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A seasonal study of zostera epibiota in the York River, Virginia

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A SEASONAL STUDY OF ZOSTERA EPIBIOTA IN THE YORK RIVER, VIRGINIA

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ABSTRACT

The invertebrate macrofauna and epiphytes occurring on *Zostera* in the lower York River, Virginia, were sampled with the aid of SCUBA for 14 consecutive months. A collecting station was located at each of three different depths within a single eelgrass bed.

Growth patterns of *Zostera* are discussed. The plants attained maximum biomass at each depth in June. Lowest biomasses occurred in January and February. Density of plants on the bottom decreased with depth, but plant elongation during spring and early summer was greatest at increased depths.

A total of 112 invertebrate species was collected, including 13 new records for Chesapeake Bay. Seasonal abundance, depth distribution and salient aspects of the ecology of each of the more abundant forms are discussed. The five most abundant non-colonial invertebrate species (*Bittium varium*, *Paracerceis caudata*, *Crepidula convexa*, *Ampithoe longimana* and *Erichsonella attenuata*) accounted for approximately 59% of the total fauna. These species dominated the epifauna throughout most of the year. Several other species, including *Balanus improvisus*, *Molgula manhattensis*, *Polydora ligni* and *Stiliger fuscata*, were abundant for only brief periods.

Twenty-nine species of epiphytic algae were identified, including 8 chlorophytes, 4 phaeophytes and 17 rhodophytes. Distinct summer and winter algal floras were evident.

Several aspects of community structure are discussed. A relatively high average index of affinity (58%) between all synchronous sample pairs indicated a generally homogeneous fauna. Diversity values, according to Shannon's information function, ranged from 1.92 to 3.90 bits/individual and averaged 3.04 bits/individual for all stations. No marked seasonal change in diversity was apparent.

Presumed trophic relationships of the more common epifaunal species are discussed. The primary sources of nutrition appeared to be 1) plankton and suspended particulate matter, 2) detritus and microorganisms on the plant blades and 3) epiphytic algae. Apparently, none of the common invertebrate species utilized living *Zostera* as a primary food source.

A SEASONAL STUDY OF *ZOSTERA* EPIBIOTA

IN THE YORK RIVER, VIRGINIA

INTRODUCTION

Eelgrass (*Zostera marina* L.) provides a substrate and shelter for a wide variety of marine organisms; it comprises, with its associated fauna and flora, a complex epibenthic community, qualitatively and quantitatively distinct from others in the area. The following is a seasonal study of the invertebrate macrofauna and common algal epiphytes found living on the photosynthetic surfaces of eelgrass in the lower York River, Virginia.

Zostera marina forms the most important north temperate seagrass system (Phillips, 1969). It is widely distributed in shallow marine and estuarine waters of protected bays and inlets in North America, Europe, Asia Minor and Eastern Asia (Burkholder and Doheny, 1968). In North America, *Z. marina* ranges along the Atlantic coast from Greenland to North Carolina and along the Pacific coast from Alaska to Northern Mexico (Setchell, 1929).

Since Setchell's classic work (1929) on the morphology and phenology of *Z. marina*, most studies of eelgrass have dealt with its widespread epidemic recession in the early 1930's and its subsequent recovery in many areas (Atkins, 1938; Addy and Aylward, 1944; Milne and Milne, 1951; and others). The "wasting disease" struck Eastern North America in 1930-31 and later spread to the west coast and to Western Europe, destroying 90% of the plants in these regions (Tutin, 1942). Although the cause of this catastrophe has not been definitely determined, Renn (1936) strongly implicated the mycetozoan parasite Labyrinthula macrocystis as the primary causal agent. A full discussion of the wasting disease is inappropriate here, but excellent bibliographies on this and other aspects of eelgrass biology are found in Phillips (1964) and McRoy and Phillips (1968).

The biological consequences of the disappearance of eelgrass have underlined its role in the marine ecosystem. The absence or decline of many Zostera associates following the epidemic has been reported by numerous authors (Dreyer and Castle, 1941; Tutin, 1942; Dexter, 1944; Wilson, 1949; Hopkins, 1957; Newell, 1963). Stauffer (1937) reported the absence in the Woods Hole, Mass., area of practically all the animals formerly found living on and among the plants, although infauna showed only a slight decline. Economically, the most important casualty was the bay scallop Aequipecten irradians which virtually disappeared from much of the United States east coast where dense beds of Zostera had provided a setting substrate for the post-veliger larvae (Gutsell, 1930).

Eelgrass has now returned to most areas from which it was eradicated, but despite general recognition of the importance of Zostera as a habitat for invertebrates, very few studies have been done on this community in North America. Most of these studies have been qualitative in nature. Allee (1923) listed 138 invertebrate species collected from Zostera beds in the Woods Hole area by numerous individuals over nine consecutive summers. No distinction was made between infauna and epifauna. MacGinitie (1935) recorded observations of the *Zostera* community as part of a larger study on the ecology of Elkhorn Slough, Calif. Brown (1962) investigated the ecology of periphyton on *Zostera* in Charlestown Pond, R.I. A few of the more common invertebrates were also noted. In a comprehensive paper on eelgrass biology, Burkholder and Doheny (1968) included a short list prepared by Dr. Patricia Dudley (Columbia University) of some invertebrates associated with the plants in South Oyster Bay, N.Y. Nagle (1968) reported on the ecology and seasonal and areal variations in abundance of amphipods on *Zostera* in the Woods Hole area and their distribution on individual plants. Some reference was made to other invertebrate groups and to algal epiphytes, although taxonomic and quantitative treatment of these was very limited.

The eelgrass community has been studied more extensively in European and Japanese waters. The composition, ecology and diurnal migration of the motile fauna of aquatic plant beds (including *Zostera*) in the Mediterranean have been investigated in some detail by Ledoyer (1962, 1966a, b) and compared with that in the English Channel (Ledoyer, 1964a, b). Environmental parameters in Mediterranean *Zostera* beds have been studied by Blois, Francaz, Gaudichon and LeBris (1961). The importance of eelgrass as a nursery ground for fish has stimulated research on the community by numerous Japanese workers, including Fuse et al. (1959); Kitamori, Nagata and Kobayashi (1959); Fuse (1962); Kita and Harada (1962); Sando (1964); and Kikuchi (1966, 1968).

Additional studies by Ledoyer (1967, 1969) have been conducted on the systematics and ecology of various crustaceans associated with Zostera and other seagrasses in Madagascar.

This study is the first in North America to provide quantitative, seasonal data on a large segment of the eelgrass community. It is primarily an attempt to elucidate temporal changes in the species composition and abundance of macroinvertebrates living on the photosynthetic surfaces of plants occurring at three depths within a single Zostera bed. Seasonal variations in the important macroscopic algal epiphytes are also recorded. The problem is approached autecologically as well as synecologically. Relative abundance, seasonal and depth distribution and general ecology of the more common species are discussed, in addition to various aspects of community structure.

HISTORICAL REVIEW OF TECHNIQUES FOR SAMPLING THE FAUNA OF AQUATIC VEGETATION

One of the most difficult aspects of a truly quantitative study of fauna living on aquatic vegetation is that of devising suitable sampling techniques. The plants must be collected without losing associated animals, some of which tend to drop off when their substrate is disturbed. Also, the plants often occur at depths which permit sampling only from a boat or by diving. Sampling in eelgrass is further complicated because it may assume different aspects with time; techniques suitable when the grass is essentially erect might not be feasible when it is prostrate and matted. The density of the plants on the bottom varies greatly through the year, so that sampling a given bottom area may give collections either overwhelmingly large or too small to be of value.

Most techniques heretofore employed to sample in aquatic vegetation have had limited quantitative value. Ekman-Birge, Petersen and other bottom grabs have often been used to collect in freshwater plant beds (Deevey, 1941; Eggleton, 1952) and in eelgrass (Kitamori et al., 1959; Kikuchi, 1966; Nagle, 1968). Phytofauna are not separated from benthos, and the plants often prevent the dredge from shutting completely, resulting in the loss of many organisms as it is hauled to the surface. In their study of animal communities in the _Zostera_ belt, Japanese investigators have used a wide variety of sampling apparatus, including beam trawls (Fuse, 1962; Kikuchi, 1966, 1968), seines (Fuse et al., 1959; Fuse, 1962), macroplankton nets (Kikuchi, 1968), and epibenthic sleds (Sando, 1964), all of which yielded only crudely quantitative results at best and did not collect forms which were firmly attached to the plants.

The simplest sampling techniques have involved gathering plants by hand, either from a small boat or while wading. Krecker (1939) collected freshwater phytofauna by reaching down from a boat and clipping the vegetation before raising it into a water-filled pan. Rosine (1955) employed a dip-net to place over submerged plants which were then broken off by hand at their bases and lifted from the water. These techniques are limited to shallow water and probably resulted in the loss of many organisms.

A variety of specially-designed devices have been utilized to improve sampling accuracy. Andrews and Hasler (1943) employed a cloth bag with a jointed-metal mouth to place over aquatic vegetation; a zippered opening permitted the hand to be inserted for clipping the plants, after which the mouth was closed to trap the animals. Gerking (1957) described two designs of rectangular open-top frames which could be placed over shallow-water plants prior to their being clipped. The samplers could be lifted from the water after enclosing the plants from below with a sliding screen door. A more elaborate mechanical device including a frame, cutter bar and attached bag was described by Gillespie and Brown (1966). O'Gower and Wacasey (1967) employed a mechanical self-closing sampler for studying both infaunal and epifaunal animal communities associated with Thalassia and Diplanthera. A "basket quadrat" consisting of a wire cubic frame was used by Kikuchi (1968) to collect eelgrass epifauna; the frame was placed over the plants, then quickly inverted after clipping the Zostera from the substratum. A drop-net quadrat designed by Hellier (1958) was used by Hoese and Jones (1963) to sample the fish and macroinvertebrates of the Thalassia community.

The use of diving gear has permitted more accurate quantitative sampling. Hagerman (1966) thus collected fauna associated with Fucus by enclosing the algae in plastic sacs, and Quade (1969) used similar means to sample the cladocerans of aquatic macrophytes. Diving was also employed by Fuse et al. (1959) to collect animals from Zostera, although their methods were not described. In his earlier investigations of marine plant communities Ledoyer (1962, 1964a, b) collected motile fauna by sweeping an insect net through shallow-water vegetation while wading; in later studies (1966a, b) he utilized SCUBA to sample in deeper water, otherwise using the same techniques. Results were "quantified" by making the same number of sweeps for each sample. An epibenthic sled which could be maneuvered by a diver was also employed in these later studies.

In the present study, before adopting the sampling methods described later, considerable time was spent in designing and testing various collecting devices, many of which incorporated features of previously-used techniques. None proved satisfactory for various reasons.

DESCRIPTION OF STUDY AREA

The study area was an extensive *Zostera* bed adjoining Big Mumfort Island (37° 16' N; 76° 31' W) in the lower York River, Virginia (Fig. 1). The area is approximately 2.7 km upriver from the George P. Coleman Bridge at Gloucester Point and directly across from the docks of the Naval Weapons Station. A smaller island (Little Mumfort) is located several hundred meters downriver. During the summer months a dense growth of eelgrass extended from below mean low water on Big Mumfort toward the main river channel for approximately 350-400 m. Eelgrass also grew in the shallows around the north end of the island but was very sparse in the generally turbid region between the island and the mainland. The Mumfort Islands were uninhabited and the area relatively undisturbed by human activity.

Sampling Stations

Preliminary investigations indicated conspicuous differences in the appearance of *Zostera* at different depths in the sampling area as well as qualitative and quantitative differences in associated fauna. To cover the full range of depths represented, three sampling stations were established in a transect extending into the river from Big Mumfort Island (Fig. 1). A gently sloping bottom with a continuous growth of eelgrass occurred along the transect. Stations were marked with

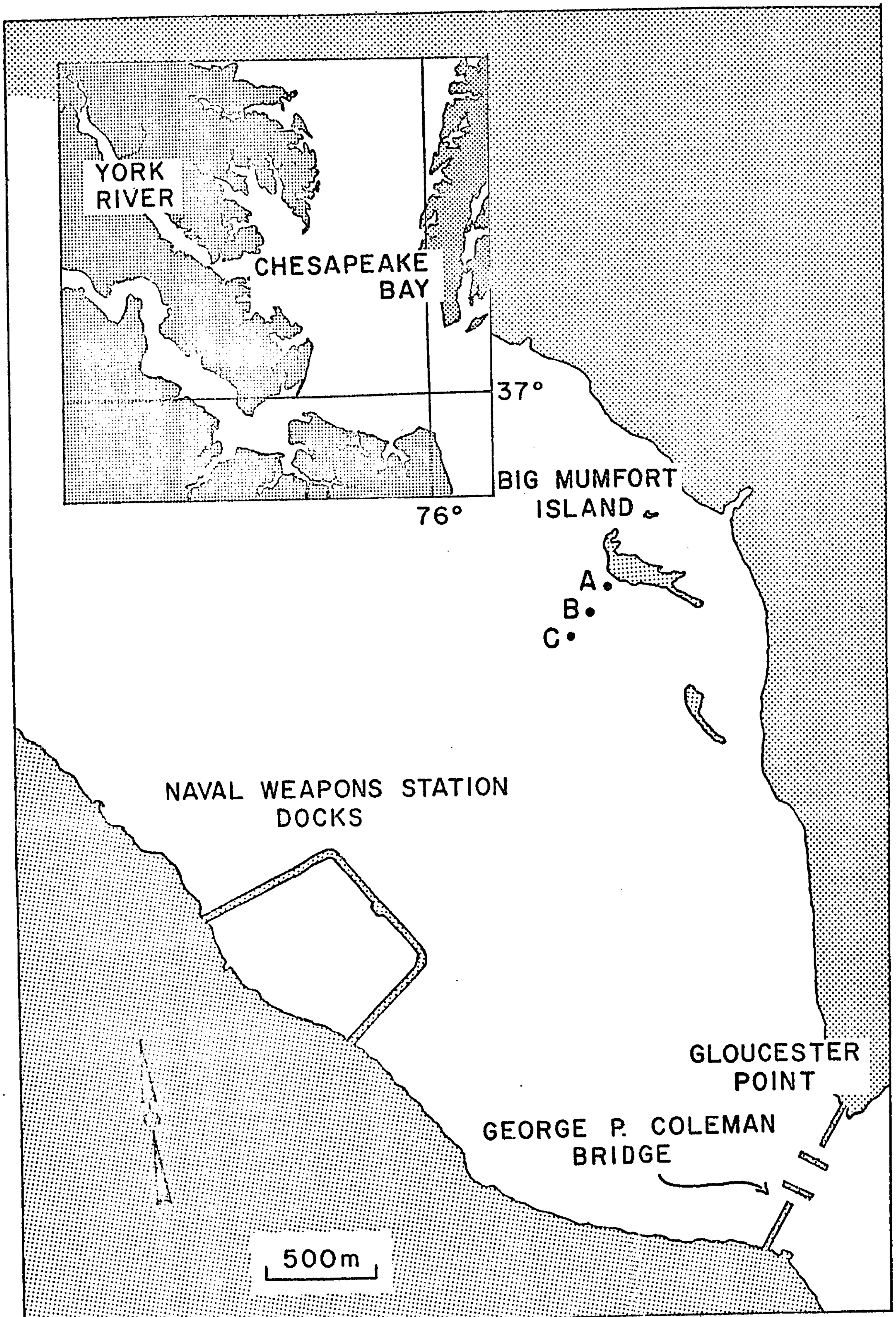


Fig. 1. Map of the area, showing location of sampling stations.

stakes which projected above water at high tide. Station A, the shallowest station, was located approximately 80 m offshore from the island. Water depth at mean low water (MLW) was about 0.7 m. Closer inshore, *Zostera* became mixed with *Ruppia maritima*, although very little of the latter was noted after the summer of 1967. Station B was approximately 120 m farther offshore where water depth at MLW was about 1.2 m. Station C, approximately 120 m farther out, was in a depth of about 1.6 m at MLW. Several meters beyond station C, *Zostera* became patchy in distribution and then absent from deeper water.

Physico-Chemical Conditions

As in other parts of the Chesapeake estuary, physical and chemical conditions were highly unstable, changing not only diurnally and seasonally but within each tidal cycle. To derive a complete picture of variations in ecologically significant environmental parameters would require continuous monitoring of these conditions. This was not feasible nor was it deemed necessary in this study since emphasis was on the descriptive aspects of temporal and spatial differences in the biota rather than on attempting to account for such differences.

Surface-water temperatures at sampling periods were determined with a stem thermometer. Values ranged from 2.8 C in early March to 28.3 in July and August (Fig. 2). More extreme temperatures were noted on other occasions: a thin layer of ice frequently overlaid the sampling area on early mornings of winter, and water temperatures as high as 30.8 C were recorded at low slack water in late summer.

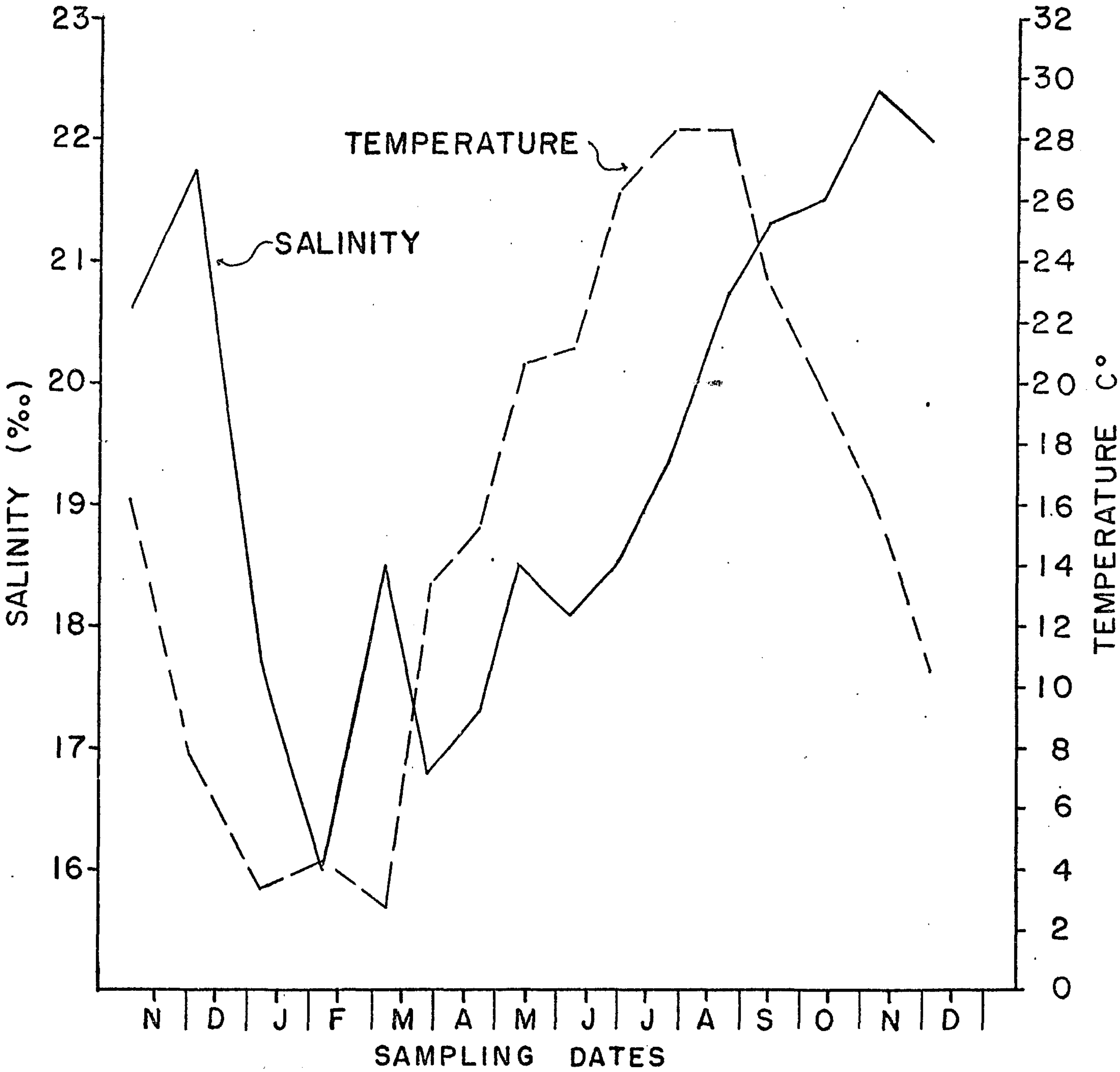


Fig. 2. Surface temperatures and salinities on sampling dates.

Surface salinities were determined in the laboratory with an induction salinometer. Values at sampling periods ranged from 16.0 to 22.4‰ (Fig. 2), salinities being generally highest in autumn and lowest in spring. Average variation in surface salinity within a tidal cycle was probably less than ± 2‰ (E. P. Ruzecki, personal communication).

Results of bottom sediment analyses for all stations, determined by fractionation (U.S. Standard Sieve Series), are shown in Fig. 3. Fine sand was the most important constituent in each case.

Mean tidal range at the Mumfort Islands, determined from Coast and Geodetic Survey tables, was approximately 0.76 m; spring tide range was about 0.91 m.

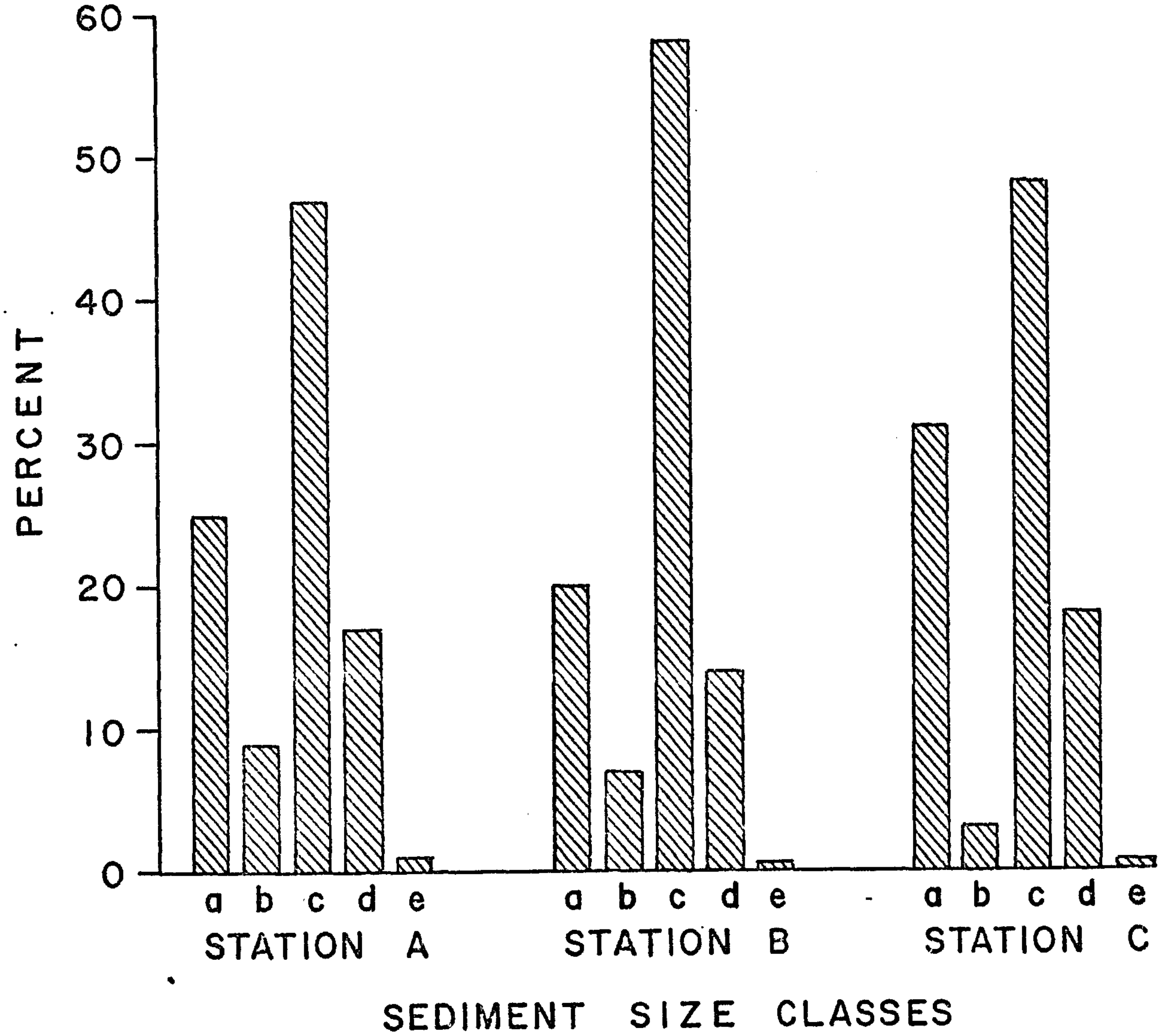


Fig. 3. Percentage composition by weight of sediment particle sizes. Wentworth size classes: (a) <0.063, silts and clay; (b) 0.125-0.063, very fine sand; (c) 0.25-0.125 mm, fine sand; (d) 0.5-0.25 mm, medium sand; (e) 1.0-0.5 mm, coarse sand.

METHODS

Field Operations

Collections consisting of one sample from each station were obtained every 21-35 days from November 1967 into December 1968. Sixteen collections were made, including at least one in every month and two each in March and June. Each sample consisted of three combined subsamples in order to ameliorate the effects of contagious distribution.

Sampling was conducted from a small boat with the aid of SCUBA, garden clippers and nine short-handled, cloth collecting bags, one for each subsample. The mouth of each collecting bag was supported by an iron ring 20 cm in diameter (Fig. 4). The bags were approximately 0.8 m deep with 0.5 mm nylon mesh netting (Nitex No. 502) sewn into the bottom.

All subsamples were obtained from within a 4-5 m radius of the station markers. Collections were made from a different quadrant on each of four successive sampling periods to minimize effects of disturbing the community.

After anchoring the boat at each station, I entered the water with the clippers, one collecting bag and a belt of lead weights sufficient to maintain stability on the bottom. Several plants were carefully gathered together about their bases, clipped off as close to the bottom as possible and eased into the bag.

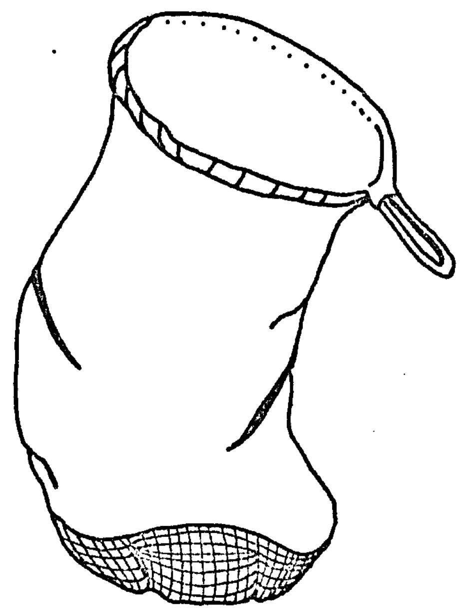


Fig. 4. Collecting bag.

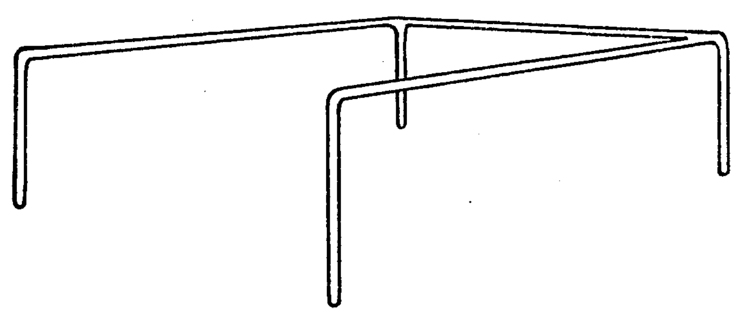


Fig. 5. $0.25m^2$ quadrat frame.

Close observation revealed little if any loss of animals from the eelgrass. A single subsample consisted of 3-8 such clippings, depending on the density of the plant cover. During winter, when the plants were sparsely distributed, a relatively large number of clippings, often consisting of only a single plant, was required to make up an adequate subsample. Between clippings, the collecting bag was rested on the bottom with the mouth effectively closed by the iron ring. When complete, the subsample was passed to an assistant in the boat. Each subsample was placed, still in its bag, into a water-filled bucket for transport to the laboratory.

From the near vicinity of each station, an additional sample was obtained for determination of Zostera biomass per unit bottom area. A 50 cm square iron frame (Fig. 5) was placed over a representative area; all plants rooted within this 0.25 m^2 quadrat were clipped at their bases, placed in a mesh bag and carried to the laboratory for drying and weighing. Quadrat samples were obtained on all but the first three collecting dates.

Whenever possible, sampling was conducted at low tide. This permitted better underwater visibility and often obviated the use of SCUBA at station A; several collecting trips were aborted due to near zero visibility in turbid water.

Regular collecting trips were supplemented by frequent visits to the sampling area for close observation with SCUBA. Macroalgae were collected primarily on these occasions.

Laboratory Procedure

In the laboratory, contents of each collecting bag were transferred to a gallon jar containing 8-10% seawater-formalin solution. Small crustaceans and other organisms adhering to the bag were removed with forceps. Animals were later washed from the eelgrass into a 0.5 mm sieve, then preserved in 7% formalin in 3-dram plastic vials according to general taxonomic groupings. Each Zostera blade was stripped of sediment, epiphytes and sessile fauna, all of which were saved. Sediment was later examined for organisms retained by a 0.5 mm screen. Cleansed plants were oven-dried at 80 C for 48 hours then weighed to the nearest 0.1 g.

All animals in each subsample were identified and counted. Macroepiphytes were identified but not treated quantitatively. For samples containing many small forms, enumeration was expedited by the use of a dissecting microscope, gridded petri dish and manual counter. The abundance of each non-colonial animal species was expressed as numbers per gram dry weight of eelgrass.

Quadrat samples for Zostera biomass determination were cleansed of sediment and organisms, oven-dried at 80 C for 48 hours, then weighed to the nearest 0.1 g.

Calculations were expedited by the use of an IBM Type 360 computer.

RESULTS

Growth Characteristics of *Zostera*

Zostera displayed a striking seasonal growth cycle. Dense beds conspicuous during summer were reduced in winter to relatively few scattered leafy shoots. Peak biomass at each station occurred in June (Fig. 6), followed by a steady decline coincident with the excision of chiefly the older plants as fall approached. Lowest biomasses among the sampling stations generally occurred at station C. Lowest biomasses at all stations occurred in late winter. With increasing water temperatures in spring, growth of shoots from the perennial underground rhizome system ensued. Flowering and fruiting occurred in April and May.

The growth pattern agrees well with that reported by Setchell (1929) who postulated several temperature-dependent periods of activity for *Z. marina* in North America. Growth and reproduction are limited to spring and summer as water temperatures rise from 10 to 20 C. Above 20 C heat rigor occurs, accompanied by death and disintegration of flowering stems and older leaves. As temperatures drop from 20 to 10 C in autumn, a period of recrudescent rigor ensues in which further disintegration is evident. Below 10 C the plants enter a period of cold quiescence.

Throughout the year, density of plants on the bottom was greatest in shallow water and decreased toward deeper water.

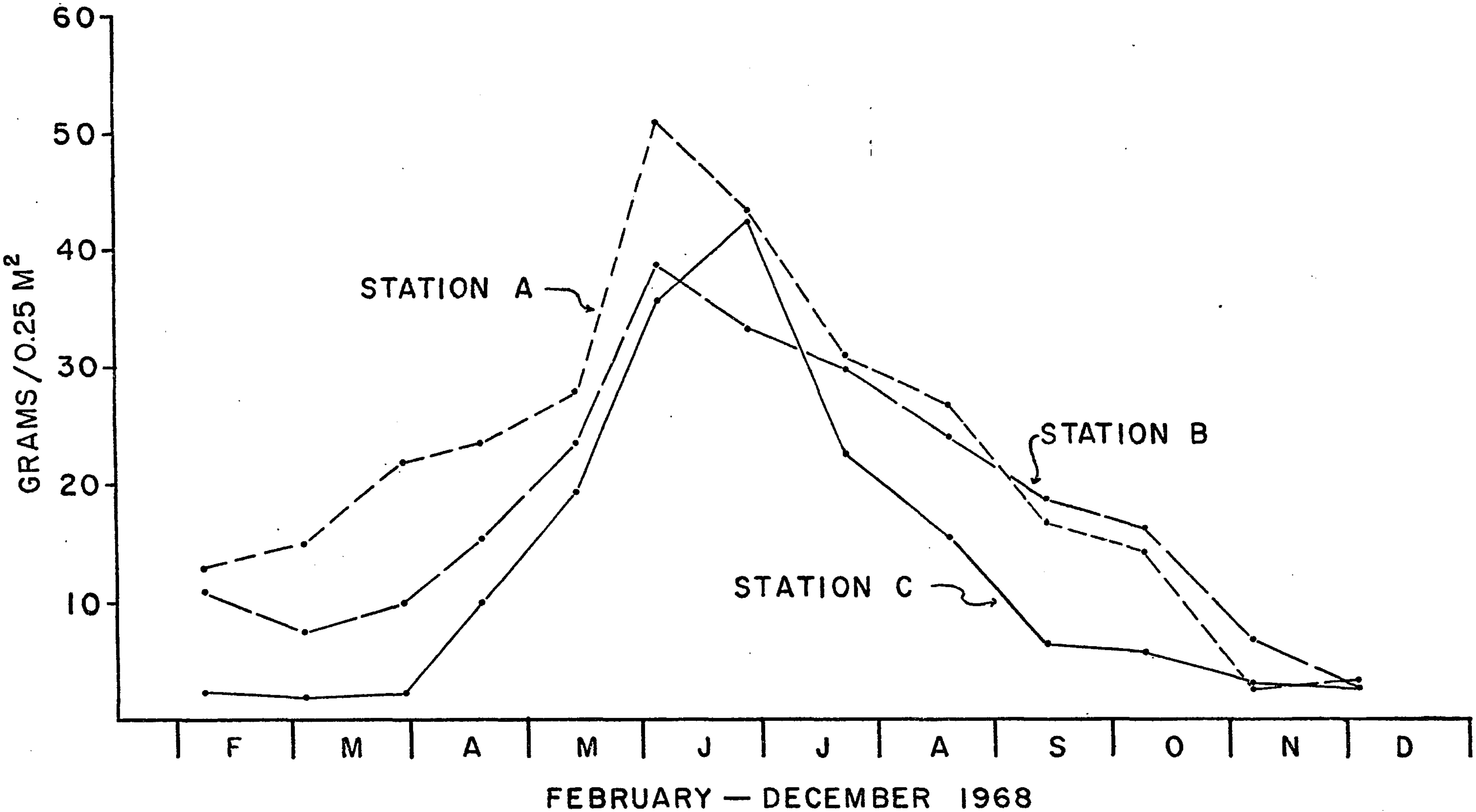


Fig. 6. Seasonal change in *Zostera* biomass.

