



**The Abundance, Seasonal Occurrence and Distribution of the  
Epizooplankton between New York and Bermuda**

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*Ecological Monographs*, Volume 32, Issue 4 (Autumn, 1962), 287-309.

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# THE ABUNDANCE, SEASONAL OCCURRENCE AND DISTRIBUTION OF THE EPIZOOPLANKTON BETWEEN NEW YORK AND BERMUDA

GEORGE D. GRICE AND ARCH D. HART

*Contribution No. 1237 of the Woods Hole Oceanographic Institution*

## TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION .....	287	Chaetognatha .....	297
METHODS .....	287	Euphausiacea .....	299
Field Procedure .....	287	Amphipoda .....	300
Laboratory procedure .....	288	Siphonophorae .....	301
HYDROGRAPHIC DATA .....	289	Other Groups .....	301
Neritic waters .....	289	DISCUSSION .....	303
Slope waters .....	289	Species occurrence .....	303
Gulf Stream .....	290	Trophic structure .....	304
Sargasso Sea .....	290	Indicators .....	305
TOTAL ZOOPLANKTON .....	291	New Records .....	305
Displacement Volumes .....	291	SUMMARY .....	305
Numerical abundance .....	292	LITERATURE CITED .....	306
COMPONENTS OF THE ZOOPLANKTON .....	293	APPENDIX .....	308
Copepoda .....	293		

## INTRODUCTION

The pioneer studies of plankton and hydrography conducted by Dr. H. B. Bigelow (1915, 1917 *et al.*) in the Gulf of Maine and waters adjacent to the northeast coast of the United States have been augmented in recent years by a few other similar and several more restricted investigations of these waters. A glance at the numerous titles dealing with zooplankton leads one to assume that the plankton fauna of the northwest Atlantic is fairly well known, as indeed the neritic plankton is.

Yet the proximity of the Sargasso Sea and Gulf Stream to the neritic and intervening slope waters off New York, each with more or less unique hydrographic conditions, makes synoptic studies not only interesting but essential if species distribution, occurrence and fluctuation are to be understood in light of the hydrography and phytoplankton production.

The present investigation is one of several concerned with the biology and chemistry of plankton in the region between New York and Bermuda and is a part of a continuing study of zooplankton in the northwest Atlantic Ocean.

It is a pleasure to acknowledge the assistance of the following persons who have generously given of their time in checking many or all of our species determinations in the indicated taxa: Siphonophorae, Dr. Mary Sears; Annelida, Dr. Phillips Dales; Amphipoda, Dr. T. E. Bowman; Euphausiacea, Dr. Brian P. Boden; species of *Lucifer*, Dr. Fenner A. Chace, Jr.; Ostracoda, Dr. E. J. Iles; and Chaetognatha, Dr. E. L. Pierce. Dr. Bowman has been especially helpful with our amphipod identification problems.

The sorting of the original collections into the

various taxonomic components was done by Mrs. Peter Saunders and Miss Louisa Schell. Miss Abigail Hooper checked the statistical data. The authors wish also to thank Dr. Bostwick H. Ketchum for reading and criticizing the manuscript. This work was supported in part by the U. S. Atomic Energy Commission (contract AT (30-1)-1918, by the U. S. Navy (Contract Nonr 3033) and by the National Science Foundation (G 8339).

## METHODS

### FIELD PROCEDURE

**CRUISES AND STATIONS.** The zooplankton was obtained on four cruises between New York and Bermuda and one cruise between New York and the Gulf Stream in 1959 and 1960 (Fig. 1, Table 1). A single Sargasso Sea sample was collected in 1960 and is considered representative of this area for this month. On each cruise zooplankton samples and usually considerable other biological and hydrographical data were collected at stations situated along a transect extending from the coastal waters off Montauk Point, New York to Sargasso Sea waters near Bermuda. Stations A-D were in shelf waters, E-HH in slope waters, II in the Gulf Stream, and JJ-NN in the Sargasso Sea. The location and water depths of each station are given in Table 2. In the present study we have not examined the samples obtained at stations MM and OO.

**PLANKTON.** The zooplankton samples were collected by a 3/4-m open net with a Clarke-Bumpus flow meter mounted in the center. Of the 56 collections, all but one were obtained by a no. 6 mesh (aperture size .23 mm) net. In September 1959 the sample from station A was obtained by a no. 2 mesh

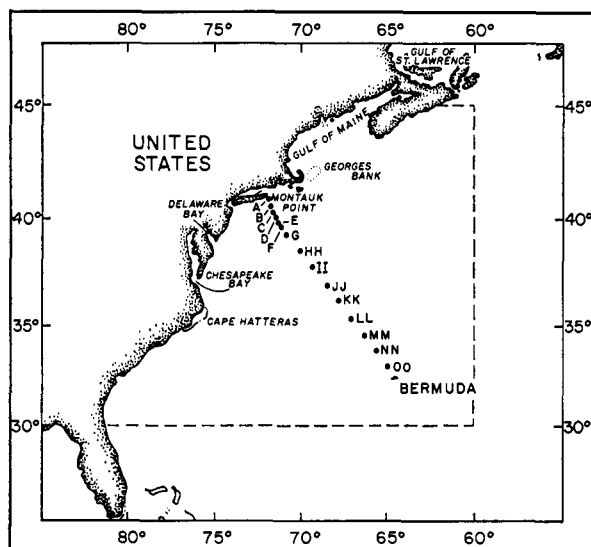


FIG. 1. Transect of zooplankton collecting stations. Species not hitherto reported from areas within dashed line considered new to this area.

(aperture size .36 mm) net; no quantitative analyses were made on this sample.

At the shelf stations (A-D) the net was lowered to as near the bottom as practicable and then raised to the surface. At the other stations, all in deep water, the maximum depth of each collection was 200 m. The oblique tows were made at ships' speeds of approximately 2 knots. The zooplankton was preserved in 5% sea water-formalin solution.

TABLE 1. Zooplankton collecting data and types of analyses made on the samples.

Ship, cruise, and date	No. samples	Stations	Types of analyses
Crawford 33 Sept. 1959 Montauk to Gulf Stream	9	A-II	Volume, counts and taxonomy, except taxonomy only on station A sample
Crawford 35 Dec. 1959 Montauk to Bermuda	10	A-C, G-LL, NN	Volume, counts and taxonomy
Crawford 38 Mar. 1960 Montauk to Bermuda	12	A-HH, JJ-LL, NN	"
Atlantis 257 July 1960 Montauk to Bermuda	12	A-JJ, LL, NN	"
Crawford 42 Aug. 1960 Montauk to Bermuda	12	A-LL	Volume only
Crawford 49 Sept. 1960 Sargasso Sea	1	KK	Volume, counts and taxonomy

The collections were obtained at various times of day and night. Except for the Gulf Stream both day and night collections were usually obtained in each area (shelf waters, slope waters, Sargasso Sea) at one station or another on a given cruise. Since the collections from neritic waters were made from the surface to the bottom, diurnal migration of the animals presumably had little effect on the composition of the catch. Examination of the collections from the Sargasso Sea showed very little variation in their

TABLE 2. Water depths and positions of zooplankton collecting stations between Montauk Point and Bermuda shown in Figure 1.

Area	Station	Depth in meters	Latitude	Longitude
Shelf waters	A	36	40°58'	71°49'
	B	64	40°44'	71°41'
	C	67	40°31'	71°35'
	D	77	40°18'	71°28'
Slope waters	E	314	40°00'	71°19'
	F	1246	39°48'	71°12'
	G	2270	39°36'	71°06'
	H	2815	38°46'	70°20'
Gulf Stream	II <sup>a</sup>	—	—	—
Sargasso Sea	JJ	4573	37°12'	68°48'
	KK	4818	36°23'	68°04'
	LL	4977	35°35'	67°20'
	MM <sup>b</sup>	5136	34°47'	66°29'
	NN	5073	33°56'	65°49'
	OO <sup>b</sup>	4853	33°05'	65°00'

<sup>a</sup> Station II in Gulf Stream, located by BT's.

<sup>b</sup> Samples from this station not examined.

total volumes from station to station. Volumes of slope collections were more variable owing to swarms of salps. Unfortunately, all four Gulf Stream collections were obtained during daylight, a fact which may account in part for the small numbers of species found in certain of the groups.

**HYDROGRAPHIC DATA.** Hydrographic data from Nansen and bathythermograph (BT) casts were collected at the stations where zooplankton was obtained on all *Crawford* cruises. On *Atlantis* 257, only BT casts were taken at the plankton collecting stations.

#### LABORATORY PROCEDURE

**SUBSAMPLING AND SORTING.** The samples were split into smaller subsamples by means of a Folsom splitter (McEwen *et al.* 1954). Usually 1/4 or 1/8 of the original sample was sorted and identified.

Each subsample was sorted into the major taxonomic components, which were placed in separate vials for later taxonomic analyses, numerical estimates of species abundance, and volume determinations.

**TAXONOMY AND COUNTS.** To make numerical estimates of species abundance, each sorted fraction of a subsample was examined and the species identified and counted. In many of the less abundant groups (annelids, euphausiids) it was possible to count all individuals in the fraction. It was not practical, however, to count all specimens in the numerically abundant taxa such as copepods and chaetognaths. Small aliquots of these groups were examined and usually the entire fraction scanned for the presence of rarer species. Forty-four samples were examined taxonomically (Table 1).

Because of fragmentation of the colonies and alternation of generation the siphonophores had to be somewhat differently treated. The total in the nectophore generation was determined by adding the

number of colonies present to either the inferior or superior nectophore count, whichever was the largest. The eudoxid generation (sexual stage) was counted by adding the number of eudoxids present to the number of bracts present. Gonophores were counted but their totals are combined with various other unidentifiable siphonophores as their numbers do not reflect the actual number of siphonophores present.

**DISPLACEMENT VOLUME.** Displacement volumes were taken of each taxonomic group in each subsample by the method of Yentsch and Hebard (1957). The displacement volumes of several subsamples which contained mostly salps were determined by first draining the water from the salps in a plankton sock and then measuring their displacement after they had been placed in a graduate containing a known quantity of water. In those samples where some groups were present in insufficient quantities for determination of volumes, these groups were combined into a miscellaneous category and a volume determination made on it. The total displacement volume of a given sample is the sum of the displacement volumes of the individual groups. The samples obtained on *Crawford* cruise 42 were not examined taxonomically and hence the displacement volumes were taken of the entire subsample. It should be pointed out that we have removed from the subsamples representative specimens for most of the species found. Where the removal of these specimens would have affected the displacement volume, we returned an equivalent number, obtained from the original sample, to the subsample prior to making a volume determination.

Volume determinations were made on 43 of the 44 samples which were examined taxonomically as well as on the 12 samples collected on *Crawford* cruise 42 in August 1960 (Table 1).

**REFERENCE COLLECTION.** The species in those groups with which we were unfamiliar were sent to cooperating specialists for corroboration of our determinations. While some specimens have been deposited in the U. S. National Museum, we have representatives of most species in a reference collection at the Woods Hole Oceanographic Institution.

### HYDROGRAPHIC DATA

Temperature and salinity data for the upper 200 m (maximum depth of plankton collecting) at representative stations in shelf, slope, Gulf Stream and Sargasso Sea waters are shown in Figures 2 to 7. Complete hydrographic data for all stations are on file at the Woods Hole Oceanographic Institution.

### NERITIC WATERS

Seasonal temperature variations were greater in the surface than in the deeper waters of the shelf (Fig. 2). Coldest temperatures were in March when the water was isothermal to the bottom. Warmest temperatures were in September and July at which times they approached those of the Sargasso Sea in March. Colder bottom waters, especially evident in July, were present throughout the year.

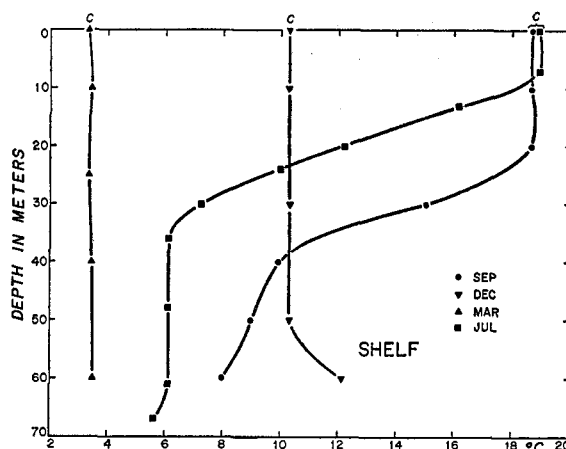


FIG. 2. Seasonal variation in temperature at a selected station in shelf waters.

Lower salinities (Fig. 6) occurred at the inshore station 25-31 ‰ and higher salinities, up to 34 ‰, were found at the offshore neritic stations. The salinity of the deeper shelf waters was somewhat higher than that of the surface. Ketchum and Corwin (1961) have discussed seasonal variation in temperatures and salinities in the continental shelf waters off New York and the hydrographic factors relating to a persistent pool of cool bottom water on the shelf in summer. We will have several occasions in the discussions below to refer to this pool of water.

### SLOPE WATERS

Large seasonal variation also occurred in surface slope waters (Fig. 3). In deeper waters, near 200 m, comparatively little seasonal temperature difference was noted. In the warmer months a thermocline was present between 10 and 40 m while in December the upper 70 m were mixed and practically isothermal. Inversions, probably representing intrusions of shelf waters, were present at some slope stations in September and July.

