THE ANNUAL CYCLE IN QUANTITY AND COMPOSITION OF THE ZOOPLANKTON OF THE SARGASSO SEA OFF BERMUDA. II. THE SURFACE TO 2,000 m[1]

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ABSTRACT

Zooplankton samples were collected at station "S" (32° 10′ N, 64° 30′ W), 24 km SE of Bermuda in 3,200 m of water, at monthly intervals from July 1968 to June 1969, over four depth intervals from the surface to 2,000 m.

In the upper 500 m highest numbers were found in October and April; between 500 and 1,000 m the highest numbers were present in July, March, and May; from 1,000 to 1,500 m the numbers were highest in August, January, and March. In the deepest waters sampled numbers were highest in July, October, March, and May.

The displacement volumes for the upper 500 m showed a pronounced April maximum; the October maximum in numbers, consisting of small copepods, was not reflected in the volumes. Larger organisms were more common in the deeper waters. In going down the water column, volumes were approximately halved over each lower depth interval, but mean numbers decreased greatly between the upper waters and those of the 500–1,000-m depth interval, indicating an increase in size of organisms between these two depth ranges.

Crustacea increased in importance and in diversity below 500 m. Copepods comprised 70% of the plankton of the upper 500 m and 85.2% in the deepest waters sampled. Pelagic ostracods were next in importance, but were relatively less numerous below 1,500 m. Highest numbers of calanoid genera and ostracod species were noted between 500 and 1,500 m. Euphausiids were most numerous between 1,500 and 2,000 m with a November maximum. Tunicates, coelenterates, chaetognaths, Foraminifera, pteropods, and various larval forms were most abundant in numbers and species in the upper waters, but occurred in small numbers below 500 m.

INTRODUCTION

A comprehensive and quantitative sampling program designed to study the total deep-water plankton community throughout the seasons appears never to have been undertaken. Usually the zooplankton collected on oceanographic expeditions is sorted into the constituent groups, which are then sent to specialists for taxonomic study without regard for the total quantities of organisms or the species of the various groups that live together at the same depths. In much of the sampling of the deeper waters trawls with coarse-mesh nets have been used, as in studies on the deep-scattering layer. The smaller zooplankton organisms not only feed the larger animals at the same and greater depths, including such carnivores as contribute to the deep-scattering layer, but provide the essential link in any conversion of microscopic detritus to fish. Our purpose has been to make a qualitative and quantitative year-round study of the microzooplankton of the 2,000-m water column and to obtain estimates of the standing crop of zooplankton in the deeper, as well as the surface, waters. An overall picture of the total zooplankton, in quantity and species composition, must be the first

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step in understanding the biological cycling of organisms and organic matter in the depths of the sea.

An oceanic station in the Sargasso Sea off Bermuda has been occupied almost continuously at regular intervals since 1957, and many hydrographic, chemical, and biological data have been collected. The zooplankton of the upper 500 m has been studied year-round (Menzel and Ryther 1961*a*, *b*; Beers 1966; Deevey 1971) and some samples have been obtained from depths down to 2,000 m. No year-round quantitative investigation has been made of the zooplankton of the deeper waters at this station, or, as far as we are aware, at any other oceanic station. Østvedt (1955) has reported qualitatively, in numbers of organisms per haul, on samples collected during 1 year over five depth ranges between the surface and 2,000 m from Weathership *M* (66° N, 2° E) in the Norwegian Sea, and Johnson (1963) has described the copepods and listed the numbers of organisms per haul for samples obtained from depths down to 2,000 m over 6 months at Drift Station Alpha in the high Polar Basin. From July 1968 to September 1970 we made monthly plankton hauls over four depth ranges between 2,000 m and the surface, using fairly fine-mesh nets; this report presents the volumetric and numerical data on the seasonal and vertical distribution of the major zooplankton groups during the first year of sampling.

We are deeply indebted to W. H. Sutcliffe, Jr., for encouragement and assistance in undertaking this study, and to the staff of the Bermuda Biological Station, especially Margaret Emmott, secretary, and George Taggett, Captain of the *Panulirus II*, for cheerful help and many favors. We are also grateful to Drew Drinkard for computer programming assistance.

METHODS

Oblique plankton hauls were made each month starting in July 1968, at station "S" (32° 10′ N, 64° 30′ W) 24 km southeast of Bermuda in 3,200 m of water from the Bermuda Biological Station's research ship, *Panulirus II*. Samples were collected over four depth intervals approximating 0–500 m, 500–1,000 m, 1,000–1,500 m, and 1,500–2,000 m. Because of the operating characteristics of the pressure-activated triggering mechanism the actual depth intervals were 0–500 m, 500–965 m, 965–1,470 m, and 1,470–1,935 m, but for convenience we shall refer to our depth levels as originally planned. The hauls of the upper 500 m were made with an open meter net of No. 2 and No. 8 nylon, equipped with a flowmeter affixed to the towing cable, on the way down and on the return. For the three lower depth intervals a 0.75-m^2 Bé (1962) plankton sampler was used, with three individually metered nets of No. 8 mesh that were pressure activated to open and close successively between 2,000 and 500 m. Around 2,600 m of cable were payed out to ensure that the triggering mechanism was properly engaged and ready to open the deep net as the unit was raised to the proper depth. While the nets were down the ship steamed ahead at 1–2 knots. Each net was towed horizontally for 10–20 min when it reached the approximate center of its depth range. An 8-hr day of ship time was required to obtain each set of samples, and of the 48 samples collected between July 1968 and June 1969 only one was lost. The ship was on station and the nets started down by 1030 to 1100 hours and were brought up usually by 1530–1630, so that any diurnally migrating organisms would have been at their daytime depth.

The 0–500-m haul sampled the waters above the permanent thermocline, where the annual temperature range was 17 to 27 or 28C, and the 500–1,000-m haul, the waters of the permanent thermocline, where temperatures decreased with depth from 16 to 7C. Over the 1,000–1,500-m depth interval, below the permanent thermocline, the temperature range was 4 to 7C; below 1,500 m the temperature remained at 4C. Below 500 m there is virtually no seasonal change in temperature. At this latitude we are dealing with surface and upper waters of seasonally variable temperature having a prevailing northerly flow at depths shallower than 800 m; below the permanent thermocline, the main mass of relatively uniform temperature and salinity is primarily North Atlantic Deep Water, with possibly some admixture of Antarctic Intermediate Water in the upper part.

The 0–500-m hauls contained estimated total numbers that ranged from 119,520 to 452,800 organisms, and the number of cubic meters of water filtered varied from 489 to 1,536. These samples were diluted to a known volume, usually 1,000 to 2,000 cc, thoroughly stirred, aliquots of 10 or 20 cc counted, and total numbers estimated. The 500–1,000-m samples contained estimated total numbers of 9,890 to 50,640 organisms, and 398 to 1,617 m^3 of water were filtered in collecting them. One of these, the October sample, was counted in its entirety and contained 12,000 organisms, but this procedure required a month's time. As a rule a 4th to a 20th of these samples was counted. The 1,000–1,500-m samples contained 3,000 to 16,000 organisms, and 386 to 1,216 m^3 of water were filtered. Usually a 10th of these samples was counted; total samples were counted on four occasions, when numbers ranged from 4,000 to 6,600 organisms. All of the organisms in the 1,500–2,000-m samples were counted, the numbers varying from 244 to 5,005 and the amount of water filtered from 338 to 660 m^3.

Dead or moulted copepod skins were counted in most of the samples. For the 0–500-m depth interval an annual mean of 14.9% of all the copepods counted were dead or moulted skins. Over the 500–1,000-m range only 12.5% of the copepods counted were skins, but the proportion then increased from 18.0% for the 1,000–1,500-m depth interval to 21.0% in the 1,500–2,000-m depth range. The proportion of skins at the deepest level was similar to that between 1,000 and 1,500 m, except for the deep January sample, which contained only 151 copepods presumed alive when caught and 1,979 copepod skins. Such a high proportion of skins was noted only on this occasion, when the deeper waters were virtually depleted of zooplankton. Since many of the skins belonged to species found over the same depth range, our data are inconclusive as to whether skins from shallower depths accumulate in deeper waters. In the following sections, numbers of organisms refer only to those believed alive when caught.