On 28 June the number of plants per 0.25 m^2 quadrat at stations A, B and C was 195, 142 and 114, respectively; by 22 July corresponding figures had fallen to 115, 105 and 45. The proportionately greater loss at station C, reflected also in biomass data (Fig. 6), may be at least partially explained by the presence on the eelgrass at station C during this interval of relatively large amounts of silt, epiphytes and sessile organisms, primarily Molgula. The heavily laden plants assumed a generally prostrate and matted aspect. Tutin (1942) postulated that such heavy investments must significantly reduce the light reaching the photosynthetic surfaces, resulting in death of the plants. This would be especially true, presumably, if the eelgrass was growing near its lower depth limit, as at station C. In January and February at station C, Zostera was extremely sparse, averaging perhaps less than one plant per 0.25 m^2.

Elongation of plants during spring and early summer was greatest at increased depths. Figure 7 illustrates average lengths of plants at each station on four sampling dates during the summer; declines were caused by loss of older plants. Such length differences between stations were not evident during fall and winter.

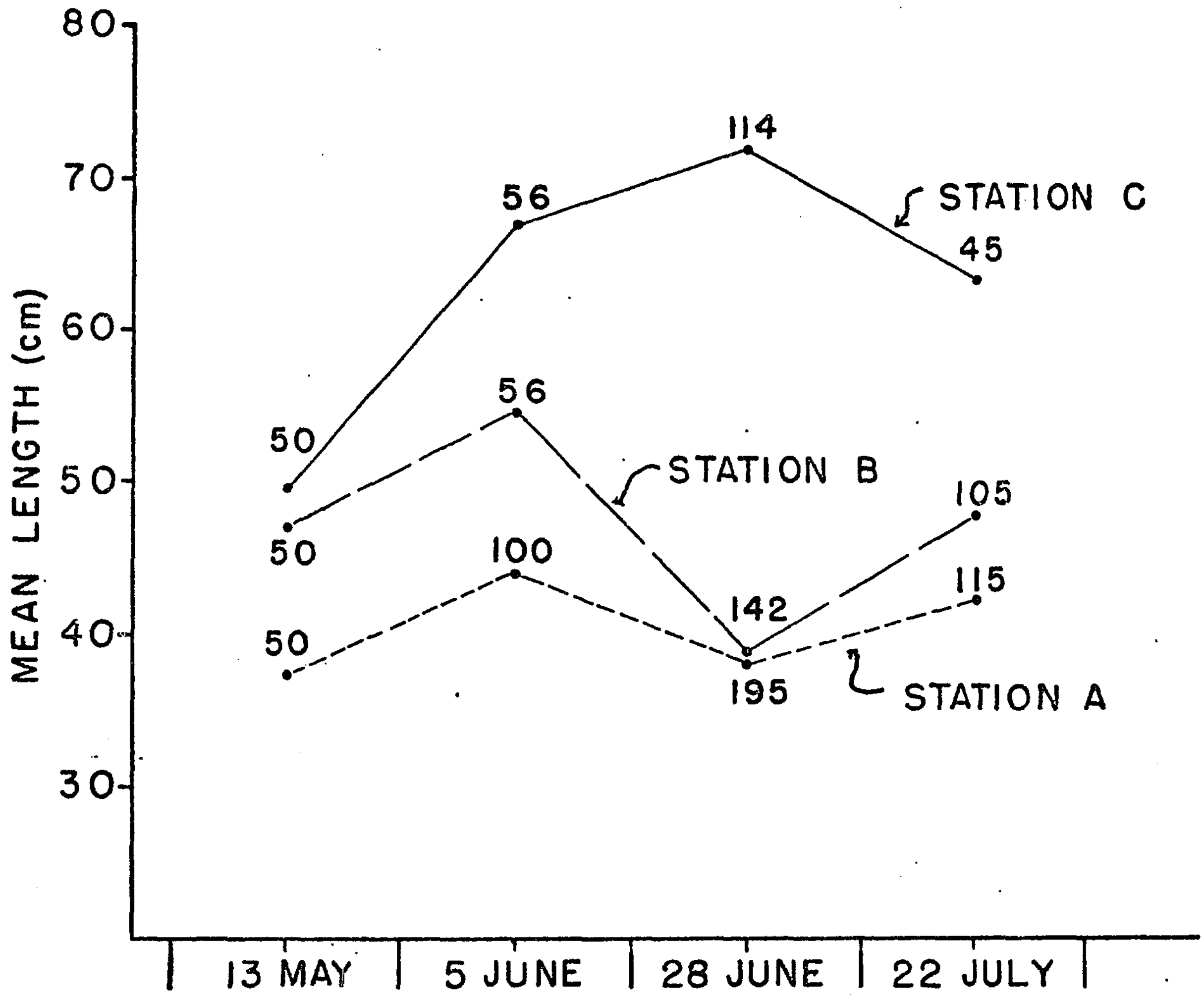


Fig. 7. Mean length of <u>Zostera</u> on four sampling dates. The number of plants on which each mean was based is indicated.

SYNOPSIS OF FAUNA

A total of 112 invertebrate species, including 167,139 non-colonial organisms, was collected from *Zostera*. Relative abundance, seasonal trends and distribution in the sample area of the more abundant forms, or others judged ecologically significant, are discussed below. Salient aspects in the biology of many species, such as breeding periodicities, life cycles and behavior, are reported, along with significant new distribution records. Collection data for each station, excluding colonial species, are recorded in Appendix Tables I-III.

Porifera

Sponges were often conspicuous members of the *Zostera* community, especially during late summer and fall. In addition to the species discussed below, *Microciona prolifera* was also common in the sampling area during summer but was always found growing on shells and other hard objects rather than the plants.

Haliclona loosanoffi was the most common sponge found on eelgrass and the only one found throughout the year. Button-sized colonies first appeared on the current year's growth of *Zostera* in late June when the sponge was considerably more abundant at stations A and B than in deeper water. Larger colonies became common throughout the sampling area in July, remaining more abundant in shallower areas. Degeneration of the normal sponge structure soon occurred, however, concomitant with the formation of yellowish hemispherical gemmules at the base of the dead and dying colonies. These resistant bodies, formed in response to adverse conditions (Wells, Wells and Gray, 1964), were first observed in late July as water temperatures exceeded 28 C. Gemmules were very abundant in late summer and fall. As temperatures decreased in September, vegetative colonies again became common, reaching maximum abundance in October and remaining common through November. During winter, H. loosanoffi persisted both as gemmules and as much reduced vegetative colonies, both stages being found primarily on old attached Zostera blades and on fragments lying on the bottom. Thus, the sponge showed a bimodal pattern in the development of normal colonies, the first peak occurring in midsummer and the second in fall, with reduced structure and gemmule formation prevailing during intervening periods.

The origin of these colonies is not clear. Although Hartman (1958) demonstrated in the laboratory that gemmules of this species may germinate directly into the normal sponge structure, Wilson (1894) reported that gemmules of some monaxonid species may give rise to ciliated larvae, similar to those produced sexually. Dispersal units of some sort were involved in the midsummer recrudescence at least, since gemmules were not previously present on young plant blades.

The life cycle of H. loosanoffi reported here is generally similar to that described by Wells et al. (1964) for this species in Hatteras Harbor, N.C., but different in many respects from that reported by Hartman (1958) for the sponge in Milford

Harbor, Conn. At Milford Harbor, over-wintering occurred only in the gemmule stage, and there was only one growth period during the year. Setting began in late summer or fall, reaching a maximum in October. Degeneration began in late October or November. Such variations in the life cycle and phenology of this species appear to be controlled primarily by water temperatures (Wells et al., 1964).

This sponge has been reported from Woods Hole, Mass. (Smith, 1964) to Beaufort, N.C., (Wells, Wells and Gray, 1960) on submerged pilings and shells. It has not been previously recorded from Chesapeake Bay.

Halichondria bowerbanki, first observed in mid-June, became increasingly common through the summer and reached maximum abundance in October and November. It was initially found only on broken *Zostera* fragments on the substratum but later invested basal portions of living plants, primarily in shallower portions of the sample area. This species decreased in abundance during December and was not present in the coldest winter months.

Halichondria bowerbanki ranges from North Carolina northward beyond Cape Cod (Wells et al., 1960). It is a common form year-round on pilings at Gloucester Point.

Mycale sp., a new record for Chesapeake Bay, was first detected in late July. It was common throughout the sample area from August until mid-December, occurring both as small patches on the *Zostera* blades and as more massive growths investing the base of the plants.

This sponge appeared similar in spiculation and texture to *M. cecilia* reported from hard substrates at Hatteras Harbor, N.C. (Wells et al., 1960, 1964). However, all specimens were distinctly bluish or lavender in color whereas those from North Carolina were a pale yellowish green or yellowish tan. Although de Laubenfels (1950) suggested that the color of this species may change with age, some question remains as to the specific designation of my specimens from the York River (Dr. H. W. Wells, personal communication).

Prosuberites microsclerus was found throughout the sample area from mid-May until mid-November. It occurred only as thin encrustations on the shells of *Urosalpinx*, to which it imparted a bright yellowish-orange color.

This species is apparently distributed along much of the United States east coast, although it has never been reported from Chesapeake Bay. Wells et al. (1964) found *P. microsclerus* encrusting *Urosalpinx*, as well as other hard substrates and algae, at Hatteras, N.C. Gemmules are reportedly formed in November and December although none were observed in this study, possibly because drills were rarely collected after early November until April.

Hydrozoa

Two hydroid species were common in the sampling area. A third, *Halocordyle tiarella*, was collected only once, though it was frequent on *Zostera* in front of the Virginia Institute of Marine Science (VIMS) at Gloucester Point.

Dynamena cornicina was found from early June through November. The stoloniferous growths heavily invested scattered *Zostera* blades throughout the study area. Calder (1968) found *D. cornicina* abundant in lower Chesapeake Bay on various substrates, particularly eelgrass. This hydroid ranges southward from Massachusetts along the east coast (Calder, 1968).

Hydractinia arge was common at all stations from April until July, with occasional colonies found as late as November. The hydroid occurred both on eelgrass and on shells of the gastropod *Bittium*, with the latter being the usual substrate. Colonies were present on approximately 15% of the year-old *Bittium* collected in May. The dying out of most of these adult snails during the summer may account for the relative scarcity of *H. arge* after June, since none of the *Bittium* in their first summer carried this hydroid.

Hydractinia arge has previously been reported from *Zostera* in Chesapeake Bay by Clarke (1882) and by Calder (1968), who also found it on *Enteromorpha* and *Bittium*. With the exception of a possible record from Woods Hole, Mass., this hydroid is known only from Chesapeake Bay (Calder, 1968).

Anthozoa

Aiptasiomorpha luciae, the only anemone commonly collected, was especially abundant during late summer and fall when several individuals often occurred on the same plant blade. This species was considerably more common at the shallower stations than at station C, with station B showing the greatest abundance (Fig. 8).

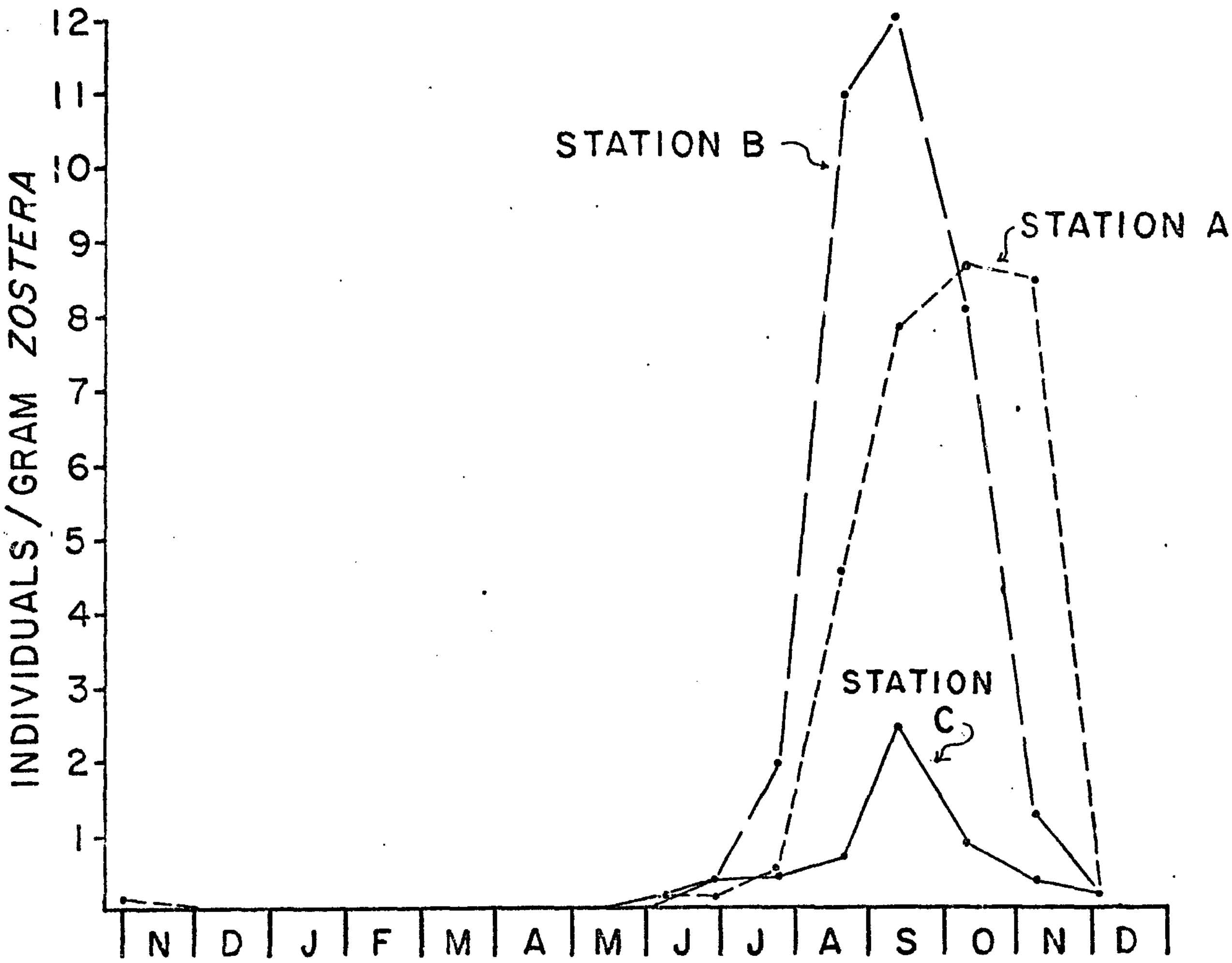


Fig. 8. Seasonal abundance of Aiptasiomorpha luciae, November 1967-December 1968.

Individuals were occasionally found attached to shells of Bittium. Two distinct color phases were evident: one had a dark green column with orange or yellow vertical stripes and no markings on the tentacles; the other had a lighter green column, no vertical stripes and tentacles marked with white blotches. Only occasional intergrades were noted.

This species, thought to be of Japanese origin, is widespread on both coasts of North America and is often found in brackish waters (Smith, 1964). It is common on shells and pilings in the Gloucester Point area.

The only other anemone encountered, Diadumene leucolena, was collected only once in a sample, although several other individuals were observed during the summer, either on Zostera or, on one occasion, on the shell of the gastropod Urosalpinx.

Turbellaria

Euplana gracilis and Stylochus ellipticus were by far the most abundant flatworms encountered. Ten individuals not belonging to these taxa remain unidentified either because of their very small size or because of damage incurred in preservation.

Euplana gracilis was present in widely varying numbers in nearly all samples from late March into December, reaching a peak abundance of 13.5 individuals/g dry wt of Zostera at station A in July. No specimens were collected in January, February and early March.

Little is known of the ecology of E. gracilis. It has been found at Woods Hole, Mass., on pilings among hydroids and sponges (Hyman, 1939) and in lower Chesapeake Bay within algal masses (Ferguson and Jones, 1949).

Stylochus ellipticus, a large green polyclad, had two peaks in abundance, occurring in November and December 1967 and in November and December 1968. The former peak was considerably more pronounced, with maximum densities reaching 10.1 individuals/g of *Zostera* at station C in November compared to maximum densities of 1.4 individuals/g at station C in November 1968. *Stylochus* was not collected from February through May but was moderately common through the summer.

This species is a well-known predator on oyster spat along the east coast and in the Gulf of Mexico (Provenzano, 1961). In oyster beds of upper Chesapeake Bay it is the dominant polyclad species (Webster and Medford, 1961). Apparently, *S. ellipticus* may also prey on organisms other than oysters. Although direct evidence is lacking, it has been strongly implicated in heavy barnacle mortalities in the Patuxent River, Md. (Cory, 1967) and at Beaufort, N.C. (MacDougall, 1943). It has also been collected from eelgrass at Prince Edward Island (Pearse and Walker, 1939) where both barnacles and, presumably, oysters were few. Although some barnacles were present during periods of *Stylochus* abundance at Mumfort Island, they were greatly outnumbered by the flatworms and it is probable that the latter were utilizing other (additional?) food sources.

Nemertea

Nemerteans were generally common on *Zostera*, especially during the warmer months. Seven species were collected, though all but a few individuals belonged to the three species discussed below.

Zygonemertes virescens was one of the two most common nemerteans found, being collected from April into December. No consistent station preference was evident, although peak abundances of 1.2 and 1.1 individuals/g of Zostera in early June and July, respectively, both occurred at station C. This was the most abundant nemertean collected from late July into November. To illustrate seasonal abundance of this and the following species (Fig. 9), all samples from each collecting period have been combined to give a single curve for each species.

Zygonemertes virescens is widespread on both coasts of the United States. It is reportedly common among algae and other growths on rocks and pilings in New England (Coe, 1943) and has been collected abundantly on eelgrass in lower Chesapeake Bay (McCaul, 1963).

Tetrastemma elegans, the other common species, was found throughout the year except in February and was generally most abundant at station C. Peak densities occurred during spring and early summer (Fig. 9).

This species is reportedly the most common nemertean at Gloucester Point where it occurs principally on eelgrass (McCaul, 1963). On the New England coast it has been collected from bryozoans, algae and other growths, as well as from Zostera (Coe, 1943).

Amphiporus ochraceus was encountered in low numbers from April through July. It was most abundant in June when it was found

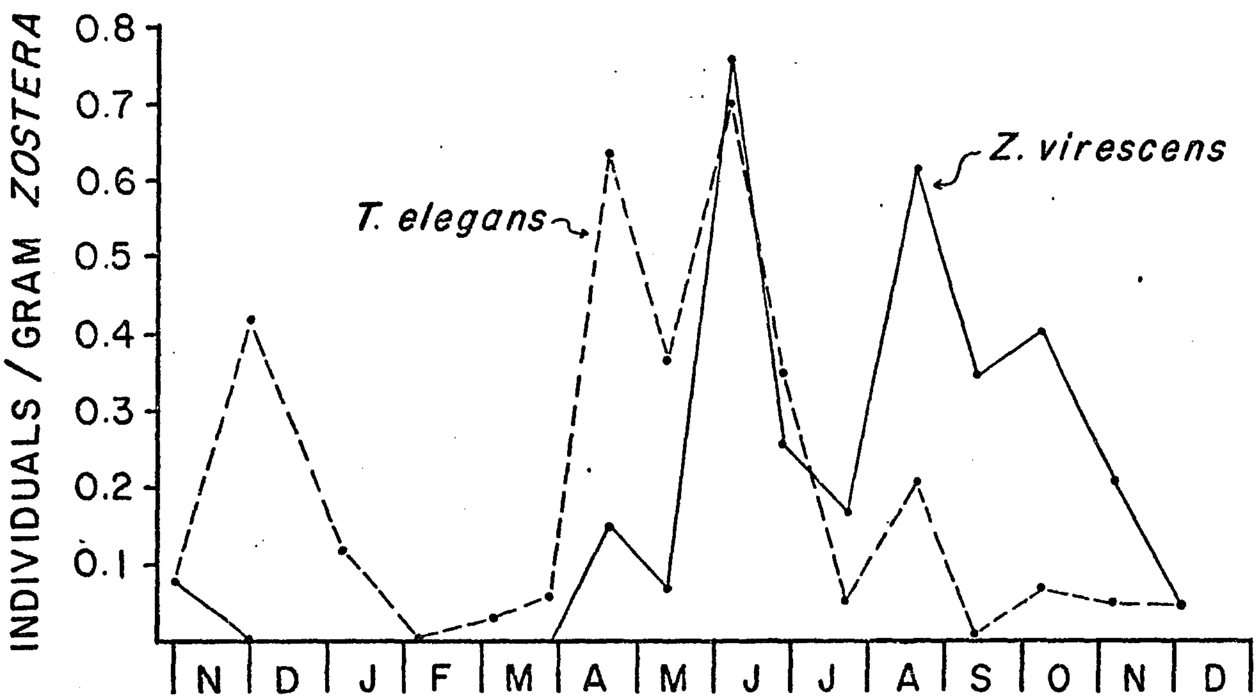


Fig. 9. Seasonal abundance of Tetrastemma elegans and Zygonemertes virescens, November 1967-December 1968. All samples pooled for each collecting period.

in both collections at every station. Maximum densities never exceeded 0.1 individuals/g dry wt of *Zostera*.

Bryozoa

Electra crustulenta, the most common bryozoan encountered, was found at all stations throughout the summer and fall. It was conspicuously more abundant in deeper portions of the sampling area. No colonies were found from January until April. The encrusting colonies occurred principally on *Zostera* blades, although the gastropods *Crepidula* and occasionally *Urosalpinx* also served as substrates.

The probable range of this estuarine species on the Atlantic coast is from Woods Hole, Mass., to Beaufort, N.C. (Maturo, 1957). Osburn (1944) reported *E. crustulenta* to be the most abundant bryozoan in Chesapeake Bay where it competed with oysters by covering surfaces on which spat could settle.

Bowerbankia gracilis occurred primarily during spring and early summer when the stoloniferous zoaria were most often found investing shells of *Crepidula convexa*. The gastropods were often completely hidden beneath a dome of close-packed tubular zoecia. Approximately 1.1% of the 969 *Crepidula* collected in May carried this bryozoan. Colonies were occasionally found on *Zostera*.

B. gracilis is widely distributed along both coasts of North America (Maturo, 1957). It is common in lower Chesapeake Bay where it can withstand salinities down to 10‰ (Osburn, 1944).

Membranipora tenuis, the only other bryozoan encountered, was found on several occasions encrusting *Zostera* at station C. This species is common in Chesapeake Bay on a wide variety of substrates and may compete with oyster spat in the same way as *E. crustulenta* (Osburn, 1944).

Polychaeta

Polychaetous annelids constituted a conspicuous and diverse component of the eelgrass epifauna. A total of 18 species was collected.

Nereis succinea was found throughout the year, but was most common from June into October (Fig. 10). During this period the worms were consistently most numerous at station C. Two sharp peaks in abundance at station C, in late June and in October, corresponded with the presence of many small individuals (<18 setigers). Smaller peaks at stations A and B, where immature forms were fewer, occurred in July and October. Adult worms occupied transparent membranous tubes attached to the surface of the *Zostera* blades, frequently in the leaf axils. The tubes were straight rather than U-shaped as reported by Pettibone (1963) for individuals living in the bottom sediments.

This euryhaline species is an extremely common estuarine form along the Atlantic coast of North America and in the Gulf of Mexico where it occupies a great variety of intertidal and subtidal habitats (Pettibone, 1963). Wass (1965) reported *N. succinea* to be probably the most widely distributed polychaete in the Chesapeake system.

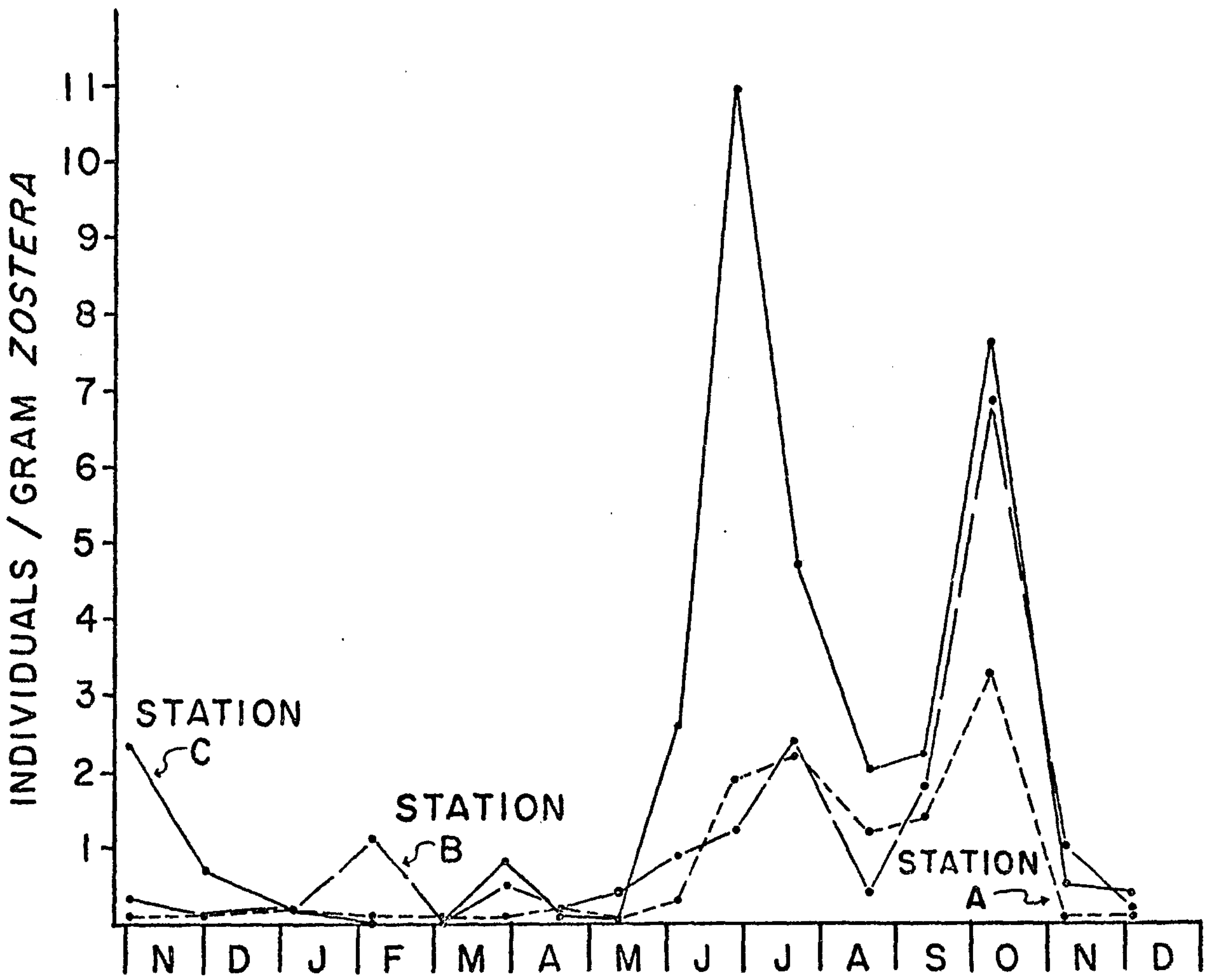


Fig. 10. Seasonal abundance of Nereis succinea, November 1967-December 1968.

Platynereis dumerilii was another common nereid found throughout the year. Overall peak abundance occurred in October when densities decreased with greater depth (Fig. 11). At stations A and B this species was very sparse from November 1967 through June 1968; numbers increased during the summer, reaching a peak in October. At station C the worms had a more sporadic occurrence, with peaks of abundance occurring in November 1967, late March and October. Young individuals (<18 setigers) were present in samples from late June through October. Several of the highly modified male and female heteronereids were collected from late June into September. Like N. succinea, these worms construct transparent membranous tubes on the surface of Zostera.

Platynereis dumerilii is a cosmopolitan species with a wide distribution in warm seas (Pettibone, 1963). Along the United States Atlantic coast south of Cape Cod it is frequently associated with attached algal masses and drifting Sargassum. It is also common on rocks and pilings among clumps of sponges, tunicates and hydroids. Ledoyer (1964a, 1966a, b) found P. dumerilii to be characteristic of Zostera and other marine phanerogam communities in the Mediterranean and the English Channel. Heteronereids have been found at Woods Hole swarming on the surface from June into September (Verrill, 1882) and at Beaufort, N.C., in June and July (Hartman, 1945).

Sabella microphthalma was collected in every sampling period except early March. This species was uncommon, however, until late June when small individuals began to appear. Peak frequencies occurred in August and September (Fig. 12) when the

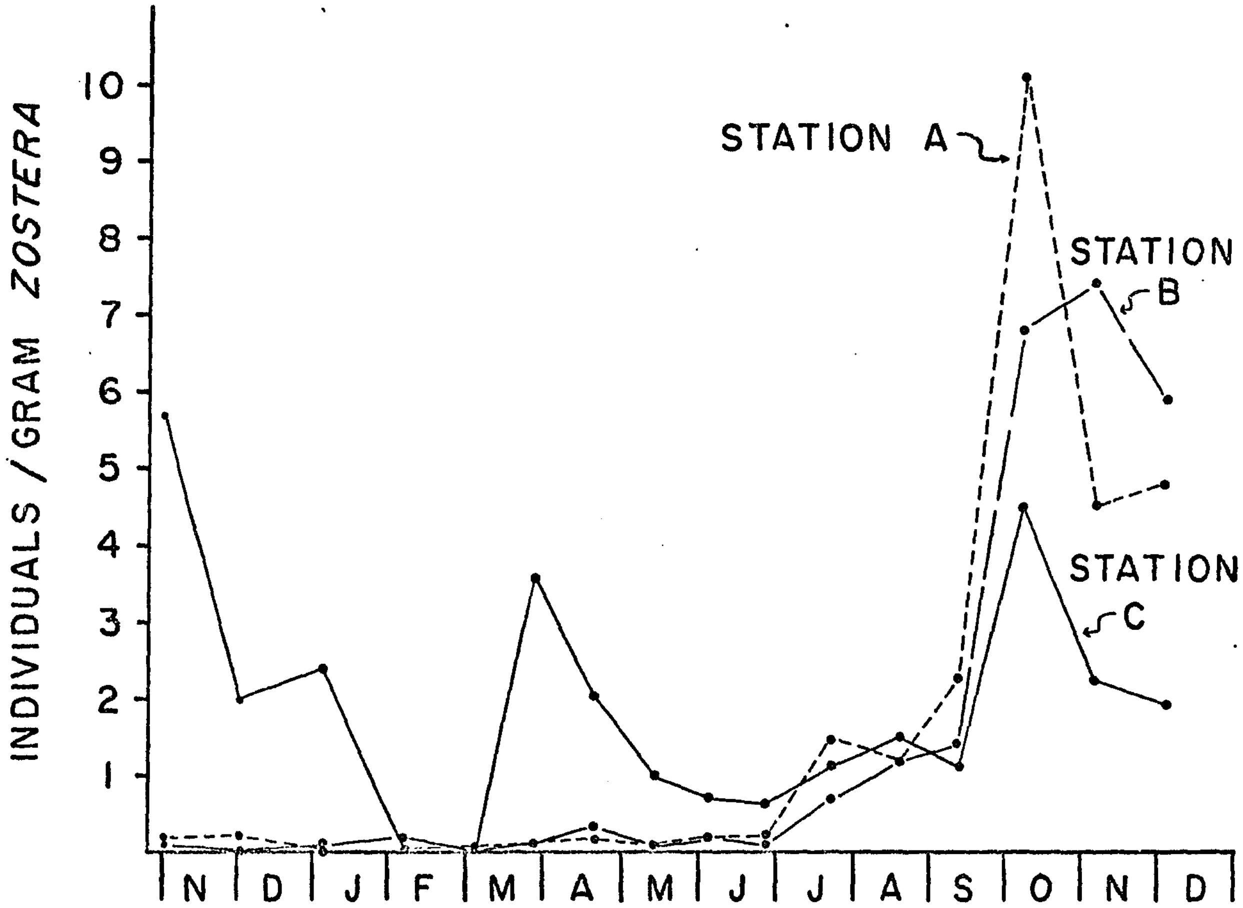


Fig. 11. Seasonal abundance of Platynereis dumerilii, November 1967-December 1968.

