows. These authors attributed this distinct zonation to the decrease in wave-induced bottom disturbance that was associated with increased water depth.

At Murrells Inlet the proportion of polychaete to peracarid crustacean species (25:36 intertidally, 83:49 subtidally) suggests a similar relationship between the degree of exposure to harsh environments and richness of the polychaete fauna (Table 1). Furthermore, numerical dominance by polychaetes was greater at subtidal stations (63% of total individuals) than at intertidal sites (55% of total individuals). The apparent success of polychaete species at Murrells Inlet compared with other sandy beach habitats may be attributed in part to the moderate impact of wave energy in this region. Roberts (1974) also noted that the fauna is more diverse and polychaetes are better represented on moderate wave energy beaches of South Carolina and Georgia than on high-energy beaches.

The degree of wave exposure effects other aspects of community structure as well. Croker (1977) found that species richness, evenness and diversity were all considerably higher on a semi-protected intertidal beach than at a moderately exposed site over the duration of a four-year study. Other studies have noted a similar relationship between species numbers and the degree of exposure (McIntyre, 1970, 1977; Croker *et al.*, 1975). After construction of the jetty at Murrells Inlet we observed increased species richness in the intertidal assemblage on the sheltered side of the jetty (Transect II). Before construction commenced in November 1977, differences in the intertidal fauna between equivalent elevations on adjacent Transects I and II were relatively minor. By February 1978, the jetty extended approximately 100 m offshore, sheltering the three intertidal stations on Transect II. This sheltering was accompanied by a marked increase in the number of species found at stations SI02 and SI03, with SR values at those stations considerably higher during February than for any intertidal collection on the other transects (Table 5).

The effects of sheltering on community structure were not as apparent along the subtidal portions of Transect II as those observed intertidally. By August, jetty construction had progressed to a point just past SS02, and although species numbers increased at SS01 and SS02 during the study, similar increases were also observed on Transect III, precluding any firm conclusions concerning the effects of sheltering on the subtidal fauna of the area. Such effects might only become apparent after a more lengthy period following jetty construction.

Various investigators have noted increased faunal richness with decreased elevation along sandy beaches (McIntyre & Eleftheriou, 1968; Trevallion *et al.*, 1970; Fincham, 1971; Holland & Dean, 1977; Matta, 1977). As noted previously, the mean low water mark is often regarded as the transitional area between different assemblages of the beach community (Dexter, 1969; Scott, 1975), with species richness often increasing abruptly below this level (Dörjes, 1972, 1977). We observed similar trends on Transects I and III, but this was not apparent on the sheltered Transect II (Table 5). Increased protection at SI02 and SI03 presumably created conditions more suitable for colonization by organisms that are otherwise prevented from inhabiting a more rigorous environment. Consequently, increased species richness at the middle and lower intertidal levels obscured the distinct transition observed between intertidal and subtidal zones on the other transects.

In summary, the widespread distribution of the dominant macroinvertebrates collected near Murrells Inlet emphasizes the importance of sampling both the intertidal and shallow subtidal areas when characterizing front beach infaunal communities in this region. Furthermore, the dominance of sandy beaches by peracarid crustaceans frequently noted in other studies was not observed at Murrells Inlet. Rather, polychaetes were the most abundant and well-represented taxon, presumably due to the moderate wave energy in this area. Jetty construction in this region enriched the intertidal assemblages in sheltered portions of the beach.

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