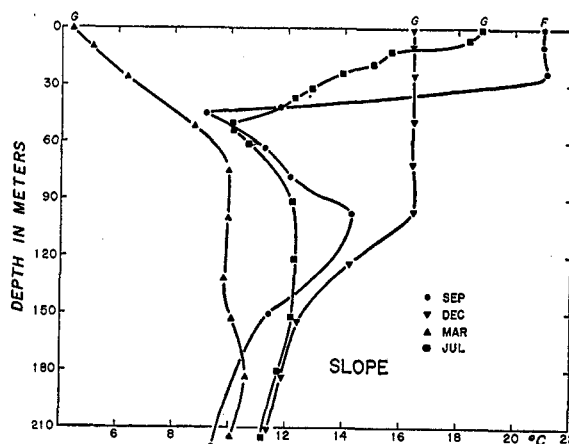


FIG. 3. Seasonal variation in temperature in the upper 200 m at selected stations in the slope water.

Salinities in the surface slope waters were variable (Fig. 6) but usually higher than those of the shelf.

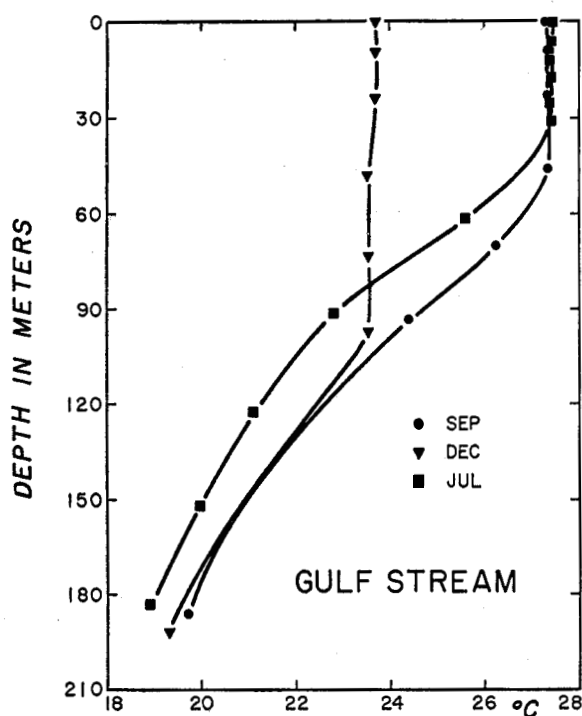


FIG. 4. Seasonal variation in temperature in the upper 200 m of the Gulf Stream.

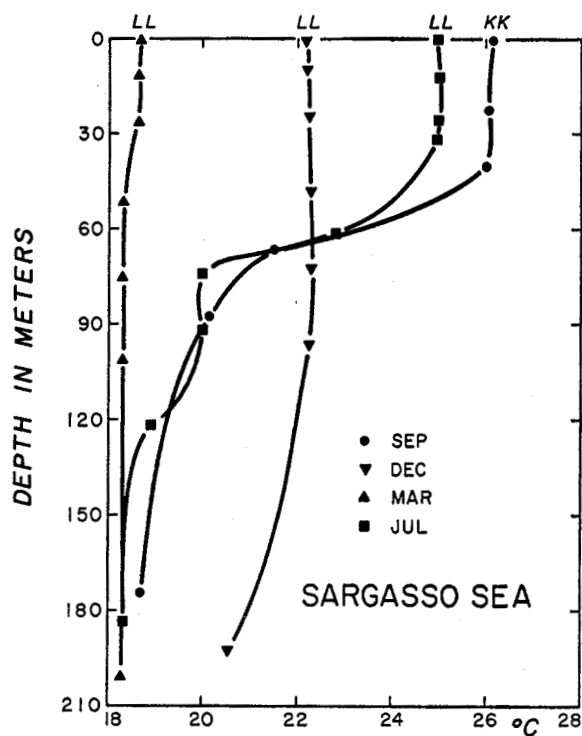


FIG. 5. Seasonal variation in temperature in the upper 200 m at selected stations in the Sargasso Sea.

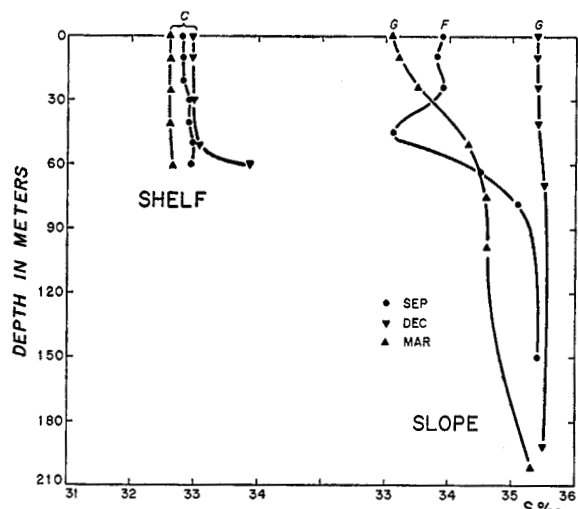


FIG. 6. Seasonal variation in salinity at a shelf station and in the upper 200 m at selected stations in the slope water.

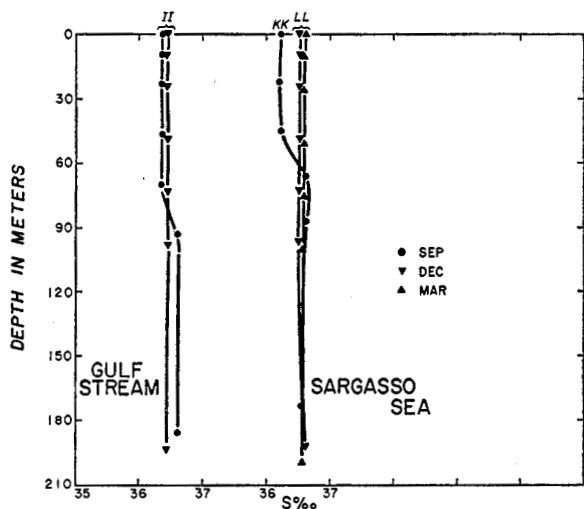


FIG. 7. Seasonal variation in salinity in the upper 200 m of the Gulf Stream and in the upper 200 m at selected stations in the Sargasso Sea.

#### GULF STREAM

Temperatures (Fig. 4) and salinities (Fig. 7) of the Gulf Stream were high and, compared to neritic and slope waters, showed little seasonal fluctuation. The minimum temperature in the upper 200 m ( $19^{\circ}$ ) was much higher than the minima of the two aforementioned areas.

#### SARGASSO SEA

The temperature (Fig. 5) and salinity (Fig. 7) of the Sargasso Sea also varied very little. In the months of December and March the waters were mixed to at least 200 m and well-developed thermoclines were present in September and July at depths of between 60 and 70 m.

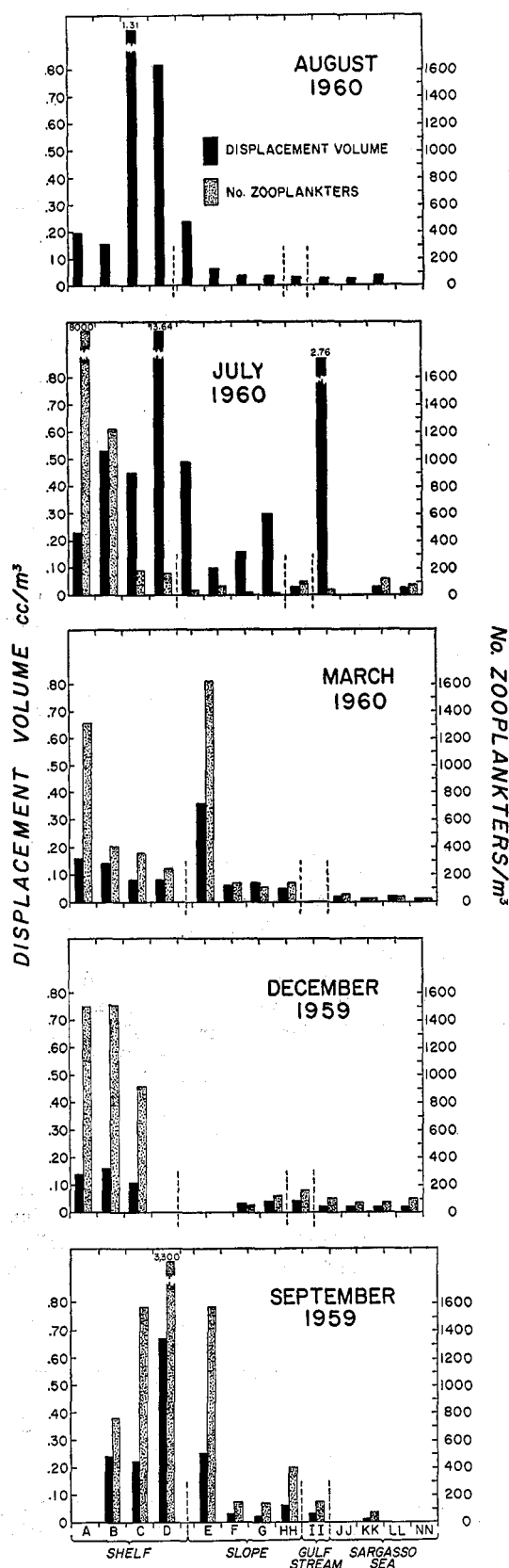


Fig. 8. Displacement volumes and numerical abun-

## TOTAL ZOOPLANKTON

## DISPLACEMENT VOLUMES

The total displacement volumes of the 55 samples are shown in Figure 8. It is immediately obvious from these data that there was spatial variation in the size of the standing crops and considerable seasonal fluctuation in the quantities found in neritic and slope waters.

INSHORE-OFFSHORE VARIATION. Inspection of the displacement volumes for each of the 5 months (Fig. 8) shows that, regardless of season, there were generally larger quantities of zooplankton in shelf waters with progressively lesser amounts in slope, Gulf Stream and Sargasso Sea waters. The only exception to this trend was in March when the mean displacement volume for the slope (.14 cc/m<sup>3</sup>) was slightly greater than that for neritic waters (.12 cc/m<sup>3</sup>). The mean seasonal values for the Sargasso Sea (.01-.03 cc/m<sup>3</sup>) were hardly different from the Gulf Stream values (.03-.04 cc/m<sup>3</sup>).

The largest standing crops were usually encountered at the shelf edge station, station D, and at the innermost slope station, station E, just beyond. In the slope waters seaward of station E there was an abrupt and often sustained decrease in volumes. The displacements at station F were 1/8 to 1/4 those at station E. Examination of the numerical abundance as well as the displacement volumes of each taxonomic group indicates that this decrease was not due to the disappearance or decline of any one group of organisms but apparently to the general reduction of zooplankton in slope waters.

Excluding 10 collections (stations D-HH and JJ, July; B-E, August) in which large quantities of salps were found and little of anything else, the mean values (cc/m<sup>3</sup>) for each of the areas based on all collections were as follows: shelf, .24; slope, .08; Gulf Stream, .03; and Sargasso Sea, .02. (We have excluded the salp-rich samples because we are not sure whether the net was clogged by them immediately upon entering the water and hence whether the subsurface zooplankton was adequately sampled.) The mean standing crop in shelf waters was therefore about 3 times greater than that of the slope, and the standing crop of the slope water was approximately 3 to 4 times greater than that of the Gulf Stream and Sargasso Sea. These values may be compared to those provided by Clarke (1940) who reported that volumetrically there was 4 times more zooplankton in coastal than in slope waters and 4 times more in slope than in Sargasso Sea waters. His data also included salps which he remarked as being unusually abundant. If salps are included in our comparisons of the mean values for each area, the shelf zooplankton (1.07 cc/m<sup>3</sup>) was 4 times more abundant than slope zooplankton (.27 cc/m<sup>3</sup>) and the latter 9 to 10 times more abundant than the Gulf Stream (.03 cc/m<sup>3</sup>) or Sargasso Sea (.02 cc/m<sup>3</sup>) zooplankton.

dance of the zooplankton. Station JJ in July is not in Sargasso Sea but in the slope water (see text).

These great differences in abundance of zooplankton from region to region should be emphasized because the displacement volumes of individual taxa discussed below will be referred to in terms of percent of total displacement volume.

**SEASONAL VARIATION.** Although the 5 series of collections were somewhat widely spaced in time, the displacement data showed that rather large fluctuations occurred seasonally especially in neritic and slope waters.

In the neritic area significantly larger mean displacement volumes occurred in the warm months of July ( $3.71 \text{ cc/m}^3$ ), August ( $.61 \text{ cc/m}^3$ ) and September ( $.38 \text{ cc/m}^3$ ) than in the cold months of December ( $.14 \text{ cc/m}^3$ ) and March ( $.12 \text{ cc/m}^3$ ). The extraordinarily large mean for July was due to salps which comprised approximately 99% of the  $13.64 \text{ cc/m}^3$  of zooplankton at station D. There was thus a 30-fold difference between the mean winter minimum and summer maximum values. This difference compares favorably to Clarke's (1940) report of 20 to 40 times more zooplankton in summer than in winter in neritic waters of this area.