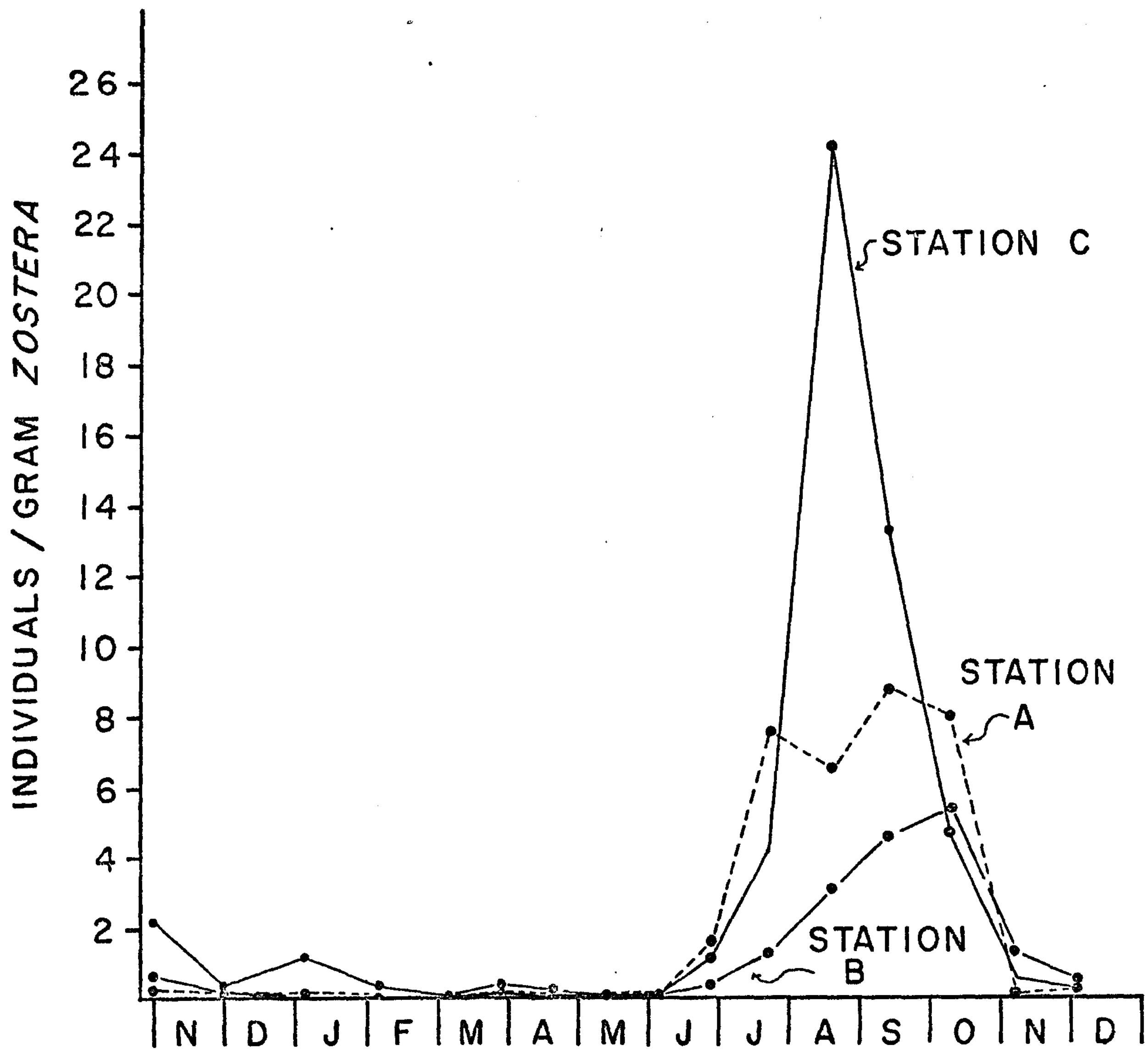


Fig. 12. Seasonal abundance of <u>Sabella</u> <u>microphthalma</u>, November 1967-December 1968.

worms were most abundant at station C and least abundant at station B. Sand grain-encrusted mucous tubes, often invested with sponge tissue, were constructed on all portions of the *Zostera* as well as in the bottom. Showy branchial crowns of these sabellids were often seen extending from the tubes during feeding. In late summer, the worms were frequently clustered, with more than one individual inhabiting the same tube.

This species is common subtidally and intertidally from New England southward into the Gulf of Mexico (Hartman, 1951). It is reportedly the most abundant sabellid in intertidal zones at Beaufort, N.C., occurring "almost anywhere a surface of attachment is present" (Hartman, 1945). In lower Chesapeake Bay it is particularly common in eelgrass beds (Wass, 1965).

Polydora ligni showed a sharp peak in abundance at each station in spring and a much smaller one in fall with numbers increasing with depth on each occasion (Fig. 13). The spring peak at stations A and B occurred in April, while at station C even greater numbers were found in May when the worms were very scarce at the shallower stations. *Polydora* occurred usually in dense colonies, the sediment tubes forming muddy patches on *Zostera* blades. The worms feed by filtering small particles from the water with their elongate tentacular palps which were usually extended from the mouth of the tubes.

This species is abundant subtidally and intertidally along both coasts of the United States where it occurs in the bottom and on the surface of various substrates (Hartman, 1945). Calder (1966) found *P. ligni* to be the most abundant polychaete

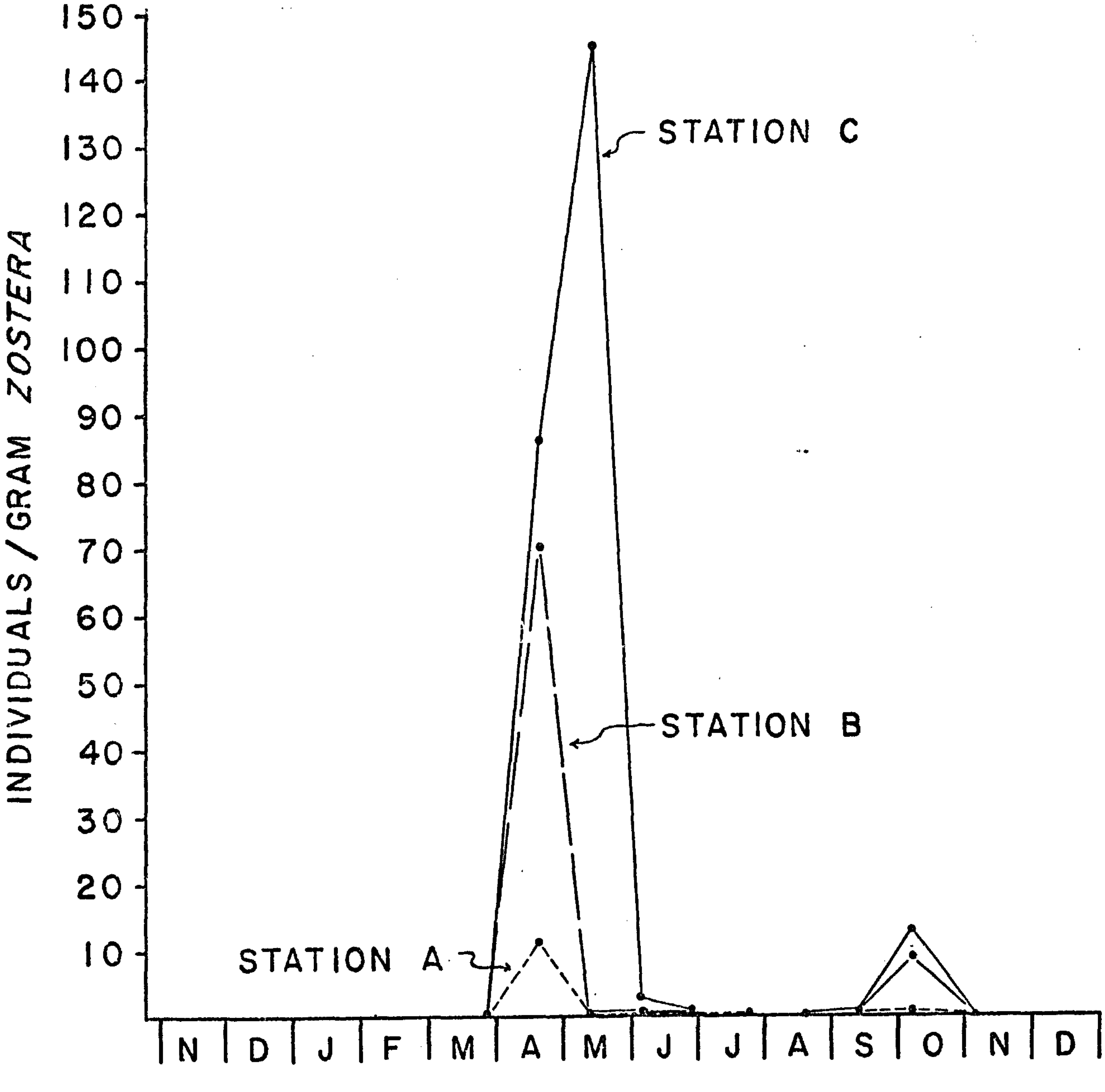


Fig. 13. Seasonal abundance of Polydora ligni, November 1967-December 1968.

throughout the year on test panels at Hampton Roads, Va. It may, in fact, be the most abundant polychaete in Chesapeake Bay (Wass, 1965).

Brania clavata was sporadically abundant at all stations from early spring through fall. Sediment tubes of this tiny syllid (length up to 4 mm) occurred on *Zostera* blades as well as on associated sponges and algae. Females brooding eggs and larvae on their dorsal surfaces were found from early June through September.

This transatlantic species is found along the United States east coast northward from Virginia where it occurs both in the bottom and on the surface of various substrates, including algae, sponges and tunicates (Pettibone, 1963). Ovigerous females have been found in the Woods Hole region from June to September and in Chincoteague Bay, Va., in May.

Hydroides hexagona was collected from mid-summer through fall with peak abundances occurring from August into October. No consistent station preference was evident: highest frequencies at station C occurred from July into September, but at station A in October. White calcareous tubes of this serpulid were most often found on *Zostera* blades but were frequently attached to shells of *Urosalpinx*; as many as six intertwining tubes were found on one shell.

This species ranges along the United States east coast southward from New England where it occurs primarily on hard substrates (Hartman, 1945). Calder (1966) reported *H. hexagona* as an important member of the fouling community at Hampton Roads, Va., in mid-summer.

Podarke obscura was collected in November 1967 and from April into December 1968 with greatest densities occurring in late summer and fall (Fig. 14). The worm showed a general increase in abundance with greater depth; highest frequencies occurred at station C in August.

This hesionid is often associated with algae and marine phanerogams from Cape Cod southward into the Gulf of Mexico (Hartman, 1945, 1951; Pettibone, 1963; Wells and Gray, 1964). It also shows commensalistic tendencies with various echinoderms and terebellid worms.

Other common but less abundant polychaete species, found primarily during late summer and fall, included *Nereiphylla fragilis*, *Exogone dispar*, *Pista palmata*, *Odontosyllis fulgurans* and *Lepidonotus variabilis*. The last two species have not been recorded from Chesapeake Bay since their original discovery there by Webster in 1879.

Prosobranchia

Bittium varium was by far the most abundant of the 10 prosobranch species encountered; it was also one of the most conspicuous elements in the eelgrass community. Individuals were found in every sample throughout the year but were most numerous during summer and fall (Fig. 15). In 14 of the 16 collecting periods highest frequencies occurred at station C where over 200 snails/g of *Zostera* were found in October. From June into October, *B. varium* was least abundant at station A.

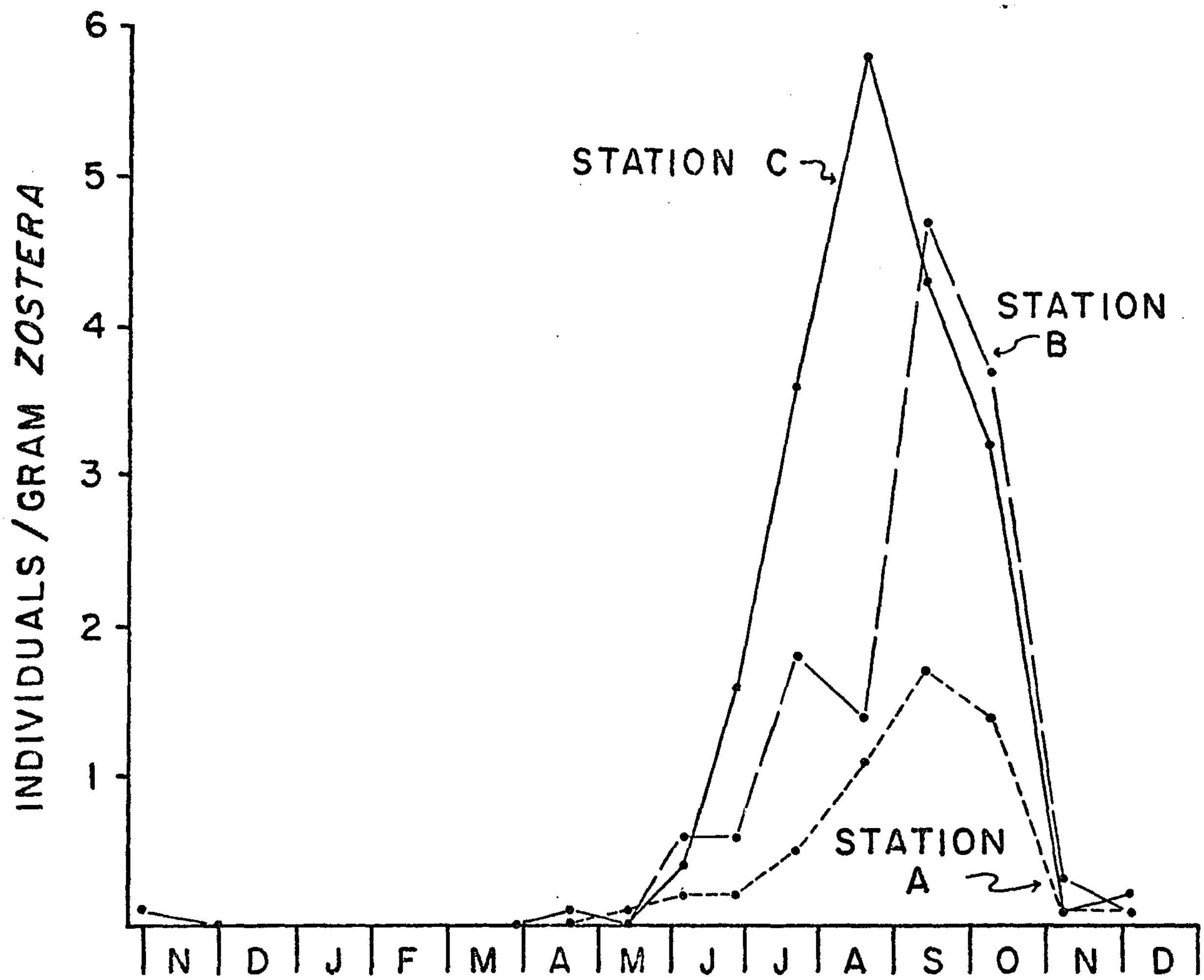


Fig. 14. Seasonal abundance of Podarke obscura, November 1967-December 1968.

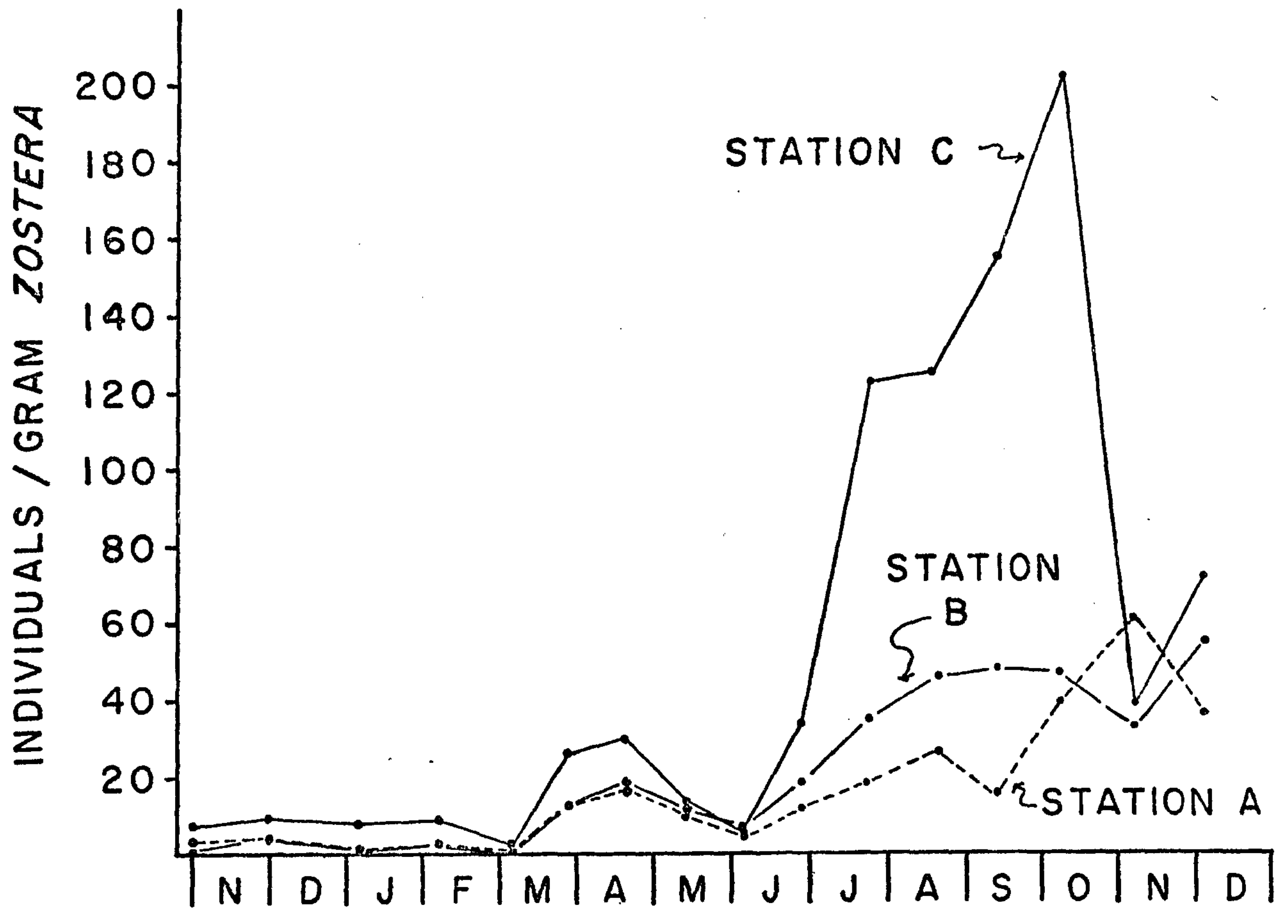


Fig. 15. Seasonal abundance of Bittium varium, November 1967-December 1968.

The life cycle of this species apparently encompasses about 1.5 years. Spiral, gelatinous egg masses were found on *Zostera* blades in May and June, often in numbers of 5-7 masses per plant. The new year-class first appeared in samples from late June and constituted an increasing proportion of the population through summer and fall (Fig. 16). Young snails were distinguishable not only by size but by the absence of such investing organisms as the hydroid *Hydractinia* and the crustose alga *Fosliella*. During winter, when relatively few *Zostera* plants were present, most *Bittium* occurred within the bottom sediments.

This detrital-feeding snail is common from Maryland to Florida and in the Gulf of Mexico (Abbott, Sandstrom and Zim, 1968). In the northern part of its range it is particularly abundant on *Zostera*; on the Texas coast *Thalassia* replaces eelgrass as its principal habitat (Nagle, 1968). A closely related species, *Bittium alternatum*, is associated with eelgrass at Woods Hole, Mass. (Nagle, 1968).

Crepidula convexa was second in abundance only to *B. varium* among the prosobranchs. This species was found throughout the year at all stations but was generally more abundant at stations A and B than at station C (Fig. 17). Peak frequencies at these shallower stations occurred in August when the population consisted primarily of individuals spawned earlier in the summer. Females were found brooding eggs from May into September. Each transparent egg capsule, usually containing 4-8 eggs or larvae, was attached by a slender stalk to the *Zostera* blade. As many as 10-15 capsules were attached to

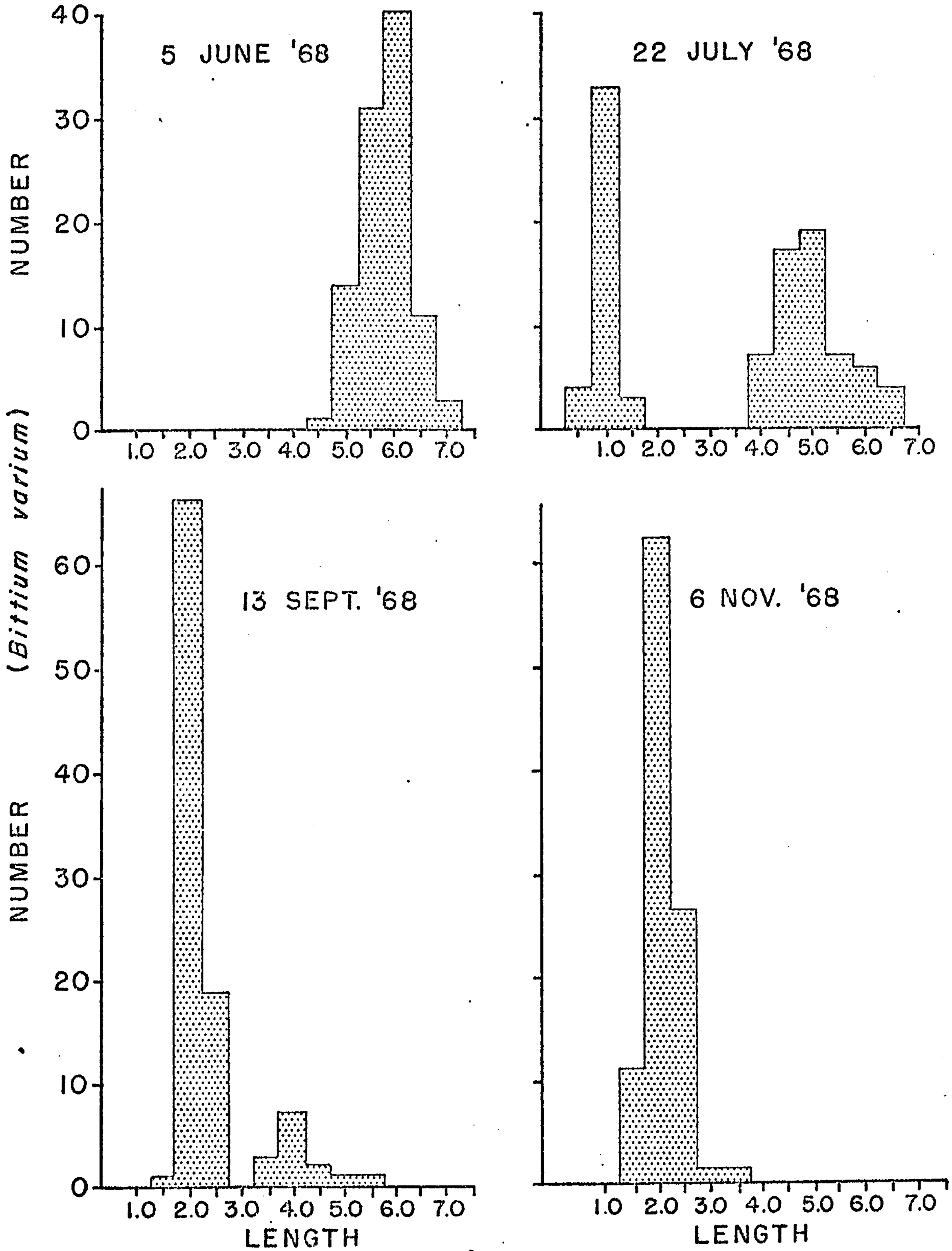


Fig. 16. Length x frequency histograms of 100 Bittium varium selected randomly from station C on each of four sampling dates.

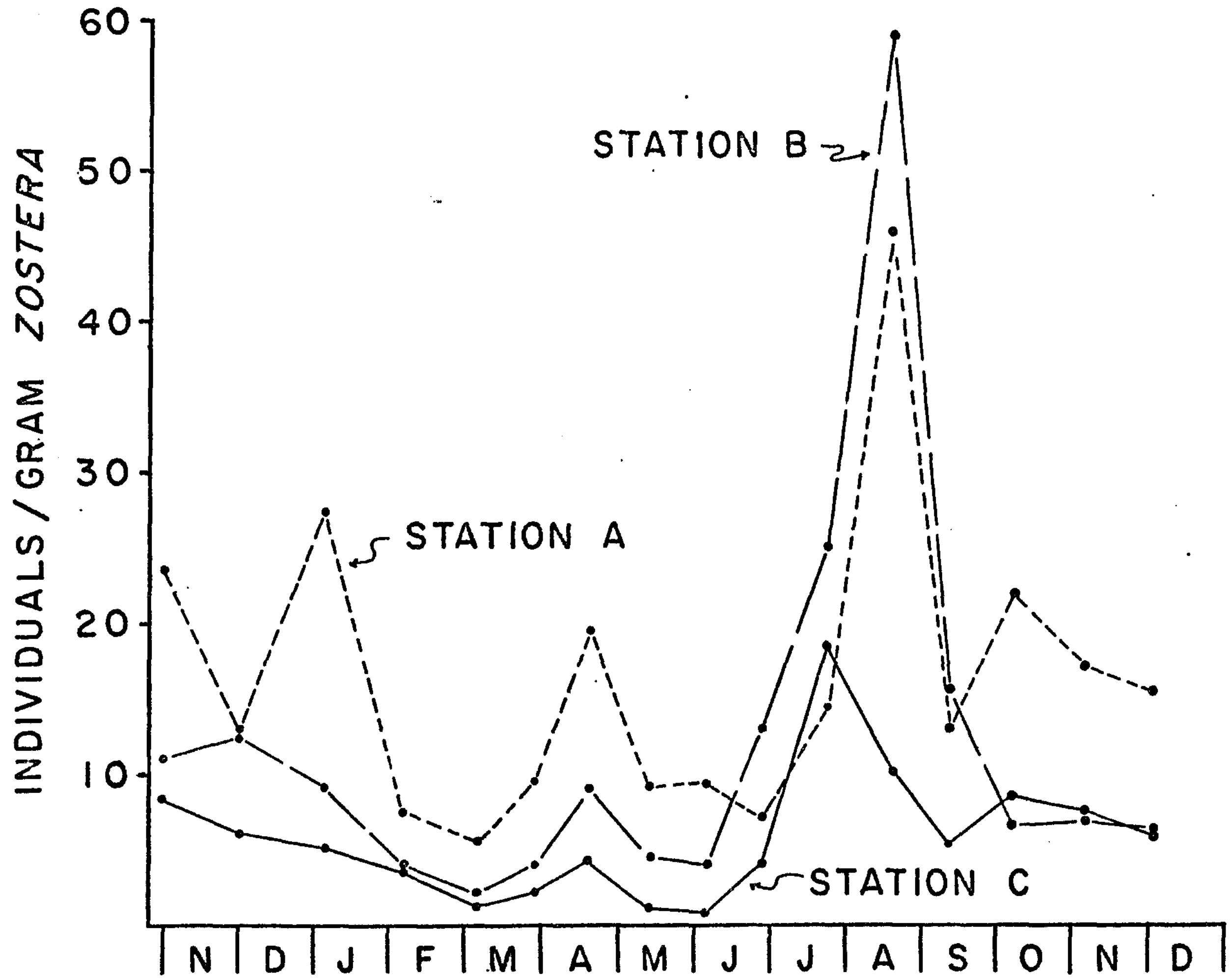


Fig. 17. Seasonal abundance of Crepidula convexa, November 1967-December 1968.

a central point and enclosed within the mantle cavity of a female. *Crepidula* were frequently found piled atop one another during the summer, usually in stacks of two, but as many as five, individuals. The snails served as substrates for many organisms, including *Bowerbankia gracilis*, *Electra crustulenta* and *Polydora ligni*, as well as several species of algae.

This species is distributed from Massachusetts to Florida and in the Gulf of Mexico (Abbott, 1954). In Chesapeake Bay it is common on *Zostera* and hard substrates (Andrews, 1956).

Urosalpinx cinerea was abundant on *Zostera* during late summer and fall but virtually absent from January through March (Fig. 18); only one individual was collected during this latter period. Snails appeared on the plants again in April and reached peak frequencies at all stations in August. *Urosalpinx* was considerably more abundant at stations B and C than at station A from July into October. Egg capsules were found on *Zostera* in May, June and July; young individuals first appeared in samples from late June.

Seasonal behavior of New England drill populations has been studied by Carriker (1954) who reported that the snails moved downward into the substratum with the onset of winter then upward again into subtidal and intertidal feeding areas as water temperatures increased in spring. Analagous vertical movements evidently occur in York River *Zostera* beds; grab samples taken in early March 1969, when the plants were very sparse, revealed numerous drills in the bottom sediments.

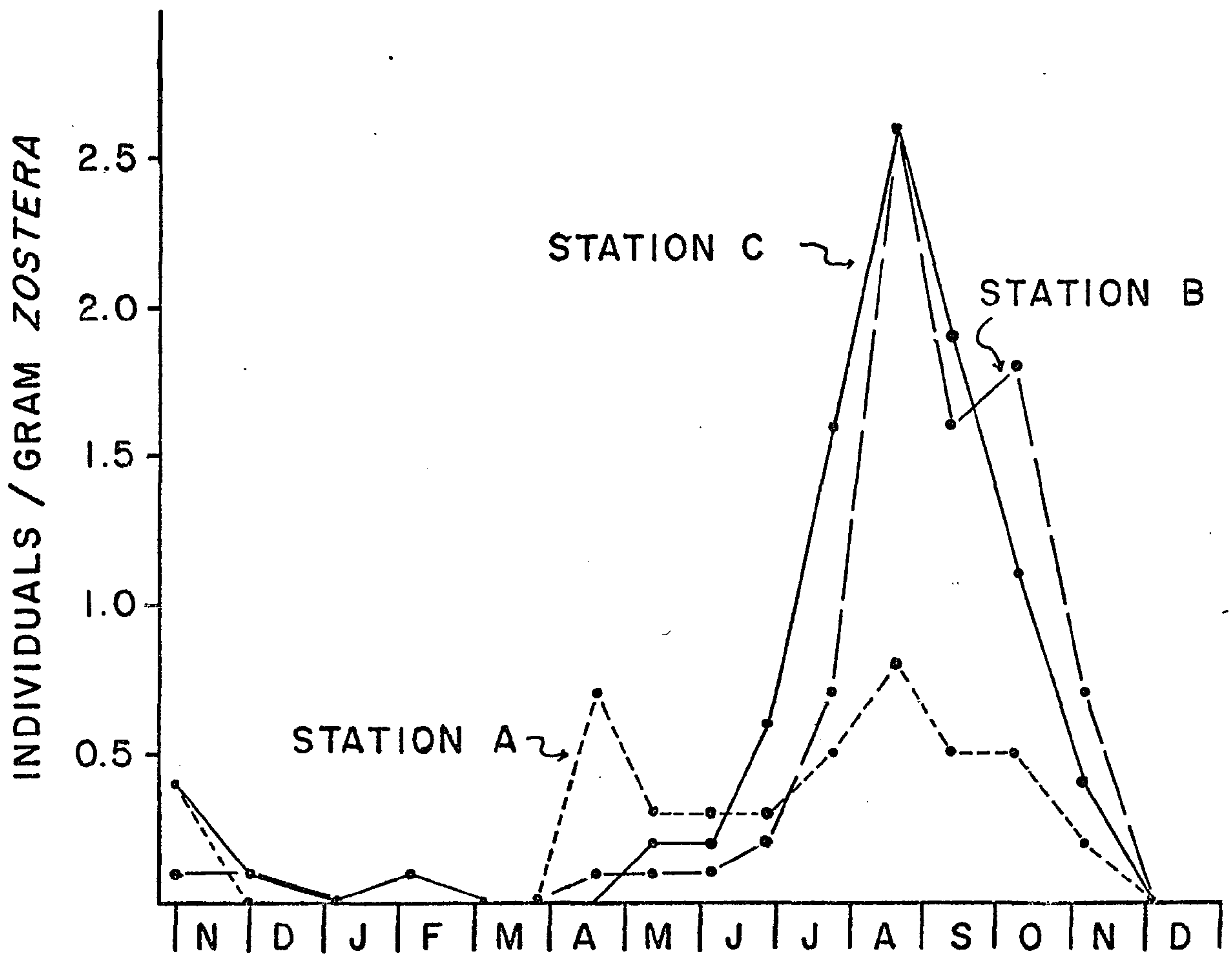


Fig. 18. Seasonal abundance of Urosalpinx cinerea, November 1967-December 1968.

