FINAL REPORT

SOUTH ATLANTIC OCS AREA
LIVING MARINE RESOURCES STUDY
PHASE III

VOLUME I

Prepared for
Minerals Management Service
Washington, D.C.
under Contract 14-12-0001-29185

Prepared by
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August 1984

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DISCLAIMER

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Preface

BACKGROUND

Hard-bottom habitats on the continental shelf off the southeastern United States have been a major focus of biological research under the Minerals Management Service (MMS) Environmental Studies Program. This research has been conducted in three phases. The first and second phases completed in October 1981 and December 1982, provided detailed background characterizations of the benthic invertebrate and demersal fish communities associated with hard-bottom areas (South Carolina Wildlife and Marine Resources Department and Georgia Department of Natural Resources [SCWMRD and GADNR], 1981; SCWMRD, 1982). Those studies also described the community structure of hard-bottom biota relative to changes in season, depth and latitude. Data obtained during the first two phases documented the importance of hard-bottom areas to offshore commercial and recreational fisheries. Additionally, those studies noted the potential effects of exploration for oil or mineral resources on hard-bottom invertebrate communities and fisheries.

In order to better understand the possible effects of energy- or mineral-related activities on recruitment of invertebrate communities and the importance of those communities to fishes, a third phase of the study was initiated in January 1983. This aspect of the study involved three major tasks. The objectives of Task I were to determine short-term and long-term colonization patterns by invertebrates and fishes on artificial hard substrates. Data obtained from Task I studies will aid in estimating recovery periods for hard-bottom communities following defaunation and provide useful information on the development of invertebrate and fish communities associated with oil production platforms. The objective of Task II was to determine how changes in sediment depth over hard substratum influence the distribution and abundance of large sponges and corals found in hard-bottom areas. Results from the Task II study should provide useful information on the potential effects of sediment redistribution by drilling activities and aid in identifying the possible location of hard bottom areas using remote sensing techniques. The objective of Task III was to examine in further detail the food habits of fishes associated with hard-bottom habitat in order to determine the dependence of these fishes on hard-bottom food resources. Fish species analyzed during the first two study phases were to be further analyzed for size- and depth-related differences in food habits and additional species were to be examined.

The remainder of this report volume is organized into three sections, each of which describes the three major Tasks. Volume II provides a listing of all data obtained from these tasks.

PROJECT ORGANIZATION AND PERSONNEL

Two institutions were involved in this study. The Marine Resources Research Institute of the South Carolina Wildlife and Marine Resources Department was the prime contractor responsible for the study design, sampling activities, data analysis, and report preparation. The Coastal Resources Division of the Georgia Department of Natural Resources was a subcontractor responsible for assisting in field sampling efforts. Project personnel and their general areas of responsibility are as follows:

SOUTH CAROLINA MARINE RESOURCES RESEARCH INSTITUTE

Name	Area of Responsibility
Beaumont, N.	Secretarial support
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Clise, M.J.	Data processing
Folsom, F.L.	Technical support, cruise logistics, diver
*Hinde, P.	Invertebrate identification; Task I, sessile community analysis, long-term colonization study, diver
*Knott, D.M.	Invertebrate identification; Task I, motile epifauna community analysis, short-term and long-term colonization studies; diver
Levisen, M.	Invertebrate identification, data management, diver
Mathews, T.D.	Water chemistry analysis
O'Rourke, C.B.	Invertebrate identification, data management
Pinckney, J.	Invertebrate identification, data management, diver
Roland, E.C.	Invertebrate identification, data management, diver
*Sedberry, G.R.	Fish and stomach content identification; Task I and III, fish community and food habits analysis; diver
Stribling, J.T.	Data processing
*Van Dolah, R.F.	Project Coordinator; project management; Task I, sessile community analysis, short-term colonization study; Task II analysis; diver
Wenner, E.L.	Invertebrate identification: Task I, community analysis

*Indicates personnel having primary responsibility for data interpretation and report preparation.

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Harris, C.D.	Diver
Kaufman, J.C.	Diver
Kroscavage, J.B.	Diver
Nicholson, F.L.	Diver
Varnedoe, D.A.	Diver

ACKNOWLEDGEMENTS

Appreciation is extended to the SCWMRD and GADNR personnel who, though not directly associated with the project, contributed to the study effort. They include the crew members of the R/V *Bagby,* R/V *Oregon,* and R/V *Lady Lisa,* who assisted in the field work; and K. Swanson who drafted the figures. Appreciation is also extended to the following taxonomic experts from other institutions, for their help in identification of organisms: C.A. Child (U.S. National Museum), R.V. Cumbee (Virginia Institute of Marine Science), R.S. Fox (Lander College), H.J. Porter (University of North Carolina), K. Sebens (Museum of Comparative Zoology), and R. Wiseman (College of Charleston). Research (Task II) in Gray's Reef National Marine Sanctuary (station IS31) was conducted under Permit GRNMS-01-83, from the Sanctuary Programs Division of the Office of Ocean and Coastal Resource Management, National Oceanic and Atmospheric Administration.

Task I: Studies of Recruitment and Community Development on Hard Substrata

INTRODUCTION

The colonization and community development of hard substrates in the marine environment has been the subject of numerous investigations (Sheer, 1945; WHOI, 1952; Aleem, 1958; Calder and Brehmer, 1967; Fager, 1971; Connell, 1972; Paine, 1974; Dayton, 1975; Jackson, 1976, 1977; Neushul et al., 1976; Osman, 1977; Sutherland and Karlson, 1977; Mook, 1980, 1981; Schoener and Schoener, 1981; Greene and Schoener, 1982). Many of these studies have employed replicate fouling panels, while others have involved the observation and manipulation of naturally occurring hard substrates.

In an effort to identify the factors controlling colonization and community development, various authors have investigated such abiotic parameters as light intensity, current velocity, substrate stability, spatial orientation, and physical disturbance (Dayton, 1971; Osman, 1977; Harris and Irons, 1982; Schoener, 1982; Vandermeulen and De Wreede, 1982). Biological interactions such as competition, predation, and herbivory have also been shown to be instrumental in directing the course of development (Connell, 1972; Paine, 1974; Dayton, 1975; Jackson, 1976; Neushul et al., 1976).

Most colonization studies have been conducted over a relatively short period of time ($\leq$ 3.5 yrs). Consequently, seasonal variation in community structure has often been difficult to distinguish from longer-term sequential development, or even random variation, in the epifaunal community. Furthermore, most of these studies have been conducted in intertidal or shallow subtidal habitats. Among the few studies that have been done in deeper subtidal waters (Aleem, 1957; Fager, 1971; Jackson, 1976; Neushul et al., 1976), none were conducted in the South Atlantic Bight.

Relatively few studies have addressed specifically the epifaunal communities associated with artificial reefs and offshore oil platforms (Carlisle et al., 1964; Turner et al., 1969; Russell, 1975; Sonnier et al., 1976; George and Thomas, 1979; Wolfson et al., 1979; Howard et al., 1980; Fotheringham, 1981; Gallaway et al., 1981; Buckley, 1982). While the earlier studies are largely descriptive in nature, some of the more recent investigations have addressed the roles of fish predation (Fotheringham, 1981), seasonal variability (Russell, 1975; Wolfson et al., 1979), bathymetric zonation (George and Thomas, 1979), and the effects of effluents on the biofouling community (Howard et al., 1980; Galloway et al., 1981). Nevertheless, few investigators appear to have considered the age of the artificial structures, their proximity to hard-bottom habitat, or the effects of surface orientation in interpreting fouling community structure.

The purpose of this study was to gain a better understanding of short-term and long-term patterns of colonization and community development on hard substrata in the South Atlantic Bight. The specific objectives of Task I were to 1) examine seasonal recruitment and short-term community development on colonization plates over the course of one year; 2) examine long-term community development on five artificial reefs ranging in age from 3.5 to 10.0 years; 3) determine the effects of spatial orientation and proximity to natural hard-bottom habitat on the colonization and community development of artificial substrates; and 4) provide qualitative and quantitative descriptions of the fish assemblages associated with the colonization platforms and the artificial reefs.

Results obtained from this study should enable management agencies to more accurately predict 1) how rapidly artificial substrates such as oil and gas platforms will be colonized by epifaunal and fish communities; 2) how proximity of these platforms to natural hard-bottom habitat (and consequently, to a potential source of recruitment) might affect the rate and pattern of community development; and 3) how quickly natural hard-bottom substrates might be recolonized following a catastrophic disturbance.

SHORT-TERM COLONIZATION STUDY

STUDY AREA

Two large steel frames with arrays of fouling plates were deployed in separate locations off the South Carolina coast during March 1983 (Figure 1.1). One frame was placed in a hard-bottom area located approximately 35 km southeast of Charleston, S.C. (32°24.7'N,79°49.6'W). This area was characterized by low-relief rock outcroppings and extensive areas of hardpan covered by a thin veneer of sand [see Powles and Barans (1980) for a more detailed description]. The other frame was placed in a sand-bottom area located approximately 16 km southwest of the hard-bottom site. Water depths in both study areas were approximately 20 m. Bottom temperatures and salinities were also similar at the two locations ranging from 13.3-25.0°C and 33.8-35.9^{o}/oo during the sampling periods (Appendix 1.1).

METHODS

Field and Laboratory Methods

Both sites were initially surveyed using an underwater television camera system (SCWMRD 1982) to identify specific locations for deployment of the frames and to document surrounding bottom type. The frames were then lowered to the bottom and anchored at each end. Helle Model 2400/1104 acoustic pingers were attached to each frame to aid in their relocation. Each frame supported 40 fouling plates oriented in alternating vertical and horizontal rows, with adjacent rows staggered to diminish effects from shading or interference from prevailing water currents (Figure 1.2). All plates measured 20 x 25 cm and were constructed of 6-mm Plexiglas sandwiched between two sheets of black, textured formica which simulated naturally occurring hard substratum. Textured formica was also used as fouling panel material by Schoener and Schoener (1981) after their pilot studies indicated that it was the most suitable material.

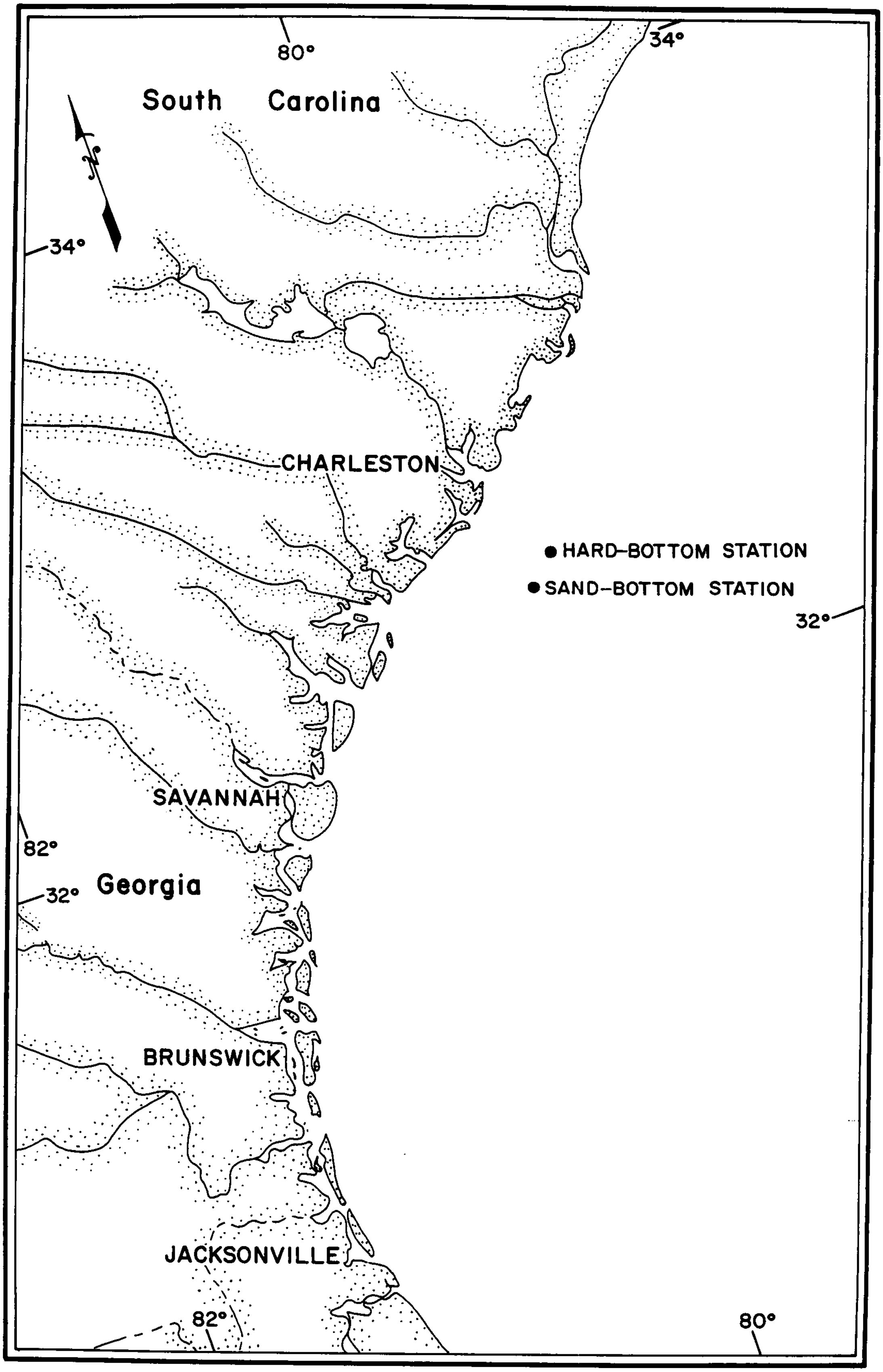


Figure 1.1 Location of fouling plate frames.

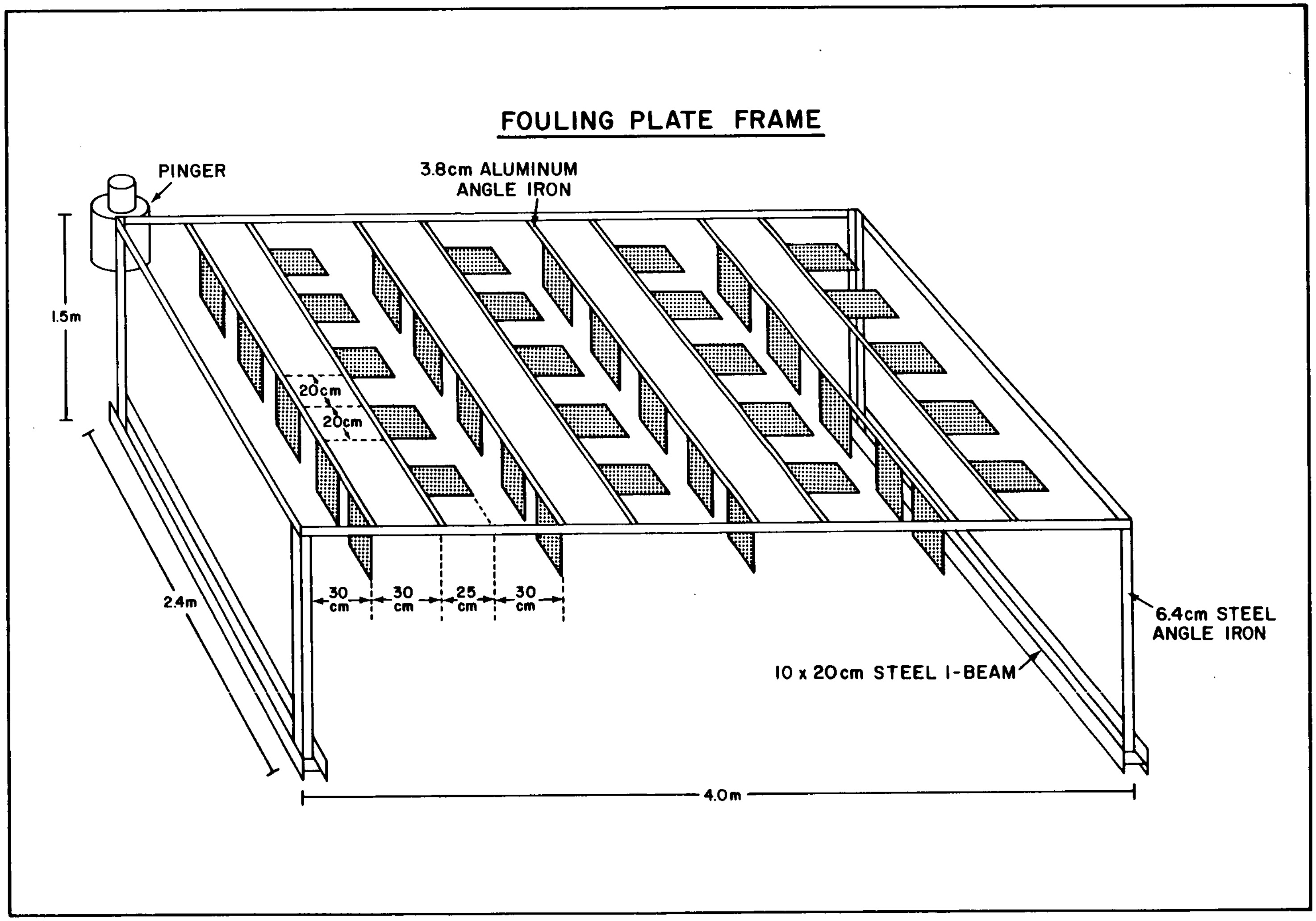


Figure 1.2 Diagram of the fouling plate frame used in the short-term colonization study.

Five replicate plates were randomly selected from each of four treatment groups for retrieval at 3-, 6-, 9-, and 12-mo intervals following the date of deployment. Two treatment groups represented plates in vertical and horizontal orientations on sand bottom, and the other two represented the same orientations on hard bottom (Figure 1.3). Before the plates were retrieved, divers fastened Plexiglas boxes (each encompassing an area of 225 cm^2) to both sides of each plate. These boxes captured the associated motile epifauna and protected the sessile growth from damage during the retrieval process. The plates were then removed from the frame, and placed in a mesh bag. Aboard the research vessel, all sessile fauna not encompassed by the Plexiglas boxes were scraped from the plates which were then preserved separately in buckets using 10% formalin in seawater. Each plate surface was tagged and assigned a unique collection number to identify the four orientations on each frame: horizontal top, horizontal bottom, vertical pinger side, and vertical opposite side (Figure 1.2). The latter two orientations arbitrarily distinguished between sides on vertical plates without regard to any specific environmental parameters.

An additional series of 10 new plates (5 horizontal, 5 vertical) were attached to each frame during the 3-, 6-, and 9-mo site visits to evaluate seasonal recruitment. These plates were collected after 3-mo exposure to provide four sets of plates submerged during the different seasons (Figure 1.3). The plates were removed from the frame using the technique described above.

Fishes observed around the frames during each sampling trip were recorded along with estimates of their abundance. Divers also recorded bottom temperatures and collected water samples for salinity and dissolved oxygen measurements. Water samples were processed aboard the research vessel using a Yellow Springs Instruments (YSI) Model 33 SCT meter for salinity and a YSI Model 51B DO meter for dissolved oxygen.

In the laboratory, three out of each treatment group of five replicate plates were randomly selected for analysis. The remaining plates were used to replace any damaged plates in a treatment group. The preservative for each plate was sieved through a 0.5-mm screen to collect all dislodged motile epifauna. The plate was then gently washed over the 0.5-mm screen to remove any motile organisms still on the plate. Fauna collected in this manner were transferred to 70% isopropanol, identified to the lowest possible taxonomic level, and enumerated. Several samples contained an unusually large number of animals and analysis of these samples was restricted to a 1/4 subsample.

Analysis of sessile biota was restricted to the central 225-cm^2 area of each plate surface to minimize effects related to the plate edges. Biota within the analyzed area were identified to the lowest possible taxonomic level and estimates of percent cover were obtained for all species using a random point-count censusing technique similar to that described by Sutherland and Karlson (1977). Each census was accomplished by submerging the plate in a tray filled with water and overlaying it with a transparent sheet of acetate plastic marked with 100 random points. One of three plastic sheets was randomly selected for the analysis of each

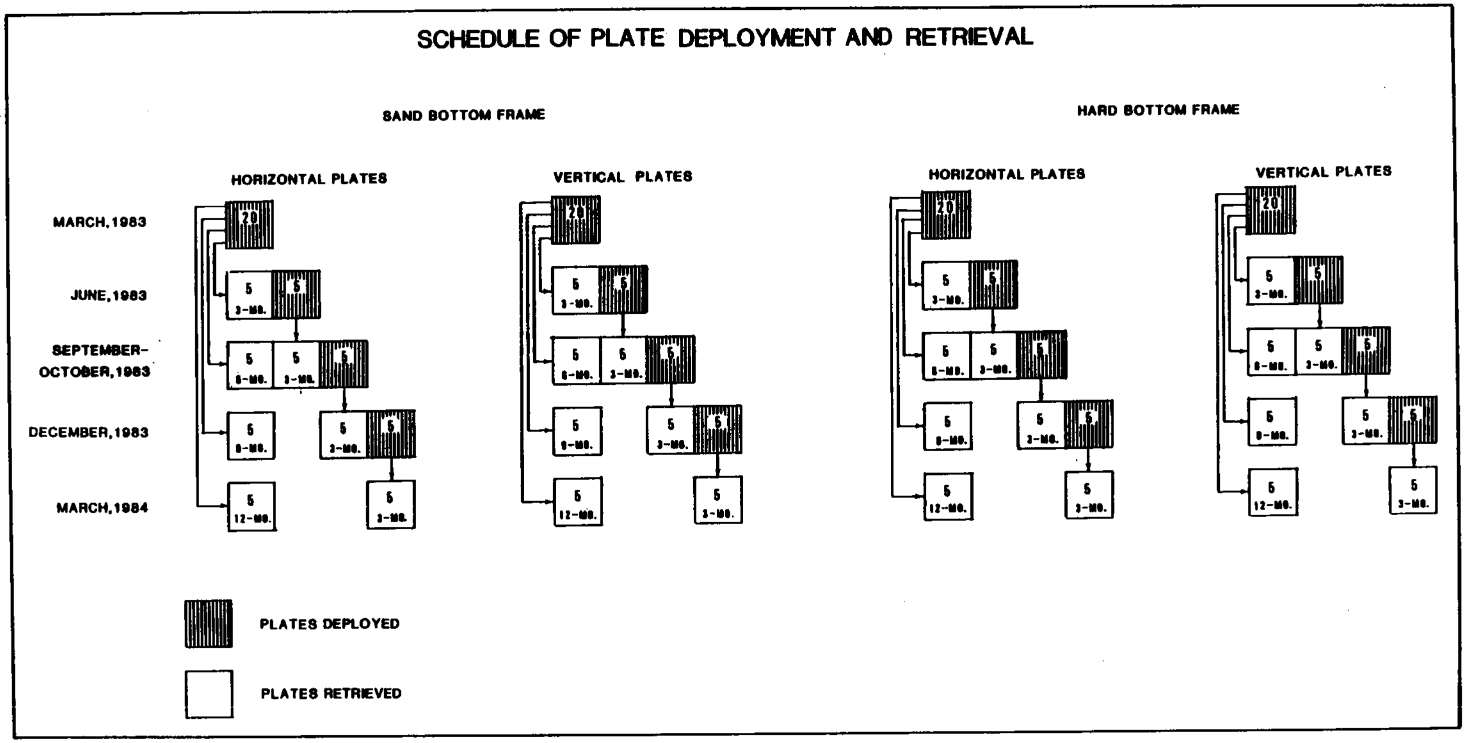


Figure 1.3 Schematic diagram of the sampling schedule used in the deployment and retrieval of plates from frames located in sand-bottom and hard-bottom areas. Numbers depicted in each block indicate the number of plates deployed and retrieved as well as the length of exposure.

plate treatment group. All points were examined under a binocular microscope and the identity of any organism(s) or the occurrence of a bare spot was noted. Dead barnacles (empty tests) were counted separately from live barnacles. Percent cover estimates were computed by dividing the number of points under which a species occurred by the total number of analyzable points on each plate (x 100). An analyzable point was considered to be one which fell within the boundaries of the 225-cm^2 area that had not been affected by the scraping process. Since more than one species occurred under many points, the sum of the percent cover estimates for all species on a plate surface frequently exceeded 100%.

The use of 100 points in the above census was based on a preliminary analysis of one horizontal fouling plate exposed for 6 months in the hard-bottom frame. The plate was chosen to represent an especially diverse assemblage of sessile organisms. Percent cover estimates of biota under 225 points (uniformly spaced on a 15 x 15-cm grid) were compared with mean estimates based on replicate sets of 100, 75, and 50 points randomly selected from the 225 original points. The results indicated that a minimum of 100 points were needed to accurately estimate cover for all species which occupied at least 5% of the plate surface (Appendix 1.2).

After completion of the point-count census, plates were scraped and the biota weighed to the nearest gram using a PN323 Mettler balance to determine total wet weight biomass on each plate surface. Biomass measurements were also obtained for the following categories: Actiniaria, Algae, Ascidiacea, Cirripedia, Hydroidea, Mollusca, Polychaeta, and Porifera.

Data Analysis

Sessile Biota - Total percent biota cover, total biomass, and number of species per plate surface were compared with respect to plate side, orientation, location, and season or duration of submergence. Comparisons of variates between plate sides (top vs. bottom, pinger vs. opposite) were made using t-tests, or the approximate t-test when variances were heterogeneous (Sokal and Rohlf, 1981). Comparisons between plate orientations (horizontal vs. vertical), plate locations (hard bottom vs. sand bottom) and among seasons or durations of plate submergence were completed using three-way (Model I) analysis of variance (Sokal and Rohlf, 1981). Based on preliminary evaluations of data normality and heterogeneity of variance, t-tests and analyses of variance were computed using the arcsin transformation for percent cover estimates, the $\log_{10}$ transformation for species number, and no transformation for biomass data. The a posteriori Ryan-Einot-Gabriel-Welsh multiple F test (Ramsey, 1978) was then used to determine significant differences between treatment group means. The level of significance for all statistical tests was $\alpha = 0.05$.

Cluster analyses were performed to determine patterns of similarity in community structure on the different plate series. Data from replicate plate surfaces were pooled and compared using the Bray-Curtis similarity coefficient (Bray and Curtis, 1957) on percent cover estimates. Data sets subjected to cluster analysis were first reduced to eliminate rare species which occurred on only one replicate set of plates and had $< 5\%$ cover on those plates. Species and collections were classified using flexible sorting with a cluster intensity coefficient (β) of -0.25 (Lance and Williams, 1967). Normal and inverse classifications were produced for the data set representing plates submerged for 3 months during different seasons, and for the data set representing plates submerged for 3, 6, 9, and 12 months. Normal classification produced dendrograms which grouped the pooled plate samples based on their degree of similarity in species composition and percent cover. Inverse classification produced dendrograms in which species were clustered based on their degree of similarity in terms of their occurrence and percent cover on the different plate surfaces.

Subsequent to cluster analysis, species groups were chosen using a variable stopping rule (Boesch, 1977). These species groups were compared with "fixed" plate groups using nodal analyses (Williams and Lambert, 1961; Lambert and Williams, 1962). The fixed plate groups represent the different treatment groups, but with both sides of a plate combined, i.e., top and bottom or pinger and opposite side. Nodal analysis evaluates the coincidence of plate and species groups by graded constancy and fidelity values. Constancy expresses the frequency with which a species group is found in a plate group and fidelity measures the degree to which a species group is restricted to a plate group.

Motile Biota - Structure of the motile epifaunal community on the plates was evaluated using a number of species diversity indices, including Shannon's diversity index (H'), evenness (J'), and species richness (SR) (Margalef, 1958; Pielou, 1975). Three-way Model I analysis of variance was used to determine the effects of orientation, location, and season (or duration) of exposure on the number of species and number of individuals on the plates. Preliminary analysis indicated that data transformation was necessary, so computations were performed on $\log_{10}$-transformed numbers of species and individuals. Means were compared among treatment groups using the Ryan-Einot-Gabriel-Welsch multiple F test on data sets in which the number of observations within cells was equal (i.e., no missing data), and Tukey's studentized range test when cell sizes were unequal. Unequal sample sizes resulted because the motile organisms from two replicate plates were inadvertently combined in the 3-mo series of sand-bottom plates deployed during the spring.

Cluster analyses were used to determine patterns of similarity in the motile fouling communities of the different plate series. Normal and inverse analyses were performed on $\log_{10}$-transformed abundance values from the 3-mo series and the 3-, 6-, 9-, and 12-mo series separately, using the Bray-Curtis coefficient and flexible sorting strategy with $\beta = -0.25$. Reduction of the data set prior to classification was accomplished by eliminating species which occurred on only one or two of the plates, provided that they also did not contribute greater than 0.1% of the total number of individuals on that particular series of plates. Following classification, the species groups were subjected to nodal analysis in order to determine their constancy and fidelity among the various plate groups.

Results and Discussion

Sessile Biota:

Seasonal Recruitment - Recruitment of fouling organisms to the plate surfaces was extensive during all seasons. The average percent cover of sessile biota observed on the plates submerged for 3-mo periods generally exceeded 90% of the analyzed surface area (Figure 1.4). Cover was significantly lower on plates submerged during the spring compared with those exposed during other seasons (Table 1.1), but the average cover on any surface was never less than 42% (Appendices 1.3-1.6). There were no significant differences in percent cover between sand-bottom and hard-bottom plates or between horizontal and vertical plate surfaces. However, a significant interaction was noted between the factors of area and season (Table 1.1, Figure 1.4). Comparisons between plate sides also indicated no differences among the vertical plates from either frame (Table 1.2). On the horizontal plates, however, biota cover was usually significantly less on the top of plates than on the bottom.

The average number of species present on the 3-mo plates was highest during the fall and lowest during the winter for both frames (Figure 1.5). Comparisons of species number in relation to season, area, and plate orientation indicated that seasonal differences were highly significant, and that the average number of species was greater on plates from the hard-bottom than the sand-bottom area (Table 1.1). A significant interaction was noted between the factors of season and area. During spring and winter, the number of species was greater on the hard-bottom plates, whereas during summer and fall, it was greatest on the sand-bottom plates (Figure 1.5). No significant differences were noted between horizontal and vertical plates (Table 1.1), or between plate sides having the same orientation with one exception (Table 1.2).

Biomass on the plates after 3-mo submergence was greatest during winter and lowest during spring and summer in both locations (Figure 1.6). As noted for percent cover and the number of species, seasonal differences observed in plate biomass were highly significant (Table 1.1). Analysis of variance of biomass on the plates indicated no significant differences related to the main effects of plate location or orientation, although significant interactions were noted between season and the factors of plate location and orientation (Table 1.1, Figure 1.6). Differences in biomass between plate sides were generally not significant, except on some horizontal plates which had greater biomass on the bottom than on the top surface (Table 1.2).

Dominant taxa observed on the plates during all seasons were barnacles and hydroids (Figures 1.7, 1.8; Table 1.3). Barnacles accounted for more than 90% of all biomass scraped from the plate surfaces (Appendix 1.7). Two species, *Balanus venustus* and *B. trigonus*, were commonly observed during the spring, summer, and fall seasons. *Balanus venustus* was always more abundant than *B. trigonus* on plates from both areas, and it was the only barnacle species observed on plates submerged during the winter. Recruitment of barnacles during the spring appeared to be greater on plates

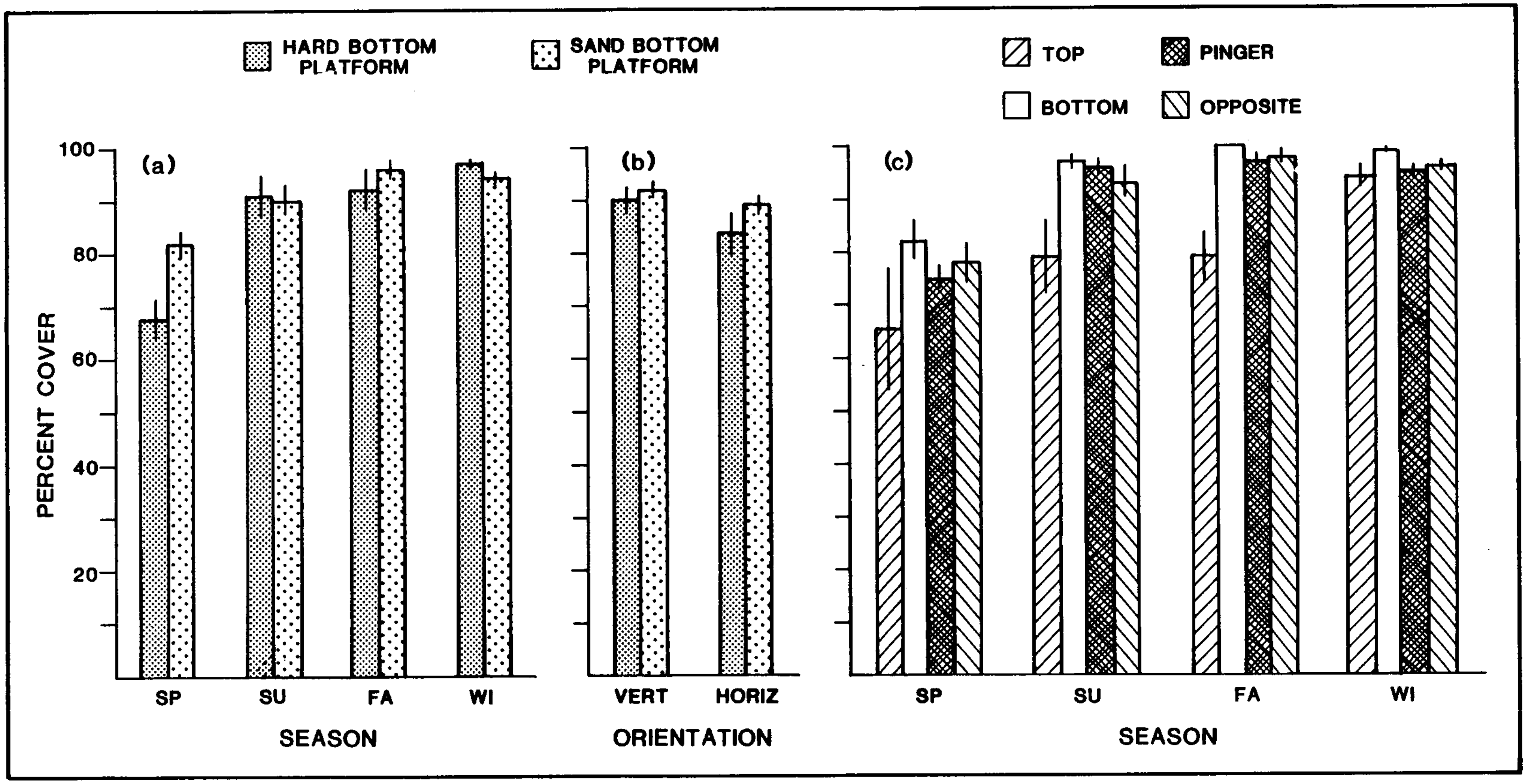


Figure 1.4 Mean percent cover of sessile biota on the 3-mo plates showing the interaction of (a) season and location, (b) orientation and location, and (c) orientation and season. Vertical lines represent the standard error of the means. SP = Spring, SU = Summer, FA = Fall, WI = Winter, Vert = Vertical plates, Horiz = Horizontal plates.

Table 1.1 Results of three-way analyses of variance (Model I) comparing percent cover, number of species, and biomass of sessile biota on horizontal and vertical plates exposed for three months during different seasons and in different locations.

SOURCE OF VARIATION	Degrees of Freedom	F Value	Results of *a posteriori* comparisons (REGW test[1])
	DEPENDENT VARIABLE: $\arcsin \sqrt{\text{percent cover/plate}}$		
Model ($r^2 = 0.50$)	15	5.27***	
Factor A: Platform Location	1	$0.00^{N.S.}$	
Factor B: Season of Exposure	3	20.79***	$\underline{\mu_{Sp}} < \underline{\mu_{Su}\ \ \mu_{Fa}\ \ \mu_{Wi}}$
Factor C: Surface Orientation	1	$1.18^{N.S.}$	
Interaction Effects			
A x B	3	2.90*	
A x C	1	$0.11^{N.S.}$	
B x C	3	$1.67^{N.S.}$	
A x B x C	3	$0.56^{N.S.}$	
	DEPENDENT VARIABLE: $\log_{10}$(No. spp./plate)		
Model ($r^2 = 0.77$)	15	17.99***	
Factor A: Platform Location	1	4.02*	$\underline{\mu_{\text{Sand bottom}}} < \underline{\mu_{\text{Hard bottom}}}$
Factor B: Season of Exposure	3	80.16***	$\underline{\mu_{Wi}} < \mu_{Sp}\ \ \underline{\mu_{Su}\ \ \mu_{Fa}}$ $\underline{\mu_{Sp}\ \ \mu_{Su}}$
Factor C: Surface Orientation	1	$2.34^{N.S.}$	
Interaction Effects			
A x B	3	5.52**	
A x C	1	$0.00^{N.S.}$	
B x C	3	$1.59^{N.S.}$	
A x B x C	3	$0.58^{N.S.}$	
	DEPENDENT VARIABLE: Biomass (g wet wt)		
Model ($r^2 = 0.86$)	15	31.72***	
Factor A: Platform Location	1	$0.04^{N.S.}$	
Factor B: Season of Exposure	3	139.34***	$\underline{\mu_{Sp}\ \ \mu_{Su}} < \underline{\mu_{Fa}} < \underline{\mu_{Wi}}$
Factor C: Surface Orientation	1	$0.13^{N.S.}$	
Interaction Effects			
A x B	3	8.07***	
A x C	1	$0.22^{N.S.}$	
B x C	3	3.97**	
A x B x C	3	7.10***	

N.S. not significant
* significant at 0.05 level
** significant at 0.01 level
*** significant at 0.001 level
[1] Ryan-Einot-Gabriel-Welsh multiple F test; means connected by underlines are not significantly different at $\alpha = 0.05$

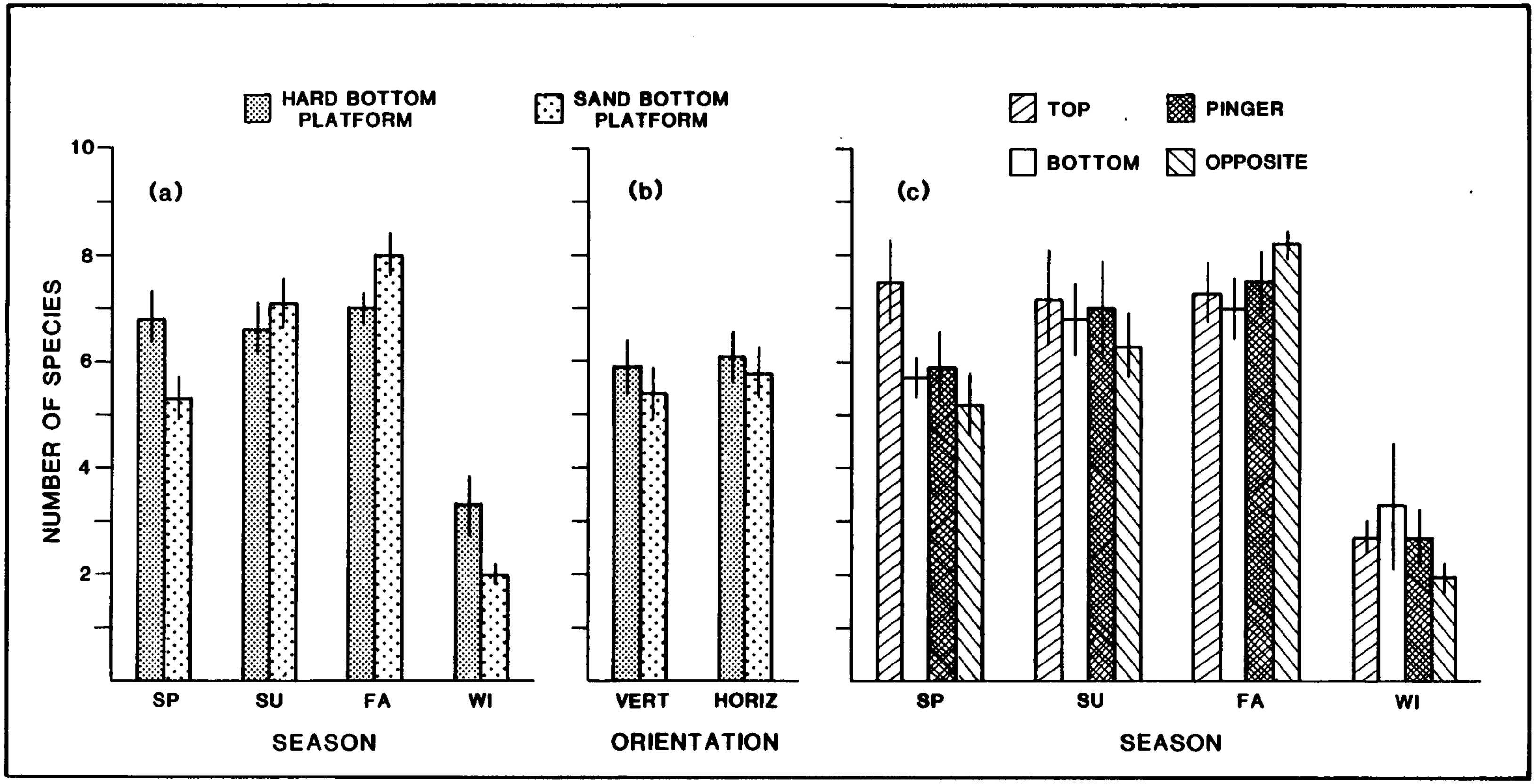


Figure 1.5 Mean number of sessile species observed on the 3-mo plates showing the interaction of (a) season and location, (b) orientation and location, and (c) orientation and season. Vertical lines represent the standard error of the means. SP = Spring, SU = Summer, FA = Fall, WI = Winter, Vert = Vertical plates, Horiz = Horizontal plates.

Table 1.2 Results of t-test comparisons of total percent biota cover, number of species, and biomass (g wet wt) of sessile biota attached to opposite sides of plates exposed for three months during the different seasons.

Plate Location	Plate Orientation	Season of Submergence	Percent Cover t_s	Percent Cover $\bar{x}$ Rank	Number of Species t_s	Number of Species $\bar{x}$ Rank	Biomass t_s	Biomass $\bar{x}$ Rank
Hard bottom	horizontal	spring	2.93*	$\mu_T < \mu_B$	1.17	N.S.	3.04*	$\mu_T < \mu_B$
Hard bottom	vertical	spring	0.69	N.S.	N.D.	N.S.	1.15	N.S.
Sand bottom	horizontal	spring	2.85*	$\mu_B < \mu_T$	1.26	N.S.	2.94*	$\mu_B < \mu_T$
Sand bottom	vertical	spring	2.00	N.S.	1.88	N.S.	0.67	N.S.
Hard bottom	horizontal	summer	1.98	N.S.	0.67	N.S.	13.26	$\mu_T < \mu_B$
Hard bottom	vertical	summer	0.09	N.S.	0.62	N.S.	0.39	N.S.
Sand bottom	horizontal	summer	3.31	N.S.	3.00*	$\mu_B < \mu_T$	6.36**	$\mu_T < \mu_B$
Sand bottom	vertical	summer	0.52	N.S.	1.01	N.S.	0.12	N.S.
Hard bottom	horizontal	fall	30.73***	$\mu_T < \mu_B$	0.36	N.S.	3.92*	$\mu_T < \mu_B$
Hard bottom	vertical	fall	0.08	N.S.	1.22	N.S.	0.61	N.S.
Sand bottom	horizontal	fall	4.17**	$\mu_T < \mu_B$	1.29	N.S.	2.10	N.S.
Sand bottom	vertical	fall	1.16	N.S.	0.29	N.S.	2.16	N.S.
Hard bottom	horizontal	winter	0.75	N.S.	0.63	N.S.	1.12	N.S.
Hard bottom	vertical	winter	0.82	N.S.	1.49	N.S.	0.42	N.S.
Sand bottom	horizontal	winter	3.93*	$\mu_T < \mu_B$	N.D.	N.S.	1.48	N.S.
Sand bottom	vertical	winter	0.35	N.S.	N.D.	N.S.	0.71	N.S.

N.D. - no difference between means
N.S. - not significant
* - significant at 0.05 level
** - significant at 0.01 level
*** - significant at 0.001 level

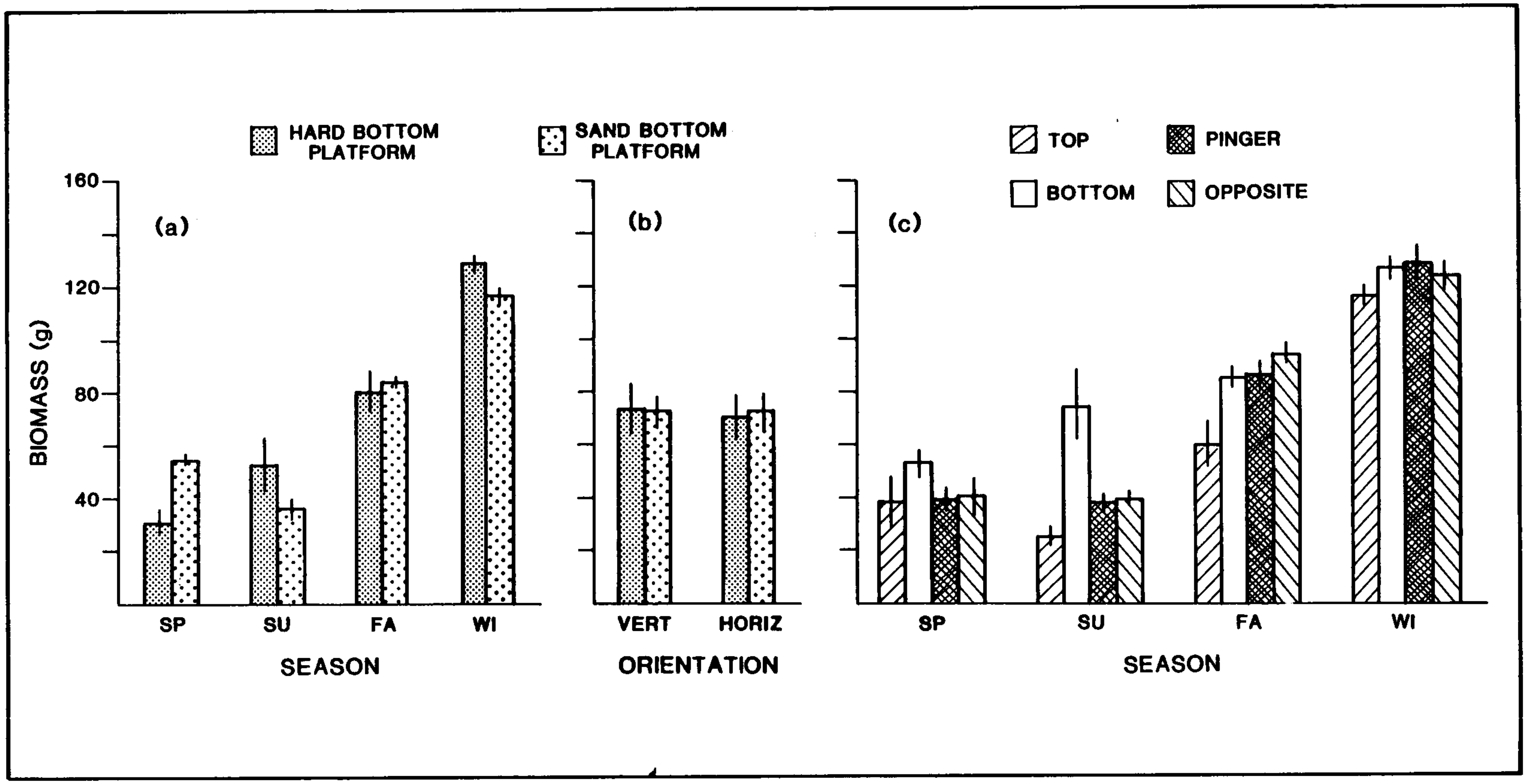


Figure 1.6 Mean biomass of sessile biota observed on the 3-mo plates showing the interaction of (a) season and location, (b) orientation and location, and (c) orientation and season. Vertical lines represent standard error of the means. SP = Spring, SU = Summer, FA = Fall, WI = Winter, Vert = Vertical plates, Horiz = Horizontal plates.

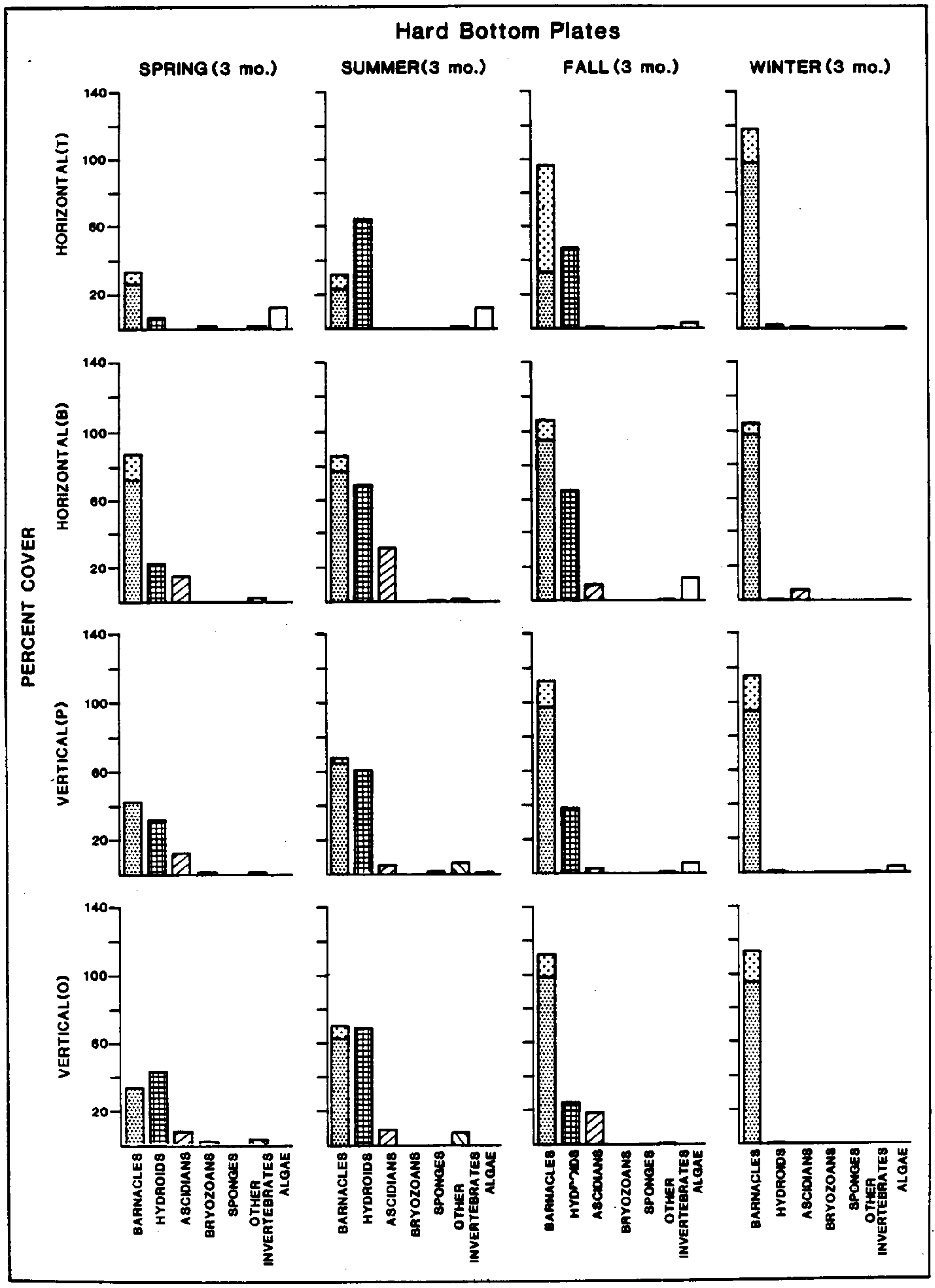


Figure 1.7 Mean percent cover of the different taxa observed on plates submerged for 3-mo periods in the hard-bottom area. The upper stippled portion of the bar diagrams representing barnacles indicates percent cover of empty barnacle tests. Plate surfaces are identified as T = Top, B = Bottom, P = Pinger, O = Opposite.

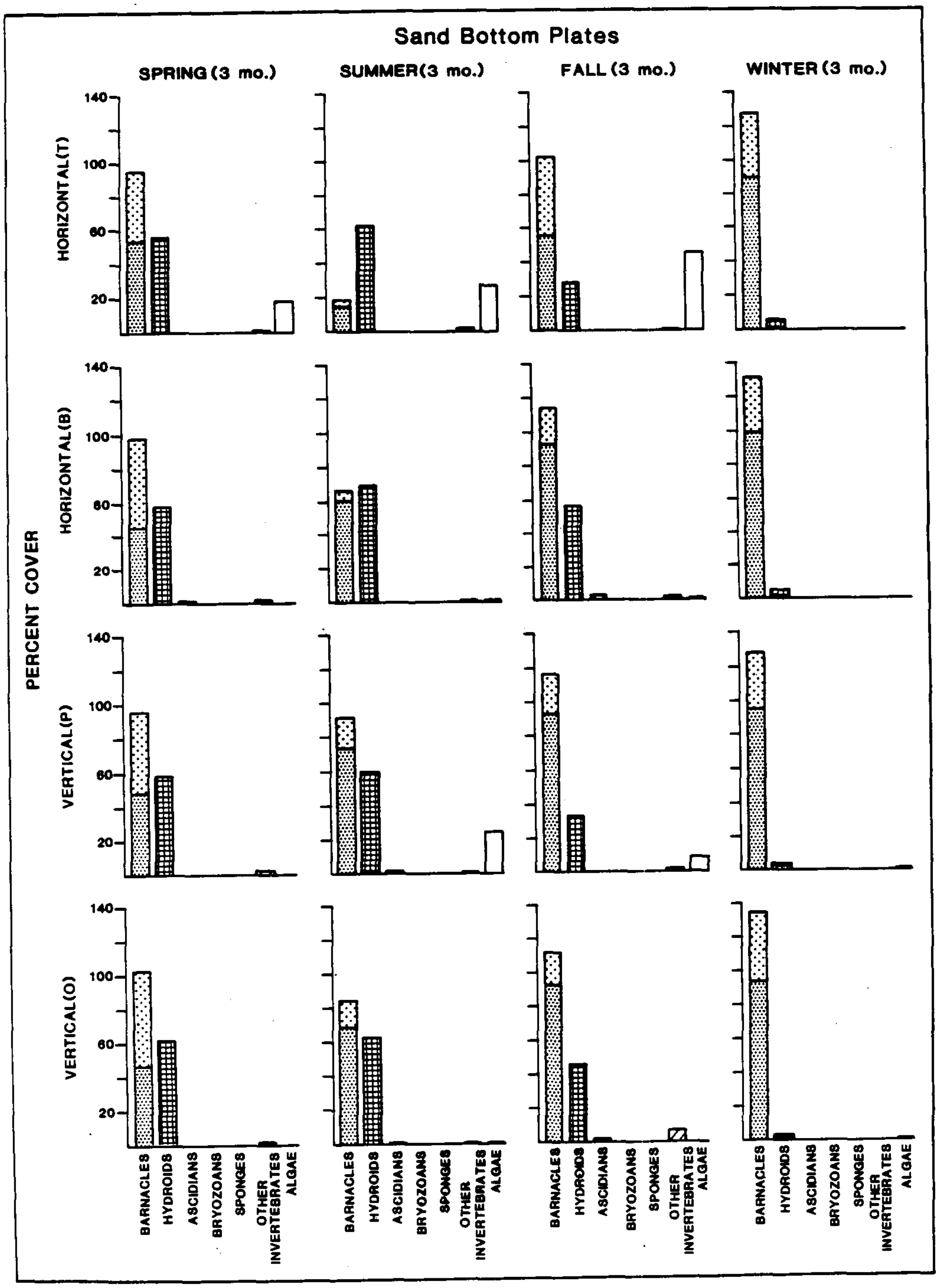


Figure 1.8 Mean percent cover of the different taxa observed on plates submerged for 3-mo periods in the sand-bottom area. The upper stippled portions of the bar diagrams representing barnacles indicates percent cover of empty barnacle tests. Plate surfaces are identified as T = Top, B = Bottom, P = Pinger, O = Opposite.

Table 1.3 Estimates of mean percent cover of sessile species which were observed under at least 1% of all points examined on the plates submerged for three months during the spring, summer, fall and winter seasons. (T = Top, B = Bottom, P = Pinger, O = Opposite; Ba = Barnacle, H = Hydroid, As = Ascidian, Al = Algae).

HARD-BOTTOM PLATFORM

	HORIZONTAL (T)				HORIZONTAL (B)				VERTICAL (P)				VERTICAL (O)			
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Balanus venustus (Ba)	22	9	37	97	34	50	93	99	24	76	96	95	18	53	96	96
Obelia dichotoma (H)	3	30	47	1	20	60	66	< 1	19	62	38			65	24	
Balanus trigonus (Ba)	4	5	1		48	36	6			1	5		18	5	1	
Clytia fragilis (H)		5			<1	33			31	1			41	1		
Symplegma viride (As)					10	28	19		9	6	1		7	9	23	
Halocordyle disticha (H)			<1								<1				7	
Turritopsis nutricula (H)						6					<1					
Ceramium strictum (Al)		2	1	1				<1			1	1				

SAND-BOTTOM PLATFORM

	HORIZONTAL (T)				HORIZONTAL (B)				VERTICAL (P)				VERTICAL (O)			
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Balanus venustus (Ba)	53	13	55	89	42	58	92	100	42	47	90	95	42	49	90	93
Obelia dichotoma (H)	55	21	13		57	6	29		57	29	32		61	17	44	
Balanus trigonus (Ba)		2	2		3	4	8		4	38	3		4	35	7	
Clytia fragilis (H)	1	6	2			22	2			23	1			15	1	
Symplegma viride (As)					<1											
Halocordyle disticha (H)		41	14			13	27			5	<1			7	<1	
Turritopsis nutricula (H)		1				38				5				30		
Ceramium strictum (Al)		23	15			<1	<1			2	1			<1		

in the sand-bottom area; however, many of the barnacles were dead when the plates were collected. The number of empty barnacle tests was lower on hard-bottom plates, but much of the barnacle cover had been removed by predators as evidenced by remaining basal plates. Thus, comparison of barnacle recruitment between areas is uncertain. Predation on barnacles attached to hard-bottom plates appeared to be highest on the top surfaces and lowest on the bottom surfaces of horizontal plates.

The density of barnacles was similar among plates collected from both frames during summer, fall, and winter (Figures 1.7, 1.8; Table 1.3). Greatest barnacle densities were present on the plates exposed during fall and winter seasons, with immature specimens often observed growing on larger barnacles, both living and dead. The percent cover of living barnacles was lower on the top surfaces in comparison with bottom and vertical surfaces during all seasons except winter.

Hydroid cover was greatest during the summer and lowest during the winter on plates from both sand-bottom and hard-bottom areas (Figure 1.3). The two species most commonly observed were *Obelia dichotoma* and *Clytia fragilis*. *Halocordyle disticha* was also abundant on sand-bottom plates during the summer and fall (Table 1.3). *Obelia dichotoma* cover was usually greater than *C. fragilis* cover on all plate surfaces, and both species formed a low mat of cover on the barnacle tests and bare surfaces (Figure 1.9). *Halocordyle* growth, on the other hand, was often much higher with this species growing in discrete clumps.

Hydroid cover on plates submerged during the spring was lower in the hard-bottom versus sand-bottom area (Table 1.3, Figures 1.7, 1.8). However, this difference was not observed during other seasons. One hydroid species, *Turritopsis nutriculata*, was only present on plates submerged during summer, and it was most abundant in the sand-bottom area. During winter, *Obelia*, *Clytia*, and *Halocordyle* were rare or absent on the plates, and only a few stalks of hydroids belonging to the family Tubulariidae were present (Appendix 1.6). No consistent patterns were noted in the distribution of hydroids on the different plate surfaces from either frame.

The only other taxa observed under more than 1% of all points analyzed in the 3-mo plate series were the ascidian *Symplegma viride*, and the alga *Ceramium strictum* (Table 1.3). *Symplegma viride*, which formed thin sheets overgrowing barnacles and bare surfaces, was most common on the underside of horizontal plates from the hard-bottom area. Ascidians were never observed on the top surfaces of 3-mo plates (Appendices 1.3-1.6). *Ceramium strictum* is a finely-branched red alga which was most abundant on the tops of horizontal plates submerged during summer and fall in the sand-bottom area. This species and other algae were also found on the vertical plates, but they rarely grew on the underside of horizontal plates.

Normal cluster analysis of species composition on the 3-mo plates resulted in distinct groupings related to season of plate submergence (Figure 1.10). Plates deployed during the winter formed Group 1, with very high similarity noted among plate surfaces regardless of location or

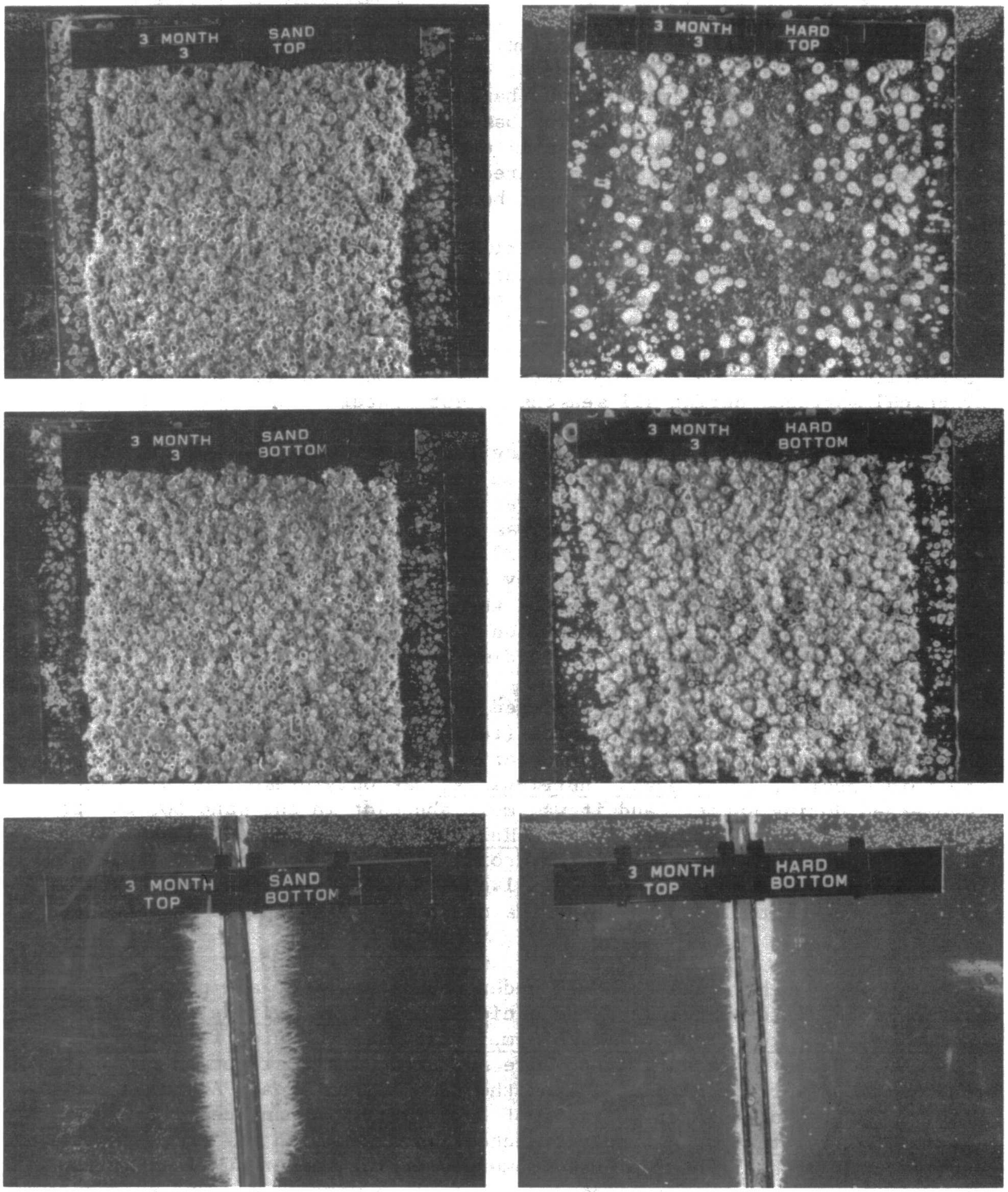


Figure 1.9 Photographs depicting sessile biota growth on the plates submerged during spring for three months in the sand-bottom and hard-bottom areas. Growth on the vertical plate surfaces (not shown) is similar to growth observed on the bottom plate surfaces in both areas. Dominant growth forms are barnacles and hydroids. The decreased growth of these taxa on the top plate surface from the hard-bottom area is most probably due to predation.

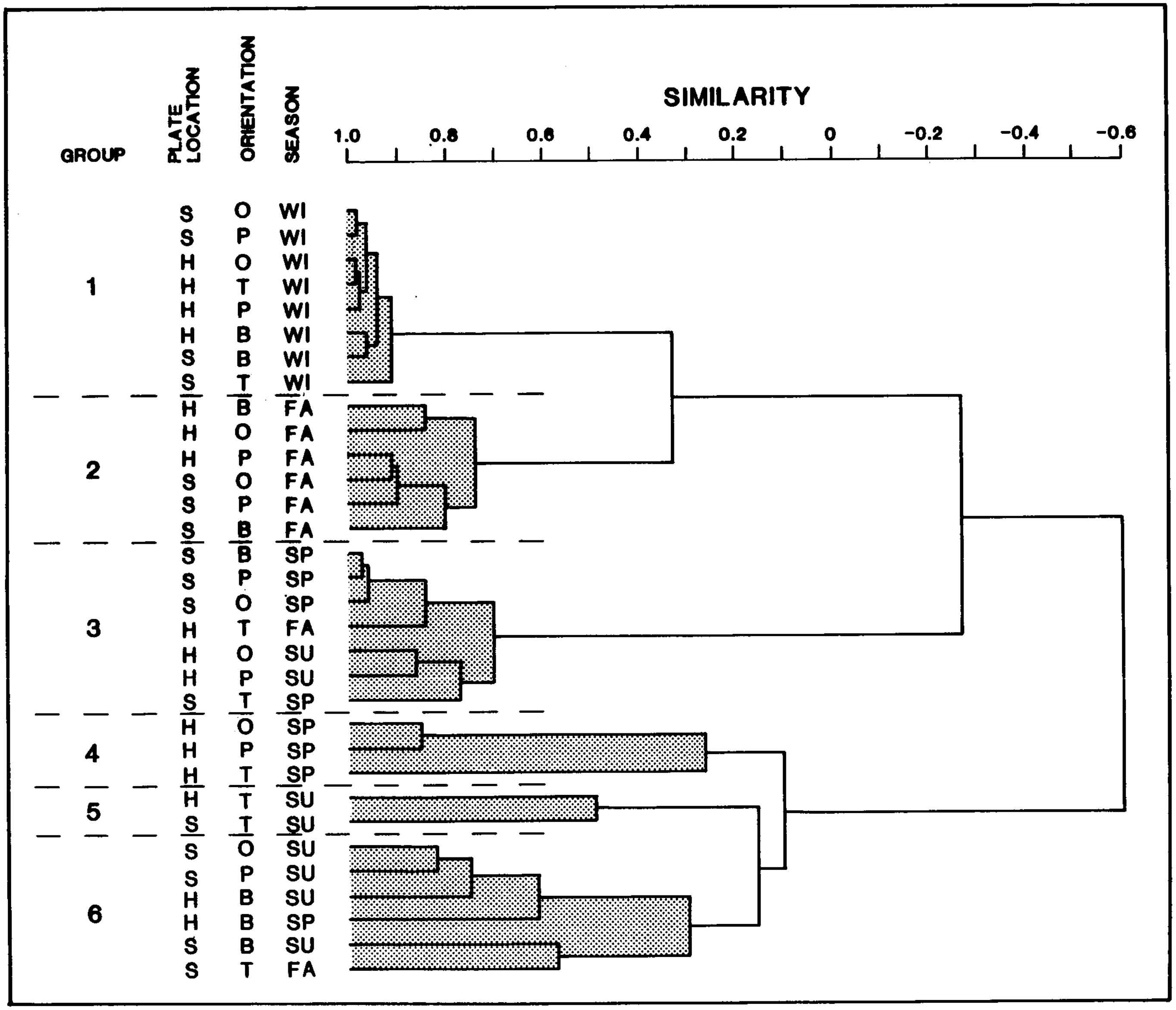


Figure 1.10 Dendrogram resulting from normal cluster analysis of percent cover estimates of sessile species attached to plates submerged for three months during the different seasons. S = Sand-bottom area, H = Hard-bottom area, T = horizontal top surface, B = horizontal bottom surface, P = vertical surface pinger side, O = vertical surface opposite side.

orientation. Six of the eight plate surfaces deployed during the fall formed Group 2, which also had relatively high similarity among entities. The two exceptions were top plate surfaces from the hard- and sand-bottom frames, which clustered in Groups 3 and 6, respectively. Cluster Group 3 included all plates deployed on sand bottom during spring, most of the vertical hard-bottom plates deployed during summer, and the one exception noted above. This group was relatively dissimilar to Groups 1 and 2 and to Groups 4-6. The latter three groups contained the other spring and summer plates from both frames, with some separation by surface orientation, season, and location. Groups 4-6 were more similar to each other than to Groups 1-3.

Inverse cluster analysis resulted in the formation of eight species groups which were relatively dissimilar to each other (Table 1.4, Figure 1.11). Group A was formed by three bryozoan species observed only rarely on the plates (Appendicès 1.3-1.6). Their distribution was restricted primarily to hard-bottom plates deployed during the spring, as noted in the nodal analysis (Figure 1.11).

Species in Group B, which included the common algae Ceramium strictum, and the hydroid H. disticha (Table 1.4), showed high constancy and moderate fidelity to sand-bottom plates during the summer and fall (Figure 1.11). Group B organisms were also noted on hard-bottom plates during fall, but their constancy and fidelity values were lower on those plates.

Species in Group C were the most frequently observed organisms on the plates (Tables 1.3, 1.4). Constancy of this species group was high on all plate groups, except during winter when few of the hydroids were observed. Due to their ubiquitous distribution among the plate surfaces, Group C species showed low fidelity to all plate groups.

Species in Group D (Table 1.4) were noted on many plate surfaces but their average percent cover on any plate series was less than 5% for all species except the serpulid worm Hydroides sp. A. Group D species were most common on 3-mo plates collected during fall, particularly on those plates from the hard-bottom area (Figure 1.11).

Species in Groups E and F also covered less than 5% of any plate surface although they were often present (Appendix 1.3-1.6). Group E species, which included the serpulid Hydroides uncinata and the hydroid Monostaechas quadridens (Table 1.4), were most common on sand-bottom plates deployed during summer. However, they were also present on plates deployed in other seasons as well (Figure 1.11, Appendices 1.3-1.6). The ascidians Distaplia bermudensis and Botryllus sp. A., and the sponge Scypha ciliata formed Group F. Nodal analysis indicated that species in this group were highly restricted to summer hard-bottom plates (Figure 1.11).