To obtain the displacement volumes the samples were strained through No. 8 nylon, placed on absorbent paper to remove excess water, and then added to known volumes of water. Since the deeper samples usually contained one or more larger organisms, such as larval fish or large crustaceans, separate displacement volumes were obtained for these animals. The figures given below for maximal displacement volumes include these larger forms; the minimal volumes are those obtained only for the microscopic plankton.

THE TOTAL ZOOPLANKTON

Table 1 lists total numbers, maximal and minimal displacement volumes, and amount of water filtered in collecting each sample. The total numbers of organisms/m^3 recorded are shown in Fig. 1. The mean crop in the upper 500 m was 107,650/m^2. This is somewhat lower than the mean recorded for 1961–1962 (Deevey 1971). An annual cycle with maximal numbers in spring is usual for these waters, the spring maximum following the winter–spring phytoplankton bloom and varying in magnitude, depending on the degree of surface cooling and subsequent mixing of the water column.

Throughout the permanent thermocline, over the 500–1,000-m depth interval, minima coincided with times of maxima in the upper waters. The crop over this depth range was 13,950/m^2.

Below the permanent thermocline there were also considerable variations in numbers during the year. The mean crop over these depths was 5,670/m^2. In the deepest waters sampled (between 1,500 and 2,000 m) the mean crop was 2,750/m^2.

The familiar seasonality of zooplankton in the upper waters is not maintained at all depths. Numbers were relatively high throughout the water column in summer, but in October when high numbers were

TABLE 1. *Amount of water filtered in m³ (A), maximal and minimal displacement volumes in cc/m³ (B), and total No./m³ (C) for the four sampling depths between the surface and 2,000 m, July 1968–June 1969*

Date	0–500 m			500–1,000 m			1,000–1,500 m			1,500–2,000 m		
	A	B	C	A	B	C	A	B	C	A	B	C
24 Jul	1,115	0.0341 0.0305	185.1	496	0.0260 0.0170	34.1	426	0.0117 0.0046	11.8	340	0.0053	8.4
20 Aug	926	0.0337	205.1	443	0.0090	29.2	386	0.0070 0.0034	13.8	338	0.0036 0.0026	6.2
12 Sep	854	0.0250	242.9	1,679	0.0104 0.0090	30.2	1,216	0.0053 0.0043	13.2	515	0.0031	2.3
15 Oct	489	0.0250	300.0	752	0.0105 0.0071	14.5	672	0.0031	6.6	552	0.0041 0.0034	8.0
16 Nov	686	0.0204	174.2	543	0.0071	21.2	580	0.0053	7.0	570	0.0047 0.0035	4.3
19 Dec	1,061	0.0160	140.8	781	0.0102	21.5	561	0.0057 0.0041	11.8	629	0.0019	2.6
20 Jan	1,536	0.0180	175.7	803	0.0091 0.0074	21.4	665	0.0139 0.0077	19.6	660	0.0047 0.0009	0.4
24 Feb	1,102	0.0190	142.7	398	0.0143 0.0103	24.9	482	0.0025	7.4	641	0.0084 0.0022	4.1
18 Mar	1,136	0.0250	211.1	551	0.0201 0.0163	47.8	455	0.0101 0.0061	17.4	355	0.0020	8.8
13 Apr	1,148	0.0775	394.4	684	0.0114 0.0109	22.0	606	0.0021	5.0	—	—	—
15 May	708	0.0380	195.5	567	0.0176 0.0150	36.5	666	0.0080 0.0057	10.7	612	0.0049 0.0036	8.2
25 Jun	748	0.0255	216.2	530	0.0233 0.0102	31.6	611	0.0067	12.0	580	0.0045 0.0043	7.2
Means:		0.0298 0.0295	215.3		0.0141 0.0108	27.9		0.0074 0.0046	11.3		0.0047 0.0027	5.5

found in surface waters, there were minimal numbers at 500–1,500 m. Between 1,000 and 1,500 m the normal seasonality is nearly reversed. High numbers were present between 500 and 2,000 m in March, when numbers were rising in the upper waters, but in April, when numbers were maximal in the upper 500 m, there was a minimum in deeper waters. These differences in seasonal response are not the consequence of vertical movements, as Fig. 1 might suggest, for the animals providing the maxima are mainly different. In general it appears that most of the organisms remain year-round at their usual depths, at least in daytime when these samples were collected.

When the total numbers obtained for the water column are averaged (Fig. 2B), the annual cycle in total numbers obtained is similar to that pictured for the 0–500-m depth interval, since numbers were much higher in the upper waters. The mean annual crop for the 2,000-m water column was 130,000/m².

The decrease in total numbers with depths is such that numbers over the 500–1,000-m depth range are around 13% of those in the upper waters. Mean numbers between 1,000 and 1,500 m are 40% those of 500–1,000-m depths, and those of the 1,500–2,000-m depth range about half of those from 1,000–1,500 m. Thus, the total numbers found in the deepest waters are only around 2.5% of those at the surface, and those from 1,000–1,500-m depths 5% of total surface numbers.

The displacement volumes obtained for the four depth intervals are illustrated in Fig. 3. As previously noted, the maximal volumes include any larger organisms that were present; the minimal volumes represent only the microscopic plankton. In the upper waters the seasonal cycle shows a pronounced April maximum (Fig. 3A), and the October maximum in numbers, which consisted almost entirely of small copepods, is not reflected in larger volumes. The mean annual crop in the upper 500 m was

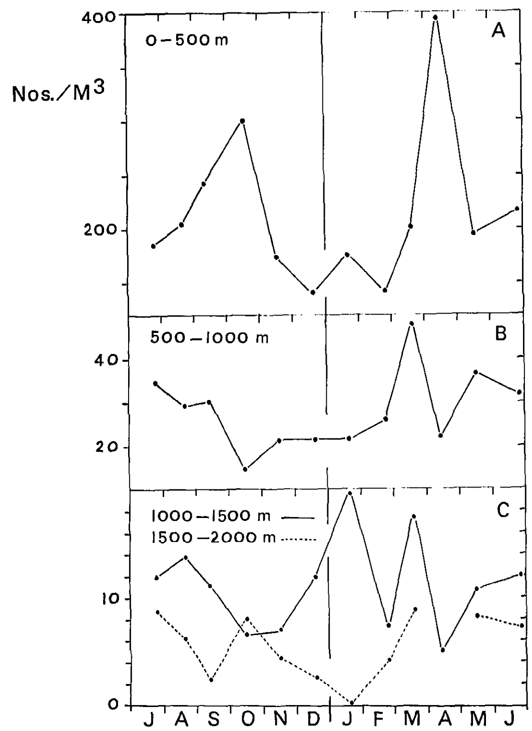

Fig. 1. Total No./m³ from July 1968 to June 1969. A. The upper 500 m. B. 500–1,000 m. C. 1,000–2,000 m.

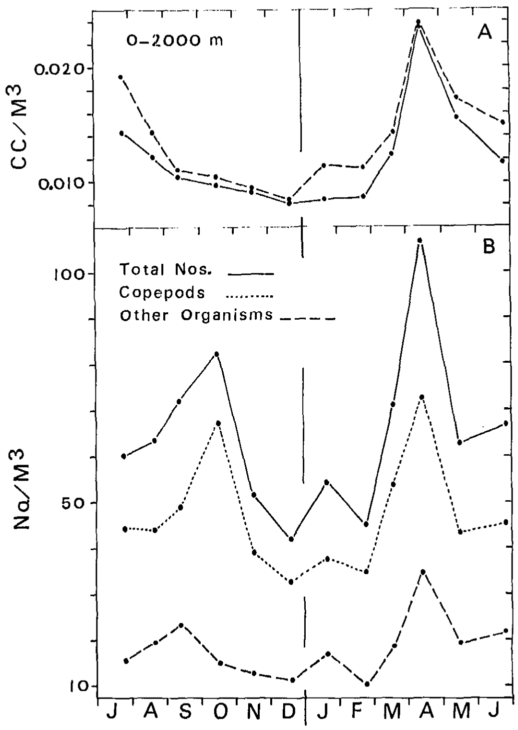

Fig. 2. A. Mean total displacement volumes in cc/m³ for the 2,000-m water column from July 1968 to June 1969. Solid line, minimal volumes; dashed line, maximal volumes including larger organisms. B. Mean No./m³ from July 1968 to June 1969 for the 2,000-m water column.