This predator ranges along the Atlantic coast from Canada to northern Florida where it feeds on barnacles, slipper limpets, small crabs and encrusting bryozoans as well as on oysters and other bivalves (Carriker, 1955). Scattered introduced populations also occur on the west coast.

Mitrella lunata was found at all stations throughout the year, but was considerably more abundant at station C than at the shallower stations (Fig. 19). Peak frequencies occurred in December 1969.

This species is common in shallow weedy bays from Massachusetts to Texas (Abbott et al., 1968). In Chesapeake Bay it is abundant in *Zostera* beds but scarce in other habitats (Wass, 1965).

Triphora nigrocincta was fairly common at all stations in late summer and fall. No individuals were collected from January until late June. Peak abundance at each station occurred in October with the appearance of young snails.

This species occurs along the United States east coast south of Massachusetts where it is often found on seaweeds at the low-tide line (Abbott, 1954).

Two other prosobranch species, *Nassarius obsoletus* and *N. vibex*, utilized eelgrass primarily as a substrate for their egg capsules. Both species were common in the area but occurred primarily on the bottom. The spinose, polygonal capsules of *N. obsoletus* were abundant in April and May in the vicinity

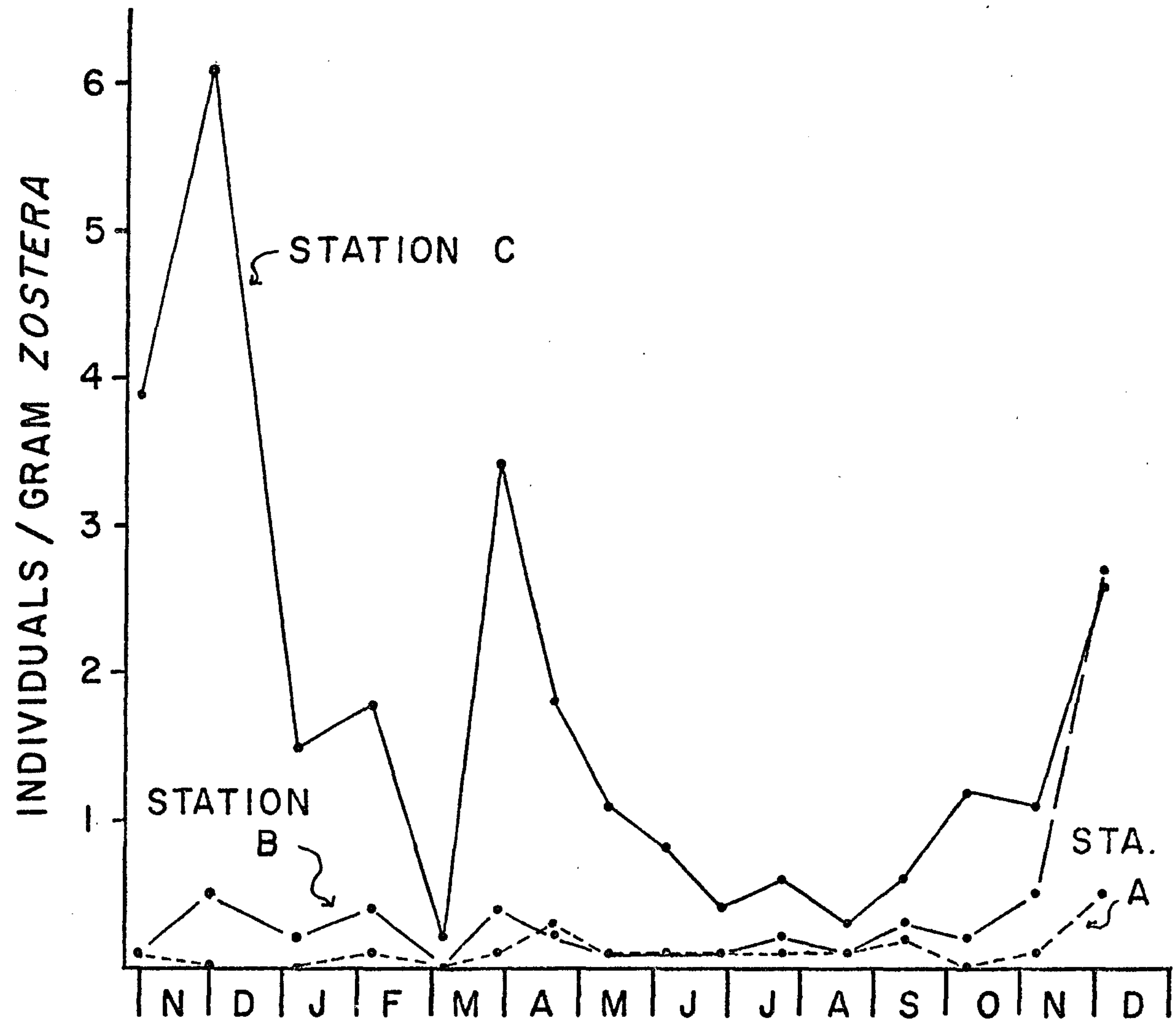


Fig. 19. Seasonal abundance of Mitrella lunata, November 1967-December 1968.

of station A and at shallower depths. Capsules of N. vibex, deposited in straight rows along the Zostera blades, were found throughout the summer at all stations.

Opisthobranchia

Thirteen species of opisthobranch gastropods were encountered, including five tectibranchs, three sacoglossans, two dorid nudibranchs, and three eolid nudibranchs. Six of these species were new records for Chesapeake Bay: Stiliger fuscata, Doris verrucosa, Tenellia fuscata, Polycerella conyma, Cratena pilata (?) and Hermaea cruciata (?). Only one specimen of each of the last two species was collected, and, because of their badly contracted conditions, their identification is uncertain. Hermaea cruciata has not been previously recorded since its original discovery in 1863 by Alexander Agassiz in Massachusetts (Dr. D. R. Franz, personal communication).

Odostomia impressa was the most common of four pyramidellids encountered. Frequencies at all stations were relatively low from November 1967 through June 1968 but showed a pronounced increase from July through October, when the abundance of these animals was greatest at station C and lowest at station A (Fig. 20).

This small predator (ectoparasite?) is common in shallow bays from Massachusetts to the Gulf of Mexico (Abbott et al., 1968). Allen (1958) reported O. impressa to be the most common pyramidellid in the Maryland waters of Chesapeake Bay where it feeds on Bittium, Crepidula, Urosalpinx and Molgula, among other invertebrates.

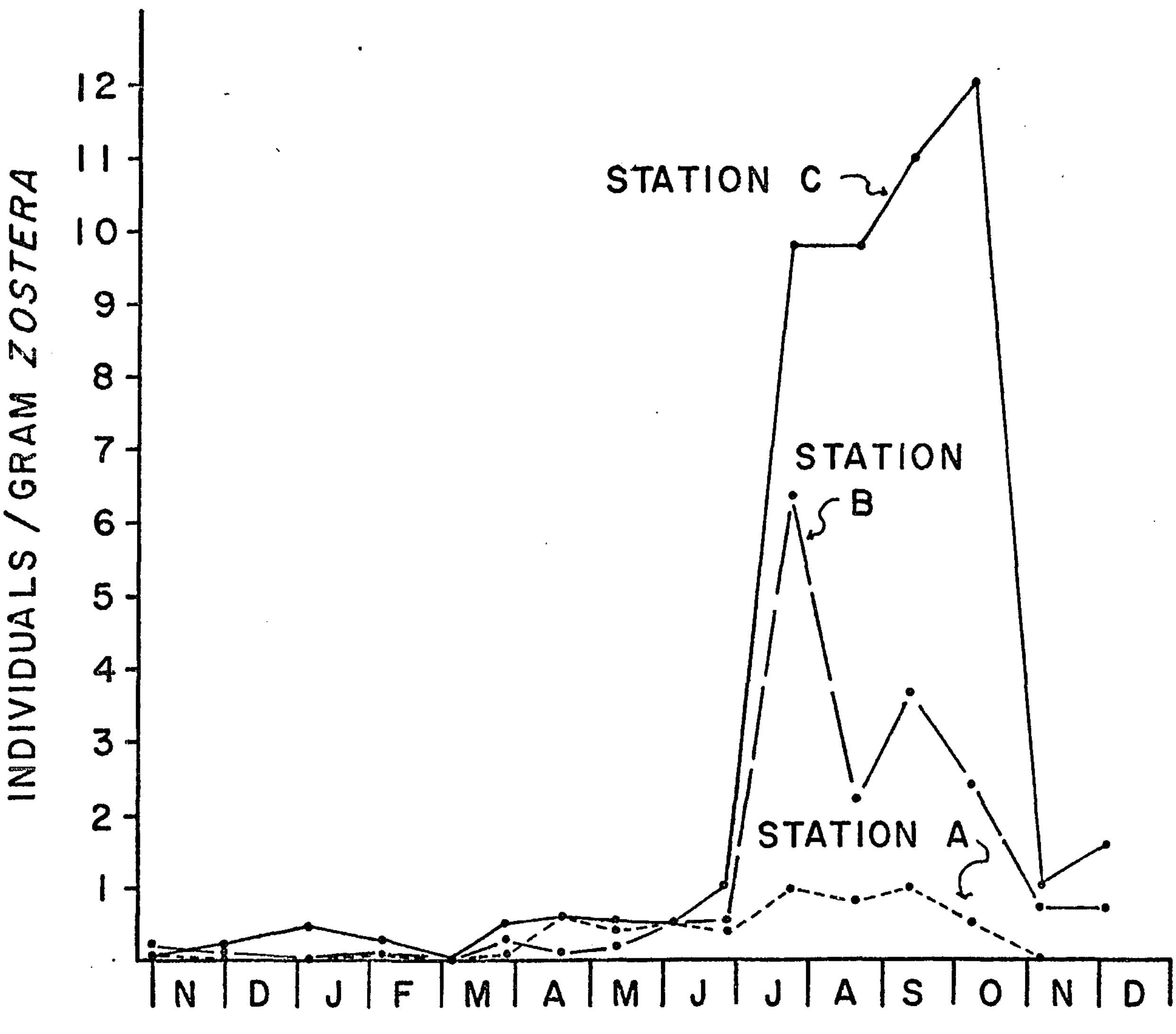


Fig. 20. Seasonal abundance of Odostomia impressa, November 1967-December 1968.

Odostomia bisuturalis was fairly common throughout most of the year, with individuals being found in every collection except that from early March. Seasonal and station distribution were generally similar to that of *O. impressa*: highest densities occurred in late summer and fall at station C. However, *O. bisuturalis* attained a peak frequency of only 3.2 individuals/g of *Zostera* compared to 12.1 for *O. impressa*.

On the Atlantic coast *O. bisuturalis* apparently reaches its southern limit in Chesapeake Bay (Allen, 1958). Although Loosanoff (1956) reported this species to prey on young oysters in New England waters, Allen (1958) was unable to induce Chesapeake Bay specimens to feed on any of a wide variety of invertebrates in the laboratory, including *Crassostrea*; rather, *O. bisuturalis* appeared to clean algae from the shells of *Bittium*. Allen concluded, however, that "additional observations are necessary to clearly define the feeding habits of *O. bisuturalis*."

Elysia catula is a small, dark sacoglossan which occurred throughout the year at all stations. This species was sporadic in abundance but reached a peak in November and December 1968 when frequencies were considerably greater at stations B and C than at station A (Fig. 21).

Chesapeake Bay appears to be the southern range limit for *E. catula* which occurs northward to Massachusetts (Franz, 1968). It is associated with *Zostera* in New Jersey waters (Franz, 1968) and in the Gloucester Point vicinity has been recorded only from that habitat (Wass, 1965).

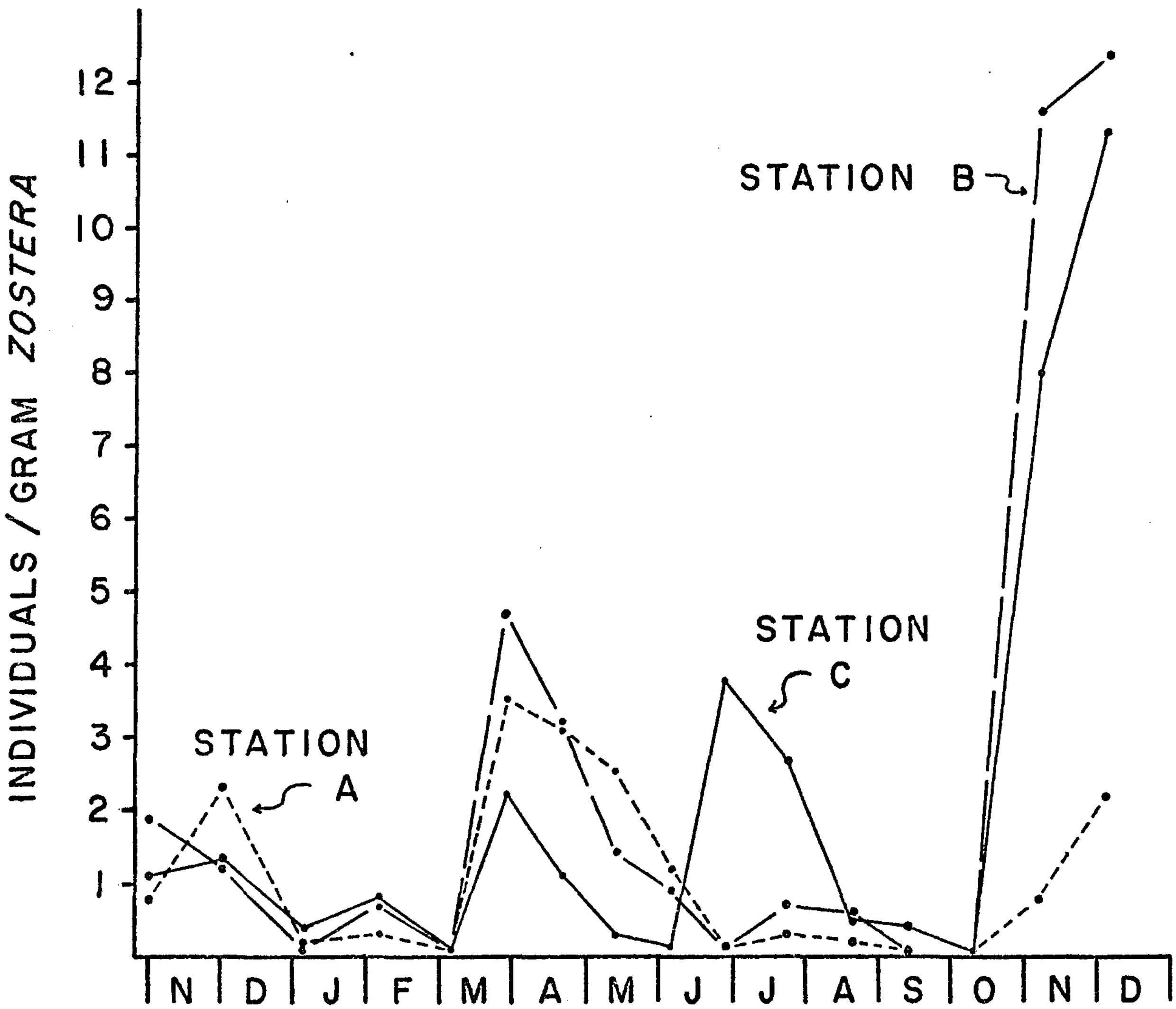


Fig. 21. Seasonal abundance of Elysia catula, November 1967-December 1968.

Stiliger fuscata is a tiny sacoglossan which made a brief but dramatic appearance in mid-summer, reaching densities of over 25 individuals/g of *Zostera* at stations B and C (Fig. 22). Considerably fewer numbers occurred at station A. This species is common on eelgrass in Connecticut where it feeds on filamentous green algae (Dr. D. R. Franz, personal communication).

Polycerella conyma, a small eolid, was collected from all stations in late June and July in maximum densities of 0.3 individuals/g of *Zostera*. Except for a few individuals found in October, this species was absent from all other collections.

The occurrence of *P. conyma* in Chesapeake Bay begins to fill a large gap in its distribution. Prior to its recent discovery at Cape May, N.J. (Franz, 1968), this species was unknown north of Florida. It reportedly feeds on the bryozoan *Bowerbankia gracilis*.

Doridella obscura was found from early June into July and again in October. Peak densities of 1.9 individuals/g of *Zostera* occurred in late June and July.

This small dorid is recorded from Vineyard Sound, Mass., to the Gulf of Mexico (Franz, 1967). It is common intertidally and subtidally in Delaware Bay where it is always found in association with and feeding on *Electra crustulenta* and other encrusting bryozoans. Wass (1965) reported *D. obscura* to be the most abundant nudibranch in lower Chesapeake Bay.

Doris verrucosa was represented in collections by only a few individuals found in August, November and December 1968. The sinuous, white egg ribbons were fairly common, however, on

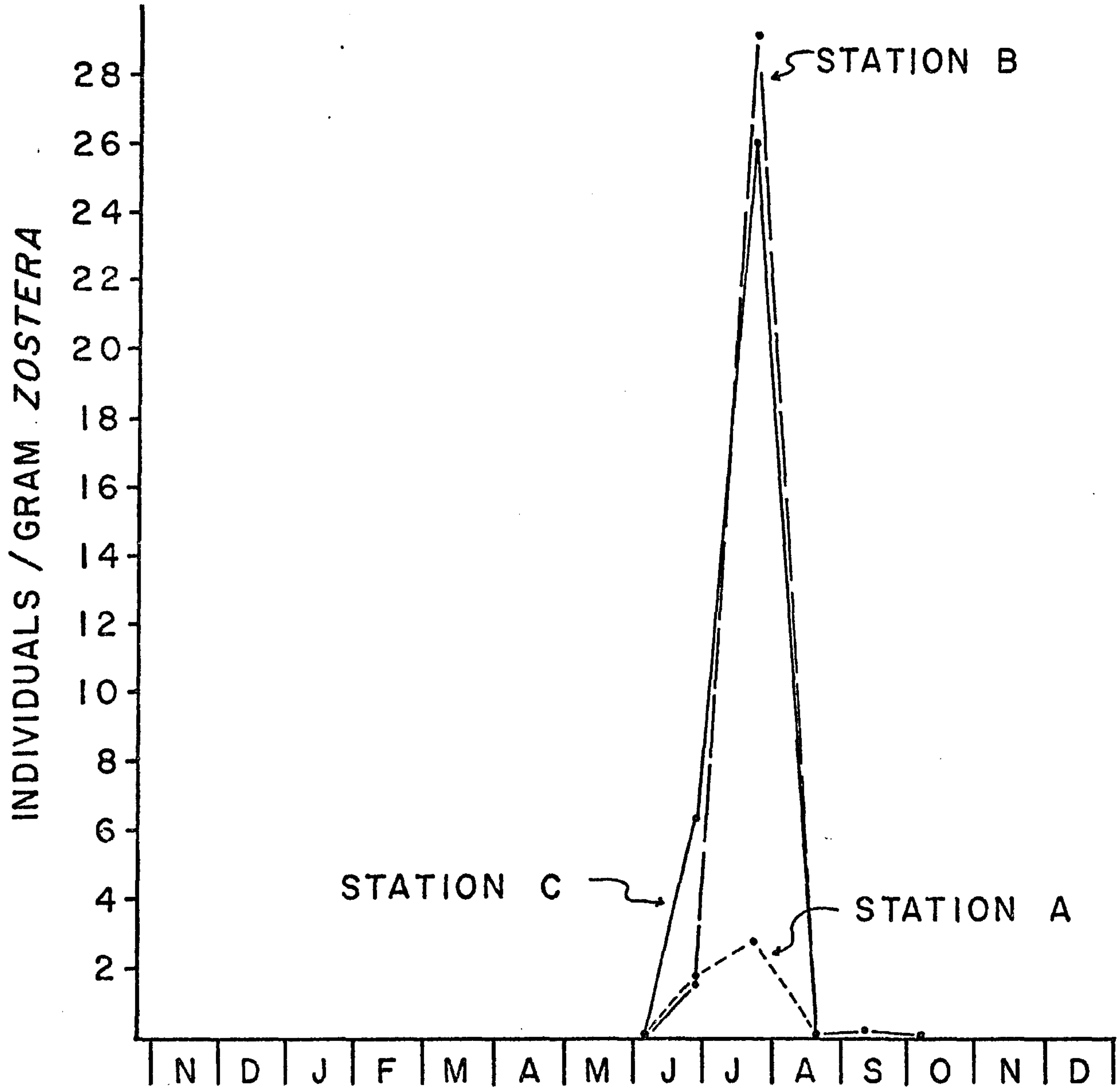


Fig. 22. Seasonal abundance of Stiliger fuscata, November 1967-December 1968.

eelgrass blades from June through July. This large, yellowish dorid appeared to be considerably more abundant in the summer following termination of this study. Field observations with face mask and snorkel often revealed 10-12 individuals within a period of approximately 10 min, while on numerous occasions over the preceding year, a total of less than six were seen.

This warm-water amphiatlantic nudibranch ranges northward along the United States east coast to Buzzards Bay, Mass. (Franz, 1970).

Pelecypoda

Since the vast majority of bivalve species have evolved as burrowers in soft-bottom habitats (Barnes, 1968), the Pelecypoda did not constitute an important component of the epifaunal community. Two species, however, were fairly frequent in collections.

Anadara transversa was found in every collection except those from February through April. A peak density of 0.4 individuals/g of *Zostera* occurred at station C in August. These bivalves ranged in length from 1.5 to 19.5 mm and were usually found attached to the cylindrical stems of the plants.

This species is common subtidally from south of Cape Cod to Florida and Texas (Abbott, 1954). In lower Chesapeake Bay it is an abundant epibenthic form reaching densities of 400 individuals/m^2 (Wass, 1965).

Mya arenaria was fairly common from January into August. Most clams were found at station A where a peak density of 0.7

clams/g of *Zostera* occurred in late March. Only young individuals, averaging 3.5 mm in length (n=42) and attached to plants by their byssal threads, were collected.

Soft-shelled clams are native to the east coast of North America from Labrador to North Carolina and have been introduced to the west coast (Abbott, 1954). Recently metamorphosed individuals are known to set on various submerged surfaces and remain attached for several months before establishing permanent burrows in the bottom (Medcof, 1950). My findings indicate that eelgrass may play an important role in providing a setting substrate for the young clams. In his research on the ecology of *M. arenaria* in the York River, Mr. Jon Lucy (VIMS, unpublished data) has provided further evidence for this: 10 transects sampled both within a *Zostera* bed and over adjacent bare bottom yielded an average of 763.7 and 39.2 clams, respectively.

Cirripedia

Balanus improvisus, the only barnacle encountered, occurred at least sparingly throughout most of the year. A sharp peak in abundance in May indicated the presence on the plants of many small, recently-set individuals (Fig. 23). Density of the young barnacles was strikingly higher at greater depths in the sample area. Following the spring set *B. improvisus* declined rapidly in numbers, probably because of predation and competition for space as well as to exfoliation of *Zostera*. By late June dead barnacles outnumbered live ones at each station.

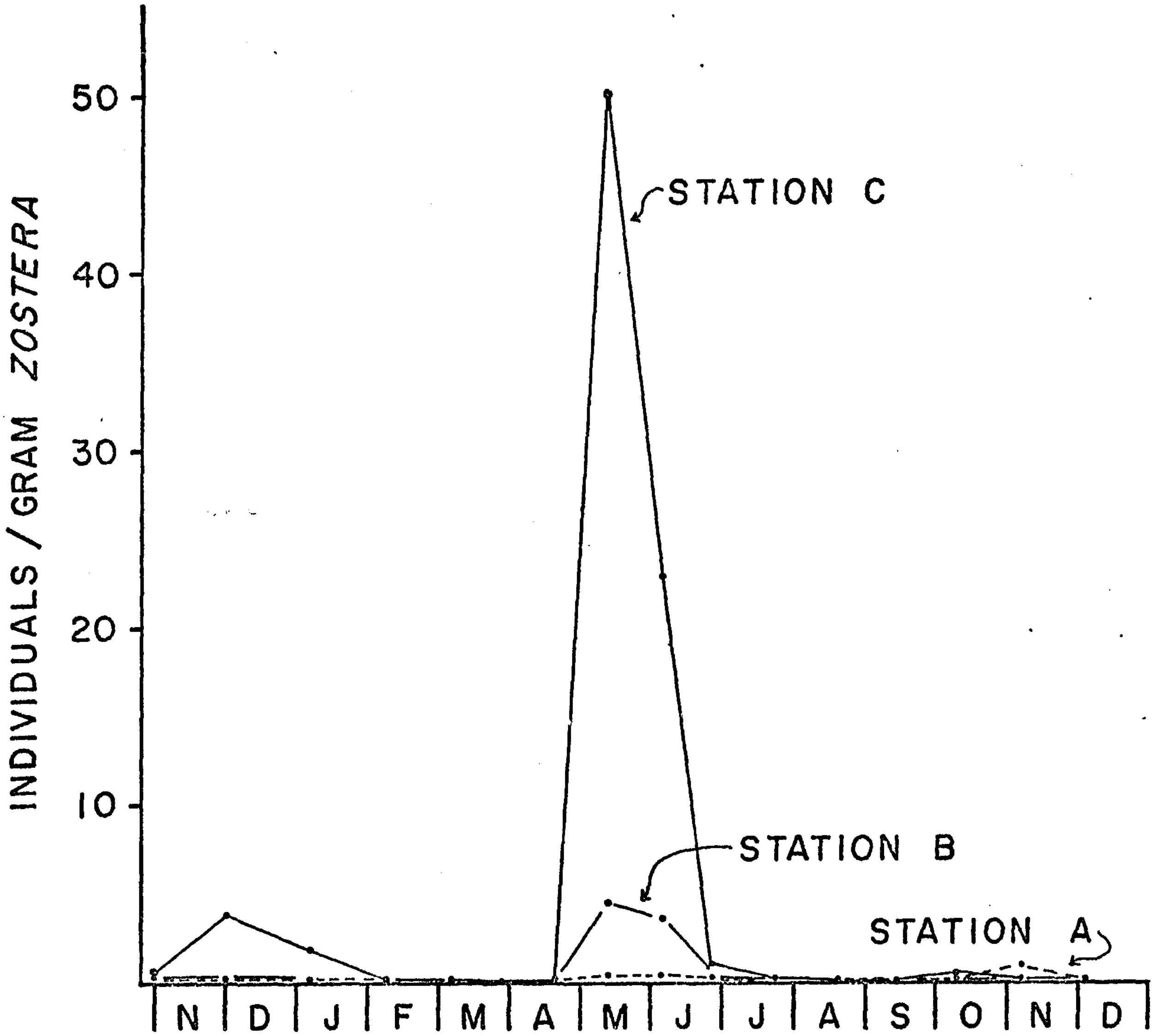


Fig. 23. Seasonal abundance of Balanus improvisus, November 1967-December 1968.

Setting of larval *B. improvisus* occurred primarily on the distal portions of the *Zostera* plants (Table 1). Fifty plants, selected randomly from each station, were divided vertically into quarter sections and the number of barnacles in each section counted. From a total of 475 barnacles, approximately 51.6% occurred in the top quarter and 90.3% in the top half.

This species has a world-wide distribution in temperate and tropical waters (Zullo, 1963) and is particularly characteristic of estuarine areas where it may penetrate to salinities of less than 1‰ (Cory, 1967). Andrews (1953) reported that *B. improvisus* is the chief fouling organism in Chesapeake Bay in salinities below 15‰; in higher salinities the population is severely reduced by competitors and predators. Two seasonal setting peaks, in spring and fall, have been reported for this species in lower Chesapeake Bay by Andrews (1953) and Calder (1966). Although a heavy spring set was evident in my study, the fall set was poorly defined except at station C in late 1967. Cory (1967) reported that in the Patuxent River, Md., the time and intensity of barnacle setting varied greatly from one location to another and from one year to another. At Beaufort, N.C., this species has only one setting period, occurring in mid-winter (MacDougall, 1943).

Mysidacea

Two mysid species were encountered, one occurring primarily in winter and spring and the other in late summer and fall. Because of the vagility of these animals, abundances recorded in Appendix Tables I-III probably represent only relative values.

Table 1. Vertical Distribution of *Balanus improvisus* on *Zostera*.

Vertical Section	Sta A	Sta B	Sta C	Total	%
Top Quarter	8	28	209	245	51.6
2nd Quarter	4	22	158	184	38.7
3rd Quarter	1	1	41	43	9.1
Basal Quarter	0	1	2	3	0.6

Neomysis americana was found from December 1967 into April 1968 and again in December 1968. Individuals were consistently most abundant at station C. Ovigerous females were collected in late March and in April.

This euryhaline species is common in temperate inshore waters along the North American coast where it plays an important role in the food chain of many commercially important fish (Hopkins, 1965). It is common in the rivers of the Chesapeake system but less so in the bay (Wass, 1965). Hopkins (1965) presented evidence for a diurnal rhythm in the vertical movements of this animal in the Indian River Inlet, Del. Individuals were abundant in the surface plankton at night but appeared to seek deeper waters during the day. Avoidance of surface waters by *N. americana* during the day has also been reported by Hulbert (1957) and Herman (1963). This adverse reaction to light may explain the relative abundance of this species at the deepest station.

Mysidopsis bigelowi, generally less abundant than the previous species, was collected in November and December 1967 and from August into December 1968. It too showed a predilection for deep water: from a total of 79 individuals collected, 77 were found at station C and the other two at station B. Ovigerous females were found in November 1967 and 1968.

This species ranges from the Gulf of St. Lawrence southward to Virginia (Tattersall, 1951). It has never been recorded from the Chesapeake estuary, although it has been found outside the mouth of the bay (Wass, 1965).

Isopoda

Paracerceis caudata was the most abundant of four isopod species collected and one of the dominant animals in the community. This small sphaeromid was found in every sample throughout the year, with greatest densities occurring from August into December 1968 (Fig. 24). No consistent station preference was evident, although the peak abundance of 54.3 individuals/g of *Zostera* occurred at station B in October. Very young animals, recently having left the internal brood pouches of the females, were found from June into September.

Paracerceis caudata apparently passes the winter in an immature stage. Adult males, easily distinguished by their characteristically notched pleotelsons and elongate outer uropods, did not appear in samples from November through March. A few mature males were present in the April collection and by mid-May they constituted approximately half of the population. Immature individuals could not be readily distinguished by sex.

Paracerceis was not listed by Guild (1961) in her summer study of *Zostera* associates at Gloucester Point, nor has it been previously recorded from the Chesapeake system. This species may therefore have only recently invaded the Bay area. Most likely, however, it has been incorrectly identified as *Sphaeroma quadridentatum*. The distinction between the two species is easily overlooked unless mature males of *P. caudata* are present in the collection.