St. John (1958) has recently summarized and compared selected zooplankton volumes (winter and summer) reported for certain areas of the North Atlantic coastal waters between Cape Hatteras and the Gulf of St. Lawrence on the American side and for areas adjacent to Iceland, Norway, and England and in the Baltic Sea on the European side of the Atlantic. Our mean March value ( $.12 \text{ cc/m}^3$ ) is identical to that for the Gulf of Maine but smaller than the January means for Cape Hatteras to Cape Fear ( $.20 \text{ cc/m}^3$ ), Cape Cod to Chesapeake Bay ( $.40 \text{ cc/m}^3$ ) and Georges Bank ( $.20 \text{ cc/m}^3$ ). Our mean is considerably larger, however, than those for European waters ( $.01$  to  $.02 \text{ cc/m}^3$ ). Using his June values for comparison with our July mean ( $3.71 \text{ cc/m}^3$ ), it is found that our value exceeds those for all regions summarized by St. John. The nearest average is that for Georges Bank ( $1.50 \text{ cc/m}^3$ ). St. John indicated that the maximum recorded zooplankton volume for a single tow in American waters is  $6.9 \text{ cc/m}^3$  as recorded by Bigelow and Sears (1939). He apparently overlooked a value of  $15.5 \text{ cc/m}^3$  reported by Clarke (1940) for one of his coastal stations. Our largest volume was  $13.64 \text{ cc/m}^3$ .

The seasonal variation in slope waters was less extreme than that in shelf waters. The maximum mean displacement volume was recorded for July ( $.76 \text{ cc/m}^3$ ) and the minimum for December ( $.04 \text{ cc/m}^3$ ), a 20-fold difference; Clarke (1940) reported a 10-fold seasonal difference in slope waters. It is almost certain that our December mean was low because it did not include a sample from station E where, as pointed out above, zooplankton volumes were very large. We feel that the December slope mean should be nearer  $.10 \text{ cc/m}^3$ , which in comparison to the summer maximum would represent a 7- to 8-fold difference in seasonal extremes.

Although admittedly based on meager data (4 collections), the displacement volume determinations for the Gulf Stream were hardly different from one another ( $.03$ -. $04 \text{ cc/m}^3$ ). Bsharah (1957), however, has shown that the volume of zooplankton in the upper 600 m of the Florida current off Miami in the period March-June was 2-3 times that for the remainder of the year, and in the upper 100 m, 4 times that of the remainder of the year.

In the Sargasso Sea we can likewise detect little, if any, seasonal fluctuations in zooplankton although here, too, our collections may be too widely spaced in time. The volumes were all extremely small and the mean values were similar to one another and to those of the Gulf Stream ( $.03$ -. $04 \text{ cc/m}^3$ ). Clarke (1940) also found little evidence of seasonal fluctuation in the samples he analyzed from the Sargasso Sea. Later Moore (1949) reported maximum zooplankton in May and June and minimum amounts in October in the waters adjacent to Bermuda. Menzel and Ryther (1961) have recently reported a distinct spring maximum in zooplankton abundance at a station located approximately 15 miles from Bermuda. Their report was based on examination of semi-monthly collections made for a period of approximately 3 years. The maximum displacement volume values for the 3-year period were approximately 21, 6 and 4 times the minimum values for each of these years.

#### NUMERICAL ABUNDANCE

The number of zooplankton per cubic meter computed for 12 major taxa is given in Figure 8. Actually the figures to which we refer as the total number of zooplankters do not include several of the minor groups (e.g., Ostracoda, Mysidacea) which were not present abundantly.

**INSHORE-OFFSHORE VARIATION.** As might be expected in light of the above discussion of displacement volumes considerably larger numbers of zooplankters were encountered in neritic waters than in Gulf Stream and Sargasso Sea waters. Abundance of zooplankton in slope waters was usually intermediate between that estimated for neritic and Sargasso Sea samples.

The trends in numerical abundance frequently followed very closely those in the displacement volume measurements. This similarity was due primarily to the large numbers of copepods which usually made up the bulk of the zooplankton.

A major exception to the similarity between volumes and numbers was in July when large volumes were not duplicated by concomitantly large numbers of zooplankton. This discrepancy was due to the predominance of salps and near absence of smaller but usually more abundant zooplankters (i.e., copepods, chaetognaths).

The decline in zooplankton offshore can probably best be illustrated by comparing average numerical abundance, based on all collections, in each of the areas. The mean number of zooplankters per  $\text{m}^3$

was as follows: neritic, 1540; slope, 310; Gulf Stream, 134; and Sargasso Sea, 71.

**SEASONAL VARIATION.** In terms of mean numerical abundance there were more zooplankters in neritic waters in September ( $1892/m^3$ ) and July ( $2401/m^3$ ) than in December ( $1312/m^3$ ) or March ( $585/m^3$ ). These values are not nearly so large as some reported for sheltered and estuarine waters of the area. For example, Deevey's (1952a) estimates for Block Island Sound, based on no. 10 net collections, varied between  $5000/m^3$  and  $34,000/m^3$ .

The numerical estimates for the slope were likewise variable but smaller in magnitude. The largest average values occurred in September ( $571/m^3$ ) and the smallest in July ( $36/m^3$ ). The March mean ( $504/m^3$ ) was similar to that of the shelf waters ( $585/m^3$ ) for this month.

Smaller values and less variation characterized the Gulf Stream. Numerical estimates ranged from 99 to  $156/m^3$  in the three collections from this area.

The numerical abundance of zooplankton estimated for Sargasso Sea samples was not as greatly variable. The minimum ( $18/m^3$ ) and maximum ( $128/m^3$ ) values differed by a factor of 7 whereas neritic samples differed by a factor of approximately 40. Comparing the means for the four months it appeared that the largest number of organisms was present in July ( $108/m^3$ ) and the least number in March ( $42/m^3$ ). As previously pointed out it is probable that our sampling was too infrequent and the spring surge of zooplankton was missed. Fish (1954) reported a yearly average of 239 zooplankters/ $m^3$  in the Sargasso Sea at a station east of Bermuda ( $35^\circ N$ ,  $48^\circ W$ ). According to data presented in his Figure 2 the total numbers of zooplankton at this station varied from approximately  $15/m^3$  to  $9000/m^3$  with a well defined augmentation period occurring in May and June. Although we did not detect such a dramatic increase our average ( $71/m^3$ ) for the Sargasso Sea was comparable to Fish's.

#### COMPONENTS OF THE ZOOPLANKTON

The abundance of the major taxonomic groups by relative displacement volumes and numbers per cubic meter are given in the Appendix (Tables 1 and 2). Three hundred and fifty-eight species were identified. A checklist of these showing the cruises and stations where each was encountered is included in a manuscript (Grice and Hart, 1962), copies of which have been deposited in the Scripps Institution of Oceanography and Woods Hole Oceanographic Institution reference libraries. A limited number are available from the authors.

The abundance of the various taxa and occurrence and seasonal fluctuation of the common species are discussed below. The references made to numbers and diversity of species do not include those which have been questionably identified unless otherwise indicated. Species not hitherto reported from the region bounded by  $30^\circ$  and  $45^\circ N$  and  $60^\circ W$  and the coast (Fig. 1) are considered new records.

#### COPEPODA

Of the taxonomic groups present in the zooplankton, copepods were 1) the largest contributors to zooplankton displacement volume, 2) the most abundant group numerically, and 3) represented by the most species.

The percentage of the zooplankton displacement volume formed by copepods (Appendix Table 1) in the 43 samples varied from near zero to 96% with a mean of approximately 51%. The numerical abundance of the copepods (Appendix Table 2), except those from samples which contained large concentrations of salps, ranged from less than  $100/m^3$  in Sargasso Sea waters to more than  $1000/m^3$  in neritic waters. The average number of all samples was  $615/m^3$ .

One hundred and thirty-three species of copepods including representatives of three orders (Calanoida, Cyclopoida and Harpacticoida) and one undescribed species (Grice, 1961) were found in the samples. Of the 44 collections analyzed taxonomically, approximately 75% of the species were present in fewer than 11 samples and only two appeared more than 25 times. Sixteen species were found in all four areas (neritic, slope, Gulf Stream and Sargasso Sea waters) whereas 22 species were restricted to one area (Table 3). Considering all occurrences, 42 species were found in neritic, 79 in slope, 61 in Gulf Stream and 92 in Sargasso Sea waters.

The following 21 species are new records for this area of the northwest Atlantic Ocean: *Arietellus setosus*, *Calocalanus contractus*, *C. styliremis*, *C. tenuis*, *Clausocalanus paululus*, *C. pergens*, *Euaetideus acutus*, *Haloptilus acutifrons*, *H. austini*, *Lophothrix latipes*, *Oithona hamata*, *O. tenuis*, *Pachos punctatum*, *Paracalanus aculeatus*, *P. nanus*, *P. pygmaeus*, *Phyllopus helgae*, *Scolecithricella dentata*, *S. vittata*, and *Temoropia mayumbaensis*.

**NERITIC WATERS.** The copepod displacement volume varied somewhat in neritic samples but with few exceptions these microcrustaceans comprised approximately 50% or more by volume of the organisms present. The mean percentage of the displacement volume in 14 neritic collections was 56.8%. In July there were large concentrations of chaetognaths, as measured volumetrically, at stations B (37.1%) and C (24.0%) and of salps at station D (99.1%); the copepods formed less than 20% of the zooplankton by volume. Chaetognaths, of course, are known predators of copepods and in our collections we commonly found them either in the process of swallowing copepods or with one or more copepods plainly visible in their digestive tracts. Apparently at stations B and C chaetognaths had made serious inroads into the copepod stock. The situation at station D, where salps (*Salpa fusiformis*) formed more than 99% of the displacement volume, is more difficult to explain. Copepods and other groups of zooplankton were sparsely represented in this collection as well as in the salp-rich collections from adjacent slope waters. It



TABLE 3. Copepod species showing widespread and restricted distribution. Species occurring less than twice omitted for neritic and Sargasso Sea.

Widespread (all areas sampled)	Restricted		
Calanoida	Neritic Calanoida	Slope Calanoida	Sargasso Calanoida
<i>Acartia danae</i>	<i>Acartia tonsa</i>	<i>Aetideus armatus</i>	<i>Candacia longimana</i>
<i>Calanus tenuicornis</i>	<i>Labidocera aestiva</i>	<i>Calanus hypertoreus</i>	<i>Clausocalanus paululus</i>
<i>Calocalanus pavo</i>	<i>Temora discaudatus</i>	<i>Clausocalanus pergens</i>	<i>Eucalanus crassus</i>
<i>Clausocalanus arcuicornis</i>		<i>Gaidius tenuispinus</i>	<i>Euchirella intermedia</i>
<i>C. furcatus</i>		<i>Heterorhabdus norvegicus</i>	<i>Gaetanus pileatus</i>
<i>Eucalanus attenuatus</i>		<i>Paraeuchaeta norvegica</i>	<i>Phyllopus helgae</i>
<i>E. pileatus</i>		<i>Pleuromamma robusta</i>	<i>Pleuromamma gracilis</i>
<i>Euchaeta marina</i>		<i>Scolecithricella minor</i>	Cyclopoida
<i>Labidocera acutifrons</i>			<i>Oithona hamata</i>
<i>Mecynocera clausi</i>			<i>O. robusta</i>
<i>Nannocalanus minor</i>			<i>Pachos punctatum</i>
<i>Paracalanus parvus</i>			Harpacticoida
<i>Temora stylifera</i>			<i>Copilia vitrea</i>
<i>Undinula vulgaris</i>			
Cyclopoida			
<i>Oithona plumifera</i>			
Harpacticoida			
<i>Macrosetella gracilis</i>			

was suggested earlier that the lack of zooplankton may be due to the inability of the salp-clogged net to filter out subsurface zooplankton. In one other neritic sample, collected in March from station B, the copepod fraction was also low (32.9%). This sample contained numerous etenophores (*Pleurobrachia pileus*), by volume 48%, which are known to be predaceous and could have locally reduced the copepod population.

At stations A and C in the same month, copepods comprised 77% and 80% of the zooplankton and etenophores were poorly represented.

Concomitant with their large displacement volumes, copepods were the most abundant neritic group numerically. The average value for all shelf samples was 1488/m<sup>3</sup>.

The three most frequently occurring species were *Centropages typicus*, *Oithona similis* and *Pseudocalanus minutus* (Table 4). Of these, *C. typicus*, a comparatively large species, probably contributed the most to the copepod displacement volume except when the smaller *O. similis* and *P. minutus* greatly predominated numerically. Five other species also occurred frequently but these were not as abundant as the preceding three (Table 4).

In September there were 35 species of copepods in the shelf samples. The most important was *C. typicus* which formed about 50% of the copepods in the four samples. The mean numerical abundance was about 1300/m<sup>3</sup>. *Calanus finmarchicus*, *Candacia armata*, *Metridia lucens*, *Oithona similis*, *Paracalanus parvus* and *Temora longicornis* were also found but none exceeded 200/m<sup>3</sup> nor formed more than 6% of the copepods at any one station. *Acartia tonsa*, an inshore and estuarine species usually not encountered far from the coast, formed 80% of the copepods at station A and *Clausocalanus furcatus*, a seasonal immigrant from oceanic waters, comprised 11% of the

copepods at station B. Neither species was encountered again in such abundance in shelf waters.

As shown in Table 3, 16 species appeared in all areas sampled and in September all 16 were present on the shelf. Their appearance in shelf waters, excepting *P. parvus*, is probably related to a shoreward drift of offshore waters which has been shown to occur during summer in the area south of Cape Cod (Bumpus, 1960). The absence of all but one of the 16 species (*P. parvus*) from the early July collections on the shelf is somewhat more difficult to explain. Possibly the inshore drift had not persisted for sufficient time to bring large and diverse populations of oceanic zooplankton to shelf waters by early July. Another explanation is perhaps that the extremely large concentrations of salps in outer-shelf and slope waters created unfavorable conditions for zooplankton in general. A comparison of Appendix Tables 1 and 2 shows that at those stations where salps predominated volumetrically (stations D-HH, JJ) other groups were poorly represented numerically. Also few species were present.

Except for *C. furcatus* none of the 16 species was important numerically in September and most had disappeared from shelf waters by December.