Among species in Groups G and H (Table 1.4), only the polychaete Filograna implexa covered more than 5% of surface area on any set of replicate plates (Appendix 1.3-1.6). Group G species were most common on plates submerged during winter and showed a moderate to high level of

Table 1.4 List of species groups resulting from inverse cluster analysis of sessile taxa on plates submerged for 3-mo periods during different seasons. A = Algae, As = Ascidians, Ba = Barnacles, Br = Bryozoans, H = Hydroids, P = Polychaetes, Po = Porifera.

Group A

Celleporaria mordax (Br)
Schizoporella cornuta (Br)
Turbicellepora dichotoma (Br)

Group B

Ceramium strictum (A)
Halocordyle disticha (H)
Colpomenia sinuosa (A)
Giffordia mitchellae (A)

Group C

Balanus venustus (Ba)
Obelia dichotoma (H)
Balanus trigonus (Ba)
Clytia fragilis (H)
Symplegma viride (As)
Turritopsis nutricula (H)

Group D

Botryllus planus (As)
Polysiphonia denudata (A)
Perophoridae A (As)
Membranipora tenuis (Br)
Serpulidae E (P)
Hydroides sp. A (P)
Styela plicata (As)

Group E

Dictyota dichotoma (A)
Spyridia hypneoides (A)
Algae S
Hydroides uncinata (P)
Monostaechas quadridens (H)

Group F

Botryllus sp. A (As)
Scypha ciliata (Po)
Distaplia bermudensis (As)

Group G

Crisia sp. (Br)
Tubulariidae B (H)
Distaplia sp. A (As)
Rhodophyta A (A)
Halecium tenellum (H)

Group H

Tubulariidae A (H)
Pomatoceros americanus (P)
Algae C
Algae O
Serpulidae P (P)
Halecium sp. (H)
Filograna implexa (P)

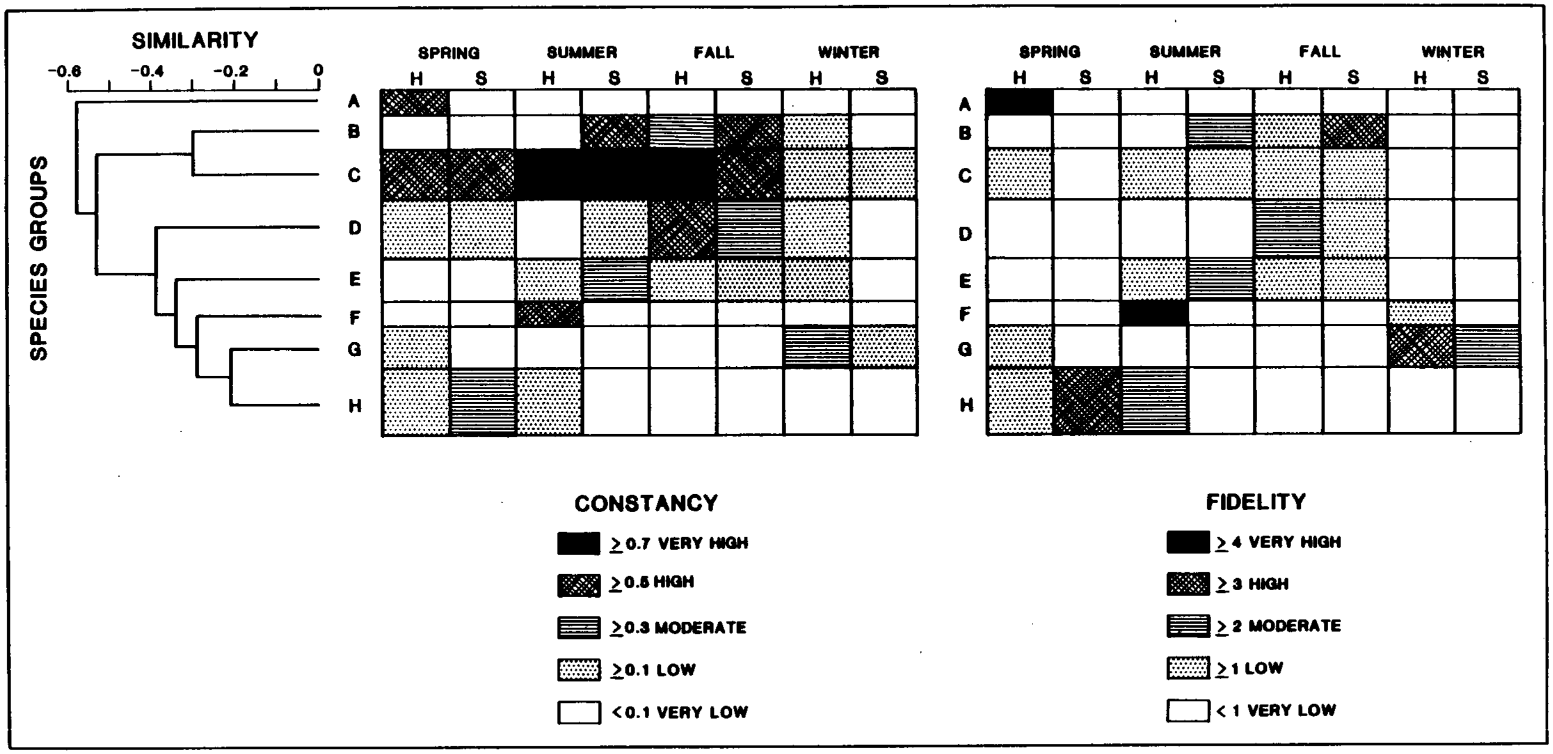


Figure 1.11 Nodal diagrams (right) showing constancy and fidelity of sessile species groups (A-H) resulting from inverse cluster analysis based on percent cover data obtained from plates submerged for 3-mo periods during the different seasons. H = Hard-bottom area, S = Sand-bottom area.

restriction to those plates (Figure 1.11). Species in Group H, on the other hand, were generally more constant and faithful to plates deployed during spring and summer.

Evaluation of all community parameters on the 3-mo plate series indicates that season of exposure has a greater influence on the composition and structure of biota colonizing hard substratum in our study area than does surface orientation or location. Sutherland (1974) and Sutherland and Karlson (1977) also noted seasonal differences in early fouling communities as they developed on plates submerged in shallower waters of North Carolina. They suggested that these differences can influence the type and structure of subsequent community development, resulting in multiple stable end points dependent on when community development began. Seasonal variations in species recruitment in their study area, however, were much greater than we observed, especially with respect to the morphology of early colonizers. In our study, barnacles and hydroids, which covered the plates with a low "mat-like" growth, were the dominant taxa noted in our study during all seasons except winter when hydroid growth was reduced. Thus, subsequent community development (after 3 mo) of hard substratum exposed during different seasons might be more similar in shelf waters off South Carolina than Sutherland (1974) noted. However, this hypothesis remains untested since the 3-mo plates were only intended to provide data on seasonal recruitment and early community development patterns.

As noted previously, faunal recruitment to hard substratum on the continental shelf of the South Atlantic Bight has not been previously studied. Many of the dominant species observed on the 3-mo plates are not major components of early developing communities in shallower waters. For example, *Balanus venustus* and *B. trigonus* were the only barnacles present on the plates in this study, with *B. venustus* covering most of the primary space on all plate surfaces. Although both species have a worldwide distribution (Zullo, 1979), neither species has been reported as the dominant barnacle covering hard surfaces in shallower subtidal waters (1-2 m) of the southeastern United States (Mook, 1976, 1980; Van Dolah et al., 1984; WHOI, 1952) or in deeper waters of other regions such as the Gulf of Mexico (Fotheringham, 1981; Gallaway et al., 1981; George and Thomas, 1979) or the Pacific (Aleem, 1957; Davis et al., 1982; WHOI, 1952).

Zullo (1979) noted that *B. venustus* is the most common subtidal barnacle of the Virginian province and that reproductive populations of *B. trigonus* are restricted to the region south of Cape Hatteras, North Carolina. Relatively little is known about the ecology of these species. On our 3-mo plates, *B. venustus* showed less seasonal variability in abundance than some of the other species, although more *B. venustus* were observed on the plates during fall and winter than during spring and summer. *Balanus trigonus*, on the other hand, was more common on the 3-mo plates during spring and summer and was rare or absent on the plates during the fall and winter. Werner (1967) suggested that *B. trigonus* is relatively intolerant of cooler temperatures which probably accounts for the lack of *B. trigonus* spat on plates submerged during the winter. Cooler temperatures did not result in substantial mortality of this species since many large *B. trigonus* were observed on the 12-mo plates exposed during winter.

Most of the hydroids growing on the 3-mo plates have been collected from other areas of the northwestern Atlantic (Fraser, 1944). The most prevalent species, Obelia dichotoma, has been observed commonly in shallower waters of South Carolina (Calder et al., 1977a, 1977b; Zingmark, 1978; Van Dolah, 1979, 1984). Several studies have noted that Obelia spp. are early colonizers on hard surfaces in both shallow and deep water (Aleem, 1957; Fager, 1971; Greene and Schoener, 1982; Vandermeulen and De Wreede, 1982). Furthermore, O. dichotoma can inhibit settlement of barnacle larvae (Standing, 1976). Thus, the reduced growth of this species and others which had similar morphologies (Clytia fragilis, Turritopsis nutricula) during the cooler months may account for the higher coverage of barnacles observed on the plates during winter. Except for the seasonal trends noted in hydroid growth, no consistent differences were observed in total hydroid cover on the plates with respect to surface orientation or proximity to hard bottom.

The effects of surface orientation were most obvious with respect to algal, ascidian, and barnacle growth. The greater cover of algae observed on top plate surfaces is similar to algal growth patterns noted by Vandermeulen and De Wreede (1982), and is most probably related to the availability of light. Ascidians, on the other hand, were restricted to the bottoms of horizontal plates and to vertical plate surfaces. This may reflect a preferential settling on surfaces which are shaded and less prone to sedimentation, predation, and competition from algae as noted by Young and Chia (1984). Predation also had an effect on the distribution of barnacles. Evidence of predation on barnacles was greatest on the tops of horizontal surfaces, which had significantly lower total biota cover and biomass than was observed on the underside of horizontal plates. Filefish, sheepshead, spadefish, black sea bass, and blennies were present around both fouling plate frames, and all of these species were occasionally observed grazing on the plates. Furthermore, diets of the latter three species are known to include barnacles and ascidians (see section III and Gallaway, 1981). Harris and Irons (1982) also found that predation was greater on the tops of horizontal surfaces and suggested that predation and siltation are the primary factors influencing communities on those surfaces.

Predation may have accounted for the large percentage of dead barnacle tests covering the plates during most seasons. Turbellarians were often observed in the motile epifaunal communities associated with the plates and certain species are known to consume barnacles (Branscomb, 1973). No obvious patterns were detected in the percentage of empty barnacle tests with respect to season, plate location, or surface orientation.

Proximity to hard-bottom habitat did not appear to have a significant influence on the total percent cover or biomass observed on the 3-mo plates, but significant differences were noted in the number of species recruited to those plates based on location. The greater number of species present on the 3-mo plates in the hard-bottom area probably reflects a greater pool of larvae from sessile species growing nearby, especially those having larvae which settle quickly. For example, ascidians were much more common on plates in the hard-bottom versus sand-bottom area. Berrill (1950) notes that the tadpole larvae of many ascidians are only in the water column for a few minutes to a few hours. Thus, fewer ascidian larvae might be expected to reach the sand-bottom plates since most of the species observed in this study are restricted to hard-bottom habitats.

Community Development - Biotic cover increased significantly with time on the 3-, 6-, 9-, and 12-mo plate series (Figure 1.12, Table 1.5). After nine months exposure, the average cover on plates from both frames exceeded 95%, which was significantly greater than the cover noted on plates submerged for 3 and 6 months, but similar to the cover noted on 12-mo plates (Table 1.5). Analysis of variance indicated that average percent cover was greater on plates from the hard-bottom versus sand-bottom area, although there was a significant interaction between area and time factors. Significant differences were noted by analysis of variance in the percent cover on vertical versus horizontal plates, but the *a posteriori* Ryan-Einot-Gabriel-Welsh Multiple F test indicated that this difference was not great enough to be detected by this test (Table 1.5). Comparisons between sides of plates indicated that cover was generally highest on the bottom of horizontal plates and lowest on the tops of those plates (Figure 1.12), but the differences were not significant with a few exceptions (Table 1.6). No significant differences were noted in the amount of biota cover on different sides of the vertical plates.

The average number of species observed on the plates increased significantly with duration of submergence (Figures 1.13, Table 1.5). After 9 months, number of species on plates from both the sand-bottom and hard-bottom locations approached or exceeded the number observed on 12-mo plates, and no significant differences were noted between the two plate groups. Significantly more species were also observed on the hard-bottom plates than on the sand-bottom plates during every sampling period (Table 1.5). The effects of plate orientation on species number, however, were not significant and there were no consistent differences in species number between sides of any plate group (Table 1.6).

Biomass increased with time on the 3-, 6-, 9-, and 12-mo plate series with greater increases noted on the hard-bottom plates (Figure 1.14). Analysis of variance indicated that differences in biomass related to submergence time and area were highly significant, and that there was significant interaction between these main effects (Table 1.5). No consistent differences were noted in biomass with respect to plate orientation. Comparisons between plate sides, however, indicated that significantly greater biomass was usually present on the bottom of horizontal plates (Table 1.6). No major differences were noted between sides of vertical plates.

Barnacles alone accounted for greater than 95% of the total biomass on 3-mo and 6-mo plates. On the 9-mo and 12-mo plates, barnacles and ascidians represented 99% of the biomass (Appendix 1.7).

As noted previously, the dominant fauna covering the 3-mo plates deployed during March were barnacles and hydroids (Figures 1.15-1.16, Table

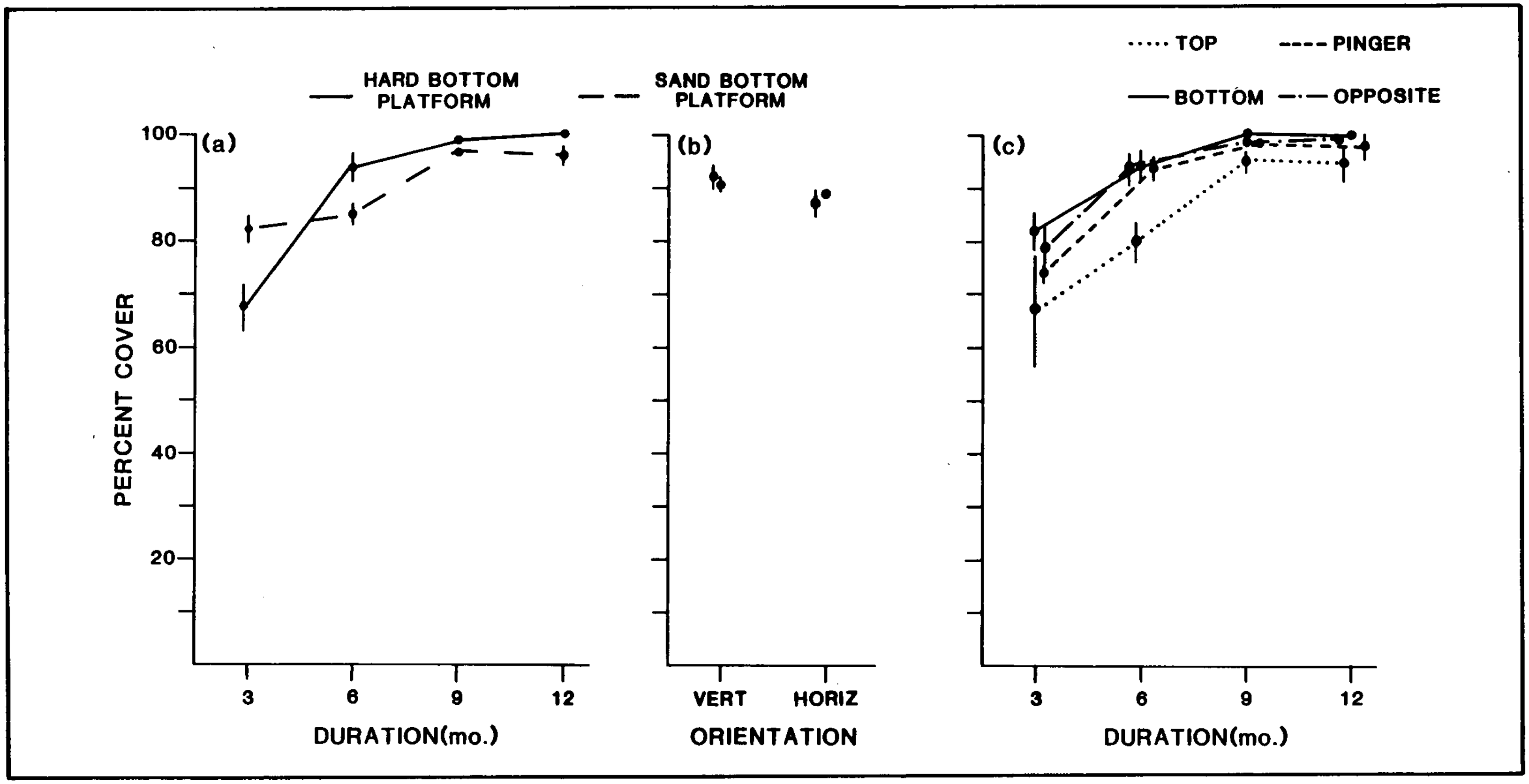


Figure 1.12 Mean percent cover of sessile biota on the 3-, 6-, 9-, and 12-mo plates showing the interaction of (a) season and location, (b) orientation and location, and (c) orientation and season. Vertical lines represent standard error of the means. Vert = Vertical plates, Horiz = Horizontal plates.

Table 1.5 Results of three-way analyses of variance (Model I) comparing percent cover, number of species, and biomass of sessile biota on horizontal and vertical plates exposed for 3-, 6-, 9-, and 12-mo intervals in different locations.

SOURCE OF VARIATION	Degrees of Freedom	F Value	Results of a posteriori comparisons (REGW test[1])
	DEPENDENT VARIABLE:	$\arcsin \sqrt{\text{percent cover/plate}}$	
Model ($r^2 = 0.73$)	15	14.78***	
Factor A: Platform Location	1	6.13*	$\underline{\mu_{Sand\ bottom}} < \underline{\mu_{Hard\ bottom}}$
Factor B: Time of Exposure	3	59.58***	$\underline{\mu_{3\ mo}} < \underline{\mu_{6\ mo}} < \underline{\mu_{9\ mo}\quad \mu_{12\ mo}}$
Factor C: Surface Orientation	1	3.90*	$\underline{\mu_{Horizontal}\quad \mu_{Vertical}}$
Interaction Effects			
A x B	3	8.76***	
A x C	1	$1.30^{N.S.}$	
B x C	3	$1.35^{N.S.}$	
A x B x C	3	$0.41^{N.S.}$	
	DEPENDENT VARIABLE:	$\log_{10}$(No. spp./plate)	
Model ($r^2 = 0.66$)	15	10.31***	
Factor A: Platform Location	1	13.01***	$\underline{\mu_{Sand\ bottom}} < \underline{\mu_{Hard\ bottom}}$
Factor B: Time of Exposure	3	43.66***	$\underline{\mu_{3\ mo}} < \underline{\mu_{6\ mo}} < \underline{\mu_{9\ mo}\quad \mu_{12\ mo}}$
Factor C: Surface Orientation	1	$0.64^{N.S.}$	
Interaction Effects			
A x B	3	$0.22^{N.S.}$	
A x C	1	$0.14^{N.S.}$	
B x C	3	$1.84^{N.S.}$	
A x B x C	3	$1.22^{N.S.}$	
	DEPENDENT VARIABLE:	Biomass (g wet wt)	
Model ($r^2 = 0.77$)	15	17.49***	
Factor A: Platform Location	1	44.75***	$\underline{\mu_{Sand\ bottom}} < \underline{\mu_{Hard\ bottom}}$
Factor B: Time of Exposure	3	61.08***	$\underline{\mu_{3\ mo}} < \underline{\mu_{6\ mo}} < \underline{\mu_{9\ mo}} < \underline{\mu_{12\ mo}}$
Factor C: Surface Orientation	1	$2.12^{N.S.}$	
Interaction Effects			
A x B	3	8.44***	
A x C	1	$2.88^{N.S.}$	
B x C	3	$0.99^{N.S.}$	
A x B x C	3	0.39	

N.S. not significant
* significant at 0.05 level
** significant at 0.01 level
*** significant at 0.001 level

[1] Ryan-Einot-Gabriel-Welsh multiple F test; means connected by underlines are not significantly different at $\alpha = 0.05$

Table 1.6 Results of t-test comparisons of total percent biota cover, number of species, and biomass (g wet wt) of sessile biota attached to opposite sides of plates exposed for 3, 6, 9, and 12 months.

Plate Location	Plate Orientation	Duration of Submergence	Percent Cover		Number of Species		Biomass	
			t_s	$\bar{x}$ Rank	t_s	$\bar{x}$ Rank	t_s	$\bar{x}$ Rank
Hard bottom	horizontal	3 mo	2.93*	$\mu_T < \mu_B$	1.17	N.S.	3.04*	$\mu_T < \mu_B$
Hard bottom	vertical	3 mo	0.69	N.S.	N.D.	N.S.	1.15	N.S.
Sand bottom	horizontal	3 mo	2.85*	$\mu_B < \mu_T$	1.26	N.S.	2.94*	$\mu_B < \mu_T$
Sand bottom	vertical	3 mo	2.00	N.S.	1.88	N.S.	0.67	N.S.
Hard bottom	horizontal	6 mo	4.61**	$\mu_T < \mu_B$	1.94	N.S.	4.07**	$\mu_T < \mu_B$
Hard bottom	vertical	6 mo	0.78	N.S.	0.97	N.S.	0.75	N.S.
Sand bottom	horizontal	6 mo	1.31	N.S.	2.79	N.S.	0.98	N.S.
Sand bottom	vertical	6 mo	1.28	N.S.	0.45	N.S.	0.62	N.S.
Hard bottom	horizontal	9 mo	2.53	N.S.	2.36	N.S.	4.43**	$\mu_T < \mu_B$
Hard bottom	vertical	9 mo	1.00	N.S.	3.96*	$\mu_O < \mu_P$	0.57	N.S.
Sand bottom	horizontal	9 mo	1.17	N.S.	0.38	N.S.	6.20**	$\mu_T < \mu_B$
Sand bottom	vertical	9 mo	0.86	N.S.	0.48	N.S.	0.12	N.S.
Hard bottom	horizontal	12 mo	1.00	N.S.	1.94	N.S.	3.06*	$\mu_T < \mu_B$
Hard bottom	vertical	12 mo	1.00	N.S.	4.38**	$\mu_O < \mu_P$	0.67	N.S.
Sand bottom	horizontal	12 mo	2.59	N.S.	1.91	N.S.	3.17*	$\mu_T < \mu_B$
Sand bottom	vertical	12 mo	0.15	N.S.	4.13**	$\mu_O < \mu_P$	0.11	N.S.

N.D. - no difference between means
N.S. - no significant difference
* - significant at 0.05 level
** - significant at 0.01 level
*** - significant at 0.001 level

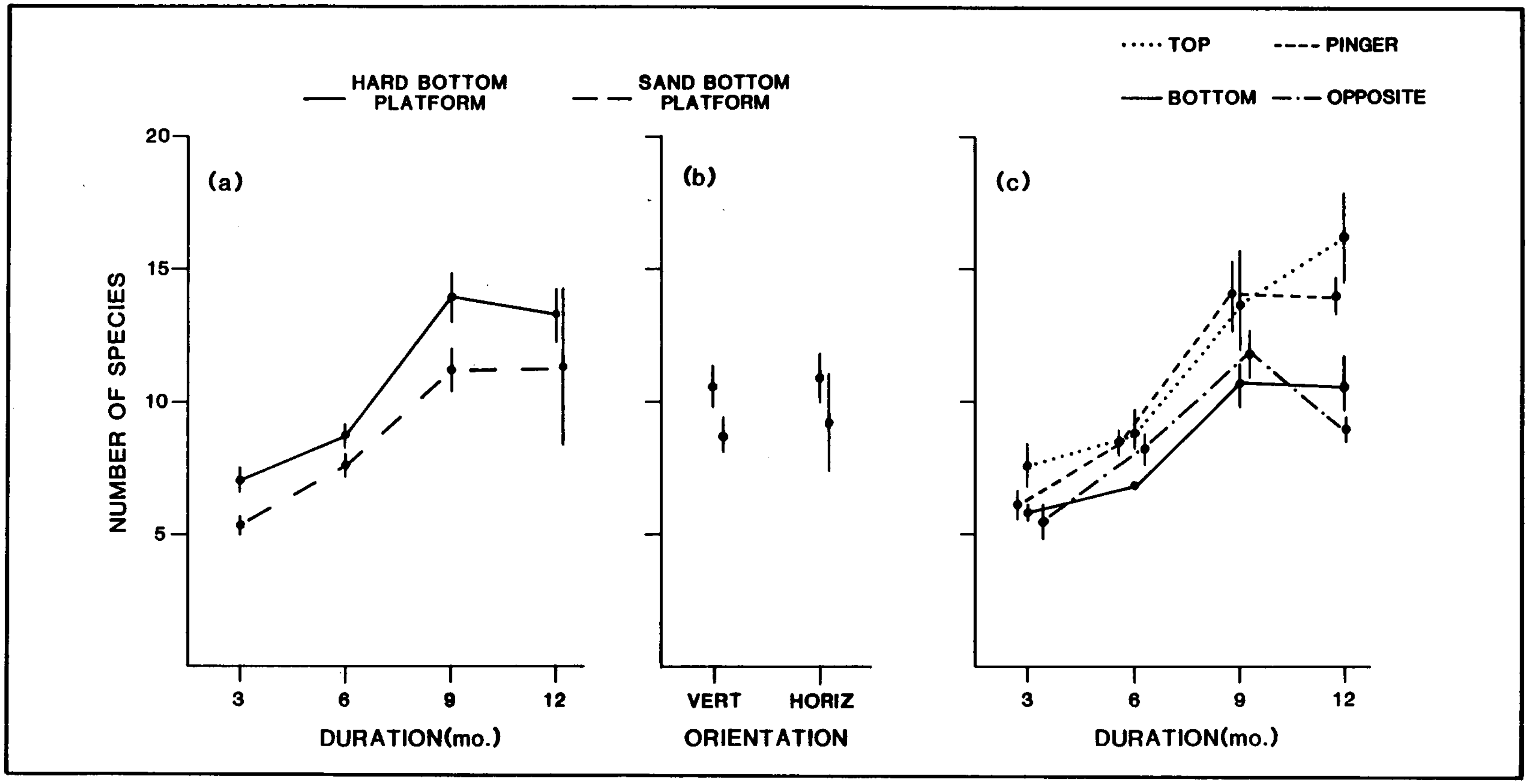


Figure 1.13 Mean number of sessile species observed on the 3-, 6-, 9-, and 12-mo plates showing the interaction of (a) season and location, (b) orientation and location, and (c) orientation and season. Vertical lines represent the standard error of the means. Vert = Vertical plates, Horiz = Horizontal plates.

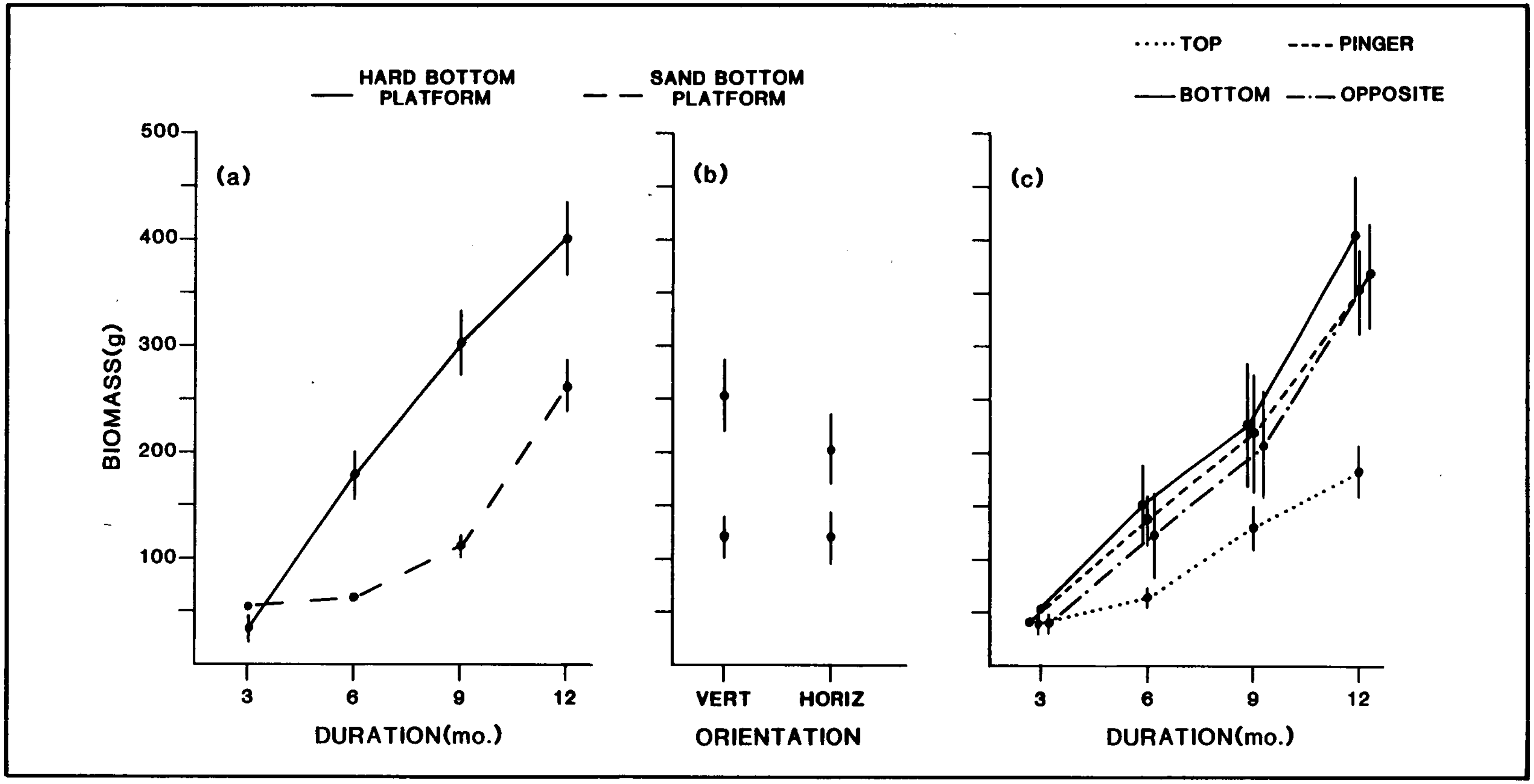


Figure 1.14 Mean biomass of sessile biota observed on the 3-, 6-, 9- and 12-mo plates showing the interaction of (a) season and location, (b) orientation and location, and (c) orientation and season. Vertical lines represent the standard error of the means. Vert = Vertical plates, Horiz = Horizontal plates.

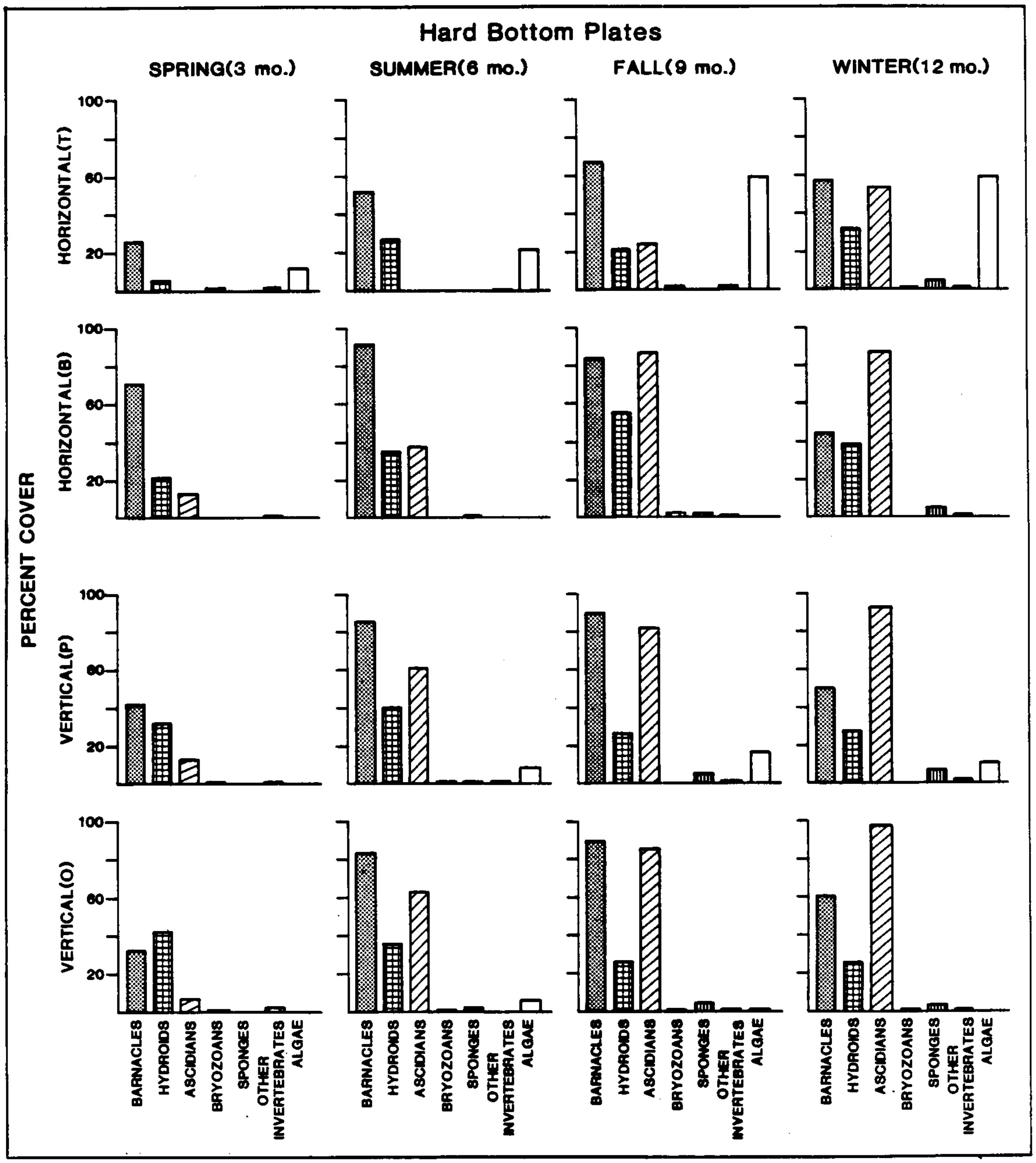


Figure 1.15 Mean percent cover of the different taxa observed on plates submerged for 3, 6, 9, and 12 months in the hard-bottom area. Plate surfaces are identified as T = Top, B = Bottom, P = Pinger, O = Opposite.

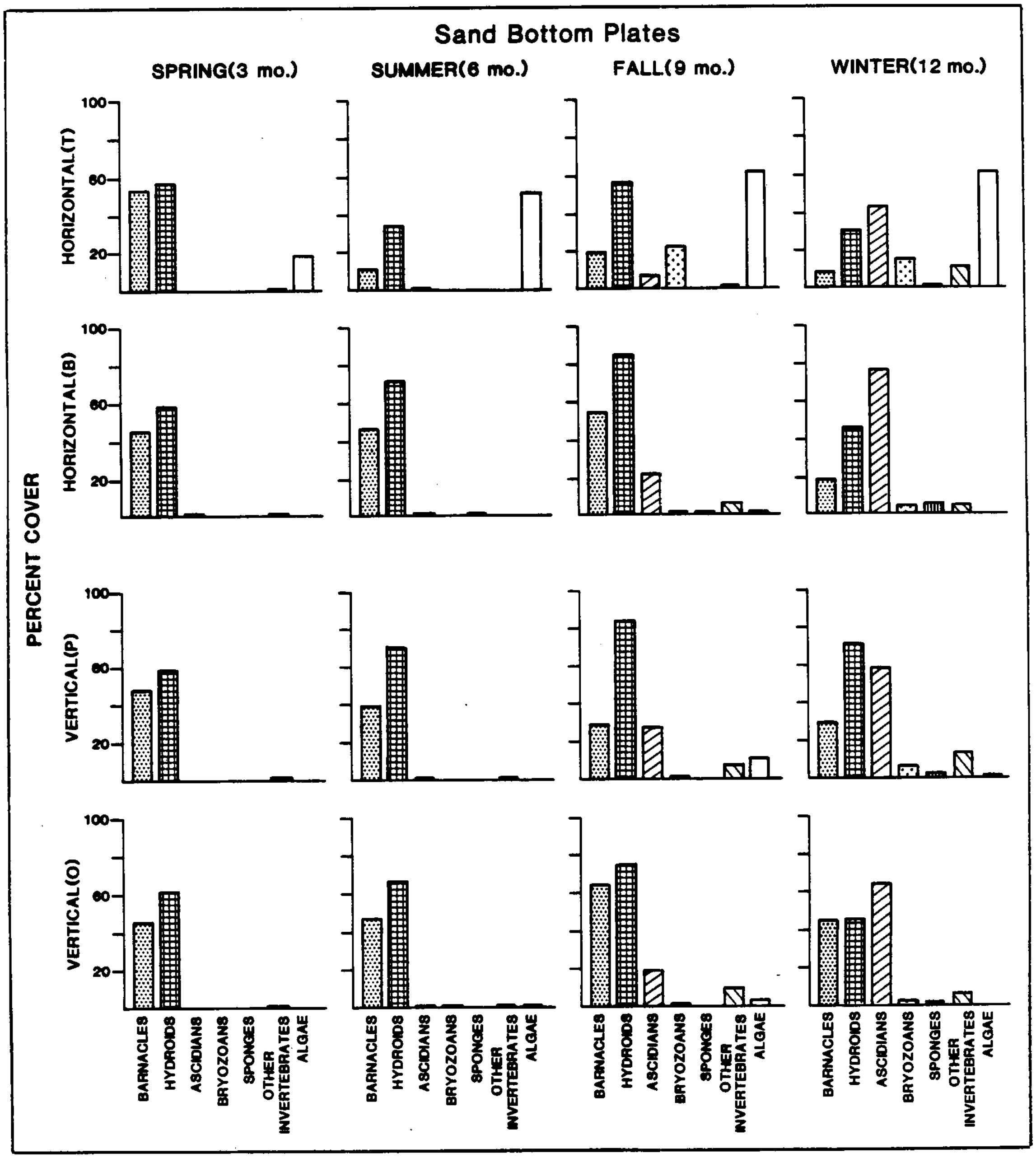


Figure 1.16 Mean percent cover of the different taxa observed on plates submerged for 3, 6, 9, and 12 mo in the sand-bottom area. Plate surfaces are identified as T = Top, B = Bottom, P = Pinger, O = Opposite.

1.7). Balanus venustus was the most common barnacle observed on the plate surfaces except on the bottom of horizontal surfaces where B. trigonus was more common. Clytia fragilis was the most common hydroid on the hard-bottom plates whereas Obelia dichtoma was more prevalent on plates in the sand-bottom area. Algae was present only on the tops of horizontal plates from both frames, and average cover never exceeded 20% of a plate surface. The algal species present under most points was Ceramium strictum, which was most common in the sand-bottom area. Nineteen other species, representing ascidians, bryozoans, and serpulid worms were present on the 3-mo plates, but only the ascidian Symplegma viride covered more than 5% of any plate surface (Appendix 1.3).

Hydroids and barnacles remained the dominant taxa on plates submerged for 6 months in the sand-bottom area, except for the top surfaces of horizontal plates which also had high algal cover (Figures 1.15-1.16, Table 1.7). Clytia fragilis and O. dichotoma were the hydroid species observed under most points, although Halocordyle disticha was also present. Balanus venustus was still the dominant barnacle species covering the sand-bottom plates. In contrast, 6-mo plates from the hard-bottom area were primarily covered by B. trigonus (Table 1.7), even though B. venustus was the most common species observed settling on the 3-mo plates collected at the same time (Table 1.3). Only the top surfaces of the 6-mo horizontal plates had greater cover by B. venustus than by B. trigonus.

Ascidian cover was also greater on the 6-mo hard bottom plates than on the 3-mo hard-bottom plates collected during the same season, or on the 6-mo sand-bottom plates (Figure 1.7, 1.15). Symplegma viride accounted for most of the ascidian cover on the hard-bottom plates although Distaplia sp. A, D. bermudensis, and Styela plicata were also present (Table 1.7). Ascidian cover was absent on the top of horizontal plates in the hard-bottom area, and accounted for < 1% of the biota cover on any surface of the sand-bottom plates. A total of 24 and 18 species were found on the hard-bottom and sand-bottom 6-mo plates, respectively (Appendix 1.8).

Species forming the primary cover on the 6-mo plates in both locations were still the dominant taxa on the 9-mo plates, which supported a total of 45 and 33 species in the hard- and sand-bottom areas, respectively (Table 1.7, Appendix 1.9). However, plates exposed for 9 months in the hard-bottom area had much greater ascidian cover than either the 6-mo hard-bottom plates or the 9-mo sand-bottom plates, which had greater hydroid cover (Figures 1.15, 1.16). Symplegma viride was the dominant ascidian on the hard-bottom plates, covering more than 70% of the vertical and horizontal-bottom surfaces (Table 1.7). This species, as well as S. plicata and D. bermudensis, was also common on the sand-bottom plates. Hydroid cover was dominated by Halocordyle disticha, especially in the sand-bottom area (Table 1.7). This species grew in tall stalks and formed a canopy over the smaller hydroids O. dichotoma and C. fragilis.

Barnacles and algae were still major components of the sessile communities on the 9-mo plates in both areas (Figures 1.15, 1.16, Table 1.7). Balanus venustus dominated the barnacle cover in the sand-bottom area whereas B. trigonus was dominant on the plates in the hard-bottom

Table 1.7 Estimates of mean percent cover of sessile species which were observed under at least 1% of all points examined on the plates submerged for 3, 6, 9, and 12 months. (T = Top, B = Bottom, P = Pinger, O = Opposite ; Ba = Barnacle, As = Ascidian, H = Hydroid, Al = Algae).

HARD-BOTTOM PLATFORM

	HORIZONTAL (T)				HORIZONTAL (B)				VERTICAL (P)				VERTICAL (O)			
	3 mo	6 mo	9 mo	12 mo	3 mo	6 mo	9 mo	12 mo	3 mo	6 mo	9 mo	12 mo	3 mo	6 mo	9 mo	12 mo
Balanus venustus (Ba)	22	39	38	25	34	25	17	14	24	23	24	17	18	33	27	17
Balanus trigonus (Ba)	4	19	36	16	48	83	75	34	19	71	77	36	18	68	76	49
Symplegma viride (As)			21	35	10	31	76	45	9	59	71	61	7	63	77	76
Obelia dichotoma (H)	3	1	2	1	20		3	7		16	11	1		12	4	
Clytia fragilis (H)		26	7		<1	25	1	14	31	10	4	10	41	4	18	14
Styela plicata (As)				15	<1		7	8		2	6	10		<1	4	12
Halocordyle disticha (H)			9				41									
Ceramium strictum (Al)		6	11	18						3	6	2		3	<1	
Hydractiniidae A (H)						<1	6	15								
Turritopsis nutricula (H)			1			10	4	1		11	7	<1		16	3	<1
Distaplia bermudensis (As)						1	8	32			2	14		<1	5	17
Champia parvula (Al)		2	32	27						<1	3	4				

SAND-BOTTOM PLATFORM

	HORIZONTAL (T)				HORIZONTAL (B)				VERTICAL (P)				VERTICAL (O)			
	3 mo	6 mo	9 mo	12 mo	3 mo	6 mo	9 mo	12 mo	3 mo	6 mo	9 mo	12 mo	3 mo	6 mo	9 mo	12 mo
Balanus venustus (Ba)	53	6	4	5	42	30	38	14	42	35	20	22	42	39	55	43
Balanus trigonus (Ba)		4	4	5	3	21	23	5	4	6	8	9	4	14	13	7
Symplegma viride (As)					3						20	6			4	
Obelia dichotoma (H)	55	8	5		57	10	3	1	57	28	16	3	61	28	24	
Clytia fragilis (H)	<1	20	1			45	20	13		15	9	7		13	4	5
Styela plicata (As)			7	36		<1	20	75		<1	7	53		<1	4	63
Halocordyle disticha (H)		4	28			7	64			34	56			18	43	
Ceramium strictum (Al)		46	39	41			1				9			1	1	
Hydractiniidae A (H)		<1	1			6	28	3			17	13			11	3
Turritopsis nutricula (H)		2				3	1	<1		7	2	2		13	<1	
Distaplia bermudensis (As)															1	
Champia parvula (Al)		1									<1					

area, even though *B. venustus* accounted for the greatest percent cover on the 3-mo hard-bottom plates during fall (Table 1.3). As noted on earlier plates, algal cover was greatest on the tops of horizontal plates. Dominant species covering plate surfaces in the hard-bottom area were *Ceramium strictum* and *Champia parvula*, but only *C. strictum* was commonly observed on sand-bottom plates.

Plates submerged for 12 months supported the most diverse fouling communities, with a total of 45 species observed on plates from the hard-bottom area and 39 species observed on plates in the sand-bottom area (Appendix 1.10). Ascidians covered most of the plate surfaces, especially in the hard-bottom area where *Symplegma viride* and *Distaplia bermudensis* overgrew and smothered many of the barnacles (Figures 1.15-1.17, Table 1.7). In contrast, *Styela plicata* was the dominant ascidian on sand-bottom plates, which supported very little *S. viride* growth and no *D. bermudensis*. Hydroid growth was reduced on the 12-mo plates and no living *H. disticha* were observed in either area. *Clytia fragilis*, *Monostaechas quadridens*, and Hydractiniidae A were the common hydroids observed on all plates except in the sand-bottom area where *M. quadridens* was rarely observed.

The alga *Ceramium strictum* continued to be an important component of the fouling community on the tops of horizontal plates submerged for 12 months (Table 1.7). Fourteen other algal species were observed on the plates, but only *Champia parvula*, *Lomentaria baileyana*, and *Polysiphonia denudata* exceeded 10% cover on any plate surface (Appendix 1.10). Other taxa observed on the plates included bryozoans, sponges, anemones, serpulid worms, and mollusks, but no species representing these taxa were observed under more than 10% of the points on a plate surface.

Normal cluster analysis of the sessile communities on the 3-, 6-, 9-, and 12-mo plates resulted in separation of plate surfaces by location, and to a lesser extent by length of exposure and orientation (Figure 1.18). Groups 1-4 contained all of the sand-bottom plate surfaces except one, and the remaining two groups were formed by plate surfaces from the hard-bottom area. Among the four groups comprising sand-bottom plates, greater dissimilarity was noted between exposure periods than between surface orientations, except for the top surfaces of plates exposed for 6, 9, and 12 months (Group 2). Group 1 represented 3-mo plates, Group 3 represented the 12-mo plates, and Group 4 represented the 6- and 9-mo plates. Plate surfaces from the hard-bottom area showed greater similarity in faunal composition among the 6-, 9-, and 12-mo exposure periods. Top surfaces, however, were relatively dissimilar to the other surfaces submerged for the same period of time. Top surfaces from all exposure periods formed Group 5 which also contained the other 3-mo plate surfaces.

Inverse cluster analysis resulted in 10 species groups which were relatively dissimilar to each other (Figure 1.19, Table 1.8). Greatest dissimilarity was noted between Groups A-C and Groups D-J. In Group A, only the ascidian *Molgula occidentalis* and the bryozoans *Aetea truncata* and *Sundanella sibogae* covered more than 5% of any plate surface. Species in this group showed high constancy and fidelity to the 12-mo sand-bottom plates based on nodal analysis (Figure 1.19). Group B contained the

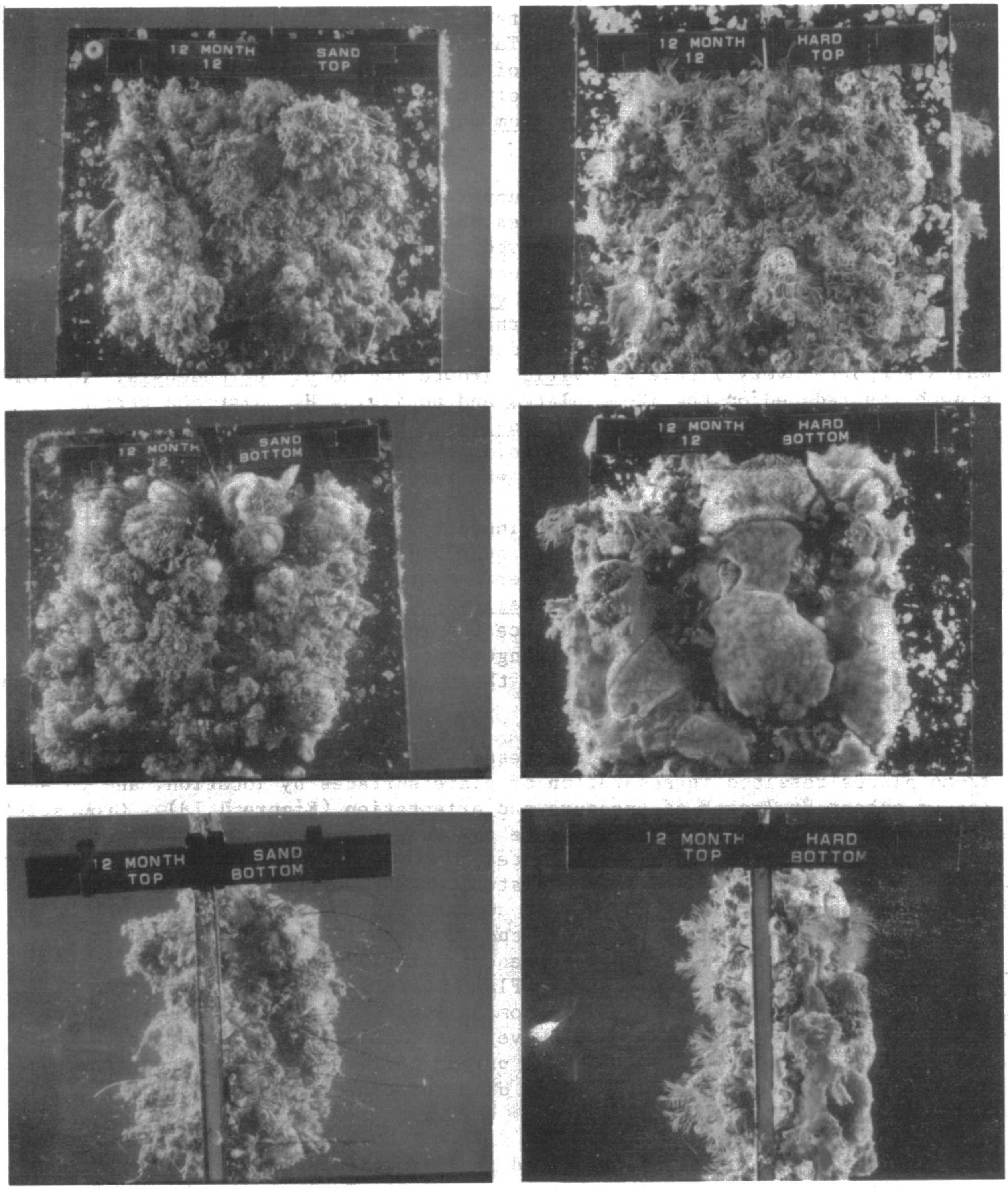


Figure 1.17 Photographs depicting sessile biota growth on the plates submerged for 12 months in the sand-bottom and hard-bottom areas. Dominant biota covering the sand-bottom plate surfaces were solitary ascideans (covered with encrusting growth), dominant biota covering the hard bottom plate surfaces were colonial ascideans. Note differences in the amount and type of grwoth between surfaces and areas.

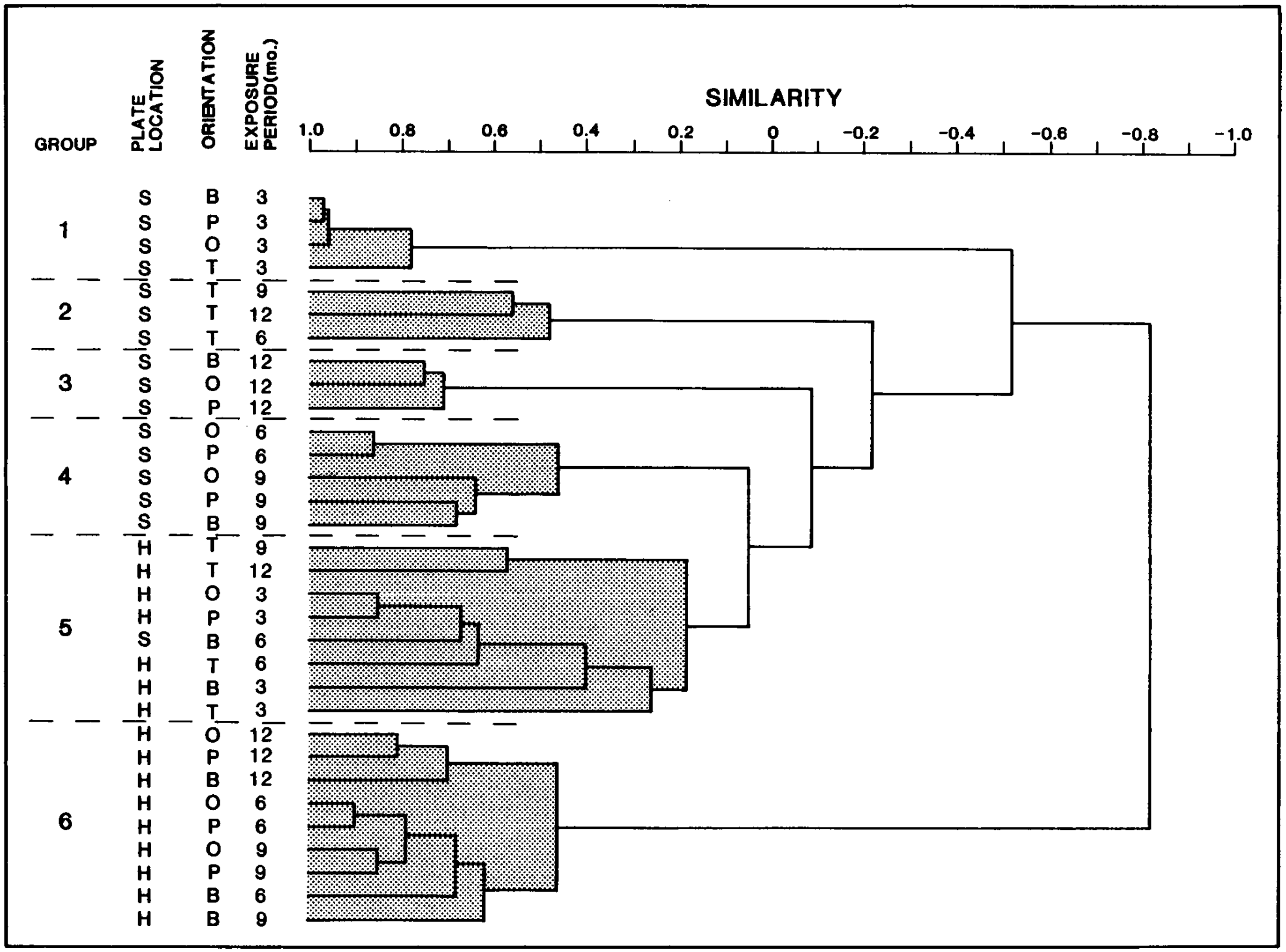


Figure 1.18 Dendrogram resulting from normal cluster analysis of percent cover estimates of sessile species attached to the plates submerged for 3, 6, 9, and 12 months. Plate locations are identified as S = Sand-bottom area and H = Hard-bottom area. Plate surface orientations are identified as T = Top, B = Bottom, P = Pinger, O = Opposite.

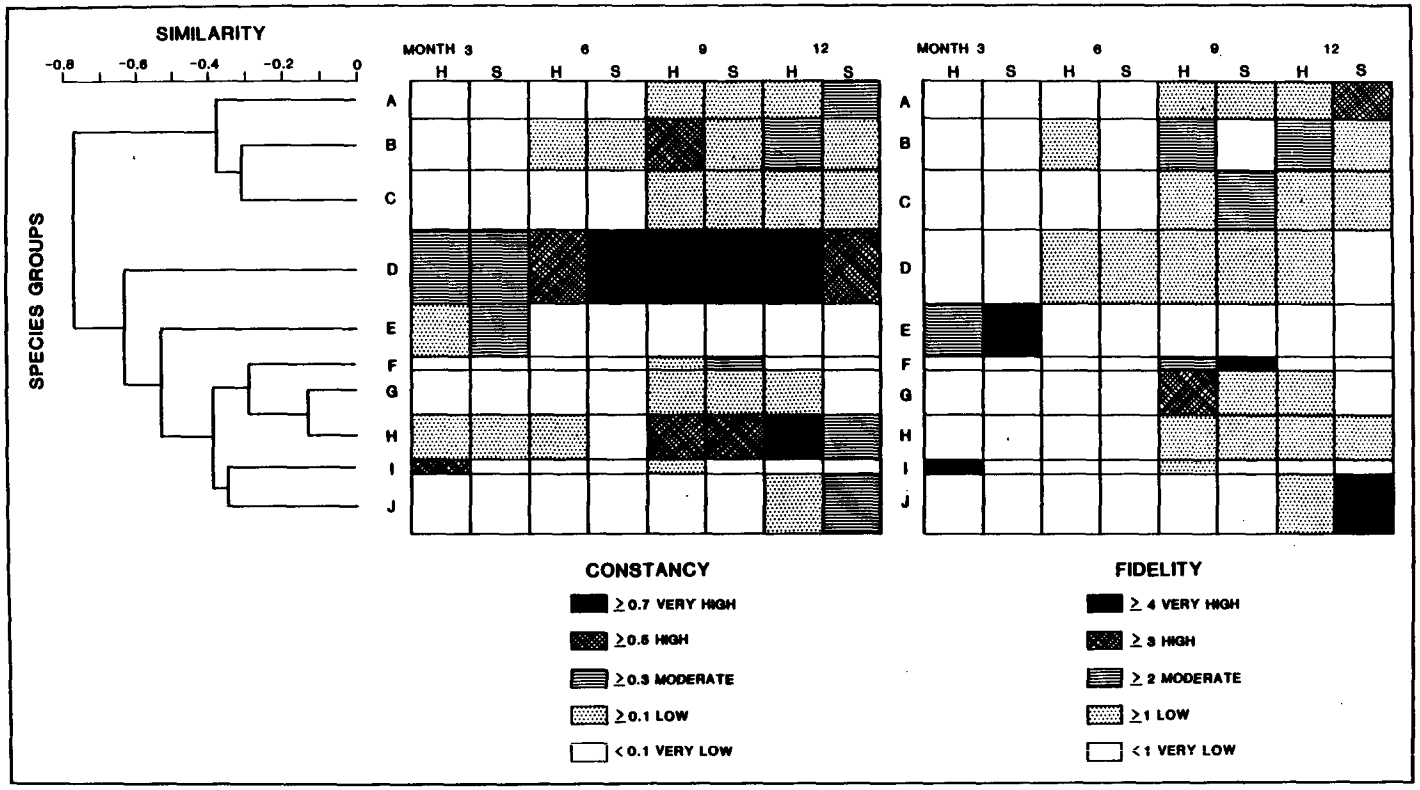


Figure 1.19 Nodal diagrams (right) showing constancy and fidelity of sessile species groups (A-J) resulting from inverse cluster analysis based on percent cover data obtained from plates submerged for 3, 6, 9, and 12 months. H = Hard-bottom area, S = Sand-bottom area.

Table 1.8 List of species groups resulting from inverse cluster analysis of taxa covering the plates submerged for 3, 6, 9, and 12 months. A = Algae, An = Anemones, As = Ascidians, Ba = Barnacles, Br = Bryozoans, H = Hydroids, M = Mollusks, P = Polychaetes, Po = Porifera.

Group A

Rhodophyta D (A)
Chone americana (P)
Molgula occidentalis (As)
Aetea truncata (Br)
Sundanella sibogae (Br)

Group B

Lomentaria baileyana (A)
Ceramiacea (A)
Halecium tenellum (H)
Monostaechas quadridens (H)
Polysiphonia denudata (A)
Champia parvula (A)
Dictyota dichotoma (A)

Group C

Dasya bailouviana (A)
Algae S
Rhodophyta E (A)
Actiniaria B (An)
Chama macerophylla (M)
Colpomenia sinuosa (A)
Spyridia hypneoides (A)
Algae U

Group D

Symplegma viride (As)
Balanus trigonus (Ba)
Styela plicata (As)
Ceramium strictum (A)
Hydractiniidae A (H)
Halocordyle disticha (H)
Balanus venustus (Ba)
Obelia dichotoma (H)
Clytia fragilis (H)
Turritopsis nutricula (H)

Group E

Tubulariidae A (H)
Pomatoceros americanus (P)
Serpulidae P (P)
Halecium sp. (H)
Algae O
Algae C

Group F

Pteria colymbus (M)
Bugula sp. A (Br)

Group G

Perophoridae A (As)
Leuconia barbata (Po)
Distaplia sp. A (As)
Turritopsis fascicularis (H)
Giffordia mitchellae (A)
Clavelina picta (As)

Group H

Scypha ciliata (Po)
Botryllus planus (As)
Distaplia bermudensis (As)
Hydroides uncinata (P)
Hydroides crucigera (P)
Hydroides sp. A (P)

Group I

Celleporaria mordax (Br)
Schizoporella cornuta (Br)

Group J

Didemnum candidum (As)
Leucosolenia botryoides (Po)
Bugula turrita (Br)
Megalomma bioculatum (P)
Actiniaria A (An)
Tubulariidae B (H)
Ascidia sp. A (As)
Turbicellepora dichotoma (Br)

hydroids *Halecium tenellum* and *Monostaechas quadridens*, and five algal species including *Champia parvula*, which occurred frequently in many plate groups (Table 1.7). Group B species showed moderate to high constancy and fidelity to 9- and 12-mo hard-bottom plates although several of the species were observed on younger plates in both the sand- and hard-bottom areas (Appendices 1.3-1.8). Of the eight species which formed Group C (Table 1.8), none of the species ever covered more than 5% of any plate surface.

The species in Group D were the dominant organisms covering the plates throughout the study (Tables 1.7, 1.8). Nodal analysis indicated that this species group was more common on the 6-, 9-, and 12-mo plates than on the 3-mo plates, but fidelity to any specific plate group was low (Figure 1.19). Species in Group E and F were relatively rare on the plates (Appendices 1.3, 1.8-1.10), and primarily restricted to the 3- and 9-mo plates respectively. Species in Groups G and H were also rarely found on the plates except for the ascidians *Distaplia* sp. A, *D. bermudensis*, and *Botryllus planus*, and the sponge *Scypha ciliata*. Both species groups were more common on the 9- and 12-mo plates (Figure 1.19). Group I contained the bryozoans *Celleporaria mordax* and *Schizoporella cornuta*, which were primarily found on the 3-mo plates from the hard-bottom area. Group J species, on the other hand, were primarily restricted to the 12-mo sand-bottom plates (Table 1.7, Figure 1.19).

In general, community development on the plates submerged during the spring appeared to be rapid, with significant changes observed in community structure over the 1-yr period. Major differences in community structure were also observed on plates from the sand-bottom versus hard-bottom areas. Initially, the dominant fouling organisms in both areas were solitary barnacles and colonial hydroids, but barnacles occupied most of the primary surface area. By the end of the 12-mo study period the percent cover of solitary species on the plates had declined in the hard-bottom area and the dominant taxa were colonial ascidians and hydroids. Many of the ascidians were competitively excluding barnacles through overgrowth. In contrast, the dominant taxa covering plates in the sand-bottom area were solitary tunicates and barnacles, and cluster analysis indicated major differences in the overall species composition on plates from the two areas.

Jackson (1977) provided evidence that colonial organisms are competitively superior to solitary forms inhabiting marine hard-substratum environments, and concluded that they can exclude solitary fauna when space is limited. Schoener (1982) and Greene and Schoener (1982), on the other hand, observed that solitary organisms eventually became dominant over colonial forms. The results of our study indicate that colonial organisms become dominant in hard-bottom areas while solitary organisms eventually dominate in sand-bottom areas. Therefore, we suggest that proximity to hard-bottom habitat (areas providing larval recruitment) has a major influence on the sessile communities developing on newly exposed hard surfaces such as oil platforms, artificial reefs, or natural rock substratum.

Sutherland (1974, 1978) also observed that both solitary and colonial organisms can dominate sessile communities. He suggested that stable points in community composition and structure are influenced by the species initially colonizing an area. Thus, seasonal differences in the species composition of early fouling assemblages on Sutherland's plates played a major role in later community development. Conversely, Mook (1981) conducted similar studies in shallow waters of Florida and concluded that differences in the early fouling assemblages had little effect on the composition of later communities. Since our study was not designed to examine the effects of seasonal recruitment on later community development, it is uncertain which of these two models of succession is operating in the South Atlantic Bight.

Community development also appeared to be influenced by plate orientation, but only with respect to the tops of horizontal plates. Those surfaces supported a large percentage of algal cover on the older plate series and overall community composition was generally more similar between sampling periods than was observed for the other plate surfaces. Evidence of greater predation was noted on the top surfaces of horizontal plates by Harris and Irons (1982) and on the top surfaces of 3-mo plates in this study, which suggests that predators may be influencing community structure on the top of older plates as well.

Sessile communities observed on the 12-mo plates probably did not represent a "climax" or stable end point in the community development. Total percent biota cover on plate surfaces approached 100% after 9 months and there were no significant differences between 9- and 12-mo plates with regard to average number of species per plate. Biomass, however, increased considerably throughout the year, and cluster analysis indicated that similarity in species composition on older (9- and 12-mo) plates was relatively low in both study areas. Dominant species on the plates also differed from those which dominated sessile communities on older artificial reefs ranging in age from 3.5 to 10 years (see section I.B). The lack of any obvious stabilization in community structure within a 1-yr period agrees with findings obtained in shallower waters of South Carolina (Van Dolah et al.,1984), where substantial shifts were observed in the structure and composition of sessile communities developing on subtidal rocks over a 4-yr period.

Finally, it is interesting to note that none of the larger sponges, octocorals, or hard corals typically found in hard-bottom areas of the South Atlantic Bight (SCWMRD,1982) were observed on the plates during the 1-yr sampling period. These species may represent later colonizers of hard substratum since at least some of the octocorals and hard corals were observed on the older artificial reefs (see section I.B.). To our knowledge, few studies have examined the colonization rates and growth of most of the sponge and coral species present in this region, but evidence from other studies in temperate waters indicates that reef corals and sponges may take several years to attain their large size (Grigg, 1974; Nicol and Reisman,1976). The apparently slow recruitment rates and slow growth rates of these organisms suggests that destruction of these communities through natural disturbance or man-induced activities may have long-term consequences.

Motile Biota:

Plates collected throughout the 12-mo period of the short-term colonization study contained 183 motile species representing 17 major invertebrate taxa (Table 1.9, Appendices 1.11-1.18). More species of polychaetes occupied the plates than any other taxon, at both the hard-bottom and sand-bottom locations. Decapod and amphipod crustaceans contributed fewer species to the overall list, as did gastropod and pelecypod mollusks. No notable difference between hard- and sand-bottom plates was apparent with respect to the relative contribution of these taxa or to the total number of species collected from each location (Table 1.9).

Plates from the two locations did differ markedly, however, with regard to the numerical abundance of the different taxa (Table 1.10). Amphipods were by far the most abundant animals on the plates, contributing greater than 90% of the 79,193 animals collected from all plates. They dominated both the hard- and sand-bottom plates, although their numerical dominance was considerably greater at the sand-bottom location, where they were more than three times as abundant as on hard bottom (Table 1.10). The difference in abundance of amphipods largely accounts for the considerable difference between locations with regard to the total number of individuals from all taxa combined (21,437 on hard-bottom plates versus 57,756 on sand-bottom plates). Polychaetes, isopods, decapods, gastropods, and pycnogonids followed amphipods in overall abundance. Each of these taxa was greatest in actual abundance and in relative abundance (percent contribution) on the hard-bottom plates. The 11 remaining taxa were represented by relatively low numbers of individuals, contributing less than 1% of the fauna on either sand- or hard-bottom plates.

Seasonal Recruitment - The numerical dominance of amphipods on the plates submerged for three months is illustrated by the fact that seven of the eight most abundant species (those contributing more than 2% of the total epifauna) were amphipods (Figure 1.20). Together, these eight species accounted for 87% of the individuals colonizing 3-mo plates, and all but one (Caprella equilibra) occurred during each season. Large seasonal variation was evident, however, in the abundance of each species (Figure 1.20).

Erichthonius brasiliensis was the most abundant species and constituted greater than 41% of the total number of organisms collected from 3-mo plates. E. brasiliensis is a common shallow-water epifaunal amphipod that constructs mud tubes attached to a variety of biotic substrates, including many sessile fouling organisms (Bousfield,1973). This species is widely distributed throughout the North Atlantic in a variety of habitats, including jetties, seagrass beds, serpulid reefs, and natural hard-bottom areas in the South Atlantic Bight and Gulf of Mexico (McKinney,1977; Wenner et al.,1983; Van Dolah et al., 1984a). Plates deployed during winter and spring were most heavily colonized by this species (Figure 1.20). During winter, recruitment was roughly equivalent on hard- and sand-bottom plates. During spring, E. brasiliensis was very abundant on sand-bottom plates but relatively scarce at the hard-bottom site.

Table 1.9 Number of species of motile invertebrates representing each of the major macroinvertebrate taxa on plates collected from the hard-bottom and sand-bottom frames.

TAXON	ALL PLATES COMBINED		HARD-BOTTOM PLATES		SAND-BOTTOM PLATES	
	Number of Species	Percent of Total	Number of Species	Percent of Total	Number of Species	Percent of Total
Polychaeta	63	34.4	44	31.4	52	35.4
Decapoda	36	19.7	32	22.9	29	19.7
Amphipoda	23	12.6	17	12.1	22	15.0
Gastropoda	19	10.4	15	10.7	13	8.8
Pelecypoda	18	9.8	11	7.9	16	10.9
Pycnogonida	7	3.8	6	4.3	5	3.4
Echinodermata	4	2.2	3	2.1	2	1.4
Isopoda	3	1.6	3	2.1	2	1.4
Sipuncula	2	1.1	2	1.4	1	0.7
Nematoda	1	0.5	1	0.7	1	0.7
Tanaidacea	1	0.5	1	0.7	1	0.7
Turbellaria	1	0.5	1	0.7	1	0.7
Nemertinea	1	0.5	1	0.7	1	0.7
Oligochaeta	1	0.5	1	0.7	-	-
Stomatopoda	1	0.5	1	0.7	-	-
Mysidacea	1	0.5	1	0.7	-	-
Ostracoda	1	0.5	-	-	1	0.7
Total Species	183		140		147	

Table 1.10 Number of individual motile invertebrates representing each of the major macroinvertebrate taxa on plates collected from the hard-bottom and sand-bottom frames.