Richardson (1905) reported numerous localities for this species ranging from New Jersey southward to Yucatan, Mexico and

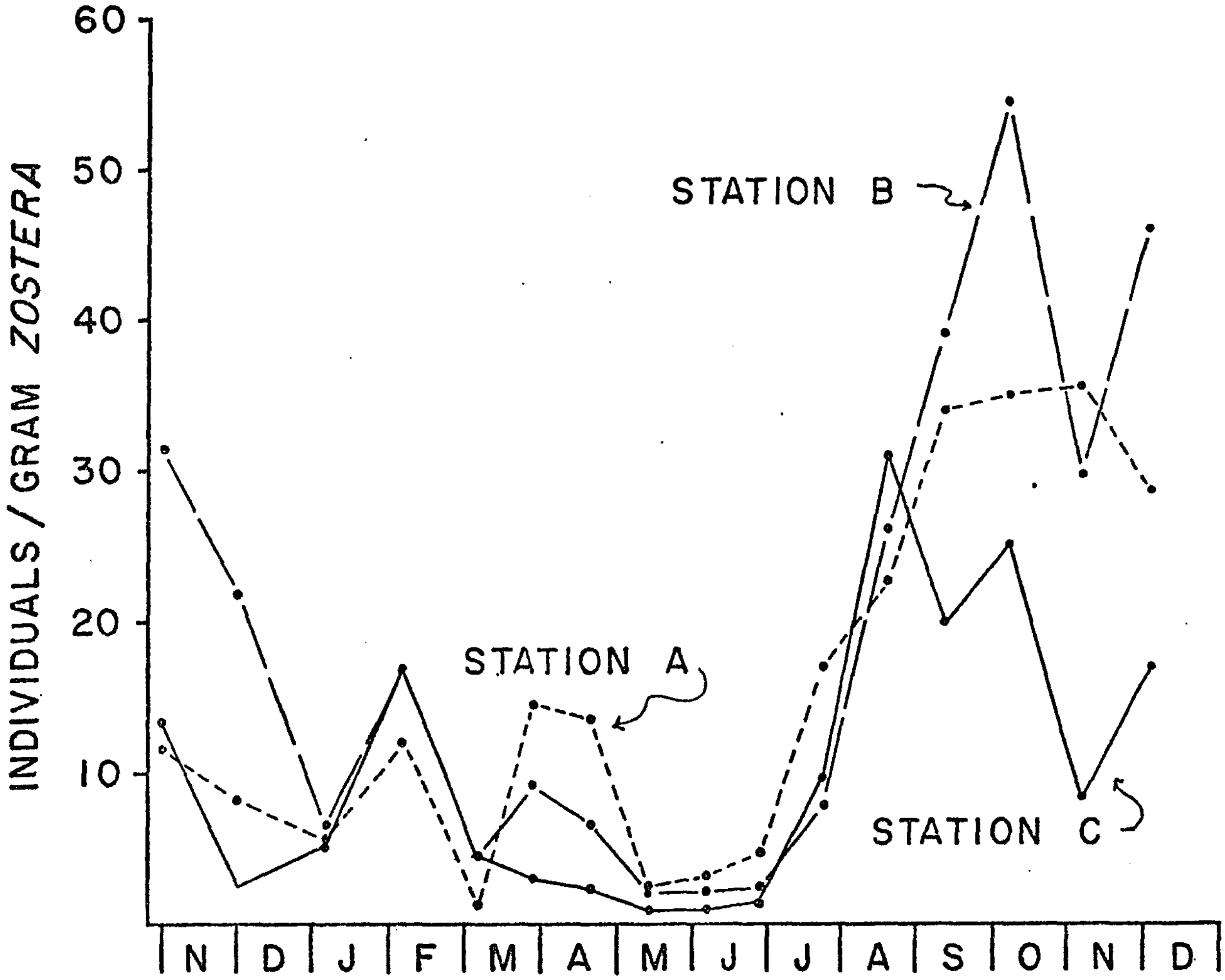


Fig. 24. Seasonal abundance of Paracerceis caudata, November 1967-December 1968.

including Bermuda and the Bahamas. It has been found in depths from the surface to 46 m among algae and grass and from coral reefs. This species has also been collected from offshore sandy bottoms in Georgia (Menzies and Frankenberg, 1966) and from sea-buoys (Miller, 1968).

Erichsonella attenuata, another very common isopod, was found throughout the year at all stations with highest densities occurring during fall and winter (Fig. 25). Ovigerous females were found from April into November. Young individuals are retained within the marsupium of the female until they reach a body length of approximately 2 mm. As many as 35-40 juveniles may be carried by one female. Unlike the preceding species, Erichsonella was occasionally seen to swim from one plant to another. This is accomplished only slowly and for short distances. Copulatory activity was observed on numerous occasions with the male lying lengthwise on top of the female while rapidly fanning its pleopods. This is followed by thrusting motions of the male's abdomen as he assumes a more lateral position.

Little information is available on the ecology of E. attenuata. It has been collected from eelgrass in South Oyster Bay, N.Y. (Burkholder and Doheny, 1968), Great Egg Harbor, N.J. (Kunkel, 1918) and at Gloucester Point, Va. (Wass, 1965).

Idotea baltica was collected throughout most of the year with highest densities generally occurring at station C. Brooding females were found from April into August. Idotea is an active swimmer and was frequently seen darting from one plant to another, although it generally remains on the grass unless

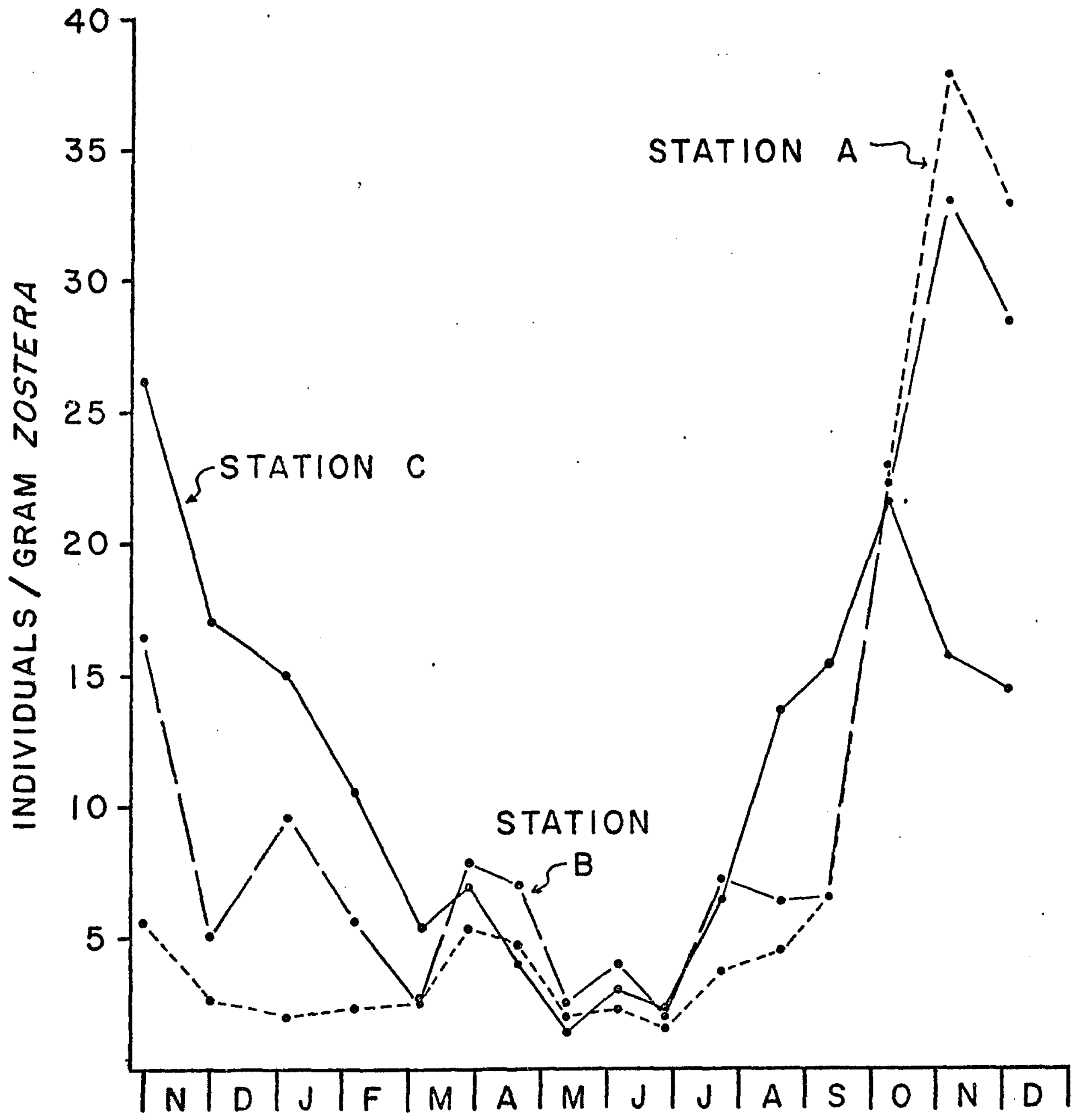


Fig. 25. Seasonal abundance of Erichsonella attenuata, November 1967-December 1968.

the latter is greatly disturbed. This swimming ability is doubtlessly beneficial for life on aquatic vegetation.

In yet other respects *Idotea*, as well as *Erichsonella*, seems particularly adapted for living on *Zostera*. Its elongate shape and greenish coloration provide effective camouflage, and the legs are well suited for grasping and moving up and down the plant blades.

Idotea baltica, a transatlantic euryhaline species generally found on floating and attached marine plants (Richardson, 1905; Dahl, 1948), is associated with *Zostera* in Oyster Bay, N.Y. (Burkholder and Doheny, 1968) and in the Mediterranean (Ledoyer, 1966a).

Amphipoda

The Amphipoda constituted a very diverse component of the epifaunal community and included several quantitatively prominent forms. Twenty-three species were collected, including two new records for Chesapeake Bay.

Ampithoe longimana, the most abundant amphipod encountered, was found throughout the year at all stations. Pronounced peaks in density at all stations, provided primarily by adults, occurred in October with secondary peaks being evident in July (Fig. 26). On both occasions the amphipods were vastly more abundant at station A than at the deeper stations. Ovigerous females were found from April into November (Fig. 27).

With the aid of glandular pereiopods (Kunkel, 1918), *A. longimana* constructs silt-impregnated web-like nests on the

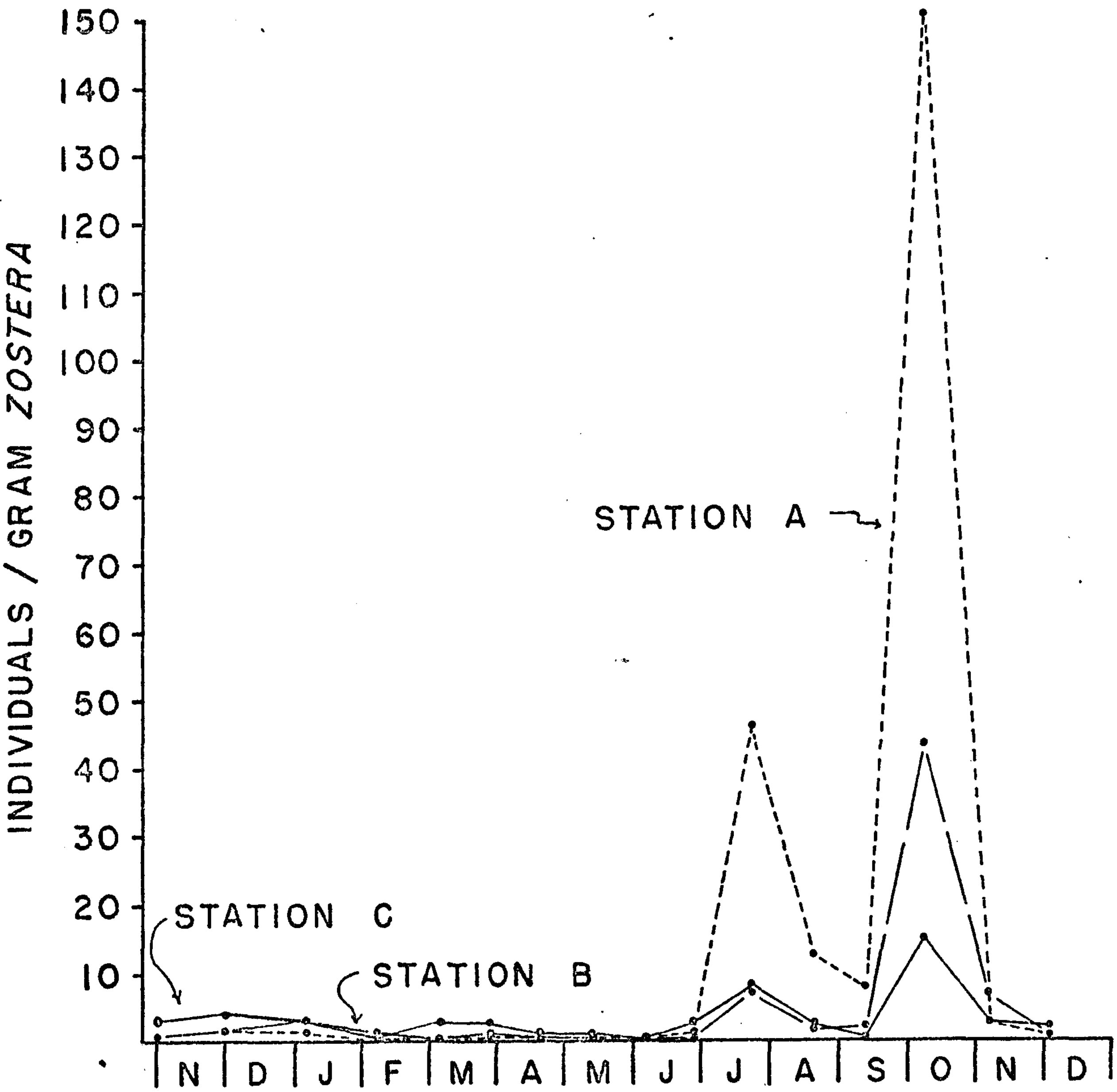


Fig. 26. Seasonal abundance of Ampithoe longimana, November 1967-December 1968.

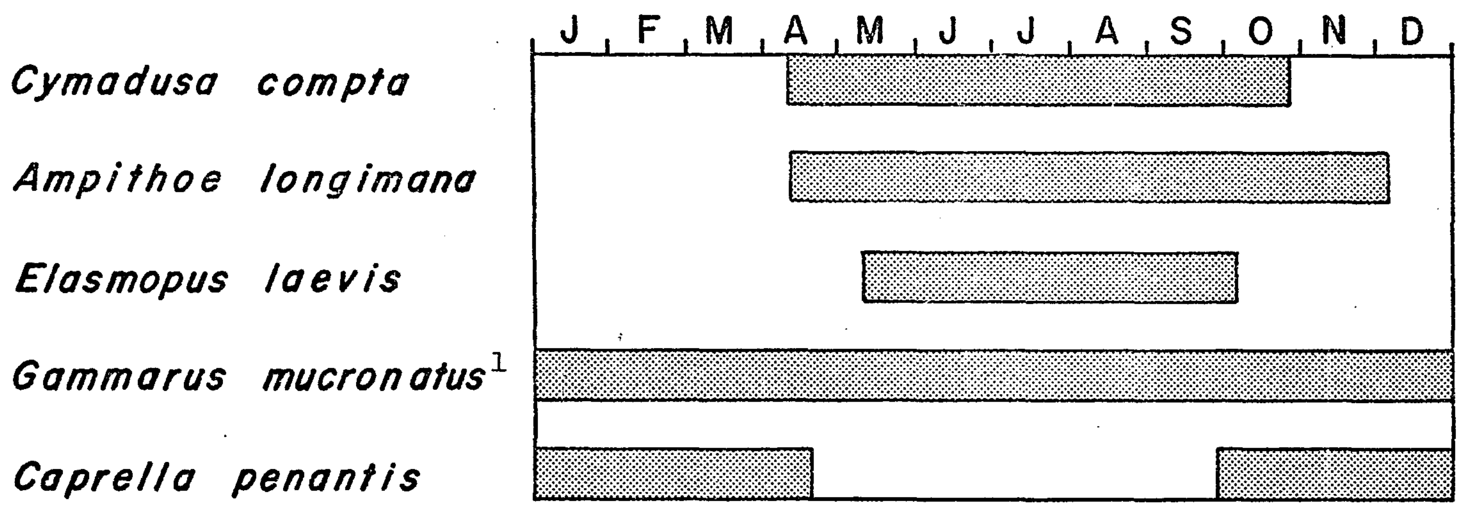


Fig. 27. Breeding seasons for five amphipod species, based on presence of ovigerous females.

[1]Only one specimen of G. mucronatus was collected during September and October but the presence of ovigerous females in the general population is assumed.

surface of the Zostera blades. Individuals were frequently observed within their nests with their antennae protruding and waving about. The first antennae are the primary olfactory sites (Holmes, 1901), and the waving of these appendages is apparently a means of sensing the environment.

When the eelgrass was generally prostrate, these amphipods and their nests were much more numerous on the undersides. This observation supports the laboratory experiments of Holmes (1901) who reported A. longimana to be negatively phototactic.

Coloration of this species was quite varied, ranging from bright green to reddish brown, although the former color greatly predominated. Holmes reported that by contraction and expansion of numerous pigmented spots, individuals could modify their color to blend with that of their background.

Nest-building habits and protective coloration of A. longimana, as well as the positively thigmotactic instincts reported by Holmes, render this species well adapted to living on Zostera. These characteristics are shared with another very abundant amphipod in this community, Cymadusa compta, to be discussed below.

Although A. longimana has been reported common in eelgrass and algae at Woods Hole (Holmes, 1901) and on the Connecticut coast (Kunkel, 1918), Feeley (1967) found it scarce in lower Chesapeake Bay, "being taken only occasionally in the lower portions of the James, York and Piankatank rivers." The discrepancy between Feeley's findings and mine can probably be attributed to most of his collections being made in deeper waters beyond the extent of eelgrass.

The breeding season reported here greatly extends that previously recorded. Ovigerous females were collected in Connecticut by Kunkel (1918) from August 13 to 17 and in Chesapeake Bay by Feeley (1967) only in June.

Cymadusa compta is very similar to A. longimana both structurally and ecologically, although Feeley (1967) reported a much lower minimum survival salinity in the York River for C. compta. These two ampithoids can be distinguished with certainty only under magnification. Although less common than A. longimana, the relative seasonal abundance and station distribution of C. compta were very similar to that of the former species (Fig. 28). Cymadusa compta also constructs nests on the Zostera blades. Ovigerous females were found from April into October (Fig. 27).

This species is found from Cape Cod to Texas and is most common in estuarine areas (Nagle, 1968). It has been collected from eelgrass at Woods Hole (Nagle, 1968), on the Connecticut coast (Kunkel, 1918) and in Chesapeake Bay (Feeley, 1967) where it is reportedly one of the most abundant shallow-water amphipods.

The breeding season reported here for this species is longer than previously found. Ovigerous females have been collected in Chesapeake Bay from June to October (Feeley, 1967) and in New England during July and August (Kunkel, 1918).

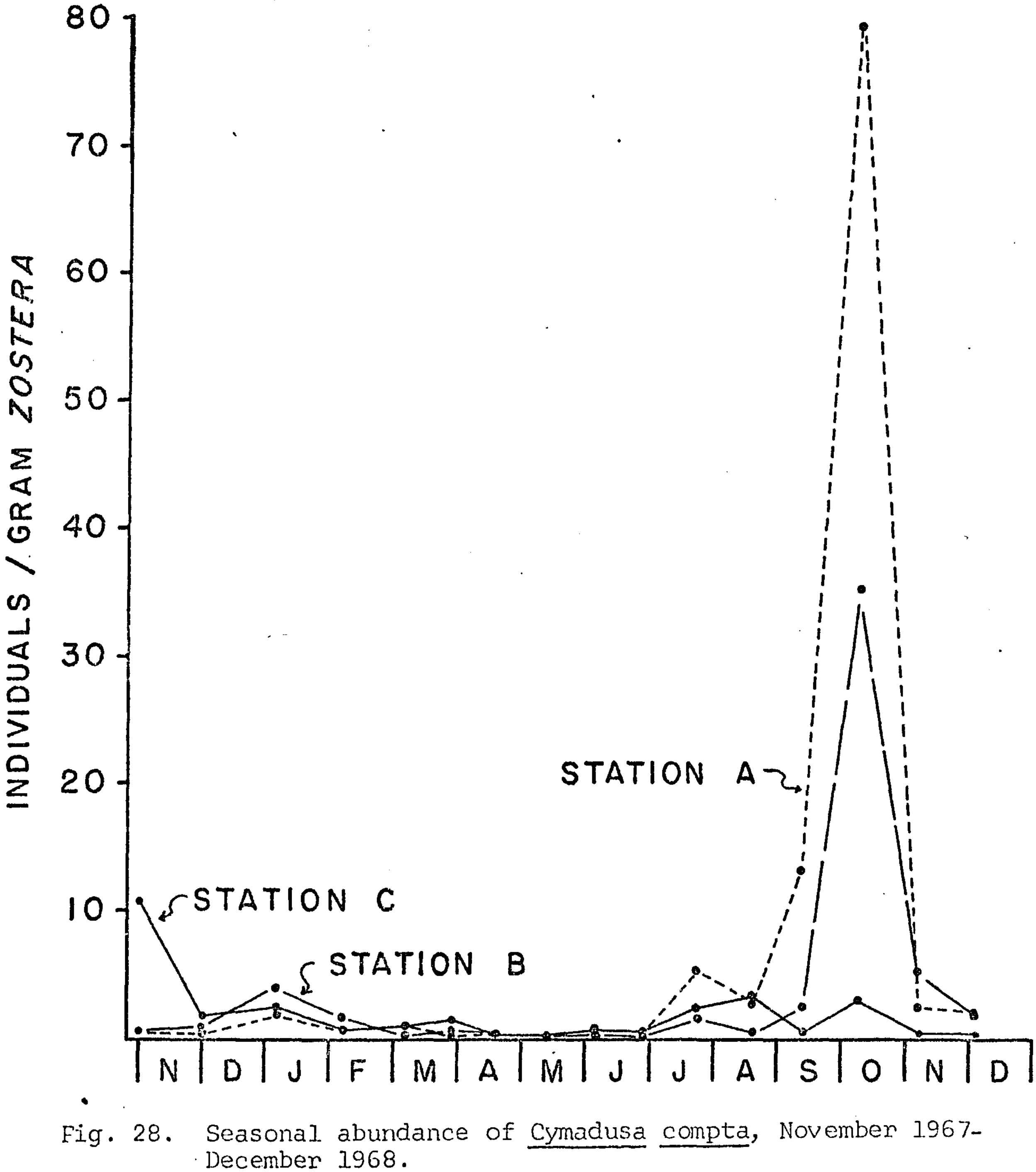


Fig. 28. Seasonal abundance of Cymadusa compta, November 1967-December 1968.

Elasmopus laevis, a very common species, was found at all stations throughout the year but was generally most abundant in late summer and fall (Fig. 29). A very pronounced peak in abundance occurred in August at station C, where considerably more very small individuals were found than at the shallower stations. Ovigerous females were collected from May into October (Fig. 27).

This species occurs commonly on pilings and among sponges and eelgrass in New England (Kunkel, 1918). According to Feeley (1967) *E. laevis* is found on eelgrass in shallow water but among hydroids and bryozoans in deeper water, where it is most abundant. He, too, collected ovigerous females from May into October.

Gammarus mucronatus was irregularly common throughout most of the sampling period, being generally most abundant at station C (Fig. 30). From September into December 1968, however, only one individual was collected.

This species apparently breeds locally throughout the year (Fig. 27). I collected ovigerous females from November 1967 into August 1968. Feeley (1967) reported breeding only from May through September.

The range of *G. mucronatus* is from the Gulf of St. Lawrence to the Gulf of Mexico (Shoemaker, 1930). Feeley (1967) reported it to be the most abundant shallow-water amphipod in lower Chesapeake Bay where it occurs primarily in *Zostera* beds. It is also associated with eelgrass in Connecticut (Kunkel, 1918) and Massachusetts (Nagle, 1968).

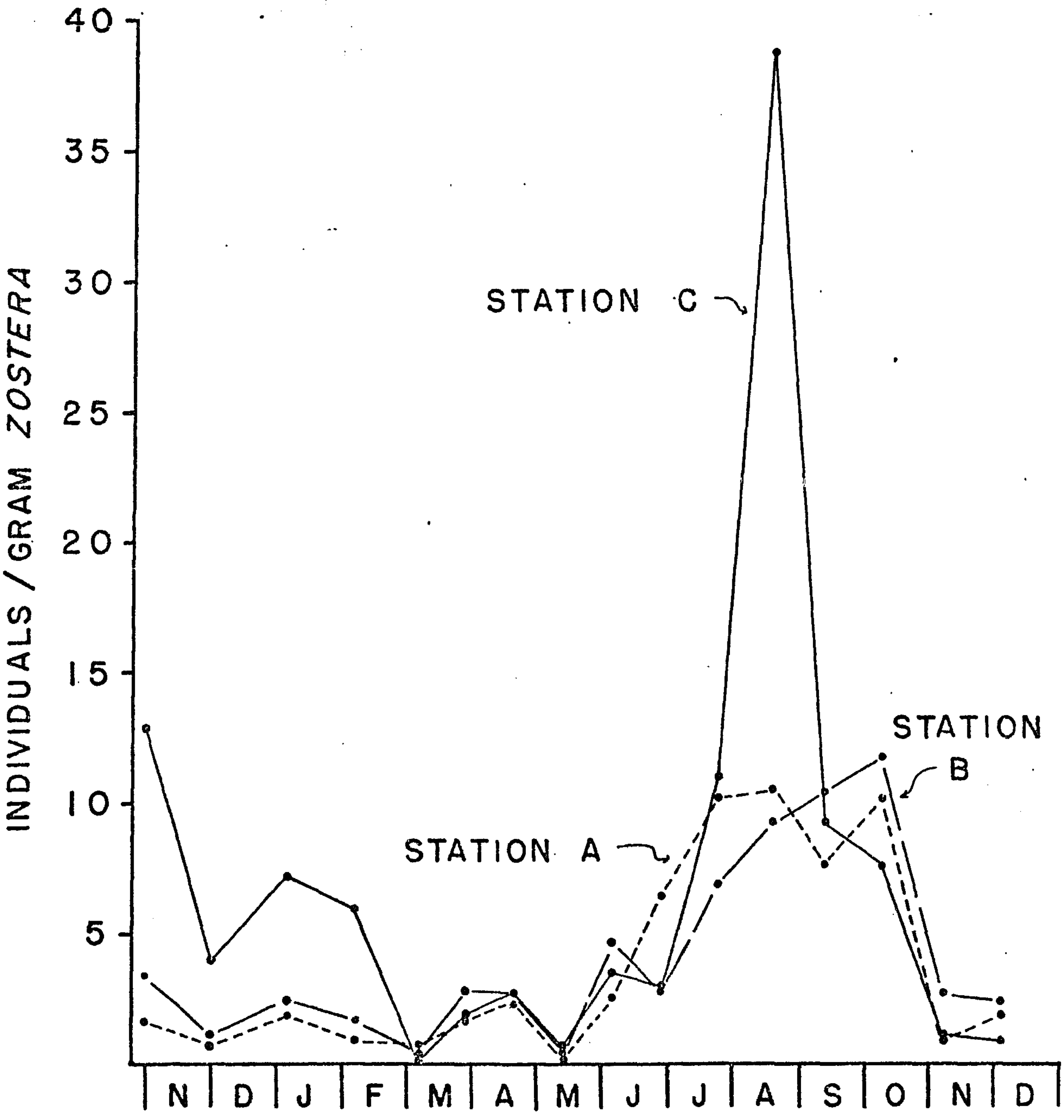


Fig. 29. Seasonal abundance of Elasmopus laevis, November 1967-December 1968.

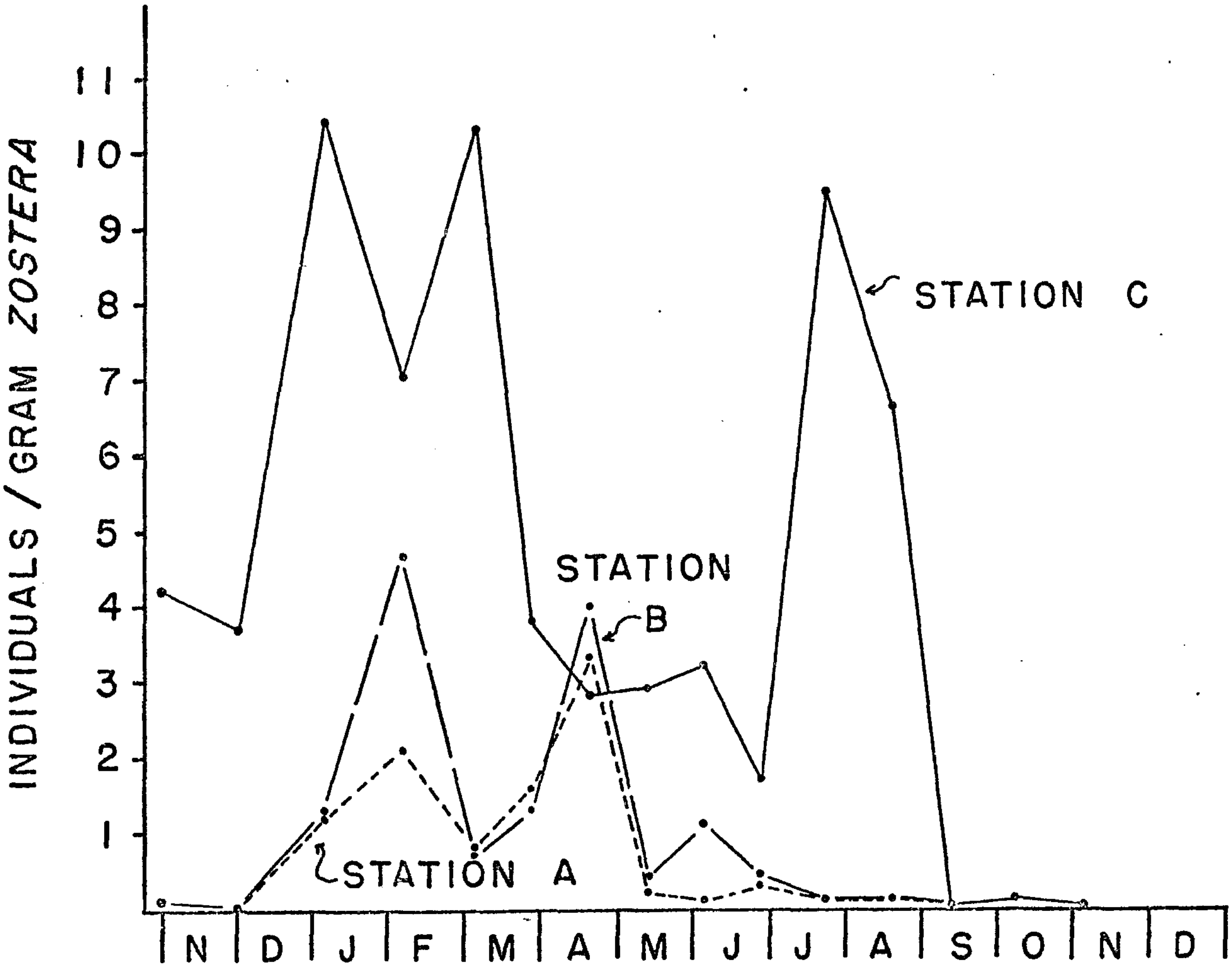


Fig. 30. Seasonal abundance of Gammarus mucronatus, November 1967-December 1968.

Caprella penantis was by far the most abundant of three caprellid species encountered. Peak densities occurred during winter and spring with relatively few individuals being collected in summer (Fig. 31). This species showed a marked increase in abundance at greater depths and was found only at station C during July, August and September, although only in scant numbers. Ovigerous females were collected from November 1967 into April 1968 and again from October into December 1968 (Fig. 27).

This species is the most common caprellid along the entire United States east coast and in the Gulf of Mexico where it occurs in a variety of habitats including pilings, sponges, eelgrass, hydroids and algae (Kunkel, 1918; McCain, 1968). At Pawleys Island, S.C., it is sometimes extremely abundant during winter on colonies of the hydroid *Tubularia crocea* (personal observation).

Several other generally less common amphipod species deserve special mention here. *Batea catharinensis* was very abundant in November 1967 at station C but was either absent or sparse in all other samples during the study period. The tube-dwelling species, *Corophium acherusicum* and *Corophium simile*, were present in low numbers throughout the year. The latter species, known only from the east coast of the United States, is apparently common nowhere (Shoemaker, 1947) and is recorded here for the first time in Chesapeake Bay. *Melita appendiculata* and *Colomastix* sp. were moderately abundant only in late summer and fall; the latter species has previously been found only in association with sponges and, significantly perhaps, its occurrence in the *Zostera*

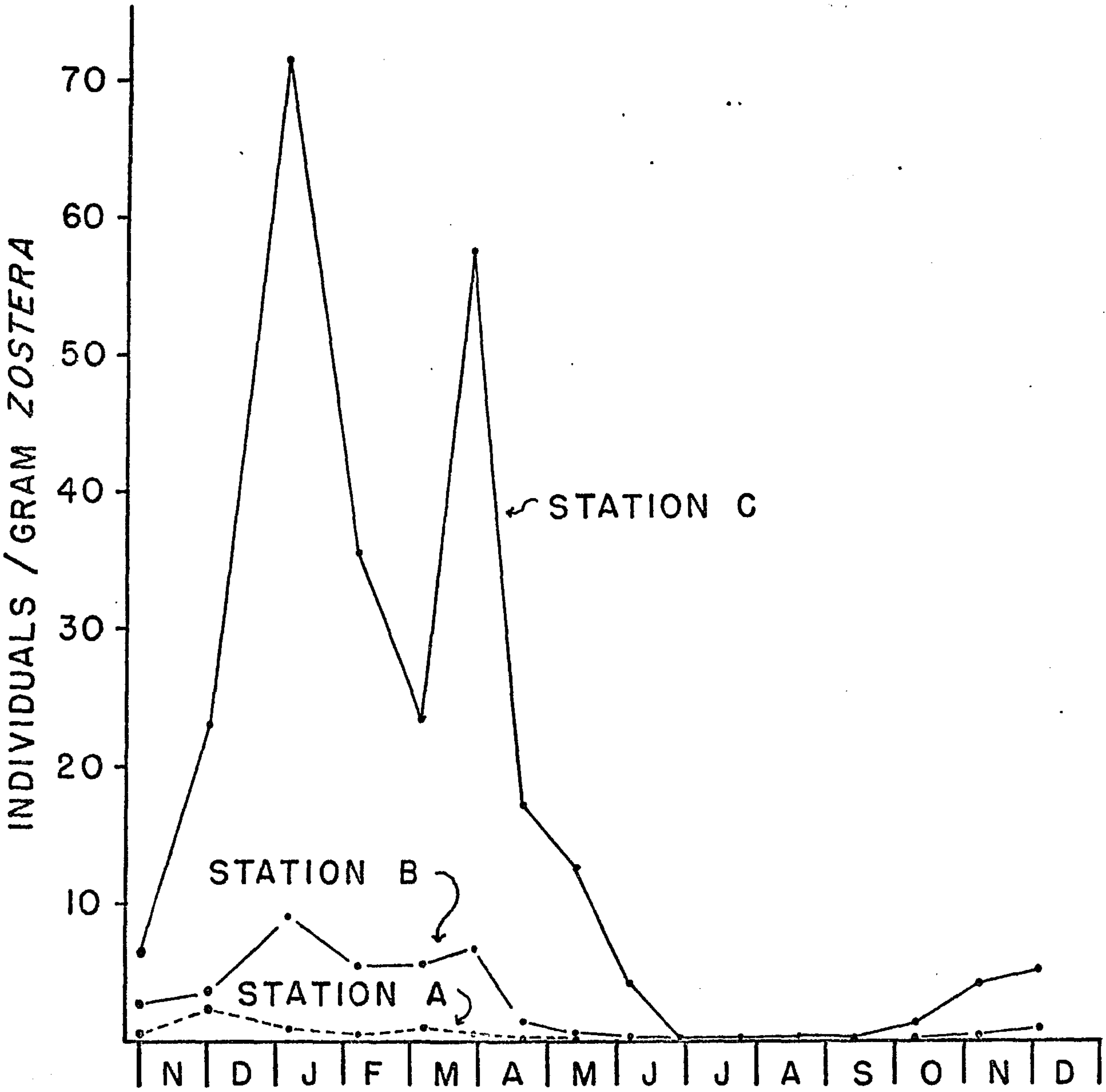


Fig. 31. Seasonal abundance of Caprella penantis, November 1967-December 1968.

community coincided with the period of maximum sponge abundance. Paracaprella tenuis and Rudilemboides sp. (currently being described as a new species by J. Stewart Nagle) occurred sparingly throughout the year. Ampelisca vadorum and Ampelisca abdita, which are normally tube-dwelling infaunal forms, were present in many samples.