In December the number of copepod species found in shelf samples was 16, 19 less than were present in September. Fifteen of the 16 were common to the September collections. The reduced diversity was largely attributable to the disappearance of most of the seasonally occurring species. *C. typicus* continued to be the most abundant species but it did not occur in as large numbers as it did in September. A mean of about 400/m<sup>3</sup> was calculated for the three samples, a figure which represents approximately 30% of the copepods. *P. minutus* and *O. similis* were about equally abundant (mean 250/m<sup>3</sup>) each forming about 20% of the copepod plankton. *C. finmarchicus*, *C. armata*,

*M. lucens* and *P. parvus* had a mean abundance of less than 100/m<sup>3</sup>. *Oithona atlantica*, a species apparently more typical of slope waters, was numerically strong at stations B and C where it comprised about 18% of the copepods.

By March there were only 10 copepod species found in shelf collections. The numerical abundance of the copepods as a group was smaller than during any other month. Nine December species (*Acartia tonsa*, *Calocalanus pavo*, *Candacia armata*, *Clausocalanus arcuicornis*, *Clytemnestra rostrata*, *Labidocera aestiva*, *Macrosetella gracilis*, *Mecynocera clausi*, *Paracalanus parvus*) were not encountered and four species not found in December appeared in the March samples. These four were *Acartia longiremis*, *Centropages hamatus*, *Temora longicornis*, and *Temora discaudatus*. *P. minutus* was the most abundant species particularly at the two inshore neritic stations where it formed 93% and 53% of the copepods at stations A and B respectively. *C. typicus*, the most abundant species in the December and September collections, was scarcely represented. The mean abundance of this species was less than 10/m<sup>3</sup> and in no collection did it exceed 6% of the copepods present.

Fifteen species of copepods were encountered in the July shelf samples including four (*Acartia clausi*, *Anomalocera patersoni*, *Euchirella rostrata* and *Microsetella norvegica*) which were not hitherto found in shelf samples and one (*Rhincalanus nasutus*) which was found there only in September. Two species (*C. armata*, *P. parvus*) which were absent from March collections reappeared in the July samples. The remaining eight species were all present in the March samples. Except possibly *P. parvus*, none of the fifteen species can be considered typically warm-water forms such as were found in samples collected during the preceding September. *P. minutus*, which predominated numerically in March, continued to be the most abundant species and again particularly at the two inshore neritic stations where it formed 69% (5451/m<sup>3</sup>) and 35% (399/m<sup>3</sup>) of the copepods at stations A and B respectively. *C. typicus* (mean 379/m<sup>3</sup>), *T. longicornis* (mean 274/m<sup>3</sup>) and *O. similis* (mean 388/m<sup>3</sup>) were about equally abundant at shelf stations A, B and C. *C. typicus* and *O. similis* each comprised a little over 30% of the copepods at station C. Only two copepod species represented by seven individuals were found in the sample collected at station D which contained a very large quantity of salps.

**SLOPE WATERS.** The mean percentage displacement volume in slope waters for all but the July samples was between 53% and 74%. As mentioned above, large concentrations of salps were present in July at offshore neritic station D where they comprised more than 99% of the zooplankton. Similarly, large populations of salps extended from station E through station JJ, excluding II, the Gulf Stream station. (During this particular cruise the Gulf Stream was located east of station JJ, which was thus situated in slope waters rather than in the Sargasso Sea.) Cope-

pods in the July slope water collections formed less than 3% of the zooplankton displacement volume in the five samples. Despite their small abundance by displacement volume in July, these microcrustaceans numerically comprised an average of about 45% of the animals in all slope water collections.

Except in the July collections at stations HH and JJ, where salps were predominant, copepods exceeded numerically all other groups. The average in all slope samples was 300/m<sup>3</sup> or about one-fifth of the mean number in neritic samples (1488/m<sup>3</sup>). The only month in which the mean number in shelf and slope waters was about equal was in March when several of the abundant species were in both areas.

Approximately twice as many copepod species (79) were collected from slope waters as from shelf waters (42). In contrast to shelf waters, characterized by large populations of copepods with numerical dominance by the same few species, the slope waters had considerably smaller copepod populations with no group of species consistently dominating. Some of the common slope species are listed in Table 4.

Although fourteen species were found only in slope water collections the samples from this area usually consisted of a mixture of Gulf Stream-Sargasso Sea and shelf species. For example, disregarding seasonal occurrences, 15 species were common to shelf and slope, 19 species to slope and Gulf Stream-Sargasso Sea, and 11 species to slope and Sargasso Sea collections. The slope water samples were made even more heterogeneous by the seasonal appearance in the epiplankton of a cold-water fauna (see below) which mixed with species of the above-mentioned areas. The slope waters were thus, biologically, an area of transition and mixing.

Of the 14 species confined to the slope, 8 occurred in two or more collections and are listed in Table 3. These 8 are species with oceanic affinities; 4 of them (*Calanus hyperboreus*, *Gaidius tenuispinus*, *Heterorhabdus norvegica* and *Paraeuchaeta norvegica*) are cold-water forms and have seldom been reported from neritic waters south of Cape Cod. The few records of these species from shelf areas as reported by Willey (1919), Bigelow (1915, 1922) and Bigelow and Sears (1939) are probably indicative of inshore movements of offshore waters. *C. hyperboreus*, a species typical of northern cold waters (Grice, 1962) appeared in the surface slope waters of the present area only during the winter cruise (March). No doubt it was present at other times of the year but in considerably deeper and colder water. In a deep tow (1800 m) which we have made in the Gulf Stream, for example, this species as well as *P. norvegica* was found in relatively large numbers.

In September 45 species were found in slope samples including all but four of the sixteen widely occurring species (Table 3) which were present in shelf samples during this month. There were also several warm-water species such as *Acartia danae*, *Candacia pachydactyla*, *Clytemnestra scutellata*, *Ctenocalanus vanus*, *Pontellina plumata*, *Rhincalanus*

*cornutus*, and *Scolecithrix danae* which gave the collections a decidedly warm-water appearance. *P. norvegica*, the only cold-water species found, was present at stations G and HH and probably near the bottom of the water column sampled (200 m) where temperatures were near 12°C. Several species, notably *C. typicus*, which were numerous on the shelf were also present in slope samples but in greatly reduced numbers. The most abundant species in slope water at this time of the year were *C. typicus* and *Clausocalanus pergens*. The former comprised over 65% of the copepods present at stations E and F with a mean abundance of approximately 1000/m<sup>3</sup> and 100/m<sup>3</sup> respectively. None were observed at stations G or HH where *C. pergens* formed 66% and 49% of the copepods, equivalent to approximately 94 and 195 animals/m<sup>3</sup> respectively.

The December slope collections contained 49 species or four more than found in September. Over half (28) of these species were common to the September collections and many of the warm-water species were still present. *P. norvegica* remained at the outer slope station (station HH) and two other cold-water species (*G. tenuispinus* and *H. norvegicus*) appeared at station G or HH. The most abundant species were *Clausocalanus arcuicornis* and *Pleuromamma borealis* which occurred in numerical strengths between 8 and 14/m<sup>3</sup> and comprised between 12% and 21% of the copepods. *Calanus tenuicornis* and *M. clausi* contributed somewhat less numerically.

Ten fewer species were present in March than in December owing to the disappearance of twelve of the widely occurring species listed in Table 3. Although several warm-water species remained (e.g., *Haloptilus longicornis*, *Scolecithrix danae*) they were at the outermost slope stations adjacent to the Gulf Stream. *C. hyperboreus*, a cold-water species, appeared at all four slope stations.

The most abundant species were two typical shelf forms, *P. minutus* and *O. similis*. The mean numerical abundances for these two were 60 and 44/m<sup>3</sup>, respectively, and they formed between 2% and 33% of the copepods at the stations where they occurred. *M. lucens* and *O. atlantica* had mean abundances of 35 and 15/m<sup>3</sup> and were thus only slightly less important numerically.

The July slope water collections contained 24 species, the least variety of any month. Only three of the wide-ranging species (Table 3) were present. The lack of diversity was discussed briefly above in connection with the July shelf samples.

Little can be said regarding numerically important species in July as the copepod population was extremely small at all slope stations (.1-70/m<sup>3</sup>). Most of the shelf species present previously in slope collections were found, but in greatly reduced concentrations.

**GULF STREAM.** Since only three collections were obtained from the Gulf Stream, little can be said concerning the seasonal occurrence of the copepods. These organisms comprised by volume approximately

50% of the zooplankton in December and July collections and 67% in the September collection. The calculated numbers of copepods in September (145/m<sup>3</sup>), December (147/m<sup>3</sup>) and July (89/m<sup>3</sup>) were close and, in conjunction with the displacement volume values, suggest a uniformity of population size in the Gulf Stream.

The total numbers of species found in the three samples were similar, 42 in September, 43 in December and 42 in July. There were 23 species common to the three samples. Seven species were relatively important numerically (Table 4). One of these, *Clausocalanus furcatus*, comprised 19%, 27%, and 13% of the species in the three collections; the others formed 12% or less. Six were present in all three collections. In view of the frequency of occurrence of a few abundant species, apparently little seasonal variation occurs in the Gulf Stream population.

No common shelf or slope water copepod was found in the Gulf Stream. As might be expected the copepod fauna of the Gulf Stream was similar to that of the Sargasso Sea. Seventeen species were restricted to Gulf Stream and Sargasso Sea samples, whereas only one was restricted to slope water and Gulf Stream samples.

**SARGASSO SEA.** The percentage of the zooplankton formed by copepods in the Sargasso Sea ranged from 34.4% to 65.1% by volume with a mean for all samples of 48.3%, the smallest mean displacement volume of the four areas sampled. The smaller displacement measurements were made on samples collected in March at stations LL and NN where the copepod fraction was about one-third of the zooplankton. Approximately one-half of the animals at these two stations were chaetognaths and siphonophores which together could have reduced the copepod stock.

The calculated numerical abundance of the copepods varied from 21 to 120/m<sup>3</sup>. The mean in all collections was 66/m<sup>3</sup>, the smallest average abundance computed for the four areas. Except for the March samples, in which there was a calculated mean of 38/m<sup>3</sup>, the average numerical abundance for the other months were close: September, 73; December, 74; and July, 103/m<sup>3</sup>.

Ninety-two species of copepods were found in the Sargasso Sea but only six occurred frequently and abundantly (Table 4). No marked seasonal variation in species composition was noted. The September, December, March and July collections contained 49, 64, 66 and 60 species, respectively, of which 30 were common to the four groups of collections. The September figure was based on one sample but the number of species found therein was of the same order as that for individual collections of the other months.

The six numerically important species were present the year round and in similar abundances. None exceeded 25% of the species in any one sample and only rarely did the percentage approach this figure. In no sample did the calculated abundance exceed 17/m<sup>3</sup>.

TABLE 4. Numerically important copepod species in neritic, slope, Gulf Stream and Sargasso Sea waters.

Neritic (14 samples)		
	Freq.	Mean no./m <sup>3</sup>
<i>Pseudocalanus minutus</i> .....	13	559
<i>Centropages typicus</i> .....	14	450
<i>Oithona similis</i> .....	13	151
<i>Temora longicornis</i> .....	8	59
<i>Paracalanus parvus</i> .....	8	39
<i>Calanus finmarchicus</i> .....	11	32
<i>Metridia lucens</i> .....	12	16
<i>Candacia armata</i> .....	9	9
Slope (15 samples)		
	Freq.	Mean no./m <sup>3</sup>
<i>Centropages typicus</i> .....	11	76
<i>Pseudocalanus minutus</i> .....	8	16
<i>Oithona similis</i> .....	6	14
<i>Metridia lucens</i> .....	11	15
<i>Clausocalanus pargens</i> .....	6	19
<i>C. arcuicornis</i> .....	7	13
<i>Pleuromamma borealis</i> .....	8	6
<i>Oithona atlantica</i> .....	12	6
Gulf Stream (3 samples)		
	Freq.	Mean no./m <sup>3</sup>
<i>Clausocalanus furcatus</i> .....	3	27
<i>Lucicutia flavicornis</i> .....	3	9
<i>Oithona plumifera</i> .....	3	9
<i>O. setigera</i> .....	3	7
<i>Calocalanus pavo</i> .....	2	9
<i>Farranula gracilis</i> .....	3	4
<i>Mecynocera clausi</i> .....	3	2
Sargasso Sea (11 samples)		
	Freq.	Mean no./m <sup>3</sup>
<i>Clausocalanus furcatus</i> .....	9	7
<i>Oithona setigera</i> .....	11	6
<i>Lucicutia flavicornis</i> .....	11	4
<i>Ctenocalanus vanus</i> .....	6	3
<i>Farranula gracilis</i> .....	6	2
<i>Mecynocera clausi</i> .....	9	2

There was considerable similarity between the species present in the Gulf Stream and in the Sargasso Sea. The most abundant species in each area was *Clausocalanus furcatus* and the list of abundant species (Table 4) included four more species which were common to both. Many of the less abundant species were also common to both areas. Of the 49, 64 and 60 species present in the Sargasso Sea in September, December and July, respectively, 30, 39 and 36 were also present in the Gulf Stream.

The March samples were characterized by reduced copepod abundance and also by the presence of two neritic slope water species, *Centropages typicus* and *Oithona atlantica*. These species occurred at station

JJ where they formed a minor part of a large assortment of tropical species. Weather conditions precluded collecting at the Gulf Stream station, station II, and therefore it is not known whether these species were likewise present in the Stream. It seems likely, however, they were incorporated into the Stream north of Cape Hatteras (the approximate southern limit of *C. typicus*), where the Gulf Stream approaches the continental shelf edge. Once in the Stream they could have been carried into the eastern edge of the Sargasso Sea by lateral mixing, although there is no hydrographic evidence for recent slope water intrusion at that particular station. No other typically neritic species were found in the Sargasso Sea.