TAXON	ALL PLATES COMBINED		HARD-BOTTOM PLATES		SAND-BOTTOM PLATES	
	Number of Individuals	Percent of Total	Number of Individuals	Percent of Total	Number of Individuals	Percent of Total
Amphipoda	71400	90.2	16688	77.8	54712	94.7
Polychaeta	2054	2.6	1164	5.4	890	1.5
Isopoda	1634	2.1	1395	6.5	239	0.4
Decapoda	1042	1.3	774	3.6	268	0.5
Gastropoda	786	1.0	460	2.1	326	0.6
Pycnogonida	723	0.9	541	2.5	182	0.3
Nematoda	572	0.7	114	0.5	458	0.8
Turbellaria	471	0.6	159	0.7	312	0.5
Nemertinea	267	0.3	56	0.3	211	0.4
Pelecypoda	184	0.2	67	0.3	117	0.2
Tanaidacea	23	<0.1	5	<0.1	18	<0.1
Sipuncula	18	<0.1	5	<0.1	13	<0.1
Echinodermata	14	<0.1	5	<0.1	9	<0.1
Oligochaeta	2	<0.1	2	<0.1	-	-
Stomatopoda	1	<0.1	1	<0.1	-	-
Mysidacea	1	<0.1	1	<0.1	-	-
Ostracoda	1	<0.1	-	-	1	<0.1
Total Number	79,193		21,437		57,756	

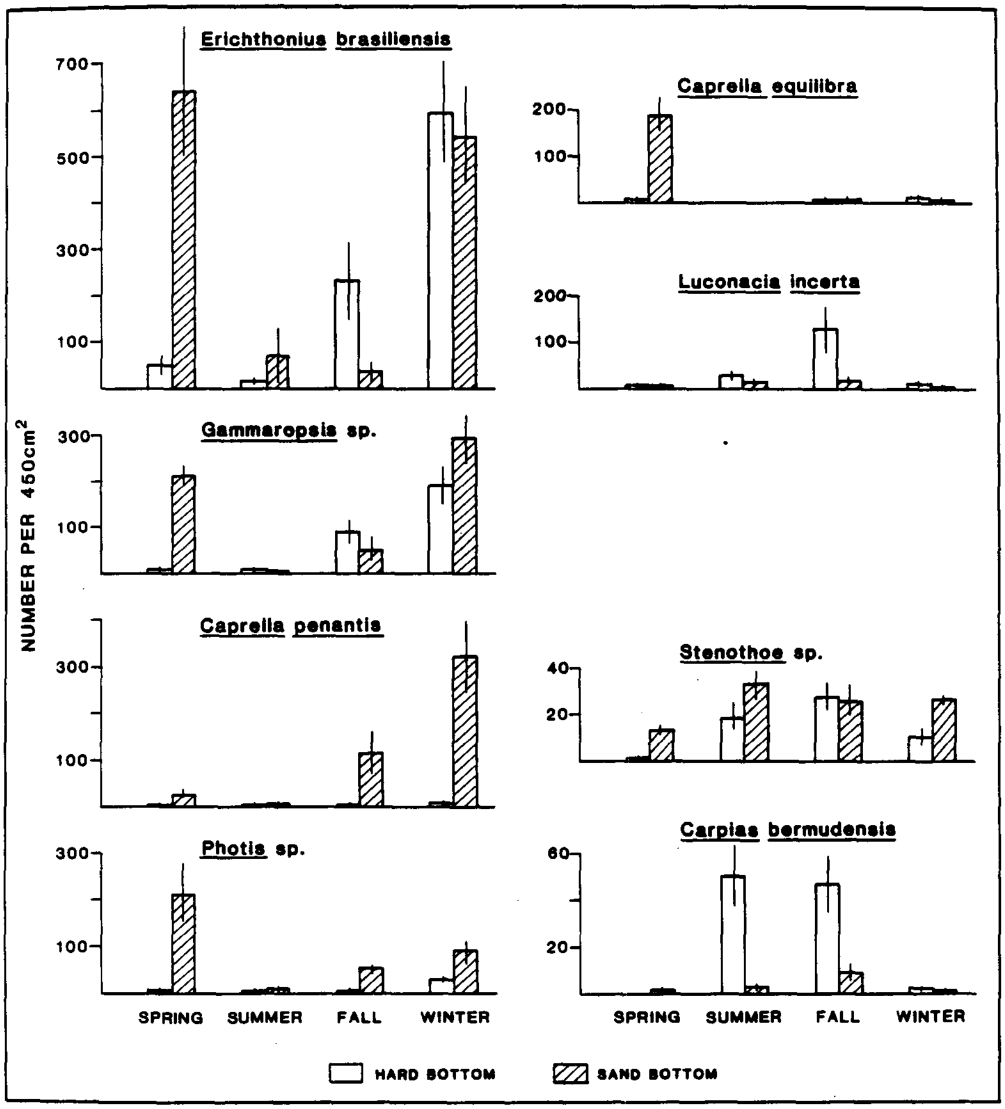


Figure 1.20 Mean density for each of the dominant motile species on 3-mo recruitment plates that were submerged during different seasons. Vertical lines represent the standard error of the means (n = 6). (Note scale difference among histograms).

The amphipod Gammaropsis sp. exhibited a seasonal pattern of occurrence parallel to that of E. brasiliensis, although it was generally far less abundant (Figure 1.20), accounting for 16% of the total number of individuals. Three other species of lesser abundance were prevalent on sand-bottom plates during either winter or spring. Caprella penantis reached peak densities during winter, while Photis sp. and Caprella equilibra densities peaked during spring (Figure 1.20). Stenothoe sp. was found in relatively low densities on plates exposed during all seasons, and was frequently more abundant on those exposed over sand bottom than over hard bottom. The caprellid amphipod Luconacia incerta and the isopod Carpias bermudensis differed in two respects from other dominant species. Both were recruited most intensively during the summer and fall, and both were considerably more abundant on plates over hard bottom than on those over sand (Figure 1.20).

The abundance of motile organisms on 3-mo plates varied significantly among seasons, and was lowest during summer and highest during winter. Faunal abundance was intermediate during spring and fall, and did not differ significantly between the two seasons (Figure 1.21, Table 1.11, Appendix 1.11).

Plates on sand bottom supported significantly more organisms than those on hard bottom, although a highly significant interaction was noted between the season and frame location, indicating that these factors were not independent (Table 1.11). Densities on the sand-bottom frame were lower than on hard bottom during summer and fall, but during winter and spring faunal abundance was much greater at the sand-bottom site. Over hard bottom, the density of motile epifauna increased regularly from spring through winter. The sand-bottom plates, on the other hand, underwent intense recruitment during spring, followed by a rapid decline during summer months and an increase during fall and winter similar to that observed on hard-bottom plates (Figure 1.21). A greater number of motile animals colonized horizontal plates than vertical ones, although this difference was less significant than those observed between locations and among seasons (Table 1.11).

Vertical and horizontal surfaces were colonized by roughly equivalent numbers of species (Figure 1.22a), and the difference between orientations was not statistically significant (Table 1.11). Sand-bottom plates were inhabited by a slightly greater number of species than those from hard bottom, but seasonal variations were more highly significant among the former (Figure 1.22a, Table 1.11). Fewer species were collected from the plates submerged during spring than from those exposed during other seaons, while the greatest number of species was observed on plates exposed during summer. Thus, more species colonized plates during the period when fewer numbers of individuals were recruited.

The patterns described above for mean numbers of species were parallel to those observed among total number of species in pooled replicate samples (Figure 1.22a, b); i.e., the lowest number of species was recruited onto vertical hard-bottom plates during the spring, while the richest collection was obtained during the summer on horizontal plates at the same location.

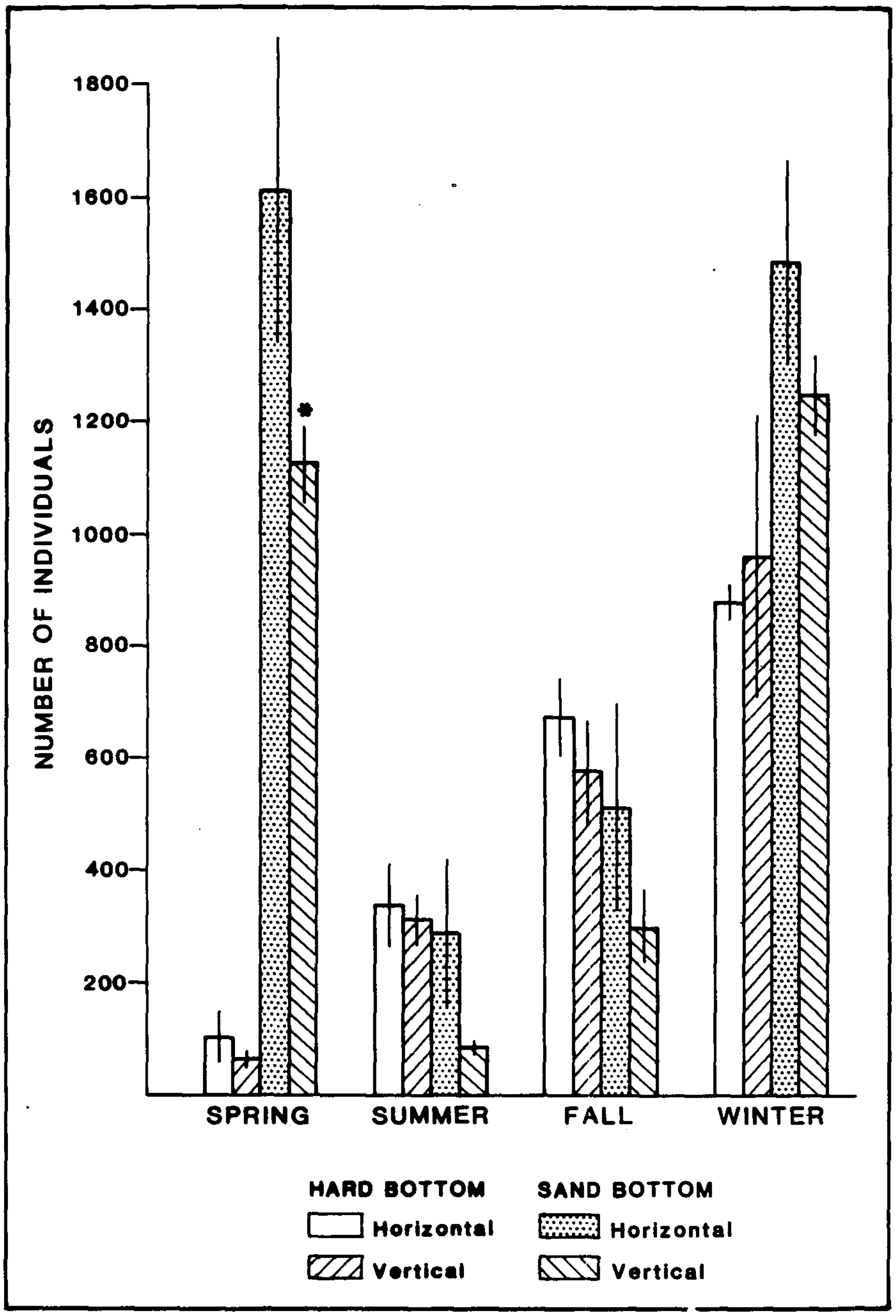


Figure 1.21 Mean abundance of motile epifauna on 3-mo recruitment plates that were submerged during different seasons. Vertical lines represent the standard error of the means (n = 3, except at * n = 2).

Table 1.11 Results of two three-way analyses of variance (Model I) comparing the number of motile invertebrate species and individuals on horizontal and vertical plates exposed for three months during different seasons at the two frame locations.

SOURCE OF VARIATION	Degrees of Freedom	F Value	Results of *a posteriori* comparisons
	DEPENDENT VARIABLE: $\log_{10}$(No. spp./plate)		
Model ($r^2 = 0.71$)	14	5.36***	
Factor A: Platform Location (Sand Bottom, Hard Bottom)	1	5.62*	$\underline{\mu_{HB}\ \mu_{SB}}^{1}$
Factor B: Season of Exposure (SPring, SUmmer, FAll, WInter)	3	16.20***	$\underline{\mu_{SP}} < \underline{\mu_{WI}\ \mu_{FA}\ \mu_{SU}}^{1}$
Factor C: Surface Orientation (Horizontal, Vertical)	1	$1.11^{N.S.}$	
Interaction Effects			
A x B	3	4.08*	
A x C	1	$0.01^{N.S.}$	
B x C	3	$0.17^{N.S.}$	
A x B x C	2	$0.05^{N.S.}$	
	DEPENDENT VARIABLE: $\log_{10}$(No. indiv./plate)		
Model ($r^2 = 0.89$)	15	17.46***	
Factor A: Platform Location (Sand Bottom, Hard Bottom)	1	14.99***	$\underline{\mu_{HB}} < \underline{\mu_{SB}}^{2}$
Factor B: Season of Exposure (SPring, SUmmer, FAll, WInter)	3	32.53***	$\underline{\mu_{SU}} < \underline{\mu_{FA}\ \mu_{SP}} < \underline{\mu_{WI}}^{2}$
Factor C: Surface Orientation (Horizontal, Vertical)	1	6.30*	$\underline{\mu_{V}} < \underline{\mu_{H}}^{2}$
Interaction Effects			
A x B	3	45.91***	
A x C	1	$1.92^{N.S.}$	
B x C	3	$0.51^{N.S.}$	
A x B x C	3	$0.63^{N.S.}$	

N.S. not significant
* significant at 0.05 level
** significant at 0.01 level
*** significant at 0.001 level

[1] Tukey's studentized range test; means connected by underlines are not significantly different at $\alpha = 0.05$.

[2] Ryan-Einot-Gabriel-Welsch multiple F test; means connected by underlines are not significantly different at $\alpha = 0.05$.

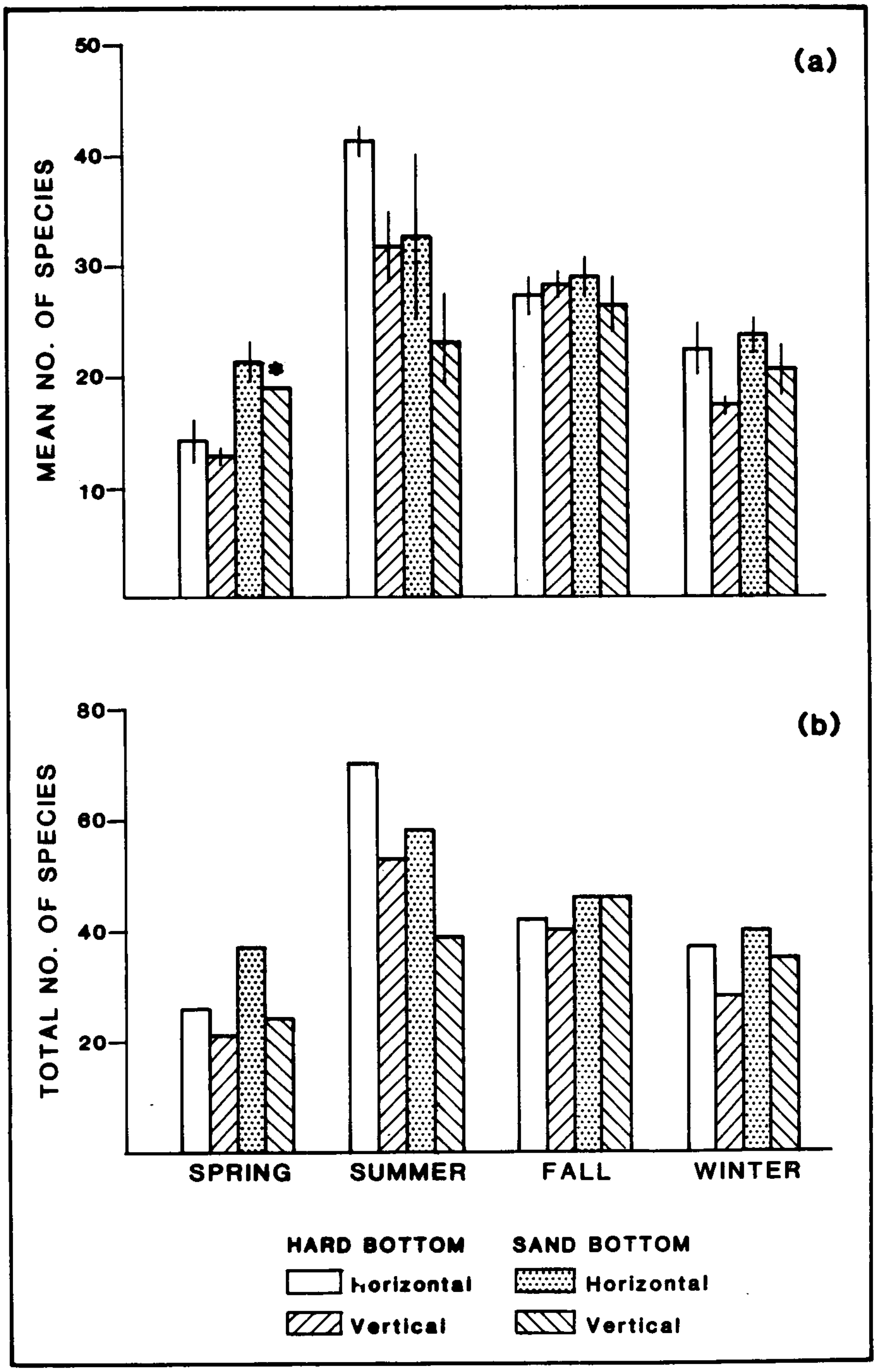


Figure 1.22 Mean number of motile species per plate (a) and total number of species on replicate plates (b) that were submerged during different seasons. Vertical lines represent the standard error of the means (n = 3, except at * n = 1).

Species diversity (H') of pooled samples showed patterns similar to those described for the number of species in each treatment group (Figure 1.23). Highest diversity was observed in the community recruited during summer, mainly as a result of greater species richness and more equitable distribution of individuals among species (Figure 1.23). Plates exposed during fall were slightly less diverse, and those collected in winter and spring exhibited even lower diversity (Figure 1.23a). The motile fauna recruited during the latter two seasons was lower in both richness and evenness, compared with summer and fall communities (Figure 1.23b, c). The lower J' values during winter and spring reflect the numerical dominance of a few species of amphipods (*E. brasiliensis*, *Gammaropsis* sp., *C. penantis*, *Photis* sp., and *C. equilibra*) (Figure 1.20).

Station groups formed using normal cluster analysis further emphasized the similarity between plates exposed during winter and spring compared with those submerged during summer and fall (Figure 1.24). Groups 1 through 4 consisted exclusively of winter and spring collections, and were highly dissimilar to the summer and fall collections of Groups 5 through 8.

Sand- and hard-bottom collections from winter (Groups 2 and 3) were most similar to the sand-bottom spring samples (Group 1) (Figure 1.24). The plates in these groups were all characterized by intensive recruitment, unlike spring hard-bottom samples (Group 4), which showed the lowest amount of recruitment of all seasons (Figure 1.21). In spite of this difference in the intensity of recruitment, the latter group was still more similar to other winter and spring collections than to those from summer and fall (Figure 1.24). Similarity was greatest among samples collected at a specific location (i.e., hard- or sand-bottom) during both summer and fall, although samples collected during the two seasons were somewhat dissimilar.

The discrete groups formed by the normal cluster dendrogram indicate distinct differences in the distribution, abundance, and composition of the motile epifauna inhabiting plates at the two locations during different seasons. The orientation of plates appeared to have the least effect on recruitment, since horizontal and vertical plates showed no consistent separation within groups formed by analysis (Figure 1.24). This is consistent with the results of the analyses of variance, which were based strictly on overall faunal abundance and richness, rather than species composition and abundance. These analyses also showed that the proximity of the plates to natural hard bottom and the season of their exposure significantly influenced recruitment, but orientation of the plates was less important (Table 1.11).

The 82 species subjected to inverse cluster analysis formed 12 groups (Table 1.12) based on their abundance and distribution among the various series of plates (Figure 1.25). Many of the numerically dominant organisms were included in Groups A and B (Table 1.12, Figure 1.20), and species from these two groups comprised greater than 91% of the total number of organisms collected from 3-mo plates. These species were mainly amphipods that were highly constant in all seasons, and consequently, showed low fidelity among all seasons (Figure 1.25). Group A included all 10 of the most abundant species except *C. equilibra*, which was included in Group B,

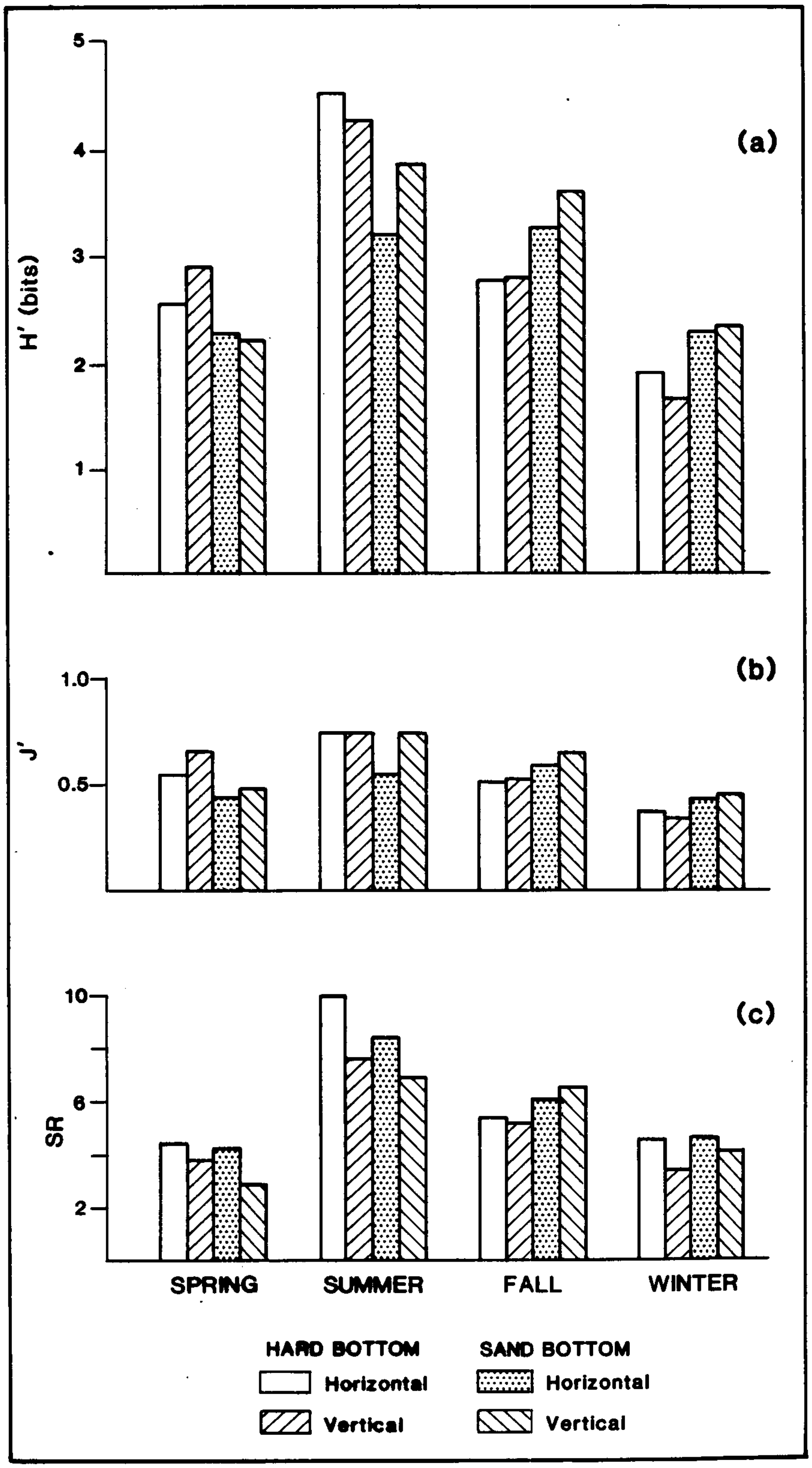


Figure 1.23 Values of (a) diversity, H'; (b) evenness, J'; and (c) species richness, SR of motile epifauna in pooled samples from 3-mo recruitment plates that were submerged during different seasons.

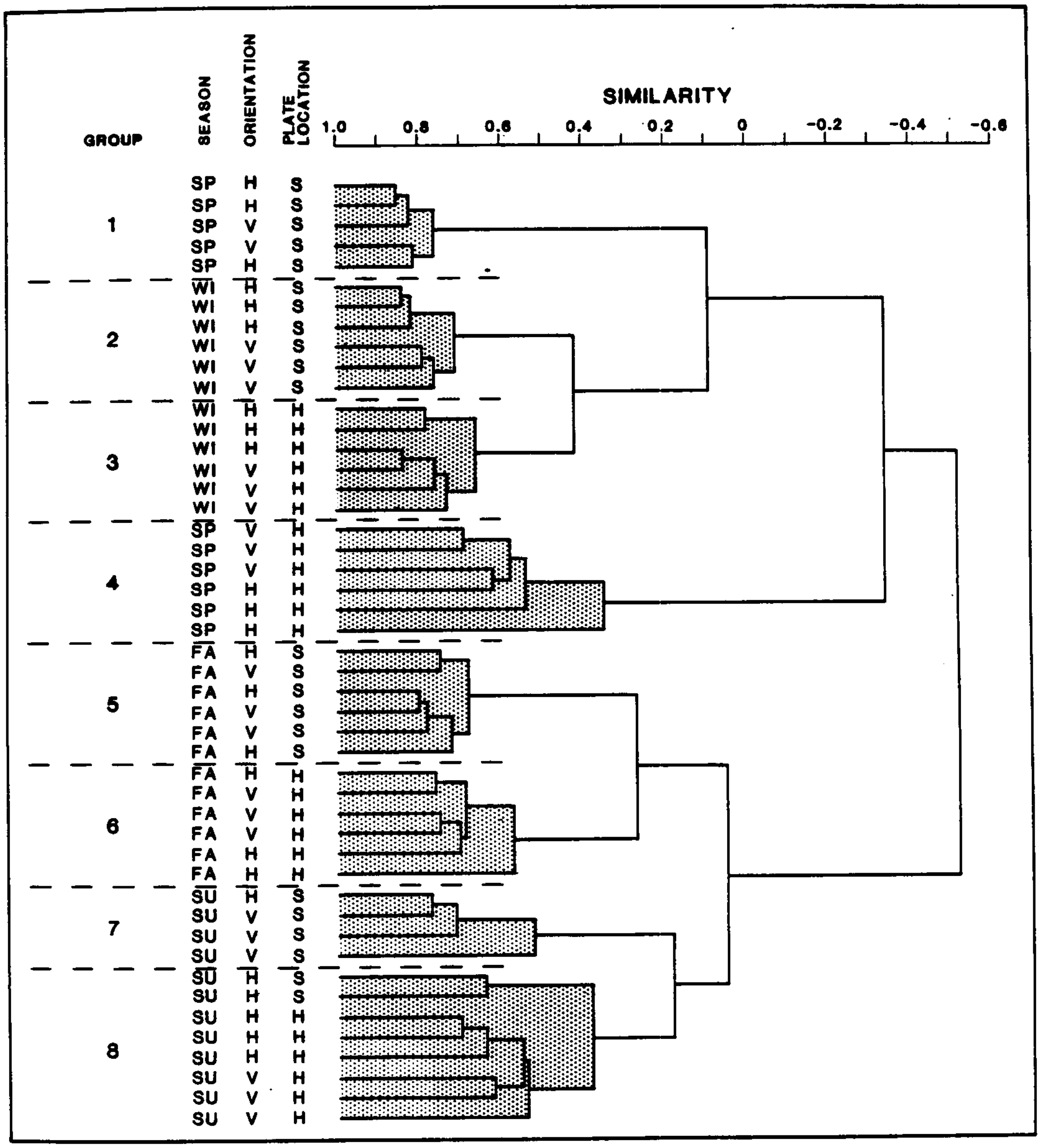


Figure 1.24 Dendrogram resulting from normal cluster analysis of motile species abundance on 3-mo recruitment plates that were submerged during spring (SP), summer (SU), fall (FA), and winter (WI). Plate orientation (H = horizontal, V = vertical) and location (S = sand bottom, H = hard bottom) are indicated.

Table 1.12 Species groups resulting from inverse cluster analysis of motile species on 3-mo recruitment plates. (A = Amphipoda; D = Decapoda; E = Echinodermata; I = Isopoda; M = Mollusca; P = Polychaeta; Py = Pycnogonida; T = Tanaidacea).

Group A

Gammaropsis sp. (Am)
Erichthonius brasiliensis (Am)
Photis sp. (Am)
Caprella penantis (Am)
Astyris lunata (M)
Elasmopus sp. A (Am)
Luconacia incerta (Am)
Stenothoe sp. (Am)
Carpias bermudensis (I)

Group B

Caprella equilibra (Am)
Nemertinea
Turbellaria

Group C

Asteroidea undet. (E)
Crepidula sp. (M)
Phyllodoce sp. (P)
Mactridae A (M)
Eulalia sanguinea (P)
Harmothoe sp. A (P)
Caprella sp. (Am)

Group D

Anoplodactylus sp. (Py)
Nudibranchia A (M)
Periclimenes iridescens (D)
Periclimenes longicaudatus (D)
Doto sp. A (M)
Armandia maculata (P)
Nereis lamellosa (P)
Nereis sp. (P)
Anoplodactylus petiolatus (Py)
Pilumnus sp. A (D)
Nematoda
Achelia sawayai (Py)

Group E

Websterinereis tridentata (P)
Pista palmata (P)
Pilumnus floridanus (D)
Syllis hyalina (P)
Costoanachis sp. A (M)
Podarke obscura (P)
Pelecypoda undet. (M)

Group F

Polycirrus carolinensis (P)
Polydora sp. (P)
Synalpheus townsendi (D)
Ceratonereis mirabilis (P)
Lima sp. (M)
Pilumnus sayi (D)
Laevicardium sp. (M)
Hiatella arctica (M)

Group G

Corophiidae (Am)
Pelia mutica (D)
Hesionidae (P)
Amphipoda undet.
Majidae A (D)
Cerithium sp. B (M)

Group H

Polydora caeca (P)
Amphipoda E
Pseudomedaeus agassizii (D)
Tanystylum calicirostre (Py)
Exogone dispar (P)

Group I

Pycnogonida undet.
Nudibranchia undet. (M)
Nudibranchia C (M)

Group J

Melita appendiculata (Am)
Phyllodocidae (P)
Caprellidae (Am)
Lembos smithi (Am)
Podocerus sp. (Am)
Malacoceros glutaeus (P)
Nereis succinea (P)
Eulalia macroceros (P)
Proceraea sp. (P)
Autolytus sp. (P)
Endeis spinosa (Py)
Ampithoe sp. A (Am)

Group K

Musculus lateralis (M)
Crepidula fornicata (M)
Chione grus (M)
Pilumnus sp. B (D)

Group L

Leptochelia sp. (T)
Pectinidae (M)
Xanthidae D (D)
Phyllodoce fragilis (P)
Pilumnus sp. (D)

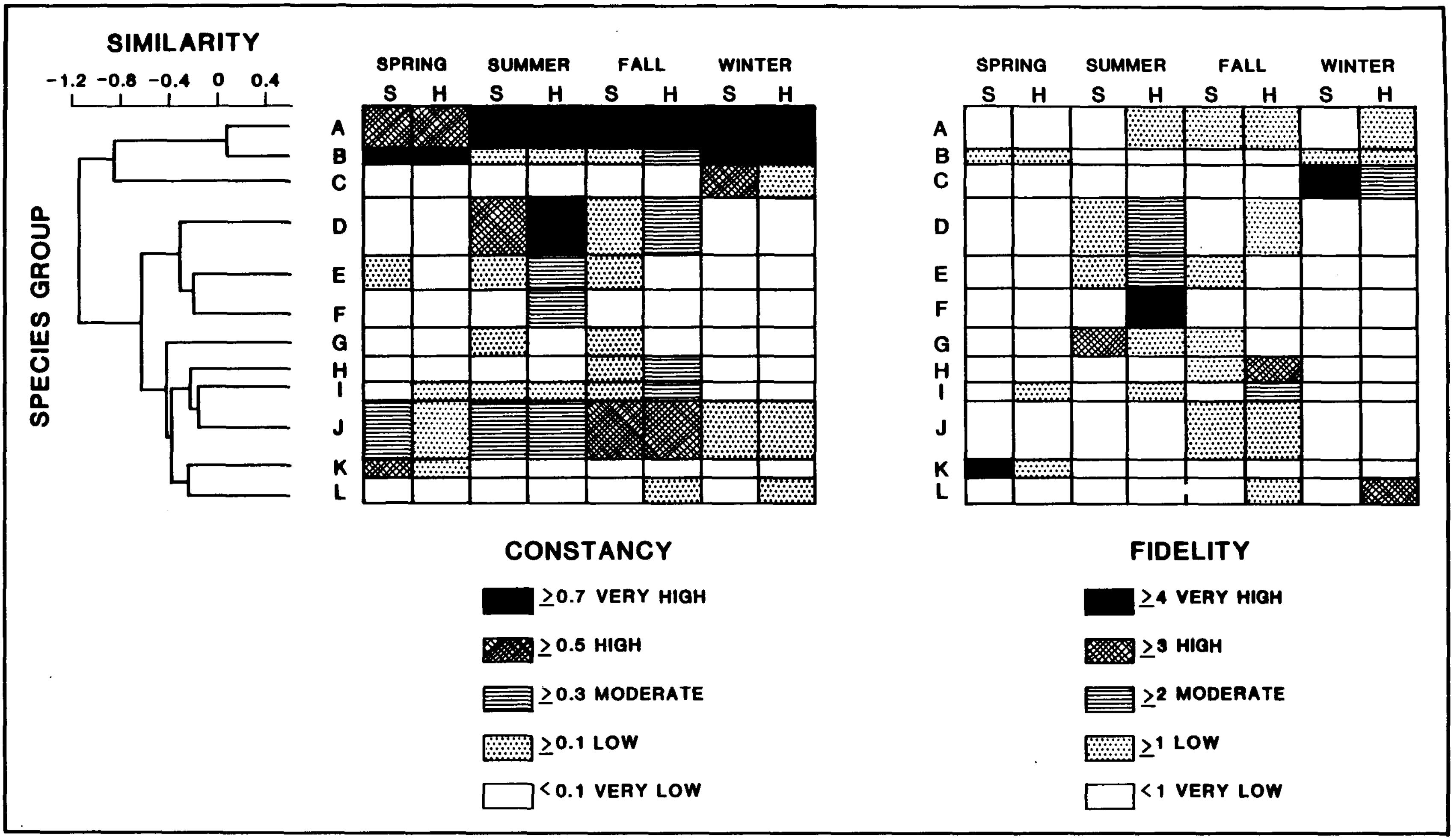


Figure 1.25 Inverse classification hierarchy of motile species, and nodal diagrams showing constancy and fidelity of species groups to 3-mo plates that were submerged during different seasons over sand bottom (S) or hard bottom (H).

a small group that had high constancy during winter and spring, but which was not restricted to any particular season or location.

Species in Group C were recruited primarily during winter, and four of the seven (Harmothoe sp. A, Crepidula sp., Mactridae A, and an undetermined asteroid) colonized plates only during that season. These species were most frequently collected from sand-bottom plates, and showed high fidelity to that location (Figure 1.25).

The remaining species groups (D through L) were quite dissimilar to those described above, and the recruitment of all species in these groups was restricted seasonally, to some degree, (Figure 1.25). Species Groups D through F had greatest constancy on summer plates, especially those over hard bottom. Group D was made up of species that were fairly abundant and which also showed moderate constancy on fall plates from hard bottom. All three of these groups were moderately to very highly restricted to the summer hard-bottom plates. The recruitment of Group G species was also highly restricted to the summer season, but these species occurred primarily on sand-bottom plates, rather than on those from hard bottom.

Groups H, I and J included species that were most constant and faithful to plates exposed during fall (Figure 1.25). The first two groups were somewhat restricted to hard bottom during that season, and two species (Tanystylum calcirostre and Nudibranchia C) were recruited only onto hard-bottom plates. Group J species were more abundant than those of Groups H and I, and were also moderately constant during spring and summer.

Among the species comprising Groups K and L were several whose recruitment was highly restricted to either sand- or hard-bottom plates during a single season (Figure 1.25). In Group K, Musculus lateralis, Crepidula fornicata, and Pilumnus sp. B were found only during spring, with the first two of these colonizing sand-bottom plates exclusively. Group L species were highly faithful to winter plates, and three of them (Phyllodoce fragilis, Xanthidae D, and Pectinidae) colonized only hard-bottom plates.

Community Development - Amphipods remained numerically dominant on plates throughout the 12-mo study period. Of the seven species of motile organisms that were particularly abundant on the 3-, 6-, 9-, and 12-mo plate series, i.e., contributed greater than 2% of the individuals, all were amphipods (Figure 1.26), and together they constituted more than 86% of the total number of individuals.

Three months after submergence, the plates were numerically dominated by Erichthonius brasiliensis, Gammaropsis sp., Photis sp., and Caprella equilibra, in that order. On 6-mo plates E. brasiliensis was still most numerous, followed by Stenothoe sp., Gammaropsis sp., and Elasmopus sp. A. This last species was initially observed on 6-mo plates, and unlike the other dominant species, it was nearly as abundant on hard-bottom as on sand-bottom plates. After nine months of exposure, E. brasiliensis had declined in abundance, and two species, Caprella penantis and Elasmopus sp. A, were more numerous, the latter of which was dominant on hard-bottom

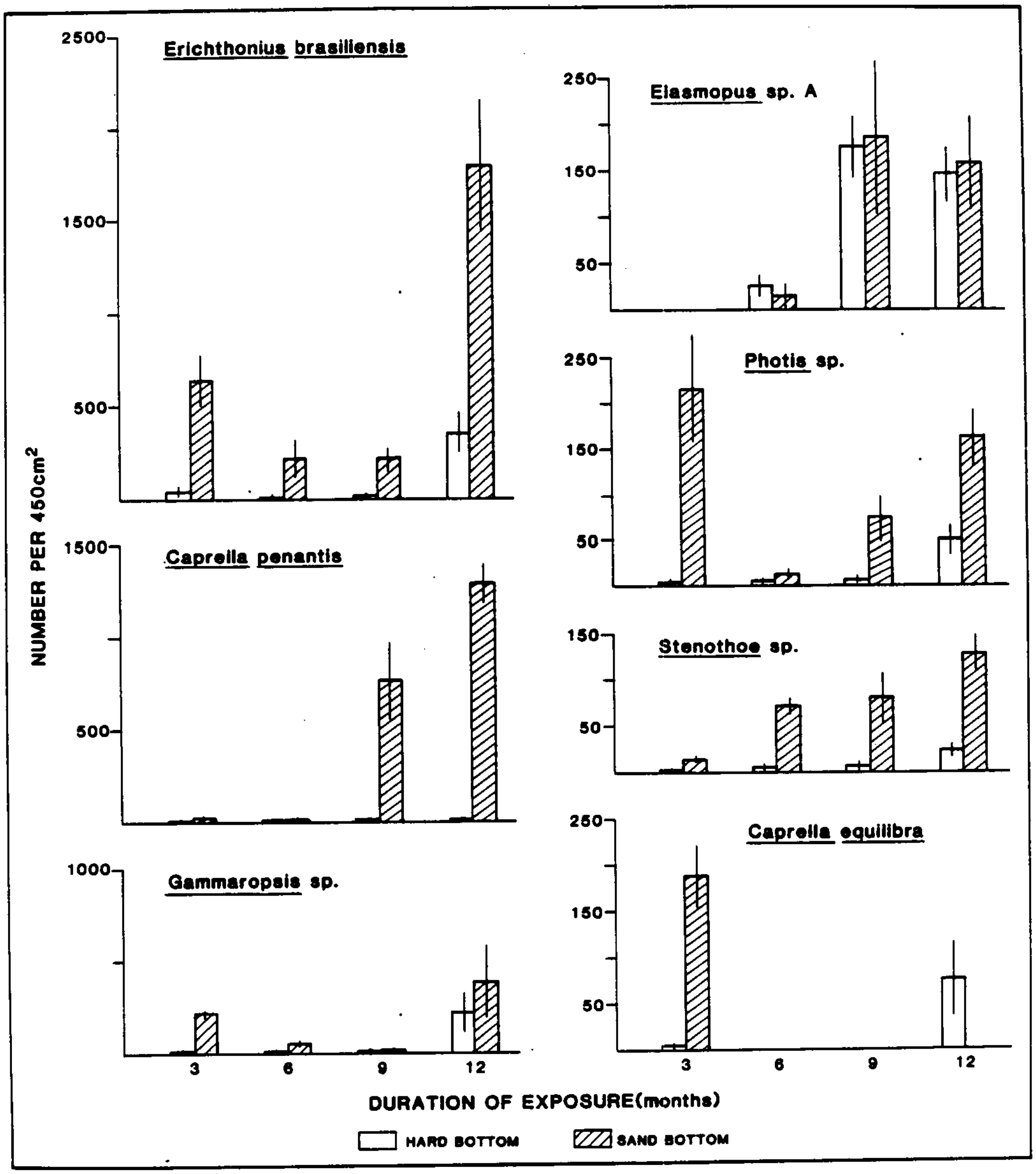


Figure 1.26 Mean density for each of the dominant motile species on plates that were submerged for 3, 6, 9, or 12 months. Vertical lines represent the standard error of the means (n = 6). (Note difference in scale of histograms).

plates. One year following initial exposure *E. brasiliensis* was once again the dominant species, with *C. penantis* ranking second in abundance.

Although most of the dominant species occurred throughout the year (note the exception above of *Elasmopus* sp. A and that of *C. equilibra,* which was absent from 6- and 9-mo plates), many exhibited patterns of abundance that were similar to those observed on 3-mo plates harvested during equivalent seasons (Figures 1.20, 1.26). Four species that showed winter and spring peaks on 3-mo plates (*E. brasiliensis,* *Gammaropsis* sp., *Photis* sp., and *C. equilibra*) also reached greatest densities during these same seasons on the plates exposed for longer periods. Similarly, *Caprella penantis* and *Elasmopus* sp. A were most abundant on 9- and 12-mo plates, coinciding with their periods of greatest seasonal recruitment. *Stenothoe* sp. increased in abundance throughout the year and was also recruited continously throughout the year onto 3-mo plates.

One consequence of the considerable variation in abundance among individual species was the pronounced fluctuation in overall density of the motile epifauna as the duration of exposure increased (Figure 1.27). The number of individuals on hard-bottom plates rose steadily throughout the 12-mo study period, while sand-bottom plates initially showed high abundance followed by a decline and subsequent rise in faunal density. This increase in density from 6 to 12 months was highly significant (Table 1.13), and paralleled the pattern of total abundance noted on 3-mo plates (Figures 1.21, 1.27). A similar parallel was noted between the two series of plates, with respect to the greater number of individuals collected from plates on sand bottom (Tables 1.11, 1.13).

Although the overall density was higher on the 6-, 9-, and 12-mo plates than on the 3-mo recruitment series (1170 versus 661 individuals per plate), some differences were noted between hard- and sand-bottom plates in this respect. For example, 6- and 9-mo hard-bottom plates supported fewer motile organisms than the 3-mo plates collected at the same time, while densities were roughly equivalent for the 12-mo and 3-mo winter plates. On sand bottom, however, 3-mo plates were always less densely occupied than the equivalent plates from the longer-duration series, and the difference was occasionally considerable, as in the case of samples taken in winter (Figures 1.21, 1.27).

The mean number of species and the total number from pooled samples were considerably lower after three months of exposure than after longer durations (Figure 1.28, Table 1.13). More species were collected from 9-mo plates than from the others, probably due to the seasonally restricted occurrence of many of the less abundant species (Appendices 1.11, 1.15-1.17). Neither the orientation of the plates nor their proximity to hard bottom significantly influenced the number of species that occupied them (Table 1.13).

Species diversity varied among the samples collected following different durations of exposure, and largely reflected the trends described in overall density and richness of the epifaunal community (Figures 1.27-1.29). Diversity (H') was generally highest in the summer following

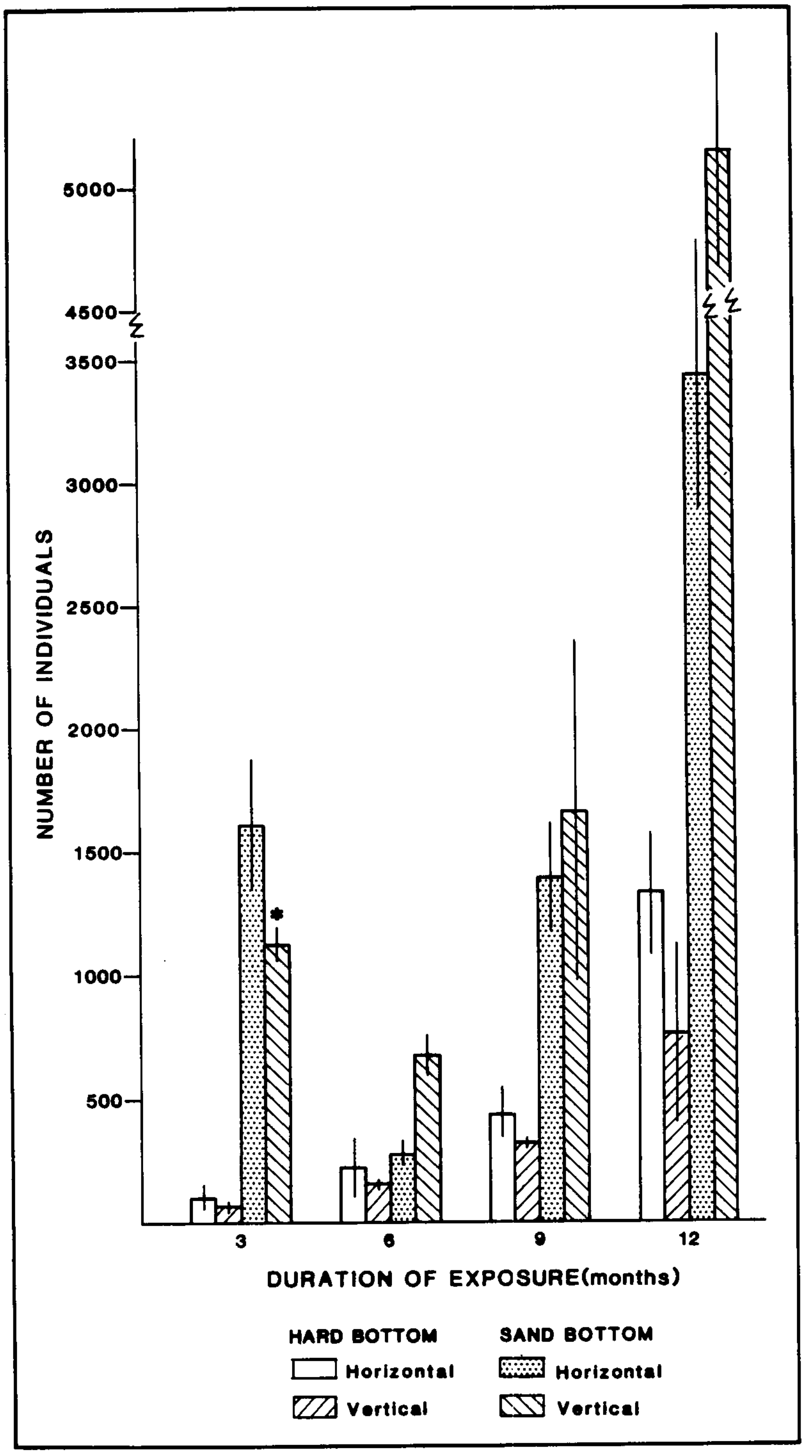


Figure 1.27 Mean abundance of motile epifauna on plates that were submerged for 3, 6, 9, or 12 months. Vertical lines represent the standard error of the means (n = 3, except at * n = 2).

Table 1.13 Results of two three-way analyses of variance (Model I) comparing the number of motile invertebrate species and individuals on horizontal and vertical plates exposed for 3, 6, 9, and 12 months at the two frame locations.

SOURCE OF VARIATION	Degrees of Freedom	F Value	Results of *a posteriori* comparisons
	DEPENDENT VARIABLE: $\log_{10}$(No. spp./plate)		
Model ($r^2 = 0.67$)	14	4.44***	
Factor A: Platform Location (Sand Bottom, Hard Bottom)	1	$3.12^{\mathrm{N.S.}}$	
Factor B: Duration of Exposure (3, 6, 9, 12 months)	3	14.15***	$\underline{\mu_3} < \underline{\mu_6 \quad \mu_{12} \quad \mu_9}$[1]
Factor C: Surface Orientation (Horizontal, Vertical)	1	$0.60^{\mathrm{N.S.}}$	
Interaction Effects			
A x B	3	$2.70^{\mathrm{N.S.}}$	
A x C	1	$0.05^{\mathrm{N.S.}}$	
B x C	3	$0.39^{\mathrm{N.S.}}$	
A x B x C	2	$0.21^{\mathrm{N.S.}}$	
	DEPENDENT VARIABLE: $\log_{10}$(No. indiv./plate)		
Model ($r^2 = 0.80$)	15	8.58***	
Factor A: Platform Location (Sand Bottom, Hard Bottom)	1	60.03***	$\underline{\mu_{HB}} < \underline{\mu_{SB}}$[2]
Factor B: Duration of Exposure (3,6,9,12 months)	3	18.13***	$\underline{\mu_6 \quad \mu_3} < \underline{\mu_9} < \underline{\mu_{12}}$[2]
Factor C: Surface Orientation (Horizontal, Vertical)	1	$0.01^{\mathrm{N.S.}}$	
Interaction Effects			
A x B	3	$2.81^{\mathrm{N.S.}}$	
A x C	1	$0.64^{\mathrm{N.S.}}$	
B x C	3	$1.36^{\mathrm{N.S.}}$	
A x B x C	3	$0.36^{\mathrm{N.S.}}$	

N.S. not significant
* significant at 0.05 level
** significant at 0.01 level
*** significant at 0.001 level

[1] Tukey's studentized range test; means connected by underlines are not significantly different at $\alpha = 0.05$.

[2] Ryan-Einot-Gabriel-Welsch multiple F test; means connected by underlines are not significantly different at $\alpha = 0.05$.

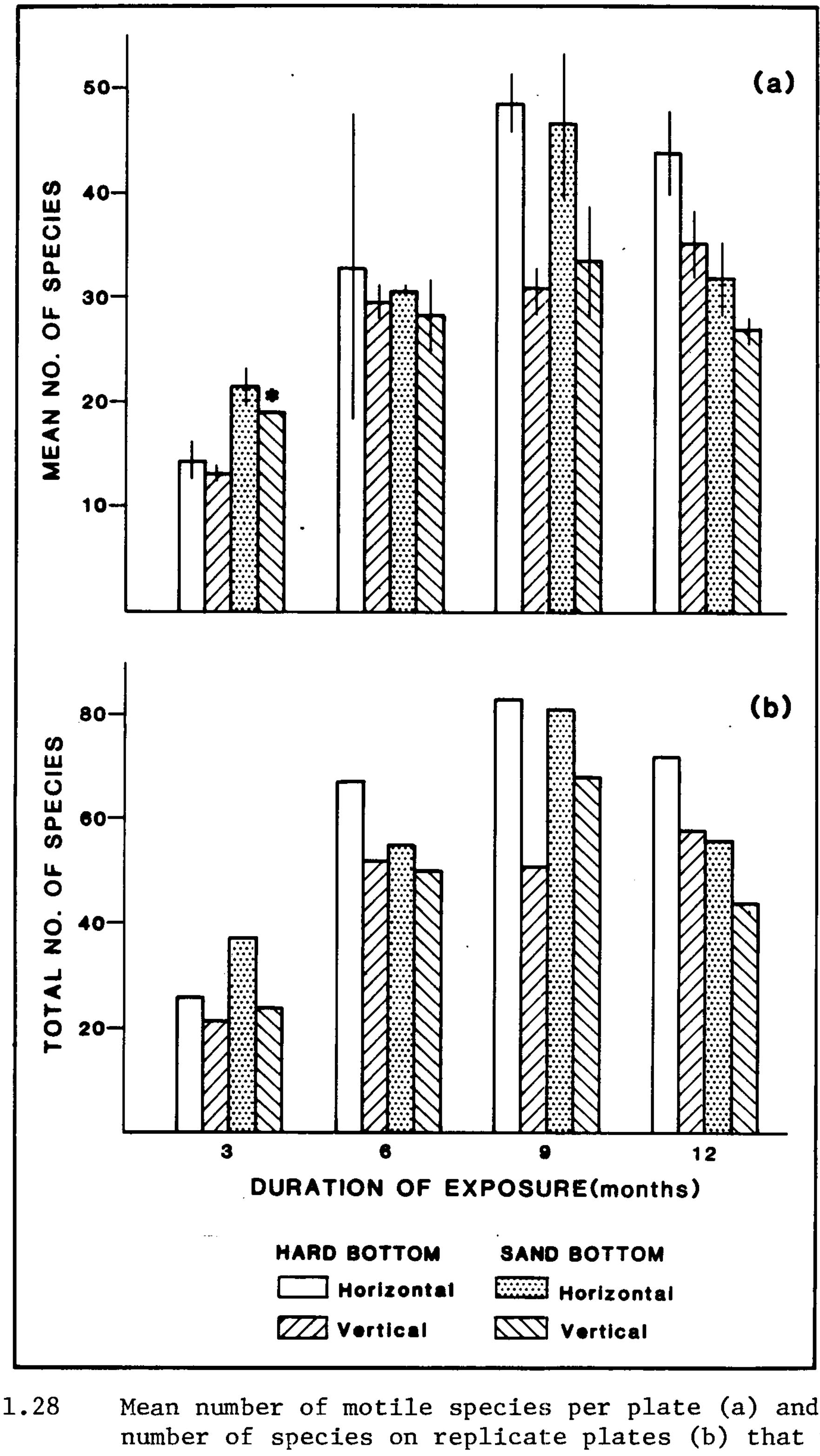


Figure 1.28 Mean number of motile species per plate (a) and total number of species on replicate plates (b) that were submerged for 3, 6, 9, or 12 months. Vertical lines represent the standard error of the means (n = 3, except at * n = 1).

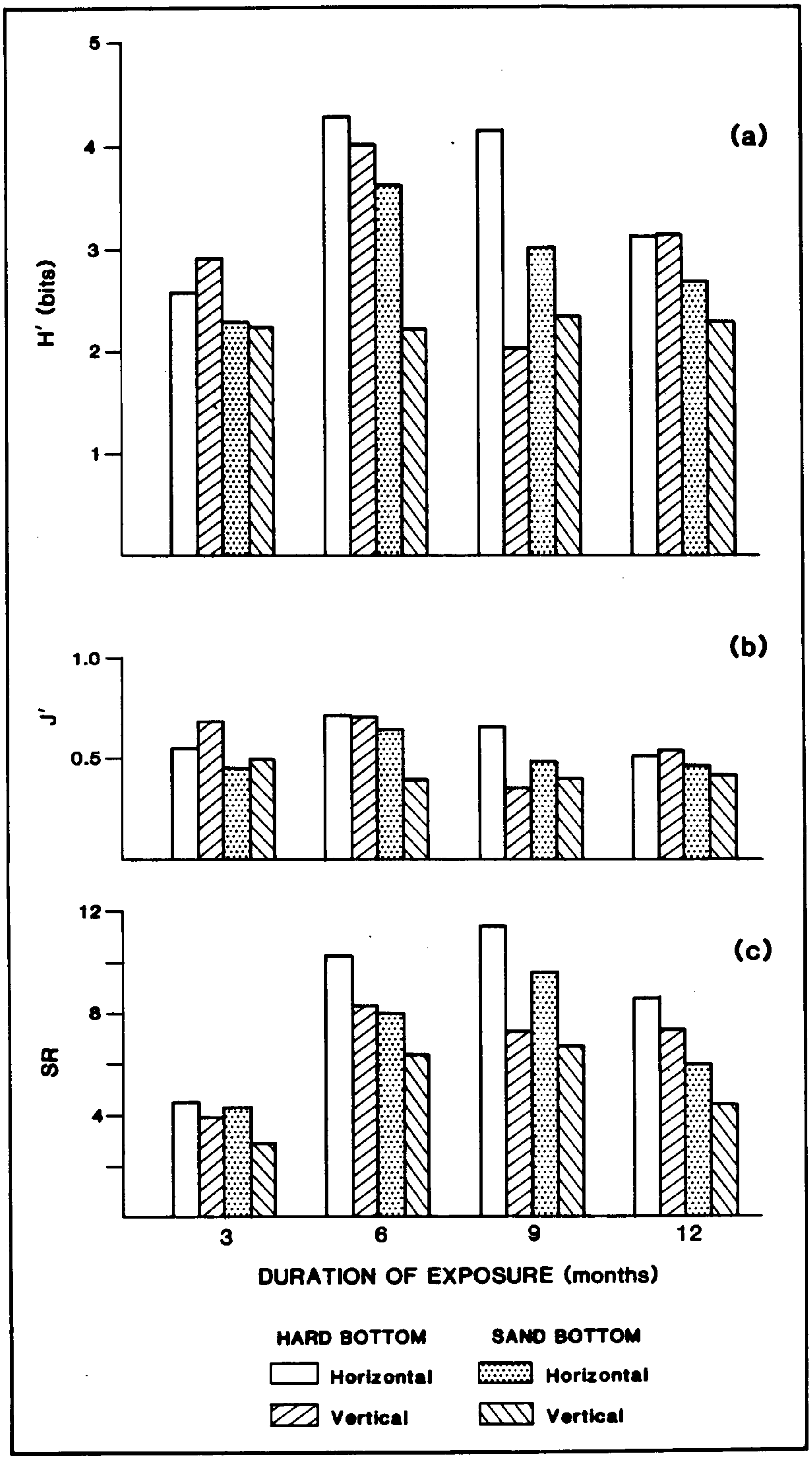


Figure 1.29 Values of (a) diversity, H'; (b) evenness, J'; and (c) species richness, SR of motile epifauna in pooled samples from plates that were submerged for 3, 6, 9, or 12 months.

six months of exposure; this corresponds to the season of greatest diversity among 3-mo recruitment plates (Figures 1.23a, 1.29a). In spite of greater species richness, 9-mo plates had lower diversity than those exposed for six months, due to the dominance of C. penantis on 9-mo plates and the consequent decrease in evenness. Diversity was lowest in the earliest stage of colonization, principally because species richness was rather low during that period.

Eight plate groups were formed in the normal cluster analysis of samples from the 3-, 6-, 9-, and 12-mo plate series (Figure 1.30). One of these (Group 3) was rather aberrant, and its single collection contained only four specimens, each repesenting a different species (Appendix 1.11). Its position in the cluster heirarchy is not significant, and it may have resulted from improper collection or treatment of the sample.

The normal dendrogram shows that changes in the community were greatest in the early phase of its development. Three-month samples (Groups 1 and 2) were highly dissimilar to those collected later in the study, and resulted primarily from the fact that these younger plates supported significantly fewer species than the others. Among the other plates, those with different exposure durations frequently showed relatively high similarity. For example, 6- and 9-mo plates on hard bottom were clustered into Groups 4 and 5, while 9- and 12-mo plates constituted Groups 7 and 8.

Sand-bottom plates were generally dissimilar to those from hard bottom with the same duration of exposure, particularly for the 3-, 6-, and 9-mo plates (Figure 1.30). This distinction was less apparent among plates exposed for 12 months, however, indicating increased similarity between the communities of these two habitats over time. As noted previously, plate orientation does not seem to be an important factor in the development of the motile epifaunal community, at least during the first year of colonization (Figure 1.30).

Thirteen groups, consisting of 104 species, were formed by inverse cluster analysis (Table 1.14). Numerically dominant amphipods were clustered into Groups A through C, along with a number of abundant species in other taxa. Group A species alone contributed more than 76% of the individuals from the 3-, 6-, 9-, and 12-mo series of plates, and together with Groups B and C represented greater than 96% of the motile epifauna collected. The amphipods of Group A were highly constant throughout the entire study period, while the species of Group B were less constant on plates exposed for only three months (Figure 1.31). None of these species were restricted to any particular season during the 12-mo exposure period. Group C species, on the other hand, were most constant during the first six months, and were moderately restricted to plates removed after only three months.

Species in Groups D and E became moderately to highly constant following the initial 3-mo exposure period, and remained so throughout the rest of the study (Figure 1.31). Species in both groups exhibited very low to moderate fidelity, with those in Group D being somewhat faithful to sand-bottom plates and those of Group E to hard-bottom ones.

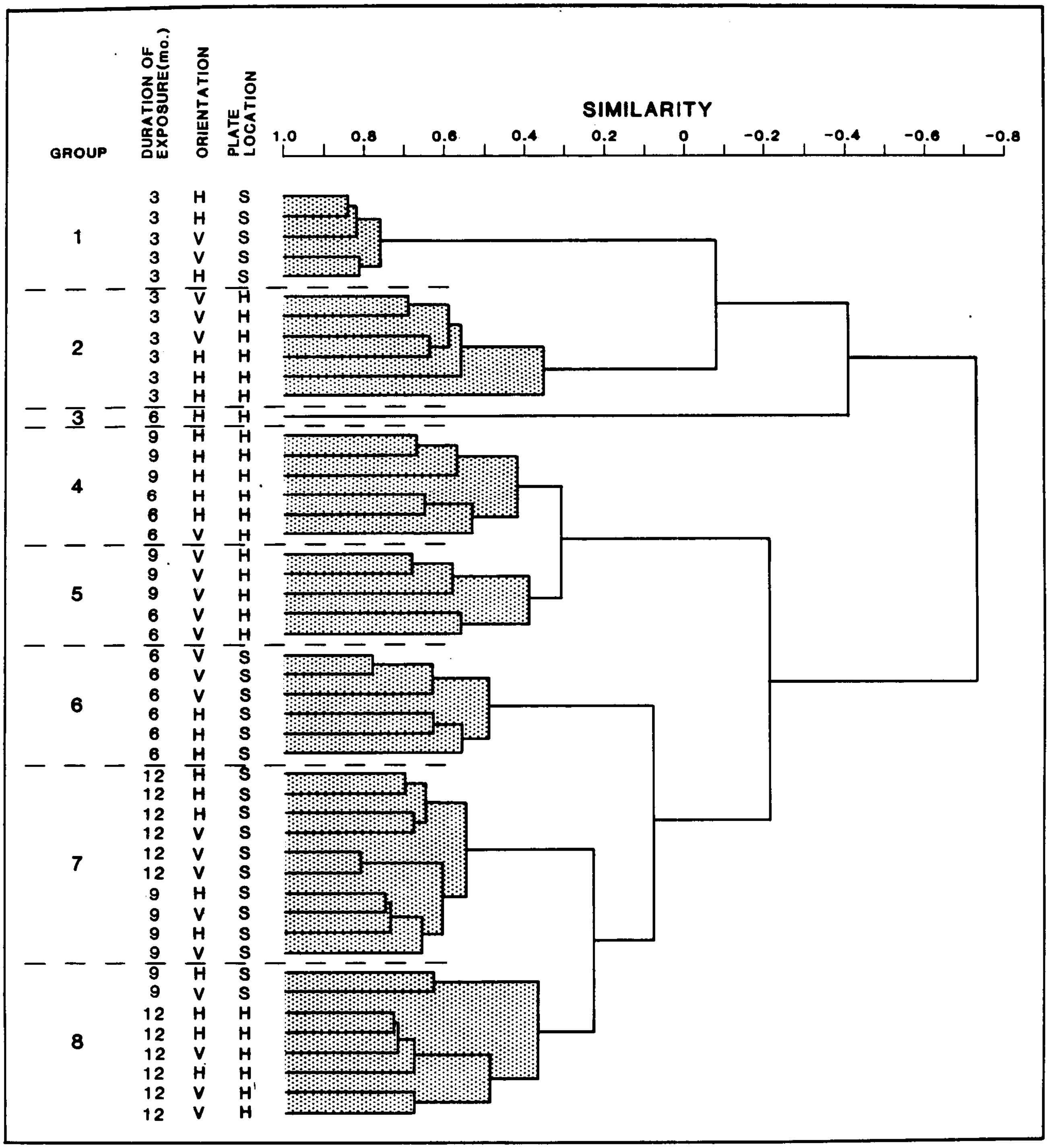


Figure 1.30 Dendrogram resulting from normal cluster analysis of motile species abundance on plates that were submerged for 3, 6, 9, or 12 months. Plate orientation (H = horizontal, V = vertical) and location (S = sand bottom, H = hard bottom) are indicated.

Table 1.14 Species groups resulting from inverse cluster analysis of motile species on the 3-, 6-, 9-, 12-mo plate series. (Am = Amphipoda; D = Decapoda; I = Isopoda; M = Mollusca; P = Polychaeta; Py = Pycnogonida; Si = Sipunculida).

Group A

Gammaropsis sp. (Am)
Photis sp. (Am)
Erichthonius brasiliensis (Am)
Stenothoe sp. (Am)
Caprella penantis (Am)

Group B

Nemertinea
Melita appendiculata (Am)
Astyris lunata (M)
Malacoceros glutaeus (P)
Nereis succinea (P)
Nereis sp. (P)
Nematoda
Luconacia incerta (Am)
Lembos smithi (Am)
Carpias bermudensis (I)
Elasmopus sp. A (Am)

Group C

Caprella equilibra (Am)
Podocerus sp. (Am)
Pilumnus sp. A (D)

Group D

Synalpheus fritzmuelleri (D)
Pilumnus dasypodus (D)
Turbellaria
Nereis lamellosa (P)
Podarke obscura (P)
Eulalia macroceros (P)
Nudibranchia A (M)
Caprellidae (Am)

Group E

Pista palmata (P)
Pilumnus floridanus (D)
Polydora sp. (P)
Syllis hyalina (P)
Exogone dispar (P)
Pilumnus sayi (D)
Autolytus sp. (P)
Synalpheus townsendi (D)
Paracerceis caudata (I)
Armandia maculata (P)

Group F

Pelia mutica (D)
Periclimenes longicaudatus (D)
Periclimenes iridescens (D)
Hiatella arctica (M)
Caecum pulchellum (M)
Eunicidae A (P)
Eunice vittata (P)

Group G

Anoplodactylus petiolatus (Py)
Anoplodactylus sp. (Py)
Achelia sawayai (Py)
Notomastus sp. (P)
Mactridae A (M)
Syllidae (P)
Capitellidae (P)

Group G (cont'd.)

Synalpheus minus (D)
Ceratonereis mirabilis (P)
Cerithium sp. B (M)
Polydora caeca (P)
Ampithoe sp. A (Am)

Group H

Phyllodoce castanea (P)
Polycirrus eximius (P)
Lembos sp. (Am)
Dorvillea sociabilis (P)
Hesionidae (P)
Nereidae (P)
Aspidosiphon gosnoldi (Si)
Owenia fusiformis (P)
Maldanidae (P)

Group I

Lima sp. (M)
Spionidae (P)
Arabella mutans (P)
Pelecypoda K (M)
Megalobrachium soriatum (D)
Xanthidae D (D)
Pycnogonida undet.

Group J

Nereis falsa (P)
Cirriformia sp. (P)
Corophiidae (Am)
Eunice antennata (P)
Stenorhynchus seticornis (D)
Thor sp. (D)
Periclimenes americanus (D)
Costoanachis lafresnayi (M)

Group K

Musculus lateralis (M)
Crepidula fornicata (M)
Majidae A (D)
Pilumnus sp. B (D)

Group L

Eulalia sanguinea (P)
Ampharete americana (P)
Pilumnus pannosus (D)
Xanthidae A (D)
Pseudomedaeus agassizii (D)
Proceraea sp. (P)
Pilumnus sp. (D)
Costoanachis sp. A (M)
Prionospio cirrifera (P)
Endeis spinosa (Py)
Polycirrus carolinensis (P)
Chione grus (M)

Group M

Doto sp. A (M)
Cerapus tubularis (Am)
Pelecypoda undet. (M)
Loimia medusa (P)
Phyllodocidae (P)
Phyllodoce sp. (P)
Sipunculida A
Nudibranchia C (M)

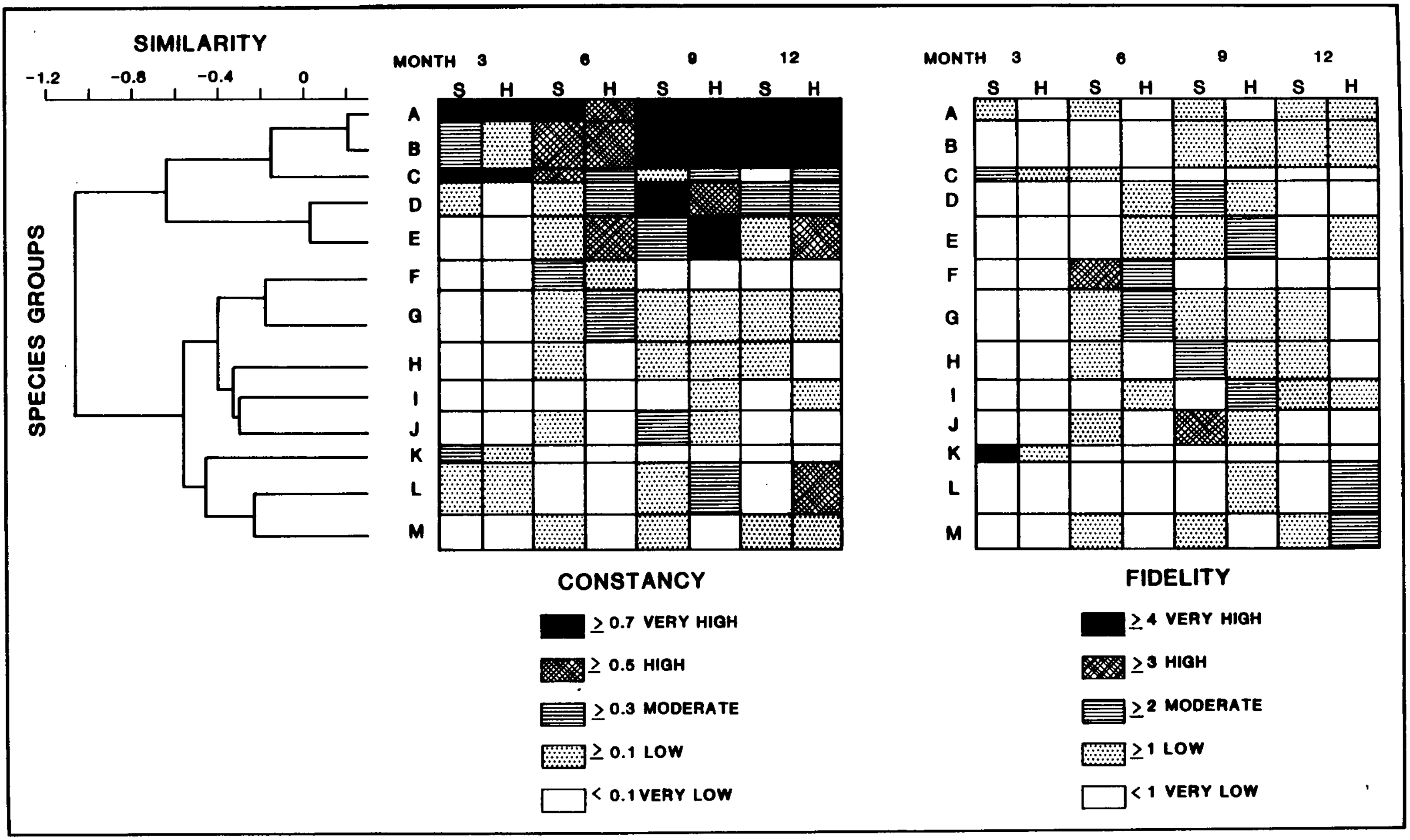


Figure 1.31 Inverse classification hierarchy of motile species, and nodal diagrams showing constancy and fidelity of species groups to sand-bottom (S) and hard-bottom (H) plates that were submerged for 3, 6, 9, or 12 months.