Decapoda

The four species of natantian decapods encountered in this study are highly mobile forms and, with my sampling techniques, difficult to assess quantitatively. Values recorded in Appendix Tables I-III, therefore, reflect at best only relative abundances.

Hippolyte pleuracantha was common in samples during fall and winter with highest densities occurring at station C. Most individuals collected were either late zoeal stages, postlarvae or juveniles. This species is very abundant in beds of vegetation in sounds and bays south of New Jersey (Williams, 1965).

Palaemonetes pugio and Palaemonetes vulgaris were found from early spring through fall. Although scarce in samples, these species, especially P. pugio, were common in several seine hauls made during the spring and summer. Adults, including ovigerous females, and larvae were represented in samples. Both species are common in estuaries from Massachusetts southward and are especially characteristic of Zostera and Ruppia beds (Williams, 1965).

Crangon septemspinosa was represented in collections by only three individuals found at station C in February and early March.

Among the reptantians, Neopanope texana sayi was the only species collected more than once. A total of 20 crabs, measuring 3-8 mm in width across the carapace, were collected from August through December 1968. This xanthid is widely distributed subtidally in Chesapeake Bay where it occupies a wide variety of habitats, especially muddy bottoms and pilings among algae (Ryan, 1956; Daugherty, 1969).

Libinia dubia was fairly common in the sample area in late summer, although only one individual was collected. On two occasions this species was observed feeding on the stinging nettle Chrysaora quinquecirrha which was extremely abundant in the river at this time. The crabs were perched atop clumps of Zostera while grasping the nettles with their chelipeds and ingesting the tentacles. Whether L. dubia had actually captured the nettles as they drifted by or whether the nettles had first become entangled in the eelgrass could not be determined. On another occasion Libinia was observed feeding on a much-damaged Aurelia aurita lying on the bottom.

Callinectes sapidus was fairly common in the area but primarily confined to the bottom. Only a single young crab was collected from the eelgrass.

Tunicata

One species of solitary tunicate, Molgula manhattensis, and two colonial forms, Botryllus schlosseri and Perophora viridis, were associated with Zostera, the last-named species being relatively uncommon and found only in late summer and early fall.

Molgula manhattensis showed two peaks in abundance: a very pronounced one in July and a much smaller one in October (Fig. 32). In July, eelgrass at station C was heavily laden with these tunicates and generally prostrate, while at the shallower stations Molgula was relatively sparse and the plants essentially erect. In October this species was more evenly distributed between stations and consisted primarily of very small individuals.

The precipitous decline of M. manhattensis at station C following the July peak apparently resulted in part from extensive exfoliation of Zostera; by mid-August the plants had thinned out considerably and many bare patches were evident. The excision of plants in response to high temperatures was probably hastened by the heavy load of Molgula. A tendency for these tunicates to slough off as they increase in size (Cory, 1967) may have contributed to their decline.

The preferential setting of larval M. manhattensis at certain depths has been reported by Cory (1967). In a two-year study of panels ($1 dm^2$) suspended in the Patuxent River, Md., 86 specimens were collected from surface panels, 534 on mid-depth panels and 832 on bottom panels at a depth of 7 m.

According to Van Name (1945) M. manhattensis is the most common simple ascidian from Massachusetts to Chesapeake Bay and beyond; it ranges south to Florida and into the Gulf of Mexico. This is one of the few ascidian species able to live in reduced

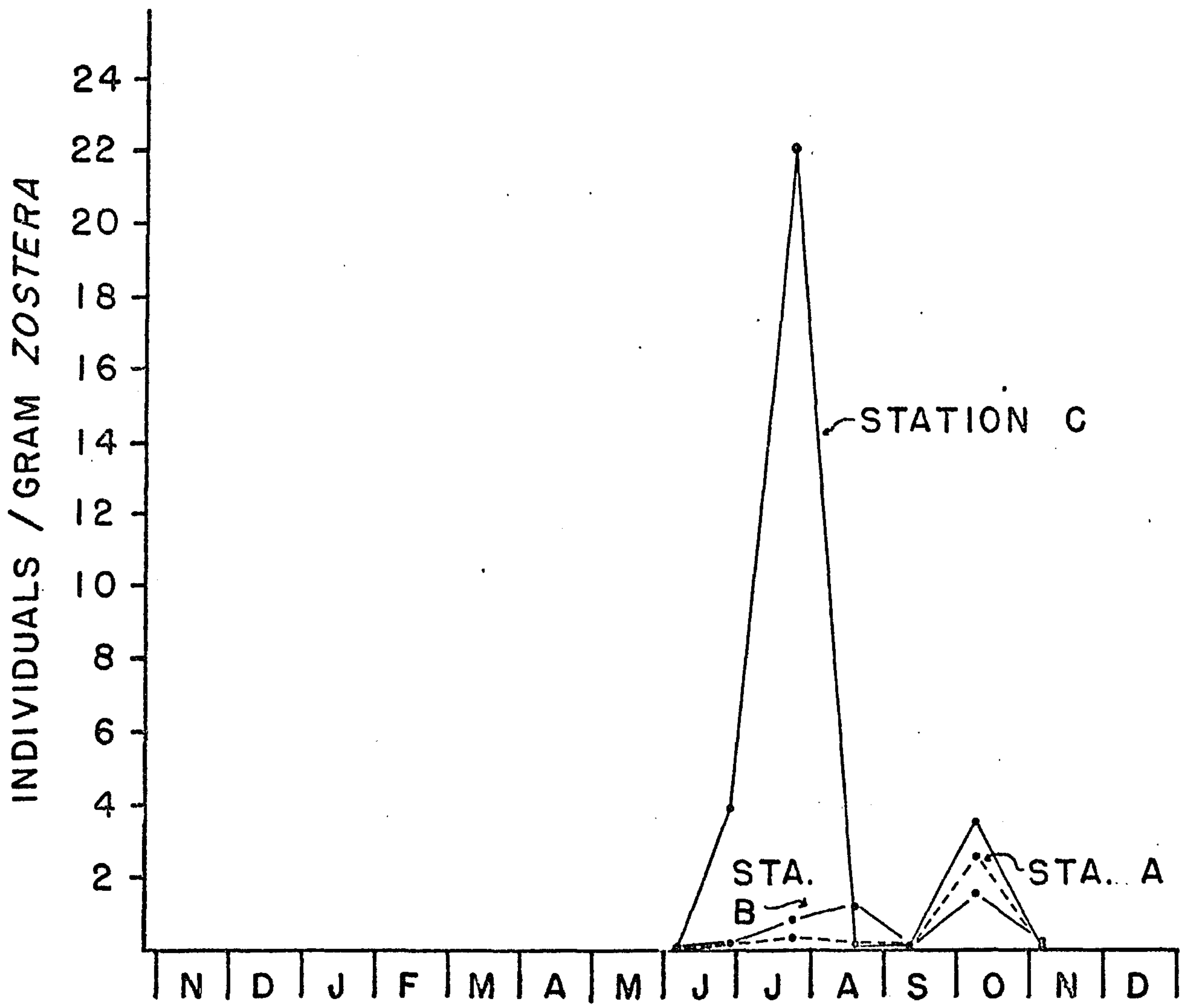


Fig. 32. Seasonal abundance of Molgula manhattensis, November 1967-December 1968.

salinities and polluted waters. MacDougall (1943) reported that *M. manhattensis* was common at Beaufort, N.C., in winter but that in mid-summer it was difficult to find a single specimen. At Hampton Roads, Va., however, Calder (1966) collected this species on test panels from May to December with a peak abundance occurring in July and August.

Botryllus schlosseri was present throughout the year, but was most common during November and December 1968 when widely-scattered large colonies were most often found investing the basal portions of *Zostera*, usually at the two shallower stations. Occasionally the prostrate blades of different plants were united by anastomosing growths of *Botryllus*.

This transatlantic species has been reported from scattered localities along the United States east coast and in the Gulf of Mexico (Van Name, 1945). It occurs on a variety of substrates including boat bottoms, pilings and floats. Distribution of *B. schlosseri* appears to be highly localized within its range, as it was not reported by MacDougall (1943) in his study of sessile invertebrates at Beaufort, N.C., nor by Andrews (1953) in his study of the fouling organisms of Chesapeake Bay. It was, however, collected by Calder (1966) on test panels at Hampton Roads, and it is fairly common on *Zostera* and hard substrates at Gloucester Point (Wass, 1965).

ALGAL ASSOCIATES

Numerous species of macroscopic algae were associated with *Zostera*, either as epiphytes or as unattached growths resting within the eelgrass bed. In both cases these algae constituted an integral part of the epibenthic community. All species collected are listed in Table 2. The more abundant forms are discussed below in relation to seasonal and depth distribution.

During the coldest winter months, the most conspicuously abundant epiphyte at all stations was *Desmotrichum undulatum* whose tan ribbon-like fronds were attached to most of the living *Zostera* blades as well as to dead fragments on the substratum. In April and early May, dying remnants of this alga were abundant at the base of the young epiphyte-free plants. Associated with *Desmotrichum* was *Elachistia* sp., whose small filamentous tufts were common primarily on the dead and prostrate *Zostera* blades. *Enteromorpha linza* was another fairly common winter form.

During June, *Champia parvula* became the first abundant epiphyte on the young *Zostera* along with scattered growths of *Agardhiella tenera*. Both species were found throughout the sample area, usually attached to basal portions of the plants. *Champia* was most abundant in shallower areas. Also common in shallow water was *Fosliella lejolisii* whose pinkish encrustations were found primarily on the shells of *Crepidula* and, less frequently, on *Bittium*.

Table 2. Macroalgae associated with *Zostera*.

Chlorophyta	
	Ulva lactuca
	Bryopsis plumosa
	Enteromorpha plumosa
	Enteromorpha intestinalis
	Enteromorpha linza
	Cladophora gracilis
	Cladophora glaucescens
	Chaetomorpha linum
Phaeophyta	
	Desmotrichum undulatum
	Asperococcus siliculosus
	Elachistia sp.
	Scytosiphon lomentaria
Rhodophyta	
	Grinnellia americana
	Porphyra leucosticta
	Agardhiella tenera
	Callithamnion byssoides
	Ceramium fastigiatum
	Ceramium rubrum
	Ceramium strictum
	Ceramium diaphanum
	Ceramium rubriforme
	Polysiphonia nigrescens
	Polysiphonia subtillisima
	Polysiphonia harveyi
	Dasya pedicellata
	Champia parvula
	Spyridia filamentosa
	Fostiella lejolisii

Approximately 68% of the adult *Crepidula* (n = 107) collected from station A in early June carried this alga. Occasional growths were found on *Zostera* blades. *Fosliella* was virtually absent from the deepest portions of the sample area. In late June other fairly common epiphytes were *Ceramium* spp. and *Polysiphonia denudata*.

During July, *Spyridia filamentosa* replaced *Champia* as the most abundant epiphyte in shallow water, although the latter species remained common throughout the summer. *Spyridia* was much less abundant in the vicinity of station C where *Ceramium strictum* and *Ceramium rubrum* were especially common. *Enteromorpha intestinalis* was conspicuously more abundant at station C than in shallower areas, and by early August it formed a green carpeting which covered the mostly prostrate *Zostera* at this locality. Within two weeks this carpeting had disappeared, and the considerably thinned-out eelgrass was nearly free of epiphytes. *Fosliella* became increasingly common during August as small crustose patches on *Zostera* at the two shallower stations.

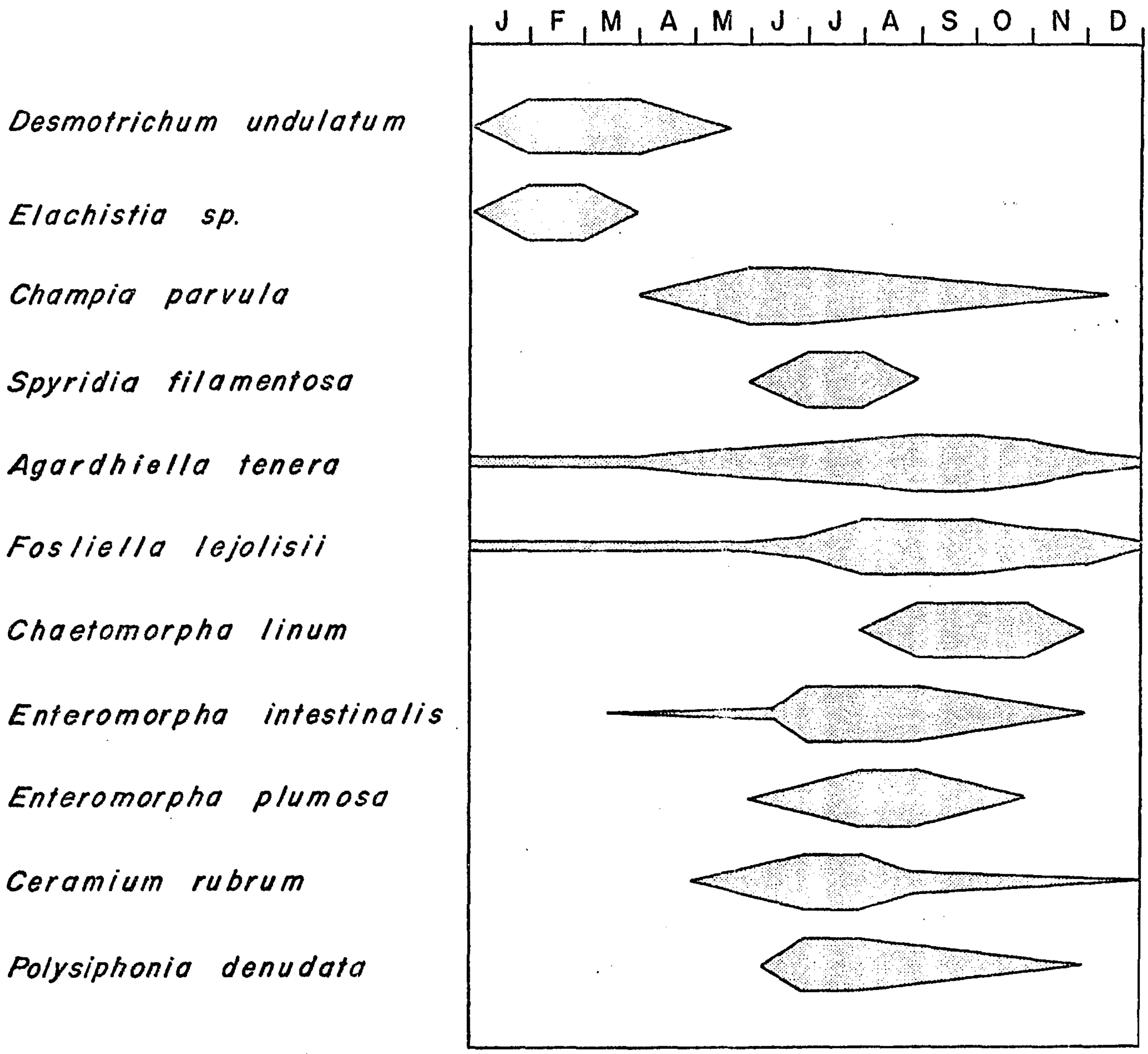
During late summer and fall, thread-like strands of *Chaetomorpha linum* became abundant throughout the sample area, especially in deeper water. Large unattached and epiphytic clumps of *Agardhiella tenera* and *Enteromorpha plumosa* were common in shallower areas, as well as the epiphyte *Polysiphonia denudata*. By December, algae were scarce within the *Zostera* bed and large drift lines of *Agardhiella* and other species had been cast ashore by heavy winds.

Thus, a distinct seasonality was evident in algae associated with *Zostera*. During winter, the brown algae predominated, primarily *Desmotrichum* and *Elachistia*, while in summer and fall red algae, such as *Champia*, *Spyridia* and *Agardhiella* were most abundant. Only a few species were present through the year, and the eelgrass was largely free of epiphytes during the periods before the advents of summer and winter species; this hiatus was evident during most of May and for a shorter period in late fall or early winter. Seasonality of the more common algal species is summarized in Table 3. These findings support the postulation of Zaneveld and Barnes (1965) that a distinct summer algal flora and a winter algal flora exist in lower Chesapeake Bay.

Several epiphytes showed a distinct differential distribution with depth. The most striking differences were between station C and the two inshore stations. *Champia* and *Fosliella* were among those more abundant at shallow depths while *E. intestinalis* and *C. rubrum* were most common in deep water.

Although microscopic forms were not included in this study, particularly luxuriant epiphytic diatom populations were sometimes evident. Filamentous sheaths of *Navicula* were abundant on *Zostera* in February and March, while periodically in summer the grass became festooned with brownish strands of *Melosira*.

Table 3. Relative seasonal abundance of common macroalgae associated with _Zostera_.



COMMUNITY STRUCTURE

Composition

Marine communities are most basically described in terms of composition and relative abundance of species. In Tables 4-6 all species of non-colonial invertebrates collected throughout the study period from stations A, B and C are ranked in order of abundance. Percentage composition of each species and cumulative percentages are also indicated.

Of the 100 species collected from all stations, the five most abundant (Bittium varium, Paracerceis caudata, Crepidula convexa, Ampithoe longimana and Erichsonella attenuata) accounted for approximately 59% of the total fauna; 95.5% of the fauna belonged to the 22 top-ranked species. Bittium varium was by far the most abundant form and constituted 26.2% of the fauna, over twice that of the second-ranked species Paracerceis caudata.

The dominant taxa, based on total numbers collected from all stations, were the Gastropoda (43.2% of fauna; 23 species), Amphipoda (18.5%; 23 species), Isopoda (16.7%; 4 species) and Polychaeta (15.0%; 18 species). These groups included approximately 93.4% of the fauna and 68% of the non-colonial species.

Although most species were common to all stations, differences in relative abundance were evident. Among common forms showing greater abundance in shallower portions of the

Table 4. Ranking by abundance of species collected at station A. Percent of total fauna and cumulative percent are indicated for each species.

Rank By No.	Species	No.	% Fauna	Cumul. %
1	*Crepidula convexa*	7860	16.26	16.26
2	*Bittium varium*	7453	15.41	31.67
3	*Ampithoe longimana*	7195	14.88	46.55
4	*Paracerceis caudata*	6534	13.51	60.06
5	*Brania clavata*	3357	6.94	67.01
6	*Erichsonella attenuata*	3039	6.29	73.29
7	*Cymadusa compta*	2972	6.15	79.44
8	*Elasmopus laevis*	2204	4.56	83.99
9	*Euplana gracilis*	1302	2.69	86.69
10	*Sabella microphthalma*	1184	2.45	89.14
11	*Aiptasiomorpha luciae*	733	1.52	90.65
12	*Platynereis dumerilii*	607	1.26	91.91
13	*Elysia catula*	505	1.04	92.95
14	*Polydora ligni*	451	.93	93.88
15	*Nereis succinea*	437	.90	94.79
16	*Gammarus mucronatus*	265	.55	95.34
17	*Stiliger fuscata*	261	.54	95.88
18	*Odostomia impressa*	209	.43	96.31
19	*Podarke obscura*	172	.36	96.66
20	*Urosalpinx cinerea*	169	.35	97.01
21	*Caprella penantis*	146	.30	97.32
22	*Triphora nigrocincta*	124	.26	97.57
23	*Zygonemertes virescens*	121	.25	97.82
24	*Hydroides hexagona*	111	.23	98.05
25	*Stylochus ellipticus*	109	.23	98.28
26	*Tetrastemma elegans*	107	.22	98.50
27	*Balanus improvisus*	93	.19	98.69
28	*Molgula manhattensis*	91	.19	98.88
29	*Odostomia bisuturalis*	73	.15	99.03
30	*Rudilemboides* sp.	48	.10	99.13
31	*Hippolyte pleuracantha*	44	.09	99.22
32	*Mitrella lunata*	40	.08	99.30
32	*Idotea baltica*	40	.08	99.39
34	*Mya arenaria*	35	.07	99.46
35	*Exogone dispar*	31	.06	99.52
35	*Polycerella conyma*	31	.06	99.59
37	*Tenellia fuscata*	23	.05	99.63

Table 4 (Continued)

Rank By No.	Species	No.	% Fauna	Cumul. %
38	*Doridella obscura*	18	.04	99.67
39	*Pista palmata*	17	.04	99.71
40	*Corophium acherusicum*	14	.03	99.73
40	*Callipallene brevirostris*	14	.03	99.76
42	*Neomysis americana*	13	.03	99.79
42	*Paracaprella tenuis*	13	.03	99.82
44	*Odontosyllis fulgurans*	10	.02	99.84
44	*Corophium simile*	10	.02	99.88
46	*Anadara transversa*	8	.02	99.88
47	*Ampelisca* sp.	7	.01	99.89
47	*Colomastix* sp.	7	.01	99.90
49	*Prionospio heterobranchia*	6	.01	99.92
50	*Amphiporus ochraceus*	5	.01	99.93
51	*Edotea triloba*	4	.01	99.94
51	*Palaemonetes pugio*	4	.01	99.94
53	*Amphiporus caecus*	3	.01	99.95
53	*Odostomia dux*	3	.01	99.96
53	*Leptochelia savignyi*	3	.01	99.96
56	*Nereiphylla fragilis*	2		
56	*Hermaea cruciata* (?)	2		99.97
56	*Palaemonetes vulgaris*	2		
59	*Diadumene leucolena*	1		
59	*Tetrastemma jeani*	1		
59	*Eumida sanguinea*	1		99.98
59	*Anachis avara*	1		
59	*Nassarius obsoletus*	1		
59	*Nassarius vibex*	1		
59	*Cratena pilata* (?)	1		
59	*Ampelisca abdita*	1		
59	*Ampelisca vadorum*	1		99.99
59	*Melita appendiculata*	1		
59	*Callinectes sapidus*	1		
59	*Neopanope texana sayi*	1		100.00

Table 5. Ranking by abundance of species collected at station B. Percent of total fauna and cumulative percent are indicated for each species.

Rank By No.	Species	No.	% Fauna	Cumul. %
1	*Bittium varium*	9927	21.70	21.70
2	*Paracerceis caudata*	7036	15.38	37.08
3	*Crepidula convexa*	6026	13.17	50.25
4	*Erichsonella attenuata*	3685	8.05	58.30
5	*Brania clavata*	2237	4.89	63.19
6	*Ampithoe longimana*	2020	4.42	67.60
7	*Elasmopus laevis*	1925	4.21	71.81
8	*Polydora ligni*	1858	4.06	75.87
9	*Stiliger fuscata*	1705	3.73	79.60
10	*Cymadusa compta*	1432	3.13	82.73
11	*Aiptasiomorpha luciae*	984	2.15	84.88
12	*Elysia catula*	711	1.55	86.43
13	*Odostomia impressa*	680	1.49	87.92
14	*Caprella penantis*	612	1.34	89.26
15	*Nereis succinea*	543	1.89	90.44
16	*Platynereis dumerilii*	525	1.15	91.59
17	*Euplana gracilis*	519	1.13	92.73
18	*Sabella microphthalma*	502	1.10	93.82
19	*Podarke obscura*	409	.89	94.72
20	*Balanus improvisus*	302	.66	95.38
21	*Gammarus mucronatus*	272	.59	95.97
22	*Urosalpinx cinerea*	247	.54	96.51
23	*Corophium acherusicum*	157	.34	96.85
24	*Molgula manhattensis*	149	.33	97.18
25	*Stylochus ellipticus*	115	.25	97.43
26	*Mitrella lunata*	109	.24	97.67
27	*Paracaprella tenuis*	103	.23	97.90
28	*Tetrastemma elegans*	94	.21	98.10
29	*Odostomia bisuturalis*	89	.19	98.29
30	*Hydroides hexagona*	69	.15	98.45
31	*Triphora nigrocincta*	65	.14	98.59
32	*Zygonemertes virescens*	64	.14	98.73
33	*Melita appendiculata*	53	.12	98.84
34	*Colomastix* sp.	49	.11	98.95
35	*Rudilemboides* sp.	47	.10	99.05
36	*Hippolyte pleuracantha*	45	.10	99.15
36	*Callipallene brevirostris*	45	.10	99.25

Table 5 (Continued)

Rank By No.	Species	No.	% Fauna	Cumul. %
38	Exogone dispar	40	.09	99.34
39	Neomysis americana	39	.09	99.42
40	Idotea baltica	36	.08	99.50
41	Corophium simile	28	.06	99.56
42	Polycerella conyma	27	.06	99.62
43	Tenellia fuscata	15	.03	99.65
44	Ampelisca sp.	14	.03	99.68
45	Prionospio heterobranchia	13	.03	99.71
45	Anadara transversa	13	.03	99.74
47	Odontosyllis fulgurans	12	.03	99.77
47	Ampelisca vadorum	12	.03	99.79
49	Lepidonotus variabilis	10	.02	99.82
50	Doridella obscura	9	.02	99.84
51	Turbellarian #2	7	.02	99.85
51	Neopanope texana sayi	7	.02	99.87
53	Amphiporus ochraceus	6	.01	99.88
53	Mya arenaria	6	.01	99.89
55	Anachis avara	5	.01	99.90
55	Edotea triloba	5	.01	99.91
57	Nereiphylla fragilis	4	.01	99.92
57	Batea catharinensis	4	.01	99.93
59	Pista palmata	3	.01	99.94
59	Ampelisca abdita	3	.01	99.94
59	Palaemonetes vulgaris	3	.01	99.95
62	Tubulanus pellucidus	2		
62	Eupleura caudata	2		
62	Nassarius vibex	2		99.96
62	Doris verrucosa	2		
62	Mysidopsis bigelowi	2		99.97
62	Stenothoe gallensis	2		
62	Stenothoe minuta	2		99.98
69	Turbellarian #3	1		
69	Eumida sanguinea	1		
69	Odostomia dux	1		
69	Turbonilla interrupta	1		99.99
69	Ericthonius brasiliensis	1		
69	Melita nitida	1		
69	Crangon septemspinosa	1		
69	Dipteran larva	1		100.00

Table 6. Ranking by abundance of species collected at station C. Percent of total fauna and cumulative percent are indicated for each species.

Rank By No.	Species	No.	% Fauna	Cumul. %
1	Bittium varium	26415	36.17	36.17
2	Polydora ligni	5805	7.95	44.12
3	Paracerceis caudata	3809	5.22	49.33
4	Elasmopus laevis	3482	4.77	54.10
5	Erichsonella attenuata	3375	4.62	58.72
6	Crepidula convexa	2915	3.99	62.71
7	Caprella penantis	2740	3.75	66.46
8	Stiliger fuscata	2361	3.23	69.70
9	Balanus improvisus	2359	3.23	72.93
10	Molgula manhattensis	1995	2.73	75.66
11	Sabella microphthalma	1816	2.49	78.15
12	Odostomia impressa	1747	2.39	80.54
13	Gammarus mucronatus	1689	2.31	82.85
14	Nereis succinea	1453	1.99	84.84
15	Brania clavata	1439	1.97	86.81
16	Ampithoe longimana	1290	1.77	88.58
17	Elysia catula	854	1.17	89.75
18	Cymadusa compta	798	1.09	90.84
19	Podarke obscura	784	1.07	91.91
20	Platynereis dumerilii	578	.79	92.70
21	Euplana gracilis	459	.63	93.33
22	Mitrella lunata	446	.61	93.94
23	Batea catharinensis	411	.56	94.51
24	Urosalpinx cinerea	350	.48	94.98
25	Odostomia bisuturalis	339	.46	95.45
26	Melita appendiculata	329	.45	95.90
27	Hydroides hexagona	291	.40	96.30
28	Idotea baltica	272	.37	96.67
29	Stylochus ellipticus	261	.36	97.03
30	Doridella obscura	260	.36	97.38
31	Neomysis americana	209	.29	97.67
32	Zygonemertes virescens	155	.21	97.88
33	Hippolyte pleuracantha	155	.21	98.09
34	Aiptasiomorpha luciae	146	.20	98.29
35	Corophium acherusicum	135	.18	98.48
36	Tetrastemma elegans	129	.18	98.66
37	Odontosyllis fulgurans	99	.14	98.79

Table 6 (Continued)

Rank By No.	Species	No.	% Fauna	Cumul. %
38	*Triphora nigrocincta*	85	.12	98.91
38	*Corophium simile*	85	.12	99.02
40	*Mysidopsis bigelowi*	77	.11	99.13
41	*Ampelisca vadorum*	71	.10	99.23
42	*Edotea triloba*	55	.08	99.30
43	*Colomastix* sp.	54	.07	99.38
44	*Exogone dispar*	45	.06	99.44
45	*Ampelisca* sp.	43	.06	99.50
46	*Rudilemboides* sp.	42	.06	99.55
47	*Anadara transversa*	33	.05	99.60
48	*Lepidonotus variabilis*	32	.04	99.64
49	*Ampelisca abdita*	31	.04	99.68
50	*Polycerella conyma*	30	.04	99.73
51	*Paracaprella tenuis*	28	.04	99.76
52	*Pista palmata*	23	.03	99.80
52	*Callipallene brevirostris*	23	.03	99.83
54	*Tenellia fuscata*	20	.03	99.85
55	*Amphiporus ochraceus*	13	.02	99.87
55	*Odostomia dux*	13	.02	99.89
57	Neopanope *texana sayi*	12	.02	99.91
58	*Nereiphylla fragilis*	10	.01	99.92
59	*Stenothoe minuta*	7	.01	99.93
60	*Nassarius vibex*	6	.01	99.94
61	*Mya arenaria*	4	.01	99.94
62	*Anachis avara*	3		99.95
62	*Doris verrucosa*	3		
62	*Monoculodes edwardsi*	3		
62	*Crangon septemspinosa*	3		99.96
62	*Palaemoneles pugio*	3		
67	*Eteone heteropoda*	2		
67	*Eumida sanguinea*	2		99.97
67	*Potamilla neglecta*	2		
67	*Caprella equilibra*	2		
71	*Turbellarian* #3	1		
71	*Turbellarian* #1	1		
71	*Tetrastemma jeani*	1		
71	*Tetrastemma vermiculus*	1		99.98
71	*Tubulanus pellucidus*	1		
71	*Prionospio heterobranchia*	1		
71	*Sabellaria vulgaris*	1		
71	*Scoloplos fragilis*	1		
71	*Ichthyobdella rapax*	1		
71	*Crepidula plana*	1		

Table 6 (Continued)

Rank By No.	Species	No.	% Fauna	Cumul. %
71	*Eupleura caudata*	1		
71	*Haminoea solitaria*	1		99.99
71	*Turbonilla interrupta*	1		
71	*Oxyurostylis smithi*	1		
71	*Corophium tuberculatum*	1		
71	*Ericthonius brasiliensis*	1		
71	*Lysianopsis alba*	1		
71	*Libinia dubia*	1		100.00

study area, Crepidula convexa ranked first (16.3% of fauna) at station A, third (13.2%) at station B and sixth (4.0%) at station C. Correspondingly, Ampithoe longimana ranked 3rd (14.9%), 6th (4.4%) and 16th (1.8%). Other common species were more abundant at greater depths. Caprella penantis ranked 21st (0.3%), 14th (1.3%) and 7th (3.8%) at stations A, B and C, respectively, while corresponding rankings for Polydora ligni were 14th (0.9%), 8th (4.1%) and 2nd (8.0%); and for Balanus improvisus, 27th (0.2%), 20th (0.7%) and 9th (3.2%).