14.75 cc/m², or 14.9 cc/m² including the larger organisms. In the previous study of the upper 500 m, a mean of 14.0 cc/m² was obtained (Deevey 1971).

Over the 500–1,000-m depth interval (Fig. 3B), the highest minimal volumes were found in July, March, and May when numbers were also highest; maximal volumes were highest in July, March, and June. The mean crop over this depth range was 5.4 cc/m² for the microzooplankton, or 7.05 cc/m² if the larger organisms are included.

Between 1,000 and 1,500-m depths (Fig. 3C) minimal volumes corresponded with minimal numbers. Larger organisms were commoner at this depth in summer, winter, and spring, and higher maximal volumes were found in July, January, March, and May. The mean minimal crop over these depths was 2.3 cc/m², the maximal 3.7 cc/m².

Between 1,500 and 2,000 m highest minimal volumes were obtained in July and June, lowest in January. Larger organisms were more numerous in winter at these depths (Fig. 3D) and the highest maximal volume was obtained in February. The mean crop in the deepest waters sampled was 1.35 cc/m² or 2.35 cc/m² including the larger organisms.

The decrease in volume with depth is not as great as in numbers, indicating an increase in size of organisms between the surface waters and 500–1,000-m depths. The mean volumes for the 500–1,000-m depth interval are 40–50% those of the upper waters, the volumes from 1,000–1,500-m depths are 40–50% those of 500–1,000-m depths, and the volumes in the deepest waters sampled are 60% those of 1,000–1,500-m depths. The volumes from the deepest level sampled are 9–15% those of the surface waters.

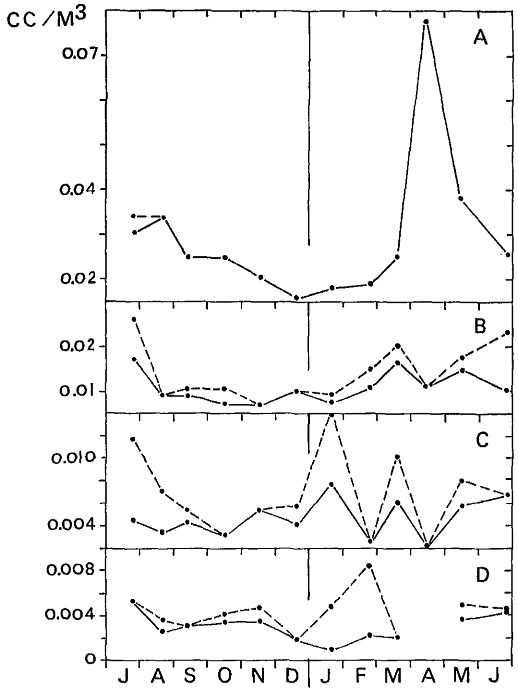

FIG. 3. Minimum (solid line) and maximum (dashed line) displacement volumes in cc/m³ of the zooplankton from July 1968 to June 1969. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m.

Thus, in going down the water column, volumes are approximately halved over each lower depth interval. Although total numbers are much higher in the surface waters, the dominant organisms there—the copepods—are all small species.

When the monthly displacement volumes for the four depth levels are averaged, the annual cycle in quantity (Fig. 2A) is similar to that for the upper 500 m, except that the April maximum is not as pronounced, since the deeper waters were depleted at that time, and relatively high volumes were present in the deeper waters in July. The mean annual crop was 24.0 cc/m², or 27.6 cc/m² including the larger organisms.

COMPOSITION OF THE ZOOPLANKTON

Table 2 gives the composition of the major zooplankton groups; the mean percentages given are the means of the monthly percentages for each depth interval, not the

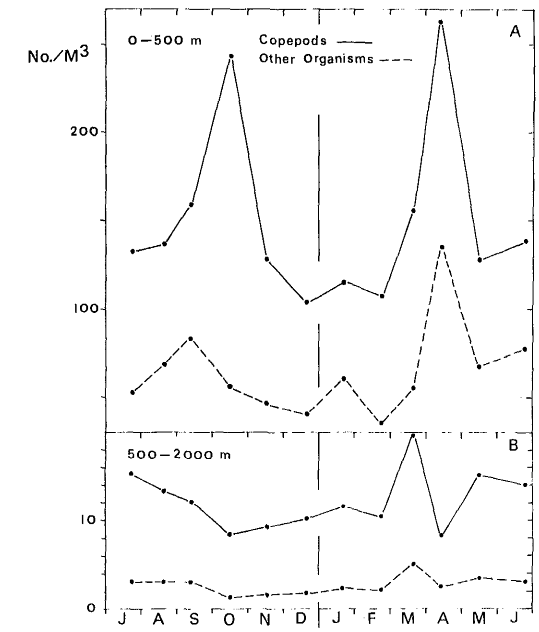

FIG. 4. Total No./m³ from July 1968 to June 1969 of copepods and all other organisms. A. The upper 500 m. B. Averaged for 500–2,000 m.

percentages of the mean total figures. Copepods constituted the major part of the zooplankton at all depths and increased in proportion with depth (though decreasing greatly in numbers) from 70% of the total plankton of the upper waters to 85% at depths of 1,500–2,000 m. The preponderance in total numbers of copepods over all other organisms throughout the water column is illustrated in Fig. 4. The October maximum in numbers in the upper waters was due entirely to an increase in numbers of copepods. All organisms were most numerous in the upper waters in April, but all other than copepods had a secondary maximum in numbers in September rather than October.

As noted, the deepest January sample consisted largely of copepod skins, and the few Protozoa counted in this sample constituted 28% of the total numbers. Excluding the January sample, copepods comprised 87.6% and total Crustacea 95.1% of the deepest samples. Pelagic ostracods ranked second to copepods throughout the

TABLE 2. *Mean annual total No./m³ (A) and mean percentages (B) of the major zooplankton groups*

	0–500 m		500–1,000 m		1,000–1,500 m		1,500–2,000 m		0–2,000 m
	A	B	A*	B	A*	B	A*	B	A
Calanoids	89.8	42.1	12.0	43.1	5.4	45.7	2.8	48.8	27.5
Other copepods	60.9	28.0	10.4	37.7	4.2	38.3	2.0	36.4	19.4
Total copepods	150.7	70.1	22.4	80.8	9.6	84.0	4.8	85.2	46.9
Ostracods	14.8	7.0	2.2	7.7	*530*	4.8	*190*	2.8	4.4
Other Crustacea (including larval forms)	7.1	3.3	1.1	3.5	*370*	3.4	*270*	4.4	2.2
Total Crustacea	172.6	80.4	25.7	92.0	10.5	92.2	5.2	92.4	53.5
Tunicates	15.1	6.5	*185*	0.6	*20*	0	*20*	0.5	3.8
Chaetognaths	6.5	3.0	*312*	1.1	*25*	2.2	*35*	0.6	1.8
Coelenterates	6.8	3.1	*309*	1.0	*100*	0.8	*13*	0.4	1.8
Larval forms (noncrustacean)	4.4	2.1	*540*	1.9	*115*	1.0	*32*	0.6	1.3
Protozoa	5.1	2.6	*690*	2.5	*320*	3.4	*160*	5.0	1.6
Miscellaneous	4.9	2.3	*103*	0.9	*20*	0.4	0		1.3
Total No./m³	215.3		27.9		11.3		5.5		65.0
Total No./m²	107,650		13,952.5		5,672.5		2,750		130,025

* Italicized numbers are $\times 10^{-3}$, i.e. No./1,000 m³.

water column. In the upper waters pelagic tunicates ranked third, but few were taken below 500 m (in our previous study tunicates ranked second and ostracods third in the upper 500 m). Coelenterates and chaetognaths were next in importance in the upper waters, followed by Protozoa, largely Foraminifera. Coelenterates were rare beneath 1,000 m, and fair numbers of siphonophores were present between 500 and 1,000 m. A few chaetognaths were commonly found throughout the water column. Foraminifera also occurred throughout the water column, and it is possible that some dead specimens (shells) may have been counted in the deeper samples. The category "other Crustacea" includes all crustacean forms except copepods and ostracods: amphipods, euphausiids, *Evadne*, *Lucifer*, isopods, microniscus larvae, and all other larval forms, such as barnacle nauplii and cyprids, pagurid larvae, unidentified crustacean nauplii and larvae, and decapod zoeae. These crustaceans occurred in appreciable numbers throughout the water column. The category "larval forms" includes all noncrustacean invertebrate larvae, such as cyphonautes larvae, polychaetes and larvae, echinoderm larvae, lamellibranch veligers, gastropod larvae, sipunculid larvae, and trochophores. These forms were quite numerous in the upper waters, but some individuals were also found throughout the water column. The "miscellaneous" category includes primarily pteropods and fish eggs and larvae; these also were found in small numbers in the deeper waters.