## CHAETOGNATHA

Chaetognaths were usually the second most important contributors to the zooplankton displacement volume and the second most abundant group numerically (Appendix Tables 1 and 2). Considering all collections their mean displacement volume was 13.4%. They were a more important element of the zooplankton in the Sargasso Sea, where they generally comprised 15% to 25% of the displacement volume, than in slope waters, where they frequently formed less than 15%.

Based on numerical abundance chaetognaths were 6 to 12 times more abundant in shelf waters than elsewhere. The average for all collections was 10.1/m<sup>3</sup> which may be compared to a mean chaetognath abundance of 8.7/m<sup>3</sup> reported by Pierce and Wass (1959) for the neritic and offshore waters of the south Atlantic coast between Cape Hatteras and southern Florida.

Of the fifteen species, two were widely distributed and occurred in all four bodies of water sampled (Fig. 9). Three species were found in shelf waters, 12 in slope waters, 9 in the Gulf Stream and 12 in the Sargasso Sea. Two species (*Sagitta decipiens* and *S. friderici*) are new records for this area of the northwest Atlantic.

NERITIC WATER. In the shelf samples chaetognaths

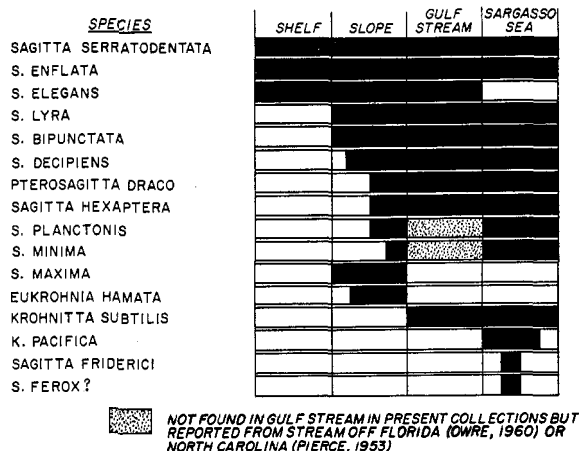


FIG. 9. Distribution of Chaetognatha.

formed a mean of 14.6% of the zooplankton displacement volume. The average abundance was 25/m<sup>3</sup>. Fewest occurred in March when they were nearly absent, for no apparent reason, from the two offshore neritic collections. The lack of chaetognaths at one other shelf station, station D, in July may be due to the large salp concentrations mentioned above in conjunction with a discussion of a similar paucity of copepods at this station.

Only three chaetognath species were represented in shelf collections, *Sagitta elegans*, *S. enflata* and *S. serratodentata*. *S. elegans* was most numerous and was present the year round. The other two species were less abundant and their occurrence was more sporadic. *S. elegans* occurred in 12, *S. serratodentata* in 9 and *S. enflata* in 5 of the 15 samples.

The seasonal variation in the shelf chaetognath population was primarily influenced by the variation in abundance of *S. elegans* and, to a lesser extent, *S. serratodentata*. The largest number of chaetognaths, based on mean values, was present in December (39/m<sup>3</sup>) and in July (37/m<sup>3</sup>). These two species were approximately equally represented in December and together accounted for about 90% of the chaetognaths. The July collections contained practically only *S. elegans* which made up 99% of the mean value for this month. Except for A, the inshore station, few chaetognaths were present in March. The mean for this month was less than 4/m<sup>3</sup> and again only *S. elegans* was represented in any number.

All three of the above chaetognath species have previously been reported from continental shelf waters between Cape Hatteras and Cape Cod (Bigelow, 1915; Bigelow and Sears, 1939; Deevey, 1952a, 1952b, 1956). Although not detected in our shelf samples, *Krohnitta subtilis*, *Eukrohnna hamata*, *Pterosagitta draco*, *Sagitta bipunctata*, *S. helenae*, *S. hexaptera*, *S. hispida*, *S. maxima* and *S. minima* have also been occasionally found in shelf waters by one or more of the above-cited authors. These species are all certainly strays into the area and are neither characteristic nor abundant members of the neritic chaetognath plankton north of Cape Hatteras. As shown in Figure 9, seven of the above nine species occurred in our extra-continental shelf collections.

**SLOPE WATERS.** Of the four areas studied, the smallest mean displacement volume (8.3%) and numerical abundance (3/m<sup>3</sup>) for chaetognaths was found in slope waters.

Twelve species of chaetognaths were encountered in slope water collections (Fig 9). Three groups can be recognized: 1) shelf species, 2) Gulf Stream-Sargasso species, and 3) endemic slope-water species.

*S. elegans*, the most numerous species in shelf waters (mean 16/m<sup>3</sup>) was also the most abundant chaetognath in slope waters (mean 1/m<sup>3</sup>). The two other shelf species, *S. enflata* and *S. serratodentata* were also found in lower concentrations in the slope water.

The Gulf Stream-Sargasso Sea component contributed seven species (*P. draco*, *S. bipunctata*, *S.*

*decipiens*, *S. hexaptera*, *S. lyra*, *S. minima*, *S. planctonis*) to the slope chaetognath fauna; all were present in very small numbers (<1/m<sup>3</sup>). The seven species are open ocean forms which, with the possible exception of *S. lyra*, were more typical of the warm Gulf Stream and Sargasso Sea waters than the generally colder slope waters. Their presence in slope collections is probably related to the mixing of the Gulf Stream and slope waters particularly in the outer parts (stations G, HH) where they more frequently appeared in the collections.

Two species (*E. hamata* and *S. maxima*) were found only in collections from the slope water. Each species occurred in five of the slope water samples, most of them collected in March. These two species have not been found in the epiplankton of the Sargasso Sea or Gulf Stream, and only occasionally, and as strays, from outer neritic waters of the present area (Bigelow, 1915; Bigelow and Sears, 1939). Pierce (1953, 1958), Pierce and Wass (1959) and Bumpus and Pierce (1955) did not find either species in the region between Cape Hatteras and south Florida. Owre (1960) reported finding a specimen of *E. hamata* in each of two fairly deep (225-275 m) collections made off Miami. The temperature at these depths was approximately 7.4° C. In view of their frequent occurrence in the epiplankton of arctic-boreal waters (e.g., Kielhorn, 1952) and in deeper waters in the region of Nova Scotia and Newfoundland (Huntsman, 1919) and in the Gulf of Maine (Bigelow, 1926; Redfield and Beale, 1940), and in view of their absence from warm and shelf waters, these species are considered good indicators of cold waters in general, and, in the present area, slope waters in particular.

**GULF STREAM.** The mean displacement volume of Gulf Stream chaetognaths was 13.9% and the mean numerical abundance was 4/m<sup>3</sup>.

There were nine species found in the three Gulf Stream samples. The most abundant species was *S. enflata* which formed between 13% and 24% of the chaetognaths in each collection. These percentages, at most, were equivalent to about 1 animal/m<sup>3</sup>. *S. elegans* reached its seaward limit in the Stream where a few stray specimens were found in the March collections. In other respects the Gulf Stream chaetognaths were very similar to those found in the Sargasso Sea.

**SARGASSO SEA.** The mean displacement volume of the Sargasso Sea chaetognaths was 18.9% with few individual collections varying much from this figure. The mean numerical abundance (3/m<sup>3</sup>) was nearly equal to that for the Gulf Stream (4/m<sup>3</sup>) as was the species composition. Of the twelve species found in Sargasso Sea collections, eight were also present in the Gulf Stream. The most abundant species was *S. serratodentata*, which, nevertheless, occurred in numbers less than 1/m<sup>3</sup>. It made up about 25% of the chaetognaths in two March collections but in all other samples it formed 15% or less. Besides this species and *S. minima*, both of which occurred in ten samples, the following species were present in all eleven

Sargasso Sea samples: *P. draco*, *S. enflata*, *S. hexaptera*, and *S. lyra*. *S. bipunctata* and *S. decipiens* were likewise present throughout the year, but in fewer samples. *K. subtilis* was absent only from the single September collection and from two of the March collections. The species named so far are typical members of the Sargasso Sea plankton and can be expected to occur at any time of the year. *S. planctonis* was the only species which apparently exhibited a well-defined seasonal occurrence. It was present in all four March collections but it was absent from all other Sargasso Sea samples. This distribution agrees with that reported by Moore (1949) who found it in maximum numbers in spring off Bermuda. It was absent or rare in his collections made in September, December and July. *Krohnitta pacifica*, *S. ferox*? and *S. friderici* occurred in less than three collections and in very small numbers.

#### EUPHAUSIACEA

Although euphausiids are important constituents of the zooplankton in boreal and antarctic waters, they were not important in the present area. They ranked fifth in mean displacement volume of all collections (4.9%) and fifth in numerical abundance (1.6/m<sup>3</sup>). Twenty-six species were found, distributed as follows: 7 in neritic waters, 13 in slope waters, 6 in the Gulf Stream and 20 in the Sargasso Sea. One species, *Thysanopoda subaequalis*, is apparently a new record for the northwestern Atlantic. Because of their infrequent occurrence and small numbers the following discussion will emphasize distribution rather than seasonal occurrence.

**NERITIC WATERS.** Euphausiids were generally a minor element in neritic waters where they formed less than 3% of the displacement volume in 11 of the 14 samples. The mean percentage of all collections was 2.0% and the average numerical abundance was 1.7/m<sup>3</sup>.

Seven species were found, all of which have previously been reported from shelf waters of this area by either Fish (1925) or Bigelow and Sears (1939). Only one of the species, *Meganyctiphanes norvegica*, appeared in as many as one-third of the neritic collections. Most of the neritic as well as offshore samples contained predominantly juvenile specimens which we have usually not attempted to identify. No species, for example, were recorded from the March shelf samples but there were more than 1 juvenile/m<sup>3</sup> calculated for three of the four collections. These juveniles were probably referable to *M. norvegica* since *Thysanoessa longicaudata*, which was present in adjoining slope samples, apparently does not breed in coastal waters (Einarsson, 1945). The infrequent occurrence of euphausiids in shelf waters is also demonstrated by the December collections which contained only one species, *Euphausia krohnii*, in one sample (station C). No euphausiids were detected at the most inshore station and only a few juveniles at the next station.

The July collections contained three species, *M.*

*norvegica*, *Thysanoessa inermis* and *T. longicaudata*. The first of these was the most frequent member of the shelf euphausiid plankton. Einarsson (1945) has remarked, in reference to the second, *T. inermis*, that it is a "pronounced coastal form." In the Gulf of Maine, this species was the most frequently occurring euphausiid (Whiteley, 1948). It was found only in shelf waters in the present collections. The third species, *Thysanoessa longicaudata*, appeared in only one July collection; otherwise it was confined to slope water. It is a boreo-arctic species which, along the American coast, ranges as far south as the slope waters off Chesapeake Bay (record cited in Hansen, 1915). Leavitt (1935) recorded it in a collection made in slope waters between 300 and 2000 m and in another slope collection made to a depth of 1400 m. Bigelow and Sears (1939) referred to it as a cold-water species and reported it from seven localities on the shelf between New Jersey and Long Island. *T. longicaudata* is, of course, more abundant in the Gulf of Maine (Bigelow, 1926) and Labrador Sea (Kielhorn, 1952), to cite just two records, than it is south of Cape Cod. Its occurrence in outer shelf waters in July may be related to the cold (6-10° C) subsurface (25 m to bottom) waters which persist on the shelf in summer (see Bigelow, 1933; Ketchum and Corwin, 1961).

The September collections contained two of the species mentioned above (*M. norvegica*, *T. inermis*) and three atypical shelf species (*Euphausia tenera*, *Nematoscelis megalops*, *Thysanoessa gregaria*). In view of the distribution (slope water, *N. megalops*; slope and Sargasso Sea waters, *E. tenera*, *T. gregaria*) of these atypical species, the presence of them in neritic samples helps to substantiate the presumed shoreward spread of offshore waters in September as also indicated by certain species of copepods (see Copepod section).

**SLOPE WATERS.** Euphausiids were relatively more important in slope waters where they comprised a mean of 8.3% of the zooplankton than they were in other three areas. The average numerical abundance was 2.2/m<sup>3</sup>, the largest average calculated for this group.

The September and December collections together contained 11 species, 6 of which were common to both months. Six species (*Euphausia tenera*, *Stylocheiron abbreviatum*, *S. affine*, *S. carinatum*, *S. suhmii*, *N. microps*) were much more frequent in Gulf Stream and Sargasso Sea waters and their presence in slope samples attests to the mixing of the warmer waters with those of the slope. Two species, *M. norvegica* and *T. gregaria*, occurred also in neritic waters; *T. gregaria* was found in the Sargasso Sea as well.

This leaves three species, *N. megalops*, *E. krohnii* and *Euphausia pseudogibba*, which were practically confined to slope waters. *Nematoscelis megalops* is particularly interesting because 11 of the 12 samples in which it occurred were from slope waters where it was also found to be breeding. Egg-bearing females were observed in September and March slope collections and females with attached spermatophores were

seen in one of the September samples. The only non-slope record for it was from station D (September). The occurrence of this species in slope water along the Atlantic coast between Cape Hatteras and Cape Cod was also indicated in the records of Hansen (1915), Tattersall (1926), Leavitt (1935) and Bigelow and Sears (1939). It is known from a single specimen collected at a depth of 270 m in the Florida current off Miami (Lewis, 1954) where temperatures are probably in the neighborhood of 10° C. In view of the above records, *N. megalops* may, as Bigelow and Sears (1939) pointed out, be "safely regarded as an indicator of water from the continental slope" in the present area.