Another way of ranking is shown in Tables 7-9. The eight most abundant animals in each sample, regardless of absolute numbers, were scored such that the first-ranked received eight points, the second-ranked, seven, . . ., etc. The dominant forms at each station were then ranked in accordance with a "biological index value" (Sanders, 1960) which is the sum of the scores in each sample. At stations A and B the four highest scoring species (though not in the same order) were Bittium varium, Crepidula convexa, Paracerceis caudata and Erichsonella attenuata, while at station C, Caprella penantis replaced Crepidula convexa which dropped to fifth position.

The biological index value is determined both by frequency of occurrence and by absolute abundance. Consequently, those species which were very abundant for only brief periods tended to rank lower on this scale than on one based solely on numbers. For example, Polydora ligni ranked second in abundance at station C but eighth in biological index value.

Table 7. Biological Index Ranking of Species at Station A.

Collection Date	1 Nov	1 Dec	5 Jan	6 Feb	5 Mar	29 Mar	19 Apr	13 May	5 Jun	28 Jun	22 Jul	19 Aug	13 Sep	8 Oct	6 Nov	3 Dec	Bio Index Value
Crepidula convexa	8	8	8	7	8	6	8	7	8	6	5	8	4	3	5	5	104
Paracerceis caudata	7	7	7	8	6	8	5	5	6	4	6	6	8	5	6	6	100
Bittium varium	5	6	3	6		7	6	8	7	7	7	7	7	6	8	8	98
Erichsonella attenuata	6	5	6	5	7	5	3	4	3					4	7	7	62
Elasmopus laevis	4		5	3	2	2			5	5	2	4	1			1	34
Brania clavata							7		4	8	4	2	6	2			33
Ampithoe longimana		1	2		1	1					8	5		8	2		28
Cymadusa compta			4	2	4								5	7	1	3	26
Elysia catula	2	3				4	1	6	1							3	20
Gammarus mucronatus			1	4	3	3	2										13
Caprella penantis	1	4			6												11
Platynereis dumerilii														1	3	4	8
Sabella microphthalma											1	3	3				7
Aiptasiomorpha luciae												1	2		4		7
Euplana gracilis									2	1	3						6
Stylochus ellipticus	4	2															6

Table 7. (Continued)

Collection Date	1 Nov	1 Dec	5 Jan	6 Feb	5 Mar	29 Mar	19 Apr	13 May	5 Jun	28 Jun	22 Jul	10 Aug	13 Sep	8 Oct	6 Nov	3 Dec	Bio Index Value
Polydora ligni							4										4
Balanus improvisus								3									3
Stiliger fuscata										3							3
Hippolyte pleuracantha				2													2
Tetrastemma [illegible]								2									2
Nereis succinea										2							2
[illegible] *impressa*								1									1

Table 8. Biological Index Ranking of Species at Station B.

Collection Date	1 Nov	1 Dec	5 Jan	6 Feb	5 Mar	29 Mar	19 Apr	13 May	5 Jun	28 Jun	22 Jul	10 Aug	13 Sep	8 Oct	5 Nov	3 Dec	Bio-Index Value
Bittium varium	3	4		3	2	8	6	8	8	8	8	7	8	7	8	8	96
Paracerceis caudata	8	8	5	8	7	7	3	4	1	4	5	6	7	8	5	7	94
Erichsonella attenuata	7	6	8	7	6	6	4	5	5	3	4	3	2	4	7	6	83
Crepidula convexa	6	7	6	4	5	3	5	7	4	7	6	8	6		3	4	81
Elasmopus laevis	5		2	2		2			6	5	2	4	3	3		1	35
Caprella penantis	4	5	7	6	8	5											35
Brania clavata							7		7	6			4				24
Elysia catula	3	1				4	1	3							5	5	22
Ampithoe longimana		3	3		2						3			6	2		19
Gammarus mucronatus			1	5	3	1	2	2									14
Cymadusa compta			4	2										5	1		12
Polydora ligni							8	2						2			12
Aiptasiomorpha luciae												5	5	1			11
Balanus improvisus								7	3								10
Stiliger fuscata										2	7						9
Platynereis dumerilii															4	3	7

Table 8. (Continued)

Collection Date	1 Nov	1 Dec	5 Jan	6 Feb	5 Mar	29 Mar	19 Apr	13 May	5 Jun	28 Jun	22 Jul	19 Aug	13 Sep	8 Oct	6 Nov	3 Dec	Bio Index Value
Stylochus ellipticus	1	3															4
Nereis americana					4												4
Setella microphthalma												2	1				3
Eupleura gracilis									2	1							3
Mitrella lunata																2	2
Odostomia impressa											1						1
Urosalpinx cinerea												1					1

Table 9. Biological Index Ranking of Species from Station C.

Collection Date	1 Nov	1 Dec	5 Jan	6 Feb	5 Mar	29 Mar	19 Apr	13 May	5 Jun	28 Jun	22 Jul	19 Aug	13 Sep	8 Oct	6 Nov	3 Dec	Bio Index Value
Bittium varium	1	6	4	5	2	7	7	6	7	8	8	8	8	8	8	8	101
Erichsonella attenuata	7	7	6	6	5	6	3	2	3			4	6	6	7	6	74
Caprella penantis		8	8	8	8	8	6	5	6						3	3	63
Paracerceis caudata	6		2	7	4	2					1	6	7	7	6	7	55
Crepidula convexa	2	5	1	2	1		4			4	5	3	2	2	4	4	39
Elasmopus laevis	5	2	3	3			1		5	1	4	7	3				34
Gammarus mucronatus			5	4	7	5	2	3	4		2						32
Polydora ligni							8	8	2					4			22
Ampithoe longimana		3			3									5	2		17
Balanus improvisus		2						7	8								17
Brania clavata							5	4		6			1				16
Neomysis americana			7	1	6	1											15
Odostomia impressa											3	2	4	3			12
Elysia catula										2					5	5	12
Stiliger fuscata										5	7						12
Mitrella lunata		5				3		1								2	11

Table 9. (Continued)

Collection Date	1 Nov	1 Dec	5 Jan	6 Feb	5 Mar	29 Mar	19 Apr	13 May	5 Jun	28 Jun	22 Jul	19 Aug	13 Sep	8 Oct	6 Nov	3 Dec	Bio Index Value
Sabella microphthalma												5	5				10
Molgula manhattensis										3	6						9
Nereis succinea									1	7				1			9
Batea catharinensis	8																8
Platynereis dumerilii						4									2	1	7
Cymadusa compta	4																4
Stylochus ellipticus	3																3
Euplana gracilis									1								1
Melita appendiculata												1					1

Faunal Affinity

A community consists of species which show a high degree of recurrence. The faunal similarity between stations on each collection date was determined by Sander's (1960) index of affinity, which is the sum of the smallest percentage frequencies of species present in both samples.

Duncan's new multiple-range test (Steel and Torrie, 1960) indicated significant differences ($P < 0.05$) in average faunal affinity between station pairs (Table 10). Stations A and B showed the highest average affinity (69.9%), followed by stations B and C (58.3%) and stations A and C (46.1%). The relative distinctiveness of station C was also generally manifested in the appearance of the eelgrass, its biomass and abundance of certain algal epiphytes.

Unusually low affinities between stations A and C and stations B and C on 13 May (Table 10; Fig. 33) were caused in part by the heavy concentration at the deepest station of recently-set *Polydora ligni* and *Balanus improvisus*.

The number of species collected from stations A, B and C (70, 76 and 88, respectively) and the average number of organisms/g of *Zostera* (96.8, 114.3 and 192.4, respectively) suggest that depth, either directly or indirectly, influences the composition of the eelgrass community.

Table 10. Percentage faunal affinity between station pairs.

Collecting Period	Station Pairs		
	A - B	B - C	A - C
1 Nov 67	63.0	48.6	40.8
1 Dec 67	76.6	43.6	46.0
5 Jan 68	53.6	52.0	31.7
6 Feb 68	74.5	64.6	52.4
5 Mar 68	53.8	64.7	41.6
29 Mar 68	76.1	56.1	42.4
19 Apr 68	64.6	75.0	50.8
13 May 68	73.2	29.7	14.5
5 Jun 68	70.3	52.8	41.4
28 Jun 68	74.7	64.5	57.3
22 Jul 68	47.9	69.4	41.0
19 Aug 68	81.0	57.2	52.3
13 Sep 68	76.8	58.9	47.4
8 Oct 68	67.0	52.7	38.3
6 Nov 68	.76.6	69.7	72.8
3 Dec 68	83.3	73.3	66.3
$\bar{x}$	69.6	58.3	46.1

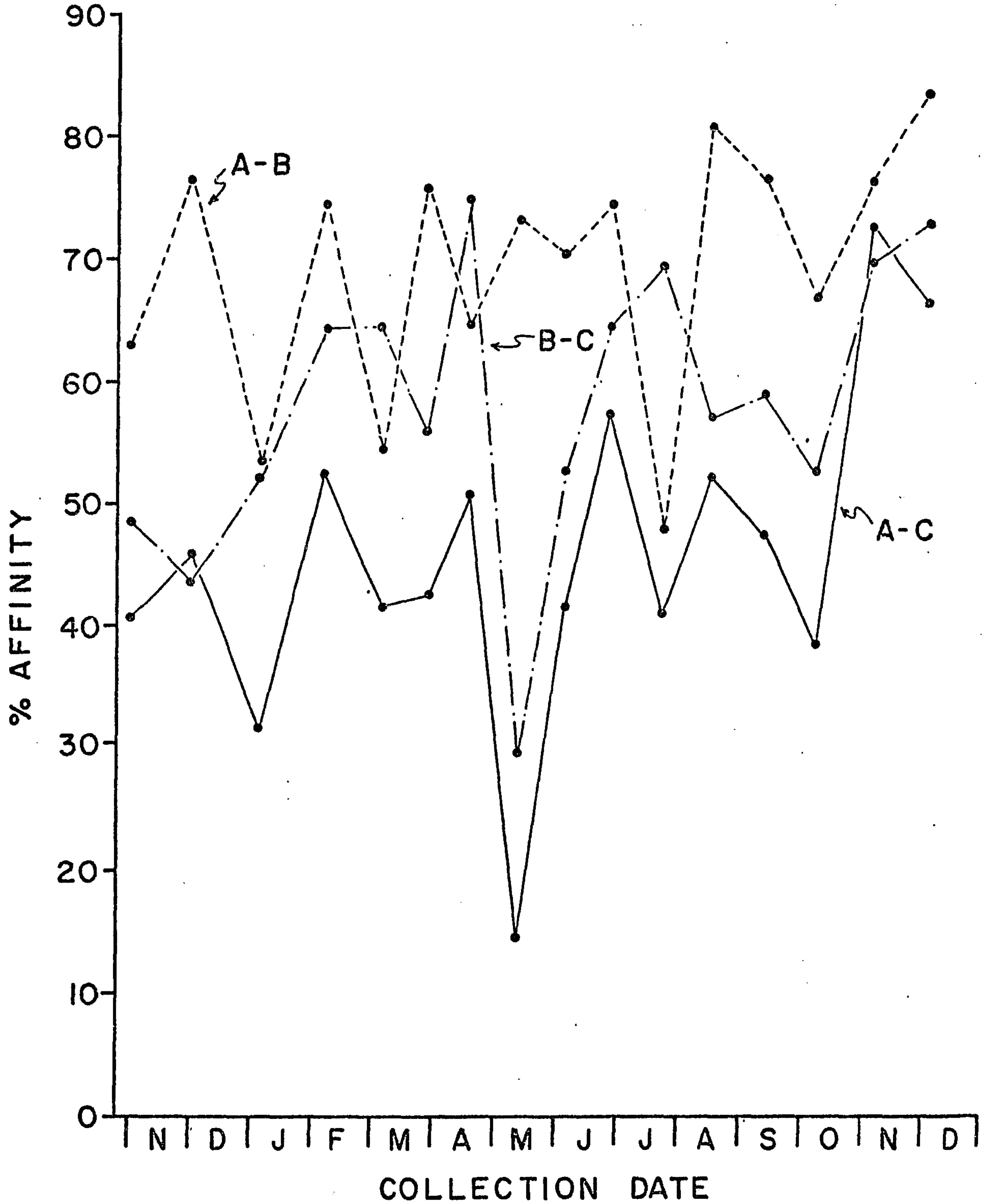


Fig. 33. Percentage faunal affinity between station pairs.

Diversity

A basic parameter of community structure is that of species diversity. Although the term has been used simply to indicate the absolute number of species within an area (Connell and Orias, 1964; Hessler and Sanders, 1967), an additional component is usually recognized, that of the apportionment of individuals among species. A hypothetical community in which most of the species are almost equally abundant is more diverse than one dominated by one or a few forms with the others being poorly represented. A commonly used diversity index (Patten, 1962; Lloyd and Ghelardi, 1964; MacArthur, 1965; Lie, 1968; Margalef, 1968; Sanders, 1968; Wilhm and Dorris, 1968) which is relatively independent of sample size, yet sensitive to both the number of forms present and the equitability of their distribution, is the information function of Shannon (Shannon and Weaver, 1963):

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

where H' = diversity in bits of information/individual

s = total number of species

p_i = n_i/n, the proportion of the sample belonging to the i^{th} species

A measure of the equitability component of diversity (ϵ), based on MacArthur's (1957) model describing a theoretical distribution of individuals among species, is provided by Lloyd and Ghelardi (1964):

$$\epsilon = s'/s$$

where ϵ = sample estimate of equitability

s' = number of equitably distributed species required to conform to MacArthur's model, given H'.

s = observed number of species

Diversity values ranged from 1.92 to 3.90 bits/individual with means of 2.97, 3.11 and 3.03 at stations A, B and C, respectively (Table 11). Average H' for all samples was 3.04. The unusually low value of 1.92, which occurred at station C in May, is attributable to the great abundance there of *Balanus improvisus* and *Polydora ligni*, which together composed approximately 42% of the sample. Both species were relatively uncommon at stations A and B.

Equitability values ranged from 0.17 to 0.73 and averaged 0.43, 0.40 and 0.36 at stations A, B and C, respectively (Table 11). Mean ϵ for all stations was 0.40. These generally low values indicate a relatively inequitable distribution of individuals among species.

Although the number of species found at each station was generally lower during winter and spring and higher during summer and fall, there was no evidence of a marked seasonal change in H' (Fig. 34). Low species numbers were often counteracted by relatively high ϵ values which tended to damp any decrease in H' (Figs. 35-37). Sager and Hassler (1969) showed that, at least for lacustrine phytoplankton populations, rare species have little effect on Shannon's index and that the major influence is the relative abundance of the most common species.

Table 11. Numbers of Species (S), Equitabilities (ε) and Diversities (H′) for all *Zostera* samples.

Date	Station A			Station B			Station C		
	S	ε	H′	S	ε	H′	S	ε	H′
1 Nov	27	0.26	2.44	34	0.26	2.67	38	0.58	3.90
1 Dec	19	0.58	2.92	25	0.36	2.71	33	0.58	3.73
5 Jan	19	0.37	2.36	26	0.54	3.31	28	0.43	3.05
6 Feb	19	0.47	2.69	22	0.59	3.19	29	0.41	3.12
5 Mar	16	0.69	2.93	15	0.73	2.89	17	0.53	2.77
29 Mar	26	0.38	2.83	26	0.38	3.23	27	0.33	2.69
19 Apr	27	0.48	3.12	30	0.27	2.62	27	0.30	2.46
13 May	27	0.37	2.81	29	0.41	3.00	29	0.17	1.92
5 Jun	34	0.47	3.48	34	0.59	3.80	37	0.46	3.54
28 Jun	40	0.43	3.53	41	0.29	3.13	45	0.40	3.67
22 Jul	37	0.41	3.40	41	0.34	3.24	50	0.28	3.26
19 Aug	35	0.40	3.24	36	0.28	2.88	51	0.25	3.23
13 Sep	30	0.53	3.45	41	0.34	3.33	45	0.18	2.54
8 Oct	35	0.37	3.14	47	0.40	3.74	52	0.19	2.85
6 Nov	27	0.33	2.65	39	0.36	3.32	30	0.43	3.16
3 Dec	20	0.40	2.55	29	0.31	2.70	34	0.26	2.65
$\bar{x}$	26.7	0.43	2.97	32.1	0.40	3.11	35.7	0.36	3.03

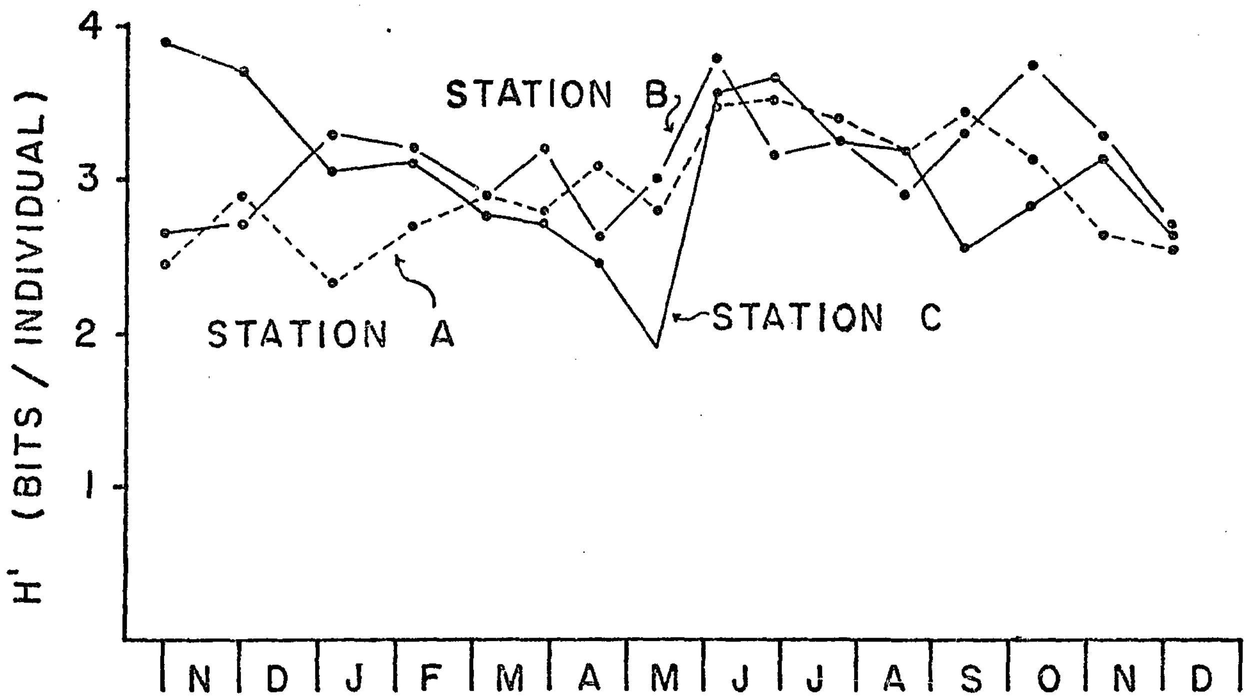


Fig. 34. Sample diversity values (H′).

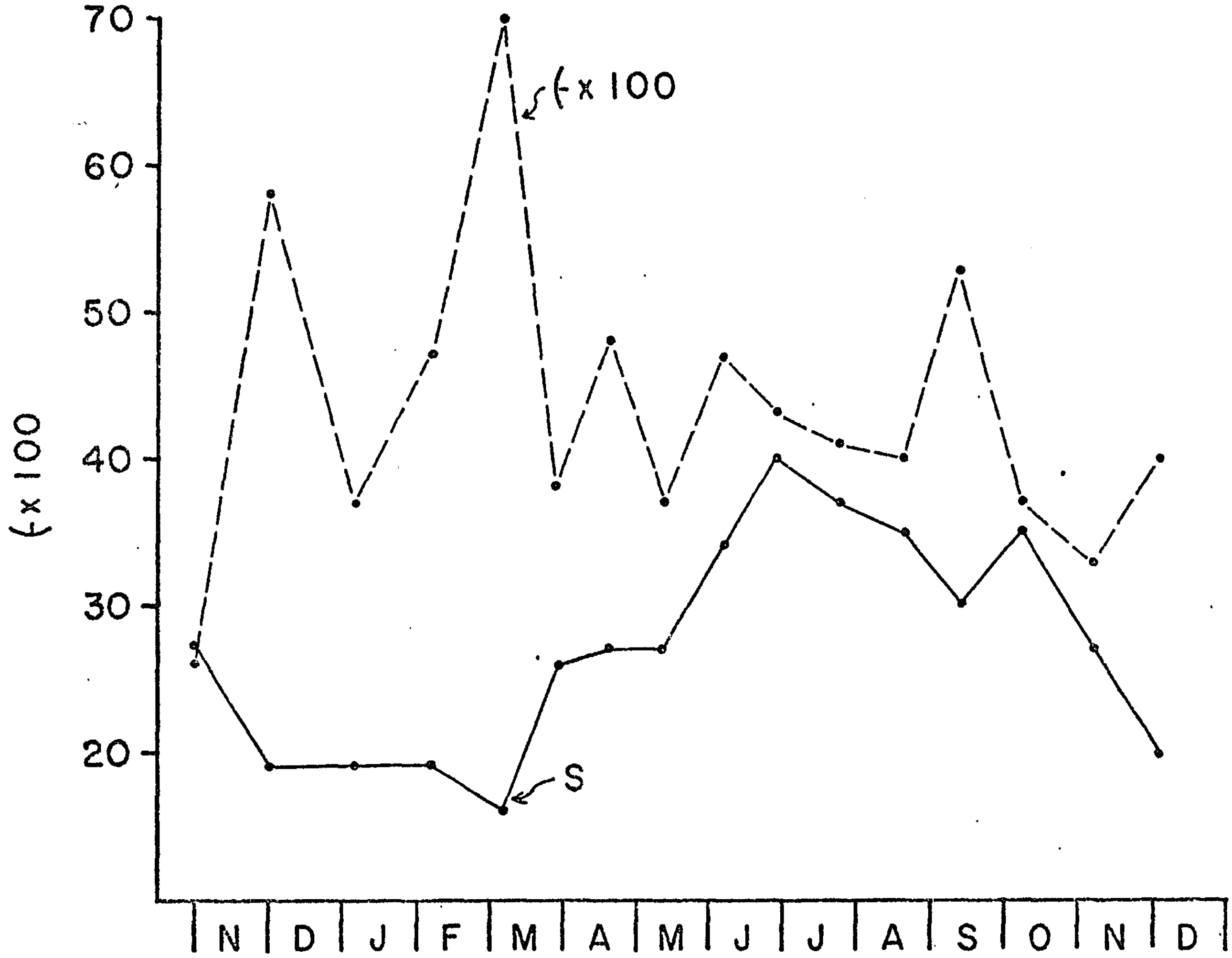


Fig. 35. Seasonal changes in number of species (S) and equitability (ϵ x 100) at station A.

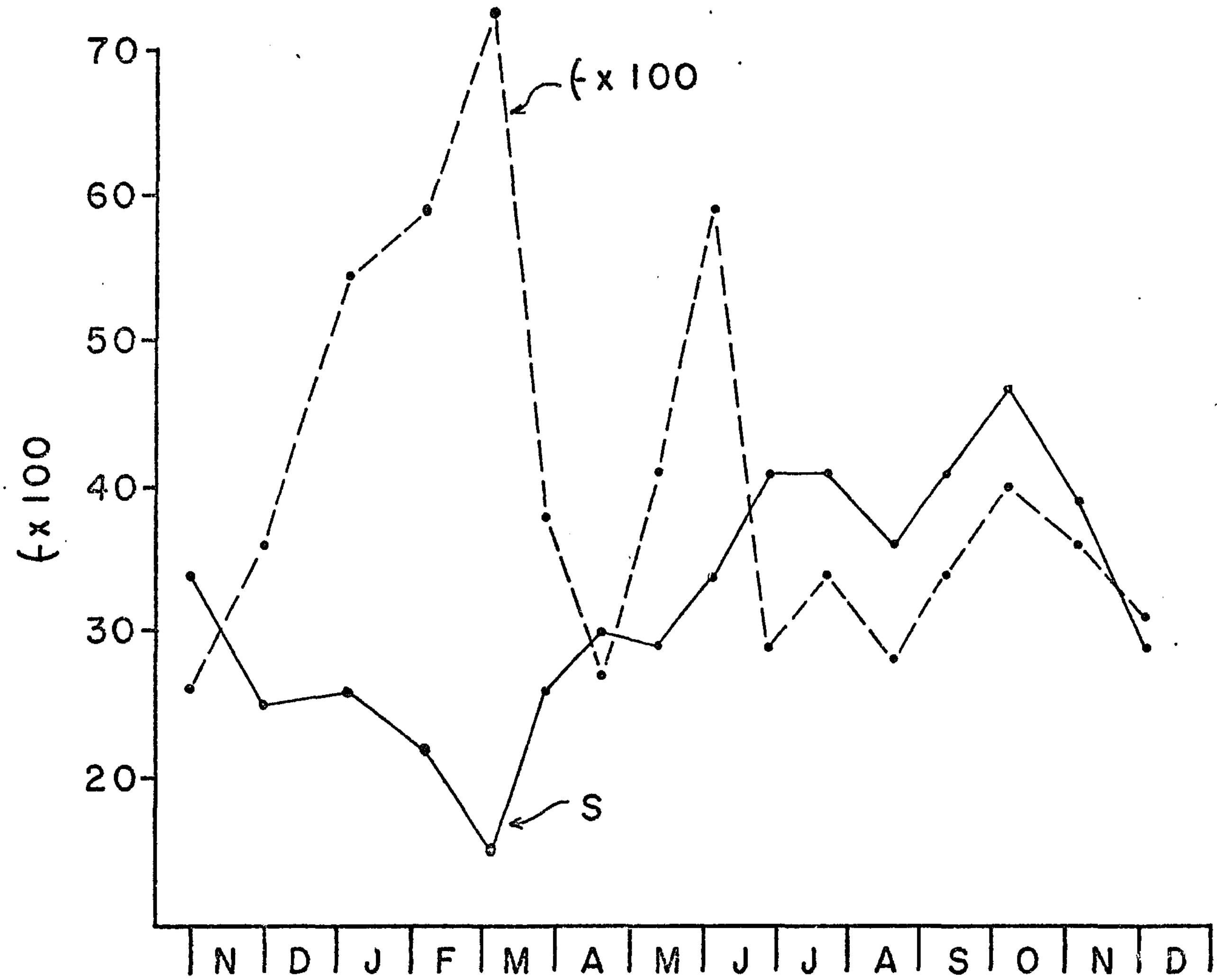


Fig. 36. Seasonal changes in number of species (S) and equitability (⨍ x 100) at station B.

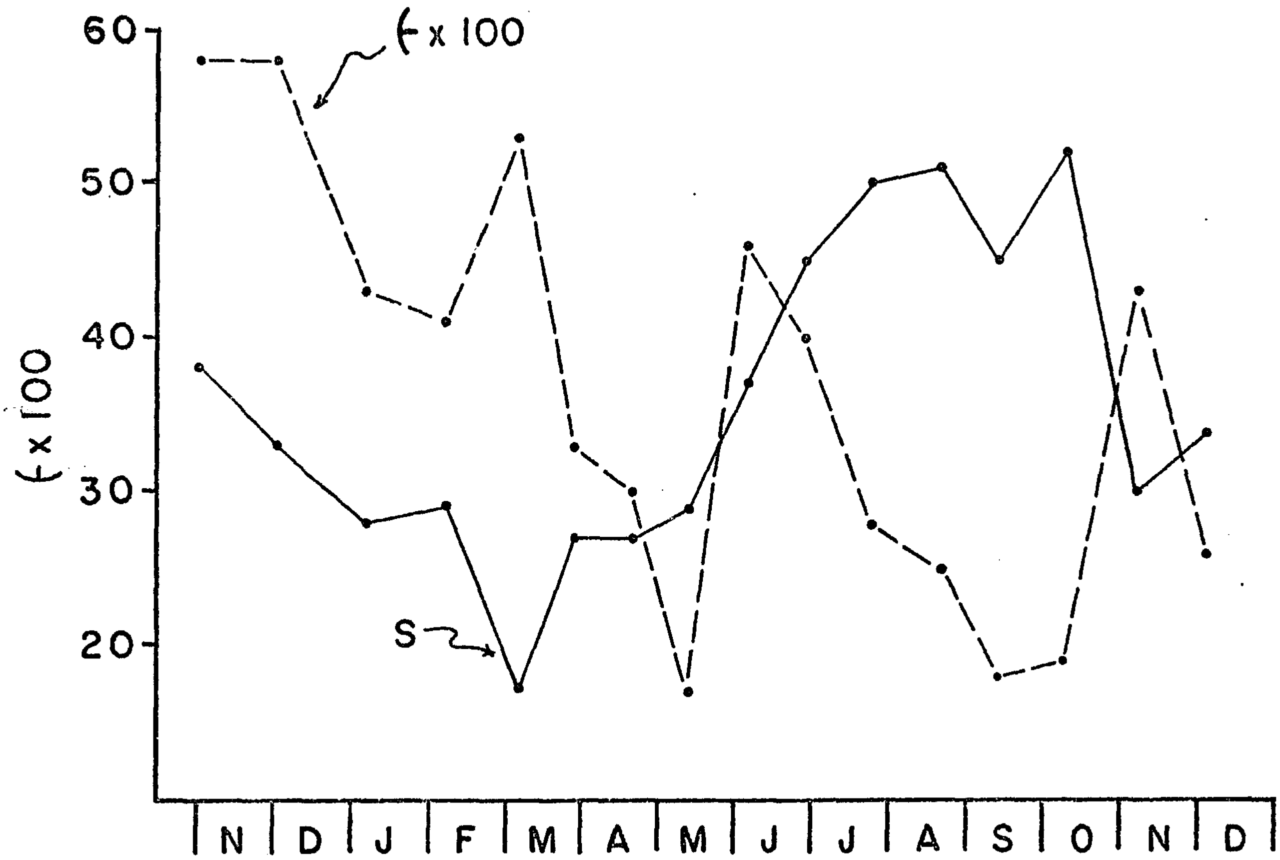


Fig. 37. Seasonal changes in number of species (S) and equitability (ϵ x 100) at station C.

DISCUSSION

The *Zostera* Community

There have been numerous attempts to define and characterize marine communities, or even to demonstrate their existence as discrete entities. No single viewpoint has gained general acceptance. Whether biotic associations are primarily biologically determined, exhibiting a high degree of interrelationship among species, or whether these assemblages are largely statistical units, determined primarily by chemical and physical factors, has been the subject of much controversy (see Jones, 1969). Fager (1963) emphasized that both the structural and functional aspects of communities must be elucidated before a complete understanding is possible. Because of the diversity of phenomena involved, Mills (1969) stressed the impossibility of defining communities in rigorous terms and proposed that the concept be applied simply to groups of organisms "occurring in a particular habitat, presumably interacting with each other and the environment, and separable by means of ecological survey from other groups." Even less restrictive is Fager's (1963) operational definition of a community as "a group of species which are often found living together."

Accordingly, it seems entirely appropriate to regard the biota living on *Zostera* as a distinct community. This does not imply that eelgrass communities everywhere, or even in the York River, have exactly the same species composition. Certain forms drop out and are replaced where environmental conditions differ. Nevertheless, a close structural similarity probably exists among the epibiotic communities of Zostera wherever the plant occurs, as similar or closely-related species fill the same ecological niches. Perusal of Ledoyer's (1962) list of fauna collected from Zostera and other seagrasses in the Mediterranean revealed a high incidence of forms congeneric or conspecific with those found in the York River. The faunal similarities are especially significant in view of the disparate hydrographic conditions of the two localities. Ledoyer (1964a) emphasized the "homogenéite spécifique remarquable" between the motile fauna of the marine phanerogams in the Mediterranean and in the English Channel.

In studies of this type, limits must be imposed on what portion of the community can feasibly be sampled. With the inclusion in at least portions of my analysis of colonial forms and epiphytes (both frequently neglected in such studies), an approach is made to a study of the whole community. Many organisms, however, such as diatoms, nematodes, ostracods, copepods and other small invertebrates, were not retained by a 0.5 mm mesh and were thereby excluded from consideration.

One of the advantages of studying Zostera epibiota is that the community lends itself to direct observation, permitting a more complete understanding of events than is possible in infaunal studies. Insights into the natural history of many forms may be gained with the aid of a face mask and snorkel. Also, the community is clearly delimited from others in the area. There are no ecotones and most of the fauna is highly characteristic of that habitat. Haven's (1967) seasonal infaunal study, conducted approximately 3 km downriver from Big Mumfort, revealed few species also found among the *Zostera* epifauna. Among the 30 most abundant forms in each study, only one (*Odostomia bisuturalis*) was common to both communities.

A study of *Zostera* epibiota also poses difficulties. Rapid changes in biotic composition necessitate frequent sampling throughout the year, especially during warmer months. Also, changes in the abundance of fauna as expressed in this study are determined not only by changes in absolute numbers but by variations in the availability of their substrate. During spring and early summer, the increase of *Zostera* biomass requires a proportionate increase in the population of a species for its numbers/g of eelgrass to remain constant. In late summer and fall the diminishing supply of eelgrass probably results in the concentration of motile fauna on the remaining plants.