Copepods

There is a great variety of species of copepods in the Sargasso Sea, and the diversity increases below 500 m, but most species occur in very small numbers. Throughout the 2,000 m, calanoids are more numerous than other copepods, of which the most important families are the Mormonillidae, Oithonidae, and Oncaeidae. Mean percentages, based on monthly figures, show that calanoid copepods comprised 59.8% of the total copepods in the upper waters, 53.5% over the 500–1,000-m depth range, 54.3% over the 1,000–1,500-m depth level, and 58.9% between 1,500 and 2,000 m. According to Wheeler (1970), calanoid copepods are also the most abundant forms below 2,000 m. Figure 5 illustrates the annual cycles in total numbers of calanoids and other copepods for the four depth levels sampled. The relative increase of other copepods between 500 and 1,500 m is evident. At each depth level the cycle

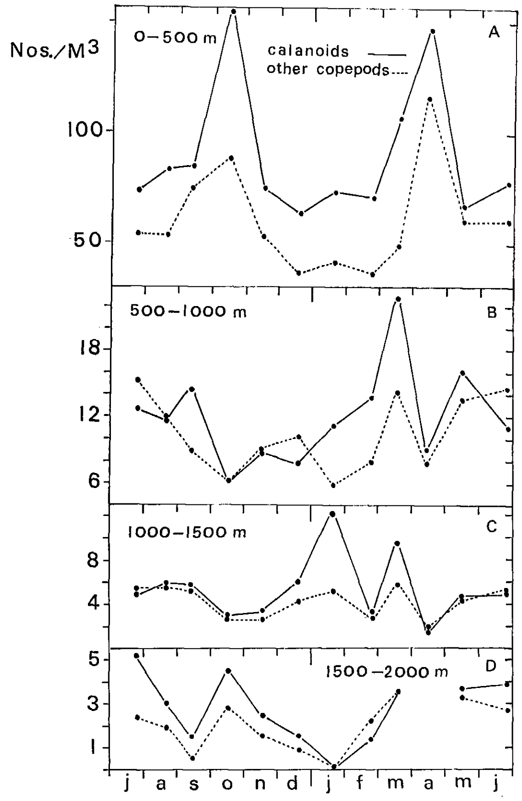

FIG. 5. Mean total No./m³ from July 1968 to June 1969 of calanoid copepods and other copepods. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m.

in numbers of copepods is similar to that shown for total numbers of zooplankton in Fig. 1. The decrease in mean numbers of copepods with depth is also similar to the decrease in total numbers. Mean numbers of copepods between 500 and 1,000 m are around 15% those of the upper waters; numbers between 1,000 and 1,500 m are around 43% those of the 500–1,000-m depth level, and numbers between 1,500 and 2,000 m are about half those from 1,000–1,500 m. Mean numbers from 1,500–2,000 m are only 3% of those from 0–500 m.

Although calanoid copepods outnumbered other copepods throughout the water column, few genera were represented by sufficient numbers to yield appreciable mean annual percentages of the total numbers (Table 3). Immature calanoids were present in every sample and constituted an appreciable percentage of the total numbers. The only noncalanoid genera numerous throughout the water column were *Oithona*, *Oncaea*, and *Mormonilla*; *Oithona* much less so below 1,000 m. *Conaea* was numerous between 500 and 2,000 m. *Oithona* and *Oncaea* were unquestionably the most numerous copepods in the upper 500 m (Fig. 6). *Mormonilla* and *Conaea* were next in abundance (Fig. 7). The tiny copepods belonging to these four genera are ubiquitous throughout the water column.

TABLE 3. *Mean annual percentages of total copepods of some copepod genera*

	0–500 m	500–1,000 m	1,000–1,500 m	1,500–2,000 m
Calanoids	59.80	53.46	54.25	58.90
Unidentified copepodites	24.34	24.50	22.54	18.62
Mecynocera	2.61	—	—	—
Pleuromamma	4.18	4.81	—	—
Calocalanus	3.53	—	—	—
Heterorhabdus	0.70	2.22	—	—
Lucicutia	4.00	0.62	—	—
Haloptilus	2.03	1.27	—	—
Clausocalanus	5.03	—	—	—
Phyllopus	—	1.06	—	—
Eucalanus	—	1.62	3.78	14.70
Metridia	—	2.27	13.46	16.57
Calanus	—	—	4.21	1.01
Rhincalanus	—	—	—	1.19
Other copepods	40.20	46.54	45.75	41.10
Oithona	18.70	14.02	4.95	0.76
Oncaea	11.57	13.43	20.17	12.00
Mormonilla	3.58	11.14	10.47	11.53
Conaea	—	7.12	9.13	16.10
Farranula	3.76	—	—	—

The seasonal cycles of the copepods in the upper 500 m have already been described (Deevey 1971). Some calanoid genera were less numerous in 1968–1969 than in 1961–1962. *Clausocalanus*, *Calocalanus*, and *Mecynocera* are epiplanktonic forms, considered contaminants in deep-water samples (Grice and Hulsemann 1965, 1967; Wheeler 1970). The annual cycle in numbers of these genera in the upper 500 m is shown in Fig. 8A. As before, *Clausocalanus* was most abundant in fall, *Calocalanus* in summer, and *Mecynocera* in late

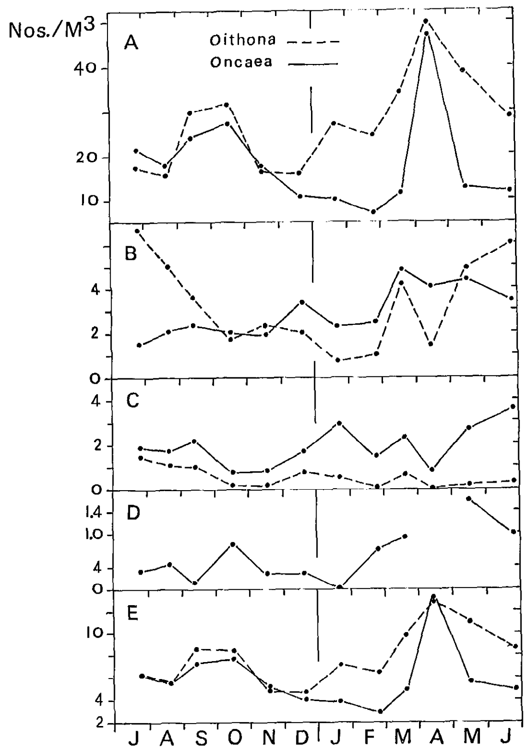

FIG. 6. Mean total No./m³ from July 1968 to June 1969 of *Oithona* and *Oncaea*. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m. E. 0–2,000 m.