The remaining groups contained species that were neither abundant nor frequently encountered on the plates (i.e., constancy was generally low; Figure 1.31). As a result of the limited occurrence of their constituent species, these groups each showed moderate to high fidelity to a particular group of plates. Species in Groups F and G, for example, were moderately to highly faithful to 6-mo plates, while those in Groups H, I, and J were somewhat restricted to 9-mo plates. Three of the four Group K species were present only during the first three months, while those in Groups L and M were restricted to the oldest plates (Figure 1.31).

Recruitment onto artificial substrates in the marine environment has been the subject of numerous investigations, many of which were reviewed by Schoener (1982) and are cited elsewhere in this report. Most of these studies, however, describe the initial colonization and subsequent development of attached sessile epifauna, and only a few have addressed, even qualitatively, the role of motile organisms in such fouling communities. The diversity and abundance of the motile epifauna evaluated in the present study suggest that this motile component may play an important part in the development of such communities in neritic waters of the South Atlantic Bight.

The 3-mo recruitment plates of the present study were rapidly colonized by a number of species that are well-adapted for immediate recruitment onto newly exposed substrates. Erichthonius brasiliensis was the most ubiquitous and abundant species on these plates and was dominant during all four seasons of the study period. A definite seasonal pattern was observed in its recruitment, with peaks occurring during winter and spring (Figure 1.20). Similar seasonality of abundance was observed by Wenner et al. (1983) in hard-bottom samples from inner-shelf stations in the South Atlantic Bight. Contrasting patterns of abundance for E. brasiliensis have been observed by others, however, and may reflect not only the seasonal reproductive periodicity of this amphipod, but the influence of life cycles of the hosts upon which it lives, as well (Hughes, 1975).

Although the occurrence of E. brasiliensis in the fouling community has been documented by others (Hughes, 1975; Fotheringham, 1981; Van Dolah et al., 1984), its overwhelming density on our colonization plates has not been observed previously. A maximum density greater than 21,800 individuals/m^2 was obtained on a 3-mo sand-bottom plate exposed during spring, while a density greater than 58,600 individuals/m^2 was observed on a plate submerged for 12 months at the same location. Hughes (1975) observed that E. brasiliensis occurred with a peak abundance of less than 200 individuals/m^2 on clumps of the hydroid Nemertesia, and its mean abundance in the hard-bottom suction samples of Wenner et al. (1983) did not exceed 350 individuals/m^2.

The rapid recruitment of E. brasiliensis, Gammaropsis sp., and Caprella penantis onto fouling plates, as observed on the 3-mo recruitment series, may be attributed in part to their reproductive strategy and morphology. Typical of peracarids in general, these species brood their offspring in a marsupium that retains the young through their early stages of development. The hatchlings eventually emerge onto the substrate in the form of young adults (Barnard, 1969). This type of development precludes the necessity of adapting behavioral or physiological mechanisms designed to allow successful substrate selection and post-larval metamorphosis, such as those observed among many sessile colonists. *Caprella penantis* is one of the most common caprellid amphipods on the east coast of the United States, and its life history and clinging behavior indicate that it is well-adapted to rapid exploitation of fouling communities (Bynum, 1978). Tubicolous gammarids are also frequently early colonists on newly submerged substrates, and are able to establish populations on surfaces with little sessile growth (McKinney, 1977).

The design of our short-term colonization study did not include the evaluation of predation effects on the structure of the fouling community. However, some comment concerning the importance of motile organisms as food items for predators is appropriate. The most abundant species among all fouling plates, *E. brasiliensis* and *C. penantis*, were consistently important in the diet of a number of fishes (Section III). The seasonal importance of *E. brasiliensis* in the diet of *Centropristis striata*, *Pagrus pagrus*, and *Stenotomus aculeatus* appeared to reflect the seasonal abundance of *E. brasiliensis* noted in Figures 1.20 and 1.26, and by SCWMRD (1982). Fotheringham (1981) noted that this species was subject to considerable predation on a submerged oil structure in the Gulf of Mexico, where it became more abundant on newly scraped surfaces when predators were excluded.

Predation pressure on fouling community amphipods may be regulated to some extent by cycles in the availability of the sessile growth forms with which they are associated. Howard et al. (1980) suggested that when colonies of the hydroid *Tubularia crocea* died off during the warmer months, the amphipods were exposed and, thus, became susceptible to increased predation. In our study, reduced cover of barnacles on 3-mo hard-bottom plates exposed during spring (Figures 1.7, 1.8) was attributed to predation, since many barnacles obviously had been dislodged, leaving only the basal attachment plates. The growth of hydroids on these same plates was also unusually low during the same season, compared with that on sand-bottom plates. No such differences existed during the other three seasons, with regard to the densities of barnacles or hydroids on sand- versus hard-bottom plates. This period of unusually sparce sessile growth on hard-bottom plates coincided with the lowest abundance of motile epifauna observed during any season, and, to some extent, it may explain the extreme differences observed in motile abundance between the two locations during that season (Figure 1.21). Such low abundances may have resulted either from direct predation on the amphipods, or from the reduction in the amount of suitable habitat due to the decline in sessile organisms as a result of predation. *Erichthonius brasiliensis*, for example, was abundant on plates from sand bottom during spring, and its tubes were attached directly to the calcareous barnacle tests in great numbers.

The results of the present study indicate that there was no orderly, directional sequence of development in the motile epifaunal community during the 12 months following submergence of the test plates. The dominant species were rapid colonizers that appeared quickly after submergence and persisted over the course of the year. Throughout that period, significant changes were observed in a number of parameters of community structure, including species richness, diversity, faunal abundance, and species composition. These changes largely reflect the recruitment and survival of the dominant constituent species. As a consequence, many trends that appeared in these parameters among 3-mo recruitment plates were similar to trends among plates which had been exposed for longer durations. One year after submergence, the motile epifaunal communities on the plates were dominated by amphipods in both the sand- and hard-bottom areas. This is similar to the epifaunal community described by George and Thomas (1979) from an oil platform in the Gulf of Mexico, in which seasonal fluctuations among a small number of dominant amphipods were also pronounced.

Fishes:

The colonization frame placed in the hard-bottom area immediately attracted fishes (Table 1.15). By the time the second dive team descended to set the anchors, a large school (several hundred individuals) of the planktivorous round scad, *Decapterus punctatus*, was hovering over the frame. Small schools of southern porgy, *Stenotomus aculeatus*, milled around beneath the frame and around nearby sponges. Individual black sea bass, *Centropristis striata*, were present in the area, but remained close to sponges and did not gather near the structure.

In contrast, no fishes were immediately attracted to the sand-bottom frame. Only one fish, an unidentified flatfish (Pleuronectiformes), was seen in the vicinity, despite the fact that considerable time (15 min) was spent entirely in search of fishes.

After 3-mo exposure, both frames had several fish species associated with them. More species were noted near the sand-bottom frame (12) than in the hard-bottom area (9). Species in the vicinity of the sand-bottom frame included those normally found on sand bottom (*Synodus foetens*, *Urophycis earlli*, *Diplectrum formosum*, *Prionotus* sp., *Hemipteronotus novacula*), as well as many hard-bottom species. Most species associated with the hard-bottom frame were fishes typically found in hard-bottom habitat.

During the 6-mo plate retrieval cruise, observations were made only on the hard-bottom frame. Seven species of fish were identified, five of which had been previously observed. *Equetus umbrosus*, a species not previously observed, was very abundant around the frame. Approximately 20 individuals of this species were closely associated with the I-beam base structures and the supporting legs. Many individuals were packed into the small scoured-out crevices under the base structures. The other new species, *Monacanthus hispidus*, was represented by one individual that was grazing on the sessile fauna growing on the frame legs.

During the 9-mo cruise only four species of fish were observed on the sand-bottom frame, two of which had not been previously observed there.

Table 1.15 Fishes observed in close proximity to the sand- (S) and hard-bottom (H) frames during initial deployment (0 mo duration) and during subsequent plate removal.

	EXPOSURE DURATION (MO) AND FRAME									
	0		3		6		9		12	
SPECIES	S	H	S	H	S	H	S	H	S	H
Synodontidae										
Synodus foetens (inshore lizardfish)			x							
Batrachoididae										
Opsanus pardus (leopard toadfish)				x						x
Gobiesocidae										
Gobiesox strumosus (skilletfish)										x
Gadidae										
Urophycis earlli (Carolina hake)			x	x						
Serranidae										
Centropristis striata (black sea bass)		x	x	x		x	x	x	x	x
Diplectrum formosum (sand perch)			x							
Carangidae										
Decapterus punctatus (round scad)		x	x	x		x				x
Seriola dumerili (greater amberjack)			x	x		x	x	x		
Lutjanidae										
Lutjanus campechanus (red snapper)							x			
Haemulidae										
Haemulon aurolineatum (tomtate)			x	x		x				
Sparidae										
Archosargus probatocephalus (sheepshead)								x		x
Diplodus holbrooki (spottail pinfish)				x						
Lagodon rhomboides (pinfish)							x			
Stenotomus aculeatus (southern porgy)	x					x				
Sciaenidae										
Equetus umbrosus (cubbyu)						x		x		
Ephippidae										
Chaetodipterus faber (Atlantic spadefish)			x	x				x		
Labridae										
Hemipteronotus novacula (pearly razorfish)			x							
Sphyraenidae										
Sphyraena barracuda (great barracuda)				x						
Blenniidae (blennies)										x
Hypleurochilus geminatus (crested blenny)										x
Triglidae										
Prionotus sp. (searobins)			x							
Pleuronectiformes (flatfish)	x									
Balistidae										
Aluterus schoepfi (orange filefish)			x							
Monacanthus hispidus (planehead filefish)			x			x				

One large Seriola dumerili (approximate weight = 12 kg) was observed swimming beneath the plates and around the frame and approximately 20 juvenile (15-20 cm total length) red snapper (Lutjanus campechanus) formed a school that hovered a few centimeters above the plates. Five species of fish were noted on the hard-bottom platform and one, Archosargus probatocephalus (approximately 10 individuals), had not been previously observed in the vicinity.

Divers on the sand-bottom platform during the 12-mo cruise found only one species, C. striata (approximately 10 individuals) associated with the structure. The hard-bottom frame had six species, two of which (Hypleurochilus geminatus and Gobiesox strumosus) had not been previously observed but were noted resting on the frame. Equetus umbrosus, which had been abundant around the plate support structures, were absent during the final visit to the frame.

In addition to the above observations, a few fishes were collected along with motile invertebrate fauna when some of the 9- and 12-mo exposure plates were retrieved. These fishes were small cryptic forms that were probably more abundant on the plates and frames than diver observations indicated. Three crested blennies, Hypleurochilus geminatus, and one leopard toadfish, Opsanus pardus were collected, and all were collected from horiontal plates. Stomach content analysis revealed that the three crested blennies had fed on an unidentified barnacle (soft parts only) as well as isopods (Carpias bermudensis) and amphipods (Photis pugnator, Cerapus tubularis, Erichthonius brasiliensis and Luconacia incerta) that were common components of the motile plate fauna. The leopard toadfish stomach was empty. Other fishes may also have fed on the plate fauna. A planehead filefish (M. hispidus) was observed to feed on attached growth and some plates that appeared to have been grazed around the edges were noted when sheepshead were present in the area. Sheepshead are heavy grazers on attached fauna and often consume species that were common on the plates (see Section III). Other fishes known to feed on attached growth, and which were present in the vicinity of the frames, were Atlantic spadefish (Chaetodipterus faber), orange filefish (Aluterus schroepfi) and planehead filefish (M hispidus) (Hildebrand and Schroeder, 1928; Randall and Hartman, 1968). Several species (C. striata, L. rhomboides, A. probatocephalus) are also predators on motile fauna associated wih sessile organisms (see Section III). Some of the predators (C. striata, C. faber) that depend heavily on hard substrate for feeding were also commonly noted near the sand-bottom platform. Because the platform provided the only obvious food source for some of these fishes, predation by these fishes may have been important in determining structure of the fouling community (Petersen, 1979).

LONG-TERM COLONIZATION STUDY

STUDY AREA

Five artificial reefs (sunken vessels) ranging in age from 3.5 to 10.0 years (Figure 1.32) were studied for evidence of long-term colonization patterns (see Table 1.16 for details of their location). All five reefs occur in very similar hydrographic regimes as evidenced by the fact that the difference in average water temperature, at a depth of 30 m, between latitudes 29°N and 34°W (a wider range of latitude than that encompassed by our study sites) was never more than 2.13°C during any 3-mo interval between 1920 and 1970 (Churgin and Halminski, 1974). During the same 50-yr period, water temperatures ranged annually from 16.18 to 29.05°C off Charleston, South Carolina and from 16.23 to 29.04°C off Jacksonville, Florida. Average salinity and dissolved oxygen values were even less variable throughout the study area. Salinities were euhaline throughout the area, ranging annually from 35.53 to 36.65 °/oo off the coast of South Carolina and from 35.66 to 36.74 °/oo off the coast of Florida. Dissolved oxygen values ranged annually from 3.41 to 5.62 ml/l off Charleston and from 3.63 to 5.64 ml/l off Jacksonville. Temperature, salinity, and dissolved oxygen values reported for each of the five artificial reefs in this study (Appendix 1.1) were generally within the ranges reported by Churgin and Halminski (1974).

The 3.5- and 8.0-yr reefs are known to be located within a few meters of natural hard bottom (Henry Ansley, personal communication). Hard-bottom habitat has also been reported 5 km east of the 6.0-yr reef and an undetermined distance north of the 10.0-yr reef.

METHODS

Field and Laboratory Methods

The sampling regime for the artificial reefs is illustrated in Figure 1.33. Four horizontal and four vertical transects were established on each vessel with polypropylene line marked in 0.5-m intervals and weighted at either end. Five close-up photographs, each encompassing an area of 225 cm^2, were taken along every horizontal and vertical transect (using a Nikonos 35-mm underwater camera system) for subsequent point-count analyses of the sessile biota. Location of the first photographed quadrat was determined by random selection and the four remaining photographs were then taken at uniform (usually 0.5-m) intervals. Biota occupying areas corresponding to the second and fourth quadrats on each transect were then scraped into separate 0.5-mm mesh bags. These scrape samples were taken for biomass measurements and to aid in the identification of sessile species appearing in the close-up photographs. Two additional photographs were taken along every transect at a distance of 1 m from the surface of the vessel. These photographs were taken to determine the density of large sessile organisms whose distributions could not be ascertained from the close-up photographs. Finally, six suction samples (three from horizontal and three from vertical surfacs) were collected from all artificial reefs

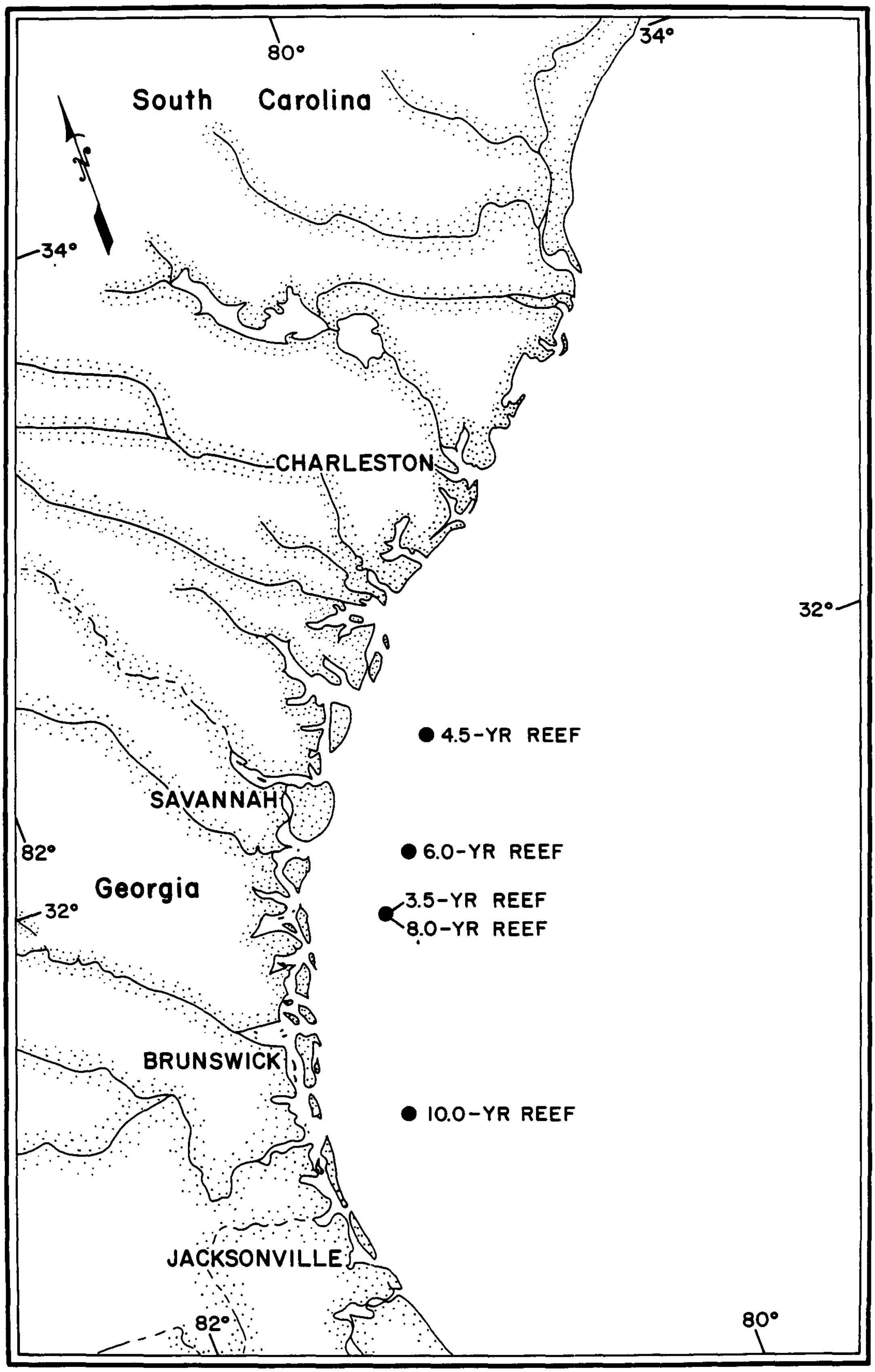


Figure 1.32 Location of sampling sites for the long-term colonization study.

Table 1.16 Summary of the location, depth, date of submergence, and sampling date for each of the five artificial reefs. Letter designations for reefs were assigned by the Georgia Department of Natural Resources.

Artificial Reef	Type of Vessel	Latitude (N)	Longitude (W)	Depth (m)	Date Submerged	Date Sampled
3.5-yr reef (Reef J)	100-ft tugboat	31°36.0'	80°47.6'	24	February, 1980	June, 1983
4.5-yr reef (Reef T)	440-ft Liberty Ship	32°0.3'	80°25.2'	31	December, 1978	September 1983
6.0-yr reef (Reef L)	90-ft barge	31°45.2'	80°36.6'	22	July, 1977	August 1983
8.0-yr reef (Reef J)	444-ft Liberty Ship	31°36.2'	80°47.6'	24	July, 1975	June, 1983
10.0-yr reef (Reef G)	100-ft tugboat	30°58.2'	80°58.8'	24	July, 1973	July, 1983

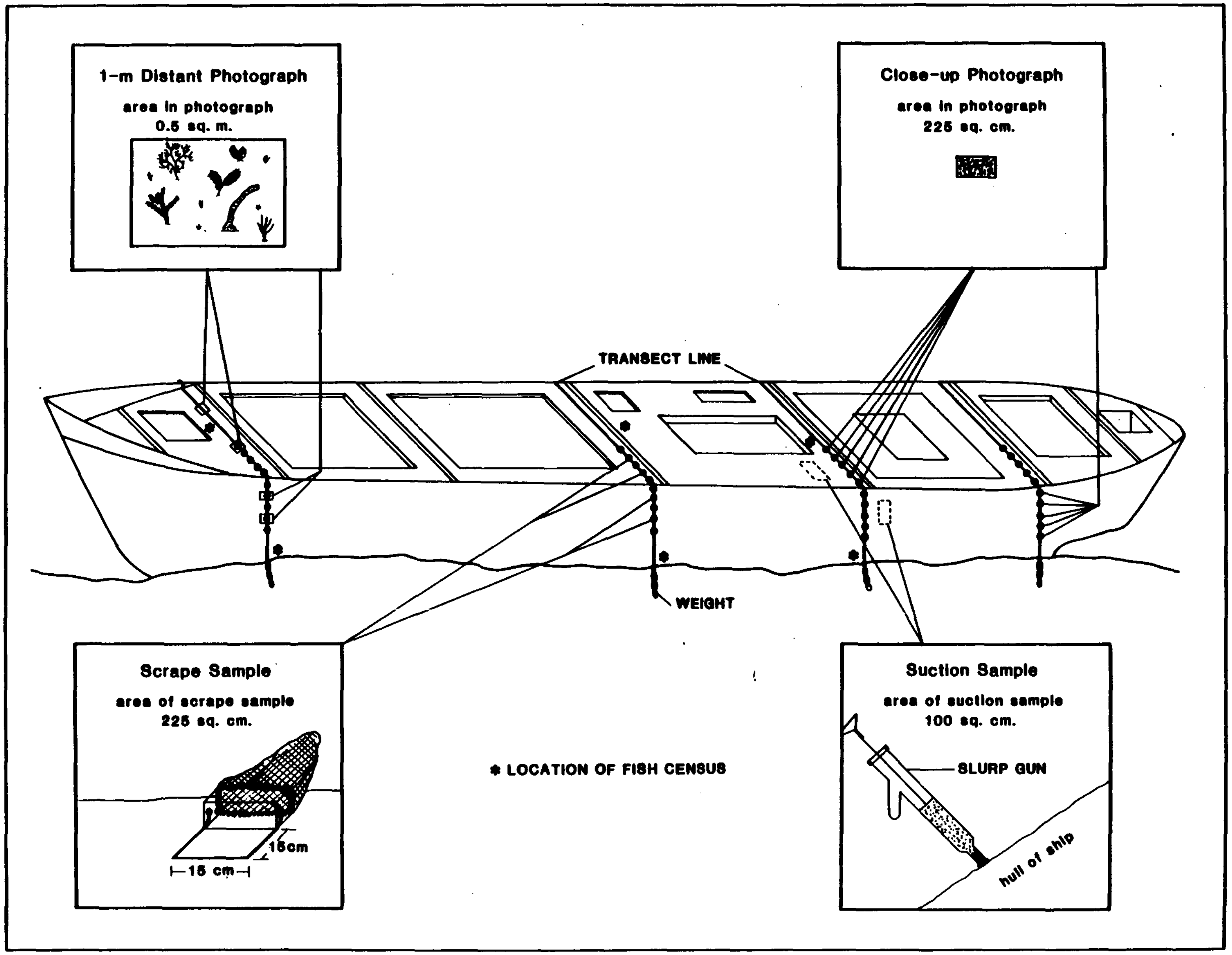


Figure 1.33 Schematic diagram of sampling regime for the long-term colonization study.

in order to capture the motile epifauna. Each sample was comprised of seven suctions taken with a modified slurp gun (Van Dolah et al. 1984). The gun was modified so that suction was obtained by venturi action; water was drawn into the gun through holes that had been drilled in the barrel and covered with 1-mm mesh screen. Suction samples were taken adjacent to three of the four transect lines. For each suction, the mouth of the gun was held flush against the surface of the vessel so that only the area encompassed by the mouth was sampled. The seven slurp gun samples collectively encompassed a total surface area of 100 cm^2. The contents of the slurp gun were injected into a plastic jug through a hole in a 1-mm mesh screen that had been fitted over the mouth of the jug to prevent fauna from escaping. Aboard the research vessel, suction samples were sieved through a 1-mm mesh screen. All samples (suction and scrape) were preserved in a buffered solution of 10% seawater formalin.

In the laboratory, suction and scrape samples were transferred to 70% isopropanol. Sessile organisms from the scrape samples were first sorted into broad taxonomic categories and then identified to the lowest possible taxonomic level. Motile organisms from the suction samples were sorted, identified, and counted.

Wet-weight biomass measurements (accurate to the nearest gram) were obtained for the following taxa sorted from scrape samples: Actiniaria, Ascidiacea, Cirripedia (soft tissue), Cirripedia (shell), Hydrozoa/Bryozoa, Mollusca (shell), Octocorallia, Porifera, and Scleractinia. Soft tissue was weighed separately from shell material for both barnacles and mollusks in an effort to derive relative proportions of living and dead organisms. The determination of accurate abundances for barnacles and mollusks was precluded by the fact that they were often highly fragmented in our scrape samples. Tubicolous polychaetes (serpulids, sabellids, and sabellariids) were not weighed separately from the other biota since it was virtually impossible to remove most of them from the organisms to which they were attached. Similarly, hydroids and bryozoans were weighed together due to the impracticality of separating them. All weight measurements were obtained using a PN323 Mettler balance.

A preliminary 225-point count, analagous to that described for the fouling plate study, was performed on one close-up photograph chosen to represent a particularly diverse assemblage of sessile organisms on the 8.0-yr reef (Appendix 1.19). As in the fouling plate study, three lower levels of sampling effort were tested by randomly selecting replicate sets of 100, 75, and 50 points from the original 225 points. The results of t-tests comparing mean percent cover estimates derived from the original and reduced data sets indicated that a minimum of 75 points was needed to accurately estimate percent cover for all species which occupied at least 5% of the area photographed. These results are similar to those obtained by Sutherland and Karlson (1977) who determined that 75 random points gave repeatable estimates of percent cover to within ± 5% on plate surfaces measuring 232 cm^2.

Photographic slides were projected on a large screen having 75 computer-generated random points. One of five different screens was randomly selected to analyze each series of five replicate photographs.

The projected surface area examined in each slide was equivalent to an actual surface area of 225 cm^2, the same area as that encompassed by a scrape sample. Organisms occurring under the 75 points in each photograph were identified to the lowest possible taxonomic level. Since the image resolution was frequently poor and canopy species often obscured the underlying biota, percent cover estimates could only be calculated for broad taxonomic categories. These included Actiniaria, Algae, Cirripedia, Hydrozoa/Bryozoa, Mollusca, Octocorallia, Porifera/Ascidiacea, Scleractinia, and Undetermined Invertebrata. Percentages were based on the total number of points analyzed which was frequently less than 75 due to the problems cited above.

Fish populations were censused on each artificial reef by divers (Figure 1.33). Fishes were identified and counted during three separate observation periods, each of which followed a short acclimation period while the divers adjusted to light conditions and assumed positions considered least likely to disturb the fishes. Fishes appeared to be undisturbed by the divers' presence during all observation periods. Each observation consisted of one two-minute count adjacent to each vertical side (port and starboard) of the hull and a four-minute count on an adjacent horizontal surface. The horizontal count was made on a line between the two points where vertical counts were made (Figure 1.33). Thus, four minutes were spent identifying and counting fishes on each surface orientation during all three observation periods, for a total of 24 minutes per reef. At each observation point, one diver kept time while the other diver counted fishes adjacent to the hull of the vessel. The divers were stationary during counts and only fishes on or adjacent to the hull and schooling fishes swimming witin three meters of the hull were counted. During observations of vertical surfaces, equal intervals of time were spent looking in opposite directions along the length of the vessel (i.e., toward the bow or stern). The divers then moved up onto the horizontal surface and positioned themselves midway between opposite sides of the hull. Counts on the horizontal surface were made for one minute while facing in each of four directions, each 90° from the previous one. Divers then swam down the opposite side of the ship and made a second vertical surface count in the same manner as the first. Fish counts were recorded on waterproof paper and transferred to standard forms in the laboratory. Presence and species composition of fishes on each reef was also documented on 8-mm film using an underwater movie camera. When possible, visual counts were supplemented with speargun and hook and line collections. Weather conditions, however, did not always permit this sampling, and fishing efforts were relatively unsuccessful. Those fishes that were collected were identified and their stomach contents were examined in the laboratory to determine the extent of their foraging on the reefs.

Data Analysis

Sessile Biota - Scrape samples were compared among artificial reefs and between surface orientations with respect to both numbers of sessile species and total biomass using separate two-way (Model I) analyses of variance for each of the two variables (Sokal and Rohlf, 1981). Biomass values were first $\log_{10}$-transformed to correct for non-normality in the data set, while species numbers were not transformed since they followed an approximately normal distribution with independent means and variances. The *a posteriori* Ryan-Einot-Gabriel-Welsch multiple F test (Ramsey, 1978) was subsequently used to make comparisons of mean values among reefs.

Close-up photographs from horizontal and vertical surfaces of the five artificial reefs were compared with respect to total percent cover. These values, expressed as a proportion of the total number of points analyzed per slide, were first subjected to an arcsin transformation before a two-way analysis of variance was performed. Since there were unequal numbers of replicate photographs, Tukey's standardized range test (Sokal and Rohlf, 1981) was used in lieu of the Ryan-Einot-Gabriel-Welsch multiple F test for *a posteriori* comparisons.

Cluster analysis was used to describe patterns of similarity in sessile species composition among scrape samples from the various reefs and surface orientations. Prior to the analysis, data from replicate scrape samples were pooled, resulting in a reduction of the total number of entities analyzed from 80 to 40. The data set was further simplified by eliminating those rare species that only occurred in one pooled scrape sample. Normal and inverse analyses were performed on presence/absence data using the Jaccard similarity coefficient (Clifford and Stephenson, 1975) and the flexible sorting strategy with a cluster intensity coefficient (β) of -0.25 (Lance and Williams, 1967).

Nodal analysis (Williams and Lambert, 1961; Lambert and Williams, 1962) was subsequently used to describe coincidences between clustered species groups and "fixed" station groups (Boesch, 1979). Each of the latter included all pooled scrape samples from either the horizontal or vertical transects on one of the five artificial reefs.

Motile Epifauna - The numbers of species and individuals in suction samples were compared among reefs and between surface orientations using separate two-way analyses of variance (Model I) for each variable. The values were transformed prior to computation using $\log_{10}(x + 1)$, since a number of zero values occurred in the data (Snedecor and Cochran, 1967). Comparisons among means were conducted using the Ryan-Einot-Gabriel-Welsch multiple F test, since all treatment groups had equal cell sizes.

Community structure was evaluated by comparing Shannon's diversity index (H'), evenness (J'), and species richness (SR) of individual and pooled replicate samples from each orientation on the five reefs. Patterns of similarity among the motile epifauna of unpooled suction samples were determined by performing cluster analyses using the Bray-Curtis coefficient and flexible sorting with $\beta = -0.25$. In order to reduce the data set, species which occurred in only 1 of the 30 suction samples were deleted prior to analysis, provided that they were also rare in abundance (i.e., none contributed greater than 1.5% of the total number of individuals). Both normal and inverse analyses were conducted on $\log_{10}$-transformed abundance values, and nodal analysis was then performed as described above.

Fishes - Abundances of fishes were compared among the reefs and between orientations using analysis of variance. Commnity structure was evaluated using the indices of diversity (H'), evenness (J'), and species richness (SR) described above. The degree of faunal similarity among reefs and between orientations was determined by performing cluster analysis using the Bray-Curtis coefficient and flexible sorting ($\beta = -0.25$).

RESULTS AND DISCUSSION

Sessile Biota

The greatest number of sessile species occurred on the 8.0-yr reef, while the fewest species were found on the 6.0-yr reef (Figure 1.34, Appendix 1.20). A comparison of mean numbers of sessile species on horizontal and vertical surfaces of the five artificial reefs indicated that two sources of variation (age of reef and surface orientation) accounted for only 45% of the total variance in the data set (Table 1.17). This suggests that some other factor(s) partially account for differences in the number of species among scrape samples. Nevertheless, the results do show that the 6.0-yr reef had significantly fewer sessile species than all except the youngest (3.5-yr) reef. Although there were no consistent trends in either the total or mean number of sessile species with increasing age of the reefs, there were significantly greater numbers of sessile species on vertical than on horizontal surfaces of all reefs combined.

Hydroids accounted for the greatest number of species overall, followed in order by bryozoans, mollusks, sponges, polychaetes, and ascidians (Table 1.18). All other taxa each contributed less than 5% to the total number of sessile species. With respect to the individual reefs, hydroids comprised the largest number of species on the 3.5-, 4.5-, and 10.0-yr reefs, while mollusks and bryozoans ranked first on the 6.0- and 8.0-yr reefs, respectively.

None of the various taxa were consistently represented by more species on one surface orientation than they were on the other. However, many of the most frequently occurring species were more common on vertical than they were on horizontal surfaces (Table 1.19). Notable exceptions to this trend were the hydroids Monostaechas quadridens and Dynamena cornicina, both of which occurred approximately twice as frequently on horizontal surfaces. The barnacle Balanus trigonus was the most frequently occurring species overall (> 95% of all collections); although, several other species occurred almost as frequently and were even more common than B. trigonus on some reefs (e.g. the hydroid Sertularella conica on the 8.0- and 10.0-yr reefs).

Normal cluster analysis of pooled scrape samples from each of the five artificial reefs generated six station groups (Figure 1.35). In general, scrape samples from similar surfaces on the same reef tended to cluster together; however, three of the six station groups included scrape samples from more than one reef, indicating a high degree of overlap in species composition among reefs.

Station Group 1 consisted solely of pooled horizontal scrape samples from the 3.5-yr reef. This group was most similar to station Group 2 which

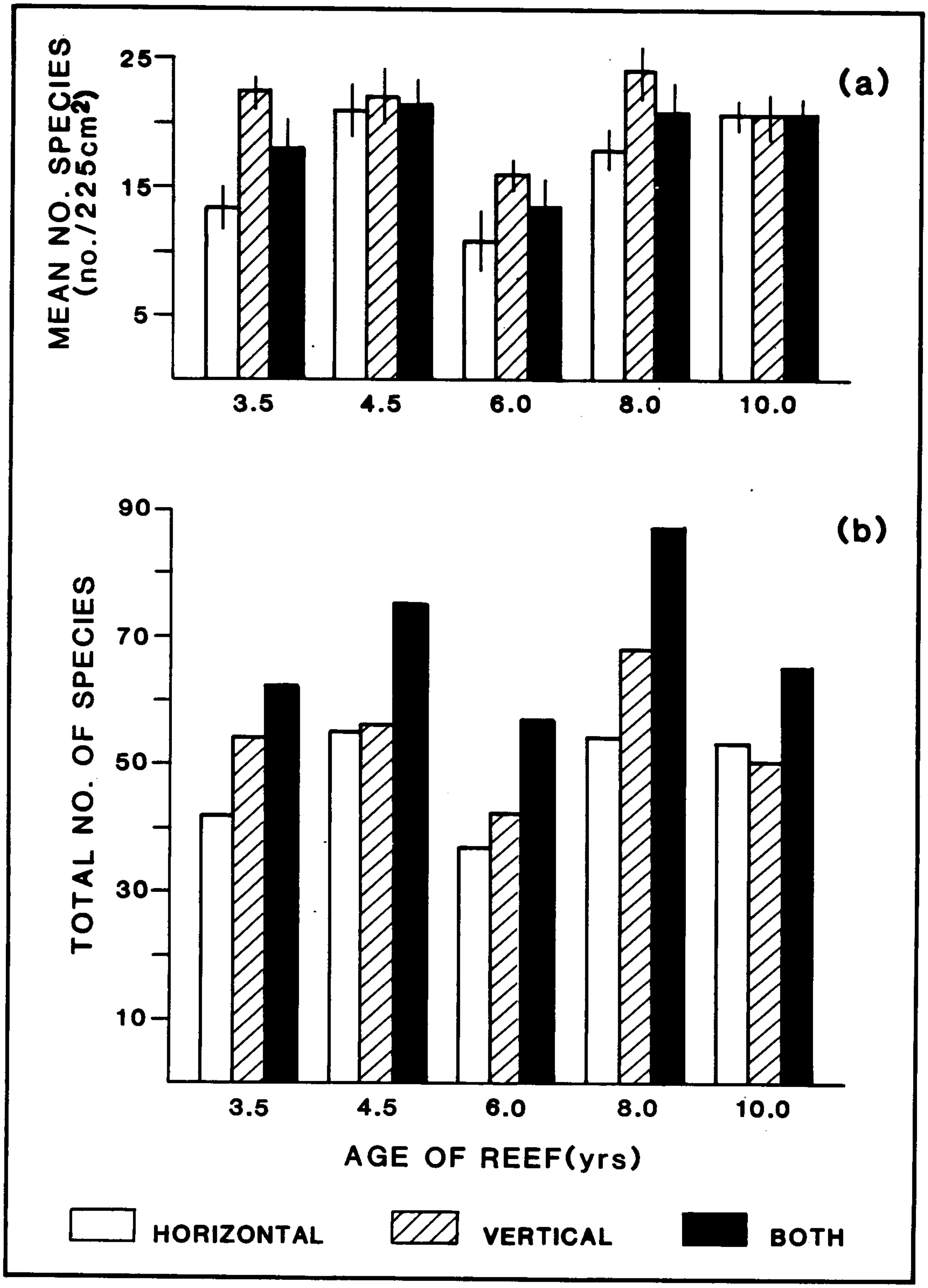


Figure 1.34 Mean number of species per scrape sample (a), and total number of species in all scrape samples (b), from horizontal (n = 8), vertical (n = 8), and both surfaces combined (n = 16) on each of the five artificial reefs. Vertical lines represent standard errors of the mean.

Table 1.17 Results of three two-way analyses of variance (Model I) comparing the number of sessile invertebrate species and biomass (g wet wt) in scrape samples and the percent cover in close-up photographs from horizontal and vertical surfaces of the five artificial reefs.

SOURCE OF VARIATION	Degrees of Freedom	F Value	Results of *a posteriori* comparisons
		DEPENDENT VARIABLE: No. spp./sample	
Model ($r^2 = 0.45$)	9	6.48***	
Factor A: Age of Reef (3.5,4.5,6.0,8.0,10.0 yrs)	4	8.09***	$\mu_{6.0}\ \underline{\mu_{3.5}\ \mu_{10.0}\ \mu_{8.0}\ \mu_{4.5}}^{1}$ $\underline{\mu_{6.0}\ \mu_{3.5}}$
Factor B: Surface Orientation (Horizontal, Vertical)	1	16.40***	$\underline{\mu_H} < \underline{\mu_V}^{1}$
Interaction Effects A x B	4	$2.38^{N.S.}$	
		DEPENDENT VARIABLE: $\log_{10}$(g wet wt./sample)	
Model ($r^2 = 0.46$)	9	6.60***	
Factor A: Age of Reef (3.5,4.5,6.0,8.0,10.0 yrs)	4	4.93**	$\underline{\mu_{6.0}} < \underline{\mu_{8.0}\ \mu_{3.5}\ \mu_{4.5}\ \mu_{10.0}}^{1}$
Factor B: Surface Orientation (Horizontal, Vertical)	1	30.15***	$\underline{\mu_H} < \underline{\mu_V}^{1}$
Interaction Effects A x B	4	$2.40^{N.S.}$	
		DEPENDENT VARIABLE: $\arcsin\sqrt{\dfrac{\text{No. biotic pts./slide}}{\text{No. pts. analyzed/slide}}}$	
Model ($r^2 = 0.65$)	9	30.75***	
Factor A: Age of Reef (3.5,4.5,6.0,8.0,10.0 yrs)	4	5.54***	$\mu_{6.0}\ \underline{\mu_{3.5}\ \mu_{4.5}\ \mu_{10.0}\ \mu_{8.0}}^{2}$ $\underline{\mu_{6.0}\ \mu_{3.5}\ \mu_{4.5}\ \mu_{10.0}}$
Factor B: Surface Orientation (Horizontal, Vertical)	1	249.71***	$\underline{\mu_H} < \underline{\mu_V}^{2}$
Interaction Effects A x B	4	5.44***	

N.S. not significant
* significant at 0.05 level
** significant at 0.01 level
*** significant at 0.001 level

[1] Ryan-Einot-Gabriel-Welsch multiple F test; means connected by underlines are not significantly different at $\alpha = 0.05$.

[2] Tukey's studentized range test; means connected by underlines are not significantly different at $\alpha = 0.05$.

Table 1.18 Percent contribution by major taxa to the total number of species collected in pooled scrape samples from horizontal (H) and vertical (V) surfaces of each reef. The total number of unique species on each surface (Σ) and on both surfaces of each reef (ΣΣ) are shown below.

TAXON	3.5-yr		4.5-yr		6.0-yr		8.0-yr		10.0-yr	
	H	V	H	V	H	V	H	V	H	V
Hydrozoa	36	26	18	23	16	14	20	13	25	24
Bryozoa	19	19	20	20	24	14	15	22	23	18
Mollusca	12	9	20	14	22	21	13	10	15	20
Porifera	14	17	13	11	8	12	15	21	9	18
Annelida	2	7	13	18	11	24	11	13	6	6
Ascidiacea	5	15	4	7	3	5	24	10	11	8
Cirripedia	5	4	4	5	8	5	2	4	4	4
Actiniaria	2	2	2	2	3	2	2	1	2	2
Octocorallia	-	-	5	-	5	2	2	-	2	-
Algae	2	2	-	-	-	-	2	-	2	-
Scleractinia	-	-	2	-	-	-	-	-	2	-
Total No. Species (Σ)	42	54	55	56	37	42	54	68	53	50
Grand Total (ΣΣ)	62		75		57		87		65	

Table 1.19 Percent frequency of occurrence for sessile species which occurred in $\geq$ 25% of all scrape samples from horizontal (H) and vertical (V) surfaces of the five artificial reefs. (An = anemone; As = ascidian; Ba = barnacle; Br = bryozoan; H = hydroid; M = mollusk; P = polychaete; Sp = sponge).

SPECIES	3.5-yr		4.5-yr		6.0-yr		8.0-yr		10.0-yr	
	H	V	H	V	H	V	H	V	H	V
Balanus trigonus (Ba)	88	100	88	100	100	100	88	100	100	88
Sertularella conica (H)	100	88	100	88	63	100	100	100	100	100
Aiptasia tagetes (An)	75	100	75	100	38	100	75	100	75	100
Crisia sp. (Br)	88	100	88	75	50	63	75	100	100	100
Amathia distans (Br)	13	100	50	100	25	63	75	100	100	100
Microporella ciliata (Br)	50	88	75	100	50	75	63	75	50	75
Chama macerophylla (M)	25	38	88	100	88	100	38	25	88	100
Filograna implexa (P)	38	100	63	100	-	100	13	75	75	88
Eudendrium sp. (H)	75	63	25	25	63	25	88	100	63	50
Hiatella arctica (M)	50	88	75	75	13	100	13	63	38	38
Monostaechas quadridens (H)	88	75	100	38	25	-	25	-	88	63
Bugula fulva (Br)	50	100	13	25	13	-	75	100	25	38
Dysidea fragilis (Sp)	25	38	63	38	-	38	-	-	100	88
Keratosa A (Sp)	-	75	-	88	-	-	13	88	25	75
Halecium dysymmetrum (H)	-	25	38	50	25	13	50	100	38	13
Chama congregata (M)	25	50	13	-	13	25	88	63	38	25
Dynamena cornicina (H)	38	25	100	25	13	38	25	-	63	-
Obelia dichotoma (H)	38	63	13	25	-	-	50	25	38	63
Balanus venustus (Ba)	38	13	50	88	13	63	-	13	13	-
Scrupocellaria regularis (Br)	-	63	100	75	-	-	13	38	-	-
Lissodendoryx isodictyalis (Sp)	13	50	13	25	13	-	25	13	38	63
Spirorbis sp. (P)	-	25	-	38	-	63	-	-	38	88
Number of replicate samples	8	8	8	8	8	8	8	8	8	8

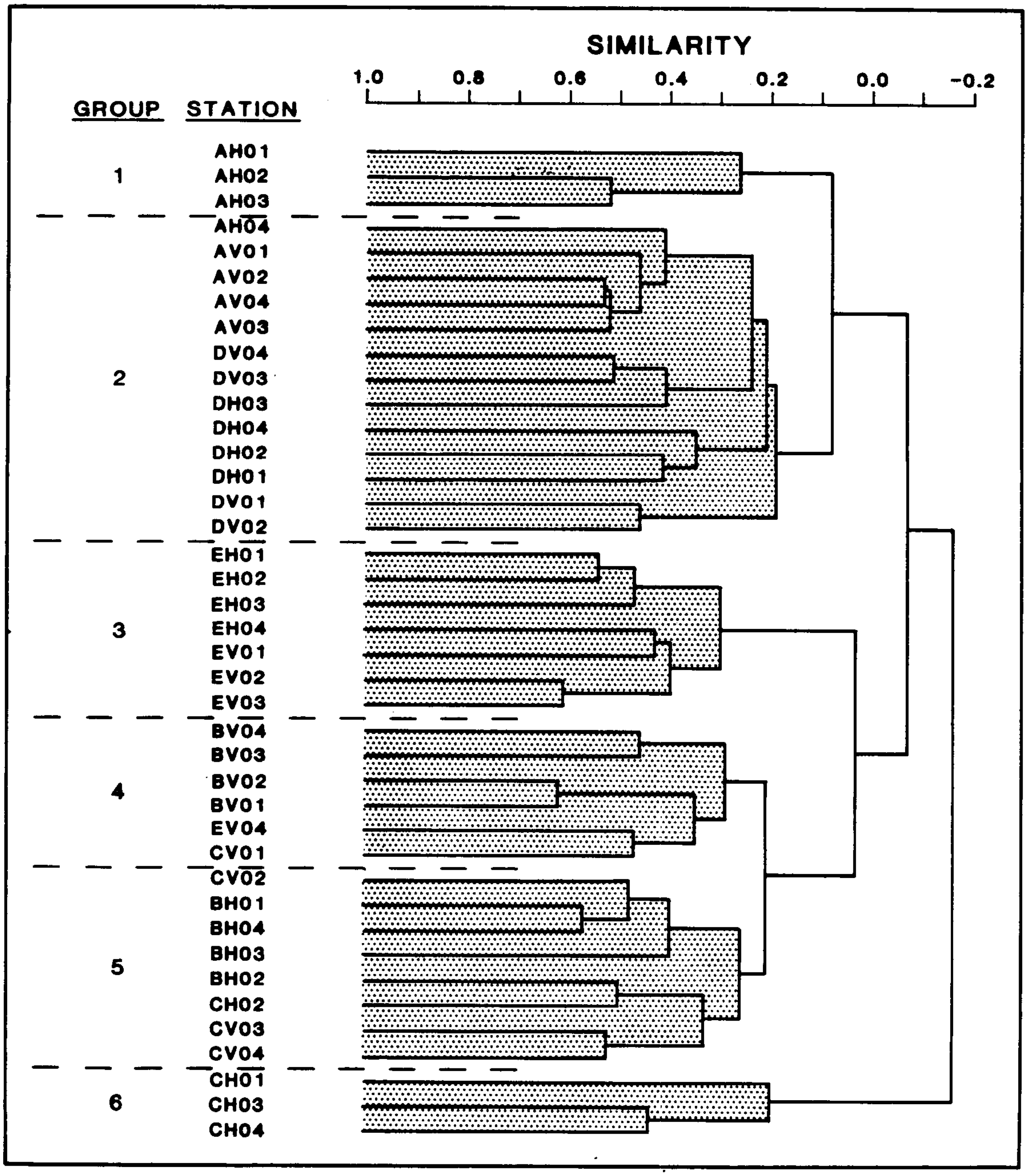


Figure 1.35 Normal classification of pooled scrape samples from horizontal (H) and vertical (V) transects on each artificial reef. (A = 3.5-yr reef; B = 4.5-yr reef; C = 6.0-yr reef; D = 8.0-yr reef; E = 10.0-yr reef).

comprised samples from both surfaces of the 3.5- and 8.0-yr reefs. Group 3 was composed entirely of scrape samples from both surfaces of the 10.0-yr reef, while Group 4 included only vertical scrape samples from the 4.5-, 6.0-, and 10.0-yr reefs. The latter group was most similar to Group 5, which included horizontal scrape samples from the 4.5-yr reef, as well as samples from both surfaces of the 6.0-yr reef. Finally, Group 6 consisted entirely of horizontal scrape samples from the 6.0-yr reef and was very dissimilar to all other groups.

Inverse cluster analysis of the 93 species remaining after data reduction produced eight species groups whose distributions among "fixed" station groups were interpreted in terms of nodal constancy and fidelity (Figure 1.36, Table 1.20). Species Group A had the highest constancy overall. The species in this group were among the 10 most frequently occurring species in all scrape samples combined (Table 1.19). With the exception of the polychaete *Filograna implexa* (which was absent from horizontal surfaces of the 6.0-yr reef), every species in Group A occurred on both surfaces of all reefs. Species in Group B were also fairly ubiquitous, with four of the five species occurring in $\geq$ 25% of all scrape samples. These species exhibited high to very high constancy (but low fidelity) on both surfaces of the two youngest reefs, on vertical surface of the 6.0-yr reef and on horizontal surfaces of the 10.0-yr reef.

Species Group C had very high constancy and high fidelity on horizontal surfaces of the 4.5-yr reef; however, only one of these species (the bivalve *Plicatula gibbosa*) was completely restricted to this particular surface. The scleractinian coral *Astrangia astreiformis* was restricted to horizontal surfaces in general, while the bivalve *Pteria colymbus* was restricted to the 4.5-yr reef where it occurred on both horizontal and vertical surfaces. Other species in Group C were generally more ubiquitous, occurring in $\geq$ 15% of all scrape samples; however, they occurred more frequently on the 3.5- and 4.5-yr reefs than elsewhere.

Group D comprised species that were only moderately constant but highly faithful on horizontal surfaces of the 6.0-yr reef. However, as in Group C, only one of the species in this group (the gastropod *Crepidula plana*) was completely restricted to that particular surface. Three species in Group D (the polychaete *Sabellaria vulgaris*, the octocoral *Telesto sanguinea*, and the bryozoan *Antropora leucocypha*) were restricted to horizontal surfaces in general, while two species (the octocoral *Telesto fruticulosa* and the hydroid *Dynamena quadridentata*) occurred primarily on horizontal surfaces but were not restricted to this orientation.

Species in Group E were characterized by high constancy (but low fidelity) on vertical surfaces of the 8.0-yr reef, and by their moderate to low constancy and fidelity elsewhere. Two species in Group E (the bivalve *Arcinella cornuta* and the sponge *Haliclona* sp.) were completely restricted to the 8.0-yr reef; however, none were restricted to a particular surface orientation. Most of the other species in this group were fairly ubiquitous and, in fact, several were among the most frequently occurring species overall.

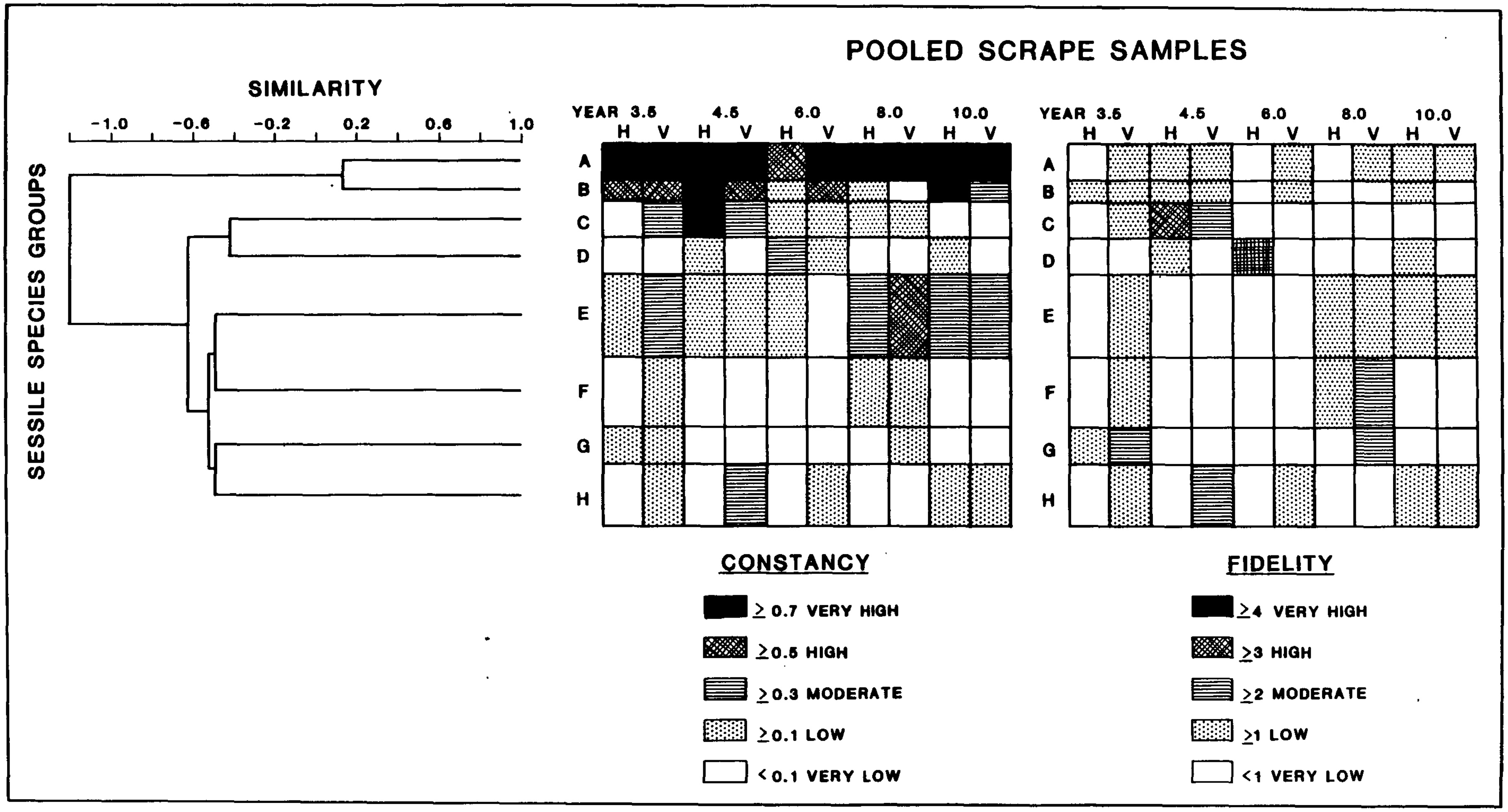


Figure 1.36 Inverse classification of sessile species in scrape samples, and nodal diagrams showing constancy and fidelity of species groups on horizontal (H) and vertical (V) surfaces of each artificial reef.

Table 1.20 Species groups resulting from an inverse classification of sessile organisms collected in scrape samples from the five artificial reefs. (An = anemone; As = ascidian; Ba = barnacle; Br = bryozoan; H = hydroid; M = mollusk; O = octocoral; P = polychaete; Sc = scleractinian coral; Sp = sponge).

Group A

Balanus trigonus (Ba)
Sertularella conica (H)
Crisia sp. (Br)
Aystasia tagetes (An)
Microporella ciliata (Br)
Filograna implexa (P)
Amathia distans (Br)
Hiatella arctica (M)
Chama macerophylla (M)

Group B

Balanus venustus (Ba)
Dynamena cornicina (H)
Monostaechas quadridens (H)
Dysidea fragilis (Sp)
Ostrea equestris (M)

Group C

Astrangia astreiformis (Sc)
Plicatula gibbosa (M)
Pteria colymbus (M)
Scrupocellaria regularis (Br)
Hydroides uncinata (P)
Nolella stipata (Br)
Gastrochaena hians (M)
Musculus lateralis (M)
Hydroides sp. A (P)
Scypha ciliata (Sp)

Group D

Sabellaria vulgaris (P)
Telesto sanguinea (O)
Crepidula fornicata (M)
Crepidula plana (M)
Xytopsues griseus (Sp)
Cumingia coarctata (M)
Telesto fruticulosa (O)
Antropora leucocypha (Br)
Dynamena quadridentata (H)

Group E

Arcinella cornuta (M)
Aetea anguina (Br)
Haliclona sp. (Sp)
Clavelina picta (As)
Chama congregata (M)
Sundanella sibogae (Br)
Bugula fulva (Br)
Keratosa A (Sp)
Obelia dichotoma (H)
Eudendrium sp. (H)
Halecium dysymmetrum (H)
Lissodendoryx isodictyalis (Sp)
Calamphora parvula (H)
Clytia fragilis (H)
Turbicellepora dichotoma (Br)
Terpios fugax (Sp)
Lithophaga bisulcata (M)
Bimeria humilis (H)
Clytia cylindrica (H)
Conopea merilli (Ba)

Group F

Molgula occidentalis (As)
Crepidula aculeata (M)
Plumularia floridana (H)
Parasmittina nitida (Br)
Poecilosclerida A (Sp)
Distaplia bermudensis (As)
Algae 0
Didemnum candidum (As)
Halichondriida B (Sp)
Aplidium sp. A (As)
Arca zebra (M)
Anomia simplex (M)
Hadromerida A (Sp)
Hypsicomus phaeotaenia (P)
Pseudovermilia sp. A (P)
Keratosa C (Sp)

Group G

Haplosclerida A (Sp)
Bimeria sp. A (H)
Schizoporella floridana (Br)
Ecteinascidia turbinata (As)
Schizoporella cornuta (Br)
Lithophaga antillarum (M)
Leuconia barbata (Sp)
Bugula turrita (Br)
Distaplia sp. (As)

Group H

Hippaliosina rostrigera (Br)
Mycale cecilia (Sp)
Hydroides crucigera (P)
Pseudovermilia occidentalis (P)
Megalomma bioculatum (P)
Turritopsis nutricula (H)
Keratosa B (Sp)
Turritopsis fascicularis (H)
Halopteris diaphana (H)
Spirorbis sp. (undet.) (P)
Microporella umbracula (Br)
Eudendrium carneum (H)
Arca imbricata (M)
Halocordyle disticha (H)
Halecium sp. (H)

Species Group F exhibited moderate fidelity (but low constancy) on vertical surfaces of the 8.0-yr reef. Although no species in this group were completely restricted to this particular surface, four (the bryozoan *Parasmittina nitida*, the polychaete *Pseudovermilia* sp. A, and the sponges Halichondriida B and Keratosa C) were restricted to vertical surfaces in general, while one species (the ascidian *Molgula occidentalis*) was restricted to the 8.0-yr reef, but not to a particular side.

Group G contained species that were moderately faithful to vertical surfaces of the 3.5- and 8.0-yr reefs; however, none were restricted to these surfaces. One species (the hydroid *Bimeria* sp.A) was found only on the 3.5-yr reef, but was collected from both horizontal and vertical surfaces. There were no other apparent trends in the distribution of these species.

Finally, species Group H exhibited moderate constancy and fidelity on vertical surfaces of the 4.5-yr reef. One species (the polychaete *Pseudovermillia occidentalis*) was restricted to vertical surfaces in general, but not to a particular reef, while another (the hydroid *Turritopsis nutricula*) was restricted to the 4.5-yr reef, but not to a particular side. Otherwise, the distribution of species in this group followed no discernable pattern.

The highest mean biomass occurred on vertical surfaces of the 10.0-yr reef, while the lowest mean biomass was recorded for horizontal surfaces of the 6.0-yr reef (Figure 1.37). The results of a two-way analysis of variance and an *a posteriori* multiple F test (Table 1.17) showed that the 6.0-yr reef was the only one whose mean biomass differed significantly from the others. Furthermore, vertical surfaces on all reefs had significantly greater biomass than horizontal surfaces. Once again, however, the fixed effects model explained only 46% of the total variance in the data.

Barnacle shell (from both living and dead specimens) accounted for the highest percentage of total wet weight overall, as well as the highest percentage of total wet weight on vertical surfaces alone (Table 1.21). Mollusk shell (primarily from living specimens) was the major component of total wet weight on all horizontal surfaces together, and on horizontal surfaces of the 6.0-, 8.0-, and 10.0-yr reefs individually. Barnacle shell ranked first on horizontal surfaces of the two youngest reefs, however. Ascidians comprised a relatively large proportion of the total biomass on the 3.5- and 8.0-yr reefs, especially on horizontal surfaces, but were not a major component of the total biomass elsewhere. All of the other taxa contributed relatively little to the total biomass, with the exception of octocorals which accounted for 11% of the total biomass on horizontal surfaces of the 6.0- and 10.0-yr reefs.

Despite considerable differences among scrape samples in the weight of the barnacle shell fraction, the biomass of the soft-tissue fraction was uniformly low. This could imply that differences in the weight of barnacle shell among reefs and between surfaces were largely due to differences in the proportion of dead barnacles, while the proportion of live barnacles remained fairly constant. This is supported by diver observations of numerous dead barnacles on all reefs. The results also suggest that the soft-tissue fraction accounted for so little of the biomass relative to the

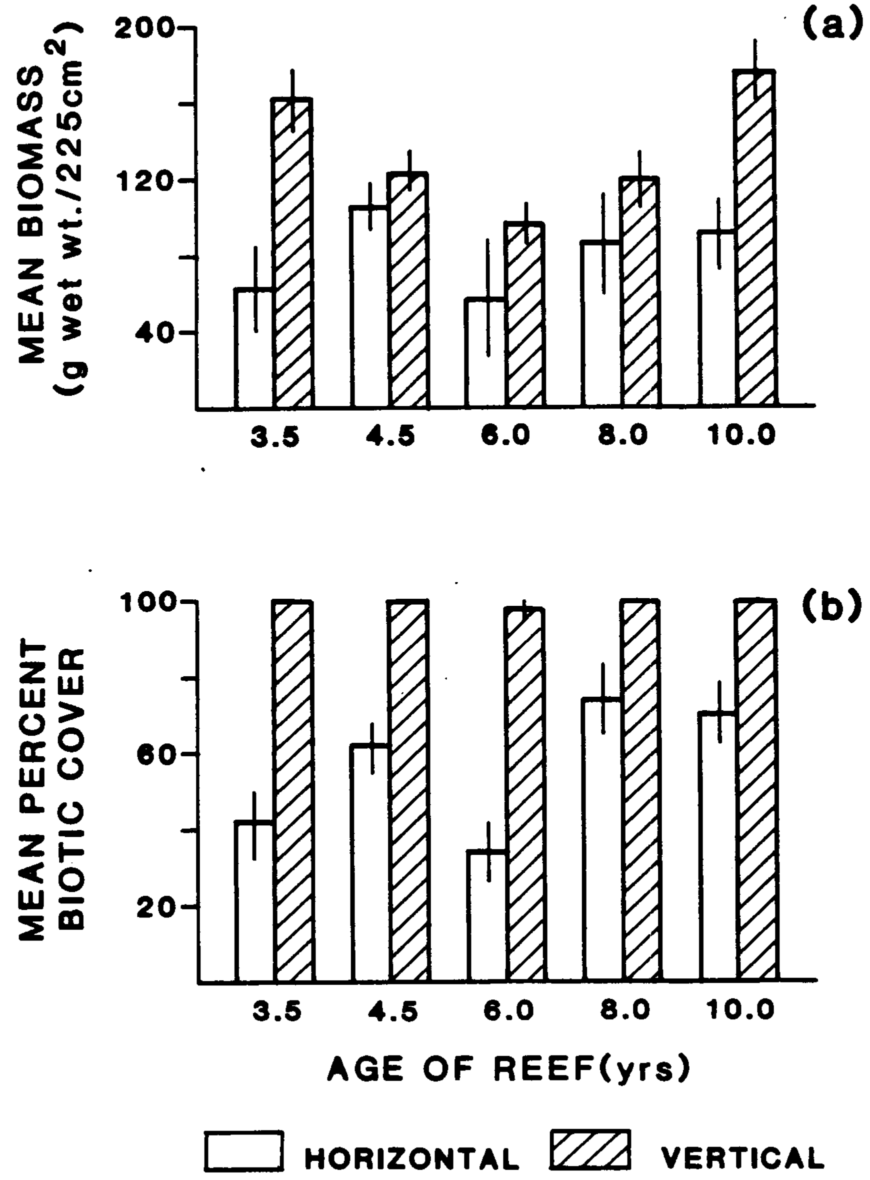


Figure 1.37 Mean biomass (g wet wt.) per scrape sample (a) and mean percent biotic cover per close-up photograph (b) taken on horizontal and vertical surfaces of each artificial reef. Vertical lines represent standard error of the mean.

Table 1.21 Percent contribution by major taxa to the total biomass (g wet wt) of sessile biota in replicate sets of horizontal (H) and vertical (V) scrape samples from each of the five artificial reefs. Taxa are listed in order of overall mean percent biomass. Total (Σ) and mean ($\bar{x}$) biomass, standard error (S.E.), and number of samples in each set of replicates (n) are shown below.

TAXON		3.5-yr		4.5-yr		6.0-yr		8.0-yr		10.0-yr	
		H	V	H	V	H	V	H	V	H	V
Cirripedia (shell)		56	72	60	74	14	84	10	65	33	75
Mollusca (shell)		3	2	32	20	64	11	24	8	41	17
Ascidiacea		31	19	< 1	< 1	< 1	< 1	51	16	1	< 1
Hydrozoa/Bryozoa		2	4	1	2	2	1	2	7	6	3
Porifera		3	2	2	< 1	2	1	6	3	3	2
Octocorallia		-	-	< 1	-	11	< 1	1	-	11	-
Mollusca (soft tissue)		2	1	2	2	5	1	2	1	2	2
Actiniaria		2	1	1	1	2	1	1	2	1	1
Cirripedia (soft tissue)		2	1	1	1	< 1	1	1	1	1	1
Algae		<1	<1	-	-	-	-	< 1	< 1	< 1	-
Scleractinia		-	-	<1	-	-	-	-	-	1	-
Total Biomass (g)	Σ	495	1291	851	982	449	761	687	952	717	1392
	$\bar{x}$	62	161	106	123	56	95	86	119	90	174
	S.E.	22	17	11	11	30	11	26	12	17	17
	n	8	8	8	8	8	8	8	8	8	8

shell fraction, that any increases in number or size of the barnacles were simply not accompanied by detectable increases in weight of the soft tissue. The same arguments can be applied to the mollusks; however, unlike the barnacles, most of the mollusks in scrape samples appeared to have been living at the time they were collected, judging from intact specimens and viscera attached to shell fragments. This suggests that differences in mollusk shell weight were largely due to changes in the proportion or size of living organisms, although these changes were not reflected in corresponding differences in soft tissue weight.

Mean percent cover was calculated from point-count data using close-up photographs from horizontal and vertical surfaces of each sunken vessel (Figure 1.37). The mean percent cover of sessile biota was invariably higher on vertical surfaces than on horizontal surfaces. Total cover on vertical surfaces was 100% on all except the 6.0-yr reef; whereas, percent cover on horizontal surfaces was lower on the three younger reefs than it was on the two older ones. Differences in total percent cover were significant, both among reefs and between surface orientations, with these two factors accounting for 65% of the total variance in the data set (Table 1.17). However, a highly significant interaction effect indicated that the two factors were not independent of one another. The results of Tukey's studentized range test show that the only significant difference among reefs was between the 6.0- and 8.0-yr reefs, while Figure 1.37 indicates that this difference was clearly dependent on surface orientation. Thus, mean percent cover on horizontal surfaces was considerably lower on the 6.0-yr reef than it was on the 8.0-yr reef, while mean percent cover on vertical surfaces was virtually the same on all reefs.

No consistent trends were observed in percent cover of the various taxa with increasing age of the reef (Table 1.22). Discounting the undetermined invertebrate cover, vertical surfaces on all reefs appeared to be dominated by hydroids and erect bryozoans. These taxa were also the most prevalent growth forms on horizontal surfaces of the 3.5- and 4.5-yr reefs. Octocorals represented the dominant cover on horizontal surfaces of the 6.0- and 10.0-yr reefs, while anemones had the highest percent cover on the 8.0-yr reef. Because of their branching, erect growth form, and high frequency of occurrence, some hydroids (notably, Halocordyle disticha and Eudendrium sp.) often obscured the underlying biota. This factor contributed to the high percent cover estimates for undetermined invertebrates and to the deceptively low percent cover estimates for barnacles and other encrusting growth forms.

The photographs taken at a distance of 1 m from the surface of each vessel indicated that there were no large sessile invertebrates such as the sponges and corals typically observed on natural hard bottom in the region [SCWMRD, 1982]. The 1-m photographs also confirmed some general impressions about the various reefs. Among these observations were: 1) a noticeably higher percent biotic cover on vertical than on horizontal surfaces, 2) a relatively high frequency of occurrence for octocorals on horizontal surfaces of the 6.0- and 10.0-yr reefs and their absence from the 3.5-yr reef, 3) more erect (as opposed to encrusting) growth on horizontal surfaces, 4) a comparatively high frequency of occurrence of

Table 1.22 Mean percent cover estimates for major taxa observed in close-up photographs of horizontal (H) and vertical (V) surfaces on each artificial reef. Taxa are listed in order of overall mean percent cover. The total number of points analyzed (Σ), mean percent biotic cover ($\overline{x}$), standard error (S.E.) and number of photographs in each set of replicates (n), are shown below.

TAXON		3.5-yr		4.5-yr		6.0-yr		8.0-yr		10.0-yr	
		H	V	H	V	H	V	H	V	H	V
Undetermined Invertebrata		15	37	34	52	11	46	19	35	22	39
Hydrozoa/Bryozoa		13	42	16	27	8	28	16	30	11	32
Porifera/Ascidiacea		10	16	10	8	2	3	12	19	12	19
Actiniaria		-	-	4	6	<1	<1	25	13	5	6
Cirripedia		4	7	-	9	1	20	<1	5	<1	5
Octocorallia		-	-	1	-	19	-	<1	-	18	-
Algae		3	-	-	-	-	-	1	-	-	-
Mollusca		-	-	-	-	<1	2	-	-	-	<1
Scleractinia		<1	-	-	-	-	-	-	-	2	-
Total No. Points Analyzed	Σ	711	1263	1092	1238	485	525	1392	1368	1063	1299
Mean Percent Biotic Cover	$\overline{x}$	42	100	61	100	33	97	74	100	70	100
	S.E.	8	0	6	<1	6	3	9	0	7	0
	n	12	19	18	19	8	9	20	19	18	20

anemones on both surfaces (especially on horizontal surfaces) of the 8.0-yr reef, and 5) a generally ubiquitous covering of seemingly dead barnacles on all reefs.

The results of the long-term colonization study indicate no consistent trends in biomass, percent cover, or number of sessile species with increasing age of the artificial reefs. These results differ markedly from those of the short-term colonization study in which significant increases occurred in all three variables with increasing duration of plate exposure (see section 1.A). Mean biomass and mean percent cover values on all artificial reefs were comparable to those on the 6-mo colonization plates which, like the artificial reefs, were sampled in summer. Mean numbers of sessile species, however, were considerably higher on artificial reefs than they were on the 6-mo colonization plates, but were only slightly higher on reefs than on the 9- and 12-mo plates. These results suggest that during the first year of substrate exposure, there are rapid increases in biomass, percent cover, and number of sessile species. Thereafter, all three variables may fluctuate seasonally, but do not appear to increase with increasing age of the substrate. Similarily, Osman (1978) found that an equilibrium number of species was attained on settling plates after 6 to 12 mo (depending on time of initial exposure) and he subsequently observed distinct seasonal fluctuations in total numbers of species, characterized by a summer high and a winter low.

With respect to individual taxa, octocorals and scleractinian corals were absent from the youngest reef as well as from all colonization plates exposed for a year or less. Anemones were present on all reefs but did not occur on any colonization plates. None of these taxa, however, exhibited any consistent trends in percent cover or biomass with respect to the age of the reefs. Sessile mollusks, however, (particularly the jewel boxes _C. macerophylla_ and _Chama congregata_) comprised a much greater proportion of the total biomass on the four older reefs than they did on the youngest reef. Furthermore, these organisms were virtually absent from all short-term colonization plates.