The occurrence of *E. krohnii* with *N. megalops* is not unusual as has been remarked by Tattersall (1926). It has also been reported from off Bermuda (Lebour, 1950) and Moore (1952) shows it as occurring in two areas in the Sargasso Sea and in the Caribbean Sea. *E. pseudogibba* is a much rarer species and the only other records of it known to us in the Atlantic north of the equator are those of Leavitt (1935, 1938).

The March and July collections contained a less diverse euphausiid assemblage than did those from September and December. Six species were present in samples from March and four in those from July. These four species were common to the two. The large group of warm-water species found in September and December samples had disappeared from slope water. *Euphausia mutica* and *Thysanoessa gregaria* were the only warm-water euphausiids present. The cold water temperatures were probably responsible for the absence of them in March and possibly the large salp concentrations can account for their scarcity in July. The other species that were present (*E. krohnii*, *M. norvegica*, *N. megalops*, *T. longicaudata*) were not unexpected in slope waters of this area.

**GULF STREAM.** Few euphausiids were found in the Gulf Stream samples (mean of 1.8% of the zooplankton) probably because all three collections were obtained in daylight hours when many species presumably had migrated away from surface waters. The average numerical abundance of 1.3/m<sup>3</sup> consisted largely of juvenile specimens.

Six species were found including four species of *Stylocheiron* (*affine*, *carinatum*, *longicorne* and *suhmii*), *Euphausia tenera* and *Thysanoessa tricuspidata*. These species have also been found in the Sargasso Sea. Additional species not recorded here were certainly present. For example, a deep tow (1800 m) made in the Gulf Stream contained 12 species including 6 which were present elsewhere only in the Sargasso Sea. Moreover, Lewis (1954) reported 20 euphausiid species from the Florida current off Miami. Sixteen of his species also occurred in the present collections from the Sargasso Sea and Gulf Stream. In short, the 6 euphausiid species are not representative of the actual diversity of this group in the Gulf Stream.

**SARGASSO SEA.** Euphausiids accounted for a mean of 4.8% of the Sargasso Sea zooplankton displacement volume. The average numerical abundance was 0.7/m<sup>3</sup>. Here, too, juveniles frequently predominated.

Twenty species were found and all but *Thysanopoda subaequalis* and possibly *Stylocheiron affine* (exact position of capture not given by Leavitt, 1938) have previously been reported from the northwestern part of the Sargasso Sea. The species most characteristic of the samples were six species referable to the genus *Stylocheiron*, *Euphausia brevis* and *E. tenera*. The other species occurred in less than 5 of the 11 collections.

#### AMPHIPODA

In 33 of the 43 collections amphipods formed 2% or less of the zooplankton displacement volume and in none of the remaining ten did they exceed 7%. The mean for all samples was 1.4%. Numerically the mean abundance was 0.7/m<sup>3</sup>. In terms of species, however, the amphipods ranked second only to copepods. Fifty-five species were found and these were distributed in the four areas as follows: shelf waters, 8; slope waters, 15; Gulf Stream, 26; and Sargasso Sea, 46. The following 13 are new records for the northwest Atlantic: *Brachyscelus acuticaudatus*, *Dairella latissima*, *Eupronoe laticarpa*, *Hyperia atlantica*, *H. fabrei*, *H. luzoni*, *H. thoracica*, *Lycaeopsis themistoides*, *Simorhynchotus antennarius*, *Streetsia longiceps*, *Vibilia borealis*, *V. gibbosa*, and *V. stebbingi*.

Although the mean amphipod abundance was small (0.7/m<sup>3</sup>) for all areas combined, there were comparatively large numbers of them present in shelf waters (mean 1.6/m<sup>3</sup>). The most frequently occurring neritic and slope water species were *Parathemisto gaudichaudii* and *P. gracilipes*; the latter was present throughout the year. *P. gaudichaudii* was probably likewise present year round, or at least occurred more frequently than we indicate. Some taxonomic confusion exists regarding the distinction between these two species in the size range of 5-6 mm. Specimens smaller than this are clearly *gracilipes* and those larger, *gaudichaudii*, but we prefer not to refer those in the indicated size range to either species until a thorough systematic study is made of the two species.

These two shelf-slope species were seasonally augmented by the appearance of Gulf Stream and Sargasso Sea species. The most notable of such intrusions occurred in September when five warm-water species (*Hyperia atlantica*, *H. fabrei*, *H. macrophthalma*, *Hyperoides longipes* and *Paraphronima gracilis*) were found in waters shoreward of the Gulf Stream. Similarly warm-water copepods and euphausiids were found in neritic and slope samples during September as noted in the discussions of them above. Only two warm-water species, *Anchylomera blossevilliei* and *Phronima semilunata*, were present in these waters in December. No adventives occurred in slope and neritic waters in March, the month of



coldest surface water temperatures, but *Hyperoche medusarum*, an arctic-boreal species, was found in one shelf sample from station B. This species persisted in neritic waters and was accompanied by two other cold-water species, *Vibilia armata* and *V. borealis*, in July. These three species were apparently collected from within the cold subsurface neritic waters (see Ketchum and Corwin, 1961), along with the boreal euphausiid, *Thysanoessa longicaudata*. Two warm-water amphipods which were also found in this month's samples were *Phronima stebbingi* (two slope samples) and *P. macropa* (one shelf sample).

A mean of 0.2 amphipods/m<sup>3</sup> was calculated for each group of collections from the Gulf Stream and Sargasso Sea. The samples had 23 species in common. Of the 26 species collected in the Gulf Stream, three were found only there and each appeared in only one sample. Twenty species were restricted to the Sargasso Sea collections, but probably all would have been detected in the Gulf Stream if more samples from this area had been analyzed. The most common Gulf Stream and Sargasso Sea species in the fourteen collections and their frequency of occurrence were *Hyperia schizogeneios* (14), *Phrosina semilunata* (14) and *Lycaeopsis themistoides* (13).

#### SIPHONOPHORAE

A mean percentage displacement volume of 7.4% was calculated for the siphonophores. The average numerical abundance including nectophore and eudoxid generations and unidentified persons was 0.8/m<sup>3</sup>. Thirty species were found at one time or another in the four areas as follows: 4 in shelf waters, 17 in slope waters, 14 in the Gulf Stream and 27 in the Sargasso Sea. *Amphicaryon ernesti*, *Galettia chuni*, *Lensia meteori*, *Nanomia bijuga*, *Rosacea plicata* and *Vogtia serrata* are new records for this area. If Bigelow's (1918) report of *Amphicaryon acaule* from off Chesapeake Bay is actually *A. ernesti* as Totton (1954) suggested, then our record for this species would not constitute a range extension.

The paucity of siphonophore species in neritic waters is consistent with the general offshore and deep-water distribution of this group of animals. The relatively small volume contribution in shelf waters (mean 0.9%) substantiates similar findings by Bigelow and Sears (1939) in their study of continental shelf zooplankton. The two species (*Diphyes bojani* and *D. dispar*) which occurred in shelf waters in September are both more typical of the Sargasso Sea and Gulf Stream and, as seen in certain species of previously discussed groups, probably indicate a shoreward spread of offshore waters. In slope waters, two other decidedly warm-water species, *Abylopsis eschscholtzii* and *A. tetragona*, appeared in this month's collections. These four warm-water species were likewise present in slope waters in December along with four other warm-water species, *Bassia bassensis*, *Chelophyes appendiculata*, *Eudoxoides mitra* and *Eudoxoides spiralis*, as well as with three species of undetermined temperature tolerances. In

March only stray specimens of *Lensia conoidea*, an apparent warm-water species, and of *Vogtia serrata*, a cold-tolerant and rare species in the present collections, were found. *Nanomia cara*, a decidedly cold-water siphonophore, occurred in most of the March shelf and slope collections. This species was also found, presumably in deeper cold waters, in three neritic and one slope water sample in July. Other species in certain of the July collections included *A. eschscholtzii*, *D. bojani*, *E. spiralis*, *Hippopodius hippopus*—all warm-water species—and several other less frequently occurring species.

As a group, siphonophores were relatively more important volumetrically in the Gulf Stream and Sargasso Sea where they comprised a mean percentage displacement of 14.4% and 17.7%, respectively, of the zooplankton than they were in neritic (0.9%) or slope (4.4%) areas. Numerically, a mean abundance of 0.9/m<sup>3</sup> was calculated for the Gulf Stream and 0.8/m<sup>3</sup> for the Sargasso Sea; both figures are comparable to shelf (1.1/m<sup>3</sup>) and slope (0.5/m<sup>3</sup>) values. All 14 of the species found in the Gulf Stream were also present in the Sargasso Sea and the 9 Sargasso Sea species which were not detected in the Gulf Stream most probably would have been found had additional material been analyzed. Five of these 9 species, for example, have been reported from the Florida current off Miami by Moore (1953). The species most likely to be encountered in the Sargasso Sea are *A. eschscholtzii*, *A. tetragona*, *B. bassensis*, *C. appendiculata*, *D. bojani*, *E. mitra*, *E. spiralis*, *H. hippopus*, and *Lensia fowleri*. These species were in all but one or two of the Sargasso Sea collections.

#### OTHER GROUPS

In contrast to the preceding five taxa, the following groups were seldom present in quantities large enough to make volume determinations and their numerical abundance was likewise generally very small. Several of these groups, however, are of interest because of their great species diversity and spatial distribution. We shall discuss them briefly in order of the number of species found in each group.

**MOLLUSCA.** Although we have identified 29 species of pelagic molluscs (10 heteropods, 19 pteropods) the identifications have not been corroborated yet by a specialist. We have therefore not attempted to determine which are new records for the present area. No heteropods were found in neritic samples and only one species, *Protatlanta souleyeti*, was recorded in slope collections. Despite the presence of 11 species in the Gulf Stream and Sargasso Sea none except *P. souleyeti*, which occurred five times, was present in more than 3 of the 14 collections.

The pteropods were likewise infrequently represented in the collections. No identified species were present in neritic samples, although several unidentified ones were found. The estimated abundance of two of these at one station (Station B, July) was 56/m<sup>3</sup>. Four species were recorded from the slope waters one of which (*Hyalocyclix striata*) was the



pteropod second most frequently encountered (6 collections). In addition to its single occurrence in slope waters (station E, September) it also occurred in two Gulf Stream and three Sargasso Sea samples. Of all pteropods, *Creseis acicula*, was present most frequently. It appeared in all three Gulf Stream and 6 of the 11 Sargasso Sea samples. All other species were recorded in six or less collections.

Molluscs were also represented in many collections by unidentified gastropod and pelecypod larvae as well as by small squids.

ANNELIDA. Of the 27 species found 24 were in the Sargasso Sea, 8 in the Gulf Stream, 8 in slope water and 1 in neritic collections. The sole shelf species, *Tomopteris helgolandica*, also occurred in several of the slope water collections. Its known distribution in the northwest Atlantic includes the Gulf of Maine (Bigelow, 1926), the waters off Nova Scotia (Huntsman, 1921 as *T. catharina*), and the Newfoundland Banks area (Apstein, 1900). It has also been found in a 300 m (wire out) collection from the Sargasso Sea (Støp-Bowitz, 1948) which contained among other species *Calanus hyperboreus*, an arctic copepod. In view of these distribution records, it appears that *T. helgolandica* is a cold-water species, and its appearance in the July neritic samples was consistent with the occurrence of certain other cold-water species during this month. Except for this species and the rarer *Lopadorhynchus henseni* and *Maupasica caeca* those annelid species found in slope waters were also present in the Sargasso Sea. Of the 24 species found in the 11 collections from the Sargasso Sea only three species were present in more than four collections. These species and their frequency of occurrence in all collections were *Sagitella kowalevskii* (7), *Tomopteris planktonis* (6) and *Vanadis minuta* (9).

Of the 27 species of annelids 13 represent range extensions to this area. These are *Lepidasthenia caroli*, *L. gramaldi*, *Lopadorhynchus krohnii*, *L. henseni*, *Maupasica caeca*, *Naiades cantrainii*, *Rhynchonerella moebii*, *R. petersii*, *Tomopteris cavallii*, *T. ligulata*, *T. nationalis*, *Torrea candida*, *Vanadis longissima*.

Included with the annelids are two species of uncertain systematic position, *Chaetosphaera falconis* and *C. nationalis*. They probably are juveniles of previously described polychaet annelids.

OSTRACODA. Fifteen species of ostracods were found. There were more species present in the Sargasso Sea (12) and Gulf Stream (9) samples than in slope (6) and neritic (no identified species) collections. The two most frequently occurring (7 samples) were *Conchoecia acuminata* and *C. curta*. They both occurred in the Sargasso Sea and Gulf Stream and *C. curta* was also found in one slope water collection. Eleven species are apparently new records for this area. They are *Archiconchoecia striata*, *Conchoecia acuticosta*, *C. atlantica*, *C. concentrica*, *C. curta*, *C. daphnoides*, *C. elegans*, *C. inermis*, *C. parthenoda*, *Halocypris brevirostris*, and *H. globosa*.

CHORDATA. This group was represented by nine identified species and several other tentatively identified ones. *Salpa fusiformis* in July comprised more than 70% of the total displacement volume in seven slope and shelf samples and in three of them the displacement exceeded 90%. These large concentrations of salps persisted into August, but chiefly in neritic waters. In September of the preceding year, no *S. fusiformis* were taken which indicates that the large summer swarms are on the wane by early fall. This distribution pattern and the fact that *S. fusiformis* has appeared in Gulf Stream and Sargasso Sea samples (but never in large numbers) suggests that the slope waters were "seeded" in early summer. When conditions became favorable, they multiplied rapidly and were carried shoreward by surface drifts. Similar large concentrations of salps in summer have been noted by Bigelow (1915), Bigelow and Sears (1939), and others.