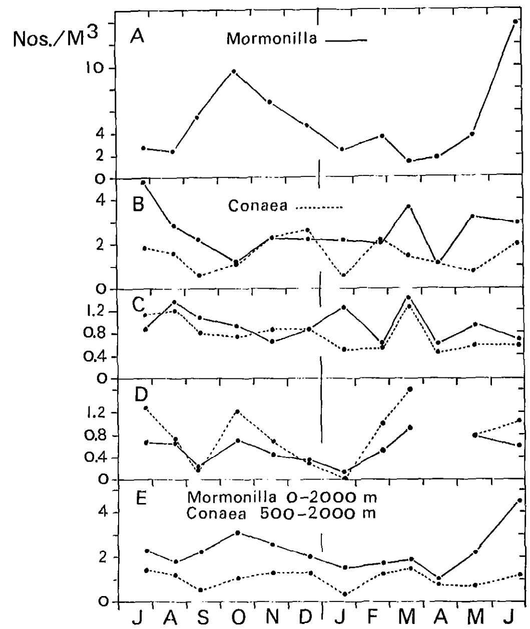

FIG. 7. Mean total No./m³ from July 1968 to June 1969 of *Mormonilla* and *Conaea*. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m. E. *Mormonilla*, 0–2,000 m; *Conaea*, 500–2,000 m.

spring and early summer. Representatives of some calanoid genera (e.g., *Haloptilus*, *Pleuromamma*, *Spinocalanus*, *Phyllopus*, *Heterorhabdus*, *Lucicutia*, *Eucalanus*, *Calanus*, and *Rhincalanus*) were found throughout the 0–2,000 m water column, usually in higher numbers over one depth level. *Heterorhabdus* and *Haloptilus* were most numerous in the upper 1,000 m (Fig. 8B, C).

Species of *Lucicutia* and *Pleuromamma* occurred throughout the water column, but both genera were most numerous in the upper 500 m (Fig. 9A, B); neither was present in appreciable numbers below 1,000 m. Species of *Metridia*, on the other hand, were found only below 500 m and were most numerous between 1,000 and 1,500 m (Fig. 9B–E).

Occasional specimens of species of *Phyllopus* were also found over the four depth levels, but *Phyllopus* occurred year-round and was commonly noted only between 500 and 1,000 m, where it was most numerous from February to June.

Species of *Calanus* and *Eucalanus* also occurred throughout the water column (Fig. 10A–E). *Eucalanus*, *Calanus*, and *Metridia* were the three most important calanoid genera below 1,000 m. In the upper waters *Eucalanus* was relatively numerous only in April at the time of the spring maximum, and at this time virtually none were found between 500 and 2,000 m. The same species were found throughout the water column, and they are therefore relatively eurythermal forms, since the temperature in the bottom waters remains at 4C year-round. Apparently *Eucalanus* spends summer and fall primarily in the deepest waters, then in winter rises to shallower depths and into the upper waters at the time of the spring maximum. In 1962, also, *Eucalanus* was numerous in the upper 500 m only in March after a late February phytoplankton

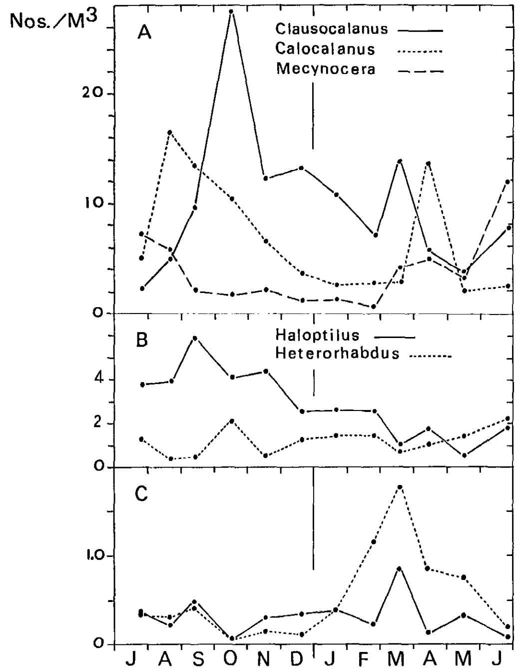

FIG. 8. Total No./m³ from July 1968 to June 1969. A. *Clausocalanus*, *Calocalanus*, and *Mecynocera* for the upper 500 m. B. *Haloptilus* and *Heterorhabdus* for the upper 500 m; C. for 500–1,000 m.

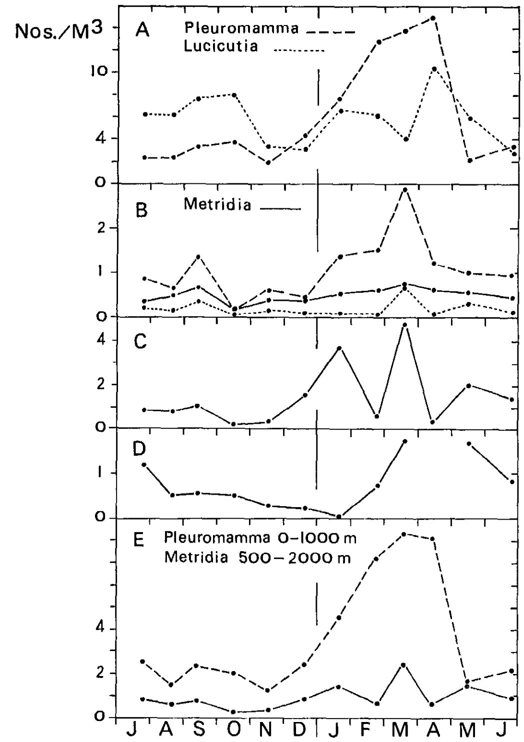

FIG. 9. Total No./m³ from July 1968 to June 1969. A. *Lucicutia* and *Pleuromamma* for the upper 500 m. B. *Lucicutia*, *Pleuromamma*, and *Metridia*, 500–1,000 m. C. *Metridia*, 1,000–1,500 m. D. *Metridia*, 1,500–2,000 m. E. Mean total No./m³ of *Pleuromamma*, 0–1,000 m; *Metridia*, 500–2,000 m.

bloom when total numbers of zooplankton were maximal.

The total numbers of *Calanus* shown in Fig. 10 include two species, *C. tenuicornis* in the upper 500 m (Fig. 10A) and *C. finmarchicus* between 500 and 2,000 m (Fig. 10B–E). Although other species of *Calanus* were occasionally noted, especially in the deeper waters, they were represented by very few specimens. *Calanus tenuicornis* was most numerous only in April and occurred in small numbers the rest of the year in the upper 500 m. *Calanus finmarchicus* was most abundant between 1,000 and 1,500 m, with a cycle in numbers similar to that of *Eucalanus* (Fig. 10C). It was not noted in the upper waters at the time of the spring maximum. Most of the specimens were late stage copepodites, as was also the case with *Eucalanus*.

Species of *Rhincalanus* were present year-round in the deeper waters between 500 and 2,000 m and were noted in the upper 500 m only in July and January. Highest numbers were found between 500 and 1,000 m in May.

Thus, throughout most of the water column, species of *Oithona*, *Oncaea*, *Conaea*, and *Mormonilla* are the most numerous forms; although calanoid copepods are somewhat more abundant, few genera occur in sufficient numbers to constitute 1% of the total numbers of copepods. Of the calanoid genera important in the deeper waters it is rather surprising that most (e.g., *Calanus*, *Eucalanus*, and *Rhincalanus*) are forms considered to be primarily herbivorous, although they can capture and eat small animals (Conover 1960; Mullin and Brooks 1967; Anraku and Omori 1963).

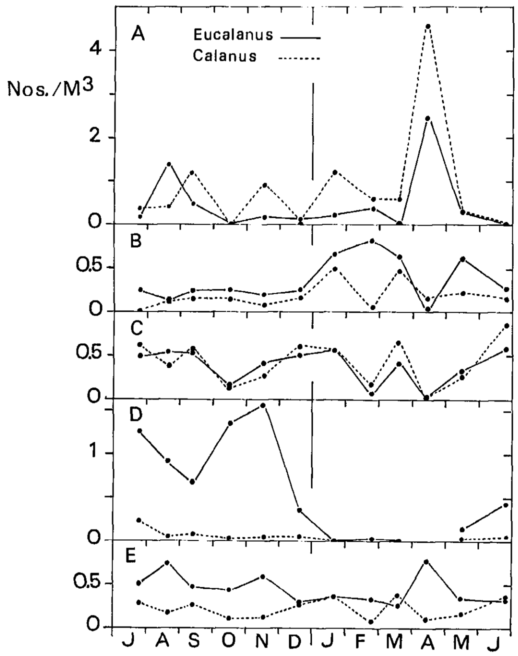

FIG. 10. Total No./m^3 from July 1968 to June 1969 of *Eucalanus* and *Calanus*. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m. E. *Eucalanus*, 0–2,000 m; *Calanus*, 500–2,000 m.