These results suggest that a number of taxa are relatively small components of the sessile biota until some time after the first year of substrate exposure. Even among the artificial reefs, the oldest of which had been exposed for 10.0 years, corals and anemones were only sporadically important constituents of the epifaunal community. The apparent absence of large sponges and corals from all artificial reefs is especially noteworthy since many of these organisms are known to occur on natural hard bottom in the immediate vicinity of at least the 3.5- and 8.0-yr reefs (Henry Ansley, personal communication). This would seem to indicate that many of the sessile species which make hard-bottom habitats so attractive to fishes are very slow to colonize new substrates or reach an appreciable size.

The delayed recruitment and growth of large epifauna is supported by the results of other studies as well (Davis et al., 1982; George and Thomas, 1979; Van Dolah et al., 1984). In our long-term colonization study, the fact that sessile mollusks comprised a relatively small proportion of the total biomass on the 3.5-yr reef, although they occurred with about the same frequency as on the older reefs, suggests that the greater biomass of mollusks on older substrates may be a function of relatively long-lived species being recruited late in the "successional" sequence and, thereafter, increasing in size rather than numbers. This pattern seems to conform to that of Connell and Slayter's (1977) "inhibition" model of succession which predicts that later species, such as the sessile mollusks in this study, will eventually succeed in establishing populations simply because they live longer and, consequently, replace earlier colonists killed by physical extremes, predation, herbivory, disease, or senescence. According to this model of succession, competitive superiority is not a prerequisite for eventual dominance by these later colonists, since the initial colonists must first have succumbed to other adversities.

Jackson (1977) observed in his study of tropical reef environments that colonial species eventually excluded solitary organisms over the course of 26 months. However, others have noted the opposite trend (i.e., a shift in dominance from colonial to solitary organisms) in the temperate subtidal waters of Puget Sound (Schoener and Schoener, 1981; Greene and Schoener, 1982). The relatively greater abundance of barnacles, bivalves, anemones, and solitary tunicates in the temperate environment accounted for the latitudinal differences between hard bottom communities. This suggests that factors other than competition for space, such as larval availability in the plankton or differential predation pressure may be more important in determining the community structure of some fouling communities.

The results of the artificial reef study bear similarities to both the tropical and temperate fouling studies. As in Jackson's (1977) study, colonial organisms (particularly hydroids, bryozoans, sponges, and certain ascidians) accounted for the greatest number of species, although the relative importance of these various taxa differed among reefs. Percent cover data also seemed to indicate that colonial organisms had achieved dominance over solitary forms; however, estimates of percent cover for individual taxa were generally unreliable due to the poor image resolution in photographs and to the presence of several canopy species that obscured much of the encrusting biota. Biomass measurements, on the other hand, indicated that solitary organisms (namely, barnacles and mollusks) comprised the greatest proportion of total biomass on all reefs. This would seem to agree more closely with Schoener and Schoener's (1981) observation of eventual dominance by solitary forms. However, if one discounts shell weight (some of which may have represented dead barnacles and mollusks), and considers only soft-tissue weight, colonial organisms comprised a greater proportion of the total biomass than solitary forms.

In summary, there was no clear competitive hierarchy with respect to colonial versus solitary organisms on any artificial reef. Both forms co-occurred in all scraped quadrats and both life history strategies were represented among the most frequently occurring species on all reefs regardless of age. The same pattern was also observed on colonization plates exposed for one year or less (although, the dominant species on colonization plates differed from those on the reefs). Clearly, solitary organisms, such as barnacles and mollusks, are more important constituents of the sessile biota in temperate than in tropical hard-bottom communities, even if only in terms of providing greater habitat heterogeneity. However, in this study colonial organisms appeared to be dominant with respect to both numbers of species and biomass excluding shell weight.

Although there were no consistent trends in biomass, percent cover, or numbers of sessile species with increasing age of the artificial reefs, these three variables were all significantly greater on vertical than on horizontal surfaces. Similarily, many of the most frequently occurring species were more common on vertical than on horizontal surfaces. This was not the case on the short-term colonization plates, where there were no significant differences between orientations. However, if top surfaces of horizontal plates had been analyzed separately from bottom surfaces (which were actually more similar to vertical surfaces in terms of their biomass, percent cover, and number of sessile species), it is likely that significant differences between some plate surfaces would have been noted. This is supported by the fact that top surfaces of plates (which were analagous to horizontal surfaces of reefs) had considerably lower biomass and percent cover values than either bottom or vertical plate surfaces, regardless of the length of plate exposure.

The greater biomass, percent cover, and number of sessile species on vertical and bottom surfaces might be caused by a number of factors. Among these are heavier predation pressure and greater sedimentation on horizontal surfaces (Harris and Irons, 1982), as well as negative phototactic behavior of settling larvae (Vandermeulen and DeWreede, 1982). With respect to differential predation between the two surface orientations, there was distinct evidence of cropping only on top surfaces of the colonization plates. No such observations were made on the artificial reefs; however, several fishes known to graze heavily on sessile epifauna were observed in large numbers on all reefs and in lower abundances near the colonization frames (see section I.A).

Harris and Irons (1982) suggest that sediment accumulation may explain the observation made by other investigators that communities on upper horizontal surfaces tend to be dominated by organisms having erect or mounding growth forms. Similar patterns were observed in the 1-m photographs of horizontal surfaces on the artificial reefs. Furthermore, among the few species that were more common on horizontal than on vertical surfaces, four had erect growth forms (the octocorals _Telesto fruticulosa_ and _T. sanguinea_, and the hydroids _Dynamena quadridentata_ and _Monostaechas quadridens_); one was an encrusting bryozoan that is epizoic on gastropod shells (_Antropora leucocypha_); and one was a tube-dwelling polychaete that constructs its tubes using sand grains (_Sabellaria vulgaris_). Thus, the ability of these organisms to inhabit horizontal surfaces may be due, in part, to various morphological characteristics or life history attributes which confer a degree of tolerance to higher sediment loads. Nevertheless, the fact that most encrusting growth forms were not excluded from horizontal surfaces suggests that sediment accumulation was rarely a limiting factor. This may be a consequence of the fact that, like _A. leucocypha_, many encrusting bryozoans, sponges, and ascidians were epizoic on barnacles, mollusks, and hydroids, all of which provided small-scale relief and, thus, protection from burial by sediments.

Superimposed on patterns related to substrate age and surface orientation, at least two other factors may have contributed to differences among the artificial reefs. One factor was related to the history of the 6.0-yr reef which was anomalous in that it had settled on the bottom upside-down. Consequently, the only surfaces accessible to sampling were the bottom and lower sides of the hull. It is likely that anti-fouling paint had been applied to these surfaces, thus inhibiting the colonization and growth of sessile organisms. This could explain the significantly lower biomass, percent cover, and fewer sessile species on both horizontal and vertical surfaces of the 6.0-yr reef.

Another factor which appears to have influenced community structure on the 3.5- and 8.0-yr reefs, was their proximity to natural hard-bottom habitat and, consequently, to a source of larval recruitment. The 8.0-yr reef had the greatest number of sessile species and highest percent cover among all artificial reefs. In addition, both the 3.5- and 8.0-yr reefs were characterized by higher ascidian biomass and a greater number of ascidian species than on the other three reefs. This may be a function of the very short-lived planktonic existence, ranging from minutes to a few hours at most, of many ascidian larvae (Berrill, 1950). This contrasts sharply with the relatively extended planktonic existence of the more ubiquitous organisms in our study such as barnacles, which can postpone settlement for several weeks (Lewis, 1972). Thus, the epifaunal communities on artificial substrates located near hard-bottom habitats seem to develop differently from those on substrates more distant from these areas. This conclusion is supported by the results of the short-term colonization study which demonstrated that fouling plates located in a hard-bottom habitat had significantly more sessile species, greater percent cover, and greater biomass than fouling plates located in a sand-bottom habitat. Furthermore, among the 3-, 6-, 9-, and 12-month plates, ascidians invariably had a higher percent cover on hard-bottom plates than on sand-bottom plates sampled during the same season.

Perhaps the most remarkable feature of the sessile biota on all artificial reefs was the consistent occurrence of one particular group of species (Group A, Table 1.20). These species are common constituents of natural hard-bottom communities elsewhere (SCWMRD,1982). The fact that they were invariably present on all artificial reefs, regardless of substratum age, suggests that a stable epifaunal community had been achieved after 3.5 years. Nevertheless, the absence of all large sessile invertebrates, many of which are also commonly found in the South Atlantic Bight (SCWMRD,1982), may indicate that the reef communities examined in this study are still undergoing succession, even after 10.0 years of substratum exposure. However, if natural and artificial substrata differ in their ability to attract and support populations of certain epifaunal invertebrates, then one might reasonably conclude that the communities developing on these substrata will never approach a common end point or "climax" community. In any case, the establishment of a reasonably persistent epifaunal community is likely to take at least three to five years, based on comparisons between long-term and short-term colonization studies.

Motile Biota:

Suction samples from horizontal and vertical surfaces of all five artificial reefs resulted in the collection of 2007 motile macroinvertebrates representing 125 species. Fourteen major taxa were represented, with decapods, polychaetes, gastropods, amphipods, and pelecypods accounting for the greatest number of species (Table 1.23). Together, these taxa constituted more than 74% of the species collected from either surface of all but the 6.0 yr-reef, where only five species were collected from vertical surfaces. The relative importance of these major taxa varied from reef to reef, while the remaining taxa were relatively insignificant, each being represented by three or fewer species. Fewer major taxa were found on the two younger reefs than on the three older ones, and the overall number of species increased with reef age (Table 1.23).

Amphipods were most abundant and represented 39% of the organisms from all samples combined. These organisms dominated the 3.5- and 8.0-yr reefs, and were followed in overall abundance by gastropods, isopods, and tanaids (Table 1.24). The ten remaining taxa were not as well represented, with each contributing less than 5% of the total number of individuals in the combined samples.

Unlike the motile epifauna on the short-term colonization plates, the artificial reef communities were not strongly dominated by a single ubiquitous species. The most abundant motile reef species was the isopod *Carpias bermudensis* which, although it was collected at all five reefs (Figure 1.38), comprised only 11% of the total number of individuals. This hard-bottom species was among the more common motile invertebrates encountered on the short-term colonization plates, where it was most abundant during summer and fall on hard-bottom plates. *Carpias bermudensis* has been collected from corals, reefs, hard bottom, and occasionally from sand in shelf waters from Bermuda to southern Florida (Miller,1968; Pires,1980; SCWMRD,1982). The greatest densities of *C. bermudensis* among the artificial reefs examined in our study occurred on the two oldest reefs, where it was most abundant on horizontal surfaces.

Second in overall abundance was the gastropod *Parviturboides interruptus*, which occurred in very high densities on the oldest reef and in much lower numbers on the 3.5- and 8.0-yr reefs (Figure 1.38). This species is commonly found living on sponges (Abbott,1974), and Van Dolah et al. (1983) described it as an important commensal of the vase sponge, *Ircinia campana*. The association with such a host and the resultant contagious distribution may explain the high variability in density of *P. interruptus* among the five artificial reefs (Figure 1.38). *Parviturboides interruptus* was found almost exclusively on the horizontal surfaces of reefs, a pattern which may also depend largely on the distribution of its host(s).

Several gammarid amphipod species were among the dominants, including *Photis* sp., *Gammaropsis* sp., *Erichthonius brasiliensis*, *Lembos websteri*, and *Elasmopus* sp. A. All of these were most numerous on the 3.5- and 8.0-yr reefs, and occurred primarily on horizontal surfaces. The tanaid

Table 1.23 Percent contribution by major taxa to the total number of motile invertebrate species collected in pooled suction samples from horizontal (H) and vertical (V) surfaces of the five artificial reefs. Taxa are ranked in descending order of the overall number of species contributing to each category.

TAXON	3.5-yr		4.5-yr		6.0-yr		8.0-yr		10.0 -yr	
	H	V	H	V	H	V	H	V	H	V
Decapoda	26	17	16	50	27	-	15	4	18	33
Polychaeta	10	17	16	12	4	20	21	13	19	8
Gastropoda	19	12	34	12	24	20	13	9	24	-
Amphipoda	32	46	9	25	13	20	26	48	17	42
Pelecypoda	-	-	16	-	13	-	6	-	8	-
Isopoda	3	4	3	-	4	-	4	9	2	8
Sipuncula	-	-	3	-	4	-	-	-	2	-
Tanaidacea	3	4	-	-	2	20	4	9	2	-
Echinodermata	3	-	-	-	2	20	4	4	3	8
Pycnogonida	3	-	-	-	-	-	2	-	-	-
Mysidacea	-	-	-	-	-	-	-	-	2	-
Turbellaria	-	-	-	-	-	-	2	-	-	-
Nematoda	-	-	3	-	2	-	2	-	2	-
Nemertinea	-	-	-	-	2	-	2	4	2	-
Total No. Species (Σ)	31	24	32	8	45	5	53	23	62	12
Grand Total (ΣΣ)	36		38		47		57		63	

Table 1.24 Percent contribution by major taxa to the total number of motile invertebrates in replicate sets of horizontal (H) and vertical (V) suction samples from each of the five artificial reefs. Taxa are listed in order of overall numerical abundance. Total (Σ) and mean ($\bar{x}$) number of individuals, standard error (S.E.), and number of replicates at each reef are shown below.

TAXON	3.5-yr		4.5-yr		6.0-yr		8.0-yr		10.0-yr	
	H	V	H	V	H	V	H	V	H	V
Amphipoda	72	71	10	25	12	17	42	49	12	47
Gastropoda	17	6	43	12	41	17	4	2	42	-
Isopoda	3	16	2	-	10	-	15	31	8	16
Tanaidacea	3	1	-	-	6	33	17	9	3	-
Decapoda	4	3	12	50	16	-	3	4	3	26
Polychaeta	1	4	10	12	3	17	4	2	10	5
Nematoda	-	-	7	-	3	-	3	-	13	-
Echinodermata	1	-	-	-	1	17	8	2	5	5
Pelecypoda	-	-	12	-	7	-	4	-	2	-
Nemertinea	-	-	-	-	1	-	<1	1	1	-
Sipuncula	-	-	2	-	1	-	-	-	<1	-
Pycnogonida	<1	-	-	-	-	-	<1	-	-	-
Mysidacea	-	-	-	-	-	-	-	-	<1	-
Turbellaria	-	-	-	-	-	-	<1	-	-	-
(Σ)	351	168	81	8	179	6	543	157	496	19
$\bar{x}$	117.0	56.0	27.0	2.7	59.7	2.0	181.0	52.3	165.3	6.3
S.E.	29.9	18.2	10.6	1.8	15.8	0	48.8	14.8	100.6	4.9
n	3	3	3	3	3	3	3	3	3	3

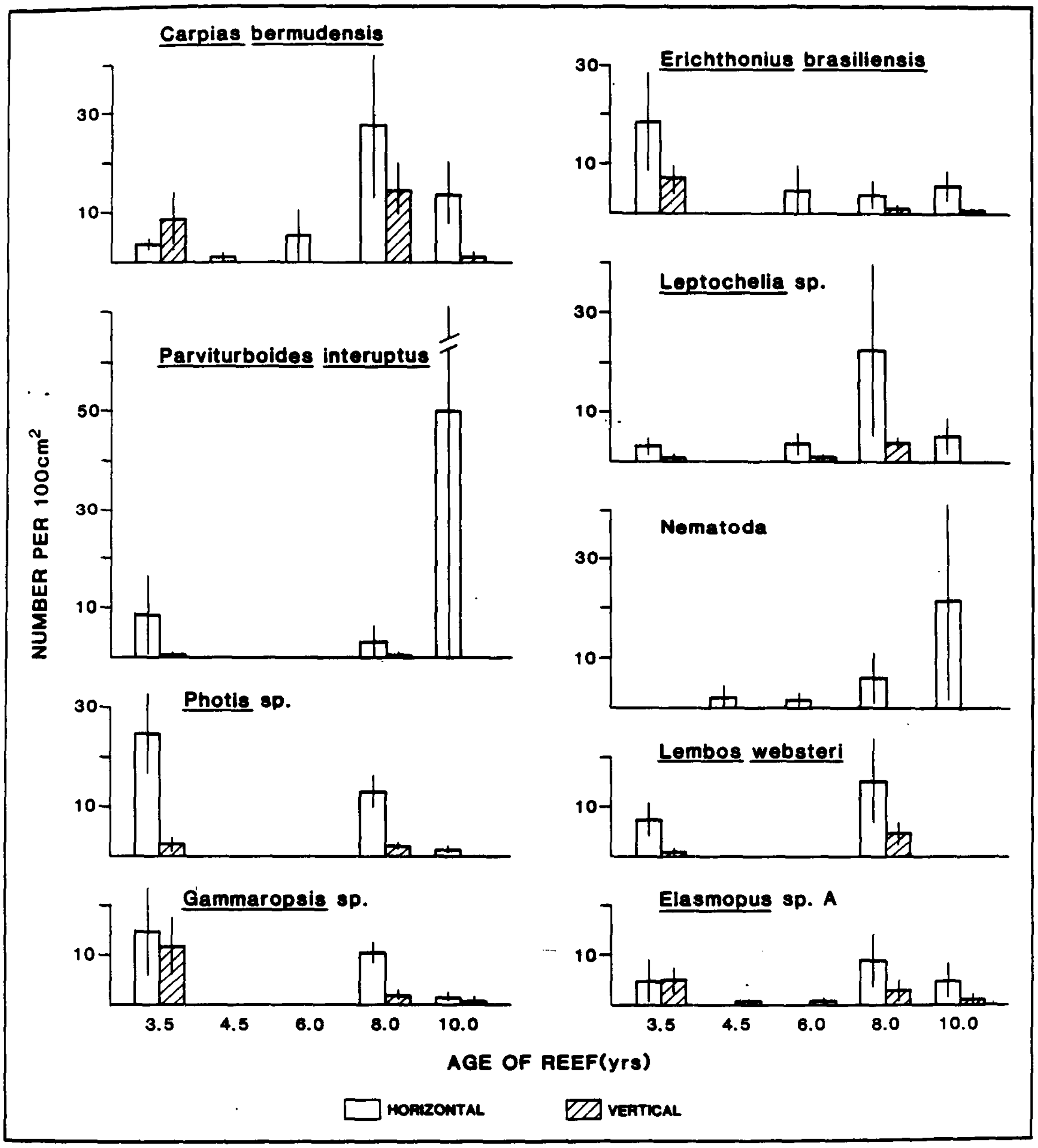


Figure 1.38 Mean density for each of the dominant motile species on both surfaces of the five artificial reefs. Vertical lines represent the standard error of the means (n = 3).

Leptochelia sp. and one or more undetermined species of benthic nematodes were particularly abundant on the 8.0- and 10.0-yr reefs, respectively. Both were most numerous on the horizontal surfaces, to which the nematodes were apparently restricted (Figure 1.38). The remaining 116 species were less abundant and none contributed greater than 4% of the total number of individuals on all reefs together. However, two of these species (the gastropods Costoanachis sp. A and Astyris lunata) were the most abundant motile organisms on the 4.5- and 6.0-yr reefs; the overall dominant species mentioned previously were often rather low in abundance on those reefs (Figure 1.38, Appendices 1.21, 1.22).

The total number of individuals (all species combined) in suction samples varied considerably among the different reefs and between orientations. Two vertical collections yielded no animals, while a maximum of 365 organisms were collected in one horizontal sample (Appendix 1.23). As suggested by the distribution patterns of the dominant species (Figure 1.38), the mean abundance of the motile fauna (all species combined) was significantly greater on horizontal surfaces than on vertical ones (Figure 1.39, Table 1.25). Among all reefs, the mean density on horizontal surfaces was 110 individuals per sample (100 cm^2), while on vertical surfaces the density was only 23.9 individuals per sample. There was also a highly significant difference among the reefs, with densities on the 3.5- and 8.0-yr reefs significantly higher than on the others (Table 1.25). A significant interaction between the reef age and surface orientation indicates that the two factors were not independent. Thus, more individuals were found on vertical surfaces of the 3.5- and 8.0-yr reefs than on vertical surfaces of the others (Table 1.25, Figure 1.39).

The number of motile species also showed considerable variation among samples, with two samples containing no species while the richest contained 37 (Appendix 1.23). The mean number of species per sample was significantly greater on horizontal portions of the reef than on vertical ones (Figure 1.40a, Table 1.25). Significant differences in the mean number of species were also noted among the various reefs (Figure 1.40a); however there was no clear pattern related to their age; however, the interaction between this factor and surface orientation was significant (Table 1.25). A distinct pattern did appear when the total numbers of species in each treatment group, rather than the means, were compared (Figure 1.40b). The total number of species (combined vertical and horizontal surfaces) varied directly with the age of the reef, with 36 species on the youngest and 63 on the oldest reef. This trend largely reflected the pattern observed on the horizontal surface alone; that is, there were few species unique to the vertical surfaces that contributed to the combined species list (Figure 1.40b). The lack of a clear trend among means may indicate that the size of individual replicates was inadequate to estimate the total number of species, particularly since pooling of the three replicates resulted in a considerable increase in the number of species, especially on horizontal surfaces (Figure 1.40a, b). Since the greater number of species is more representative of the actual species richness of the motile community, pooled-replicate samples were used in comparisons of species diversity, evenness, and richness on each surface of all reefs (Figure 1.41).

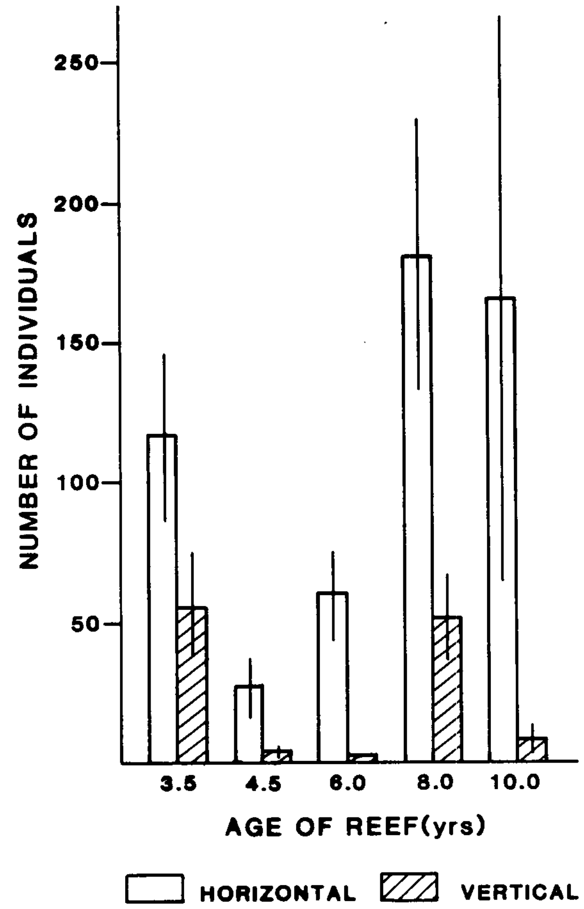


Figure 1.39 Mean abundance of motile epifauna in suction samples from both surfaces of the five artificial reefs. Vertical lines represent the standard error of the means (n = 3).

Table 1.25 Results of two two-way analyses of variance (Model I) comparing the number of motile invertebrate species and individuals in suction samples from horizontal and vertical surfaces of the five artificial reefs.

SOURCE OF VARIATION	Degrees of Freedom	F Value	Results of REGW[1] multiple F tests
	DEPENDENT VARIABLE: $\log_{10}[(\text{No. spp./sample}) + 1]$		
Model ($r^2 = 0.80$)	9	8.91***	
Factor A: Age of Reef (3.5,4.5,6.0,8.0,10.0 yr)	4	5.34**	$\mu_{4.5}\ \mu_{6.0}\ \mu_{10.0}\ \mu_{3.5}\ \mu_{8.0}$
Factor B: Surface Orientation (Horizontal, Vertical)	1	44.72***	$\underline{\mu_V} < \underline{\mu_H}$
Interaction Effects A x B	4	3.52*	
	DEPENDENT VARIABLE: $\log_{10}[(\text{No. indiv./sample}) + 1]$		
Model ($r^2 = 0.85$)	9	12.40***	
Factor A: Age of Reef (3.5,4.5,6.0,8.0,10.0 yr)	4	11.47***	$\underline{\mu_{4.5}\ \mu_{6.0}\ \mu_{10.0}} < \underline{\mu_{3.5}\ \mu_{8.0}}$
Factor B: Surface Orientation (Horizontal, Vertical)	1	53.95***	$\underline{\mu_V} < \underline{\mu_H}$
Interaction A x B	4	2.95*	

*significant at 0.05 level
**significant at 0.01 level
***significant at 0.001 level

[1] Ryan-Einot-Gabriel-Welsch; means connected by underlines are not significantly different at $\alpha = 0.05$

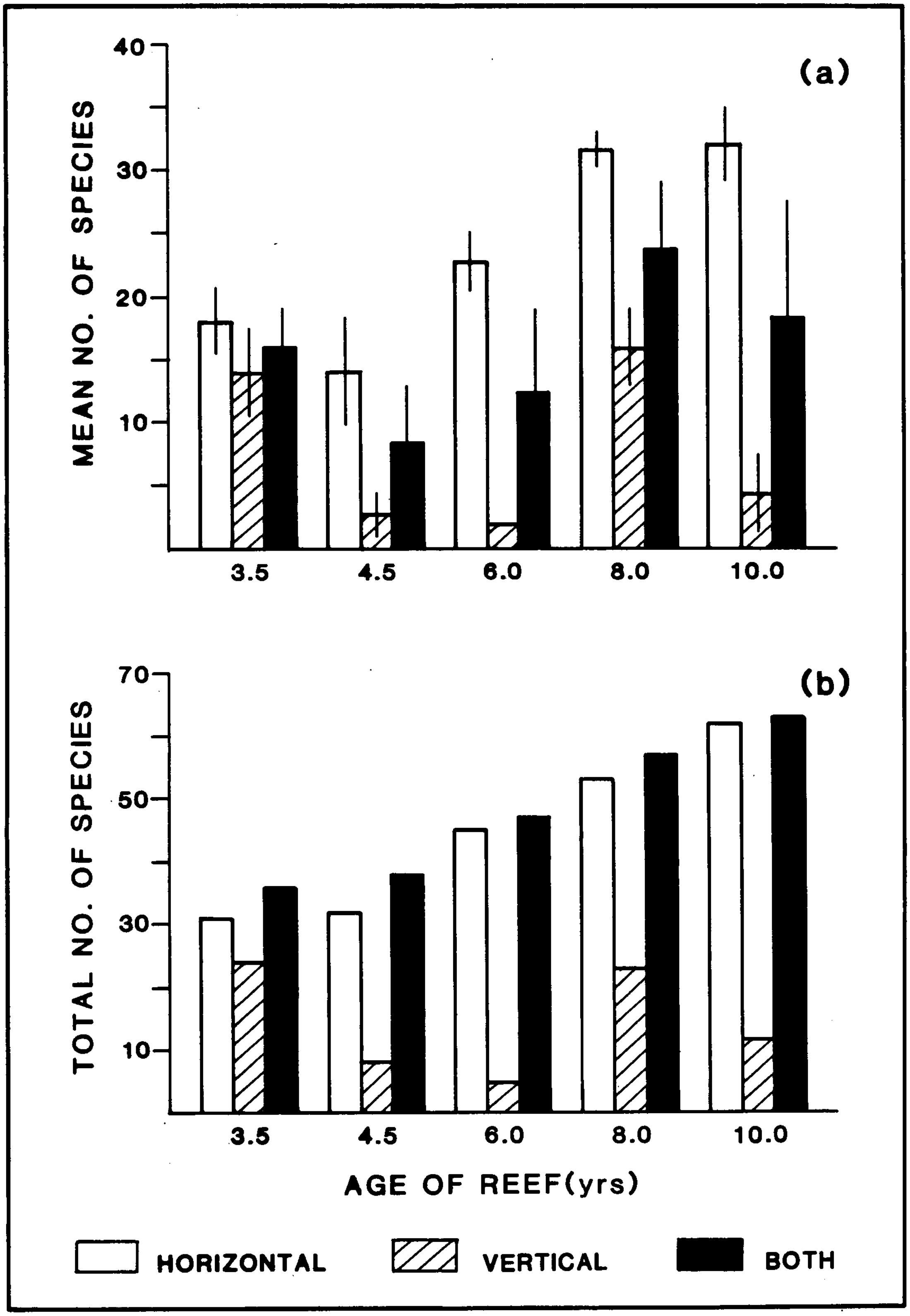


Figure 1.40 Mean number of motile species per suction sample (a) and total number of species in pooled suction samples (b) from horizontal (n = 3), vertical (n = 3), and both surfaces combined (n = 6) on each of the five artificial reefs. Vertical lines represent the standard error of the means.

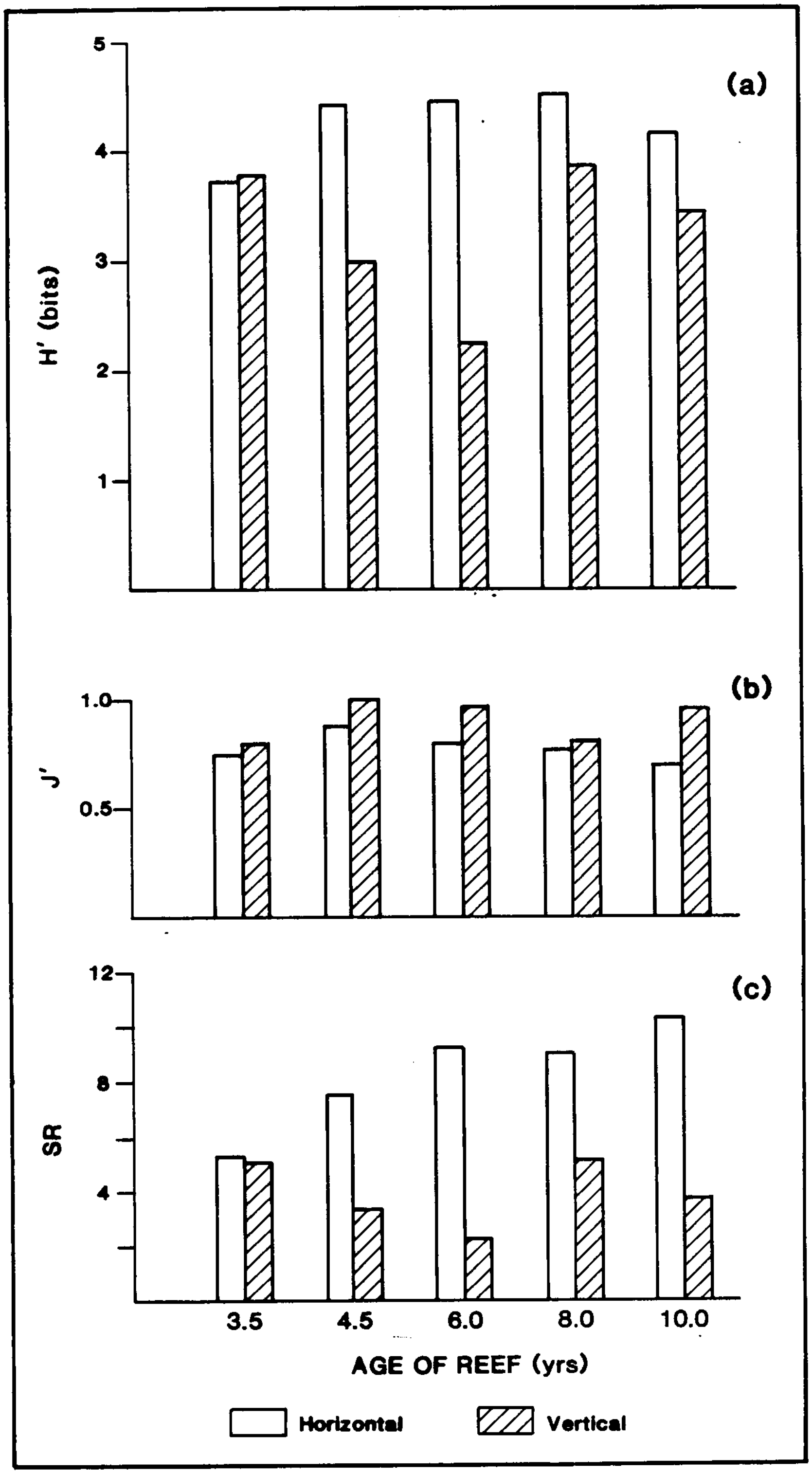


Figure 1.41 Values of diversity (H'), evenness (J'), and species richness (SR) of motile epifauna in pooled suction samples from each of the five artificial reefs.

Species diversity ranged from 2.3 to 4.5 bits among all reefs, and showed similar differences between horizontal and vertical surfaces on all except the youngest reef (Figure 1.41a). The communities on horizontal surfaces were consistently more diverse than those on vertical ones (Figure 1.41a), despite the more equitable distribution of individuals among species on vertical surfaces, where J' frequently approached its upper limit of 1.0 (Figure 1.41b). The higher diversity on the horizontal surfaces was largely due to greater species richness on that surface; values of SR ranged from 5.3 to 10.3 for horizontal surfaces and from 2.2 to 5.1 for vertical orientations (Figure 1.41c). Such marked differences did not occur on the 3.5-yr reef, where values of H', J', and SR were nearly identical on horizontal and vertical surfaces.

There were consistent trends in diversity observed among the reefs, largely as a result of the differences noted between vertical and horizontal orientations. For example, the lowest diversity among horizontal samples was observed on the 3.5-yr reef, while the same reef exhibited the greatest diversity among vertical collections (Figure 1.41a). Evenness of species representation (J') was primarily a function of the number of individuals in each collection. Samples from the horizontal surfaces of 3.5-, 8.0-, and 10.0-yr reefs were frequently dominated by a small number of species and consequently had low J' values, while vertical samples from the 4.5-, 6.0-, and 10.0-yr reefs contained the fewest individuals and exhibited the greatest evenness (Figures 1.39, 1.41b). Patterns of species richness were generally parallel to the trends described previously for the total number of species in pooled samples from both horizontal and vertical surfaces (Figures 1.40b, 1.41c). On horizontal surfaces SR increased with reef age, and on vertical surfaces richness was geater on the 3.5-yr and 8.0-yr reefs than on the others.

Although it showed no clear patterns of similarity related to reef age, the normal cluster dendrogram further illustrates the similarity between the motile epifaunal communities of the 3.5- and 8.0-yr reefs. Station Groups 1 through 3 consisted of collections from those two reefs, and were similar to one another, but quite dissimilar to the others which were composed principally of collections from the 4.5-, 6.0-, and 10.0-yr reefs. All but one collection in station Groups 1 and 2 were from horizontal surfaces, and most contained a greater number of individuals than collections in the remaining groups (Appendix 1.23). Vertical collections from the 3.5- and 8.0-yr reefs were slightly dissimilar to these horizontal ones, and formed Group 3.

The remaining station groups included samples from the 4.5-, 6.0-, and 10.0-yr reefs and were less similar to one another than the first three groups were (Figure 1.42). As noted above, horizontal samples were largely separated from vertical ones. Horizontal samples comprised station Group 4, while all but one sample in Groups 5 through 7 were vertical collections that contained very low numbers of motile invertebrates (Figure 1.42, Appendix 1.23). Group 5, for example, consisted of two collections which contained no animals and two others which, prior to data reduction, included only two individuals. The similarity coefficients among all four of these collections were zero, resulting in an uncommon lack of internal hierarchy for station Group 5 (Figure 1.42).

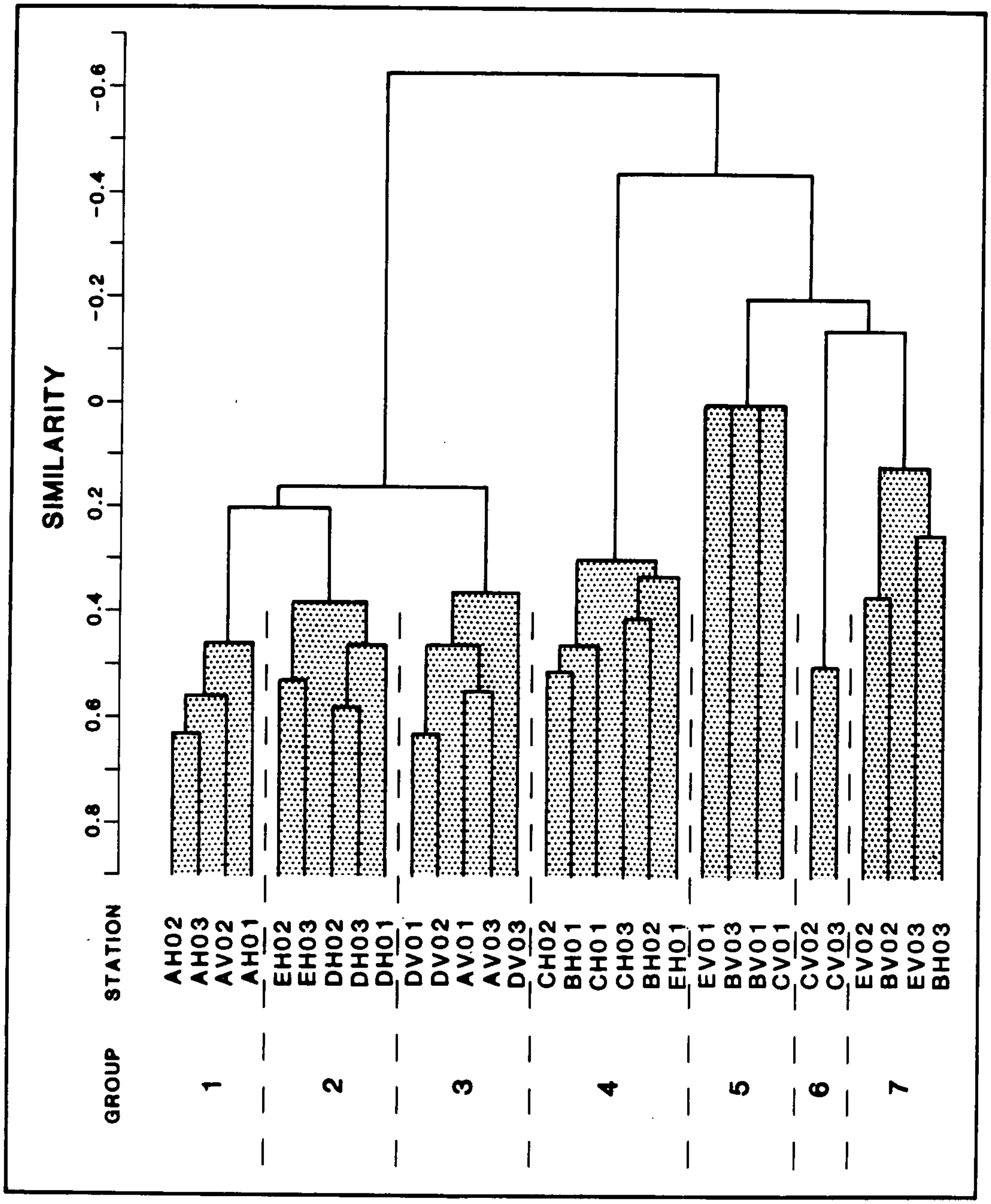


Figure 1.42 Normal cluster dendrogram of suction samples from horizontal (H) and vertical (V) surfaces of each artificial reef. (A = 3.5-yr reef; B = 4.5-yr reef; C = 6.0-yr reef; D = 8.0-yr reef; E = 10.0-yr reef).

The 74 motile species that remained following data reduction were placed into 10 species groups based on inverse classification (Table 1.26). Species Groups A through D were very dissimilar to the others, and their constituent species occurred less frequently on vertical than on horizontal surfaces of the artificial reefs (Figure 1.43). Three of these groups (A, B, and D) were moderately constant on horizontal surfaces of only one or two reefs, and consequently showed high fidelity to those sites (A at the 6.0-yr, B at the 10.0-yr, and D at the 4.5-yr reef). The species in these groups were low in abundance (Appendices 1.21 and 1.22), and none contributed greater than 0.5% of the total number of motile epifauna collected from the reefs.

Groups E and F, on the other hand, consisted of many numerically abundant species (Table 1.26, Appendices 1.22, 1.23). Eight species of peracarid crustaceans were contained in Group E: one isopod (*Carpias bermudensis*), a caprellid amphipod (*Caprella penantis*), several gammarid amphipods (*Gammaropsis* sp., *Erichthonius brasiliensis*, *Elasmopus* sp. A, *Lembos websteri*, *Photis* sp.), and a tanaidacean (*Leptochelia* sp.). Together, these species comprised more than 48% of the total number of individuals. They were ubiquitous on the 3.5-, 8.0- an 10.0-yr reefs, where they generally occurred on both surface orientations, accounting for the low or very low fidelity observed at all sites (Figure 1.43).

Group F included the second most abundant organism, *Parviturboides interruptus*, as well as many of the slightly less abundant species such as *Costoanachis* sp. A, *Astyris lunata*, and nematodes. This group differed from Group E mainly in its low constancy among vertical surfaces of all reefs. Higher constancy on the horizontal surfaces of the two oldest reefs resulted in moderate fidelity of Group F species to those sites (Figure 1.43).

Species in three of the remaining groups (G, I, and J) showed similar distribution patterns. Their constancy was moderate to high and they were highly restricted to the horizontal surface of one of the two oldest reefs (Figure 1.43). Several species in Group J, including *Exogone dispar*, *Jaeropsis coralicola*, *Apseudes* sp. A, and Pelecypoda J, were collected only from the 8.0-yr reef, while *Synalpheus* sp. and *Caecum pulchellum* of Group G were restricted to the 10.0-yr reef. Species in Group J also differed from those in most other groups, with regard to their numerical abundance; they were more abundant than all species other than those in Groups E and F. Finally, Group H species occurred most frequently on both surfaces of the 3.5-yr reef and were moderately restricted to that location. Only this group and Group E were composed exclusively of species which were collected from both horizontal and vertical orientations.

As previously noted, the motile species in marine fouling communities are often not considered, particularly in studies of large submerged structures such as the artificial reefs in the present study. Historically, investigators have relied primarily upon *in situ* diver observations and have made little attempt, other than anecdotally, to describe the motile organisms on the reef (Carlisle et al.,1964). Others have included qualitative descriptions of a few of the larger motile

Table 1.26 Species groups resulting from inverse cluster analysis of suction samples from the artificial reefs. (Am = Amphipoda; D = Decapoda; E = Echinodermata; I = Isopoda; M = Mollusca; P = Polychaeta; Si = Sipunculida; T = Tanaidacea).

Group A

Paracerceis caudata (I)
Inachoides forceps (D)
Pinnixa sp. (D)
Pagurus hendersoni (D)
Lembos sp. (Am)
Podocerus sp. (Am)
Natica pusilla (M)

Group B

Ophiuroidea undet. (E)
Cerithiopsis sp. (M)
Turridae K (M)
Pilumnus sp. A (D)
Gastropoda U (M)
Lima sp. (M)
Periclimenes iridescens (D)

Group C

Epitonium humphreysi (M)
Neopanope sayi (D)
Elasmopus sp. (Am)
Apseudes sp. (T)
Synalpheus townsendi (D)
Nudibranchia (M)
Leucothoe spinicarpa (Am)

Group D

Odontosyllis fulgurans (P)
Epitonium candeanum (M)
Crassispira albomaculata (M)
Pagurus sp. (D)
Costoanachis avara (M)
Epitonium sp. C (M)
Paguristes sp. (D)
Capitellidae (P)
Lembos smithi (Am)
Aspidosiphon gosnoldi (Si)

Group E

Caprella penantis (Am)
Gammaropsis sp. (Am)
Erichthonius brasiliensis (Am)
Elasmopus sp. A (Am)
Lembos websteri (Am)
Photis sp. (Am)
Carpias bermudensis (I)
Leptochelia sp. (T)

Group F

Costoanachis sp. A (M)
Pagurus carolinensis (D)
Astyris lunata (M)
Ophiothrix angulata (E)
Melanellidae (M)
Syllis spongicola (P)
Pelecypoda K (M)
Ophiuroidea A (E)
Nematoda
Prionospio cirrifera (P)
Chione grus (M)
Parviturboides interruptus (M)

Group G

Syllis gracilis (P)
Synalpheus sp. (D)
Caecum pulchellum (M)
Majidae A (D)
Nemertinea

Group H

Proceraea sp. (P)
Syllis hyalina (P)
Pseudomedaeus agassizii (D)
Stenothoe sp. (Am)

Group I

Exogone dispar (P)
Maera sp. A (Am)
Armandia maculata (P)
Podarke obscura (P)
Branchiosyllis exilis (P)
Pilumnus sp. (D)

Group J

Melita appendiculata (Am)
Corophiidae (Am)
Jaeropsis coralicola (I)
Luconacia incerta (Am)
Elasmopus levis (Am)
Apseudes sp. A (T)
Pelecypoda J (M)
Amphipoda undet.

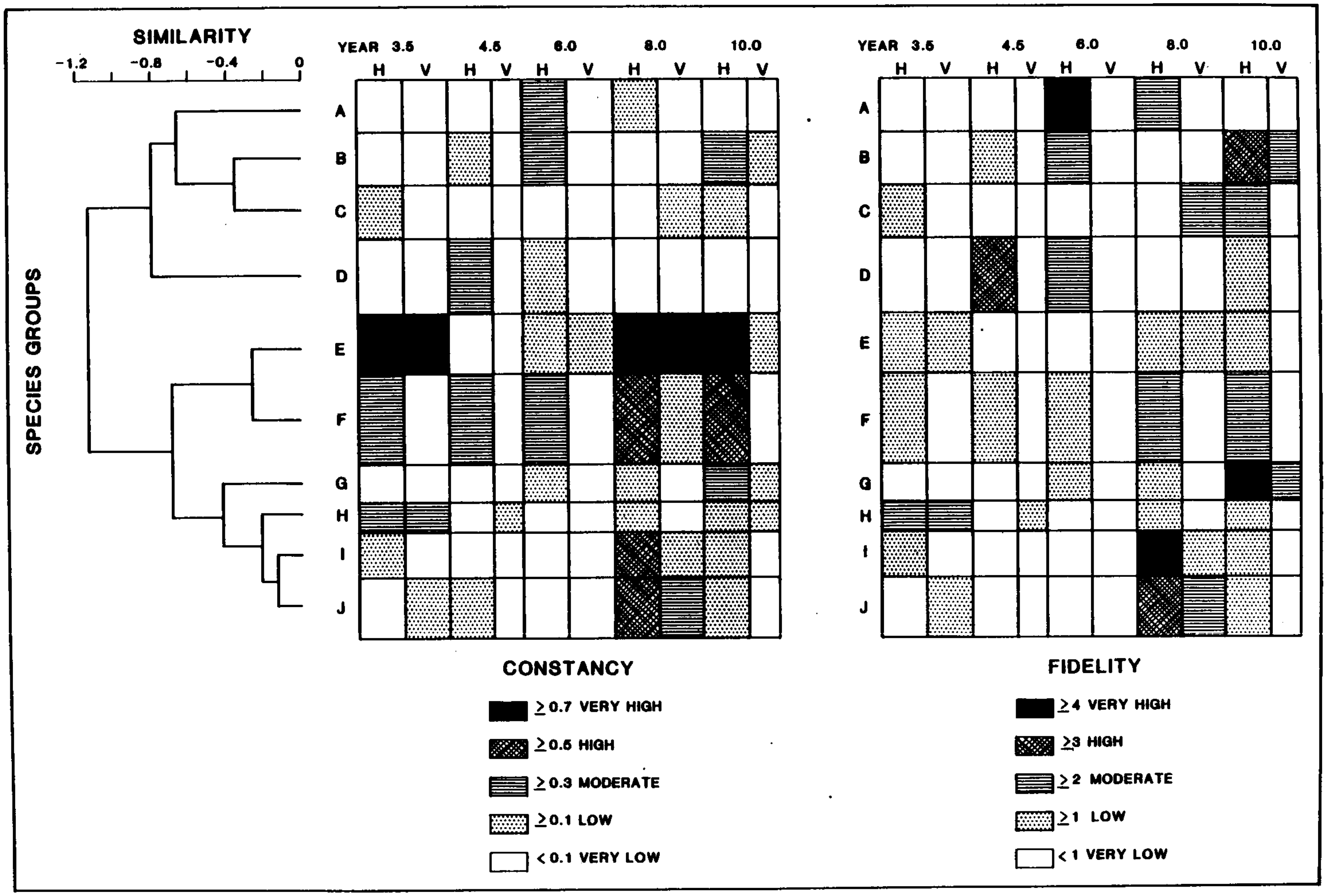


Figure 1.43 Inverse classification hierarchy of motile species in suction samples, and nodal diagrams showing constancy and fidelity of species groups on horizontal (H) and vertical (V) surfaces of each artificial reef.

organisms that are readily apparent to divers (Turner et al., 1969; Russell, 1975), but have ignored the smaller, more abundant motile forms. Certain motile species are known to be predators on sessile fouling organisms, (e.g., *Asterias, Lytechinus, Stylochus, Cancer,* and various nudibranchs) and have, consequently, received more attention than other constituents of the motile epifauna (Pearse and Chess, 1969; Harris and Irons, 1982). Recently, however, a growing number of studies, such as those on the biofouling communities of oil production platforms in the Gulf of Mexico (George and Thomas, 1979; Fotheringham, 1981), have included analyses of the smaller motile species such as amphipods and polychaetes.

A comparison of the various community structure parameters of the motile reef epifauna in the present study reveals no evidence to suggest that this community has reached a stable endpoint on any of the reefs. The number of species and species richness (SR) increased directly with the duration of reef submergence, and showed no indication of approaching an equilibrium. The constituent fauna of the older reefs also represented a broader range of invertebrate taxa than the younger reefs (Table 1.23).

A number of other differences were observed among reefs that were not obviously related to the duration of their submergence. Motile epifauna on the 4.5- and 6.0-yr reefs was considerably less abundant than on the others, and the dominant species on those two reefs also differed considerably from the others (Appendices 1.21, 1.22). Furthermore, vertical surfaces of the 4.5- and 6.0-yr reefs supported considerably fewer species, and as a consequence, were less diverse than vertical surfaces of other reefs.

Normal classification of suction samples indicated that the 3.5-yr reef was most similar to the 8.0-yr reef. The high similarity between the sessile fouling communities of these two reefs, as well as their proximity to one another and to natural hard bottom, has been previously described (see previous section). The density of motile epifauna on these reefs was significantly greater than on others, and the tube-building amphipods *Photis* sp., *Gammaropsis* sp., and *Erichthonius brasiliensis* were particularly abundant. These species, along with a number of other amphipods, rapidly colonized the plates of the short-term colonization studies, where they dominated the epifaunal community (Section I.A). Greatest densities of *E. brasiliensis* were observed during winter on 12-mo sand-bottom plates, where the dominant sessile organism was the ascidian *Styela plicata.* Amphipod tubes were densely aggregated on the tunic of these ascidians, indicating their suitability for attachment. A similar association may explain, in part, the extreme abundance of tubicolous amphipods on the 3.5- and 8.0-yr reefs, since ascidians also reached their greatest biomass on horizontal surfaces of these two reefs (see previous section).

Normal cluster analysis (Figure 1.42) also illustrates the distinct dissimilarity between horizontal and vertical surfaces of the reefs. The mean number of motile species on the top of the reefs was more than three times greater than on the sides. Furthermore, the mean density of the motile epifauna was more than four times as great on the top. This contrasts sharply with the sessile community, whose species richness, cover, and biomass were all significantly greater on the sides of the reefs. Reasons for these differences in the effect of orientation on sessile and motile organisms are not obvious. However, there is evidence to suggest that sediment accumulation on the top surfaces of the reefs may have served to increase the diversity of microhabitats available to small motile species, particularly infaunal organisms that might be excluded from vertical surfaces. Wenner et al. (1983) noted that such a layer of sediment over hard substrate may have contributed to the high diversity of motile invertebrates on natural hard bottom in this region. Sedimentation may also be the cause of the similarity in H' and SR between horizontal and vertical surfaces on the youngest (3.5-yr) reef. If the rate of sedimentation was roughly equivalent on all reefs, then the youngest would be expected to show less enhancement of microhabitat diversity on its top surface and, thus, smaller differences in species diversity between surfaces.

A comparison of the motile epifauna on the reefs with that on the relatively young plates reveals a number of similarities in those communities. Overall faunal density on the plates (21,000 individuals/m^2) was much higher than on the reefs (6,700 individuals/m^2) when averaged over the entire 12-mo study period. However, plates collected in late spring and summer (corresponding to the time of reef sampling) had a density of motile fauna (6,500 individuals/m^2) that was very close to the average density observed among reefs. Reefs and plates sampled during the same season also supported a comparable number of species. Spring and summer plates averaged 31-33 species per plate (450 cm^2), while the number of species in pooled reef samples, which have a somewhat greater surface area (600 cm^2), ranged from 36 to 63. Considerable overlap was observed in the species composition of the plate and reef communities, with a number of tube-dwelling gammarid amphipods being abundant on both artificial substrates. Caprellid amphipods, however, were much more abundant on the plates, and the dominance of amphipods was, in general, more extreme on the younger substrates. Overall species diversity (H'), however, was comparable between summer plates and reef samples (Figures 1.23, 1.29, 1.41). The differences observed between horizontal and vertical reef surfaces with respect to diversity, total abundance, and species richness, were not apparent among the plates. Reasons for this are not obvious, but it is probable that the effects of sedimentation were more important in determining community structure on the reefs than on the much younger plates, which had accumulated little sediment.

Fishes:

Approximately 71,500 fishes representing 22 families and 38 species were observed during fish counts on the five artificial reefs (Table 1.27). Dominant species were (by rank abundance) *Decapterus punctatus* (49,760 individuals), *Selar crumenophthalmus* (9,330), *Haemulon aurolineatum* (3,961), *Sardinella aurita* (3011), *Chaetodipterus faber* (990), *Lagodon rhomboides* (430), *Diplodus holbrooki* (409), *Stenotomus aculeatus* (380), *Sphyraena barracuda* (185), *Centropristis striata* (140), *Scomberomorus maculatus* (126)and *Equetus umbrosus* (84). Of the top five species, *Decapterus punctatus* was the most abundant species on all five reefs and

Table 1.27 Number of individuals of fishes observed on three transects across each artificial reef.

Family Species (Common name)	NUMBER OF INDIVIDUALS AGE OF REEF 3.5-yr	 4.5-yr	 6.0-yr	 8.0-yr	 10.0-yr
Orectolobidae					
Ginglymostoma cirratum (nurse shark)					1
Clupeidae					
Sardinella aurita (Spanish sardine)	3000			11	
Engraulidae					
Undetermined (anchovies)	1200	1000		200	
Batrachoididae					
Opsanus sp. (toadfishes)		1		1	
Serranidae					
Centropristis ocyurus (bank sea bass)		1	3		
Centropristis striata (black sea bass)	37	28	10	59	6
Mycteroperca microlepis (gag)		2	2	1	11
Serranus subligarius (belted sandfish)	4	8	5	11	10
Carangidae					
Caranx hippos (crevalle jack)		11			
Caranx sp. (jacks)		13			
Decapterus punctatus (round scad)	6510	14100	6400	12650	10100
Selar crumenophthalmus (bigeye scad)	70	7503	156	1	1600
Seriola dumerili (greater amberjack)	11	5		24	2
Lutjanidae					
Lutjanus campechanus (red snapper)			3		
Rhomboplites aurorubens (vermilion snapper)					1
Haemulidae					
Haemulon aurolineatum (tomtate)	615	1988	925	76	357
Sparidae					
Archosargus probatocephalus (sheepshead)			1		3
Calamus leucosteus (whitebone porgy)	7		9		1
Diplodus holbrooki (spottail pinfish)	34	30	146	13	186
Lagodon rhomboides (pinfish)		1		429	
Stenotomus aculeatus (southern porgy)	250	95	35		
Sciaenidae					
Equetus umbrosus (cubbyu)	28	1	9	1	45

Table 1.27 (Continued)

Family Species (Common name)	NUMBER OF INDIVIDUALS AGE OF REEF 3.5-yr	 4.5-yr	 6.0-yr	 8.0-yr	 10.0-yr
Mullidae					
Mullus auratus (red goatfish)		2			
Pseudupeneus maculatus (spotted goatfish)					3
Ephippidae					
Chaetodipterus faber (Atlantic spadefish)	94	4	169	628	95
Chaetodontidae					
Chaetodon ocellatus (spotfin butterflyfish)		2			
Pomacanthidae					
Holacanthus bermudensis (blue angelfish)					1
Pomacentridae					
Chromis enchrysurus (yellowtail reeffish)				1	
Labridae					
Halichoeres bivittatus (slippery dick)	9	9	30		29
Sphyraenidae					
Sphyraena barracuda (barracuda)	19	33	4	18	111
Sphyraena borealis (northern sennet)		1			
Blenniidae					
Undetermined (blennies)	6	2		5	1
Scombridae					
Scomberomorus cavalla (king mackerel)			1		
Scomberomorus maculatus (Spanish mackerel)	1	125			
Scomberomorus sp.	19			8	
Bothidae					
Paralichthys sp. (flounders)				2	
Balistidae					
Balistes capriscus (gray triggerfish)			2		
Ostraciidae					
Lactophrys quadricornis (scrawled cowfish)			1		
Total N	11914	24965	7911	14139	12563
Number of taxa	18	24	19	19	19

there was no significant difference among reefs in abundance per observation period for this species ($P > .05$, ANOVA). *Selar crumenophthalmus* was most abundant on the 4.5- and 10.0-yr reefs but was common on all other reefs, with the exception of the 8.0-yr structure. *Haemulon aurolineatum* showed significant ($p < .05$, ANOVA) differences in abundance among reefs, being more common on the younger reefs. Atlantic spadefish, *Chaetodipterus faber*, were most abundant on the 8.0-yr reef, but no significant difference was observed among reefs with respect to mean number per observation period. The other dominant fishes varied in abundance among the reefs.

Several species of commercial and recreational importance, including species that were priority species on natural reefs during Phases I and II of the Living Marine Resources Study, were also common on the artificial reefs. Black sea bass (*Centropristis striata*) were observed on all the reefs and reached their maximum abundance at similar depths on natural reefs (SCWMRD and GDNR 1981, SCWMRD 1982). Gag (*Mycteroperca microlepis*) were also occasionally seen. Three red snapper (*Lutjanus campechanus*) were observed on the 6.0-yr reef. Although this was not a large number of specimens, it exceeded the total number caught or observed at similar depths during Phases I and II. Hook-and-line catches (below) also indicated that red snapper may be more abundant on inner-shelf artificial reefs than on natural inner-shelf hard bottom. Perhaps the greater relief provided by artificial reefs is more attractive to red snapper than are the low-relief ledges normally found at inner-shelf hard-bottom sites. Only one vermilion snapper (*Rhomboplites aurorubens*), another priority species, was observed hovering just above the forward deck at the 10.0-yr reef.

Several other species of commercial and recreational importance were attracted to the artificial reefs. Sheepshead (*Archosargus probatocephalus*) were occasionally noted during fish counts, and casual observations during other dives indicated that they are probably more abundant than the counts indicate. Atlantic spadefish (*Chaedodipterus faber*) were very abundant on the reefs and king and Spanish mackerels (*Scomberomorus* spp.) were also frequently sited. Flounders (*Paralichthys* spp.) and grey triggerfish (*Balistes capriscus*) were infrequently observed.

Dominant species exhibited various degrees of association with the reef structures. Pelagic species such as *Decapterus punctatus*, *Selar crumenophthalmus*, *Sardinella aurita*, and engraulids formed large schools that hovered over horizontal deck surfaces or alongside the hull. Some pelagic species such as *Seriola dumerili* and *Sphyraena barracuda* swam individually or in small groups over and alongside the sunken vessels. Other pelagic species such as *Scomberomorus* spp. and *Caranx* spp. were only briefly associated with the reef as they rapidly passed over individually or in small schools.

Dominant demersal species such as *Haemulon aurolineatum*, *Lagodon rhomboides*, *Chaetodipterus faber*, and *Diplodus holbrooki* occurred in large and small schools that hovered or swam slowly very close to the surface of the vessel. *Haemulon aurolineatum* occurred more frequently over horizontal surfaces or near the top of the hull on vertical surfaces, whereas Chaetodipterus faber appeared to occur more frequently next to vertical surfaces (Table 1.28).

Other demersal fishes were even more closely associated with the surface of the vessel and some of these were sedentary species that did not move even when disturbed. For example, Centropristis spp. and Mycteroperca microlepis moved very little and would return to an area if chased away. They tended to remain close to vertical surfaces on or just above the ocean bottom. Archosargus probatocephalus, Equetus umbrosus, Chaetodon ocellatus, and Halichoeres bivattatus also showed littled movement and would return to the same location if disturbed. Serranus subligarius moved only when disturbed and settled immediately to the substrate less than a meter away. Unlike many other species that were associated with vertical surfaces, Serranus subligarius rested with its abdomen on the substrate, whether the substrate was vertical or horizontal. Demersal fishes such as Opsanus sp. and blennies were sedentary and rarely moved even if disturbed.

No significant differences were observed in abundance of all fishes between reefs or between orientations, i.e., vertical versus horizontal (all reefs combined) (Tables 1.29 and 1.30). Even with pelagic fishes (a source of wide variation in counts) excluded, there were no significant differences in demersal fish abundance between reefs or substrate orientations.

Diversity values were generally low and younger artificial reefs tended to have the highest H' values (Table 1.31). Numbers of species noted on each reef were similar in magnitude to the number of species that eventually colonized an artificial reef (Liberty Ship) in the Gulf of Mexico during two years of submergence (Lukens 1981). Artificial reefs in the South Atlantic Bight are also apparently colonized at an early stage and reach an equilibrium number of species in less than 3.5 years (the age of the youngest reef). Lukens (1981) noted an increased number of species on an artificial reef as water temperatures in the Gulf of Mexico increased throughout the summer. The maximum number of species recorded on any reef in the present study (24) was observed on the 4.5-yr reef. This was the last reef censused during the summer (7-8 September 1983) and water temperature was higher than that observed at any other reef (Appendix 1.1).

The composition and abundance of dominant fishes was similar among the reefs and no obvious distribution patterns were noted among fish species based on cluster analysis (Figure 1.44). Reefs of different ages often grouped together based on orientation (Groups 1, 4, 5, 6, 9), but in other instances observations on a single reef grouped together regardless of orientation (Groups 7, 8). Other groupings consisted of observations from different orientations on more than one reef (Group 3). Inverse and nodal analysis (not presented) provided little insight into community structure since species generally grouped by abundance and only a few rare species were faithful to any reef. Because an equal amount of effort was expended in counting fishes on both orientations, observations on each reef were combined to compare overall similarity (Bray-Curtis) between reefs (Figure 1.45). Again, no clear relationship was noted between the age of reefs and the ichthyofauna associated with them. The greatest similarity in faunal

Table 1.28 Abundance of fishes observed during fish counts on vertical and horizontal surfaces of all artificial reefs combined.

SPECIES	VERTICAL	HORIZONTAL
Ginglymostoma cirratum	1	
Sardinella aurita		3011
Engraulidae	900	1500
Opsanus sp.	1	1
Centropristis ocyurus		4
Centropristis striata	94	46
Mycteroperca microlepis	15	1
Serranus subligarius	20	18
Caranx hippos	11	
Caranx sp.		13
Decapterus punctatus	26760	23000
Selar crumenophthalmus	2503	6827
Seriola dumerili	18	24
Lutjanus campechanus	3	
Rhomboplites aurorubens		1
Haemulon aurolineatum	1671	2290
Archosargus probatocephalus	4	
Calamus leucosteus	13	4
Diplodus holbrooki	222	187
Lagodon rhomboides	215	215
Stenotomus aculeatus	315	65
Equetus umbrosus	73	11
Mullus auratus		2
Pseudupeneus maculatus	3	
Chaetodipterus faber	693	297
Chaetodon ocellatus	2	
Holacanthus bermudensis	1	
Chromis enchrysurus	1	
Halichoeres bivittatus	20	57
Sphyraena barracuda	147	38
Sphyraena borealis		1
Blenniidae	9	5
Scomberomorus cavalla		1
Scomberomorus maculatus	125	1
Scomberomorus sp.		27
Paralichthys sp.	2	
Balistes capriscus	2	
Lactophrys quadricornis	1	
Total N	33845	37647
Number of taxa	30	27

Table 1.29 Analysis of variance of the mean number of individuals ($\log_e + 1$) per observation between artificial reefs. One observation= one horizontal fish count or two vertical fish counts on a reef.

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARE	F
Between reefs	4	3.089	0.772	2.32
Between observations within reefs	25	8.330	0.333	
Total	29	11.419		

Table 1.30 Analysis of variance of the mean number of individuals ($\log_e + 1$) per observation between reef surface orientation, i.e., counts adjacent to vertical hull surfaces vs. counts on horizontal deck surfaces. One observation = one horizontal count or two vertical counts on a reef.

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARE	F
Between orientations	1	0.058	0.058	0.14
Between observations within an orientation	28	11.361	0.406	
Total	29	11.419		

Table 1.31 Community structure values [(number of individuals, number of species, Shannon diversity (H'), evenness (J') and species richness (SR)] for pooled counts of fishes at each artificial reef.

Age of Reef	Number of Individuals	Number of Species	H'	J'	SR
3.5-yr	11,914	18	1.88	0.45	1.81
4.5-yr	24,965	24	1.60	0.35	2.27
6.0-yr	7,911	19	1.08	0.25	2.01
8.0-yr	14,139	19	0.73	0.17	1.88
10.0-yr	12,563	19	1.07	0.25	1.91

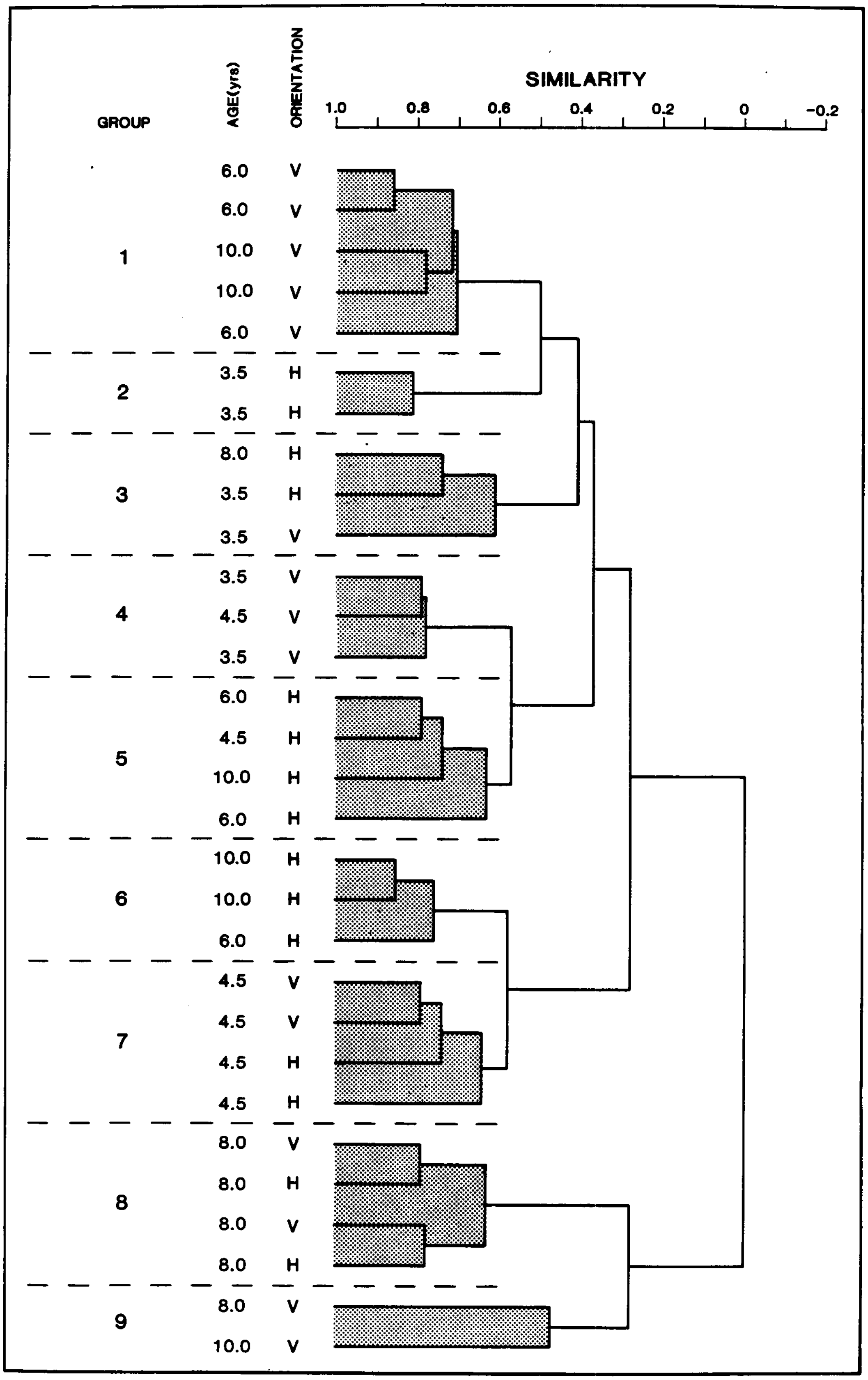


Figure 1.44 Normal cluster analysis of observations of fishes on horizontal (H) and vertical (V) surfaces of the artificial reefs.