During winter months many of the epifauna apparently move into the bottom sediments. Petersen grab samples taken in early March 1969 from areas free of *Zostera* yielded numerous specimens of *Bittium varium*, *Erichsonella attenuata*, *Paracerceis caudata* and other forms.

The relatively high affinity indices, averaging 58% for all synchronous sample pairs, indicate a generally homogeneous fauna. Other published values include 31.2% affinity for the *Ampelisca* community and 37.2% affinity for the *Nephthys-Nucula* community, both in Buzzards Bay, Mass. (Sanders, 1958). McCloskey (1968) reported affinities from 36.0% to 64.8% between two samples of the *Oculina* coral community from each of four locations. Monthly samples of York River infauna taken at four depths throughout the year yielded average affinities between all synchronous sample pairs from 19.1% to 54.7% (Haven, 1967).

The significance of my diversity values is difficult to assess. Although definite patterns of diversity appear to exist in nature (MacArthur, 1965), caution should be used in comparing values from different studies. Diversities are often highly dependent on screen size (Lie, 1968), since whole groups of organisms may be retained or lost, and geographic variations in diversity are significant only within similar habitats (Sanders, 1968). It is interesting, nevertheless, to compare values obtained in this study with those from other communities. In his study of York River infauna, Haven (1967) reported a range in H' from 2.0 to 4.2, with a yearly mean of 3.50. Samples of the pelagic *Sargassum* community had highly variable diversities ranging from 1.03 to 5.12, with a mean of 2.51 (Fine, 1969). H' calculated from Dexter's (1969) data describing the intertidal sandy beach community was an unusually low 0.95; one species comprised 83.4% of the total fauna. Relatively high yearly mean diversities of 3.99 and 3.75 were obtained at two soft-bottom benthic stations in Arthur Harbor, Antarctica (Lowry, 1969).

Numerous explanations have been offered to explain within- and between-habitat differences in diversity (see Grassle, 1967). Generally, however, diversities appear to correlate with environmental stability (Connell and Orias, 1964; Sanders, 1968; Dexter, 1969). Uniform, low-stress environments seem to foster higher diversities than do those where conditions are highly and irregularly variable. One might expect, therefore, that in *Zostera* communities in the lower York River, where salinities are reduced and variable and where water temperatures may range from near 0 C to over 30 C during the year, diversities would be low compared to those in non-estuarine eelgrass beds. Low equitabilities are characteristic of high-stress environments (Sanders, 1968). In this context, it is perhaps significant that my values ($\bar{\epsilon} = 0.40$) were considerably lower than those reported by Fine (1969) for the epifauna of pelagic *Sargassum* ($\bar{\epsilon} = 0.73$).

Trophic Structure

A community analysis is not complete without reference to the trophic relationships of at least the more common organisms. Although a detailed study of feeding habits was not conducted, some general conclusions, based primarily on information available in the literature, can be made. A somewhat tentative food web involving the epifaunal community is illustrated in Fig. 38.

Three primary food sources were utilized by *Zostera* associates: 1) detritus and microorganisms found on the plant surfaces, 2) suspended particulate organic matter and plankton and 3) epiphytic algae. Of the 22 most abundant species collected, comprising over 95% of the total fauna, 21 were dependent on at least one of these sources; the other (*Odostomia impressa*) was ectoparasitic on various invertebrates. Apparently, none of the

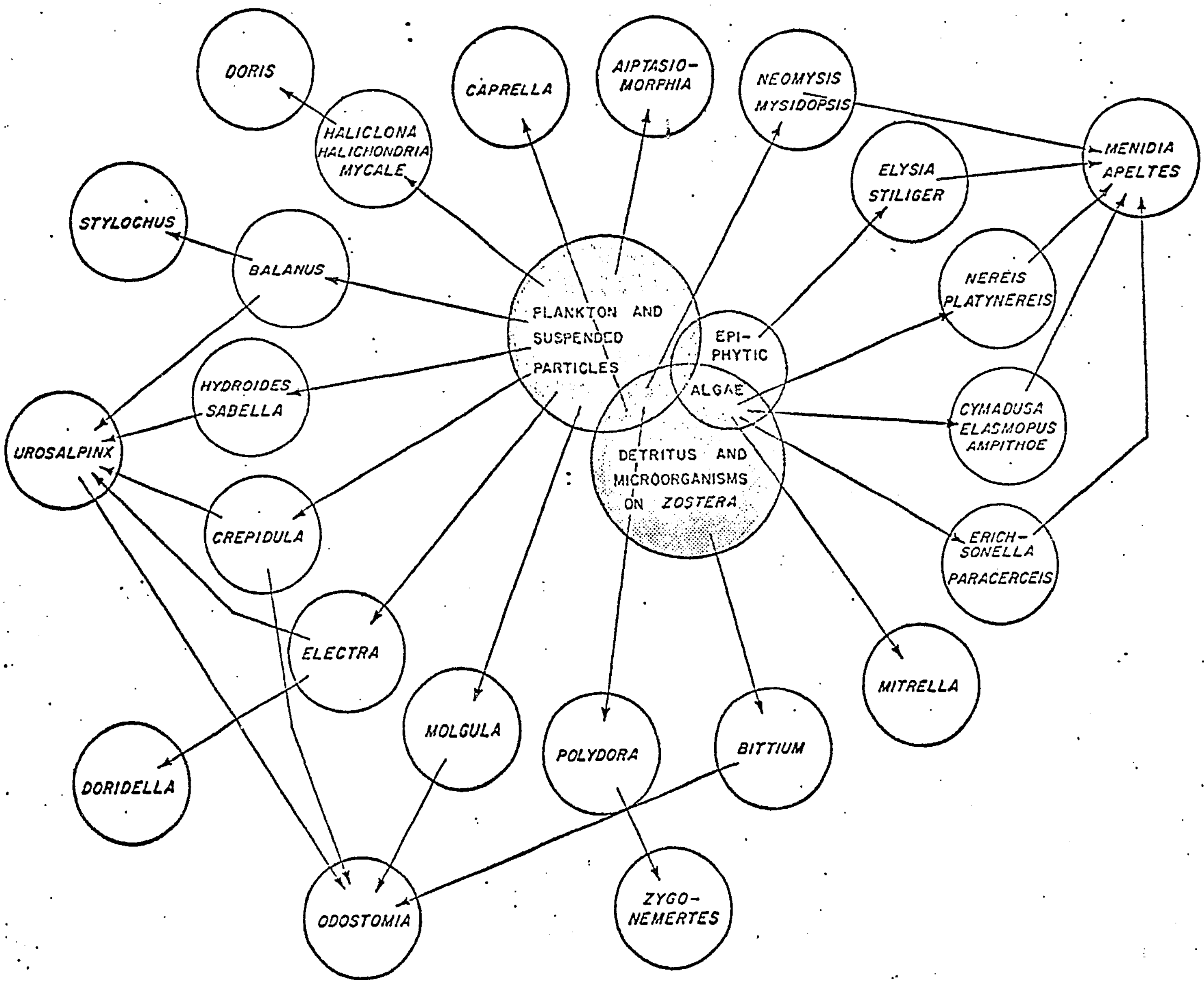


Fig. 38. Presumed trophic relationships of common epifaunal genera.

common species fed to an appreciable extent on living Zostera. A similar conclusion was reached by MacGinitie (1935) in his survey of Zostera associates in Elkhorn Slough, Calif.

Surface scrapings of eelgrass frequently revealed an astonishing number of nematodes, rotifers, diatoms and other microorganisms in addition to considerable quantities of sediment and detritus. This material was grazed by a wide variety of animals, including Bittium varium, Triphora nigrocincta and other detritus-feeding snails, along with numerous amphipod and polychaete species. The isopods Erichsonella attenuata, Paracerceis caudata and Idotea baltica apparently also utilized this food.

Common suspension feeders included sponges, tunicates and bryozoans; the barnacle Balanus improvisus; the polychaetes Hydroides hexagona and Sabella microphthalma; and Crepidula convexa, one of the few filter-feeding gastropods. Many animals, such as the caprellid amphipods, mysid shrimps and the polychaete Polydora ligni, probably fed both on suspended particles and on detrital material investing the plant blades.

The macroscopic algae were apparently not as important food sources as the aforementioned categories but doubtlessly at least supplemented the diet of numerous species, including the polychaetes Platynereis dumerilii and Nereis succinea, numerous small crustaceans and the gastropod Mitrella lunata. The sacoglossans, Elysia catula and Stiliger fuscata, reportedly feed exclusively on filamentous green algae (Hyman, 1967). Epiphytes also served as detritus traps, benefiting many non-herbivorous species.

Urosalpinx cinerea and Odostomia impressa were probably the chief predators among the epifauna; both reportedly (Allen, 1958; Wood, 1968) feed on a wide variety of invertebrates. Other predators included Stylochus ellipticus, whose prey is uncertain, and the nemerteans, chiefly Zygonemertes virescens and Tetrastemma elegans, which feed on polychaetes and other small invertebrates (Barnes, 1968).

Numerous fishes which preyed primarily on epifauna were common during the summer. Most abundant were the common silversides (Menidia menidia), the four-spined stickleback (Apeltes quadracus) and the pipefish (Syngnathous fuscus). Stomach analyses of these and other common species revealed diets consisting chiefly of amphipods, mysids and other small crustaceans. Polychaete worms were less frequently eaten.

SUMMARY

1. The invertebrate macrofauna and epiphytes occurring on *Zostera* in the lower York River, Virginia were sampled with the aid of SCUBA for 14 consecutive months. A collecting station was located at each of three different depths within a single eelgrass bed.

2. Eelgrass attained maximum biomass at each depth in June. Lowest biomass occurred in January and February. Density of plants on the bottom decreased with depth. Plant elongation in spring and early summer was greatest at increased depths.

3. A total of 112 invertebrate species were collected, including 13 new records for Chesapeake Bay. Seasonal abundance, depth distribution and salient aspects of the ecology of each of the more abundant forms are discussed.

4. Twenty-nine species of epiphytic algae were identified, including 8 chlorophytes, 4 phaeophytes and 17 rhodophytes. Distinct summer and winter algal floras were evident.

5. The five most abundant non-colonial invertebrate species (*Bittium varium*, *Paracerceis caudata*, *Crepidula convexa*, *Ampithoe longimana* and *Erichsonella attenuata*), accounted for approximately 59% of the total fauna. These species dominated the epifauna throughout most of the year.

6. Several epifaunal species, including *Balanus improvisus*, *Molgula manhattensis*, *Polydora ligni* and *Stiliger fuscata*, were very abundant for only brief periods.

7. The number of species and the average number of organisms/gram of *Zostera* increased at greater depths in the sampling area.

8. A relatively high average index of affinity between all synchronous sample pairs indicated a generally homogeneous fauna.

9. Diversity values, according to Shannon's information function, ranged from 1.92 to 3.90 bits/individual and averaged 3.04 bits/individual for all stations. No marked seasonal change in diversity was apparent.

10. Presumed trophic relationships of the more common epifaunal species are discussed. The primary sources of nutrition appeared to be (1) plankton and suspended particulate matter, (2) detritus and microorganisms on the plant blades and (3) epiphytic algae. Apparently, none of the common invertebrate species utilized *Zostera* as a primary source of nutrition.

APPENDIX

Table I. Non-colonial Species and Numbers of Individuals Collected From Station A.

Collection Date g Zostera	1 Nov 39.8	1 Dec 22.6	5 Jan 23.4	6 Feb 18.3	5 Mar 18.5	29 Mar 25.7	19 Apr 30.1	13 May 36.4	5 Jun 57.8	28 Jun 64.0	22 Jul 49.3	19 Aug 38.8	13 Sep 22.9	8 Oct 26.6	6 Nov 13.5	3 Dec 12.0
Anthozoa																
Aiptasiomorpha luciae	1								5	8	23	173	179	230	113	1
Diadumene leucolena												1				
Turbellaria																
Euplana gracilis	4	2				1			89	111	665	155	17	241	10	6
Stylochus ellipticus	62	38	4							1					1	3
Nemertea																
Zygonemertes virescens							8	4	25	26	26	17	2	13		
Tetrastemma elegans	2	3				2	10	16	32	28	7	6			1	
Amphiporus ochraceus									3	2						
Amphiporus caecus											3					
Tetrastemma jeani									1							
Polychaeta																
Brania clavata						1	550	2	141	800	696	225	462	470	10	
Sabella microphthalma	11	3	3			1		5		108	376	258	202	212	2	3
Polydora ligni						2	390	12	14	3	1		9	20		
Nereis succinea	1	2	4	2	2	2	5	3	17	122	109	46	33	87	1	1
Podarke obscura								2	9	15	27	41	38	38	1	1
Hydroides hexagona	4						1				2	24	17	64		
Platynereis dumerilii	7	5			2		6	3	12	13	74	45	53	269	61	57

Table I. (Continued)

Collection Date g *Zostera*	1 Nov 39.8	1 Dec 22.6	5 Jan 23.4	6 Feb 18.3	5 Mar 18.5	29 Mar 25.7	19 Apr 30.1	13 May 36.4	5 Jun 57.8	28 Jun 64.0	22 Jul 49.3	19 Aug 38.8	13 Sep 22.9	8 Oct 26.6	6 Nov 13.5	3 Dec 12.0
Polychaeta (Cont.)																
Exogone																
dispar										7	8	4	5	7		
Pista																
palmata											6	3		5	3	
Odontosyllis																
fulgurans													2	8		
Prionospio																
heterobranchia								1		4			1			
Nereiphylla																
fragilis												1	1			
Eumida																
sanguinea										1						
Prosobranchia																
Crepidula																
convexa	913	297	516	136	105	242	583	330	540	451	721	1789	232	581	238	186
Bittium																
varium	107	85	35	46	6	329	516	346	242	772	921	1050	584	1046	812	556
Urosalpinx																
cinerea	16						21	10	15	21	26	32	11	14	3	
Triphora																
nigrocincta										2	2	2		84	17	17
Mitrella																
lunata	1			2		1	10	3	4	3	1	2	5		2	6
Anachis																
avara													1			
Nassarius																
obsoletus						1										
Nassarius																
vibex												1				
Opisthobranchia																
Elysia																
catula	31	52	5	6		91	92	90	69	9	15	8			11	26

Table I. (Continued)

Collection Date g Zostera	1 Nov 39.8	1 Dec 22.6	5 Jan 23.4	6 Feb 18.3	5 Mar 18.5	29 Mar 25.7	19 Apr 30.1	13 May 36.4	5 Jun 57.8	28 Jun 64.0	22 Jul 49.3	19 Aug 38.8	13 Sep 22.9	8 Oct 26.6	6 Nov 13.5	3 Dec 12.0
Opisthobranchia (Cont.)																
Stiliger																
fuscata										124	137					
Odostomia																
impressa	4			1		2	18	13	27	28	47	31	24	14		
Odostomia																
bisuturalis	3	3				3	12	4	7	1	4	20	8	5		3
Polycerella																
conyma											11					
Tenellia																
fuscata									2	11	10					
Doridella																
obscura									4	5	4			5		
Odostomia																
dux												1		2		
Hermaea																
cruciata	2															
Cratena																
pilata															1	
Pelecypoda																
Mya																
arenaria			1		2	19	3		7	3						
Anadara																
transversa	1							4	1			2				
Cirripedia																
Balanus																
improvisus	1	3		1				27	47			1		1	12	
Mysidacea																
Neomysis																
americana			6		6	1										
Tanaidacea																
Leptochelia																
savignyi									1	2						

Table I. (Continued)

Collection Date g Zostera	1 Nov 39.8	1 Dec 22.6	5 Jan 23.4	6 Feb 18.3	5 Mar 18.5	29 Mar 25.7	19 Apr 30.1	13 May 36.4	5 Jun 57.8	28 Jun 64.0	22 Jul 49.3	19 Aug 38.8	13 Sep 22.9	8 Oct 26.6	6 Nov 13.5	3 Dec 12.0
Isopoda																
Paracerceis caudata	465	187	81	218	19	373	405	80	172	285	849	874	777	929	479	341
Ericnsonella attenuata	228	62	46	43	49	136	143	73	133	98	185	172	150	613	515	393
Idotea baltica							1	2	10	24	2	1				
Edotea triloba											2		1	1		
Amphipoda																
Ampithoe longimana	10	31	32	9	10	21	7	8	1	78	2276	484	175	4011	37	5
Cumacusa compta	19	9	41	12	16	7	5	2	6	19	253	111	299	2116	31	26
Elasmopus laevis	62	15	45	17	13	41	69	6	144	402	500	411	177	269	12	22
Gammarus mucronatus			28	39	15	42	100	8								
Caprella penantis	21	55	19	10	19	16	5	1	3	22	6	2				
Rudilemboides sp.			1		2				7	29			1	7	1	
Corophium acherusicum			1	1		3		4						5		
Paracaprella tenuis				1		1	3		3	5						
Corophium simile	1					1	3			3			2			
Colomastix sp.														3	4	
Ampelisca abdita			1													
Ampelisca vadorum		1														
Melita appendiculata				1												

Table I. (Continued)

Collection Date g *Zostera*	1 Nov 39.8	1 Dec 22.6	5 Jan 23.4	6 Feb 18.3	5 Mar 18.5	29 Mar 25.7	19 Apr 30.1	13 May 36.4	5 Jun 57.8	28 Jun 64.0	22 Jul 49.3	19 Aug 38.8	13 Sep 22.9	8 Oct 26.6	6 Nov 13.5	3 Dec 12.0
Decapoda																
Hippolyte pleuracantha	2	7	9	12	3									1		10
Palaemonetes pugio				1	1	1	1									
Palaemonetes vulgaris							1								1	
Neopanope texana sayi														1		
Pycnogonida																
Callipallene brevirostris	1											9		3	1	
Urochordata																
Molgula manhattensis										2	12	6		69		1

Table II. Non-colonial Species and Numbers of Individuals Collected From Station B.

Collection Date g *Zostera*	1 Nov 28.4	1 Dec 22.8	5 Jan 15.4	6 Feb 11.1	5 Mar 12.9	29 Mar 16.6	19 Apr 21.9	13 May 22.6	5 Jun 37.3	28 Jun 53.9	22 Jul 55.3	19 Aug 33.3	13 Sep 20.0	8 Oct 29.9	6 Nov 14.9	3 Dec 13.5
Anthozoa																
Aiptasiomorpha																
luciae									3	15	105	364	240	238	18	1
Turbellaria																
Euplana																
gracilis						2	6	2	97	79	31	26	4	236	35	1
Stylochus																
ellipticus	52	32	6							2		2		3	6	12
Turbellarian #2													7			
Turbellarian #3															1	
Nemertea																
Tetrastemma																
elegans	1	3					24	3	38	12	2	8			1	2
Zygonemertes																
virescens	3							2	28	2	5	10	8	6		
Amphiporus																
ochraceus									4	2						
Tubulanus																
pellucidus									2							
Polychaeta																
Brania																
clavata							798	2	239	544	227	73	214	121	19	
Polydora																
ligni						2	1531	10	31	5			5	273	1	
Nereis																
succinea	7	2	3	12		8	5	8	33	64	130	12	35	206	15	3
Platynereis																
dumerilii	2		2	2		2	7	3	7	1	39	40	28	203	110	79
Sabella																
microphthalma	18	3				5	3	1	2	21	69	100	94	159	19	8
Podarke																
obscura							1		23	31	97	47	93	112	4	1
Hydroides																
hexagona		2									8	21	17	19	2	

Table II. (Continued)

Collection Date g Zostera	1 Nov 28.4	1 Dec 22.8	5 Jan 15.4	6 Feb 11.1	5 Mar 12.9	29 Mar 16.6	19 Apr 21.9	13 May 22.6	5 Jun 37.3	28 Jun 53.9	22 Jul 55.3	19 Aug 33.3	13 Sep 20.0	8 Oct 29.9	6 Nov 14.9	3 Dec 13.5
Polychaeta (Cont.)																
Exogone																
dispar	2									33	1		2	2		
Prionospio																
heterobranchia										12	1					
Odontosyllis																
fulgurans											1	3	2	4	1	1
Lepidonotus																
variabilis			1					1		1			2	4		1
Nereiphylla																
fragilis												2	1	1		
Pista																
palmata													1	2		
Eumida																
sanguinea														1		
Prosobranchia																
Bittium																
varium	55	79	12	24	8	215	414	255	254	1010	2465	1556	952	1389	494	745
Crepidula																
convexa	314	290	124	45	28	67	171	107	143	713	1370	1967	305	198	100	84
Urosalpinx																
cinerea	4	1					2	3	5	11	36	86	32	55	11	1
Mitrella																
lunata	4	11	3	4		6	5	3	2	4	10	3	6	5	7	36
Triphora																
nigrocincta		1								1	1	1	1	44	3	13
Anachis																
avara													2	3		
Eupleura																
caudata													2			
Nassarius																
vibex							1					1				

Table II. (Continued)

Collection Date g Zostera	1 Nov 28.4	1 Dec 22.8	5 Jan 15.4	6 Feb 11.1	5 Mar 12.9	29 Mar 16.6	19 Apr 21.9	13 May 22.6	5 Jun 37.3	28 Jun 53.9	22 Jul 55.3	19 Aug 33.3	13 Sep 20.0	8 Oct 29.9	6 Nov 14.9	3 Dec 13.5
Opisthobranchia																
Stiliger fuscata										87	1617		1			
Elysia catula	55	28	1	8	1	78	69	32	34	8	37	19			173	168
Odostomia impressa	5	3		1		5	21	5	18	27	355	74	73	73	11	9
Odostomia bisuturalis	2	1	1	2		1	5	1	3	2	7	12	16	18	7	11
Polycerella conyma										9	15			3		
Tenellia fuscata										7	8					
Doricella obscura									1					8		
Doris verrucosa																2
Odostomia dux															1	
Turbonilla interrupta											1					
Pelecypoda																
Anadara transversa	1		1								7	1	1	1	1	
Mya arenaria			1	1		2	1		1							
Cirripedia																
Balanus improvisus	14	3	4	1	2			107	142	24	1	2		2		
Mysidacea																
Neomysis americana			19	5	12											3
Mysidopsis bigelowi																2

Table II. (Continued)

Collection Date g Zostera	1 Nov 28.4	1 Dec 22.8	5 Jan 15.4	6 Feb 11.1	5 Mar 12.9	29 Mar 16.6	19 Apr 21.9	13 May 22.6	5 Jun 37.3	28 Jun 53.9	22 Jul 55.3	19 Aug 33.3	13 Sep 20.0	8 Oct 29.9	6 Nov 14.9	3 Dec 13.5
Isopoda																
Paracerceis caudata	895	499	101	181	59	152	145	46	75	112	434	866	782	1624	442	623
Erichsonella attenuata	464	113	150	63	31	120	151	56	144	110	396	210	132	667	493	385
Idotea baltica		1			1	1	2	3	8	12	1	6	1			
Edotea triloba				1		1	1		1	1						
Amphipoda																
Ampithoe longimana	16	32	46	12	8	18	5	2	1	14	386	46	35	1295	94	10
Elasmopus laevis	82	24	39	19	7	47	60	9	177	139	384	308	208	350	39	33
Cymadusa compta	16	20	61	19	3	12	5	1	3	1	84	11	46	1051	74	25
Caprella penantis	74	81	141	61	73	113	33	9	8	1	2				4	12
Gammarus mucronatus	1		20	52	9	22	87	10	40	22	6	3				
Corophium acherusicum	1		3		1	2	10	1		1			6	131	1	
Paracaprella tenuis	6	3	4	2		1		1	5		4	6		61	10	
Melita appendiculata	5												25	19	4	
Colomastix sp.	2		1									2	1	9	34	
Rudilemboides sp.	4			4		2	1		5	8	10			2	1	
Corophium simile	8	1	1			1	1	3		1			1	9	2	
Ampelisca sp.		1				1		2	2	3				5		
Ampelisca vadorum											5	3		4		

Table II. (Continued)

Collection Date g Zostera	1 Nov 28.4	1 Dec 22.8	5 Jan 15.4	6 Feb 11.1	5 Mar 12.9	29 Mar 16.6	19 Apr 21.9	13 May 22.6	5 Jun 37.3	28 Jun 53.9	22 Jul 55.3	19 Aug 33.3	13 Sep 20.0	8 Oct 29.9	6 Nov 14.9	3 Dec 13.5
Amphipoda (Cont.)																
Batea catharinensis	4															
Ampelisca abdita	3															
Stenothoe gallensis														2		
Stenothoe minuta	1														1	
Ericthonius brasiliensis					1											
Melita nitida											1					
Decapoda																
Hippolyte pleuracantha	2	2	8	7										23		3
Neopanope texana sayi													1	5		1
Palaemonetes vulgaris													1		2	
Crangon septemspinosa							1									
Pycnogonida																
Callipallene brevirostris	1											12	10	20	2	
Insecta																
Dipteran larva											1					
Urochordata																
Molgula manhattensis			4							8	44	42	1	47	3	

Table III. Non-colonial Species and Numbers of Individuals Collected From Station C.

Collection Date g Zostera	1 Nov 13.8	1 Dec 11.9	5 Jan 5.5	6 Feb 10.6	5 Mar 6.4	29 Mar 7.3	19 Apr 22.5	13 May 24.0	5 Jun 43.5	28 Jun 60.9	22 Jul 76.3	19 Aug 40.0	13 Sep 25.4	8 Oct 14.1	6 Nov 14.2	3 Dec 13.2
Anthozoa																
Aiptasiomorpha																
luciae										17	28	24	62	11	4	
Turbellaria																
Euplana																
gracilis							3		111	73	117	16	72	60	6	1
Stylochus																
ellipticus	140	35	2						11	16	8			13	20	16
Turbellarian #3														1		
Turbellarian #1														1		
Nemertea																
Zygonemertes																
virescens	4						3		53	18		42	14	10	9	2
Tetrastemma																
elegans	5	15	5		1	1	14	12	28	22		20	1	5		
Amphiporus																
ochraceus							1	3	6	3						
Tetrastemma																
jeani								1								
Tetrastemma																
vermiculus			1													
Tubulanus																
pellucidus								1								
Polychaeta																
Polydora																
ligni						3	1947	3479	116	55	4		8	193		
Sabella																
microphthalma	31	3	6	3		1				64	321	970	338	66	9	4
Nereis																
succinea	32	8	1	4	1	6	2	1	111	672	357	80	57	109	7	5
Brania																
clavata							331	103	100	436	200	105	126	32	5	1
Podarke																
obscura	1								18	98	277	232	109	45	2	2

Table III. (Continued)

Collection Date g *Zostera*	1 Nov 13.8	1 Dec 11.9	5 Jan 5.5	6 Feb 10.6	5 Mar 6.4	29 Mar 7.3	19 Apr 22.5	13 May 24.0	5 Jun 43.5	28 Jun 60.9	22 Jul 76.3	19 Aug 40.0	13 Sep 25.4	8 Oct 14.1	6 Nov 14.2	3 Dec 13.2
Polychaeta (Cont.)																
Platynereis																
dumerilii	79	24	13	8		26	47	23	30	38	84	58	29	63	31	25
Hydroides																
hexagona										7	114	121	43	6		
Odontosyllis																
fulgurans	3									1		46	33	14		2
Exogone																
dispar										19	12	12	1	1		
Lepidonotus																
variabilis		1										20	6	3	2	
Pista																
palmata											1	20	1	1		
Nereiphylla																
fragilis											4	4	1	1		
Eteone																
heteropoda									1	1						
Eumida																
sanguinea											1	1				
Potamilla																
neglecta	1												1			
Prionospio																
heterobranchia											1					
Sabellaria																
vulgaris														1		
Scoloplos																
fragilis						1										
Hirudinea																
Ichthyobdella																
rapax						1										
Prosobranchia																
Bittium																
varium	90	111	45	103	9	190	672	338	247	2069	9244	4986	3960	2864	539	948

Table III. (Continued)

Collection Date g *Zostera*	1 Nov 13.8	1 Dec 11.9	5 Jan 5.5	6 Feb 10.6	5 Mar 6.4	29 Mar 7.3	19 Apr 22.5	13 May 24.0	5 Jun 43.5	28 Jun 60.9	22 Jul 76.3	19 Aug 40.0	13 Sep 25.4	8 Oct 14.1	6 Nov 14.2	3 Dec 13.2
Prosobranchia (Cont.)																
Crepidula convexa	115	72	27	38	8	16	93	25	33	255	1403	400	132	119	104	75
Mitrella lunata	54	72	8	19	1	25	40	27	33	26	48	11	16	17	15	34
Urosalpinx cinerea	6	1						5	7	35	122	104	48	15	6	
Triphora nigrocincta	1										18	22	13	16	2	13
Nassarius vibex						1	2		2	1						
Anachis avara	1										1					1
Crepidula plana												1				
Eupleura caudata												1				
Opisthobranchia																
Stiliger fuscata										385	1976					
Odostomia impressa	1	4	3	3		4	13	12	23	63	747	390	279	170	14	21
Elysia catula	15	16	2	9		16	24	6	6	231	209	20	11	27	113	149
Odostomia bisuturalis	2	7	6	5		2	4	2	14	1	59	115	82	26	11	3
Doridella obscura									1	115	143			1		
Polycerella conyma										15	15					
Tenellia fuscata									3	9	8					
Odostomia dux	1	2	3	3								2	1	1		

Table III. (Continued)

Collection Date g Zostera	1 Nov 13.8	1 Dec 11.9	5 Jan 5.5	6 Feb 10.6	5 Mar 6.4	[illegible] Mar [illegible]	19 Apr 22.5	13 May 24.0	5 Jun 43.5	28 Jun 60.9	22 Jul 76.3	19 Aug 40.0	13 Sep 25.4	8 Oct 14.1	6 Nov 14.2	3 Dec 13.2
Opisthobranchia (Cont.)																
Doris verrucosa													1	2		
Haminoea solitaria										1						
Turbonilla interrupta										1						
Pelecypoda																
Anadara transversa		1						1	2	1	9	15	2			2
Mya arenaria						1					2	1				
Cirripedia																
Balanus improvisus	6	46	10	2		1		1200	1002	75	7			6	3	1
Mysidacea																
Mysidopsis bigelowi	22	12										1	1	7	28	6
Neomysis americana		10	83	31		18	11									14
Cumacea																
Oxyurostylis smithi		1														
Isopoda																
Paracerceis caudata	188	27	28	176	29	21	50	21	29	87	718	1241	503	354	115	222
Erichsonella attenuata	361	205	82	111	34	51	91	31	132	134	492	537	395	305	223	191
Idotea baltica		2	2	2	3	2	2	24	38	43	126	27	1			
Edotea triloba			2	2	1	5		1	3	3	29	5	3			1
Amphipoda																
Elasmopus laevis	177	46	39	62		14	61	16	155	164	829	1552	234	106	15	12

Table III. (Continued)

Collection Date g *Zostera*	1 Nov 13.8	1 Dec 11.9	5 Jan 5.5	6 Feb 10.6	5 Mar 6.4	29 Mar 7.3	19 Apr 22.5	13 May 24.0	5 Jun 43.5	28 Jun 60.9	22 Jul 76.3	19 Aug 40.0	13 Sep 25.4	8 Oct 14.1	6 Nov 14.2	3 Dec 13.2
Amphipoda (Cont.)																
Caprella penantis	89	274	393	374	150	421	386	302	182	5	9	10	1	19	59	56
Gammarus mucronatus	58	44	57	74	66	28	63	70	140	103	722	263		1		
Ampithoe longimana	39	47	17	9	17	17	18	22	6	136	613	87	4	?11	31	16
Cumadusa compta	148	21	13	8	5	11	1	5	16	31	369	119	7	38	3	3
Batea catharinensis	394	6	1	1							1	6		2		
Melita appendiculata	2	1		1							3	304	8	7	3	
Corophium acherusicum	4						1		2	7		99	14	8		
Corophium simile	7		3	2				1	10	3	6	23	14	15		1
Ampelisca vadorum		1							1		34	33		2		
Colomastix sp.												8	16	15	12	3
Ampelisca sp.								1	17	6		6	5	8		
Rudilemboides sp.	5		1	2		1	1			15	17					
Ampelisca abdita	5										26					
Paracaprella tenuis	1	3		1			1			10				11		1
Stenothoe minuta	2							5								
Monoculodes edwardsi					3											
Caprella equilibra		2														
Corophium tuberculatum											1					

Table III. (Continued)

Collection Date g *Zostera*	1 Nov 13.8	1 Dec 11.9	5 Jan 5.5	6 Feb 10.6	5 Mar 6.4	29 Mar 7.3	19 Apr 22.5	13 May 24.0	5 Jun 43.5	28 Jun 60.9	22 Jul 76.3	19 Aug 40.0	13 Sep 25.4	8 Oct 14.1	6 Nov 14.2	3 Dec 13.2
Amphipoda (Cont.)																
Ericthonius																
brasiliensis																1
Lysianopsis																
alba												1				
Decapoda																
Hippolyte																
pleuracantha	70	19	18	9	3								1	22	1	12
Neopanope																
texana sayi												1		6	2	3
Crangon																
septemspinosa				1	2											
Palaemonetes																
pugio					1				1				1			
Libinia																
dubia												1				
Pycnogonida																
Callipallene																
brevirostris												8	12	3		
Urochordata																
Molgula																
manhattensis	16									239	1686	4		50		

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