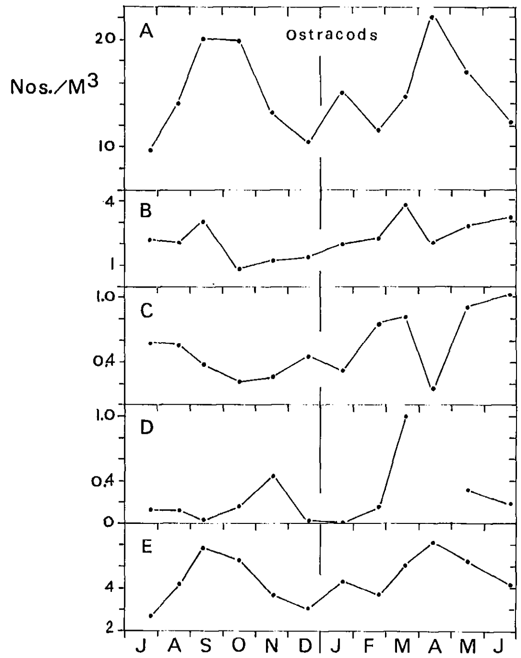

FIG. 11. Total No./m^3 from July 1968 to June 1969 of ostracods. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m. E. 0–2,000 m.

Specimens of these genera taken from the deeper waters appeared well fed. Also, these genera belong to the families Calanidae and Eucalanidae, considered by Grice and Hulsemann (1965) as restricted to "really shallow depths." Some members of these families, including *Mecynocera*, *Nannocalanus minor*, and *C. tenuicornis* are indeed epipelagic, but other species of *Calanus*, and the species of *Eucalanus* and *Rhincalanus*, may occur throughout the water column below 500 m in the Sargasso Sea and cannot be contaminants from shallower depths where they were found in smaller numbers or not at all. Leavitt (1938) also noted these genera at depths down to and below 2,000 m. It is impossible to determine whether any of the tiny cyclopoids were contaminants from shallower depths; this is quite possible, but the fact that *Oithona* decreased sharply in numbers below 1,000 m and that *Conaea* normally occurred only below 500 m would imply that the overall picture of depth distribution is correct.

Ostracods

As a group pelagic ostracods were second in importance after copepods throughout the water column (Table 2). Mean total numbers decreased more sharply below 1,000 m than did those of copepods. Between 500 and 1,000 m numbers were about 15% those of the upper 500 m; numbers between 1,000 and 1,500 m were only 25% those between 500 and 1,000 m; for the deepest level sampled, numbers were only 35% of those from 1,000–1,500-m depths. The seasonal cycle in total numbers of ostracods is illustrated in Fig. 11. In the upper 500 m total numbers varied between 7.7/m^3 in July to 21.9/m^3 in April; from 500–1,000 m highest numbers ranged between 0.8/m^3 in October and 3.7/m^3 in March; below 1,000 m highest numbers were found in February, March, May, and June over

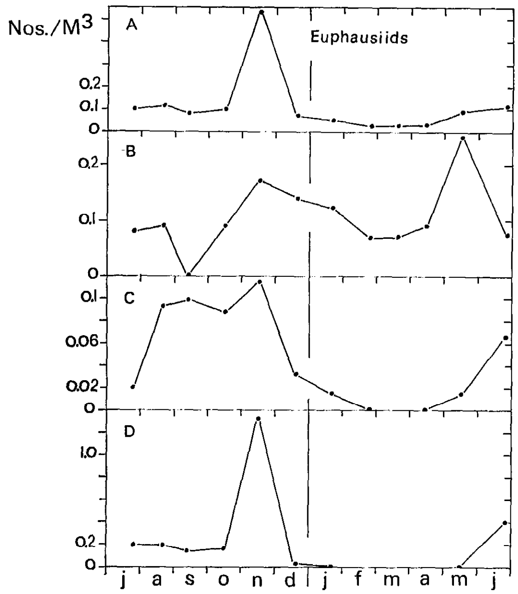

FIG. 12. Total No./m^3 from July 1968 to June 1969 of euphausiids. A. 500–2,000 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m.

1,000–1,500-m depths, and in March in the deepest waters sampled. The numbers for the 2,000-m water column (Fig. 11E) varied from 2.6/m^3 in July to 6.1/m^3 in April, with an annual mean of 4.4/m^3, or 8,800/m^2.

Six genera of ostracods were represented in the samples: *Macrocypridina* within the upper 1,000 m; species of *Halocypris, Halocypria, Archiconchoecia,* and *Conchoecia* throughout the water column; and *Euconchoecia* only in the upper waters. The greatest number of species was found between 500 and 1,000 m—in the waters of the permanent thermocline: 27 species in the upper 500 m, 46 between 500 and 1,000 m, 37 between 1,000 and 1,500 m, and only 22 between 1,500 and 2,000 m. In all, some 58 species have thus far been recorded at station "S." In a previous study, ostracods comprised 7.2% of the total zooplankton of the upper 500 m, and an annual mean of 17.76/m^3 was obtained; 43 species were described (Deevey 1968).

Other Crustacea

The samples also include nauplii, unidentified larvae, amphipods, isopods, the cladoceran *Evadne spinifera,* the sergestid shrimp *Lucifer typus,* euphausiids, large unidentified decapods, and various larval forms such as decapod zoeae, microniscus larvae, and barnacle nauplii and cyprids. These forms are considered together in Table 2. Throughout the year and down to 1,500-m depths crustacean nauplii were quite numerous with maximal numbers in April in the upper waters and in March between 500 and 1,000 m. In deeper waters no seasonal trend was discernible. Unidentified crustacean larvae were also most numerous in April in the upper waters and were found in small numbers down the water column. Amphipods also occurred throughout the water column in small numbers but were most numerous in November–December and May–June in the upper 500 m. A few isopods were noted only between 1,000 and 1,500 m. *Evadne spinifera* was present from July to October, with highest numbers in July (2.2/m^3) and October (2.9/m^3) in the upper 500 m. *Lucifer typus* was recorded in the surface waters only in August, April, and May.

Euphausiids were the largest organisms that occurred commonly in the deeper samples (Fig. 12). In the upper 500 m they were noted only in December and March. In general, most euphausiids were below 1,500 m in daytime (Fig. 12D), and few were taken throughout the water column in winter. The highest number recorded from any depth was 1.3/m^3 in November from the 1,500–2,000-m depth interval. The mean crop obtained for the 500–2,000-m water column was 158.0/m^2. Our nets were too fine meshed to sample these crustaceans adequately; probably the majority of the specimens caught were immature.