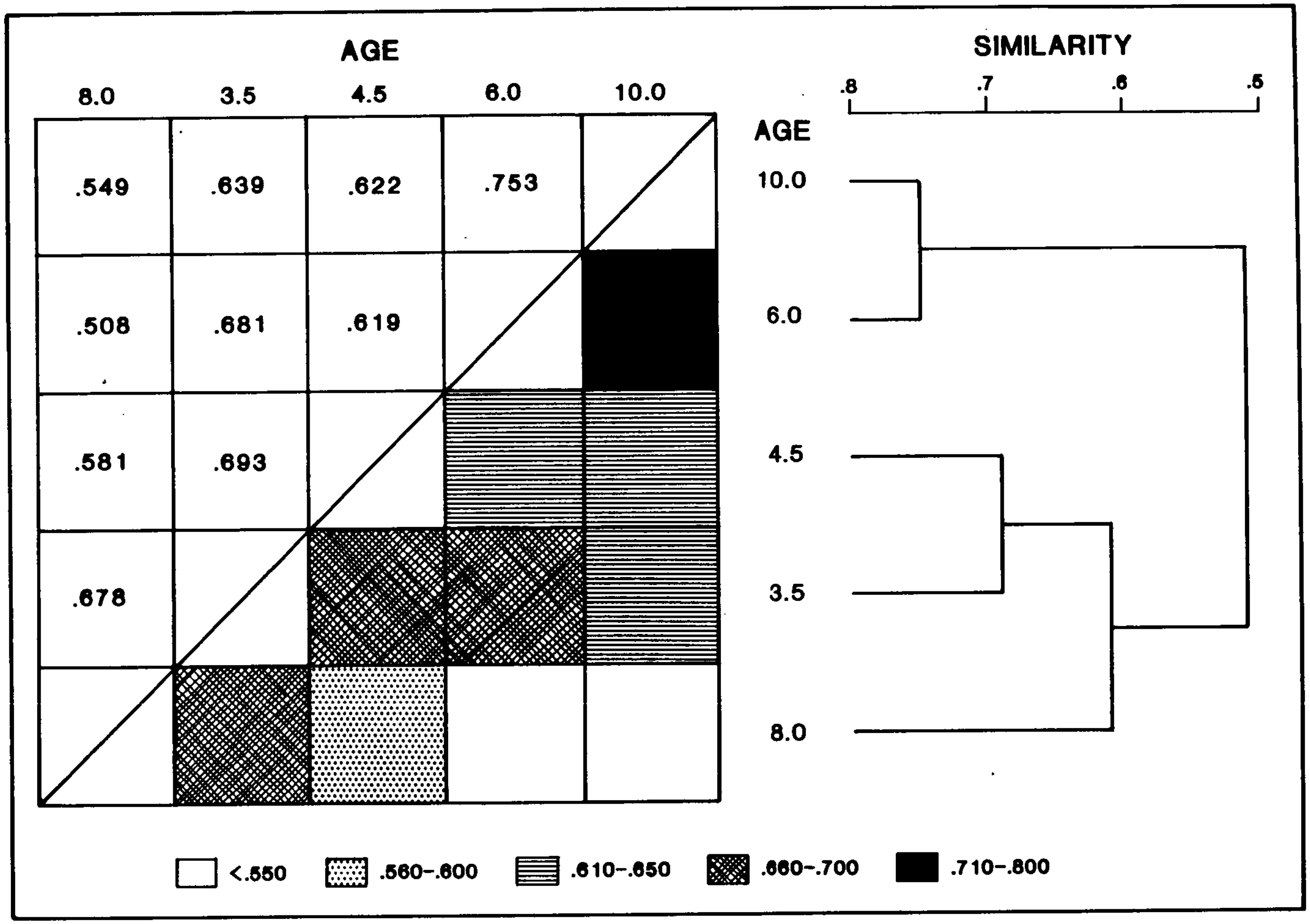


Figure 1.45 Bray-Curtis similarity between reefs and normal cluster hierarchy among reefs of various ages.

composition was between the 6.0-yr and 10.0-yr reefs. Although they were similar in ichthyofauna the reason for this similarlity is unclear. They were widely separated in distance and time of deployment, and their configuration (barge vs. tug) was quite different. These two reefs were similar to one another (and different from other reefs) in that they both had large numbers of automobile tires adjacent to the ships' hull. The effect of these tires on attraction of fishes to the reef is unknown. Two species, *Archosargus probatocephalus* and *Calamus leucosteus*, were found only on the 6.0-and 10.0-yr reefs only and this may have contributed to the relatively high similarity between these reefs.

The youngest reef (3.5 yr) had relatively high similarity to most of the reefs but was most similar to the 4.5-yr reef and least similar to the oldest reef. The higher similarity of the 3.5-yr reef to the 4.5 yr reef may be a result of the similar age of the reefs or of their proximity to one another (Figure 1.32).

The fact that the artificial reefs were similar in ichthyofauna despite their different ages is not surprising in light of the nature of the fish fauna at those depths and latitudes. Demersal fish assemblages on natural hard-bottom reefs in similar depths off Georgia and South Carolina, appear to be highly influenced by seasonal changes in water temperature. Far fewer fishes are present at those depths in winter than in summer, indicating a high degree of seasonal migration at those depths (Sedberry and Van Dolah 1984). Fishes associated with artificial reefs in the same depths probably undertake seasonal migrations as well, moving offshore in winter and returning to the reef in summer. Seasonal variations in the fish fauna probably outweigh any variation in community structure due to age of the reef. In addition, previous studies in the Gulf of Mexico have shown that artificial reefs are rapidly colonized by fishes (recruitment rates of 2-5 species per month) and reach a maximum number of species in less than two years (Lukens 1981). Community structure and species composition of fishes on artificial reefs in the South Atlantic Bight appears to be similar to that observed in the Gulf of Mexico. The five artificial reefs were probably colonized very rapidly, approaching equilibrium in less than 3.5 years.

Several species were collected for food habits analysis by spear or hook and line on the artificial reefs. In addition to those listed in Tables 1.32 and 1.33, four red snapper, *L. campechanus*, one sand perch (*Diplectrum formosum*), and an oyster toadfish, *Opsanus tau*, that had empty stomachs were collected. All of the red snapper were collected from the 4.5-yr reef and the oyster toadfish and sand perch were collected from the 10.0-yr reef.

Black sea bass (*C. striata*) were collected at all reefs that were sampled for fishes (4.5-, 6.0- and 10.0-yr reefs). Black sea bass fed to some extent on sessile and motile reef epifauna, as evidenced by the presence of *Didemnum candidum* and *Ophiothrix angulata* in stomachs. One specimen had consumed a large grasshopper-like insect, many of which were seen floating on the surface at the 4.5-yr reef.

Table 1.32 Frequency of occurrence (F), percent numerical abundance (N) and percent volume displacement (V) of food items in black seabass (*C. striata*), tomtate (*H. aurolineatum*), pigfish (*O. chrysoptera*), whitebone porgy (*C. leucosteus*) and spottail pinfish (*D. holbrooki*) stomachs collected from the artificial reefs.

	Centropristis striata			*Haemulon aurolineatum*			*Orthopristis chrysoptera*			*Calamus leucosteus*			*Diplodus holbrooki*		
FOOD ITEM	F	N	V	F	N	V	F	N	V	F	N	V	F	N	V
Cnidaria															
Hydrozoa															
Monostaechus quadridens													100.0	100.0	100.0
Annelida															
Polychaeta															
Chloeia sp.										50.0	50.0	60.0			
Diopatra cuprea				16.7	10.5	3.1									
Glycera sp.	25.0	3.4	24.9												
Onuphis nebulosa							50.0	13.3	11.9						
Pseudeurythoe ambigua				16.7	5.3	3.1									
Total Polychaeta	25.0	3.4	24.9	33.3	15.8	6.2	50.0	13.3	11.9	50.0	50.0	60.0			
Arthropoda															
Crustacea															
Stomatopoda larvae				33.3	21.0	9.3									
Mysidacea															
Bowmaniella portoricensis				16.7	10.5	2.2									
Isopoda															
Carpias bermudensis				16.7	5.3	0.2									
Amphipoda															
Caprella penantis				16.7	5.3	0.2									
Elasmopus sp. A							50.0	13.3	11.9						
Erichthonius brasiliensis				16.7	10.5	0.2	50.0	46.7	11.9						
Stenothoe georgiana							50.0	6.7	0.8						
Total Amphipoda				16.7	15.8	0.3	50.0	66.7	24.6						
Decapoda															
Majidae				16.7	5.3	15.5	50.0	6.7	19.8						
Pagurus sp.										50.0	50.0	40.0			
Pelia mutica	25.0	6.9	3.3												
Periclimenes longicaudatus				16.7	10.5	3.4	50.0	6.7	4.0						
Portunus sp.				16.7	5.3	46.6									
Processa fimbriata				16.7	5.3	0.8									
Trachypenaeus constrictus				16.7	5.3	15.5									
Xanthidae							50.0	6.7	39.7						
Total Decapoda	25.0	6.9	3.3	66.7	31.6	81.8	100.0	20.0	63.5	50.0	50.0	40.0			

Table 1.32 (Continued).

	Centropristis striata			*Haemulon aurolineatum*			*Orthopristis chrysoptera*			*Calamus leucosteus*			*Diplodus holbrooki*		
FOOD ITEM	F	N	V	F	N	V	F	N	V	F	N	V	F	N	V
Insecta															
Orthoptera	25.0	6.9	3.3												
Echinodermata															
Ophiuroidea															
Ophiothrix angulata	25.0	3.4	0.6												
Holothuroidea															
Ocnus pygmaeus	25.0	3.4	5.0												
Chordata															
Ascidiacea															
Didemnum candidum	25.0	3.4	11.0												
Pisces															
Engraulidae	25.0	75.9	38.7												
Number of stomachs examined:		9			20			2			6			4	
Examined stomachs with food:		4			6			2			2			1	

Table 1.33 Frequency of occurrence (F), percent numerical abundance (N), and percent volume displacement (V) of food items in pinfish (*L. rhomboides*), southern porgy (*S. aculeatus*), grey triggerfish (*B. capriscus*) and scrawled cowfish (*L. quadricornis*) stomachs collected from the artificial reefs.

	Lagodon rhomboides			*Stenotomus aculeatus*			*Balistes capriscus*			*Lactophrys quadricornis*		
PREY ITEM	F	N	V	F	N	V	F	N	V	F	N	V
Porifera												
Keratosa										100.0	7.7	31.6
Mycale cecilia										100.0	7.7	31.6
Total Porifera										100.0	15.4	63.2
Cnidaria												
Hydrozoa												
Dynamena cornicina										100.0	7.7	0.8
Crustacea												
Mysidacea												
Bowmaniella portoricensis				100.0	37.5	33.3						
Cumacea												
Cyclaspis varians				100.0	12.5	11.1						
Oxyurostylis smithi				100.0	12.5	11.1						
Total Cumacea				100.0	25.0	22.2						
Tanaidacea												
Leptochelia sp.										100.0	15.4	<0.1
Amphipoda												
Ampelisca cristata				100.0	12.5	11.1						
Leucothoe spinicarpa										100.0	23.1	0.2
Photis pugnator										100.0	7.7	0.0
Rudilemboides naglei				100.0	12.5	11.1						
Stenothoe georgiana										100.0	7.7	<0.1
Total Amphipoda				100.0	25.0	22.2				100.0	38.5	0.3
Decapoda												
Pilumnus sp.										100.0	7.7	0.2
Reptantia undetermined							100.0	100.0	100.0			
Total Decapoda										100.0	7.7	0.2
Bryozoa												
Crisia sp.				100.0	12.5	22.2				100.0	7.7	4.0
Chordata												
Ascidiacea												
Distaplia bermudensis										100.0	7.7	31.6
Pisces												
Engraulidae	100.0	100.0	100.0									
Number of stomachs examined:		6			1			1			1	
Examined stomachs with food:		1			1			1			1	

The haemulids *H. aurolineatum* and *O. chrysoptera* fed on infaunal and sand-bottom species (e.g. *Diopatra cuprea*, *Bowmaniella portoricensis*, *Stenothoe georgiana*, *Trachypeneus constrictus*) as well as species associated with hard substrates, such as *Caprella penantis*, *Erichthonius brasiliensis* and *Processa fimbriata* (Bousfield, 1973; Gardiner, 1975; Williams, 1984). Tropical reef-dwelling haemulids forage extensively on open sandy areas adjacent to reefs (Randall, 1967; Section III this Volume) and haemulids associated with artificial reefs in the South Atlantic Bight apparently exhibit the same behavior. Other species of fish examined from the artificial reefs (*C. leucosteus*, *D. holbrooki*) also fed on a combination of reef invertebrates and sand-dwelling organisms, or on sand-dwelling organisms exclusively (*S. aculeatus*). Although sample sizes in the present study were very small, previous studies have shown the importance of soft-bottom prey to these abundant reef-inhabiting fishes (Carr and Adams, 1972; Section III this volume). Apparently these fishes are attracted to artificial structures for reasons other than feeding on sessile and associated motile epifauna.

The scrawled cowfish, *Lactophrys quadricornis*, had a diet dominated by sponges, ascidians, and an amphipod (*Leucothoe spinicarpa*) that dwells in sponges (Pearse, 1932). Although not collected in the present study, several other species associated with the reefs probably graze heavily on the attached fauna. Randall and Hartman (1968) found that *Chaetodipterus faber*, a very abundant artificial reef species, had a diet composed (by volume) of sponges (32.7%), anthozoans (27.1%), ascidians (12.6%) and other sessile biota (10.5%). Motile species formed a small part (17.1%) of the diet. *Archosargus probatocephalus* also feeds extensively on sessile fauna (Section III). Other artificial reef fishes that have a diet dominated by sessile invertebrates include *Holacanthus bermudensis* (94.6% sponge, by weight) and *Chaetodon ocellatus* (Feddern, 1968; Allen, 1979). The heavy predation pressure exerted by these fishes on sessile reef biota, particularly in the summer, may explain the lower biomass of sessile biota on the artificial reefs versus the 9- and 12-mo colonization plates sampled in fall and winter, when sessile invertebrate-feeding fishes were lower in abundance.

IMPLICATIONS OF TASK I RESULTS RELATED TO OFFSHORE OIL AND GAS DEVELOPMENT

The potential effects of oil and gas development on hard-bottom communities in the South Atlantic Bight have been discussed at length in previous reports to the Bureau of Land Management/Minerals Management Service (SCWMRD and GADNR, 1981; SCWMRD, 1982). Briefly stated, a number of adverse effects on hard-bottom communities may result from the discharge of drilling muds or from the occurrence of accidental oil spills. In extreme cases, these events could result in the complete defaunation of nearby benthic habitats. The results of the present study suggest two possibilities for the recovery of hard-bottom communities from total devastation, both of which pre-suppose the absence of any lingering toxicity in the sediments or water column and the absence of any permanent alteration of the substratum.

In the first case, if one assumes that natural and artificial hard substrata are equally suitable for the colonization and growth of epifaunal invertebrates, then the results of this study can be used to predict recovery rates on natural hard bottom in similar hydrographic regimes. Based on this assumption our data indicate that, even after 10 years of recolonization and growth following a catastrophic disturbance, the re-established sessile epifaunal community will still be undergoing "succession" toward a mature state resembling the original "climax" community. This conclusion is based upon the absence of large sessile invertebrates (i.e., certain sponges and corals) from all artificial substrata including the oldest (10.0-yr) reef. These organisms are common constituents of natural hard-bottom communities in the South Atlantic Bight and would be expected to occur in mature artificial reef communities, as well. The delayed recruitment and slow growth of sponges and corals is also supported by the results of other studies (Davis et al., 1982; George and Thomas, 1979; Grigg, 1974; Nicol and Reisman, 1976; Van Dolah et al., 1984). On the other hand, the rapid establishment of gammaridean and caprellid amphipod populations on the colonization plates examined in this study suggests that the recovery of the motile epifauna in natural hard-bottom areas could proceed quickly following a disturbance. Most of the species that dominated the plates during the first 12 months of substratum exposure exhibit opportunistic life-history strategies that enable them to rapidly exploit newly available resources. This suggests that they would probably become well established early in the recovery of hard-bottom habitats.

Alternatively, if natural and artificial hard substrata differ in their ability to attract and support populations of certain epifaunal invertebrates, then the results of this study cannot be confidently used to predict recovery rates on natural hard bottom. Furthermore, if specific historical events such as differential predation or physical disturbance alter the course of community development, as Sutherland (1974) suggests they might, then the epifaunal community which becomes established following a catastrophic disturbance may never resemble the original "climax" community. Nevertheless, the consistent occurrence of numerous sessile invertebrate species on all artificial reefs ranging in age from 3.5 to 10.0 years, and the lack of consistency in species composition among colonization plates exposed for one year or less, suggests that it may take as long as three to five years before a reasonably persistent epifaunal community becomes re-established. In order to test this hypothesis, however, further research is needed to examine seasonal trends on the artificial reefs and to examine colonization and growth on a variety of artificial substrata exposed for different periods of time ranging from 1.0 to 3.5 years.

Aside from the potentially lethal effects of oil and gas development on hard-bottom communities, production platforms and drill cuttings would substantially increase the amount of hard substrata available for colonization, particularly in sand-bottom areas where there is little or no emergent rock. The results of this study suggest that barnacles and hydroids would be recruited rapidly during all seasons to new substrata deployed in either hard-bottom or sand-bottom habitats. Barnacles would probably dominate the sessile fauna initially, with populations of longer-lived, less opportunistic species (e.g., certain bivalves and solitary ascidians) eventually becoming established over a longer period of time. It is likely, however, that colonial organisms, such as hydroids, bryozoans, and colonial ascidians, would ultimately dominate the sessile biota, as barnacles and other solitary organisms were overgrown. The total biomass and number of sessile species would be expected to increase rapidly during the first year of substratum exposure and thereafter stabilize at a level which would probably be higher on production platforms placed in hard-bottom areas than on those in sand-bottom areas. Additionally, the proximity of platforms to existing hard-bottom habitat will probably influence community structure by increasing the likelihood of colonization by larvae having a narrow range of dispersal from parent populations.

Due to their small size and resultant instability, drill cuttings would be more susceptible to frequent physical disturbance than either production platforms or natural hard bottom. Consequently, the sessile community colonizing drill cuttings would probably never achieve equilibrium but rather would continually represent an early stage in the successional development of hard-bottom communities. One might expect such a community to resemble the epifaunal assemblage observed on the short-term colonization plates exposed during the same season as that of the most recent physical disturbance. Conversely, one might expect the epifaunal community colonizing a relatively stable production platform to more closely resemble that of the older artificial reefs. With respect to the motile epifauna, it is reasonable to expect that the opportunistic gammaridean and caprellid amphipods would persist as the dominant motile organisms on frequently disturbed drill cuttings, and would initially dominate the motile fouling community on production platforms, as well. Subsequent changes in the motile community would be related to the growth of sessile organisms which provide additional microhabitats and to physical factors such as the rate of sediment accumulation.

Finally, with respect to the ichthyofauna, all of the fishes examined in this study depend on hard-bottom habitat for food and/or shelter during at least part of their life history (see Task III). Consequently, any damage to hard-bottom reefs and their associated epifauna could seriously deplete fish populations associated with these habitats. Nevertheless, if risks to the environment are minimized, our results suggest that oil and gas production platforms would enhance fish populations in the South Atlantic Bight. Structures placed in hard-bottom areas would probably attract fish more quickly than those placed in sand-bottom areas; however, it is likely that within a few months several fishes typically associated with natural hard-bottom habitat would be observed in the vicinity of structures placed in either hard-bottom or sand-bottom areas. These would probably include many of the numerically dominant species observed on artificial reefs in this study such as round scad, bigeye scad, Spanish sardines, anchovies, tomtate, Atlantic spadefish, pinfish, and spottail pinfish. Several species of economic importance such as black sea bass, Spanish mackerel, king mackerel, gag, red snapper, vermilion snapper, sheepshead, and grey triggerfish might also be found in the vicinity of production platforms. The lack of any significant difference in fish abundance among the five artificial reefs examined in this study suggests that natural hard-bottom habitats recovering from complete defaunation and newly submerged production platforms are likely to be colonized by highly motile fishes within three to four years and thereafter support fish populations that are comparable in size to those found on older platforms or in mature hard-bottom communities.

SUMMARY AND CONCLUSIONS

- The objectives of Task I were to 1) examine seasonal recruitment and short-term community development on colonization plates over the course of one year, 2) examine long-term community development on five artificial reefs ranging in age from 3.5 to 10.0 years, 3) determine the effects of spatial orientation and proximity to natural hard-bottom habitat on the colonization and community development of artificial substrates, and 4) provide qualitative and quantitative descriptions of the fish assemblages associated with the colonization plate frames and artificial reefs.

- Short-term colonization patterns were evaluated by deploying arrays of fouling plates in two locations near Charleston: one in sand-bottom habitat and one in hard-bottom habitat. Replicate series of plates oriented both vertically and horizontally were collected from each area at 3-mo intervals to obtain data on community development patterns over a 1-yr period. Additional plate series were deployed during the year to determine variations in seasonal recruitment patterns. All plates were collected using a technique designed to capture the associated motile epifauna. In the laboratory, sessile biota attached to each plate surface were identified and estimates of percent cover were obtained for each species using a random-point censusing method. Plate surfaces were then scraped to measure total biomass. Motile epifauna washed from the plates were identified and enumerated.

- Long-term colonization patterns were evaluated by examining the sessile biota, motile epifauna, and fishes on five artificial reefs ranging in age from 3.5 to 10.0 years. Replicate scrape, suction, and photographic samples were collected on horizontal and vertical surfaces of each reef. Fishes were enumerated by divers who made three timed counts on both surfaces of each reef. The sessile organisms in scrape samples were sorted to major taxa, weighed, and identified. The motile epifauna in suction samples were identified and counted. Estimates of percent cover for major taxa were determined from close-up photographs using a random point-count method.

- Results of the short-term study indicated that recruitment of sessile organisms to the plates was significantly different between some seasons with respect to percent cover, biomass, and the number of species. A greater number of species colonized plates in the hard-bottom as opposed to the sand-bottom area but major differences were not observed between areas with respect to total biota cover or biomass. Plate orientation (horizontal vs. vertical) did not significantly affect biota cover, biomass, or the number of species on a plate, except between sides of horizontal plates which had less growth on the top surfaces.

- Dominant taxa colonizing the plates during all seasons were barnacles and hydroids. Barnacles were least abundant on the plates during spring and hydroids were least abundant during winter. Algal and ascidian cover was greatest on the bottom of horizontal plates in the hard-bottom area. Dominant species colonizing the plates were often different from those colonizing hard surfaces in shallower subtidal waters of the same region or in deeper waters of other regions.

- Evaluation of all community parameters on the plates submerged for three months indicated that the species composition and percent cover of biota colonizing hard substratum in the study area were influenced more by season than by orientation or location. However, the latter two factors did have some influence on the composition and cover of certain taxa. Effects of orientation were related to evidence of fish predation which appeared to be greatest on the top surfaces of horizontal plates. Effects related to location were primarily observed in the number of species found on the plates which may be a function of proximity to areas of larval recruitment.

- Total biota cover, biomass, and total number of species increased significantly with time on the plates submerged from 3 to 12 months. Significant differences in these parameters were also noted between areas. Additionally, species composition changed markedly with time and differed between the two areas. Early community development in both areas was similar, but after 1 year colonial species were the dominant taxa covering plates in the hard-bottom area and solitary species were the dominant taxa covering plates in the sand-bottom area. Differences in species composition indicated that proximity to hard-bottom habitat has a major influence on communities developing on newly-exposed hard surfaces.

- Sessile communities observed on the 12-mo plates probably did not represent a "climax" or stable end point in community development based on comparisons with older artificial reefs. Additionally, none of the larger sponge and coral species typically found in hard-bottom habitat of the South Atlantic Bight had settled on plate surfaces after 1 year which suggests that they may be later colonizers.

- Recruitment of motile epifauna on the plates was rapid and amphipods, particularly tubicolous and clinging species, heavily dominated the community on 3-mo plates. The level of recruitment was seasonally variable, with heaviest colonization during winter and spring. Many of the seasonal variations were attributed to reproductive periodicity of the dominant species. The overall abundance of motile organisms was greater on sand plates, although this was not the case during all seasons. Heavy predation on hard-botom plates set out in spring may account for some of the differences noted. The orientation of plates appeared unimportant with regard to the intensity of recruitment and to the number of species colonizing the plates.

- Structure of the motile epifaunal community on recruitment plates also reflected seasonal patterns of dominance by a few species. Although the number of motile organisms on winter and spring plates was high, fewer species were recruited during those months; thus, evenness and diversity were lower than in other seasons. Normal cluster analysis revealed distinct differences in community structure and composition among the plates. These differences were related primarily to the overall abundance of epifauna, although the hierarchy of plate similarity in the dendrogram indicated that species composition of the newly recruited community differed seasonally, as well.

- Comparison of the motile epifauna on plates submerged for durations of 3 to 12 months indicated that changes in the community during this period were also related to periodic fluctuations in abundance of a few species. Peaks of overall motile density on plates submerged for different lengths of time correspond closely with the seasonal pattern observed on the 3-mo recruitment plates. The mean density of motile epifauna on plates submerged for 3 to 12 months were greater than on 3-mo plates, and may be related to the increased growth of sessile organisms noted on the older plates.

- Values of overall community structure parameters for the 6-, 9-, and 12-mo plates paralleled those of the 3-mo plates which were submerged during the corresponding season, illustrating the continued influence of seasonal variability in recruitment patterns. The overall faunal abundance remained higher on sand-bottom plates than on those over hard-bottom throughout the year, possibly as a result of the greater initial predation on those plates. As observed on 3-mo plates, spatial orientation appeared to have little influence on community development.

- Normal cluster analysis of samples taken throughout the 12-mo study revealed that changes in the motile epifaunal community were greatest in the early phase of its development, but diminished with time. However, no directional sequence of development was apparent during this period, and the motile epifauna remained an amphipod-dominated community characterized by seasonal variation in the recruitment and abundance of relatively few species.

- The colonization plate frame in the hard-bottom area immediately attracted fishes but recruitment was slower in the sand-bottom area. After 3 months, several fish species were associated with both frames and many of the fishes were observed feeding on biota attached to the plates and frames. Most of the fishes found around both platforms were species typically associated with hard-bottom habitat in the South Atlantic Bight.

- The results of the long-term colonization study indicated that there were no consistent trends in biomass, percent cover, or number of sessile species with increasing age of the artificial reefs. Several taxa, including octocorals, scleractinian corals, anemones, and sessile bivalves were present on the artificial reefs, but were absent from short-term colonization plates, suggesting that a number of taxa are late colonizers and/or slow to mature. This pattern conforms with Connell and Slayter's (1977) "inhibition" model of succession, although no inhibitory effects by early colonists were conclusively demonstrated.

- There was no clear competitive hierarchy with respect to colonial versus solitary organisms on any artificial reef. Species representing both life history strategies co-occurred in all scraped quadrats. Solitary organisms, primarily the barnacle *Balanus trigonus*, accounted for the greatest proportion of total biomass on all reefs; however, colonial organisms appeared to be dominant with respect to both numbers of species and biomass excluding shell weight.

- Biomass, percent cover, and number of sessile species were all significantly greater on vertical than on horizontal surfaces. This may be a function of several factors, including heavier predation pressure and greater sedimentation on horizontal surfaces as well as negative phototaxis of settling larvae.

- The 6.0-yr reef had significantly lower biomass, fewer sessile species, and lower percent cover on both horizontal and vertical surfaces than any of the other reefs. This may have been due to our sampling of hull surfaces that had been treated with anti-fouling paint which, in turn, may have inhibited the settlement and growth of sessile organisms.

- The proximity of the 3.5- and 8.0-yr reefs to hard-bottom habitat appears to have influenced community structure by increasing the likelihood of settlement by larvae having short-lived planktonic existences and, thus, a narrow range of dispersal from breeding populations. This may explain the higher biomass and greater number of ascidian species on these two reefs.

- The consistent occurrence of several species on all artificial reefs, regardless of substratum age, and the lack of consistency in species composition among colonization plates exposed for one year or less, suggests that the establishment of a reasonably persistent epifaunal community may take as long as three to five years. However, the absence of large sessile invertebrates commonly found in natural hard-bottom areas of the South Atlantic Bight suggests that the artificial reef communities examined in this study are still undergoing succession, even after 10.0 years of substratum exposure.

- The motile community of the artificial reefs consisted primarily of amphipods, gastropods, and isopods. Unlike the epifauna of the short-term colonization plates, the reef communities were not heavily dominated by a small number of species. Mean faunal densities and mean number of species on the reefs were similar, however, to those observed on plates collected during the same season that reefs were sampled.

- Species richness of motile epifauna increased with increasing reef age, although no other parameters of community structure were related to this factor. Two reefs (the 3.5-yr and 8.0-yr reefs) were quite similar to one another, and their proximity to each other and to natural hard bottom was noted. Faunal density and diversity were considerably greater on these reefs than on others, and normal cluster analysis also revealed high similarity between them. The considerable abundance of tubicolous amphipods on these reefs may be related to the amount of suitable habitat provided by sessile species.

- Unlike the sessile reef biota, the motile epifauna was significantly more diverse and abundant on horizontal than on vertical surfaces. Cluster analysis illustrated the distinct dissimilarity between samples from these two orientations, as well. These differences may be related to the effects of sedimentation, since a moderate accumulation of sediment on the top of a reef could provide a greater variety of microhabitats for motile species.

- Dominant fishes (by number) on the artificial reefs included schooling forage fishes such as round scad (*Decapterus punctatus*), bigeye scad (*Selar crumenophthalmus*), Spanish sardine (*Sardinella aurita*) and anchovies

(Engraulidae). Other abundant fishes included tomtate *(Haemulon aurolineatum)*, Atlantic spadefish *(Chaetodipterus faber)*, pinfish *(Lagodon rhomboides)*, and spottail pinfish *(Diplodus holbrooki)*, which are also abundant on natural reefs.

- Several species of economic importance were also observed on the artificial reefs, including Atlantic spadefish, black sea bass *(Centropristis striata)*, Spanish mackerel *(Scomberomorus maculatus)*, king mackerel *(S. cavalla)*, gag *(Mycteroperca microlepis)*, red snapper *(Lutjanus campechanus)*, vermilion snapper *(Rhomboplites aurorubens)*, sheepshead *(Archosargus probatocephalus)* and grey triggerfish *(Balistes capriscus)* .

- No significant differences in abundance of fishes were observed between reefs or between orientations (i.e., horizontal vs. vertical) of the adjacent substrate.

- Diversity values were low for the fish community and younger reefs tended to have the highest diversity.

- Cluster analysis of vertical and horizontal fish counts on all reefs combined usually grouped observations according to orientation, although some observations grouped by reef without regard to orientation and a few observations from different reefs and orientations grouped together. Cluster analysis of counts pooled for each observation period (three for each reef, vertical and horizontal combined) also demonstrated high similarity among all reefs, and no relationship in similarity between age of the reef and its ichthyofauna.

- The similarity noted in the ichthyofauna of the reefs is probably a result of latitudinal and depth similarity and the fact that artificial reefs are generally colonized by highly motile fishes in less than two years.

- The results of this study suggest that the recovery of hard-bottom habitats from catastrophic disturbances induced by oil- and gas-related activities could take anywhere from three to more than ten years, depending on substratum characteristics and the rapidity with which drilling muds and/or toxic substances are dispersed.

- Aside from the potentially lethal effects of oil and gas development on hard-bottom communties, production platforms and drill cuttings would substantially increase the amount of hard substrata available for colonization, particularly in sand-bottom areas where there is little or no emergent rock.

- Epifaunal communities which are either developing on recently deployed production platforms or recovering from a catastrophic disturbance on natural hard bottom will initially be dominated by opportunistic organisms such as barnacles, hydroids, and caprellid and gammaridean amphipods. Opportunistic species would continue to dominate frequently disturbed drill cuttings, while longer-lived, less opportunistic species would eventually become established on the relatively stable production platforms. It is likely, however, that colonial organisms such as hydroids, bryozoans, and colonial ascidians would ultimately dominate the sessile biota as barnacles and other solitary organisms were overgrown. Additionally, the proximity of new substrata to existing hard-bottom habitat will probably influence community structure by increasing the likelihood of colonization by larvae having a narrow range of dispersal from parent populations.

- Finally, with respect to the ichthyofauna, our results indicate that oil and gas production platforms would enhance fish populations in the South Atlantic Bight, but only if risks to the environment were minimized.

- Structures placed in hard-bottom areas would probably attract fish more quickly than those placed in sand-bottom areas; however, it is likely that within a few months several fishes typically associated with natural hard-bottom habitat would be observed in the vicinity of structures placed in either hard-bottom or sand-bottom areas. These would probably include many of the numerically dominant species observed on artificial reefs in this study as well as several species of economic importance.

- The lack of any significant difference in fish abundance among the five artificial reefs examined in this study suggests that natural hard-bottom habitats recovering from complete defaunation and newly submerged production platforms are likely to be colonized rapidly and support fish populations that are comparable in size to those found on older platforms or in mature hard-bottom communities.

Task II: A Study of Sponge and Coral Distribution in Relation to Sediment Depth Over Hard Substratum

INTRODUCTION

Hard-bottom areas in the South Atlantic Bight and other regions generally support a diverse assemblage of sessile fauna, including many large sponge and coral species. Because of their size, these sponges and corals significantly increase the complexity of hard-bottom habitat which in turn enhances the attractiveness of these areas to reef fishes. Although sponges and corals usually require exposed hard substratum for attachment, these taxa have been commonly observed growing in areas where the hard bottom is covered with a veneer of sandy sediments (Continental Shelf Associates, 1979; Henry and Giles, 1980; Powles and Barans, 1980; Reed, 1980; SCWMRD, 1982). Based on observations made during previous investigations off the South Carolina and Georgia coasts (SCWMRD and GADNR, 1981; SCWMRD, 1982), the distribution of sponges and corals within a reef area is patchy and appears to be limited by the depth of sediment over the hard substratum.

Several studies have demonstrated that increased sedimentation can adversely affect the distribution and growth of sponges and corals by inhibiting settlement, slowing growth, and causing mortality through clogging filtering structures or complete burial (Jones and Endean, 1973, 1976; Storr, 1976; Taylor, 1977; Bak, 1978). However, specific information is lacking on the thickness of sediment over hard substratum that will prevent the growth of sessile fauna, especially those species common in the South Atlantic Bight. The purpose of this study was to define the relationship between the depth of sediment and the distribution of sponges and corals within several representative hard-bottom habitats. Data obtained should prove useful in (1) identifying the possible location of hard-bottom communities in other areas using remote-sensing techniques designed for geological assessment, and (2) evaluating the potential effects of increased sediment loads resulting from industrial activities on existing hard-bottom communities.

STUDY AREAS

Six hard-bottom reefs, located off the coasts of South Carolina and Georgia, were selected for study: three in relatively shallow shelf waters and three in deeper waters of the middle shelf (Figure 2.1, Table 2.1). Four of the sites (IS31, IS32, MS32, MS33) were also sampled during the Year I and Year II study periods.

Station IS31 was located within the Gray's Reef National Marine Sanctuary. Based on previous observations (SCWMRD, 1982), this area had a very irregular bottom topography with numerous rock ledges of moderate to high relief (0.5-2 m) which were often separated by wide expanses of sand. A very thin layer of sand was usually present on top of the ledges. Sessile faunal growth observed in the area was patchy and usually densest on or adjacent to the ledges. The density of sponges and corals in this area

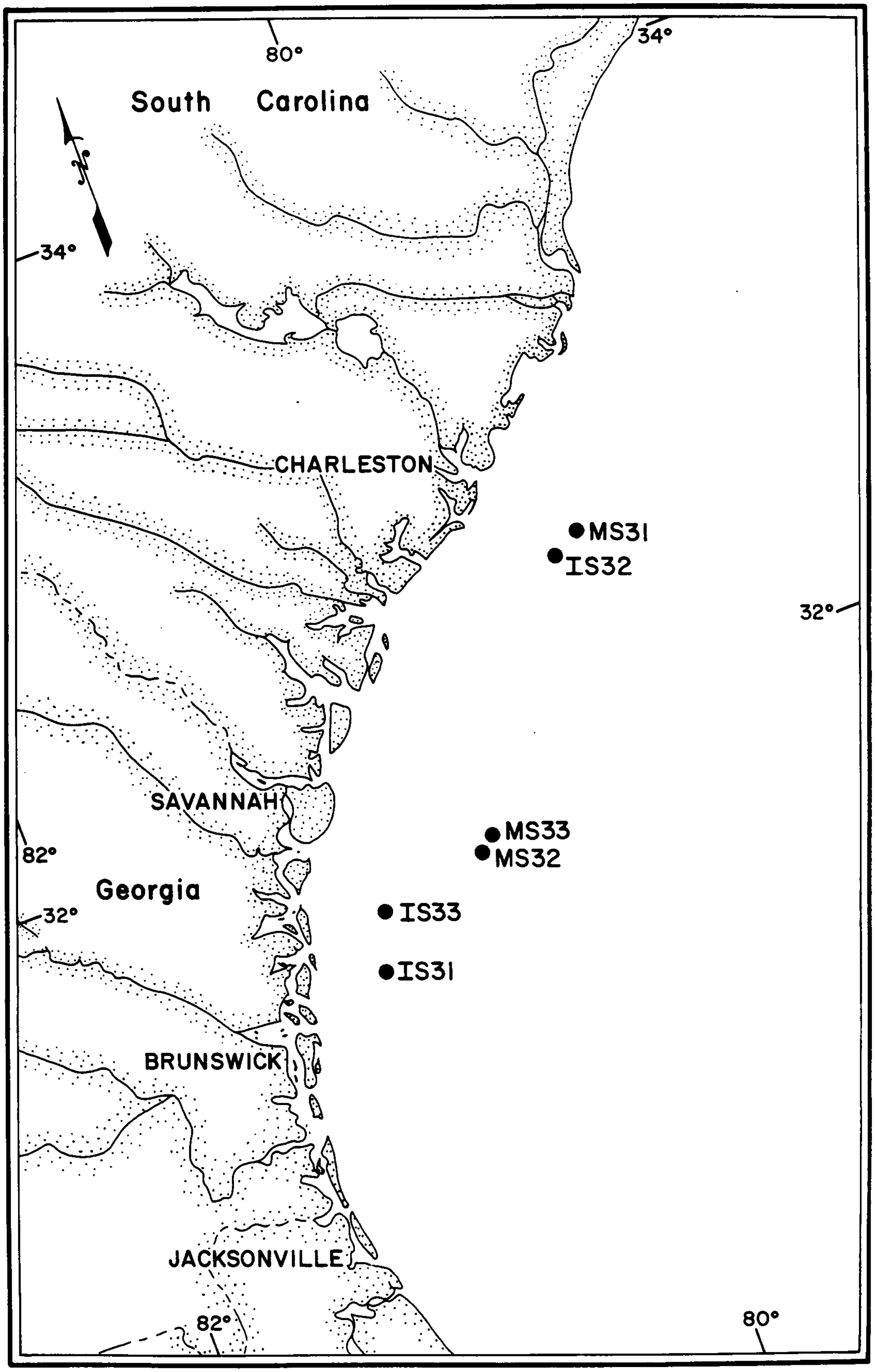


Figure 2.1 Location of sampling sites for the Task II study.

Table 2.1 Station and collection information for the Task II study.

STATION	COLLECTION NUMBER	DATE	DEPTH (m)	LATITUDE (N)	LONGITUDE (W)	NUMBER OF QUADRATS
MS31	63830001	24 May 1983	25	32°32.3'	79°33.6'	8
MS31	63830002	25 May 1983	25	32°32.3'	79°33.6'	8
MS31	63830003	27 May 1983	25	32°32.3'	79°33.6'	3
IS31	63830159	26 July 1983	21	31°24.1'	80°52.8'	8
IS31	63830160	17 August 1983	21	31°24.1'	80°52.8'	8
IS32	63830161- 162	8 August 1983	21	32°29.6'	79°42.5'	8 8
IS32	63830163	9 August 1983	21	32°29.6'	79°42.5'	8
IS31	63830164	18 August 1983	21	31°24.1'	80°52.8'	8
MS32	63830233	13 September 1983	33	31°41.1'	80°20.7'	8
MS32	63830234	19 September 1983	33	31°41.4'	80°20.8'	8
MS32	63830235	20 September 1983	33	31°41.4'	80°20.8'	5
IS33	63830236- 237	7 November 1983	21	31°36.0'	80°47.4'	8 7
MS33	63830320	4 October 1983	36	31°44.1'	80°13.7'	8
MS33	63830321	5 October 1983	36	31°44.1'	80°13.7'	6
MS33	63830322	6 October 1983	36	31°44.1'	80°13.7'	8

generally decreased with distance from the ledges, grading into areas with sparse growth or into areas of sandy bottom and no sessile growth. Hunt (1974) and Henry and Van Sant (1982) provide more detailed descriptions of Gray's Reef.

Station IS32 was an extensive area of rock hardpan covered by a layer of sand which varied in thickness throughout the study site. No emergent rock ledges or other outcroppings were observed within the study area and faunal growth ranged from patches of dense sessile growth to areas with sparse growth. Sessile biota observed at this station were more uniformly distributed, however, than observed at the other stations where outcroppings were present.

Station IS33 was located near the Georgia artificial reef "J", an area also sampled in the Task I study. This hard-bottom area was characterized by a single, moderate-relief (1 m) sand-covered ledge which had dense growth on top of the ledge grading into sparser growth with increased distance from the outcropping. The decrease in density of faunal growth away from the ledge was typical of other hardpan areas in the region.

Bottom topography was more similar among the middle-shelf stations than among the inner-shelf stations. These deeper sites all had well-defined ledges and outcroppings separated by patches of sand bottom with little or no sessile growth. As noted at the inner-shelf sites, sessile fauna was most dense on top of the ledges and less growth was observed with increased distance from the outcroppings. Station MS31 and MS32 had low- to moderate-relief ledges (0.5-1 m) which were distributed irregularly, whereas station MS33 had one primary, continuous ledge of high relief (1-2 m) which spanned the study area. The tops of ledges at all middle-shelf sites were covered with sandy sediments, although sediment cover was minimal on the outcroppings at MS31. This station also had less encrusting growth on the ledges compared to the other middle-shelf sites.

METHODS

At each study site divers placed polypropylene transect lines, marked in 1-m intervals, along the bottom so that they traversed areas with high and low densities of sessile fauna (Figure 2.2). When placing the lines, divers attempted to span a gradient of faunal density without biasing the position of lines with respect to the distribution of particular species. Both ends of the transect lines were anchored to the bottom and the total distance between anchors was noted. A quadrat frame was then placed on the transect line (Figure 2.2), within which estimates of sponge and coral density and sediment depths were made. Placement of the first quadrat along each transect was determined by random selection among the first five meter marks from one end of the line. The remaining quadrats were then spaced at equidistant intervals along the transect line between the first quadrat and the terminal anchor. Whenever possible, eight quadrats were assessed on each transect. Transect length varied from 9-58 m, with length dependent primarily on the distance from an area with dense growth to an area of sand bottom with no sessile growth.

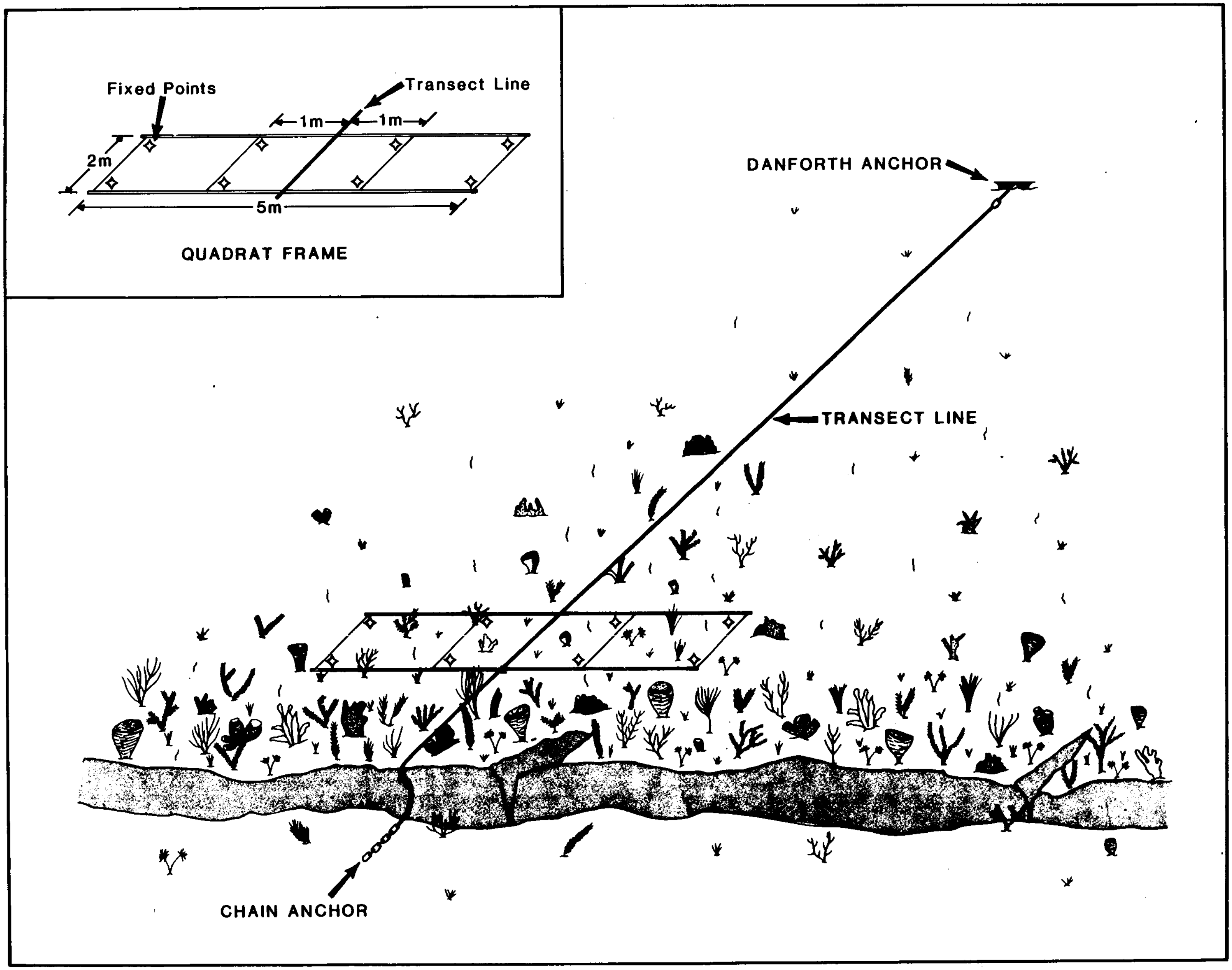


Figure 2.2 Depiction of the transect line and quadrat frame used in the Task II study. Symbols (◇) within the quadrat frame show the location of fixed-point sediment depth measurements within the quadrat areas (see text).

The overall dimensions of the quadrat frame used on each transect were 2 x 5 m (Figure 2.2). Sponges and hard corals were counted in the two 2 x 2.5 m quadrat areas on each side of the line. Octocorals were counted in the smaller 1 x 2 m quadrat areas on each side of the line because they were usually much more abundant.

Measurements of sediment depth were taken at eight fixed locations within the quadrat frame (Figure 2.2) by pushing a graduated 30-cm metal probe, into the sediment until hard bottom was contacted. Depth was recorded as 30+ cm if no hard substratum was detected within the length of the probe. These fixed-point measurements provided four estimates of sediment depth within each 5-m^2 quadrat used for counts of sponges and two estimates of sediment depth within each 2-m^2 quadrat used for counts of octocorals.

Additional measurements of sediment depth were also collected at sites of attachment for each species. Sediment depth was measured using the probe at the base of four representative specimens within each area bounded by the 2 x 5 m quadrat frame.

The sponge species counted at inner-shelf and middle-shelf stations were *Ircinia campana*, *I. ramosa*, *Homaxinella* sp., *H. waltonsmithi*, and *Haliclona oculata*. Octocoral species counted in the quadrats were *Titanideum frauenfeldii*, *Leptogorgia virgulata*, *Lophogorgia* spp. and *Muricea pendula*. Counts of the latter two genera were combined in all analyses because divers often had difficulties distinguishing among specimens of these genera. The only hard corals counted in the quadrats were *Oculina varicosa* and *Solenastrea hyades*. These hard corals were only found in quadrats at the IS stations.

Correlations between the density of sponges or corals and estimates of average sediment depths in the quadrats were evaluated using the Spearman rank correlation test (Sokal and Rolf, 1981). Each species was tested separately by station and for all stations combined within each depth zone.

RESULTS AND DISCUSSION

Approximately 5000 sponges and corals were counted in the 597 quadrats surveyed at inner-shelf (IS) and middle-shelf (MS) stations (Appendix 2.1-2.6). Octocorals were considerably more abundant than sponges at all sites and densities of both taxa were greatest at IS stations (Tables 2.2, 2.3). Hard corals were less common then octocorals or sponges at any of the study sites.

The species of octocoral most frequently encountered at all stations was *Titanideum frauenfeldii* (Table 2.2). Densities of *T. frauenfeldii* were approximately three times greater at IS stations than at MS stations, and 91.8% of all specimens observed were present in quadrats with an average sediment depth $\leq$ 5.0 cm. Within the quadrats which contained this species, the density of *T. frauenfeldii* was not significantly correlated with estimates of average sediment depth although a slight negative correlation was noted at most sites (Table 2.4). *Titanideum frauenfeldii* were never

Table 2.2 Summary of coral densities in relation to average sediment depths within quadrats assessed at inner-shelf (IS) and middle-shelf (MS) stations.

AVERAGE SEDIMENT DEPTH (cm) PER QUADRAT	NUMBER OF QUADRATS SAMPLED		NUMBER OF SPECIMENS IN ALL QUADRATS										NUMBER OF QUADRATS WITHOUT CORALS	
			<u>Titanideum frauenfeldii</u>		<u>Leptogorgia virgulata</u>		<u>Lophogorgia sp./ Muricea pendula</u>		<u>Oculina varicosa</u>		<u>Solenastria hyades</u>			
	IS	MS	IS	MS	IS	MS	IS	MS	IS	MS	IS	MS	IS	MS
0-1.0	55	30	919	246	64	2	29	66	115		7			2
1.1-2.0	27	8	364	112	32		32	7	45		8			1
2.1-3.0	20	5	421	19	5		8	14			2		1	
3.1-4.0	10	7	133	133	5		1	5	5		2			1
4.1-5.0	9	1	125		8		2		1					1
5.1-6.0	2	8	52	12				10						3
6.1-7.0	2	6	22	40				1						2
7.1-8.0		6		28				8						3
8.1-9.0		6		2				4						3
9.1-10.0		6		9				1						3
10.1-11.0		2				1		2						1
11.1-12.0		4		25				1						2
12.1-13.0		1												1
13.1-14.0		3		2				4						2
14.1-15.0		2		14										1
15.1-16.0		1												1
16.1-17.0		3		9										1
17.1-18.0		1		7										8
18.1-30.0+		13												13

Table 2.3 Summary of sponge densities in relation to average sediment depths within quadrats assessed at inner-shelf (IS) and middle-shelf (MS) stations.

AVERAGE SEDIMENT DEPTH (cm) PER QUADRAT	NUMBER OF QUADRATS SAMPLED		NUMBER OF SPECIMENS IN ALL QUADRATS										NUMBER OF QUADRATS WITHOUT SPONGES	
			Ircinia ramosa		*Ircinia campana*		*Homaxinella* sp.		*Homaxinella waltonsmithi*		*Haliclona oculata*			
	IS	MS	IS	MS	IS	MS	IS	MS	IS	MS	IS	MS	IS	MS
0-1.0	37	10	177	21	34	19	228	3	341	9	19		3	
1.1-2.0	47	10	85	24	10	22	113	1	147	7	19		11	5
2.1-3.0	19	8	15	26	2	15	51	3	64	4	10		5	1
3.1-4.0	13	8	14	15	9	25	29	12	59	7	11		3	
4.1-5.0	7	10	6	17		17	5	7	9	5	2		3	4
5.1-6.0	3	10		13		8		8		5			3	4
6.1-7.0		7		17		7				1				4
7.1-8.0		5								1				3
8.1-9.0		3				1		2		1				1
9.1-10.0		8		15		10		3		2				5
10.1-11.0		5		7						2				3
11.1-12.0		3		2		2								2
12.1-13.0		2												2
13.1-14.0		0												-
14.1-15.0		3		9		4				1				2
15.1-16.0		4												4
16.1-17.0		1												1
17.1-18.0		2		1						1				1
18.1-19.0		0												-
19.1-20.0		0												-
20.1-21.0		1				1		1						
21.1-30.0+		6												6

- (no quadrats sampled)

Table 2.4 Summary of statistical results obtained from Spearman Rank correlation analyses of specimen density versus average sediment depth within the quadrats.

		CORALS					SPONGES		
Species Name	Station	No. of Quadrats with Specimens	Spearman r_s	Probability	Species Name	Station	No. of Quadrats with Specimens	Spearman r_s	Probability
Titanideum	IS31	44	-0.07	0.61	*Ircinia ramosa*	IS31	6	-0.17	0.75
frauenfeldii	IS32	45	0.13	0.39		IS32	38	-0.37	0.02*
	IS33	30	-0.02	0.93		IS33	17	-0.57	0.02*
	IS (combined)	119	-0.03	0.96		IS (combined)	61	-0.50	0.0001**
	MS31	17	-0.16	0.55		MS31	21	0.13	0.59
	MS32	12	-0.17	0.59		MS32	9	-0.50	0.17
	MS33	27	-0.21	0.30		MS33	8	-0.06	0.89
	MS (combined)	56	-0.16	0.24		MS (combined)	38	-0.01	0.95
Leptogorgia	IS31	27	-0.03	0.88	*Ircinia campana*	IS31	5	0.54	0.34
virgulata	IS32	12	-0.30	0.34		IS32	19	-0.01	0.95
	IS33	4	-0.26	0.74		IS33	4	0.00	1.00
	IS (combined)	43	-0.11	0.48		IS (combined)	28	-0.06	0.78
	MS31	1	NT	-		MS31	23	-0.21	0.33
	MS32	1	NT	-		MS32	9	-0.14	0.72
	MS33	0	-	-		MS33	7	-0.43	0.34
	MS (combined)	2	NT	-		MS (combined)	39	0.08	0.63
Lophogorgia sp./	IS31	26	0.15	0.45	*Homaxinella* sp.	IS31	2	NT	-
Muricea pendula	IS32	5	-0.87	0.06		IS32	35	0.07	0.68
	IS33	0	-	-		IS33	11	-0.52	0.10
	IS (combined)	31	-0.06	0.76		IS (combined)	48	-0.24	0.12
	MS31	24	-0.43	0.04*		MS31	4	0.94	0.05*
	MS32	11	-0.59	0.05*		MS32	5	0.16	0.80
	MS33	0	-	-		MS33	5	0.45	0.45
	MS (combined)	35	-0.42	0.01**		MS (combined)	14	0.42	0.14
Oculina	IS31	8	-0.42	0.29	*Homaxinella*	IS31	24	0.19	0.38
varicosa	IS32	27	-0.37	0.06	*waltonsmithi*	IS32	39	-0.12	0.46
	IS33	5	-0.63	0.25		IS33	18	0.01	0.94
	IS (combined)	40	-0.48	0.002**		IS (combined)	81	-0.25	0.02*
	MS (combined)	0	-	-		MS31	4	-0.32	0.68
						MS32	7	-0.06	0.90
Solenastrea	IS31	13	0.26	0.39		MS33	12	-0.63	0.03*
hyades	IS32	0	-	-		MS (combined)	23	-0.47	0.02*
	IS33	0	-	-					
	IS (combined)	13	0.26	0.39	*Haliclona*	IS31	11	0.00	1.00
	MS (combined)	0	-	-	*oculata*	IS32	16	0.03	0.90
						IS33	15	0.37	0.17
						IS (combined)	42	0.18	0.24
						MS (combined)	0	-	-

NT = Not tested
* = Significant at 0.05 level
** = Significant at 0.01 level

observed in quadrats with an average sediment depth > 7.0 cm at IS stations or > 18.0 cm at MS stations (Table 2.2).

Similar patterns of distribution were noted for the whip coral, *Leptogorgia virgulata* (Table 2.2). More than 99% of all *L. virgulata* colonies counted during this study were found at inner-shelf sites and 84% of those specimens were present in quadrats with an average sediment depth ≤ 2.0 cm. Only 1 of the 117 *L. virgulata* specimens counted were present in quadrats with an average sediment depth > 5.0 cm. As noted for *T. frauenfeldii*, the density of *L. virgulata* showed a slight negative correlation with average sediment depths in quadrats which contained this species, although these correlations were not statistically significant.

The only other large octocorals commonly observed at the study sites were the fan-shaped gorgonians, *Lophogorgia* spp. and *Muricea pendula*. These octocorals were equally abundant in both depth zones, and most colonies (84%) were found in quadrats with an average sediment depth ≤ 5.0 cm (Table 2.2). No fan corals were observed in quadrats with average sediment depths > 14.0 cm. Furthermore, there was a significant negative correlation between colony density and sediment depth in quadrats at the middle-shelf sites where 54% of all colonies were found (Table 2.4). A negative correlation was also noted at station IS32, although this correlation was less significant based on Spearman rank correlation analysis.

The hard corals, *Oculina varicosa* and *Solenastrea hyades*, were encountered only along transects at the inner shelf stations, and neither species was observed in quadrats with an average sediment depth > 5.0 cm (Table 2.2). A significant negative correlation was noted between *O. varicosa* density and average sediment depth in the quadrats when data from all IS stations were combined (Table 2.4), and 96% of all colonies counted were found in quadrats with an average sediment depth ≤ 2.0 cm. *Solenastrea hyades* was only found at station IS31, and no significant correlation was noted between the density of this species and sediment depth in the quadrats (Table 2.4).

All five sponge species assessed in this study were observed at IS stations, whereas only four of the species were encountered at the deeper MS stations (Table 2.3, Appendices 2.1-2.6). Of these sponges, only the large vase sponge *Ircinia campana* and the finger sponge *Haliclona oculata* were commonly detected on television transects conducted previously at inner- and middle-shelf stations (SCWMRD and GADNR, 1981; SCWMRD, 1982). Other large sponge species which have been observed at hard-bottom sites, such as the loggerhead sponge *Spheciospongia vesparium* and the barrel-shaped sponges *Cliona* spp. (SCWMRD, 1982), were not encountered along transects established at IS and MS stations.

The vase sponge *I. campana*, and the irregularly shaped sponge, *I. ramosa*, were common at both the IS and MS stations. *Ircinia campana* was more abundant at the deeper MS sites whereas *I. ramosa* was more abundant at the shallower IS sites (Table 2.3). Of the 464 *I. ramosa* counted at all sites, approximately 93% were found in quadrats with an average sediment depth ≤ 7.0 cm. There was generally a negative correlation between *I.*

ramosa density and average sediment depth within the quadrats where this species was observed (Table 2.4), and this correlation was highly significant for sponges counted at the IS stations (combined). The distribution of I. campana was not significantly correlated with sediment depth at any of the stations sampled, but 90% of all specimens counted were located in quadrats with an average sediment depth ≤ 7.0 cm.

The finger sponge Homaxinella sp. and the flabellate sponge Homaxinella waltonsmithi were observed at all stations sampled, but both species were much more abundant at the shallower IS sites than at the deeper stations (Table 2.3). Approximately 98% of all specimens representing each species were found in quadrats having an average sediment depth ≤ 5.0 cm. The density of Homaxinella sp. showed no consistent correlation with average sediment depth in quadrats at the different stations, although a significant positive correlation was noted at one station (Table 2.4). The density of H. waltonsmithi, on the other hand, was negatively correlated with sediment depth at most stations and significant negative correlations were observed when the data obtained at stations in each depth zone were combined (Table 2.4).

The only other large sponge species commonly observed at the study sites was the finger sponge Haliclona oculata. This species was found only in IS quadrats, although it has been observed in middle-shelf hard-bottom areas during previous studies (SCWMRD, 1982). The majority of H. oculata (91%) were observed in quadrats with an average sediment depth ≤ 4.0 cm, but no significant correlation between sediment depth and sponge density was noted for this species (Table 2.4).

The lack of any consistent association between sponge or coral density and the average depth of sediment in quadrats sampled at the inner- and middle- shelf sites is probably due to the patchy distribution of hard substratum along the transects. Sediment depths at the fixed locations measured within each quadrat were often quite variable and, in many instances, patches of bare sand with sediment depths > 30 cm were present in quadrats which also had rock substratum with little or no sediment cover. Although quadrats with one or more fixed-point measurements > 30 cm were excluded from statistical analyses, the estimates of mean sediment depth based on the fixed-point measurements did not always accurately reflect the sediment depths where most organisms were found.

Measurements taken at the base of sponges and corals found in the quadrats provide more information on the distribution of these species with respect to sediment depth. A total of 1230 measurements were made adjacent to sponge and coral specimens at the six stations. The data obtained indicate a clear relationship between sediment depth and the presence of the sessile species examined (Figures 2.3-2.5, Appendix 2.7-2.8). Of the 578 corals measured, only one specimen of L. virgulata was found in sediment > 8.0 cm deep and more than 95% of the specimens representing each species were attached to rock covered by sediment ≤ 5.0 cm deep. Similarly, among the 652 sponges measured, only one specimen of I. campana was observed in sediment > 8.0 cm deep and more than 93% of the specimens representing each species were found attached to rock covered by sediment ≤ 5.0 cm deep. Furthermore, in both depth zones the majority of all sponge and coral

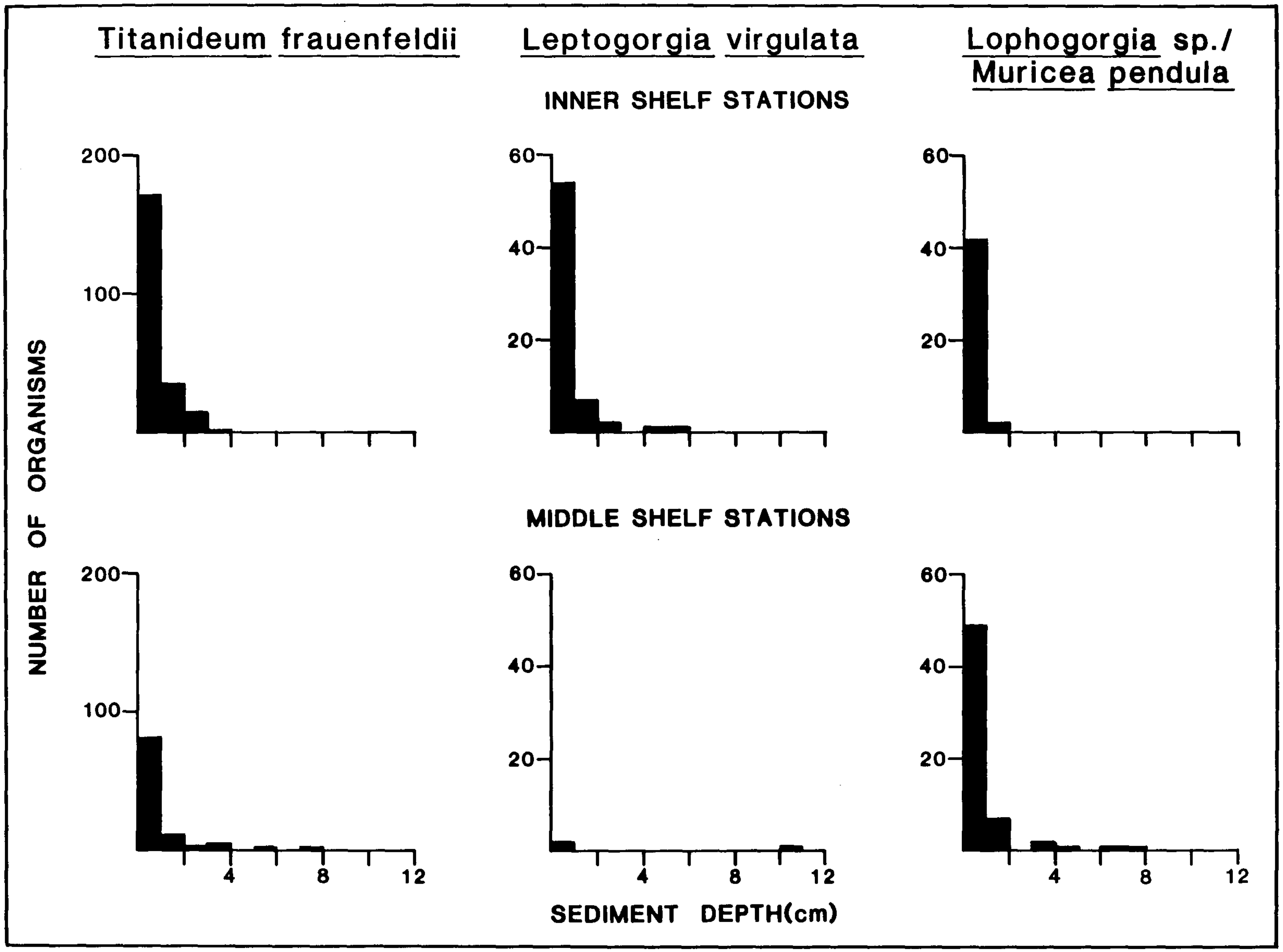


Figure 2.3 Frequency distribution of octocorals observed attached to hard substratum covered by different sediment depths. Sediment depths represent measurements taken at the base of each specimen counted.

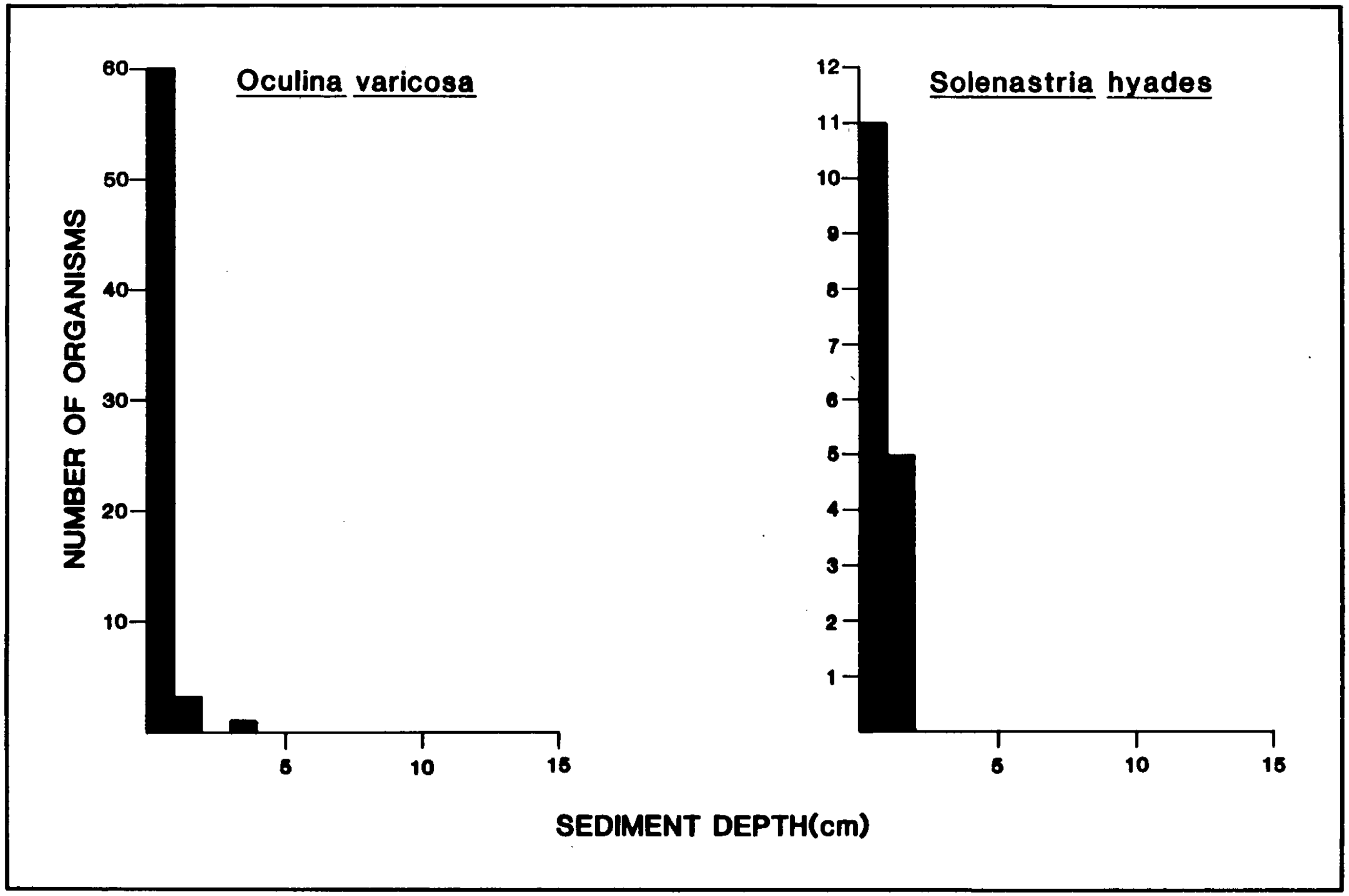


Figure 2.4 Frequency distribution of hard corals observed attached to hard substratum covered by different sediment depths. Sediment depths represent measurements taken at the base of each specimen counted.

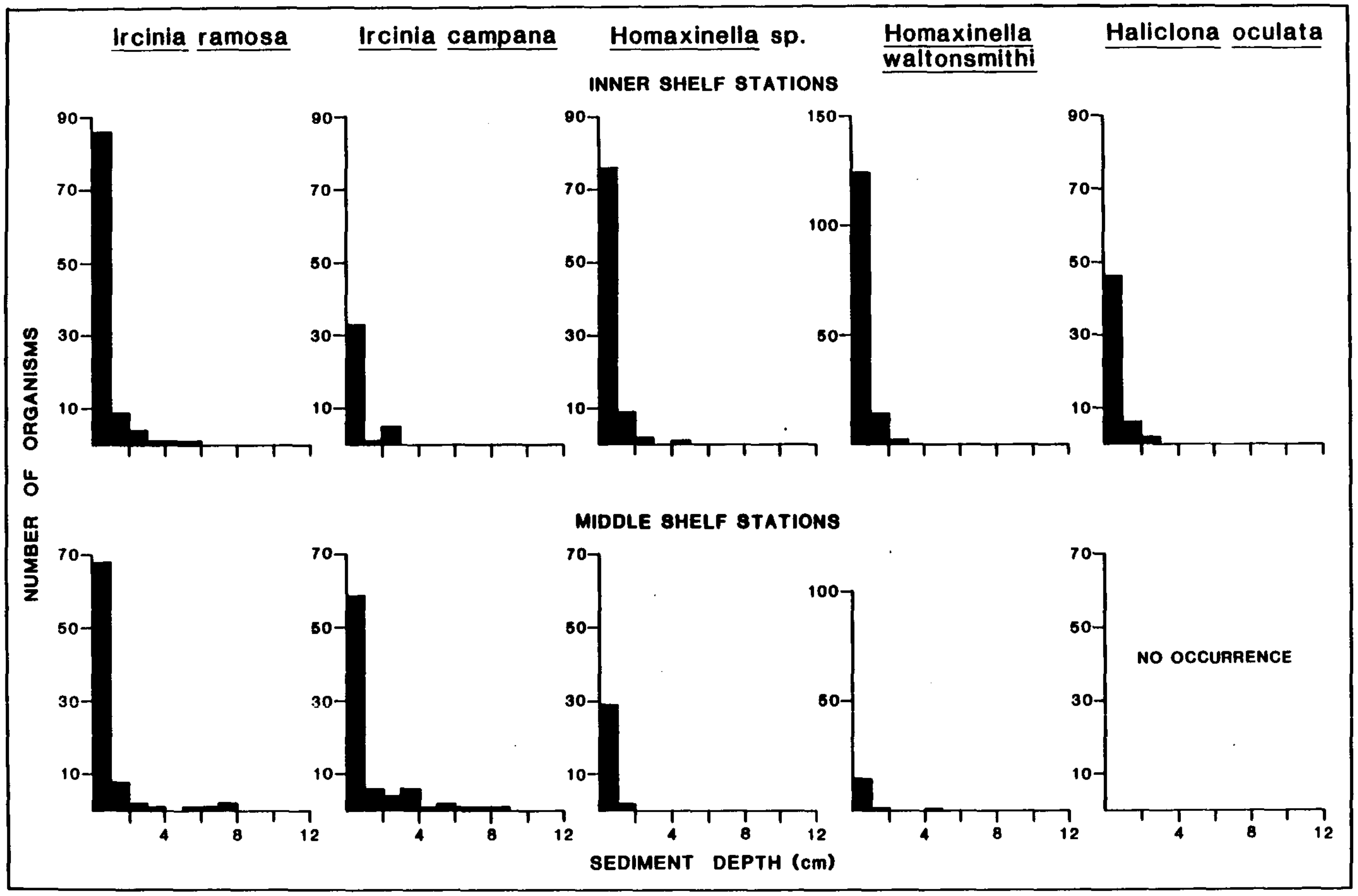


Figure 2.5 Frequency distribution of sponges observed attached to hard substratum covered by different sediment depths. Sediment depths represent measurements taken at the base of each specimen counted.

specimens were found attached to rock having 0-1 cm of sediment cover.