Sears and Clarke (1940) state that the large concentrations of salps found in neritic waters are due to local propagation and not to unusually large mixing of slope with shelf water. The possibility that these large numbers of salps created unfavorable environmental conditions for other groups has been alluded to in the discussions of certain of the major groups. *Thalia democratica* was another common but far less abundant salp. It appeared in all but two of the September collections but was detected only in Gulf Stream and Sargasso Sea samples during the other months.

Three species of doliolids were found at a few scattered stations in all four areas.

The not too infrequent occurrence in fair numbers of unidentified juvenile cephalochordates in eleven Gulf Stream and Sargasso Sea collections was of interest because of the coastal and benthic habitat of the adults. Cephalochordates have been noted before in oceanic plankton samples including many from the Sargasso Sea where Moore (1949) reported *Amphioxides pelagicus* as occurring throughout the year. He also drew attention to a paper by Goldschmidt (1933) in which it was stated that this species is a larval form but probably not referable to either of the two known Bermuda species. The occurrence of juveniles in two of the three Gulf Stream samples suggests that immature specimens of the Caribbean species, *Branchiostoma caribaeum*, are brought northward and may be conspecific with those juveniles found in the Sargasso Sea. *B. caribaeum* occurs along the Atlantic coast as far as Chesapeake Bay where Hubbs (1922) described it as a new species (*B. virginiae*). Bigelow and Farfante (1948) considered *B. virginiae* and another of Hubbs' species, *B. floridae* (from Florida coastal waters), as synonyms for *B. caribaeum*.

Of the chordate species, *Salpa maxima* and *Doliolum mirabilis* have apparently not been reported from this area of the northwestern Atlantic Ocean. Deevey (1952b) has referred to a paper by Garstang (1934) in which it was suggested that *D. mirabilis*

and *D. nationalis*, also recognized in our collections, may be referable to the same species in which case our *mirabilis* would not be a new record for this area.

Juvenile fishes and fish eggs have also appeared in many of the collections from all areas. We have not attempted to identify any of these.

CLADOCERA. Six species were identified, all of which have previously been reported from the present area by Sharpe (1910), Fish (1925), Bigelow and Sears (1939), Deevey (1948, 1952a, 1952b, 1960a) and Lochhead (1954). Our records for these species are mostly confined to neritic waters where they were more abundant. *Evadne nordmanni* and *E. spinifera* were both taken in extra-neritic samples, however, the former in three July slope collections and the latter in one July Sargasso Sea collection. Although we first thought it to be an unusual occurrence, we found that Hansen (1899) had previously reported *E. spinifera* from the Sargasso Sea.

MEDUSAE. The five identified species were, with but few exceptions, relatively unimportant constituents of the zooplankton. At stations A, B and C in July, however, a species of *Obelia* was present in large numbers and comprised volumetrically 23%, 23%, and 43%, respectively, of the zooplankton. The mean numerical abundance at these three stations was 375/m<sup>3</sup>. Although not as abundant, *Aglantha digitale* was the most frequently occurring medusa. It was obtained from ten shelf and slope water collections in March and July. *Solmundella bitentaculata*, which was found in one sample, has not hitherto been reported from this area.

DECAPODA. Three pelagic decapods (*Gennadus elegans*, *Lucifer faxonii*, *L. typus*) all of which have been previously found in the present area were encountered in our collections. The first is a bathypelagic species (Bouvier, 1908) that occurred in only two March slope-water samples. It was probably captured near the lower limit of our 200 m collection inasmuch as it was not encountered in any of the 100 m collections made by Waterman *et al.* (1939) in their study of the diurnal movement of deep-water plankton which was carried out in the general area of our station HH, but it was encountered in significant numbers between depths of 200 and 1000 m. The two species of *Lucifer* appeared together in many collections from outer slope, Gulf Stream and Sargasso Sea waters but only *L. faxonii* was found in neritic waters. *L. faxonii* apparently penetrates farther inshore than *L. typus* as the former has been reported from Block Island Sound (Deevey, 1952a) and from the Delaware Bay region (Deevey, 1960a) although Bigelow and Sears (1939) found *L. typus* in a few neritic collections.

Of course the larvae of benthic decapods, especially brachyurans, as well as those of pelagic species also appeared in many collections. We have not attempted to identify them.

MYSIDACEA. *Mysidopsis bigelowi* and *Neomysis americana* each appeared in one March collection. Both have previously been found in this area and

these records have been summarized by Tattersall (1951).

CTENOPHORA. Two species of ctenophores, *Pleurobrachia brunnea* and *P. pileus*, occurred in several of the March and July samples. A swarm of *P. pileus* was present at station B in March and accounted for nearly 50% of zooplankton displacement volume. *P. pileus* has been reported from this area by several investigators (e.g., Bigelow, 1917; Fish, 1925), but there appears to be only one prior record of *P. brunnea* (Cowles, 1930).

STOMATOPODA. *Alima hyalina*, apparently not hitherto found in this area, occurred in one Sargasso Sea collection; "alima" and "erichthus" larvae were found several times.

UNIDENTIFIED ZOOPLANKTON. Several foraminifera and radiolaria species were observed in about one-half of the collections but no species were identified. Fourteen species of foraminifera are known to occur in Sargasso Sea water near Bermuda (Bé, 1960). A brachiopod larva was found in one and an unidentified cirriped larva in six collections from the Sargasso Sea. At least two isopod species were observed in three samples and an echinopluteus and tornaria larvae were detected in two Sargasso and two Gulf Stream collections.

## DISCUSSION

### SPECIES OCCURRENCE

One of the obvious features of the occurrence of the 361 epizooplankton species was the great number encountered in the Sargasso Sea (268 species) in comparison to the slope (169) and neritic (81) waters. The number of species found in the Gulf Stream (157) is certainly not representative of this warm current and, as pointed out in the discussion of the major groups, simply reflects the small number (3) of samples examined. Little emphasis will thus be placed on the Gulf Stream species or their abundance in this discussion.

The great diversity in the Sargasso Sea was the result of the occurrence of many species in most groups rather than an unusually large representation in a few groups. The only groups with fewer species in the Sargasso Sea than in the other three areas were Cladocera, Medusae, Decapoda, Mysidacea and Ctenophora but these were relatively non-diverse taxa elsewhere. Only very few species in each of these groups were found in all four areas.

The latitudinal diversity in biotas, especially among animals, has been referred to by many authors and recently by Fischer (1960). He pointed out that tropical biotas because of long-time environmental stability have evolved and diversified more rapidly than polar and temperate biotas which have been subjected to periodic climatic fluctuations. Dunbar (1960) has also referred to the stable conditions of tropical waters and the long-term and seasonal oscillations of temperate and polar seas in relation to the evolution of the fauna.

The present study provides additional examples of

diversity vs. stability. The slope and especially the neritic water can be considered regions of oscillation (seasonally) and the Sargasso Sea a region of relatively stable conditions (see Hydrographic Data).

It was not uncommon to find more than 100 species of zooplankters in an individual Sargasso Sea collection whereas never more than 40 were encountered in a neritic sample. The species in shelf material, unlike that of the Sargasso Sea, varied seasonally. During the winter cruise the maximum number of species found in any neritic sample was only 18. The species composition of slope samples also varied depending on the season and on whether offshore or inshore zooplankton predominated. Generally the numbers of species present were higher than those found in neritic waters and lower than in Sargasso Sea samples. In September approximately the same number of species occurred throughout the shelf and slope areas, largely owing to the presence of offshore copepods, the most diverse group, which had apparently been carried shoreward by indrafts of offshore water.

The large species diversity and concomitant small number of individuals and thus small zooplankton standing crops as found in the Sargasso Sea are typical of tropical epizooplankton. Menzel and Ryther (1961) have found, in their studies of plankton near Bermuda, that nearly 100% of the production is used by the zooplankton. Where phytoplankton production is comparatively low it is interesting that so many species can co-exist despite the relatively prolonged periods of environmental stability which would permit the evolution of new species and the exploitation of many niches. One would suspect, in view of the small number of individuals of each species, that the major competition is perhaps intraspecific rather than interspecific. The many species of herbivorous copepods, for example, may have very specialized food requirements, as Deevey (1960b) has suggested for two copepod species found in the Sargasso Sea near Bermuda.

The small species diversity in shelf waters may be related to instability and seasonal alternation of the environment. Although no estimates have been made of the proportion of the large production by phytoplankton over the shelf which is utilized by the zooplankton, it seems safe to assume that considerable surplus must exist, especially during times of blooms. In Long Island Sound no more than 26% of the net phytoplankton production is utilized by zooplankton (Riley, 1956).

#### TROPHIC STRUCTURE

The trophic structure of neritic and Sargasso Sea waters can be discussed in light of the abundance of the major groups and the position each occupies in the food chain. The slope water epizooplankton is considered a mixture of neritic and Gulf Stream-Sargasso Sea species with a seasonally appearing cold-water element and for this reason is not discussed below. The Gulf Stream zooplankton composition is also not discussed because our analyses are based on only three samples.

The species comprising many taxa cannot collectively be assigned to specific segments of the food chain. There are, for example, herbivorous, carnivorous and omnivorous species of copepods although it is assumed here that the bulk of this group is herbivorous. Similar diverse feeding habits are found among euphausiids and amphipods. It should be emphasized that in all four areas the copepods were the most important single component of the zooplankton.

**NERITIC WATERS.** In shelf waters, where the largest quantities of zooplankton were found, the copepod plankton frequently comprised more than 60% of the total zooplankton volume. The few abundant species (Table 4) were herbivorous or omnivorous but at times some predatory species (*Candacia armata*) were numerous. In one sample, for example, this species comprised about 10% of the copepod volume. Occasionally salps which are obligate herbivores appeared in large numbers and in one summer collection they formed 99% by volume of the zooplankton. They were practically absent, however, from December and March samples. The only other group of frequent volumetric importance in shelf waters were the three species of carnivorous chaetognaths which varied in abundance between less than 1% to as much as 49%. In summary, using mean values, the neritic zooplankton was composed of approximately 9% salps (herbivores), 57% copepods (mostly herbivores), 15% chaetognaths (carnivores), 1% amphipods (mostly carnivores) and 2% euphausiids (omnivores).

**SARGASSO SEA.** The most important group in the Sargasso Sea, where least quantities of zooplankton were found, was again the copepods which formed between 34% and 65% of the displacement volume in individual samples. Although the volumetrically dominant species were most certainly herbivores or omnivores some predatory ones (*Candacia* and *Euchaeta* spp.) occurred. The near absence of large concentrations of obligate herbivores, such as found in shelf waters, was noteworthy. Two probably exclusively carnivorous groups, chaetognaths and siphonophores, formed large proportions of the zooplankton. In individual samples chaetognaths comprised between 11% and 30% and siphonophores between 8% and 27% of the total zooplankton volumes. Other taxa were of little importance volumetrically. Using mean percentage data the Sargasso Sea zooplankton consisted of approximately 50% mostly herbivorous or omnivorous copepods, 19% carnivorous chaetognaths, 18% carnivorous siphonophores, 2% mostly carnivorous amphipods and 5% omnivorous euphausiids.

Aside from total quantities of zooplankton and, of course, species composition, the chief difference between shelf and Sargasso Sea zooplankton populations was in the relative abundance of the herbivorous groups. Well over one-half by volume of the shelf zooplankton consisted of predominantly herbivorous animals while in the Sargasso Sea only about one-half of the zooplankton belonged to this trophic level. It

has already been pointed out that nearly all of the Sargasso Sea phytoplankton is utilized by phytophagous zooplankton. It appears from the relative quantities of the herbivorous groups that there is also no excessive surplus of herbivores and this, when considered in conjunction with the near complete utilization of phytoplankton, suggests that an efficient, if not delicate relationship, exists between producers and consumers in these tropical waters.

#### INDICATORS

If the usual distribution of zooplankton species in a large area is fairly well known, it is then possible to recognize unusual or expatriated occurrences and perhaps to relate these to transport by water. Such species, often referred to as "indicators," need not be endemic to certain water masses in order to be useful in implying water movement. In the present investigation an effort was made, in conjunction with literature references, to ascertain which of the species occurred regularly in sufficient abundance in certain areas so that they could be considered indicators when found elsewhere. Since certain oceanic copepods can breed in coastal waters, at least in southern coastal waters (St. John, 1958), some knowledge of the reproductive cycle and longevity of the species is often valuable in deciding whether it is indicating recent or possibly old intrusions of water into an area.

The samples collected from shelf waters in September and December contained 21 species with oceanic or offshore affinities. Included in this group in September were 15 of the 16 warm-water copepods listed in Table 3 (*Paracalanus parvus* excluded), 2 euphausiids (*Euphausia tenera*, *Thysanoessa gregaria*), 1 amphipod (*Hyperia atlantica*), 2 siphonophores (*Diphyes bojani*, *D. dispar*) and 1 tunicate (*Thalia democratica*).

The copepods, because of their abundance, are perhaps the most important group for making inferences concerning the hydrography of this area. Deevey (1952b, 1960a) recognized 6 Gulf Stream copepods in Block Island Sound and 10 of southern origin outside Delaware Bay. These species are included in our list of 16 warm-water species and occurred also in late summer and fall. Our list of warm-water species would have been longer had we identified the several species of *Corycaeus* and *Oncaea*, two essentially tropical genera. Apparently the inshore movement of the offshore waters when it occurs is a widespread feature of the hydrography of this area.

It has already been pointed out that surface currents, as deduced from drift bottles released off New York, show an inshore movement of offshore waters during the summer period (Bumpus, 1960).