Tunicates

Pelagic tunicates ranked third in mean percent although second in mean numbers in the upper 500 m and were numerous only in the upper waters. Occasional doliolids and appendicularians were found in the deeper samples, but, since they were usually tangled in clumps with other organisms, it was difficult to decide whether

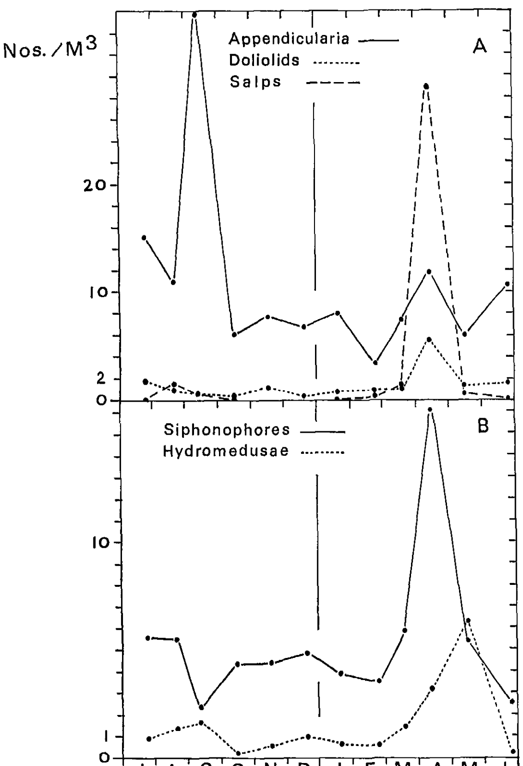

FIG. 13. A. Total No./m^3 from July 1968 to June 1969 of Appendicularia, salps, and doliolids for the upper 500 m. B. Total No./m^3 from July 1968 to June 1969 of siphonophores and hydromedusae for the upper 500 m.

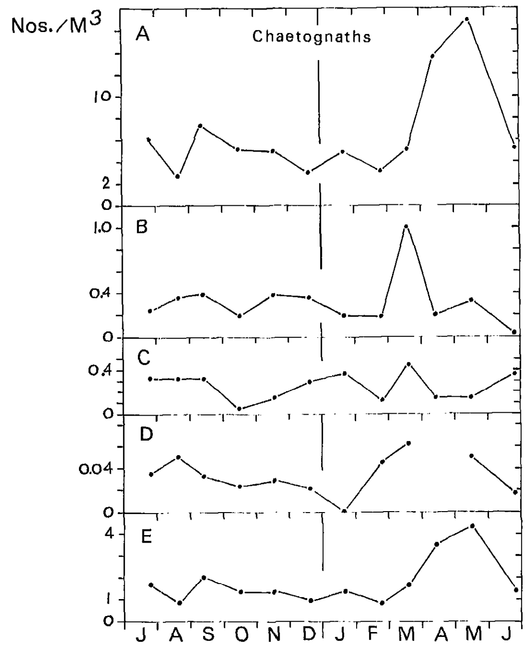

FIG. 14. Total No./m^3 from July 1968 to June 1969 of chaetognaths. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 1,500–2,000 m. E. 0–2,000 m.

they had been alive when caught. Doliolids and salps were numerous only in April (Fig. 13A). Appendicularians comprised 71% of the tunicates in the surface waters and were more numerous year-round. *Fritillaria* was most abundant in September and June, *Oikopleura* in September and April. The mean total number of tunicates obtained for the year for the upper 500 m was 15.1/m^3, of Appendicularia 10.8/m^3.

Coelenterates

Siphonophores and hydromedusae together ranked fourth in abundance in the upper 500 m, although almost equal numbers of chaetognaths were present, and chaetognaths were somewhat more abundant below 500 m. Their seasonal cycles in the upper waters show siphonophores most numerous in April and hydromedusae in May (Fig. 13B). Occasional hydromedusae were found throughout the water column, but siphonophores were usually somewhat more numerous. In the upper waters siphonophores constituted 78% of the coelenterates and gave a mean of 5.3/m^3 for the year. Between 500 and 1,000 m highest numbers of siphonophores were noted in March and May; the annual mean obtained was 0.3/m^3. Small numbers were also found throughout the year below 1,000 m, but some of the specimens counted from the deeper waters may have been dead when caught.

Chaetognaths

Table 2 lists the percentages of chaetognaths in the total zooplankton from the four levels sampled and the total numbers per cubic meter are shown in Fig. 14. Mean total numbers for the 2,000-m water column gave a seasonal cycle similar to that in the upper 500 m, with an annual mean of 1.8/m^3 or 3,540/m^2.

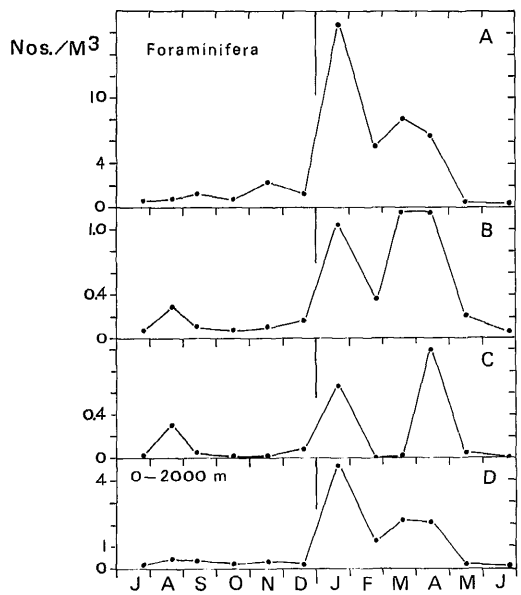

FIG. 15. Total No./m^3 from July 1968 to June 1969 of Foraminifera. A. 0–500 m. B. 500–1,000 m. C. 1,000–1,500 m. D. 0–2,000 m.

In 1961–1962 chaetognaths constituted the same percentage (3.0%) of the total zooplankton of the upper 500 m, but numbers were slightly higher and gave an annual mean of 8.4/m^3 (Deevey 1971). Ten species were noted in the upper waters of which *Sagitta minima* was the most abundant; *S. lyra* has been found throughout the water column below 500 m, and *S. macrocephala* was the species most commonly observed between 500 and 1,500 m. Species of *Eukrohnia* also occur in the deeper waters, and *Krohnitta subtilis* has been recorded from down to 1,000–1,500-m depths.

Foraminifera

Foraminifera were the most abundant Protozoa taken in the samples, although some Radiolaria and other forms were noted, especially in deeper waters. Bé (1960) has described the seasonal cycles of the temperate and subtropical species that occur at station "S," the former being most abundant in winter–spring, the latter in fall. Apparently only small numbers of subtropical species were present in 1968, since there was no fall maximum, unlike 1961 when Foraminifera were more numerous in fall than in winter–spring. Total numbers for the upper 500 m gave an annual mean of 3.7/m^3. Foraminifera occurred throughout the water column (Fig. 15). Mean annual numbers were 0.4/m^3 for 500–1,000 m, 0.2/m^3 for 1,000–1,500 m, and 0.08/m^3 for 1,500–2,000-m depths, the annual mean for the 2,000-m water column being 1.1/m^3, or 2,200/m^2. Since the cycles in the deeper waters follow so closely that in the upper 500 m, perhaps some of the specimens counted from the deeper samples were dead shells.

Other forms

Polychaetes and polychaete larvae were found throughout the water column all year. In the upper 500 m they were most numerous in August and from April to June, with mean numbers for the year of 1.4/m^3; between 500 and 1,000 m the annual mean was 0.3/m^3; between 1,000 and 1,500 m it was 0.04/m^3; in the deepest waters, 0.02/m^3. Over all the depth levels polychaetes constituted less than 1% of the total zooplankton.

Gastropod larvae were most abundant in the upper 500 m in July, October, and June, and only occasionally were noted below 1,000 m. Cyphonautes larvae occurred throughout the water column primarily in summer and fall and were most numerous in the upper waters in November and December and between 500 and 1,000 m in September. Echinoderm larvae were most abundant in September in the upper 500 m, and rarely were found in deeper waters. Brachiopod larvae were found occasionally at any depth, and squid larvae were noted infrequently between 500 and 1,500 m.

Fish eggs were noted occasionally throughout the water column, especially in August, November, December, and February. Fish larvae were most numerous in the upper waters in August, but were most frequently noted between 500 and 1,000 m and occasionally down to the deepest level.

Pteropods occurred throughout the water column, but in very small numbers below 500 m. In the upper 500 m highest numbers of $31.3/m^3$ were recorded in June when *Spiratella* (= *Limacina*) *inflata* was abundant ($29.6/m^3$). The mean number obtained for the year was $3.9/m^3$. *Desmopterus papilio* occurred between 500 and 1,000 m from July to January and was once noted from 1,500–2,000-m depths. Occasional gymnosomes were noted at any depth between November and February. The species of pteropods and their seasonal cycles at station "S" have been discussed by Chen and Bé (1964) and also by Deevey (1971).