Several previous studies have noted that sponges and corals are intolerant of heavy sediment loads in the water column or on the bottom (e.g. Bakus, 1968; Roy and Smith, 1971; Jones and Enden, 1973, 1976; Taylor, 1977; Bak, 1978); however, these studies generally do not define specific limits of sediment cover which would inhibit the growth or distribution of these taxa. Other studies have noted the presence of sponges and corals in areas covered by sandy sediments, but made no mention of the sediment depth (Wells et al., 1960; Nicol and Reisman, 1976; Storr, 1976; Vacelet and Vasser, 1977; Reed, 1980).

Results obtained from this study indicate that the predominant sponge and coral species growing in hard-bottom areas of the South Atlantic Bight can tolerate a layer of sediment over the rock substratum, but all of the species are restricted by the depth of sediment cover. Only one of the 1230 specimens measured at their points of attachment was ever observed growing where sediment thickness exceeded 8 cm, and all sponges and corals were absent from quadrats with average sediment depths exceeding 21 cm. Furthermore, the data support the hypothesis that sponge and coral densities are inversely correlated with the depth of sediment over hard substratum.

To our knowledge, data comparable to those reported in this study have not been published previously. Wiedenmayer (1977) examined shallow water sponges of the western Bahamas and noted that many species of the same genera we studied (e.g. *Ircinia*, *Haliclona*) were found in areas with a "...sediment veneer up to 4 inches thick." He also qualitatively noted that the frequency of sponges and stony corals in these areas was dependent on the thickness of the sediment veneer. Occurrence of the most common sponge, *Spheciospongia vesparium*, dropped markedly when the sediment veneer exceeded 2-3 inches and the common coral, *Siderastrea radians*, was confined to areas where the sediment veneer was less than one inch in thickness. Thus, Wiedenmayer's observations support the data obtained in our study although different species were examined.

Storr (1976) indicates that clean, exposed rock is essential for the attachment of several sponge species. Similarly, Bayer (1961) notes that most gorgonian corals require solid substratum for growth when waters are turbulent. However, bare rock substratum was rarely observed at our study sites and it is not clear how the extensive sponge and coral assemblages we observed in these areas became established. It is possible that the species assessed in our study can attach and grow on rocky substratum having some sediment cover, but no data exist on what sediment thickness would preclude settlement. Alternatively, it is possible that shifts in sediments within these areas result in short-term exposure of bare rock, thus allowing settlement and growth. Once established, the sponges and corals can tolerate shifts in sediment cover around their base of attachment as long as these shifts do not result in burial of the specimen. In either case, the negative correlation noted between sediment depth and the density of most species observed in this study suggests that increased sediment depth over hard substratum inhibit the attachment and/or survival of these species.

IMPLICATIONS OF TASK II RESULTS RELATED TO OFFSHORE OIL AND GAS DEVELOPMENT

Drilling muds released from exploration and production platforms are known to have an adverse affect on benthic fauna due to (1) the toxicity of their chemical constituents, and (2) changes in the physical environment resulting from increased turbidities and sedimentation rates (see SCWMRD, 1982; Duke and Parrish, 1984 for reviews). While this study does not address the toxic effects associated with drilling muds, the data indicate that sponges and corals commonly found in hard-bottom areas of the South Atlantic Bight may be very sensitive to the accumulation of sediment on the bottom. Furthermore, organisms growing in areas with deeper natural sediment cover might be even more susceptable to mortality from increased sedimentation due to industry-related activities or natural events. Obviously, a number of factors such as water depth, current velocity, and proximity of the discharge pipe would influence the rate of sedimentation in a hard-bottom area near a platform. However, our data suggest that if sediment depths over hard substratum exceed 5 cm, then sponges and corals will be absent or present only in low densities.

Exploration for petroleum or mineral resources requires extensive surveys of bottom conditions in lease blocks where activities are proposed. In addition to comprehensive geophysical surveys of sub-bottom conditions, television and still-camera systems have often been deployed to evaluate biological resources. Although these devices are excellent for mapping the location of hard-bottom fauna, they provide only a limited field of view and they usually must be towed slowly. Thus, considerable time and effort is required to map an area for epifaunal growth. Side-scan sonar and sub-bottom profiling instruments often can be used to rapidly map hard-bottom subtrata, but give no information on the presence, absence, or distribution of epifaunal growth that may be present. The data obtained in this study, used in conjunction with geological survey techniques to measure sediment depth over hard substratum, should be helpful in predicting the presence of hard-bottom epifauna.

SUMMARY AND CONCLUSIONS

- The purpose of this study was to evaluate the relationship between sediment depth over hard substratum and the distribution of predominant sponge and coral species inhabiting hard-bottom areas of the South Atlantic Bight.

- Six hard-bottom reefs located on the continental shelf off South Carolina and Georgia were sampled: three of the sites were located in relatively shallow waters of the inner shelf while the other three were located in deeper waters of the middle shelf. At each study site, replicate transect lines were laid out so that they traversed areas with high and low densities of sessile fauna. Large quadrats were then assessed at uniform intervals along each transect to assess sponge and coral density within 5-m^2 and 2-m^2 areas, respectively, and to assess average sediment depth based on fixed-point measurements in each quadrat. Additional sediment depth measurements were also obtained at the attachment sites of several representative specimens of each species assessed.

- Approximately 5000 sponges and corals were counted in 597 quadrats surveyed at the 6 sites. Octocorals were more abundant than sponges at all stations and hard corals were relatively uncommon. Densities of all octocoral species (*Titanideum frauenfeldii*, *Leptogorgia virgulata*, and *Lophogorgia* spp./ *Muricea pendula*), one hard coral species (*Oculina varicosa*) and most sponge species (*Ircinia ramosa* , *I. campana* , and *Homaxinella waltonsmithi*) were negatively correlated with sediment depth at most stations, although not all correlations were statistically significant. Densities of the hard coral *Solenastrea hyades* and the sponges *Homaxinella* sp. and *Haliclona oculata* were more variable with respect to average sediment depth in the quadrats. However, no sponges or corals were observed in quadrats with average sediment depths exceeding 21 cm.

- Measurements collected at the bases of 1230 sponges and corals representing all of the above species showed a clearer relationship between species distribution and sediment depth. Most specimens were found attached to hard substratum with 0-1 cm of sediment cover. Additionally, more than 95% of the corals and 93% of the sponges were observed attached to rock with $\leq$ 5.0 cm of sediment.

- Results obtained in this study suggest that increased thickness of sediment over hard substratum inhibit the attachment and survival of the sponge and coral species assessed, and that specimens growing in deeper sediments could be more susceptible to additional sedimentation from natural or industry-related activities. The data obtained should also be helpful in locating areas where hard-bottom fauna might be growing using remote assessment techniques such as side-scan sonar and sub-bottom profiling systems.

Task III: A Study of Food Habits of Hard-Bottom Fishes

INTRODUCTION

The importance of hard-bottom habitat to commercial and recreational fisheries in the South Atlantic Bight has been well documented (Struhsaker, 1969; Ulrich et al., 1976; Miller and Richards, 1980; Grimes et al., 1982; Wenner, 1983; Sedberry and Van Dolah, 1984; Chester et al., 1984). In addition, large populations of unexploited forage and bait fishes are closely associated with these hard-bottom reefs (Struhsaker, 1969; SCWMRD, 1982; Wenner, 1983; Sedberry and Van Dolah 1984). Although the nature of the attraction of fishes to hard-bottom reefs is complex and poorly understood, several factors are considered to be important in the association between fishes and the relief provided by hard bottom and its associated epifauna. Hard-bottom reefs may provide shelter from predators for small fishes associated with the reef, a substrate on which to deposit eggs or establish cleaning stations, and an abundance of epifaunal organisms on which benthic-feeding fishes can prey.

The first two phases of the present study involved an investigation of the food habits of several of the most important fishery species, in order to understand the importance of hard-bottom habitat as feeding grounds for these fishes. Species examined included black sea bass, red snapper, vermilion snapper, gag and scamp groupers, and red porgy (SCWMRD and GADNR, 1981; SCWMRD, 1982). Two additional species, southern porgy (the most abundant species collected) and whitebone porgy (an abundant and economically important species) were also studied. These studies were aimed primarily at describing seasonal differences in the food habits of those fishes. During Phase III, the study was expanded to further describe length- and depth-related changes in the food habits of these important hard-bottom fishes and to quantify the importance of hard-bottom organisms as prey for these fishes by making selectivity comparisons between stomach samples and benthic samples. In order to better understand the complex interactions between fish and epibenthic communities, stomachs of several additional species of fish that were collected during the two-year baseline study were also analyzed. These species included important fishery species, as well as additional hard-bottom fishes. The purpose of this report is to present the results of these food habits studies.

METHODS

Fishes analyzed for food habits were collected during seasonal cruises in 1980 (two cruises, one in winter and one in summer) and 1981 (four cruises, one each in winter, spring, summer, and fall) from the 11 hard-bottom stations sampled in the first two phases of the Living Marine Resources Study (Figure 3.1). Stations were located in each of three depth zones representing the inner shelf (16-22 m depth, three stations), middle shelf (23-37 m depth, four stations) and the outer shelf (46-69 m depth, four stations). Fishes were collected with a variety of gears including trawls, traps, hook-and-line, and

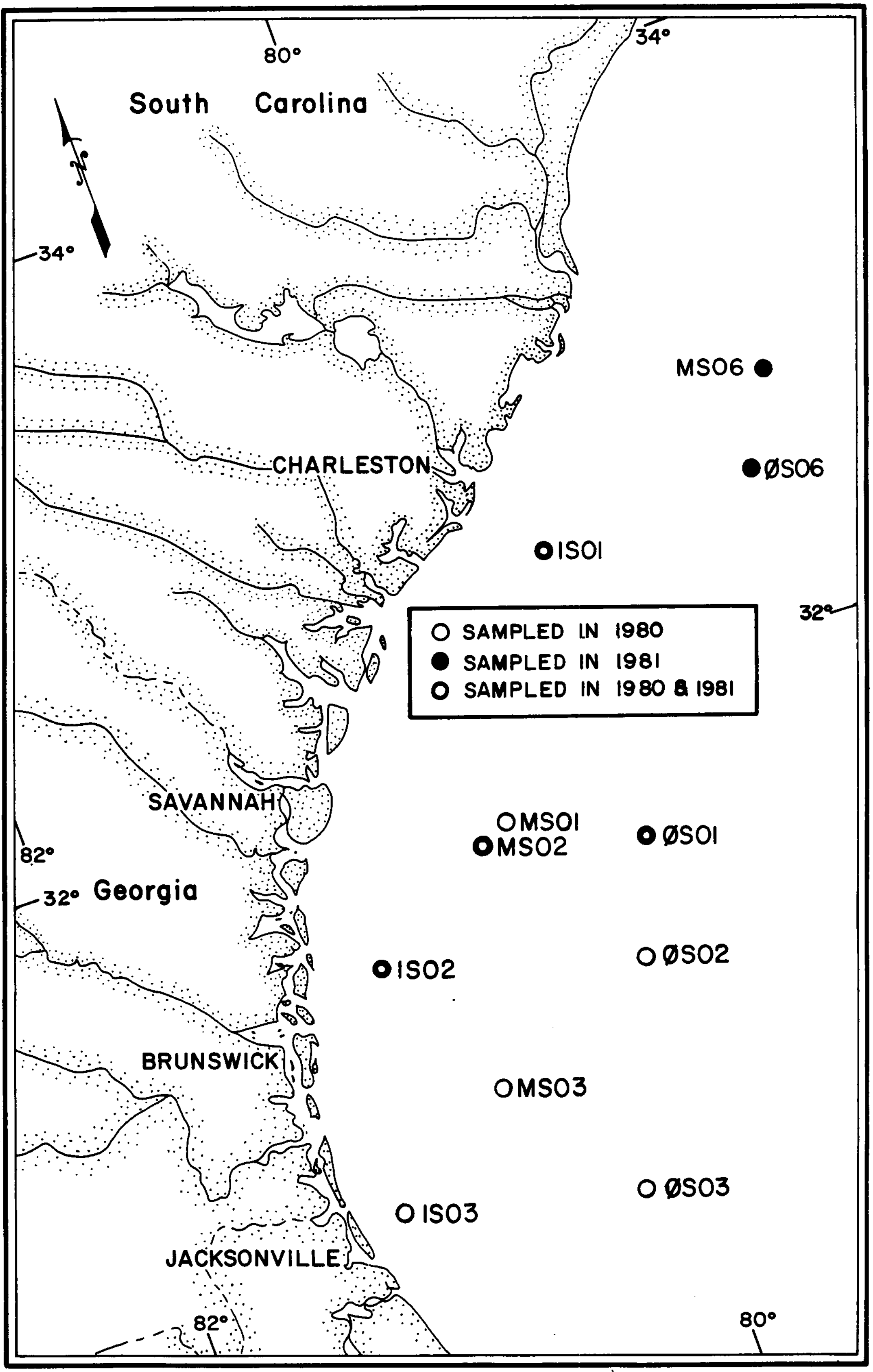


Figure 3.1 Stations sampled for fishes in 1980 and 1981.

speargun, but most fishes utilized for food habits study were collected by trawl. Only inner- and middle-shelf stations and the outer-shelf station OS01 could be sampled by trawl. Sampling for fishes was conducted on hard-bottom habitat which was mapped for each station using underwater television. Detailed descriptions of station locations and sampling techniques are described in the final reports of the first two phases (SCWMRD and GADNR, 1981; SCWMRD, 1982; see also Wenner et al., 1983; Sedberry and Van Dolah, 1984; and Wenner et al., in press).

Species for which seasonal food habits were described in the final reports of those studies were: Centropristis striata (black sea bass), Mycteroperca microlepis (gag), M. phenax (scamp), Lutjanus campechanus (red snapper), Rhomboplites aurorubens (vermilion snapper), Calamus leucosteus (whitebone porgy), Pagrus pagrus (red porgy), and Stenotomus aculeatus (southern porgy). Additional species analyzed for the present report were Diplectrum formosum (sand perch), Apogon pseudomaculatus (twospot cardinalfish), Haemulon aurolineatum (tomtate), Archosargus probatocephalus (sheepshead), Lagodon rhomboides (pinfish), and Equetus lanceolatus (jackknife-fish). These additional species included fishes that are important in hard-bottom fisheries or that dominated by number or weight of trawl catches in the 1980-1981 cruises (Table 3.1).

Fishes were usually identified and measured (standard length, SL) at sea and their stomachs were excised if not conspicuously empty. Stomachs were individually labeled and preserved in 10% seawater-formalin. Small individuals were preserved whole and dissected in the laboratory. Stomachs were washed in tap water and transferred to 50% isopropanol in the laboratory, where contents of individual stomachs were sorted by taxa and counted. For sheepshead (Archosargus probatocephalus) which have no clearly defined stomach, the contents of the anterior fourth of the digestive tract were examined. Colonial forms and fragments of animals were counted as one organism unless abundance could be estimated by counting pairs of eyes (crustaceans), otoliths (fishes), or other parts. Volume displacement of food items was measured using a graduated cylinder, or estimated by using a 0.1-cm^2 grid (Windell, 1971).

Since methods of food habits quantification are variously biased (Hynes, 1950; Pinkas et al., 1971; Windell, 1971), the relative contribution of different food items to the total diet was determined using three methods: (1) percent frequency occurrence (F), (2) percent numerical abundance (N), and (3) percent volume displacement (V). Percent frequency occurrence indicates what prey species are being fed upon but gives no indication of quantity. It is useful, however, for describing the food habits of predators that feed on large numbers of colonial forms, which cannot be counted. Percent numerical abundance provides a quantitative estimate of the abundance of prey items in a predator but does not give an accurate estimate of energy value because of wide variations in the size of individuals of a prey species. Percent volume is not affected by frequency or numbers of individuals and more accurately reflects foods consumed by the predator population as a whole. Volumetric measurements, however, are subject to errors due to digestion and also mask the importance of smaller food items, particularly if a few very large predators that consumed a few large prey are present in the samples. For some predators that feed heavily on colonial forms, frequency and volume may more

Table 3.1 Fishes selected for food habits analysis and percent of the total trawl catch of demersal teleost fishes during the six sampling periods in 1980 and 1981. Data from the eight trawled stations are combined.

	Percent of Total Demersal Teleost Catch by:			
	Number	(Rank)	Weight	(Rank)
Serranidae (sea basses)				
Centropristis striata (black sea bass)	0.95	(5.0)	2.69	(7.0)
Diplectrum formosum (sand perch)	0.34	(13.0)	0.40	(18.0)
Mycteroperca microlepis (gag)	0.02	(46.5)	1.80	(8.0)
Mycteroperca phenax (scamp)	< 0.01	(95.0)	0.10	(32.0)
Apogonidae (cardinalfishes)				
Apogon pseudomaculatus (twospot cardinalfish)	0.30	(15.0)	0.02	(50.0)
Lutjanidae (snappers)				
Lutjanus campechanus (red snapper)	0.04	(33.0)	1.15	(14.0)
Rhomboplites aurorubens (vermilion snapper)	17.66	(2.0)	9.43	(3.0)
Haemulidae (grunts)				
Haemulon aurolineatum (tomtate)	16.31	(3.0)	10.78	(2.0)
Sparidae (porgies)				
Archosargus probatocephalus (sheepshead)	0.05	(29.0)	1.22	(11.0)
Calamus leucosteus (whitebone porgy)	0.59	(8.0)	4.66	(4.0)
Lagodon rhomboides (pinfish)	0.40	(12.0)	0.56	(17.0)
Pagrus pagrus (red porgy)	0.21	(17.0)	1.40	(9.0)
Stenotomus aculeatus (southern porgy)	52.07	(1.0)	49.06	(1.0)
Sciaenidae (drums)				
Equetus lanceolatus (jackknife-fish)	0.53	(9.0)	1.21	(12.0)
Total demersal teleosts caught:	150,184		8134.691 kg	
Total percent of demersal teleost caught:	89.47		84.48	
Total number of demersal teleost species:	161		161	

accurately describe the food habits; whereas for infaunal feeders that feed on similarly-sized small items, numerical abundance estimates are most accurate. For these reasons, a combination of the three measures of food value were used to describe the food habits of fishes examined.

Percent frequency, number and volume were calculated for prey species and for prey items grouped into higher taxonomic categories. To avoid excessive tabular material, values are only presented for those prey items that occurred with a frequency of at least one percent or which made up at least one percent of the total number or volume of prey.

In order to determine the dependence of demersal fishes on hard-bottom prey organisms, stomach samples were compared to benthic samples using Ivlev's index of electivity (Ivlev, 1961), calculated as follows:

$$E = \frac{P^1 - P^2}{P^1 + P^2}$$

where P^1 is the percentage of the diet composed of a given prey taxon and P^2 is the percentage of the food complex in the environment (i.e., in benthic samples) composed of the same prey taxon. Electivity values range from -1 to +1. Negative values imply that the prey species is avoided by the predator or that it is unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species that occur in a different habitat than that sampled by the benthic sampler. A value near zero implies no selectivity by the predator, i.e., the fish is feeding on the prey in proportion to the prey's relative abundance.

The electivity index was calculated for species that were numerically dominant in benthic samples or in fish stomach samples. Benthic samples and stomach collections were pooled by depth zone (inner, middle and outer shelf) for comparison. Benthic samples were obtained at the 11 hard-bottom sites during 1980 and 1981 with a suction sampler (inner and middle shelf) or a grab (outer shelf). Details of benthic sampling are provided in the Year I and Year II final reports (SCWMRD and GADNR, 1981; SCWMRD, 1982) and are only summarized here. Briefly, divers obtained five replicate suction samples at each inner- and middle-shelf station by scraping the area enclosed by a 0.1 m^2 quadrat box while simultaneously sucking with an airlift device similar to that described by Chess (1979). Suction samples were collected in 1.0-mm mesh bags.

At the outer shelf stations (OS01, OS02, OS03, and OS06) where water depth precluded the use of the suction device operated by divers, quantitative 0.1 m^2-samples were collected with a modified Smith-McIntyre grab (Kahlsico No. 214WA250). After retrieval, each sample was placed into a 1.0-mm sieve and washed to remove the finer sediment.

Sampling invertebrates with the suction sampler proved to be a very simple, yet effective, technique. Samples were quantitative because suctioning was confined to the surface area within the walled box placed on the substratum. The Smith-McIntyre grab, which was substituted for the suction sampler at deeper stations, was less reliably quantitative because the volume of sediment sampled was not consistent for all collections, especially when the grab hit hard bottom without a sand veneer. In spite of these limitations, the grab sampler was the only effective means of sampling outer shelf stations, and provided the only quantitative benthic collections on which to calculate electivity.

A modification of this technique was used, in addition to the above, to calculate electivity indices for the species that fed on motile epifauna and on sessile forms, and for those species that fed primarily on plankton. For those predators that fed on sessile forms, presence or absence of sessile species in fish stomachs was compared to presence or absence of those prey in dredge samples. Dredge samples consisted of two replicate tows during each cruise at each of 11 stations with either a 60 cm x 37 cm mouth opening rock dredge or a 90 cm x 37 cm opening Cerame-Vivas dredge. For the selectivity analysis, calculations of percent occurrence were done only for those taxonomic groups of sessile organisms that were analyzed in dredge samples (i.e., barnacles, hydroids, sponges, bryozoans, and ascidians). Abundance of sessile animals in any sample was considered to be one if the species occurred in the dredge or stomach sample.

For plankton feeding fishes, electivity comparisons were made with suction/grab samples as well as with samples obtained with an epibenthic plankton sled. This sled had a mouth opening of 0.5 m^2 and runners which permit it to sample 5 cm off the bottom. The sled also had a mouth-opening mechanism designed to fish only when it was in contact with the bottom. A .947 mm mesh net was attached to the sled, and two ten-minute tows were made per station at night to minimize visual net avoidance. Sled collections for invertebrates were made only in 1981. These samples were analyzed for decapods, stomatopods, cumaceans, and mysids, and comparisons with fish stomachs were limited to these taxa. Further details of fish and invertebrate sampling can be found in the Phase I and Phase II final reports (SCWMRD and GADNR, 1981; SCWMRD 1982).

Similarity in diet between predators was measured using the Bray-Curtis measure (Bray and Curtis, 1957), expressed as:

$$S_jk = 1 - \frac{\sum_i |X_{ji} - X_{ki}|}{\sum_i (X_{ji} + X_{ki})}$$

where S_{jk} is the similarity in diet between the predators j and k; X_{ji} is the abundance of the i^{th} prey for predator j; and X_{ki} is the abundance of the i^{th} prey for predator k. Because sample sizes of predators were unequal, abundance of prey items was standardized as percent numerical abundance for each predator (Clifford and Stephenson, 1975; Boesch, 1977). Only prey items that were identified to species were included in the similarity analyses. Similarity values are presented in trellis diagrams.

Similarity in diet among all predators was also determined using numerical classification techniques (cluster analysis) on the data matrix generated by the Bray-Curtis measure. Each predator was treated as a collection, and all predators were subjected to normal cluster analysis. Similarity among groups of predators was expressed in the form of dendrograms generated using flexible sorting with $\beta = -0.25$ (Lance and Williams, 1967; Clifford and Stephenson, 1975).

RESULTS AND DISCUSSION

Of the 1952 stomachs from 14 fish species examined, 1316 (67.4%) contained food. Results from the analysis of these stomachs are presented below in descriptions for each species.

Centropristis striata

Black sea bass, an important commercial and recreational species, were abundant in the study area and made up a large portion of trawl catches (Table 3.1). They were most abundant in trawl tows at inner-shelf stations (mean catch per tow of 11.9), frequent at the middle shelf (5.4 per tow) and rare at the outer shelf (< 0.1 per tow).

Approximately 220 species of prey were identified in 441 black sea bass stomachs during the two-year study. Amphipods, decapods, and fishes dominated the diet (Appendix 3.1, Table 3.2). Amphipods were frequently found in large numbers but, because of their small size, contributed little to the food volume. Caprellids and the epifaunal tube-dwelling *Erichthonius brasiliensis* were the most abundant amphipods consumed. Decapods were the most frequently consumed higher taxon and ranked second in number and volume. Brachyurans (e.g. *Pilumnus sayi)* were the most important decapods. Fishes made up the greatest prey volume and were frequently consumed, but in small numbers. Most fish remains in black sea bass stomachs could not be identified to species. Ascidians, ophiuroids, and polychaetes were also commonly found in stomach samples.

Amphipods dominated in frequency, number, and volume in the smallest size class of black sea bass (Table 3.2). Although amphipods were frequently found in high numbers in larger black sea bass, decapods and fishes contributed the greatest volume of prey for larger black sea bass. Ascidians were also important in the diet of larger black sea bass, and cephalopods were consumed in small amounts by all size classes.

Black sea bass fed heavily on amphipods which were not as abundant in suction samples as they were in stomachs (Table 3.3). Electivity values were usually positive for amphipods and other crustaceans that made up the diet of black sea bass. Polychaetes, such as *Exogone dispar* and *Filograna implexa* , that dominated in benthic samples were not utilized as prey by black sea bass. This is probably a result of the small size of these polychaetes (Day, 1967; Gardiner, 1975). In addition, the most abundant benthic invertebrate, *F. implexa,* constructs reef-like aggregations of calcareous tubes in which they dwell and thus are only available to specialized predators with crushing molars that are lacking in black sea bass. Selectivity analysis indicates that black sea bass appear to prefer motile epifaunal amphipods.

Table 3.2 Percent frequency occurrence (F), percent number (N) and percent volume (V) of higher taxonomic groups of food in the diet of *Centropristis striata*, by length interval.

	LENGTH INTERVALS (mm SL)														
	50-100			101-150			151-200			201-250			>250		
PREY TAXON	F	N	V	F	N	V	F	N	V	F	N	V	F	N	V
Algae				1.7	<0.1	<0.1	0.7	0.1	<0.1						
Anthophyta				1.7	<0.1	0.1									
Foraminifera				1.7	0.1	<0.1									
Porifera							4.4	0.4	1.8	4.3	0.8	1.5	3.6	1.0	0.3
Cnidaria															
Hydrozoa				6.9	0.2	0.2	8.7	0.8	0.1	11.4	2.1	<0.1	21.4	6.1	0.1
Anthozoa				3.4	0.1	0.6	4.4	0.4	0.2	2.9	0.5	0.1	7.1	2.0	3.7
Annelida				22.4	0.7	22.0	12.3	1.3	2.7	5.7	1.1	0.4	7.1	2.0	<0.1
Mollusca															
Gastropoda							2.9	0.4	<0.1	7.1	1.3	1.2			
Pelecypoda				6.9	0.3	1.0	9.4	1.2	4.1	8.5	2.4	1.9	7.1	5.1	1.3
Cephalopoda	5.3	0.2	6.8	1.7	<0.1	<0.1	4.4	0.4	9.7	2.9	0.5	6.3	7.1	3.1	5.7
Crustacea															
Copepoda				1.7	0.7	0.1	1.4	0.7	<0.1	1.4	0.3	<0.1			
Cirripedia				1.7	<0.1	0.9	7.2	1.1	0.8	4.3	1.1	0.1			
Stomatopoda										1.4	0.3	<0.1			
Mysidacea	5.3	2.6	3.6	5.2	0.4	0.3	2.2	0.9	<0.1	1.4	0.3	<0.1			
Cumacea	5.3	0.2	0.4	1.7	0.2	<0.1	0.7	0.1	<0.1						
Tanaidacea							0.7	0.1	<0.1						
Isopoda	26.3	1.1	6.3	17.2	1.9	1.6	4.4	1.4	0.1	1.4	0.3	<0.1			
Amphipoda	94.7	93.8	74.8	51.7	86.8	15.1	33.3	64.5	1.8	20.0	40.8	0.3	10.7	32.6	0.1
Decapoda	36.8	1.5	5.1	65.5	6.1	30.6	71.0	15.5	35.2	52.9	27.6	19.9	53.6	22.4	24.7
Sipunculida							1.4	0.1	0.4						
Bryozoa				3.4	0.1	0.1	8.0	0.7	0.3	5.7	1.1	0.2	10.7	5.1	0.1
Echinodermata															
Echinoidea							0.7	0.1	<0.1						
Ophiuroidea	15.8	0.6	3.0	17.2	1.0	5.2	8.7	0.8	0.6	5.7	1.1	0.8			
Holothuroidea				1.7	<0.1	0.6				4.3	0.8	3.3			
Chaetognatha							2.2	2.8	0.1						
Chordata															
Ascidiacea				6.9	0.2	3.1	15.9	1.6	8.7	21.4	4.8	17.1	21.4	8.2	15.1
Cephalochordata				1.7	<0.1	0.2									
Pisces				17.2	0.7	18.3	30.4	4.7	33.5	40.0	12.9	46.9	42.9	12.2	48.8
Number of stomachs examined:		24			73			190			105			49	
Examined stomachs with food:		19			58			138			70			28	
Mean length of fish with food:		81.3			132.4			174.8			223.7			274.4	

Table 3.3 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction samples and *Centropristis striata* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in either depth zone, for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction Samples						
Chone americana	-	0.33	-1.00	-	0.81	-1.00
Erichthonius brasiliensis	51.82	2.89	0.89	6.94	0.30	0.92
Exogone dispar	-	3.71	-1.00	-	0.47	-1.00
Filograna implexa	-	20.42	-1.00	-	63.87	-1.00
Luconacia incerta	0.36	3.27	-0.80	2.12	1.03	0.34
Malacoceros glutaeus	-	0.41	-1.00	-	0.81	-1.00
Podocerus sp. A	0.84	2.87	-0.94	0.59	0.27	0.38
Syllis spongicola	-	2.15	-1.00	-	1.90	-1.00
Total	53.02	36.05		9.65	69.46	
Dominant Species - Stomachs						
Caprella equilibra	17.06	1.55	0.83	10.71	0.34	0.93
Caprella penantis	-	0.07	-1.00	2.12	0.42	0.67
Erichthonius brasiliensis	51.82	2.89	0.89	6.94	0.30	0.92
Luconacia incerta	0.36	3.27	-0.80	2.12	1.03	0.34
Paracerceis caudata	1.04	0.54	0.31	-	0.08	-1.00
Pilumnus sayi	0.84	0.07	0.85	1.29	0.02	0.97
Photis pugnator	1.79	2.68	-0.20	0.59	0.80	-0.15
Phtisica marina	-	0.01	-1.00	2.94	0.03	0.98
Total	72.91	11.08		26.71	3.02	

Diplectrum formosum

Sand perch, which were occasionally taken in the trawl (Table 3.1), were most abundant at middle-shelf stations (mean catch per tow of 3.4) and were frequently trawled at inner-shelf stations (2.7 per tow), especially during the warmer seasons (summer and fall). Because of their rarity at the outer shelf (0.1 per tow), no stomachs were collected at those stations.

Sand perch fed on about 35 species (Appendix 3.2). Small crustaceans were the most frequently occuring prey items in the 40 stomachs examined (Table 3.4). Mysids and decapods were the most frequently consumed prey and they also ranked high volumetrically. Bowmaniella portoricensis was the primary mysid eaten and several natantians and brachyurans were important decapods. Cumaceans and amphipods were frequently consumed in large numbers but contributed little to the volume of food because of their small size. Several other taxa of invertebrates and fishes were consumed (Appendix 2.3, Table 3.4).

Sand perch less than 168 mm SL fed mainly on mysids and decapods, and these two taxa were also important in the diet of larger fish (Table 3.4). Decapods dominated in sand perch greater than 167 mm SL.

Like black sea bass, sand perch fed heavily on motile crustaceans but consumed more mysids and cumaceans than amphipods. Most of the benthic invertebrate species that were important as food for sand perch were uncommon in benthic samples, and electivity values for these species were positive (Table 3.5). On the other hand, most dominant hard-bottom invertebrates were rare in the diet of sand perch. The prey of sand perch also included a few pelagic species (e.g. chaetognaths) that were not collected in bottom samplers. Although sand perch are commonly captured and observed with other hard-bottom fishes (Bortone, 1971; Sedberry and Van Dolah, 1984), they apparently prefer sandy areas adjacent to hard-bottom reefs (Moe and Martin, 1965; Bortone, 1971). Much of the prey of sand perch were infaunal sand-dwelling species (cephalochordates, cumaceans, some of the decapods and mysids), and sand perch, while abundant near and on hard-bottom reefs, apparently do not feed heavily on epifauna associated directly with hard bottom.

Mycteroperca microlepis

Gag were not abundant in trawl catches, but ranked in the top ten species by weight because of their large size (Table 3.1). Trawl catches probably do not reflect the true abundance of gag, and underwater television observations have indicated abundances that are an order of magnitude greater than that noted in trawl catches (Sedberry and Van Dolah, 1984). Diver observations during Task II dives (section II, this volume) have indicated that gag (30-100 cm SL) are very abundant at middle-shelf depths.

Only a limited number of gag stomachs were available for analysis. This is due to the difficulty of capturing them as described above and to the problem of obtaining intact stomachs from deep-living physoclistic fishes, which often regurgitate their food when raised to the surface. Twenty-six stomachs which were believed to contain food were preserved, but on closer examination in the laboratory, only 13 of these contained food.

Table 3.4 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Diplectrum formosum*, by length interval.

	LENGTH INTERVALS (mm SL)					
	< 168			≥ 168		
PREY TAXON	F	N	V	F	N	V
Cnidaria						
Hydrozoa	6.2	0.7	0.4			
Anthozoa	6.2	0.4	3.2			
Annelida						
Polychaeta	12.5	0.7	0.9			
Mollusca						
Pelecypoda	18.8	1.8	0.2			
Crustacea						
Copepoda	6.2	0.4	0.1			
Mysidacea	56.2	63.0	21.7	82.4	80.5	21.3
Cumacea	25.0	17.4	4.3	47.1	9.7	1.0
Amphipoda	43.8	9.4	2.3	11.8	1.3	0.4
Decapoda	43.8	3.6	19.3	35.3	3.9	76.0
Bryozoa				5.9	0.6	0.1
Echinodermata						
Ophiuroidea				5.9	0.6	0.1
Chaetognatha				11.8	2.6	0.3
Chordata						
Ascidiacea	6.2	0.4	32.5			
Cephalochordata	12.5	1.4	4.9			
Pisces	12.5	0.7	10.2	5.9	0.6	0.8
Number of stomachs examined:		16			23	
Examined stomachs with food:		16			17	
Mean length of fish with food:		151.5			182.3	

Table 3.5 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction samples and *Diplectrum formosum* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in either depth zone, for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction Samples						
Chone americana		0.33	-1.00		0.81	-1.00
Erichthonius brasiliensis		2.89	-1.00	0.53	0.30	0.28
Exogone dispar		3.71	-1.00		0.47	-1.00
Filograna implexa		20.42	-1.00		63.87	-1.00
Luconacia incerta		3.27	-1.00	1.60	1.03	0.21
Malacoceros glutaeus		0.41	-1.00		0.81	-1.00
Podocerus sp. A		2.87	-1.00	0.53	0.27	0.34
Syllis spongicola	—	2.15	-1.00	—	1.90	-1.00
Total	0.00	36.05		2.66	69.46	
Dominant Species - Stomachs						
Bowmaniella portoricensis	68.73	0.09	0.99	62.57	0.10	0.99
Branchiostoma caribbaeum			0.00	2.14	.01	0.99
Caprella equilibra	6.56	1.55	0.62		0.34	-1.00
Cyclaspis varians	0.39	<0.01	0.98	1.60	<0.01	0.99
Ervilia concentrica			0.00	2.14		1.00
Leptochela papulata		0.04	-1.00	2.14	0.09	0.92
Mysidopsis bigelowi	3.47		1.00			0.00
Mysidopsis furca		<0.01	-1.00	2.67		1.00
Ovalipes stephensoni	0.39		1.00	1.60		1.00
Oxyurostylis smithi	18.15	0.67	0.93	6.42	0.14	0.96
Sicyonia typica		0.02	-1.00	2.14	<0.01	0.99
Tozeuma serratum	0.39	—	1.00	—	—	
Total	98.08	2.38		83.42	0.69	

Gag fed mainly on fishes, which dominated the diet in frequency, number, and volume (Appendix 3.3, Table 3.6). Although many fish remains could not be identified, it is apparent that schooling forage fishes such as *D. punctatus* (round scad), *E. teres* (round herring), *S. aurita* (Spanish sardine), and small vermilion snapper (*R. aurorubens*) were important prey items. Fishes were by far the most important prey for the two size classes of gag examined (Table 3.6). Because gag fed mainly on fishes, no selectivity comparison was made with benthic samples. Gag are top-level carnivores on hard-bottom reefs and feed on schooling and pelagic fishes that are abundant on these reefs in the South Atlantic Bight (SCWMRD, 1982). Previous studies from other geographic areas have indicated that dominant pelagic fishes in those areas also dominate as prey items in gag stomachs (Saloman and Naughton, MS). It is noteworthy that several small vermilion snapper, an economically important species, were found in gag stomachs. The impact of gag predation on vermilion snapper populations is unknown.

Mycteroperca phenax

Scamp, like gag, is an economically important species that was rarely collected with any sampling gear. Only four were captured during the two-year study. Underwater television observations (SCWMRD, 1982) and diver observations (Sections I and II) indicate that scamp are much rarer than are gag at inner- and middle-shelf depths.

Of the four scamp captured, two had empty stomachs. Of the remaining two, one had eaten a fish that was digested beyond identification. The other scamp examined had fed on fishes (one *Stenotomus aculeatus* and one unidentified), squid (one *Loligo plei*), and a sea urchin (Cideroida). It is apparent that scamp, like gag, are top-level carnivores.

Because of the limited number of scamp stomachs collected, it was impossible to determine size-related changes in food habits. However, fishes are the most important food for individuals exceeding 153 mm SL in other species of *Mycteroperca* (Randall, 1967; Saloman and Naughton, MS), and are probably important prey for scamp in the South Atlantic Bight.

Apogon pseudomaculatus

The twospot cardinalfish is a small species that was frequently taken in the trawl. During the first year of the Living Marine Resources Study they were collected only in the summer. In the second year, they were rare in trawl catches in winter and spring but were commonly collected during summer and fall. Individuals were frequent at the inner (mean catch per tow of 1.2) and outer (1.8 per tow) shelf, but were most abundant at middle-shelf stations (3.4 per tow) where all stomachs were collected. All twospot cardinalfish were collected at night, which is probably related to behavior. Tropical cardinalfishes occupy enclosures in the reef during the day and emerge at night to feed on plankton (Hobson, 1965; Livingston, 1971). *Apogon pseudomaculatus* apparently demonstrates similar behavior in the South Atlantic Bight and is available for capture by trawl only at night.

Table 3.6 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Mycteroperca microlepis*, by length interval.

	LENGTH INTERVALS (mm SL)					
	< 730			≥ 730		
PREY TAXON	F	N	V	F	N	V
Cnidaria						
Hydrozoa	14.3	8.3	<0.1			
Anthozoa				16.7	9.1	<0.1
Mollusca						
Gastropoda	14.3	8.3	0.1			
Cephalopoda				16.7	9.1	7.2
Crustacea						
Decapoda	14.3	16.7	0.4			
Chordata						
Pisces	85.7	66.7	99.5	83.3	81.8	92.8
Number of stomachs examined:		20			6	
Examined stomachs with food:		7			6	
Mean length of fish with food:		588.7			893.5	

Of the 53 Apogon pseudomaculatus stomachs examined, 44 contained food (Appendix 3.4, Table 3.7). Amphipods were the most frequently occurring prey taxon and were also the most abundant prey. Many of the species of amphipods that were consumed are known to swarm in the water column at night (Williams and Bynum, 1972). Decapods, cumaceans, and mysids were also important prey for twospot cardinalfish which apparently prey upon these crustaceans during nocturnal foraging activity. Many of the species of these taxa are also hyperbenthic organisms, i.e., they swarm in the water column at night and are important prey for nocturnally foraging fishes (Jones, 1957; Anger and Valentin, 1976; Arntz, 1978; Watling, 1979; Stuck et al., 1979a, b; Williams, 1984).

Small twospot cardinalfish fed mainly on amphipods, decapods, and cumaceans, whereas larger fish fed more heavily on decapods (Table 3.7). Fishes were preyed upon in small amounts by both size classes.

Dominant benthic invertebrates, primarily polychaetes (except L. incerta) at middle-shelf stations, were not found in twospot cardinalfish stomachs (Table 3.8). Instead, twospot cardinalfish selectively fed on small crustaceans. Comparison of percent numerical contribution by species of cumaceans, mysids, stomatopods, and decapods in stomachs to the percent contribution by these organisms in sled samples revealed that A. pseudomaculatus fed heavily on species of crustaceans that swarm just above the bottom at night (Table 3.9), when they are available for capture by the sled and by A. pseudomaculatus.

Lutjanus campechanus

Red snapper were frequently taken in the trawl, but in small numbers. They ranked relatively high in demersal teleost weight because of their large size. Red snapper were most abundant at middle-shelf stations (mean catch per tow of 0.7) and were rarer at outer-shelf (0.2 per tow) and inner-shelf (< 0.1 per tow) depths. As was true for the large groupers (gag and scamp), few red snapper stomachs were collected during the study. This was due mainly to net avoidance and regurgitation. The red snapper that were collected had been feeding mainly on fishes, which made up the greatest food volume by far (Appendix 3.5, Table 3.10). Schooling forage fishes such as round scad (D. punctatus) and Spanish sardine (S. aurita) were the most abundant prey species consumed. Crustaceans were the most frequently consumed invertebrate prey but they contributed little to the prey volume. Most invertebrates were consumed by smaller size classes of red snapper and the largest fish fed mainly on other fishes (Table 3.10). Bradley and Bryan (1975) noted similar results for red snapper in the Gulf of Mexico. Because red snapper feed very little on hard-bottom epifauna, selectivity analysis was not performed.

Table 3.7 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Apogon pseudomaculatus*, by length interval.

	LENGTH INTERVALS (mm SL)					
	< 45			≥ 45		
PREY TAXON	F	N	V	F	N	V
Annelida						
Polychaeta	3.8	0.5	0.4			
Crustacea						
Stomatopoda	3.8	0.5	1.9			
Mysidacea	57.7	11.4	3.9	16.7	10.3	4.2
Cumacea	50.0	27.5	6.0	22.2	8.8	1.8
Isopoda	7.7	1.0	0.3	22.2	5.9	2.7
Amphipoda	69.2	49.3	45.1	55.6	26.5	17.7
Decapoda	46.2	9.0	30.9	72.2	45.6	66.2
Chordata						
Cephalochordata	3.8	0.5	9.3			
Pisces	3.8	0.5	2.3	5.6	2.9	7.5
Number of stomachs examined:		29			24	
Examined stomachs with food:		26			18	
Mean length of fish with food:		39.6			50.3	

Table 3.8 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant species in suction samples and *Apogon pseudomaculatus* stomachs at middle shelf stations. Dominant species included those that ranked in the five most abundant species in stomach or benthic samples pooled for all seasons and years.

	MIDDLE SHELF		
	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction Samples			
Chone americana	-	0.81	-1.00
Filograna implexa	-	63.87	-1.00
Luconacia incerta	-	1.03	-1.00
Malacoceros glutaeus	-	0.81	-1.00
Syllis spongicola		1.90	-1.00
Total	0.00	68.42	
Dominant Species - Stomachs			
Ampelisca cristata	8.60	-	1.00
Carinobatea carinata	20.43	-	1.00
Cyclaspis varians	16.49	0.01	0.99
Mysidae C	5.38	-	1.00
Oxyurostylis smithi	6.45	0.14	0.96
Total	57.35	0.15	

Table 3.9 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant species of decapods, cumaceans, mysids and stomatopods in sled samples and *Apogon pseudomaculatus* stomachs at middle shelf stations. Dominant species included those that ranked in the five most abundant species of decapods, stomatopods cumaceans and mysids in stomach or sled samples pooled for all seasons.

	MIDDLE SHELF		
	Fish Stomachs	Sled Samples	E
Dominant Species - Sled Samples			
Bowmaniella portoricensis	6.82	10.45	-0.21
Lucifer faxoni		6.79	-1.00
Mysidopsis furca	5.30	4.45	0.08
Periclimenes iridescens	3.79	3.75	0.01
Promysis atlantica		7.24	-1.00
Total	15.91	32.68	
Dominant Species - Stomachs			
Bowmaniella portoricensis	6.82	10.45	-0.21
Cyclaspis varians	34.85	1.45	0.92
Leptochela papulata	4.55	2.07	0.37
Mysidopsis furca	5.30	4.49	0.08
Oxyurostylis smithi	13.63	1.19	0.84
Total	65.15	19.65	

Table 3.10 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of <u>Lutjanus campechanus</u>, by length interval.

	LENGTH INTERVALS (mm SL)					
	< 357			≥ 357		
PREY TAXON	F	N	V	F	N	V
Algae	4.4	2.4	0.4	5.9	3.7	<0.1
Mollusca						
Gastropoda						
Crustacea						
Ostracoda	4.4	2.4	<0.1			
Stomatopoda	4.4	2.4	28.8			
Cumacea	4.4	2.4	<0.1			
Isopoda	4.4	2.4	<0.1			
Amphipoda	8.7	11.9	<0.1	11.8	2.5	<0.1
Decapoda	34.8	28.6	2.9	5.9	1.2	0.4
Chordata						
Pisces	52.2	47.6	67.8	70.6	92.6	99.6
Number of stomachs examined:		41			27	
Examined stomachs with food:		23			17	
Mean length of fish with food:		231.6			442.2	

Rhomboplites aurorubens

Vermilion snapper were very abundant in trawl catches. They were relatively infrequent at inner-shelf stations (mean catch per tow of 12.4), where catches were dominated by juveniles (< 11 cm fork length, FL) which were only collected during the warmer seasons (summer and fall). An exception was station IS03, where a large number (N = 931) of older fish ($\bar{x}$ FL = 16.5 cm) were caught by trawl during winter of 1980. Vermilion snapper were most abundant at middle-(243.7 per tow) and outer-shelf (140.1 per tow) stations where larger fish ($\bar{x}$ FL = 14.7 and 12.1 cm) dominated.

Approximately 115 species of prey were identified in 356 vermilion snapper stomachs, with most prey items representing planktonic and nektonic organisms (Appendix 3.6, Table 3.11). Decapods dominated in frequency and abundance and consisted mainly of planktonic forms. Amphipods, mainly planktonic hyperiids and caprellids (e.g. *Lestrigonus bengalensis*, *Phtisica marina*), and planktonic copepods were frequently consumed in large numbers, but made up little of the food volume because of their small size. Cephalopods, fishes, and decapods made up most of the prey volume and mysids, cumaceans, and doliolids were also frequently consumed.

Decapods, copepods, and other small crustaceans dominated the diet of the smaller (1-100 mm) size classes of vermilion snapper (Table 3.11). Larger vermilion snapper had a diet composed mainly of fishes and cephalopods, but decapods were also frequently consumed by larger fish.

Like *Apogon pseudomaculatus* , *Rhomboplites aurorubens* appears to forage in the water column. Many of the prey species consumed by *Apogon pseudomaculatus* were also important prey for vermilion snapper, especially for smaller individuals. Vermilion snapper are well adapted to foraging in the water column (Davis and Birdsong, 1973; Grimes, 1979) and Grimes (1979) also noted a diet dominated by planktonic organisms in vermilion snapper he examined. He noted that small juveniles (< 100 mm TL) had a diet dominated volumetrically by copepods, whereas decapods dominated volumetrically in fish less than 100 mm SL in the present study. *Rhomboplites aurorubens* is probably a nocturnal forager (Grimes, 1979) and feeds on both holoplanktonic species as well as species such as mysids, sergestids, and cumaceans, which are planktonic at night.

Vermilion snapper, like twospot cardinalfish, fed very little on hard-bottom invertebrates collected in suction and grab samples (Table 3.12). Polychaete species collected in those samples were not consumed at all by vermilion snapper and consisted mainly of tube-reef building species (*F. implexa*) and species associated with sponges and corals (*E. dispar* and *S. spongicola*) (Gardiner, 1975). Vermilion snapper apparently do not forage directly on hard-bottom reefs, but feed mainly on pelagic swarms of small crustaceans, as well as on some epibenthic species. A comparison of the relative abundance of cumaceans, mysids, stomatopods, and decapods in fish stomachs to their abundance in sled samples indicate that vermilion snapper prefer crustaceans that swarm in the water column at night, particularly the cumacean *O. smithi* and mysid *P. atlantica* at inner-shelf stations, and the decapods *L. faxoni* and *L. papulata* at middle- and outer-shelf stations

Table 3.11 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Rhombop'ites aurorubens*, by length interval.

	LENGTH INTERVALS (mm SL)											
	1-50			51-100			101-150			151-200		
PREY TAXON	F	N	V	F	N	V	F	N	V	F	N	V
Cnidaria (tentacles)							2.9	0.3	0.9			
Annelida	7.1	1.6	2.1	10.9	0.4	2.8	13.3	2.2	2.8	10.9	1.4	2.2
Mollusca												
Gastropoda	7.1	0.9	0.2	1.8	0.1	<0.1	5.7	1.6	1.0	6.3	1.4	0.2
Pelecypoda							2.9	1.2	0.2			
Cephalopoda				1.8	0.1	1.0	4.8	0.6	24.2	12.5	1.0	37.0
Crustacea												
Ostracoda	28.6	3.7	1.5	24.4	29.1	3.6	7.6	1.0	0.1	3.1	0.2	<0.1
Copepoda	82.1	33.9	12.0	60.0	15.3	4.0	41.0	13.1	1.0	17.2	2.0	<0.1
Cirripedia	21.4	6.1	4.2	20.0	1.3	0.5	11.4	2.6	2.5	18.8	4.8	3.4
Stomatopoda	25.0	2.8	9.6	20.0	4.6	8.4	3.8	0.4	1.5	4.7	0.3	0.4
Mysidacea	21.4	1.9	4.6	12.3	0.7	0.5	20.0	16.0	4.0	12.5	1.5	0.1
Cumacea	3.6	0.9	0.8	7.3	0.4	0.4	21.0	21.7	5.0	15.6	4.3	0.4
Isopoda	3.6	0.2	0.2							6.2	0.5	0.1
Amphipoda	35.7	20.3	12.7	49.1	12.9	6.2	49.5	14.2	4.0	48.4	11.6	1.2
Decapoda	35.7	25.0	31.1	70.9	29.4	42.0	52.4	14.1	19.0	59.4	14.3	10.3
Sipunculida							1.9	0.2	0.1	1.6	0.1	<0.1
Chaetognatha	21.4	1.6	3.4	10.9	1.3	0.9	11.4	2.3	0.8	17.2	2.3	0.2
Chordata												
Thaliacea	3.6	0.2	0.4	9.1	1.5	1.6	5.7	2.0	0.4	14.1	25.0	1.7
Larvacea										3.1	0.2	<0.1
Cephalochordata				1.8	0.1	0.2	2.9	1.0	0.2	6.2	0.4	0.2
Pisces	7.1	0.7	17.1	43.6	2.9	27.8	21.9	5.5	32.4	40.6	28.9	42.7
Number of stomachs examined:		37			81			138			96	
Examined stomachs with food:		28			55			105			64	
Mean length of fish with food:		36.4			77.8			131.1			165.5	

Table 3.12 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction samples and *Rhomboplites aurorubens* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in any depth zone, for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF			OUTER SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction Samples									
Chone americana	-	0.33	-1.00	-	0.81	-1.00	-	0.59	-1.00
Erichthonius brasiliensis	0.09	2.89	-0.94	-	0.30	-1.00	-	0.13	-1.00
Erichthonius sp. A	-	0.08	-1.00	-	-	-	-	3.75	-1.00
Exogone dispar	0.44	3.71	-0.79	-	0.47	-1.00	-	0.01	-1.00
Filograna implexa	-	20.42	-1.00	-	63.87	-1.00	-	21.91	-1.00
Luconacia incerta	-	3.27	-1.00	0.05	1.03	-0.90	-	0.18	-1.00
Malacoceros glutaeus	-	0.41	-1.00	-	0.81	-1.00	-	0.02	-1.00
Phyllochaetopterus socialis	-	0.21	-1.00	-	0.12	-1.00	-	12.40	-1.00
Pista palmata	-	0.09	-1.00	-	0.08	-1.00	-	8.60	-1.00
Podocerus sp. A	-	2.87	-1.00	-	0.26	-1.00	-	0.14	-1.00
Spiophanes bombyx	-	0.39	-1.00	-	0.46	-1.00	-	5.81	-1.00
Syllis spongicola	-	2.15	-1.00	-	1.90	-1.00	-	1.38	-1.00
Total	0.53	36.82		0.05	70.11		0.0	54.92	
Dominant Species - Fish Stomachs									
Bowmaniella portoricensis	0.18	0.09	0.32	1.80	0.10	0.89	0.50	0.22	0.37
Leptochela papulata	0.35	0.04	0.81	3.45	0.09	0.95	1.86	0.12	0.88
Lucifer faxoni	12.05	0.18	0.97	9.79	0.01	>0.99	0.62	0.04	0.87
Oxyurostylis smithi	15.74	0.67	0.92	2.46	0.14	0.89	-	-	-
Phtisica marina	0.09	0.01	0.75	1.80	0.03	0.97	7.20	0.40	0.90
Phyllodoce longipes	1.14	0.06	0.89	0.05	0.04	0.10	0.12	0.20	-0.22
Promysis atlantica	11.79	-	1.00	0.05	<0.01	0.88	-	-	-
Rudilemboides naglei	1.06	0.05	0.91	-	<0.01	-1.00	-	0.04	-1.00
Total	42.40	1.10		19.40	0.42		10.30	1.02	
Stomachs with food:		49			138			68	

(Table 3.13). Grimes (1979) also proposed night feeding to explain the abundance of nocturnally active crustaceans in vermilion snapper stomachs.

Haemulon aurolineatum

Tomtate were very abundant in trawl catches over hard bottom and ranked among the top three demersal species by number and weight (Table 3.1). They were most abundant at middle- and inner-shelf stations (171.4 and 121.6 per tow, respectively) while few were collected at the outer shelf (3.5 per tow). They are also occasionally caught in trawls directed at sampling sand bottom (Wenner et al., 1980).

Haemulon aurolineatum had a generalized diet and approximately 120 species of prey were found in the 154 stomachs examined. Polychaetes and amphipods were the most important food and were eaten with almost the same frequency (Appendix 3.7, Table 3.14). Polychaetes, however, made up a larger volume of prey because of their large size. Decapods were also frequently consumed, but made up a small percentage of the volume and number of prey items. Pelecypods were the most abundant prey and cephalochordates, while infrequently consumed, made up a large portion of food volume because of their large size. Fishes also constituted a large portion of food volume and copepods, though small in volume displacement, were often eaten in large numbers. Ophiuroids were frequently consumed but were usually represented in stomachs by small arm fragments.

Small (1-100 mm SL) tomtate had a diet dominated numerically by very small crustaceans (copepods) and volumetrically by fishes and decapods (Table 3.14). Amphipods were the most abundant prey taxon for 101-150 mm tomtate and polychaetes made up the greatest volume of food. Large (151-200 mm SL) tomtate primarily consumed pelecypods, which were the most abundant taxon, and cephalochordates, which were abundant in the diet and made up the greatest prey volume.

Many hard-bottom invertebrates that were abundant in suction samples at inner- and middle-shelf sites (too few stomachs were collected at the outer shelf for analysis) were not important in the diet of tomtate (Table 3.15). Of the eight dominant hard-bottom invertebrate species, only two (the polychaete Chone americana and the corophoid amphipod Erichthonius brasiliensis) at inner-shelf sites and one (the caprellid amphipod Luconacia incerta) at middle-shelf sites made up a greater percentage of the diet than they did of benthic samples. On the other hand, benthic invertebrates that were common in stomachs were generally not abundant in benthic samples and electivity values were usually positive.

Tomtate are apparently not completely dependent on hard-bottom habitat for prey. Some of the most abundant prey species are pelagic (e.g. brachyuran megalopae, copepods). Most benthic prey are infaunal species which are restricted to soft sediments. Armandia maculata, a dominant prey species on the inner shelf, is a deposit-feeding polychaete that burrows in soft sediments (Fauchald and Jumars, 1979). Ervilia concentrica, an important prey species on the middle shelf, was not collected at any of the 11 hard-bottom stations. This bivalve is common in soft sediments (Porter, 1974). The cephalochordate Branchiostoma caribaeum, a common prey species on

Table 3.13 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant species of decapods, cumaceans, mysids and stomatopods in sled samples and *Rhomboplites aurorubens* stomachs. Dominant species include those that ranked in the five most abundant species of decapods, stomatopods, cumaceans and mysids in stomach or sled samples pooled for all seasons.

	INNER SHELF			MIDDLE SHELF			OUTER SHELF		
	Fish Stomachs	Sled Samples	E	Fish Stomachs	Sled Samples	E	Fish Stomachs	Sled Samples	E
Dominant Species - Sled Samples									
Bowmaniella portoricensis	0.30	5.56	-0.90	5.52	10.45	-0.31	4.30	5.45	-0.12
Lucifer faxoni	20.57	66.77	-0.53	29.93	6.79	0.63	5.38	12.29	-0.39
Mysidopsis furca	-	0.67	-1.00	0.17	4.49	-0.93	-	22.28	-1.00
Neopontonides beaufortensis	-	4.10	-1.00	-	3.35	-1.00	-	0.77	-1.00
Periclimenes iridescens	-	3.18	-1.00	-	3.75	-1.00	-	0.84	-1.00
Pontophilus gorei	-	-	-	-	0.03	-1.00	-	7.33	-1.00
Promysis atlantica	20.12	2.57	0.77	0.17	7.24	-0.95	-	0.63	-1.00
Thor manningi	-	0.05	-1.00	-	0.43	-1.00	-	2.44	-1.00
Total	40.99	82.90		35.15	36.63		9.68	52.03	
Dominant Species - Stomachs									
Bowmaniella portoricensis	0.30	5.56	-0.90	5.52	10.44	-0.31	4.30	5.45	-0.12
Cyclaspis varians	1.05	0.05	0.91	3.18	1.45	0.37	-	0.41	-1.00
Lucifer faxoni	20.57	66.77	-0.53	29.93	6.79	0.63	5.38	12.29	-0.39
Leptochela papulata	0.60	0.39	0.21	10.54	2.07	0.67	16.13	1.61	0.82
Neopontonides beaufortensis	-	4.10	-1.00	-	3.35	-1.00	-	0.77	-1.00
Oxyurostylis smithi	26.88	1.38	0.90	7.52	1.19	0.73	-	0.42	-1.00
Promysis atlantica	20.12	2.57	0.77	0.17	7.24	-0.95	-	0.63	-1.00
Solenocera atlantidis	-	-	-	-	0.03	-1.00	4.30	1.12	0.59
Total	69.52	80.82		56.86	32.56		30.11	22.70	
Stomachs with food:		49			138			68	

Table 3.14 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of <u>Haemulon aurolineatum</u>, by length interval.

	LENGTH INTERVALS (mm SL)								
	1 - 100			101 - 150			151 - 200		
PREY TAXON	F	N	V	F	N	V	F	N	V
Algae	4.8	0.4	2.6						
Cnidaria									
Hydrozoa							6.2	0.3	<0.1
Anthozoa				8.3	1.1	3.0	6.3	0.3	0.4
Turbellaria				12.5	4.0	6.3	4.2	0.7	0.1
Annelida	19.0	1.5	11.4	62.5	15.6	35.9	50.0	9.4	13.5
Mollusca									
Gastropoda				8.3	1.1	4.7	2.1	0.2	<0.1
Pelecypoda				4.1	0.6	<0.1	12.5	57.2	8.0
Cephalopoda							2.1	0.1	1.1
Arthropoda									
Pycnogonida				4.2	0.6	0.1			
Copepoda	47.6	77.1	14.4	4.2	0.6	<0.1	4.2	0.3	<0.1
Stomatopoda	19.0	1.9	14.7	12.5	1.7	2.2	6.2	0.3	4.0
Mysidacea							6.2	0.3	0.1
Cumacea	4.8	0.4	0.2				6.2	0.3	<0.1
Tanaidacea				4.2	0.6	<0.1			
Isopoda				12.5	1.7	0.1	6.2	0.3	0.2
Amphipoda	33.3	6.0	7.3	79.2	58.3	7.7	39.6	5.9	0.5
Decapoda	19.0	9.8	20.8	33.3	5.6	11.3	39.6	3.2	5.6
Sipunculida	4.8	0.4	0.7						
Bryozoa				8.3	1.1	0.4	6.2	0.3	<0.1
Echinodermata									
Echinoidea							2.1	0.1	<0.1
Ophiuroidea	14.3	1.1	1.7	25.0	5.0	8.0	22.9	1.4	1.0
Chaetognatha	4.8	0.4	0.4						
Chordata									
Cephalochordata				4.2	0.6	2.4	6.2	18.4	51.1
Pisces	4.3	1.1	26.0	16.7	2.2	17.8	12.5	0.7	14.1
Number of stomachs examined:		28			44			79	
Examined stomachs with food:		21			24			48	
Mean length of fish with food:		71.5			138.2			168.3	

Table 3.15 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction samples and *Haemulon aurolineatum* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in either depth zone, for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction Samples						
Chone americana	0.36	0.33	0.04	0.09	0.81	-0.79
Erichthonius brasiliensis	9.32	2.89	0.53	0.19	0.30	-0.23
Exogone dispar	0.72	3.71	-0.68	-	0.47	-1.00
Filograna implexa	-	20.42	-1.00	-	63.87	-1.00
Luconacia incerta	0.36	3.27	-0.80	1.77	1.03	0.26
Malacoceros glutaeus	-	0.41	-1.00	-	0.81	-1.00
Podocerus sp. A	-	2.87	-1.00	-	0.27	-1.00
Syllis spongicola	-	2.15	-1.00	-	1.90	-1.00
Total	10.76	36.05		2.05	69.46	
Dominant Species - Stomachs						
Armandia maculata	10.75	0.22	0.96	0.19	0.03	0.75
Branchiostoma caribaeum	-	-	-	15.69	0.01	0.99+
Caprella equilibra	2.87	1.55	0.30	1.40	0.34	0.61
Erichthonius brasiliensis	9.32	2.89	0.53	0.19	0.30	-0.24
Ervilia concentrica	0.36	-	1.00	48.18	-	1.00
Luconacia incerta	0.36	3.27	-0.80	1.77	1.03	0.26
Melita appendiculata	4.66	0.43	0.83	-	0.27	-1.00
Photis pugnator	2.87	2.68	0.03	-	0.80	-1.00
Stenothoe georgiana	1.43	0.01	0.99	0.65	0.03	0.91
Total	32.62	11.05		68.07	2.81	

the middle shelf that was very rare in benthic samples, is also an infaunal sand-bottom species (Hildebrand and Schroeder, 1928). Thus a large portion of the prey of *Haemulon aurolineatum* are not hard-bottom epifaunal species, suggesting that tomtate are not restricted to hard-bottom habitat for food resources. Although numerous in hard-bottom areas, *Haemulon aurolineatum* has been characterized as a reef-related species; i.e., it uses the reef for only part of each day (Parrish and Zimmerman, 1977). Randall (1967) found sand-dwelling organisms in 16 tomtate stomachs he examined, but the habitat of the decapods, the predominant prey, could not be inferred from his results. Parrish and Zimmerman (1977) noted a diet dominated by sand-flat invertebrates for an unspecified number of tomtate collected in the Caribbean. Parrish and Zimmerman (1977) reported nocturnal foraging, with tomtate occupying the reef during the day. During extensive Task I and Task II daytime scuba dives off of South Carolina and Georgia, no tomtate that exhibited foraging behavior were observed and large schools were often noted "stacked up" at the edge of rock ledges protruding out into sand areas. Apparently, nocturnal feeding behavior descibed for tomtate in the Caribbean is also typical for the species in the South Atlantic Bight. Tomtate forage, apparently at night, on sand-bottom areas of the shelf or in sand patches often found adjacent to rock outcrops, returning to the reefs for shelter during the day. This behavior probably results in considerable energy transfer, in the form of feces, from open-sand bottom areas of the shelf onto hard-bottom reefs. The fact that some hard-bottom amphipods (*E. brasiliensis* , *L. incerta, M. appendiculata,* and *P. pugnator)* were common in tomtate stomachs and that many additional hard-bottom species (e.g. hydroids, alpheid decapods, and bryozoans) were occasionally eaten indicates that tomtate also forage to a limited extent on hard bottom.

Archosargus probatocephalus

Archosargus probatocephalus were only occasionally caught by trawl at inner- (1.7 per tow) and middle-shelf (0.2 per tow) stations (Table 3.1). Underwater television and diver observations, however, indicate that they are common at inner- and middle-shelf stations, and they are occasionally observed at the outer shelf. Their low abundance in trawl catches probably reflects their cryptic habits.

The 42 sheepshead guts examined contained a diversity of sessile and motile organisms. Bryozoans, pelecypod mollusks, and barnacles (Cirripedia) were the most frequently consumed taxa and each occurred in more than 70 percent of stomachs with food (Appendix 3.8, Table 3.16). Amphipods and ascidians were also frequently consumed and several other taxa occurred in more than 50% of the stomach samples. Amphipods and barnacles were the most abundant prey; however many colonial organisms could not be counted. Bryozoans, ascidians, echinoids, and pelecypods made up most of the prey volume. Most organisms eaten by sheepshead were sessile forms that are firmly attached to the substrate or to other sessile animals. These included all hydroids and anthozoans, some polychaetes (e.g. *Hydroidea* spp.), some pelecypods (e.g. *P. colymbus, Arca* spp.), barnacles, some amphipods (e.g. *Cerapus tubularis)* , and all bryozoans and ascidians. It is apparent that sheepshead are heavy grazers on hard-botom reefs. Most fishes had full guts at all times of the day and a large volume of food was usually present in the entire gut.

Table 3.16 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Archosargus probatocephalus*, by length intervals.

	LENGTH INTERVALS (mm SL)					
	< 346			≥ 346		
PREY TAXON	F	N	V	F	N	V
Foraminifera	22.2	0.8	<0.1	27.3	1.7	<0.1
Cnidaria						
Hydrozoa	55.6	2.3	0.3	54.6	2.7	0.1
Anthozoa	66.7	1.7	2.6	36.4	1.0	0.6
Annelida						
Polychaeta	50.0	4.8	0.3	63.6	3.6	0.1
Mollusca						
Gastropoda	44.4	7.0	0.4	45.4	5.6	0.2
Pelecypoda	72.2	5.3	2.4	81.8	4.8	16.6
Arthropoda						
Pycnogonida	5.6	0.1	<0.1			
Cirripedia	77.8	14.4	3.0	72.7	13.6	3.0
Isopoda	5.6	0.1	<0.1			
Amphipoda	61.1	44.9	0.4	72.7	47.2	0.2
Decapoda	38.9	5.0	2.2	54.6	4.4	3.0
Sipunculida	5.6	0.1	<0.1			
Bryozoa	83.3	9.3	76.2	72.7	11.4	8.6
Echinodermata						
Echinoidea	11.1	0.3	<0.1	27.3	0.7	22.5
Ophiuroidea	22.2	0.6	0.1	9.1	0.2	<0.1
Holothuroidea	5.6	0.3	0.7	9.1	0.2	0.2
Chordata						
Ascidiacea	55.6	2.8	11.4	81.8	2.9	44.9
Number of stomachs examined:		23			13	
Examined stomachs with food:		18			11	
Mean length of fish with food:		304.7			410.9	

Attached sessile fauna dominated the volume of prey in both size groups of sheepshead examined, though larger attached pelecypods (e.g., *Arca* spp.) made up a greater portion of the diet of larger fish than that of smaller sheepshead (Table 3.16). Barnacles were consumed in nearly the same frequency, number, and volume in both size classes. Amphipods were consumed in large numbers by both size classes, and gastropods were consumed more by smaller fish.

The sessile colonial invertebrates that dominated in sheepshead stomachs were not enumerated in suction samples, and selectivity comparisons (Table 3.17) to those samples were limited to the most abundant motile epifauna found in sheepshead stomachs and suction samples. In general, most amphipod crustaceans consumed by sheepshead were eaten in relatively greater numbers than their proportion in the benthos. At middle-shelf stations, all dominant amphipods and mollusks (*A. lunata, M. lateralis)* were positively selected by sheepshead. In contrast, polychaetes that were abundant in suction samples were not consumed by sheepshead. *Exogone dispar* and *F. implexa* were the only common hard-bottom polychaetes to be consumed by sheepshead. These species, and other small motile crustaceans and mollusks found in sheepshead guts may have been incidentally ingested along with sessile fauna.

Sessile invertebrates were generally more frequent in dredge samples than in sheepshead stomachs, and electivity values were usually negative (Table 3.18). Octocorals *(L. virgulata, L. hebes, T. frauenfeldii,* and *T. fruticulosa)* were very frequent in dredge collections in both depth zones but, with the exception of *T. fruticulosa,* they were not frequently consumed. Bryozoans such as *Crisia* sp. A and *S. cornuta* were consumed in proportion to their frequency at middle-shelf depths, but this was not true at inner-shelf stations. The reasons for this pattern are unknown.

Little has been published previously regarding the food of sheepshead. Amphipods, copepods, and polychaetes were found in 11 stomachs of small juvenile sheepshead (< 50 mm) from inshore seagrass beds around Tampa Bay (Springer and Woodburn, 1960). Springer and Woodburn (1960) found that larger juveniles (51-100 mm) fed mainly on mollusks and crustaceans, and some small crustaceans and algae were also noted. Smaller sheepshead (< 300 mm, N = 4) collected from inshore waters of South Carolina (1 m depth) fed on algae and mollusks (mussels, *Brachiodontes exustus)* that were abundant on the rock jetty where they were collected (Van Dolah et al., 1984). Sheepshead apparently occupy inshore waters as juveniles where they feed heavily on algae and mollusks and move to offshore reefs as adults, where algae becomes less important in their diet as well as in the benthic community.