#### NEW RECORDS

Although it was stated in the Introduction that the zooplankton of this area is fairly well known, this knowledge applies more to the continental shelf and adjacent waters than to the Gulf Stream and Sargasso

Sea. The number of species newly recorded for the area (Fig. 1), excluding the pelagic molluscs, is as follows: 21 copepods, 13 amphipods, 13 annelids, 11 ostracods, 5 siphonophores, 2 chaetognaths, 2 chordates, 1 euphausiid, 1 medusa and 1 stomatopod. Thus 70 species or approximately 20% of the 358 identified zooplankton species found represent new records for this region of the northwest Atlantic Ocean. More than two-thirds were found in the Gulf Stream and northwest Sargasso Sea, two areas poorly known taxonomically.

#### SUMMARY

Quantitative zooplankton samples and hydrographic data were collected seasonally at thirteen stations located in neritic, slope, Gulf Stream and Sargasso Sea waters between the coast of New York and Bermuda in 1959 and 1960.

The total zooplankton displacement volumes were much higher in neritic and inner slope waters than elsewhere. The mean ( $\text{cc}/\text{m}^3$ ) for each area was: neritic, 1.07; slope, .27; Gulf Stream, .03; and Sargasso Sea, .02. Larger mean volumes were found in warm months than in cold months in neritic waters where a 30-fold difference between the maximum ( $3.71 \text{ cc}/\text{m}^3$ ) and minimum ( $.12 \text{ cc}/\text{m}^3$ ) occurred. Less extreme seasonal fluctuation (.76 to .04  $\text{cc}/\text{m}^3$ ) was noted in slope waters and much less in Gulf Stream (.04 to .03  $\text{cc}/\text{m}^3$ ) and Sargasso Sea waters (.04 to .01  $\text{cc}/\text{m}^3$ ).

The numerical abundance of the zooplankton was much larger in neritic than in Gulf Stream and Sargasso Sea waters. The slope waters usually had numerical abundances between that of neritic and Sargasso Sea waters. The mean abundance in each area ( $\text{no.}/\text{m}^3$ ) was: neritic, 1540; slope, 310; Gulf Stream, 134; and Sargasso Sea, 71.

The 358 identified species, with the numbers that have not previously been recorded from the northwest Atlantic Ocean given in parentheses, were distributed in the various taxa as follows: 133(21) copepods, 55(13) amphipods, 30(5) siphonophores, 29 molluscs, 27(13) annelids, 26(1) euphausiids, 15(2) chaetognaths, 15(11) ostracods, 9(2) chordates, 6 cladocera, 5(1) medusae, 3 decapods, 2 mysids, 2 ctenophores, and 1(1) stomatopod. Eighty-one species were found in neritic, 169 in slope, 157 in Gulf Stream and 268 in Sargasso Sea waters.

Copepods were the most important constituents of the zooplankton in all areas. They formed a mean of 51% by volume and a mean of  $615/\text{m}^3$  by number in all collections. Chaetognaths (13%,  $10/\text{m}^3$ ) were usually second in abundance. Other groups formed considerably less proportions of the zooplankton although occasionally salps predominated in shelf and slope waters.

Approximately 65% of the neritic and 50% of the Sargasso Sea zooplankton consisted of predominantly herbivorous groups. In the Sargasso Sea the quantities of phytoplankton utilized by zooplankton and the relative abundance of herbivorous zooplankton indi-

cates that an efficient relationship exists between producers and consumers in these tropical waters.

Based on the distribution of 21 species, including 15 copepods, it was shown that there was a general inshore movement of offshore waters in the fall. From examination of prior reports of species occurrence it was postulated that such indrafts of offshore waters when they occur are a widespread feature of the hydrography of the northeast Atlantic coast between Delaware and Block Island Sound.

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## APPENDIX

TABLE 1. Major taxonomic groups by percent of total displacement volume. X indicates that the group was too small to permit a volume determination or that it was included with several other groups in a "miscellaneous" category.

Station	Copepoda	Chaetognatha	Euphausiacea	Amphipoda	Siphonophorae	Pteropoda	Heteropoda	Annelida	Salpidae	Decapoda
<i>Crawford cruise 33—(Sept. 1959)</i>										
A <sup>a</sup>	—	—	—	—	—	—	—	—	—	—
B	47.5	15.8	1.0	1.6	2.2	1.2	0	X	14.7	6.8
C	68.9	8.4	1.3	2.0	4.9 <sup>c</sup>	X	0	0	9.0	3.7
D	86.1	7.4	1.1	1.9	1.9 <sup>c</sup>	0	0	X	0.7	0.1
E	85.3	5.4	4.0	0.3	1.0 <sup>c</sup>	1.4	X	0	0	1.2
F	59.7	25.4	7.0	2.1	X	0	0	0	X	X
G	63.7	12.7	2.5	0	15.9	0	0	0	5.1	0
HH	62.0	10.1	13.8	0.6	1.5	X	0	X	0.6	3.9
II	67.0	11.5	1.4	1.0	13.2	X	X	1.0	X	X
KK <sup>b</sup>	40.4	18.0	0.8	5.1	11.8	X	X	2.4	X	2.2
<i>Crawford cruise 35—(Dec. 1959)</i>										
A	89.3	6.3	0	3.8	0	0	0	X	0	X
B	48.6	48.8	X	1.7	X	0	0	0	0	X
C	81.9	10.8	0.9	6.4	X	0	0	X	0	X
G	60.3	28.7	3.9	X	2.1	0	0	X	X	X
HH	45.8	2.9	45.6	X	4.9	0	0	X	X	0
II	51.7	21.2	2.6	1.9	8.8	X	X	5.6	X	1.4
JJ	65.1	14.4	5.6	1.1	8.4	X	0	1.4	X	1.1
KK	59.5	11.2	5.3	1.3	15.1	X	0	X	X	1.1
LL	47.3	19.2	3.6	6.4	13.9	X	0	X	X	X
NN	53.7	19.2	1.5	1.9	21.7	X	X	X	X	X
<i>Crawford cruise 38—(Mar. 1960)</i>										
A	77.3	19.8	1.2	0	0	0	0	X	0	X
B	32.9	11.1	X	X	X	0	0	0	0	0
C	79.9	X	3.0	0	X	0	0	X	0	X
D	95.8	0	2.1	X	X	0	0	X	0	X
E	81.3	12.3	1.9	3.2	X	0	0	X	0	0
F	82.3	5.9	4.1	0.8	4.5	X	0	X	0	2.3
G	47.9	4.8	35.2	1.6	5.3	2.2	0	0.7	0	2.3
HH	83.4	10.7	4.2	X	X	X	0	0	X	X
JJ	48.9	29.8	3.4	1.8	12.4	X	X	X	X	0.4
KK	46.0	17.3	14.2	0.8	16.2	X	0	1.4	X	X
LL	34.4	21.6	11.8	1.8	27.0	X	X	X	X	X
NN	35.5	24.2	4.8	3.0	25.0	X	X	2.3	X	X
<i>Atlantis cruise 257—(July 1960)</i>										
A	56.5	15.0	0	0	0	0	0	X	0	0.5
B	19.3	37.1	9.5	0.1	0.2	3.9	0	0.9	0	1.7
C	12.0	24.0	8.3	1.1	3.0	X	0	1.4	2.8	0.6
D	X	0.1	0.1	0.1	0.5	0	0	0	99.1	X
E	3.1	1.5	1.2	X	2.3	0	0	X	88.7	0
F	5.4	2.7	1.2	X	15.6	X	X	X	72.1	X
G	2.4	1.1	0.2	2.1	9.4	0	X	0	83.5	X
HH	0.9	0.4	X	0.7	4.0	X	0	0	93.2	X
II	49.2	9.1	1.3	2.6	21.4	X	X	0.8	X	1.5
JJ	X	X	0	0	0	0	0	0	99.0+	0
LL	44.0	21.8	0.8	2.1	22.5	X	X	5.8	X	0.5
NN	56.6	10.8	1.1	1.1	21.2	X	X	3.4	0	0.8

<sup>a</sup> Percentage not shown since no. 2 net used for collection; all others are no. 6 net.<sup>b</sup> Crawford cruise 49 (September 1960).<sup>c</sup> Includes some medusae.

## APPENDIX

TABLE 2. Number of animals per cubic meter in several common groups of the zooplankton.

Station	Copepoda	Chaetognatha	Euphausiacea	Amphipoda	Siphonophorae			Pteropoda	Heteropoda	Annelida	Salpidae	Decapoda
					N°	E°	U°					
Crawford cruise 33—(Sept. 1959)												
A <sup>a</sup>	—	—	—	—	—	—	—	—	—	—	—	—
B	705	27.7	1.18	2.92	0.492	0.769	0	0.584	0	0.030	25.5	15.5
C	1550	11.5	1.68	1.59	0.396	0.305	0.030	0.152	0	0	3.72	3.69
D	3280	31.6	8.41	2.68	0.026	0.557	0.079	0	0	0.106	0.328	0.504
E	1550	5.37	21.6	0.344	0.034	0.017	0.051	7.82	0.035	0	0	0.826
F	150	1.04	1.59	0.177	0	0.014	0.066	0	0	0	0.170	0.074
G	142	0.819	0.390	0	0.143	0.143	0.195	0	0	0	0.780	0
HH	397	2.23	0.922	0.201	0.088	0.084	0	0.037	0	0.023	0.207	0
II	145	0.842	1.24	0.238	0.295	0.081	0.194	0.113	0.006	0.226	0.025	0.201
KK <sup>b</sup>	72.8	2.77	0.223	0.211	0.242	0.080	0.196	0.061	0.007	0.331	0.003	0.238
Crawford cruise 35—(Dec. 1959)												
A	1490	11.5	0	4.66	0	0	0	0	0	0.018	0	0.149
B	1420	90.7	0.030	1.98	0.060	0	0.030	0	0	0	0	0.121
C	895	14.1	0.383	7.74	0.056	0	0	0	0	0.028	0	0.028
G	47.2	6.26	0.550	0.049	0.176	0.098	0.216	0	0	0.098	0.009	0.019
HH	114	3.70	0.849	0.013	0.097	0.027	0.034	0	0	0.062	0.007	0
II	147	5.14	1.50	0.246	0.456	0.170	0.277	0.076	0.013	0.358	0.018	0.238
JJ	89.6	3.32	1.08	0.138	0.290	0.170	0.145	0.094	0	0.164	0.019	0.290
KK	59.8	2.49	1.10	0.113	0.623	0.142	0.160	0.032	0	0.338	0.014	0.060
LL	56.8	5.42	1.20	0.092	0.575	0.145	0.053	0.030	0	0.122	0.031	0.076
NN	90.3	3.43	1.35	0.302	0.678	0.339	0.208	0.052	0.005	0.313	0.016	0.078
Crawford cruise 38—(Mar. 1960)												
A	1300	11.4	3.35	0	0	0	0	0	0	0.044	0	0.089
B	406	4.09	0.089	0.044	0.044	0	0	0	0	0	0	0
C	382	0.017	1.44	0	0.105	0	0	0	0	0.017	0	0.035
D	230	0	1.45	0.045	0.045	0	0	0	0	0.045	0	0.022
E	1610	11.8	1.23	0.888	0.044	0	0	0	0	0.014	0	0
F	143	0.577	0.943	0.065	0.024	0.008	0	0.008	0	0.008	0	0.008
G	100	0.831	1.49	0.207	0.085	0.012	0	0.697	0	0.012	0	0.012
HH	143	0.513	1.10	0.005	0.005	0.005	0	0.035	0	0	0.006	0.017
JJ	78.3	3.44	0.749	0.276	0.368	0.135	0	0.004	0.004	0.145	0.002	0.060
KK	20.9	1.04	0.156	0.014	0.297	0.046	0.023	0.002	0	0.067	0.001	0.009
LL	38.8	2.27	0.761	0.246	0.632	0.279	0.057	0.072	0.001	0.285	0.001	0.011
NN	16.0	1.33	0.107	0.103	0.273	0.118	0	0.006	0.003	0.052	0.002	0.013
Atlantis cruise 257—(July 1960)												
A	7900	72.8	0	0	0	0	0	0	0	0.359	0	8.09
B	1140	39.8	0.022	0.109	0.175	0	0	56.1	0	1.67	0	3.58
C	140	36.9	5.88	0.384	1.057	0	0	8.52	0	0.865	0.004	0.807
D	0.448	0.640	0.256	0.256	3.45	7.49	0	0	0	0	173	0.192
E	31.9	2.59	1.22	0.403	0.840	0.470	1.44	0	0	0.033	5.11	0
F	70.5	1.12	0.420	0.143	0.973	0.399	0.409	0.102	0.010	0.040	1.66	0.010
G	6.82	0.665	0.268	0.419	0.380	0.290	0	0	0.005	0	5.42	0.011
HH	0.397	0.264	0.284	0.170	0.378	0.548	0	0.018	0	0	13.4	0.018
II	89	5.38	1.29	0.223	0.714	0.285	0.571	0.095	0.047	1.05	0.085	0.214
JJ	0.136	0.081	0	0	0	0	0	0	0	0	31.3	0
LL	120	4.17	0.484	0.399	0.723	0.637	0.361	0.072	0.006	1.08	0.007	0.080
NN	83.2	3.07	0.243	0.272	0.160	0.160	0	0.055	0.027	0.573	0	0.080

<sup>a</sup> No./m<sup>3</sup> not computed since no. 2 net used for collection; all others are no. 6 net.<sup>b</sup> Crawford cruise 49 (September 1960).<sup>c</sup> N=Nectophore generation; E=Eudoxid generation; U=unidentified.