DISCUSSION

That there is a seasonal cycle in quantity of zooplankton in the subtropical waters of the Sargasso Sea has been well established for the upper 500 m (Menzel and Ryther 1961*a*; Deevey 1971). The most prominent and consistent feature of the cycle is a spring maximum, in which many kinds of animals participate. In the upper waters the magnitude of the spring maximum is related to the extent of the winter–spring phytoplankton bloom and in turn to the degree of environmental change. Insofar as there are seasonal variations of atmospheric origin at this latitude, there are seasonal cycles in quantity and species of plankton in the upper waters. The great majority of species involved are epiplanktonic, restricted to the upper several hundred meters.

By contrast, below 400–500 m, or at most 800 m, there is no seasonal change in temperature or salinity. Except for the vertical migrations of living animals and the gravitational sinking of organic detritus, there would appear to be little interchange between the seasonally controlled upper waters and the waters within and below the permanent thermocline. Nevertheless, the quantity of zooplankton varied considerably throughout the year below 500 m (*see* Figs. 1 and 3, in particular). Figure 4, which gives the total numbers of copepods and all other organisms for the upper 500 m and averaged for 500–2,000-m depths, shows that in general numbers were higher in the deeper waters when they were lower in the upper waters, and vice versa. Between 500 and 1,500 m, numbers were low in October and April, when they were maximal in the upper 500 m. Throughout the water column below 500 m (Fig. 4B) copepods and all other organisms were most numerous in March, before the April maximum in the surface waters, but the quantity of zooplankton in the deeper waters also increased after the April maximum.

We do not know whether these variations were directly related to seasonal changes in the upper waters, since, with the notable exception of the seasonal depth distribution of *Eucalanus* (Fig. 10), most of the species appear to remain year-round at their own depth levels below 500 m. Some forms, such as species of *Metridia* (Fig. 9B–E), that were not noted in the upper waters and were most numerous between 1,000 and 2,000 m, showed a definite cycle in numbers during the year, with maxima between January and May. Until the annual cycles of particular deep-water species can be looked at in more detail we cannot say whether these variations are related to seasonal changes in the upper waters. They may instead reflect variations in horizontal transport, thus echoing seasonal changes at higher latitudes where the water mass is formed rather than off Bermuda (*see* Leavitt 1938). Some of the observed cycles of seasonal abundance suggest such a relation, others do not, and the variety of patterns clearly needs further study.

The quantity of zooplankton in the Sargasso Sea, reputedly sparse in the upper waters, decreases markedly with depth, more so in numbers than in volumes. The greatest decrease in numbers occurs between the upper waters above 500 m, which are subject to seasonal change, and those of the permanent thermocline between 500 and 1,000 m. Below 1,000 m numbers and volumes are approximately halved over each lower depth level (Fig. 16). The great majority of organisms are concentrated in the upper several hundred meters. However, previous investigations in these waters have indicated that more than 50% of the zooplankton is found below 500 m. Menzel and Ryther (1961*a*) sampled with

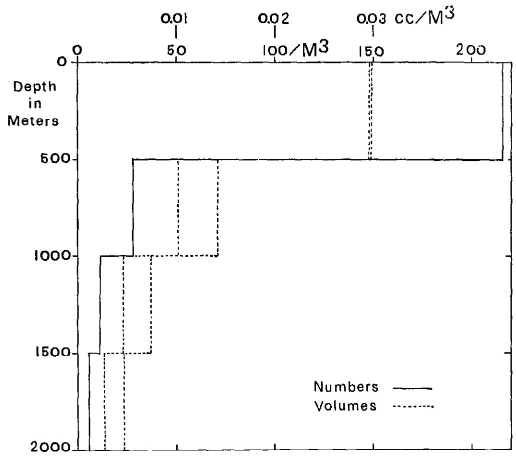

FIG. 16. Mean annual maximal and minimal displacement volumes in cc/m^3 and mean annual total No./m^3 for the four depth intervals between the surface and 2,000 m.

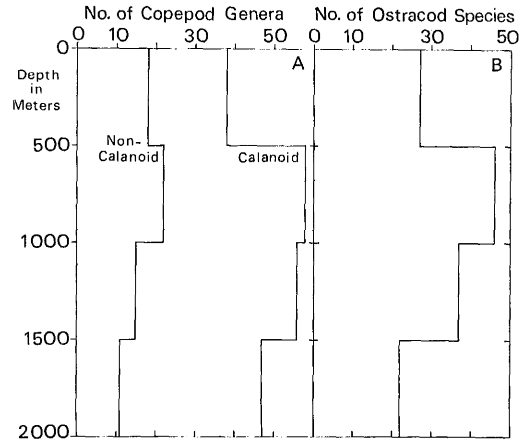

FIG. 17. The number of copepod genera (A) and of ostracod species (B) noted for the four depth ranges between the surface and 2,000 m.

a No. 2 net over several depth levels down to 2,000 m in June, August, and February at station "S" and found that an average of 63% of the zooplankton dry weight occurred below 500 m; the distribution of zooplankton displacement volumes and ash-free dry weights was similar. Leavitt (1938) reported that more than 50% of the macrozooplankton was found below 500 m in waters north of Bermuda. Relatively coarse nets would not have adequately sampled the minute organisms that comprise the bulk of the plankton of the upper waters, and it is true that larger organisms are more abundant below 500 m. Figure 16 shows that the decrease in mean volumes between the upper waters and the 500–1,000-m depths is not nearly as great as the decrease in mean numbers, and this indicates an increase in size of organisms below 500 m. The dominant organisms in the upper waters are small copepods, ostracods, and Appendicularia. The range in size of organisms is greater below 500 m; tiny calanoids and ostracods occur throughout the water column, but large and exceptionally large species are also present. Our data indicate that the mean total number of microzooplankton between 500 and 2,000 m is only a fourth that of the upper 500 m; the mean minimal volumes are only 61%, the maximal volumes 88%, of the mean volume obtained for the upper 500 m. Our mean displacement volumes for 1,000–2,000-m depths are of the same order of magnitude as those recorded by Grice and Hulsemann (1965, 1967), who obtained a mean volume of 0.005 cc/m^3 for samples collected between 30° and 40° N in the Atlantic.

However, when the 2,000-m water column is considered as a whole, appreciable quantities of zooplankton are present. In mean total numbers, 65 organisms/m^3 occur throughout this column—130,000 beneath a square meter of sea surface; these include 27.5 calanoid copepods/m^3 or nearly 55,000/m^2, 4.4 ostracods/m^3 or 8,800/m^2—a total of 53.5 crustaceans/m^3 or over 100,000/m^2. In comparing the quantity of zooplankton in the Sargasso Sea with quantities recorded for New England coastal waters, the mean annual minimal volume obtained, 24.0 cc/m^2, is half the mean volume recorded for Georges Bank (Riley and Bumpus 1946), but, over a water column a hundred times longer, is almost 20% greater than that obtained for central Long Island Sound (Deevey 1956, 1971).

A great variety of organisms live within the upper 500 m of the Sargasso Sea (Moore 1949; Grice and Hart 1962; Deevey 1971). Some of these, such as the tunicates, chaetognaths, coelenterates, and pteropods, are more abundant in species as well as numbers in the upper waters, but in the deeper waters the Crustacea have proliferated into myriad forms. In the case of ostracods and copepods the increase in diversity with depth is notable, and the greatest diversity has thus far been found in waters of the permanent thermocline. Figure 17 illustrates our present data for the distribution with depth of numbers of copepod genera and ostracod species and shows that highest numbers have been found between 500 and 1,500 m. In the case of the ostracods, there are fewer species at the deepest level than within the upper 500 m, but there are more calanoid genera in the deepest waters than in surface waters. In the upper 500 m at station "S," 42 calanoid genera were recorded (Deevey 1971); the upper waters may have more, but it is unlikely that as many will be found as in deeper waters. Calanoid species diversity reportedly decreases below 2,000 m, but many new species from deep waters have been described recently (Grice and Hulsemann 1965, 1967, 1968; Park 1970; Wheeler 1970).

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