Calamus leucosteus

Whitebone porgy were common in all three depth zones, but they were more abundant at middle- and outer-shelf stations (5.6 and 5.8 per tow, respectively) than on the inner shelf (2.6 per tow). Whitebone porgy stomachs (N = 219) contained approximately 105 species of invertebrates and fishes. Decapods were the most important prey and ranked first in frequency, number, and volume (Appendix 3.9, Table 3.19). Hermit crabs (Paguridae) were the

Table 3.17 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction samples and *Archosargus probatocephalus* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in either depth zone, for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction Samples						
Chone americana	-	0.33	-1.00	-	0.81	-1.00
Erichthonius brasiliensis	19.25	2.89	0.74	17.65	0.30	0.97
Exogone dispar	1.13	3.71	-0.53	-	0.47	-1.00
Filograna implexa	-	20.42	-1.00	1.84	63.87	-0.94
Luconacia incerta	5.28	3.27	0.24	12.55	1.03	0.85
Malacoceros glutaeus	-	0.41	-1.00	-	0.81	-1.00
Podocerus sp. A	0.75	2.87	-0.58	0.31	0.27	0.07
Syllis spongicola	-	2.14	-1.00	-	1.90	-1.00
Total	26.41	36.04		32.35	69.46	
Dominant Species - Stomachs						
Astyris lunata	-	0.20	-1.00	2.45	0.20	0.85
Caprella equilibra	11.70	1.55	0.77	1.22	0.34	0.56
Cerapus tubularis	-	0.02	-1.00	5.00	0.05	0.98
Erichthonius brasiliensis	19.25	2.89	0.74	17.65	0.30	0.97
Luconacia incerta	5.28	3.27	0.24	12.55	1.03	0.85
Musculus lateralis	2.26	0.03	0.97	0.71	0.05	0.88
Photis pugnator	6.42	2.68	0.41	13.06	0.80	0.88
Total	44.91	10.64		52.64	2.77	

Table 3.18 Frequency occurrence (percent of samples containing the species) and electivity values (E) for dominant sessile species (including cnidarians, sponges, barnacles, bryozoans and ascidians) in dredge samples and *Archosargus probatocephalus* stomachs. Dominant species include those that ranked in the five most frequent species within stomach or benthic samples in either depth zone, for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Dredge Samples						
Balanus trigonus	50.00	85.19	-0.26	50.00	75.86	-0.21
Crisia sp. A	93.75	74.07	0.11	93.75	96.55	-0.01
Leptogorgia virgulata	6.67	88.89	-0.86	-	24.14	-1.00
Lophogorgia hebes	-	85.19	-1.00	-	41.38	-1.00
Microporella ciliata	31.25	81.46	-0.45	31.25	82.76	-0.45
Monostaechas quadridens	6.25	77.78	-0.85	6.25	86.21	-0.86
Styela plicata	37.50	88.89	-0.41	37.50	34.48	0.04
Synthecium tubitheca	12.50	-	1.00	12.50	75.86	-0.72
Thyroscyphus marginatus	6.25	14.81	-0.41	6.25	75.86	-0.85
Titanideum frauenfeldii	-	96.30	-1.00	-	62.07	-1.00
Dominant Species - Stomachs						
Balanus trigonus	46.67	85.19	-0.29	50.00	75.86	-0.21
Balanus venustus	26.67	74.07	-0.47	62.52	31.03	0.34
Crisia sp. A	46.67	74.07	-0.23	93.75	96.55	-0.01
Nellia tenella	6.67	-	1.00	50.00	31.03	-0.23
Schizoporella cornuta	26.67	70.37	-0.45	87.50	72.41	0.09
Sundanella sibogae	6.67	14.81	-0.39	50.00	6.90	0.75
Telesto fruticulosa	26.67	59.26	-0.39	68.75	27.59	0.43
Turbicellepora dichotoma	13.33	62.96	-0.65	68.75	62.07	0.05

Table 3.19 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Calamus leucosteus*, by length interval.

	LENGTH INTERVALS (mm SL)											
	101-150			151-200			201-250			251-300		
PREY TAXON	F	N	V	F	N	V	F	N	V	F	N	V
Algae							3.2	0.3	<0.1			
Porifera										2.4	0.3	0.4
Cnidaria												
Hydrozoa				4.4	0.6	<0.1				2.4	0.3	<0.1
Anthozoa	37.5	9.8	10.0	10.9	4.4	14.8	14.5	2.4	5.8	17.1	3.1	10.0
Nemertinea				2.2	1.1	12.7	1.6	0.2	0.3			
Annelida	25.0	9.8	6.9	47.8	9.4	11.6	48.4	8.8	6.8	46.3	11.1	9.7
Mollusca												
Gastropoda	12.5	2.4	0.2	58.7	26.9	16.2	66.1	24.9	11.2	53.7	17.2	9.3
Pelecypoda	12.5	9.8	14.4	21.7	4.2	12.0	22.6	5.8	7.6	22.0	6.8	8.3
Cephalopoda				2.2	0.3	0.1						
Crustacea												
Ostracoda										2.4	0.6	<0.1
Copepoda							1.6	0.2	<0.1			
Cirripedia	37.5	17.1	17.2	8.7	2.5	2.5	14.5	10.4	5.0	14.6	12.0	4.4
Stomatopoda	12.5	2.4	1.0				1.6	0.2	0.2	4.9	0.9	0.2
Mysidacea				8.7	1.7	0.2						
Cumacea				8.7	1.1	0.1	3.2	0.6	<0.1	7.3	0.9	<0.1
Isopoda							1.6	0.2	<0.1			
Amphipoda				17.4	4.2	0.8	29.0	4.3	0.5	19.5	3.1	0.2
Decapoda	50.0	26.8	43.3	71.7	31.7	14.2	71.0	23.0	11.4	70.7	32.9	23.6
Sipunculida	12.5	17.1	6.9	23.9	6.7	4.2	33.9	9.5	11.4	7.3	1.5	1.2
Brachiopoda				2.2	0.8	0.2	3.2	0.6	0.1	2.4	0.3	<0.1
Bryozoa							14.5	1.8	0.4	2.4	0.6	0.2
Echinodermata												
Asteroidea				4.4	0.6	5.7	12.9	1.6	7.6	22.0	3.1	11.0
Echinoidea							4.8	0.5	0.4	7.3	0.9	3.8
Ophiuroidea	12.5	2.4	<0.1	15.2	1.9	0.8	21.0	2.1	2.4	17.1	2.2	0.4
Holothuroidea										7.3	1.2	11.9
Chordata												
Ascidiacea										2.4	0.3	4.2
Pisces	12.5	2.4	0.1	8.7	1.1	4.0	19.4	2.7	29.8	4.9	0.6	1.6
Number of stomachs examined:		11			62			86			57	
Examined stomachs with food:		8			46			62			41	
Mean length of fish with food:		125.2			183.7			223.5			270.3	

dominant decapods in whitebone porgy stomachs and they were consumed along with their gastropod shells, which were often damaged during ingestion. Gastropods were also an important prey and sipunculids, especially those species that occupy gastropod shells (A. gosnoldi), were frequently consumed. The motile gastropod shell is apparently a visual stimulus to whitebone porgy which results in ingestion of the shell regardless of its inhabitant. Other important prey for whitebone porgy included polychaetes, pelecypods, barnacles, and fishes.

Whitebone porgy demonstrated little change in food habits with increasing age (Table 3.19). Decapods were frequently consumed by all size classes. Gastropods and sipunculids were also consumed by all size classes. Fishes increased in volumetric importance in the diet of fish up to a length of 250 mm, but were not frequently consumed by the largest fish.

Invertebrate species that were most abundant in suction and grab samples were generally not consumed by whitebone porgy in any of the three depth zones (Table 3.20). Rather, whitebone porgy fed selectively on "shelled invertebrates" that were relatively uncommon in suction and grab samples. Most of those prey species were occasionally collected at the hard-bottom stations, indicating that they are part of the hard-bottom community.

Published information on the diet of Calamus leucosteus is lacking. Randall (1967) reported on the food habits of several other West Indian species of Calamus and noted a high incidence of shelled invertebrates such as mollusks and echinoids. He also stated that Calamus spp. feeding on hermit crabs were largely gastropod feeders as well. Sipunculids were also occasionally consumed. Fishes of the genus Calamus have broad molariform teeth (Gregory, 1933) that are used to crush the shells of gastropods, hermit crabs, and other invertebrates equipped with hard protective shells.

Lagodon rhomboides

The pinfish is an abundant species along the southeast coast and is found in a variety of inshore marine and estuarine habitats (Hansen, 1970). Offshore they are associated with artificial and natural hard-bottom reefs. During trawl sampling in 1980 and 1981, pinfish were occasionally taken at inner-shelf stations (mean catch per tow of 6.2) but were rare at middle- (1.1 per tow) and outer-shelf (< 0.1 per tow) stations. All stomachs were collected at inner-shelf stations.

Pinfish stomachs (N = 20) contained about 35 species of invertebrates, most of which were benthic species. Amphipods were the most frequently eaten taxon and ranked first in abundance and second in volume (Appendix 3.10, Table 3.21). The corophoid amphipod E. brasiliensis, which was abundant in the diet of many other hard-bottom fishes, was the dominant amphipod in pinfish stomachs. Chaetognaths and cumaceans were also common prey items and several other taxa were also consumed.

Amphipods were frequently consumed by both size classes of pinfish, however they made up little of the prey volume in stomachs of larger fish (Table 3.21). Decapods and chaetognaths were more important in the diet of larger pinfish.

Table 3.20 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction and grab samples and *Calamus leucosteus* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in any depth zone for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF			OUTER SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction/Grab Samples									
Chone americana	-	0.33	-1.00	-	0.81	-1.00	-	0.59	-1.00
Erichthonius brasiliensis	0.20	2.89	-0.87	0.18	0.30	-0.25	0.66	0.13	0.66
Erichthonius sp. A	-	0.08	-1.00	-	-	-	0.66	3.75	-0.70
Exogone dispar	-	3.71	-1.00	-	0.47	-1.00	-	0.01	-1.00
Filograna implexa	-	20.42	-1.00	-	63.87	-1.00	-	21.91	-1.00
Luconacia incerta	-	3.27	-1.00	-	1.03	-1.00	-	0.18	-1.00
Malacoceros glutaeus	-	0.41	-1.00	-	0.81	-1.00	-	0.02	-1.00
Phyllochaetopterus socialis	-	0.21	-1.00	-	0.12	-1.00	-	12.40	-1.00
Pista palmata	-	0.09	-1.00	-	0.08	-1.00	-	8.60	-1.00
Podocerus sp. A	-	2.87	-1.00	0.18	0.27	-0.19	-	0.14	-1.00
Spiophanes bombyx	-	0.39	-1.00	-	0.46	-1.00	-	5.81	-1.00
Syllis spongicola	-	2.14	-1.00	-	1.90	-1.00	-	1.38	-1.00
Total	0.20	36.81		0.36	70.12		1.32	54.92	
Dominant Species - Stomachs									
Costoanachis avara	2.15	0.21	0.98	3.27	< 0.01	0.99	-	-	-
Aspidosiphon gosnoldi	12.13	1.63	0.76	3.99	0.46	0.79	0.33	0.09	0.57
Glottidia pyramidata	0.20	0.01	0.88	-	0.01	-1.00	2.31	0.07	0.94
Iridopagurus dispar	-	-	-	0.36	0.01	0.97	4.29	0.07	0.97
Leptochela papulata	-	0.04	-1.00	2.54	0.09	0.93	0.33	0.12	0.46
Marginella hartleyanum	4.70	0.14	0.94	0.18	0.01	0.87	-	0.03	-1.00
Onuphis nebulosa	-	0.01	-1.00	-	0.05	-1.00	2.64	0.56	0.65
Osachila tuberosa	-	<0.01	-1.00	-	<0.01	-1.00	1.98	0.02	0.98
Pagurus carolinensis	2.35	0.40	0.71	4.36	0.30	0.87	2.97	0.07	0.96
Pagurus hendersoni	6.46	0.26	0.92	5.81	0.11	0.96	1.65	0.11	0.88
Total	27.99	2.70		20.51	1.05		16.50	1.14	

Table 3.21 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Lagodon rhomboides*, by length interval.

	LENGTH INTERVALS (mm SL)					
	≤ 130			> 130		
PREY TAXON	F	N	V	F	N	V
Cnidaria						
Hydrozoa	14.3	0.2	0.8	42.9	1.0	1.1
Annelida						
Polychaeta	28.6	0.9	4.2	28.6	2.3	1.6
Mollusca						
Gastropoda	28.6	0.7	0.5	14.3	1.3	0.5
Pelecypoda	14.3	0.2	0.2	42.9	1.0	0.8
Crustacea						
Ostracoda	14.3	0.2	0.2			
Copepoda	14.3	0.9	0.3	28.6	1.3	0.2
Cirripedia				14.3	0.7	3.8
Mysidacea	14.3	0.5	0.6	14.3	0.3	0.5
Cumacea	28.6	3.0	9.4	42.9	10.4	8.6
Tanaidacea	14.3	0.2	0.2			
Isopoda	14.3	0.9	4.6	14.3	0.3	0.4
Amphipoda	85.7	66.0	46.3	85.7	13.7	6.2
Decapoda	14.3	0.2	0.3	14.3	0.3	12.6
Bryozoa				42.9	1.0	0.6
Chaetognatha	28.6	26.0	32.5	28.6	66.2	63.1
Number of stomachs examined:		11			10	
Examined stomachs with food:		7			7	
Mean length of fish with food:		123.7			136.7	

Because pinfish fed heavily on pelagic species such as copepods and chaetognaths (Appendix 3.10), electivity values for invertebrates that dominated in suction samples at the inner-shelf stations were mostly negative (Table 3.22). However, some of the dominant species in pinfish stomachs made up a higher proportion of total prey individuals than they did of individuals in benthic samples. Thus, electivity values were relatively high for the crustaceans E. brasiliensis and O. smithi. Other species (C. equilibra and P. pugnator) were consumed in nearly the same proportion as their relative abundance in suction samples.

Previous life history studies on pinfish have been limited to inshore habitats, which are usually occupied by pinfish from early spring to late fall, after which time the fish move to offshore spawning grounds (Hildebrand and Schroeder, 1928; Caldwell, 1957; Hansen, 1970). In nearshore habitats small (< 100 mm) pinfish feed in grass beds on small crustaceans and other benthic invertebrates, often ingesting large quantities of vegetation (Hansen, 1970). Larger fish (> 100 mm) from the same habitat have a diet dominated by plant material (Stoner and Livingston, 1984). Pinfish have also been observed grazing on rocks and pilings (Caldwell, 1957). The herbivorous habit of pinfish is apparently related to the availability of grass beds and the availability of crustacean prey versus the protection afforded crustaceans by suitable sea grasses (Stoner, 1982). Because there are no seagrasses on offshore hard-bottom areas, pinfish feed on invertebrates (which have more energy value than sea grasses), as has been noted in inshore areas where seagrasses are absent, or only those grasses (Halodule wrightii) that afford little protection to prey are present (Stoner, 1982).

Pagrus pagrus

The red porgy is an abundant species at middle- and outer-shelf depths in the South Atlantic Bight, where it supports a substantial fishery (Manooch, 1977). This species is commonly taken by hook and line at those depths (Manooch, 1977) and they were occasionally collected in the trawl at middle-shelf (mean catch per tow of 1.4) and outer-shelf (5.6 per tow) stations. None were collected at inner-shelf stations.

Approximately 80 species of prey were found in the 323 red porgy stomachs examined and this species was a generalized predator on motile organisms. Decapods and fishes were the preferred prey of red porgy (Appendix 3.11, Table 3.23). Decapods ranked first in frequency and number (second in volume) and fishes, by far, made up the greatest volume of prey. Natantian, anomuran, and brachyuran decapods appeared to be of nearly equal importance in the diet. Many fishes could not be identified but schooling species (Clupeidae, D. punctatus, R. aurorubens, and S. aurita) were the most frequently eaten fishes. Several seahorses (Hippocampus sp.) were also ingested.

Polychaetes were also frequently consumed, and cephalopods ranked third in prey volume. Amphipods ranked second in abundance in stomachs but contributed little to prey volume. Numerous other motile taxa as well as some sessile species (hydroids, anthozoans, barnacles) were preyed upon.

Table 3.22 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction samples and *Lagodon rhomboides* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples at inner shelf stations, for collections pooled for all seasons and years.

	INNER SHELF		
	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction Samples			
Erichthonius brasiliensis	37.06	2.89	0.86
Exogone dispar	-	3.71	-1.00
Filograna implexa	-	20.42	-1.00
Luconacia incerta	1.63	3.27	-0.33
Podocerus sp. A	0.14	2.87	-0.91
Total	38.83	33.16	
Dominant Species - Stomachs			
Caprella equilibra	1.36	1.55	-0.06
Erichthonius brasiliensis	37.06	2.89	0.86
Luconacia incerta	1.63	3.27	-0.33
Oxyurostylis smithi	5.31	0.67	0.78
Photis pugnator	2.86	2.68	0.03
Total	48.22	11.06	

Table 3.23 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Pagrus pagrus*, by length interval.

	LENGTH INTERVALS (mm SL)																				
	51-100			101-150			151-200			201-250			251-300			301-350			>350		
PREY TAXON	F	N	V	F	N	V	F	N	V	F	N	V	F	N	V	F	N	V	F	N	V
Algae				2.6	0.8	29.9													10.0	3.3	0.2
Foraminifera										2.7	0.8	<0.1	2.1	0.8	<0.1						
Porifera										8.1	2.3	8.3									
Cnidaria																					
Hydrozoa							5.3	1.6	0.1	2.7	0.8	<0.1	6.4	1.1	<0.1						
Anthozoa				2.6	0.8	1.1	5.3	1.6	0.2	5.4	1.6	2.4	8.5	2.3	1.8	12.0	6.8	0.7	10.0	3.3	11.2
Annelida	66.7	6.6	27.8	43.6	18.0	21.0	5.3	4.9	0.7	37.8	14.8	8.3	23.4	7.1	4.0	24.0	13.6	1.0	30.0	13.3	0.3
Mollusca																					
Scaphopoda										2.7	0.8	<0.1									
Gastropoda				2.6	0.8	0.9				8.1	2.3	0.4	6.4	1.1	0.1						
Pelecypoda				2.6	1.6	0.7	5.3	1.6	0.1				2.1	0.4	0.3						
Cephalopoda													2.1	0.4	2.5	4.0	1.7	14.4			
Crustacea																					
Ostracoda													2.1	1.1	<0.1						
Copepoda				2.6	0.8	0.1				2.7	1.8	<0.1	2.1	0.4	<0.1						
Cirripedia				5.1	1.6	0.7	5.3	16.8	1.6	2.7	1.0	<0.1	4.3	20.3	1.4	4.0	1.7	<0.1			
Stomatopoda				7.7	4.1	2.1	5.3	3.7	3.4										10.0	3.3	<0.1
Mysidacea	16.7	2.6	1.5	5.1	2.5	0.1				13.5	4.9	0.5	4.3	0.8	<0.1	8.0	3.4	<0.1	10.0	3.3	<0.1
Amphipoda	50.0	71.7	11.5	35.9	25.4	1.6	31.6	11.9	0.2	8.1	12.7	0.5	10.6	2.3	<0.1	8.0	3.4	<0.1			
Decapoda	50.0	8.6	17.0	53.8	26.6	25.0	52.6	26.6	10.6	54.0	21.3	10.7	51.1	40.2	8.0	48.0	32.2	7.3	30.0	26.7	1.5
Sipunculida										2.7	1.1	<0.1									
Bryozoa	16.7	1.3	0.1							10.8	3.3	0.3	6.4	1.5	<0.1	4.0	1.7	<0.1			
Brachiopoda				2.6	2.5	0.1															
Echinodermata																					
Asteroidea													2.1	0.4	<0.1						
Echinoidea							10.5	3.3	2.3	2.7	0.8	0.5	12.8	2.3	3.1	8.0	3.4	1.1			
Ophiuroidea				15.4	4.9	1.9	10.5	3.3	2.7	16.2	4.7	0.7	6.4	1.1	0.2	4.0	1.7	<0.1	20.0	6.7	0.4
Holothuroidea																4.0	1.7	0.9			
Chaetognatha				2.6	0.8	<0.1															
Chordata																					
Ascidiacea										2.7	0.8	2.1	4.3	0.8	0.6	4.0	1.7	2.3			
Cephalochordata	33.3	7.9	41.1	5.1	2.5	2.4				5.4	2.3	0.8	6.4	3.8	0.5						
Pisces	16.7	1.3	0.3	18.0	5.7	11.5	57.9	24.6	78.0	43.2	21.9	64.3	38.3	12.0	77.4	56.0	27.1	72.4	50.0	20.0	85.4
Number of stomach examined:		7			58			29			67			94			46			22	
Examined stomachs with food:		6			39			19			37			47			25			10	
Mean length of fish with food:		91.2			129.3			174.9			220.0			277.4			326.9			379.1	

The diets of smaller size classes of red porgy were dominated volumetrically by cephalochordates, decapods, and polychaetes (Table 3.23). Fishes were most important volumetrically in the diet of all size classes over 150 mm SL. Decapods were frequently eaten by all size classes but were progressively replaced by fishes in the volume of food eaten by larger size classes of red porgy. Amphipods were a significant dietary component only in the smallest size classes.

Dominant species of benthic invertebrates from hard-bottom habitats were generally not important in the diet of red porgy (Table 3.24). Less abundant hard-bottom invertebrates (motile amphipods, mysids, and decapods) that were most abundant in the benthic portion of the diet of red porgy were, however, usually postively selected. Fishes, which were not sampled with the suction and grab samples, were also preferred, especially by larger red porgy.

Manooch (1977) also studied the foods of red porgy off North Carolina and South Carolina and, in contrast to the present study, noted a diet in adult fish (> 202 mm total length, TL, according to his definition) dominated by invertebrates. While invertebrates made up 72.6% of the prey volume in red porgy examined, they only accounted for 25.8% of the total prey volume in the present study. Decapods were, however, the most important invertebrate prey in both studies. Manooch (1977) also noted a high frequency of crustaceans in small (46-162 mm TL) red porgy, a finding duplicated in the present study.

Manooch (1977) further reported that 92% by volume of the food of red porgy consisted of benthic or "semibenthic" (defined as "nektonic but...associated with the substrate") organisms. Red porgy in the present study appeared to feed more on nekton ("free swimming and...found primarily up in the water column" by his definition). Assuming that copepods, chaetognaths, and some fishes (Clupeidae, *D. punctatus*, *S. aurita*, and *R. aurorubens*) can be considered "nektonic", 24.1% of the prey of red porgy in the present study were nektonic. It is apparent that the diet of red porgy is not completely dependent on hard-bottom benthos. Nevertheless, there is a close tie between red porgy and hard-bottom reefs with respect to prey species and red porgy often prey on nektonic species that are abundant in the vicinity of hard bottom.

Stenotomus aculeatus

The southern porgy was the most abundant species collected by trawl during the first two years of the Living Marine Resources Study. It was more abundant at middle-shelf stations (mean catch per tow of 562.8) than at inner-shelf stations (376.8 per tow). Southern porgy were rare at the outer shelf (0.9 per tow). Stomachs were, however, collected from all three depth zones.

Table 3.24 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction and grab samples and *Pagrus pagrus* stomachs. Dominant benthic species included those that ranked in the five most abundant species within stomach or benthic samples in either depth zone, for collections pooled for all seasons and years.

	MIDDLE SHELF			OUTER SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction/Grab Samples						
Chone americanus	-	0.81	-1.00	0.19	0.59	-0.50
Erichthonius sp. A	-	-	-	5.75	3.75	0.21
Filograna implexa	-	63.87	-1.00	-	21.91	-1.00
Luconacia incerta	-	1.03	-1.00	-	0.18	-1.00
Malacoceros glutaeus	-	0.81	-1.00	-	0.02	-1.00
Phyllochaetopterus socialis	-	0.12	-1.00	-	12.40	-1.00
Pista palmata	-	0.08	-1.00	-	8.60	-1.00
Spiophanes bombyx	-	0.46	-1.00	-	5.81	-1.00
Syllis spongicola	-	1.90	-1.00	-	1.38	-1.00
Total	0.00	69.08		5.94	54.64	
Dominant Species - Stomachs						
Amphinomidae B	2.10	-	1.00	0.60	0.02	0.93
Bowmaniella portoricensis	2.94	0.10	0.93	1.19	0.22	0.68
Branchiostoma caribaeum	7.56	0.01	0.99	0.79	0.09	0.79
Erichthonius brasiliensis	0.42	0.30	0.16	1.39	0.13	0.82
Erichthonius sp. A	-	-	-	5.75	3.75	0.21
Leptochela papulata	3.78	0.09	0.95	11.90	0.12	0.98
Photis pugnator	-	0.80	-1.00	4.56	0.96	0.65
Phtisica marina	0.84	0.03	0.93	4.37	0.39	0.83
Renilla reniformis	1.26	-	1.00	-	-	-
Total	18.90	1.33		30.55	5.68	

Approximately 120 species of prey, mainly motile invertebrates, were found in the 247 stomachs examined. Amphipods and polychaetes were the primary foods (Appendix 3.12, Table 3.25). Amphipods ranked first in frequency and number (second in volume) and polychaetes ranked first volumetrically (second in frequency and fifth in number). The ubiquitous corophoid *E. brasiliensis* and the caprellids *P. marina* and *C. equilibra* were the most abundant amphipods in the diet. Approximately 30 species of polychaetes were noted in the stomachs analyzed and each was consumed in low numbers. Pelecypods, copepods, and chaetognaths were abundant in southern porgy stomachs. Decapods and cephalochordates were frequently consumed and made up a large portion of prey volume.

Small southern porgy (51-100 mm SL) fed mainly on amphipods and polychaetes (Table 3.25). Numerous tiny, recently-set pelecypod mollusks (*E. concentrica*) were also consumed. Fish that ranged in length from 101 to 150 mm SL also fed mainly on amphipods and polychaetes, but cephalochordates made up a large volume of food. Cephalochordates made up the greatest prey volume for the largest fishes.

The most abundant species in suction and grab samples were generally not abundant in southern porgy stomachs and, in most cases, were not consumed at all (Table 3.26). The exceptions were *E. brasiliensis*, which was selected by southern porgy in all three depth zones, and *L. incerta* which was selected at middle shelf depths. In addition, many of the prey species of southern porgy were pelagic (chaetognaths, copepods) and were not collected by suction or grab samplers. The overall most abundant prey species, *E. concentrica* was consumed only at middle-shelf stations and was not collected in benthic samples at any hard-bottom station. On the other hand, many hard-bottom crustaceans, such as *E. brasiliensis*, *C. equilibra*, and *P. marina* were higher in relative abundance in fish stomachs than in benthic samples. It appears that southern porgy forage extensively on both sand-bottom (*E. concentrica*, *B. caribaeum*, *G. pyramidata*, *O. smithi*) and hard-bottom (*C. equilibra*, *E. brasiliensis*, *L. incerta*) species. Although southern porgy forage extensively on sand bottom, their diet is not dominated by sand-bottom species as was the case for tomtate. Approximately 25% and 50% of the prey of southern porgy at inner- and middle-shelf depths, respectively, were individuals of species commonly taken in suction samples. For tomtate the corresponding figures were only 11% and 2% (Table 3.15). Like tomtate, southern porgy may be important in transferring energy between sand- and hard-bottom areas, but to a lesser degree.

Although no previous studies of the food habits of *S. aculeatus* are available for comparison, southern porgy appear to have food habits similar to the closely related species, *S. caprinus* (longspine porgy) and *S. chrysops*

Table 3.25 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Stenotomus aculeatus*, by length interval.

	LENGTH INTERVALS (mm SL)								
	51-100			101-150			151-200		
	F	N	V	F	N	V	F	N	V
Algae				0.8	<0.1	<0.1	8.3	0.5	0.3
Cnidaria									
Hydrozoa	2.7	0.1	0.4	6.4	0.3	0.2			
Anthozoa	2.7	0.1	0.4	1.6	0.1	<0.1			
Nemertinea	2.7	0.1	0.6						
Annelida	32.4	2.8	23.6	50.8	7.8	27.0	66.7	7.3	16.0
Mollusca									
Gastropoda	5.4	0.2	0.5	6.4	0.4	0.6			
Pelecypoda	5.4	54.9	7.3	8.9	5.8	1.8	16.7	1.0	3.0
Pycnogonida				0.8	<0.1	0.1			
Crustacea									
Ostracoda				4.0	0.2	<0.1			
Branchiura				0.8	<0.1	<0.1			
Copepoda	37.8	17.2	2.7	23.4	9.6	0.8			
Cirripedia				2.4	0.2	0.9			
Stomatopoda				4.0	0.2	0.4			
Mysidacea	21.6	1.5	4.8	22.6	3.1	3.6	8.3	0.5	0.5
Cumacea	2.7	0.1	< 0.1	16.9	1.5	0.6	25.0	41.3	15.3
Tanaidacea	2.7	0.1	< 0.1	1.6	0.1	0.1			
Isopoda	2.7	0.2	2.0	4.8	0.2	0.2			
Amphipoda	37.8	15.8	20.0	68.6	40.7	15.0	66.7	13.1	6.3
Decapoda	27.0	3.0	12.2	44.4	6.2	7.9	25.0	1.5	2.3
Sipunculida	27.0	1.8	11.0	10.5	0.7	4.4	16.7	1.0	3.2
Brachiopoda	2.7	0.1	<0.1	1.6	0.1	0.1			
Bryozoa	2.7	0.1	0.1	1.6	0.1	0.1			
Echinodermata									
Asteroidea				0.8	<0.1	0.2			
Ophiuroidea	16.2	0.7	4.0	19.4	1.0	3.2	16.7	1.0	1.7
Chaetognatha				11.3	17.4	7.5	33.3	24.8	7.7
Chordata									
Ascideacea				1.6	0.1	2.7			
Thaliacea	2.7	0.1	0.1	1.6	0.2	0.2			
Cephalochordata	2.7	0.1	<0.1	13.7	2.6	15.3	41.7	6.8	43.6
Pisces	18.9	0.8	10.0	14.5	1.2	7.0			
Number of stomachs examined:		43			183			20	
Examined stomachs with food:		37			124			12	
Mean length of fish with food:		92.3			125.7			166.6	

Table 3.26 Relative abundance (percent of total number of individuals) and electivity values (E) for dominant benthic species in suction and grab samples and *Stenotomus aculeatus* stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in either depth zone, for collections pooled for all seasons and years.

	INNER SHELF			MIDDLE SHELF			OUTER SHELF		
	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E	Fish Stomachs	Benthic Samples	E
Dominant Species - Suction/Grab Samples									
Chone americana	-	0.33	-1.00	0.11	0.81	-0.76	-	0.59	-1.00
Erichthonius brasiliensis	20.13	2.89	0.75	1.41	0.30	0.65	1.19	0.13	0.80
Erichthonius sp. A	-	0.08	-1.00	-	-	-	1.19	3.75	-0.52
Exogone dispar	0.40	3.71	-0.81	-	0.47	-1.00	-	0.01	-1.00
Filograna implexa	-	20.42	-1.00	-	63.87	-1.00	-	21.90	-1.00
Luconacia incerta	0.40	3.27	-0.78	3.32	1.03	0.53	-	0.18	-1.00
Malacoceros glutaeus	-	0.41	-1.00	-	0.81	-1.00	-	0.02	-1.00
Phyllochaetopterus socialis	-	0.21	-1.00	-	0.12	-1.00	-	12.40	-1.00
Pista palmata	-	0.09	-1.00	-	0.08	-1.00	-	8.60	-1.00
Podocerus sp. A	2.85	2.87	0.00-	0.16	0.27	-0.24	-	-	-
Spiophanes bombyx	-	0.39	-1.00	-	0.46	-1.00	-	5.81	-1.00
Syllis spongicola	1.08	2.14	-0.33	-	1.90	-1.00	-	1.38	-1.00
Total	24.86	36.81		5.00	70.12		2.38	54.77	
Dominant Species - Stomachs									
Bowmaniella portoricensis	0.86	0.09	0.81	2.99	0.10	0.93	2.38	0.23	0.82
Branchiostoma caribaeum	1.43	-	1.00	2.88	0.01	0.99	5.95	0.09	0.97
Caprella equilibra	4.96	1.55	0.52	0.60	0.34	0.27	-	0.03	-1.00
Erichthonius brasiliensis	20.13	2.89	0.75	1.41	0.30	0.65	1.19	0.13	0.80
Ervilia concentrica	-	-		33.64	-	1.00	-	-	-
Glottidia pyramidata	-	0.01	-1.00	0.05	0.01	0.77	2.38	0.07	0.94
Latreutes parvulus	4.16	0.16	0.93	0.05	0.06	-0.09	-	-	-
Luconacia incerta	0.40	3.27	-0.78	3.32	1.03	0.53	-	1.18	-1.00
Lumbrineris coccinea	-	0.26	-1.00	-	0.06	-1.00	2.38	0.04	0.96
Metharpinia floridana	0.11	-	1.00	-	0.01	-1.00	3.57	0.30	0.85
Oxyurostylis smithi	5.36	0.67	0.78	0.11	0.14	-0.14	-	-	-
Photis pugnator	1.48	2.67	-0.29	0.27	0.81	-0.49	7.14	0.96	0.76
Phtisica marina	0.57	0.01	0.96	10.92	0.03	0.99	4.76	0.40	0.85
Spio sp. A	3.25	0.39	0.78	-	<0.01	-1.00	-	0.02	-1.00
Total	42.71	11.97		56.24	2.90		29.75	3.45	
Stomachs with food:		77			85			12	

(scup). Longspine porgy, which occur mainly on mud bottom in the Gulf of Mexico (Caldwell, 1955), also feed on polychaetes and crustaceans (Henwood, et al. 1978). Although Henwood et al. (1978) did not identify prey to a level that would enable a determination of prey habitat, it is likely that those prey represent typical soft-bottom species. Scup are found in a variety of marine and estuarine habitats in the Middle Atlantic Bight and southern New England (Morse, 1978). Scup collected on sandy bottom off Delaware and New Jersey had a diet that is very similar to that of southern porgy in terms of higher taxonomic categories; however, the species consumed are sand dwellers, reflecting the habitat where the fish were collected (Sedberry, 1983). It is apparent that southern porgy feed on the same types of prey as its congeners and that the species consumed are representative of the habitat in which the fish were collected. In addition to being a dominant species in hard-bottom habitats on the inner and middle shelf, southern porgy are also a dominant species in sand-bottom habitat in the same depths, although they are not nearly as abundant as they are on hard bottom (Wenner et al., 1980). Stenotomus aculeatus is apparently a more opportunistic species (than are other hard-bottom fishes) with regard to prey and habitat and can take advantage of both habitats on the shelf as dwelling and feeding areas.

Equetus lanceolatus

The jackknife-fish is a common inhabitant of hard-bottom habitat, but little is known regarding its habits or life history. During the first-year study it was a dominant species at middle-shelf stations and was most abundant in winter. In the second year only a few were collected in the trawl. Overall it was most abundant at middle-shelf stations (9.5 per tow), rare at inner-shelf stations (0.1 per tow), and absent at the outer-shelf station. All stomachs were collected from the middle shelf.

Jackknife-fish, like other sciaenids, are characterized by the possession of an expansive physoclistous swimbladder (Chao, 1978). For this reason most specimens examined at sea had regurgitated their food when brought up from depth. Of the stomachs that were preserved for analysis in the laboratory, only 13 contained food and most of these contained only traces of food, apparently because of regurgitation. As a result, only limited results were obtained (Appendix 3.13, Table 3.27). Because of the low numbers of prey individuals and species, selectivity analysis was not performed.

Jackknife-fish fed on about ten species of prey, all of which were polychaetes or crustaceans. Decapods were the most important crustaceans eaten, while mysids, cumaceans, and amphipods were frequently consumed as well. Polychaetes were more important for larger fish, and cumaceans were consumed more by smaller fish (Table 3.27).

Although nothing is known about the feeding behavior of E. lanceolatus, the closely related species Pareques viola and Equetus acuminatus, as well as other reef sciaenids, are known to hide under ledges during the day, emerging at night to feed on crustaceans and polychaetes (Longley and Hildebrand, 1941; Hobson, 1965; Randall, 1967; Thomson et al., 1979; Hobson et al., 1981). Perhaps because of this behavior, no E. lanceolatus were observed during the daytime Task II dives. Jackknife-fish, like related species, probably shelter under ledges during the day and emerge at night to

Table 3.27 Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Equetus lanceolatus*, by length interval.

	LENGTH INTERVALS (mm SL)					
	< 185			≥ 185		
PREY TAXON	F	N	V	F	N	V
Annelida						
Polychaeta	40.0	13.0	19.1	100.0	59.3	56.3
Crustacea						
Mysidacea	20.0	4.4	4.8	25.0	7.4	3.8
Cumacea	60.0	52.2	13.4	12.5	7.4	0.4
Isopoda	20.0	4.4	1.3			
Amphipoda	60.0	13.0	5.7	25.0	7.4	0.5
Decapoda	60.0	13.0	55.7	50.0	18.5	39.0
Number of stomachs examined:		8			8	
Examined stomachs with food:		5			8	
Mean length of fish with food:		161.8			197.1	

feed. The frequency of mysids and cumaceans in their stomachs is also evidence of nocturnal foraging (see sections on Apogon pseudomaculatus and Rhomboplites aurorubens).

Overlap in Diet

Comparison of diet overlap between predators indicated that a few predators were similar in diet to one or several other predators whereas most fishes had relatively low diet overlap (Figure 3.2).

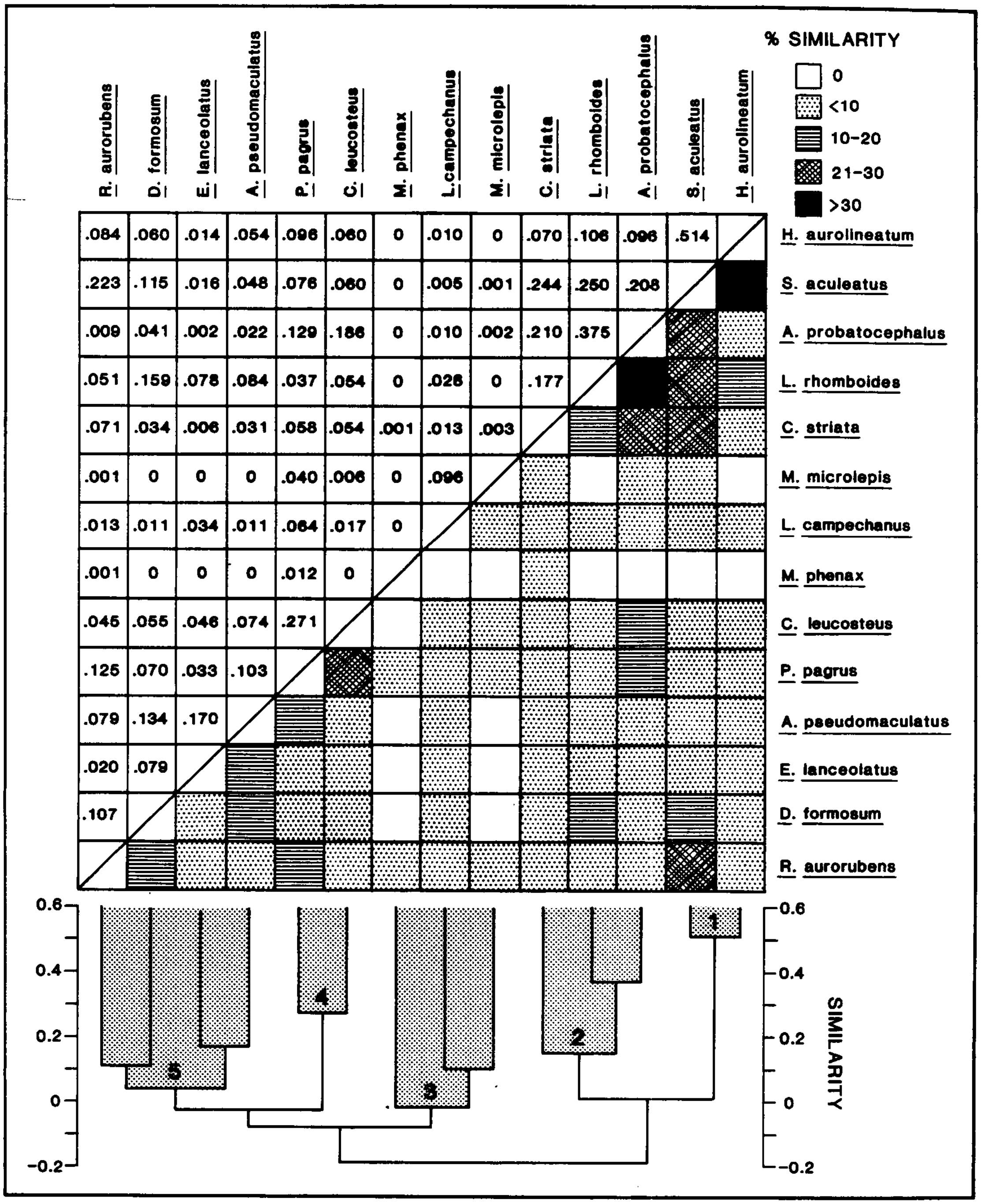
Not surprisingly, H. aurolineatum and S. aculeatus had the highest overlap in diet (Group 1, Figure 3.2). These species fed extensively on infaunal invertebrates and although H. aurolineatum preyed on infauna much more than S. aculeatus did, both of these predators fed more on infauna than did other fishes. Dominant prey shared in common included Ervilia concentrica, Calanopia americana, Branchiostoma caribaeum, Erichthonius brasiliensis, and chaetognaths. Stenotomus aculeatus also had relatively high diet overlap with several other species, including Rhomboplites aurorubens, Centropristis striata, Lagodon rhomboides, and, to a lesser extent, Archosargus probatocephalus.

Archosargus probatocephalus and L. rhomboides were also relatively high in diet overlap (Group 2). The motile amphipod E. brasiliensis was the most abundant prey species for both predators and Photis pugnator was also abundant in the diet of both of these sparid fishes. In addition, both species, especially A. probatocephalus, fed on sessile epifauna which were not heavily utilized by other species. Lagodon rhomboides has previously been characterized as a grazer on attached organisms (Caldwell, 1957) and it is apparent from the present study that A. probatocephalus is a grazer on sessile fauna as well. Centropristis striata also had a diet dominated numerically by E. brasiliensis and also fed on sessile and other motile species consumed by L. rhomboides and A. probatocephalus. Group 2 predators consumed some motile epifauna that were also consumed by Group 1 and were joined to the latter group at a lower level of similarity.

Mycteroperca microlepis, M. phenax, and Lutjanus campechanus were highly piscivorous and formed a separate predator group (Group 3), although diet similarity values were quite low. Lutjanus campechanus consumed some invertebrates in addition to fishes and demonstrated low similarity in diet to most other predators. Mycteroperca phenax had little similarity in diet to other predators, but this may be due to small sample size.

The sparids Calamus leucosteus and Pagrus pagrus had a relatively high similarity in diet (Group 4). The barnacle Balanus trigonus was an abundant species in the diet of both predators, and other species such as Erichthonius sp. A were consumed more by these predators than by other fishes.

A final group (Group 5) consisted mainly of species that appear to be nocturnal foragers on mysids, cumaceans, and decapods that swarm in the water column at night. Although some predators in this group (e.g., R. aurorubens) had higher diet similarity to species outside the group (e.g., S. aculeatus and P. pagrus), predators in this group fed more on planktonic and



	R. aurorubens	D. formosum	E. lanceolatus	A. pseudomaculatus	P. pagrus	C. leucosteus	M. phenax	L.campechanus	M. microlepis	C. striata	L. rhomboides	A. probatocephalus	S. aculeatus	H. aurolineatum
H. aurolineatum	.084	.060	.014	.054	.096	.060	0	.010	0	.070	.106	.096	.514	
S. aculeatus	.223	.115	.016	.048	.076	.060	0	.005	.001	.244	.250	.208		
A. probatocephalus	.009	.041	.002	.022	.129	.186	0	.010	.002	.210	.375			
L. rhomboides	.051	.159	.078	.084	.037	.054	0	.028	0	.177				
C. striata	.071	.034	.006	.031	.058	.054	.001	.013	.003					
M. microlepis	.001	0	0	0	.040	.006	0	.096						
L. campechanus	.013	.011	.034	.011	.064	.017	0							
M. phenax	.001	0	0	0	.012	0								
C. leucosteus	.045	.055	.046	.074	.271									
P. pagrus	.125	.070	.033	.103										
A. pseudomaculatus	.079	.134	.170											
E. lanceolatus	.020	.079												
D. formosum	.107													
R. aurorubens														

Figure 3.2 Bray-Curtis similarity values and classification hierarchy (flexible sorting) for predators, based on prey similarity.

hyperbenthic organisms then did other predators, and were grouped together for this reason. *Apogon pseudomaculatus* was most similar to *Equetus lanceolatus. Ampelisca cristata, Oxyurostylis smithi* and *Bowmaniella portoricensis* were abundant in the diet of these predators, both of which are believed to forage at night when those benthic crustaceans are active. Within this group, *Rhomboplites aurorubens* was most similar in diet to *Diplectrum formosum.* Although *R. aurorubens* is believed to be a nocturnal forager (Grimes, 1979), *D. formosum* demonstrates diurnal feeding activity (Bortone, 1981). Whereas *R. aurorubens* is well adapted for water column foraging (Davis and Birdsong, 1976; Grimes, 1979), *D. formosum* is a more sedentary species that usually occupies a "home area" (Bortone, 1971). Diurnal activity in *D. formosum* consists of active excavation of sediments (Bortone, 1971) and pursuit of hyperbenthic organisms while those benthic organisms occupy their daytime habitat in the sediments. *Rhomboplites aurorubens,* on the other hand, pursues many of these same prey at night when they swarm in the water column.

Previous investigators who have studied the food habits of reef-fish communities have generally classified species into distinct feeding types. Hiatt and Strasburg (1960) studied the food habits of 56 species of fishes in the Marshall Islands and grouped those fishes into algal feeders (including grazers, browsers, and incidental algal feeders), detritus feeders, scavengers, plankton feeders, carnivores (fossorial, benthic, mid-water, and roving), coral feeders (browsers and grazers), and omnivores (facultative and incidental). Hobson (1974) classified 102 species of tropical Hawaiian fishes as generalized carnivores (nocturnal, crepuscular and diurnal predators), specialized predators (ambush predators, stalkers, sensory specialists, diurnal planktivores, diurnal benthivores), and herbivores. Randall (1967) examined the stomach contents of 212 species of West Indian fishes and grouped species into the following categories: 1) plant and detritus feeders, 2) zooplankton feeders, 3) sessile animal feeders, 4) "shelled" invertebrate feeders, 5) generalized carnivores on motile invertebrates and fishes, 6) ectoparasite feeders, and 7) fish feeders.

Classification (cluster analysis) of predators in the present study according to prey composition generally grouped the fishes into distinct feeding types similar to Randall's (1967) classification. Diurnal or nocturnal feeding behavior of some species, however, resulted in different feeding types clustering together in the same group. *Rhomboplites aurorubens* for example can be considered a zooplankton feeder (Randall, 1967), as its diet was dominated by strictly planktonic organisms such as hyperiid amphipods, calanoid copepods, sergestid decapods, planktonic ostracods, doliolids, and chaetognaths. *Rhomboplites aurorubens* also fed heavily on hyperbenthic species (mysids, cumaceans, etc.) in the water column at night. *Diplectrum formosum* was classified in a group with the planktivorous species *R. aurorubens.* Although *D. formosum* also fed mainly on hyperbenthic cumaceans and mysids, this species is a diurnal feeder (Bortone et al., 1981) and thus probably feeds on these crustaceans when they are burrowed in the sediments. *Diplectrum formosum* should be considered a generalized carnivore on motile benthic animals, although its diet most closely overlapped that of a planktivore. The feeding of *R. aurorubens* and *D. formosum* demonstrates temporal partitioning of the same food resource, which diminishes competition among fishes occupying the same reef.

Apogon pseudomaculatus also fed heavily on hyperbenthic crustaceans, and Randall (1967) and others have considered apogonids to be zooplankton feeders. Equetus lanceolatus fed on hyperbenthic crustaceans and appears to be nocturnally active. This species, however, appears to be better adapted to benthic feeding (Chao, 1978). Equetus lanceolatus may feed on hyperbenthic crustaceans just as these emerge from the bottom at night. The frequent consumption of strictly benthic species (e.g., Glycera sp.) also indicates that E. lanceolatus is a benthic feeder. Although it grouped with A. pseudomaculatus based on prey similarity, E. lanceolatus feeds differently and should be classified as a generalized carnivore (perhaps nocturnal or crepuscular) on motile benthic invertebrates (Randall, 1967).

The sheepshead, Archosargus probatocephalus was the only species studied that could be considered a sessile animal feeder. Sessile invertebrates dominated the volume of prey in sheepshead guts by far. Many individuals of motile crustaceans that are associated with the sessile prey of sheepshead were incidentally consumed, but they made up little of the prey volume. These motile species were mainly amphipods that build tubes on sessile organisms (E. brasiliensis, C. tubularis) or that cling to and feed on sessile organisms (C. equilibra) (see section I, fouling plate study). Some species that were primarily generalized predators on motile invertebrates and fishes were grouped with sheepshead in the cluster analysis (Figure 3.2). These fishes, pinfish (Lagodon rhomboides) and black sea bass (Centropristis striata), consumed many of the same motile prey as sheepshead, and fed to a lesser extent on sessile fauna. Pinfish consumed hydroids and black sea bass frequently consumed ascidians.

Other generalized predators on motile organisms were southern porgy (Stenotomus aculeatus) and tomtate (Haemulon aurolineatum). These fishes, particularly H. aurolineatum, fed extensively on infaunal invertebrates. Haemulon aurolineatum is a nocturnal forager over sand flats and returns to the reef during the day. On the other hand, southern porgy appear to be diurnal feeders. Of the stomachs collected, those collected between 0800 hrs and 1199 hrs local time had the highest percentage (84%) of non-empty stomachs and most of those collected between 1200 hrs and 1599 hrs local time (83%) also contained food. In contrast, only 41% of stomachs collected between 2000 hrs and 0399 hrs local time contained food. In addition, the related species S. caprinus in the Gulf of Mexico and S. chrysops in the Middle Atlantic Bight show definite diurnal feeding activity (Henwood et al., 1978; Sedberry, 1980).

Calamus leucosteus appeared to be the only predator with a diet dominated by "shelled" invertebrates. These invertebrates included mollusks, barnacles, pagurids and sipunculids. Many other species of Calamus are also considered to be shelled invertebrate feeders (Randall, 1967). Calamus leucosteus was grouped with red porgy, Pagrus pagrus, in the cluster dendrogram. Both predators had a sessile barnacle species (Balanus trigonus) as an abundant prey in the diet, but they fed on few other sessile organisms. Red porgy fed mainly on motile decapods and fishes and can be classified as a generalized predator on motile organisms.

Three species of fish analyzed in the present study formed a group (Group

3, Figure 3.2) of fish feeders. This group included two groupers, gag (*Mycteroperca microlepis*) and scamp (*M. phenax*); and the red snapper (*L. campechanus*). These apex predators fed mainly on smaller planktivorous fishes that form large schools in hard-bottom areas. These fishes also occasionally consumed other demersal fishes and smaller individuals often fed on invertebrates.

No fishes in the present study were considered plant and detritus feeders. Sheepshead and pinfish consume plant material in coastal habitats, but the relative lack of plant material (or the increased relative abundance of animal prey) on hard-bottom areas off South Carolina and Georgia (SCWMRD, 1982) resulted in a scarcity of plant material in the diet of these fishes. Although cordgrass (*Spartina alterniflora*), a source of food for many estuarine detritus-feeding fishes (Darnell, 1961), accumulates under rock outcrops and in crevices in some inner-shelf hard-bottom areas (Office of Coastal Zone Management, 1980), vascular plant detritus was found in only one stomach (of black sea bass) and was probably ingested incidentally.

Although none of the fishes studied fed on plant material, several species that Randall (1967) included in this group also occur on hard-bottom reefs in the South Atlantic Bight (SCWMRD and GADNR, 1981; SCWMRD, 1982; Sedberry and Van Dolah, 1984). These include the seaweed blenny (*Parablennius marmoreus*), orange filefish (*Aluterus schoepfi*), scrawled filefish (*A. scriptus*), orangespotted filefish (*Cantherhines pullus*), and the fringed filefish (*Monacanthus ciliatus*).

No evidence of ectoparasite picking was noted among the fishes examined. Eating of ectoparasites is a very specialized coevolutionary predation form that is usually limited to the highly complex fish communities of tropical coral reefs (Ehrlich, 1975). The sharksucker, *Echineis naucrates*, occurred on the hard-bottom reefs but, although it is a parasite picker (Randall, 1967; Cressy and Lachner, 1970), it does not establish "cleaning stations" on the reefs. Juvenile spottail pinfish (*Diplodus holbrooki*), a common hard-bottom species, also pick ectoparasites from fishes (Carr and Adams, 1972).

Interaction of Fishes with the Benthos

It is apparent, even from the relatively small number of species examined, that there is a great variety of feeding types among fishes in hard-bottom habitat. The diversity of feeding types and feeding habitats results in a comparatively low diet overlap and allows many species of fishes to coexist in the relatively scarce (as opposed to sand-bottom habitat) hard-bottom areas of the South Atlantic Bight. Although many fishes are abundant on hard bottom, the degree of their dependence on this habitat varies. In the South Atlantic Bight, some of the fishes studied are found only on natural or artificial reefs for at least part of their life history. Others are found on open shelf areas but are much more abundant on hard-bottom reefs. During the first two years of this study (SCWMRD and GADNR, 1981; SCWMRD, 1982) the three most abundant fishes in trawl catches were *S. aculeatus*, *R. aurorubens* and *H. aurolineatum* (ranking first, third, and second, respectively, by weight). Two of these species, *S. aculeatus* and *H. aurolineatum*, are occasionally taken in trawls over sand bottom (Wenner et al., 1980) but they are not nearly as abundant as they are in hard-bottom habitat (Sedberry and Van Dolah, 1984). Since these two species feed heavily on sand-dwelling infauna (Figure 3.3) they are apparently not completely dependent on hard-bottom habitat. *Rhomboplites aurorubens*, on the other hand, is more restricted to reef habitat, and does not range far from a home reef (Fable, 1980). Wenner et al. (1980) collected only 12 specimens in 40 trawl tows in sand-bottom habitat on the southeastern continental shelf. *Rhomboplites aurorubens* did not, however, feed directly on hard-bottom fauna and is its diet was dominated volumetrically by copepods, planktonic or hyperbenthic decapods, cephalopods, and fishes, many of which were not strictly hard-bottom species. The attraction of *R. aurorubens* to hard-bottom reefs may be behavioral rather than trophic.

Other fishes that had a diet dominated volumetrically by animals that are not restricted to hard bottom were *D. formosum*, *A. pseudomaculatus*, and *E. lanceolatus*. These fishes fed on sand-bottom benthic crustaceans and (especially *A. pseudomaculatus*) hyperbenthic crustaceans that swarm in the water column at night.

Piscivorous species, such as *L. campechanus*, *M. microlepis*, and *M. phenax*, while not feeding directly on hard-bottom invertebrates, fed heavily on fishes that are abundant in hard-bottom habitats. Hard-bottom fishes also dominated the diet of larger *P. pagrus*, although juveniles fed more heavily on epifaunal invertebrates.

Other fishes appeared to depend more on hard-bottom habitat for feeding. *Calamus leucosteus* fed on a combination of hard-bottom epifauna, infaunal invertebrates and fishes. *Lagodon rhomboides* consumed many species of hard-bottom invertebrates; however, chaetognaths dominated the diet of this species volumetrically. Black sea bass were more dependent on hard bottom for food than *C. leucosteus* or *L. rhomboides* and ate many species of sessile and motile hard-bottom invertebrates and fishes. *Archosargus probatocephalus* fed exclusively on hard-bottom sessile invertebrates and associated motile fauna.

Predation can be an important factor in regulating the structure of sessile communities (Petersen, 1979). Most predators in the present study were not, however, generalized grazers on sessile biota. A notable exception was the sheepshead, *Archosargus probatocephalus*, which may be important in contributing to the high diversity of the hard-bottom sessile fauna. Sutherland (1978) reported that *Schizoporella unicornis* (= *S. errata* of later authors), an encrusting bryozoan very similar in form and functional role to *S. cornuta*, and the ascidian *Styela plicata* are able to colonize available space to the exclusion of other species. *Styela plicata* is also capable of invading space occupied by other species. Both of these species served to stabilize the fouling community at a low diversity level (Sutherland 1978). *Styela plicata* and *S. cornuta* (similar to *S. unicornis*) may function in a similar manner if left undisturbed in hard-bottom habitat, i.e. they may monopolize and stabilize the community. However, these two species were the top-ranking prey, by volume, for sheepshead. If these species function in hard-bottom areas as they do in shallow-water fouling communities (Sutherland, 1978) then sheepshead are probably very important in controlling the structure of sessile invertebrate communities in hard-bottom habitats by reducing the abundance of these competitively superior species.

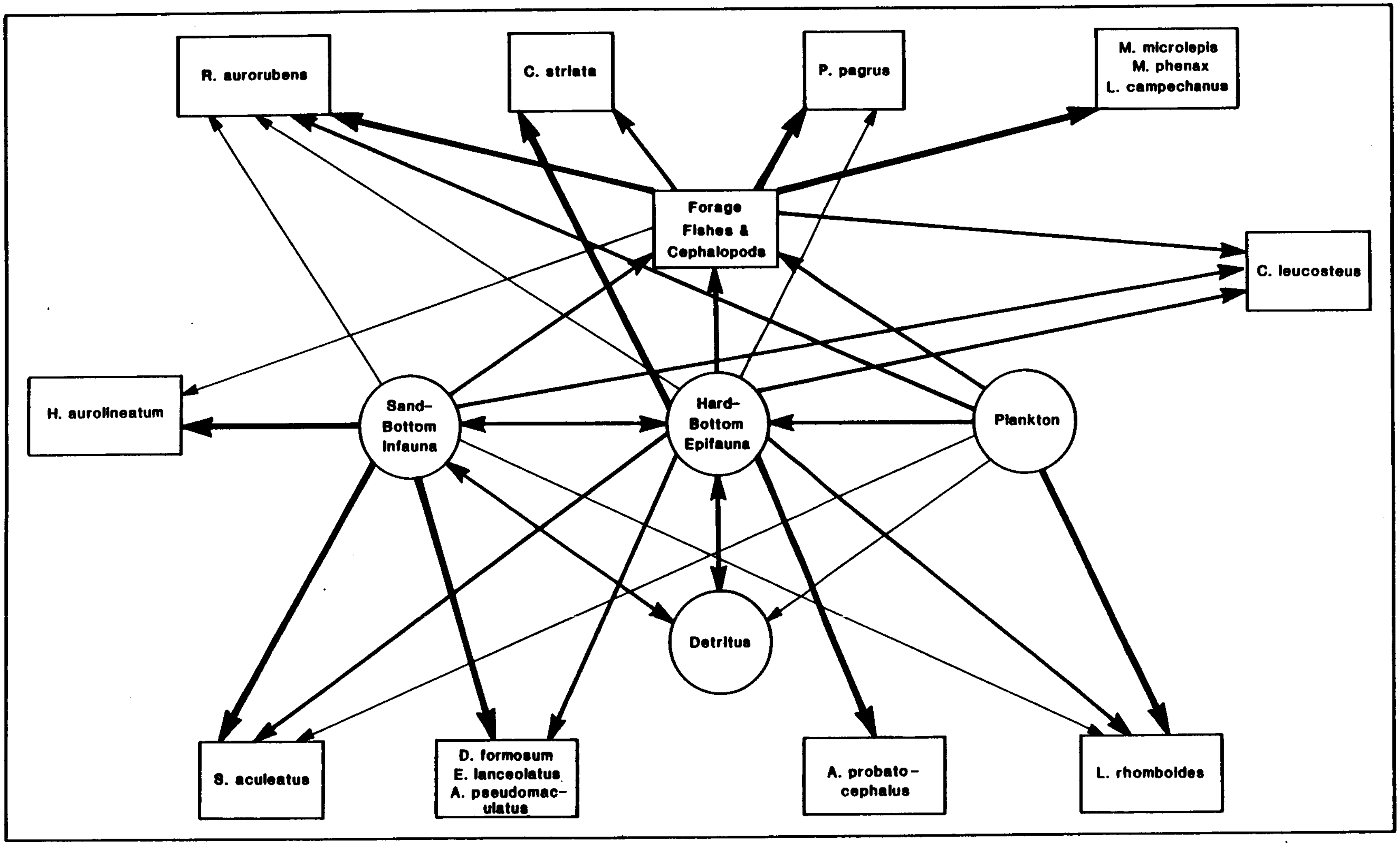


Figure 3.3. Schematic food web depicting alternate food sources for live-bottom fishes and the relative importance of each source for each species. Wider lines indicate major food sources; narrower lines indicate less important food sources.

Other predators studied appear to have less effect on hard-bottom epifaunal communities. Many fed extensively on infauna or nekton. Those that fed on epifauna often selected prey species that are prolific and opportunistic (as indicated by their early colonizing ability) inhabitants of hard-bottom communities, such as E. brasiliensis and C. equilibra.

IMPLICATIONS OF TASK III RESULTS RELATED TO OFFSHORE OIL AND GAS DEVELOPMENT

The overall effects of oil development on fish populations in the South Atlantic Bight are unknown at this time, but some generalizations can be made based on Task III results and previous MMS studies. Potential detrimental effects that act directly on fishes have been discussed in the Year 1 and Year 2 reports and will not be detailed here. Briefly, these include destruction of habitat, lethal and sublethal contamination by acute or chronic exposure to drilling fluids and oil from spills, and noise pollution. In addition to direct effects on fishes, oil production activities can negatively affect food chains on the continental shelf, with subsequent reductions in fish populations and modification of prey community structure.

Many hard-bottom fishes, such as D. formosum, H. aurolineatum, S. aculeatus and E. lanceolatus, feed heavily on sand-bottom areas of the shelf, and certain others, such as L. rhomboides and C. leucosteus, have a diet that includes sand-bottom species. These fishes would be adversely affected by drilling operations in sand areas adjacent to hard-bottom reefs. Haemulon aurolineatum, S. aculeatus and L. rhomboides, while not important commercial species, are often caught by recreational fisherman, and H. aurolineatum is the most commonly caught grunt in the recreational headboat fishery (Manooch and Barans, 1982). These species are most abundant at inner- and middle-shelf depths and drilling on hard bottom and adjacent sand areas at those depths could damage living space and feeding grounds of these species. Calamus leucosteus is an important species in the trawl fishery (Waltz et al., 1982) and would be affected by any negative impact on its habitat, which includes hard-bottom areas in all three depth zones.

Species such as C. striata and, especially A. probatocephalus, that depend heavily on hard-bottom reefs for their source of food could be severely affected if drilling into hard bottom were to eliminate the reefs by physical destruction of the reef structure. Burial of reef organisms as a result of drilling could also eliminate the food supply for these fishes. Centropristis striata is an important commercial and recreational species at inner- and middle-shelf depths, and A. probatocephalus is fished recreationally in inshore waters. Negative impacts of oil development at inner- and middle-shelf depths could threaten populations of these important species.

Apogon pseudomaculatus and *R. aurorubens* feed in the water column and very little on hard-bottom invertebrates. Both species, however, are highly dependent on hard-bottom habitat. At night, *Apogon pseudomaculatus* feeds on benthic invertebrates that swarm in the water column and during the day it uses the reef for shelter. *Rhomboplites aurorubens* feeds on a variety of planktonic and nektonic animals, at least some of which (e.g., forage fishes) are concentrated near hard-bottom reefs. The dependence of this important fishery species on hard-bottom habitat is also evident from trawl surveys and tagging studies (Wenner et al., 1980; Fable, 1980; Sedberry and Van Dolah, 1984). Juveniles and adults are found mainly at middle and outer shelf stations, and juveniles also occur on the inner shelf. Although drilling activities in the three depth zones that may smother hard bottom invertebrates might not affect the feeding of *R. aurorubens*, activities that reduce water quality and hence, plankton and nekton productivity will likely reduce *R. aurorubens* populations.

The piscivores *M. microlepis*, *M. phenax*, *L. campechanus* and, to a lesser extent *P. pagrus*, feed very little on hard-bottom invertebrates, although they are dependent on reef habitat for most of their life history and tagging studies have shown that *L. campechanus* and *P. pagrus* move only short distances from a home reef (Fable, 1980; Grimes et al., 1982). Although they do not feed extensively on hard-bottom epifauna, they do feed on forage fishes that school on hard-bottom reefs. This and their relatively sedentary behavior makes them susceptible to disturbance of their habitat. These species are most abundant at middle- and outer-shelf depths and petroleum development activities at those depths could have adverse affects on their populations.

Because fishes are attracted to hard-bottom reefs (whether for food, shelter, or due to innate behavior), damage to this habitat will probably affect fish populations and thus the community structure of these reefs. Disturbance to the habitat itself, such as destruction of undercut ledges and crevices, will reduce sheltering places for fishes such as *A. pseudomaculatus* and *E. lanceolatus*. Smothering and burial of sessile species and associated motile fauna will affect fishes that feed on the reefs. Water column discharges and spills that increase turbidity may lower productivity and decrease the efficiency of particulate plankton feeders such as *R. aurorubens* and forage fishes such as *Decapterus punctatus* that are important prey for piscivorous species. Toxic hydrocarbons and metals may reduce populations of heavy grazers on epifauna (such as *A. probatocephalus*) which may, in turn, affect invertebrate community structure.

Although drilling operations on South Atlantic Bight hard-bottom reefs have not been studied directly, evidence from studies in the Gulf of Mexico suggest that these activities, under normal operation, may have few detrimental effects (Boland et al., 1983). Provided there are no major spills or similar accidents, platforms act as artificial reefs and attract fishes. In open areas of the shelf, platforms attract a diverse reef community to an otherwise relatively barren habitat. Some drilling operations near to natural reefs in the Gulf of Mexico (Boland et al., 1983) have produced no detectable detrimental effects (e.g., sessile growth mortality or excessive sedimentation). If such were the case in the South Atlantic Bight, drilling and production platforms installed in the vicinity of hard-bottom reefs would provide additional relief, more habitat, and an artificial substrate on which epifaunal invertebrates (potential prey for fishes) could grow. In the absence of detrimental effects such as spills, these platforms would probably enhance fish populations in the immediate vicinity.

SUMMARY AND CONCLUSIONS

- Food habits, prey selectivity, and trophic relationships of several species of hard-bottom fishes were studied by analyzing the stomach contents of specimens collected from 11 hard-bottom stations. Food habits were described for each species and food selectivity was quantified by comparing stomach contents to benthic samples from the same habitat. Fishes were collected in three depth zones, defined as inner shelf (16-22 m depth, three stations), middle shelf (23-37 m depth, four stations), and outer shelf (46-69 m depth, four stations). The species examined represented a variety of feeding types and included species of economic importance, as well as other species representative of the hard-bottom ichthyofauna in the South Atlantic Bight. Species examined included four serranids (*Centropristis striata*, *Diplectrum formosum*, *Mycteroperca microlepis*, and *M. phenax*), an apogonid (*Apogon pseudomaculatus*), two lutjanids (*Lutjanus campechanus* and *Rhomboplites aurorubens*), one haemulid (*Haemulon aurolineatum*), five sparids (*Archosargus probatocephalus*, *Calamus leucosteus*, *Lagodon rhomboides*, *Pagrus pagrus*, and *Stenotomus aculeatus*), and a sciaenid (*Equetus lanceolatus*).

- Black sea bass (*C. striata*) had a generalized diet of motile epibenthic hard-bottom species, mainly amphipods, decapods, and fishes. Black sea bass fed selectively on a few species of amphipods but generally avoided species of polychaetes that dominated the hard-bottom invertebrate fauna. Smaller black sea bass ate relatively more small crustaceans (amphipods) and larger fish fed more on decapods and fishes.

- Sand perch (*D. formosum*), both large (< 168 mm) and small individuals, fed on motile crustaceans (mysids and decapods) most of which are sand-dwelling species. Consequently, selectivity values for those species were high, while values for most hard-bottom invertebrates were negative. Sand perch apparently feed in sandy areas often found between ledges in hard-bottom areas.

- Gag (*M. microlepis*), scamp (*M. phenax*), and red snapper (*L. campechanus*) fed mainly on fishes. These predators are top-level carnivores that did not feed directly on hard-bottom invertebrates to any extent. They fed on species that are abundant schooling forage fishes associated with hard bottom habitat.

- The twospot cardinalfish (*A. pseudomaculatus*) is an abundant small tropical species that is diurnally cryptic, emerging at night from hiding places in the reef to feed. They fed mainly on small benthic crustaceans that also emerge at night and are active in the water column. Dominant benthic invertebrates (mainly polychaetes) were not consumed, but many planktonic mysids, cumaceans, and decapods were selected. Smaller crustaceans (amphipods) were eaten by smaller fishes whereas larger twospot cardinalfish ate larger decapods.

- Vermilion snapper (R. aurorubens), an abundant and economically valuable species, fed mainly on planktonic and nektonic species. Planktonic species consisted mainly of amphipods, copepods, and thaliaceans as well as crustaceans (mysids and cumaceans) that are nocturnally planktonic. Most of the dominant benthic invertebrates were not consumed. Small vermilion snapper consumed small crustaceans but larger individuals preferred fishes, cephalopods, and larger crustaceans.

- Tomtate (H. aurolineatum) had a generalized diet of motile invertebrates. Polychaetes, amphipods, decapods, pelecypods, and cephalochordates were the most important prey. Most prey species were infaunal sand-dwelling species that were not found in hard-bottom invertebrate samples. Smaller tomtate ate small crustaceans and fishes while larger fish consumed mainly pelecypods and cephalochordates. Tomtate are nocturnal feeders that leave the reef to forage on adjacent sandy areas, returning to the reef during the day.

- Sheepshead (A. probatocephalus) fed mainly on sessile invertebrates, including bryozoans, pelecypods, barnacles, and ascidians. Dominant hard-bottom polychaetes were generally not consumed, but dominant amphipods were positively selected for. Common sessile prey species were consumed less frequently than their occurrence in benthic samples. Sessile fauna dominated the diet of large and small sheepshead.

- Whitebone porgy (C. leucosteus) fed on motile benthic invertebrates, mainly species with hard shells, such as pagurids, gastropods, sipunculids, barnacles, and pelecypods. Fishes were also consumed by larger individuals. Whitebone porgy selectively fed on shelled invertebrates and selectivity values for dominant hard-bottom invertebrates (polychaetes and amphipods) were negative.

- Small pinfish (L. rhomboides) fed primarily on amphipods, cumaceans, and polychaetes, while larger pinfish fed mainly on chaetognaths and decapods. Most species of crustaceans in the diet were positively selected, but polychaetes that dominated benthic samples were avoided.

- Red porgy (P. pagrus) is an economically important species that is abundant at middle- and outer-shelf depths. Red porgy fed on motile organisms, primarily decapods and fishes. Small red porgy fed on amphipods, cephalochordates, and decapods, whereas larger fish had a diet dominated by fishes. Red porgy selectively fed on motile crustaceans that were relatively scarce in benthic samples.

- Southern porgy (S. aculeatus) was the most abundant species in trawl catches and was found in all three depth zones. They fed mainly on amphipods and polychaetes. Cephalochordates were important prey for larger individuals. Southern porgy fed mainly on infaunal sand-dwelling or pelagic animals, and selectivity values for hard-bottom invertebrates were generally negative. A few species of hard-bottom amphipods were selectively eaten.

- Jackknife-fish (*E. lanceolatus*), a common inner- and middle-shelf species, fed mainly on polychaetes and decapods. Cumaceans were important in the diet of smaller fish, but larger individuals consumed more polychaetes.

- Overlap in diet was relatively low among the fishes studied. Tomtate and southern porgy were most similar in diet, and both fed extensively on infaunal organisms. Black sea bass, pinfish, and sheepshead formed a group that fed on sessile organisms and their associated motile fauna. Three piscivorous species (gag, scamp, and red snapper) clustered together. Red porgy and whitebone porgy showed a low level of diet similarity, but had a few sessile and motile species in common. Several fishes (vermilion snapper, sand perch, jackknife-fish, and twospot cardinalfish) fed on a variety of infaunal and planktonic prey and were grouped together in the cluster analysis. The variety of available food sources, including infauna, epifauna (sessile and motile), plankton, and nekton in hard-bottom habitat, as well as diel partitioning of food resources, resulted in low diet overlap.

- Energy production activities that destroy rock outcrops or smother hard-bottom invertebrates will reduce habitat for fishes such as *A. pseudomaculatus* and *E. lanceolatus* that shelter under ledges and prey for fishes like *C. striata* and *A. probatocephalus* that graze heavily on hard-bottom invertebrates. The discharge of drilling muds on adjacent sand-bottom areas may bury infaunal organisms that are a food source to many other fishes, such as *S. aculeatus* and *H. aurolineatum*. Drilling activities that decrease water quality and productivity by increasing turbidity will affect particulate plankton feeders, such as *R. aurorubens* and the many forage fishes on which piscivorous species such as *Mycteroperca* spp. and *L. campechanus* feed. On the other hand, if detrimental effects are minimized, production platforms could act as artificial reefs and provide additional habitat and food for hard-bottom fishes.

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