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PLANKTON STUDIES

BULLETIN

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Plankton Studies

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The Zooplankton of the Surface Waters of the Delaware Bay Region

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ABSTRACT

The zooplankton samples on which this study is based were obtained from 1929 to 1935 at a number of stations in the lower part of Delaware Bay and outside the Bay by horizontal tows, usually five minutes at the surface and five minutes subsurface, with a meter net of fairly coarse mesh (#2 or #0 silk, or both). Consecutive monthly data, including the species present and the estimated numbers and displacement volumes per 10 minute tow, are available for January 1930 through July 1933. In general, outside the Bay, maximal numbers and volumes were found in summer and late fall or early winter, minimal numbers and volumes in late winter or spring. In the Bay the annual cycles in total quantity were less regular; usually there was a spring minimum and maxima in early summer, fall or winter. Despite differences in the seasonal cycles, the relative quantity of zooplankton varied similarly from year to year outside and in Delaware Bay. The mean annual volumes obtained in and outside the Bay for 1930 and 1933 were considerably greater than those for 1931 and 1932.

Copepods were by far the dominant organisms. Other groups of importance in the Bay were the larvae of bottom invertebrates, chaetognaths, fish eggs and hydromedusae. Outside the Bay, aside from these groups, Cladocera and tunicates were seasonally abundant. All of the species have been listed in tabular form with their periods of occurrence. Fifty-six different copepods were recorded. In the Bay *Acartia tonsa* was dominant and *Centropages hamatus* and *Pseudodiaptomus coronatus* were second in importance. Outside the Bay *Centropages typicus* was dominant and *Paracalanus parvus* and *Pseudocalanus minutus* were the next most abundant species. The seasonal cycles of all the important species have been considered. Six species of marine Cladocera were recorded, of which *Penilia avirostris* was seasonally most abundant. Eight species of pelagic tunicates were found outside the Bay; of these *Oikopleura dioica* and *Doliolum nationalis* appeared each summer or fall. The chaetognaths which occurred regularly were *Sagitta elegans*, *S. serratodentata* and *S. enflata*. Larval forms, largely crustacean, were more abundant in the Bay than outside. Fish eggs were most numerous from May to July. Two protozoans, *Acanthometron* sp. and *Noctiluca* sp., were briefly exceedingly abundant. Other groups occasionally noted include pelagic polychaetes, isopods, the ostracod *Euconchoecia chierchiaie*, the penaeid *Lucifer faxoni*, the heteropod *Oxygyrus keraudreni*, and the pteropods *Clione limacina*, *Limacina retro-versa* and *Creseis virgula*.

Because of the wide annual temperature range in the waters of the Delaware Bay region, about 0-25° C, few organisms occur throughout the year. Four copepods, *Acartia tonsa*, *Pseudodiaptomus coronatus*, *Centropages typicus* and *Paracalanus parvus*, are considered year-round species. The known temperature ranges, including the range over which breeding occurs and the extreme recorded limits, of 14 species of copepods are presented and compared with the known geographic and seasonal occurrences of these species from 50° to 30° N Lat. *Acartia tonsa* and *Pseudodiaptomus coronatus* have the widest breeding range, 30-31° C; *Paracalanus parvus* and *Centropages typicus* are next with a range of 24-26°. Colder water species such as *Pseudocalanus minutus*, *Temora longicornis*, and *Acartia clausi* apparently do not reproduce at temperatures exceeding 20° C. Their latitudinal and seasonal occurrence appears to be limited primarily by temperature and secondarily by competition with associated species. Warmer water species, capable of reproducing over an exceptionally wide temperature range, of which *Acartia tonsa* is an example, are probably limited in their seasonal occurrence at the northern part of their range by competition with dominant colder water species. In the area here considered, other factors such as hydrographic conditions or food do not appear to be as important in limiting seasonal or latitudinal ranges.

INTRODUCTION

From 1929 to 1935, hundreds of zooplankton samples were collected at over 40 stations in the Delaware Bay region. These were obtained on the *SELMA W* by Captain Julius Widerstrom under the direction of Robert A. Nesbit of the U.S. Bureau of Fisheries and Albert E. Parr, then Director of the Bingham Laboratory, during investigations into the distribution and relative quantities of fish eggs and larvae, particularly those of the weakfish. This large zooplankton collection has since been stored in Peabody Museum at Yale University. Several years ago it was decided to study part of this material, and through the kindness of Yngve H. Olsen the pertinent data were turned over to me. Acknowledgment is made to the U.S. Bureau of Fisheries for making these collections possible.

Although these samples are not quantitative, the data obtained are of value for several reasons. For $3\frac{1}{2}$ years, hauls were made at monthly intervals. Thus variations in abundance and in species composition are known for a fairly long period, and since samples were collected both in and outside the Bay it is possible to note the changes in species composition in passing from the Bay to the waters outside. Also, there has been no general survey of the zooplankton of the inshore coastal waters of the middle Atlantic states. Although Cowles (1930) has listed many of the species and Wilson (1932a) has studied the copepods of Chesapeake Bay and the waters outside, no data are available for some of the important zooplankton groups, such as Cladocera and pelagic Tunicata. This report is concerned with the zooplankton of the lower Bay and of the waters outside; our knowledge of the zooplankton of the Delaware River and of the upper to lower Bay should be considerably augmented by quantitative collections made on quarterly cruises from November 1951 to August 1953 at a series of stations from Philadelphia to Overfalls Shoal by investigators at the University of Delaware (Cronin, 1954). Shuster (1959) has recently reviewed the work on the Delaware River estuary.

METHODS

The hauls were made with a fairly coarse meshed net one meter in diameter. The mesh size of the silk used is not known, but it was probably either No. 0 or No. 2 silk, or both. Ten minute tows (five minutes surface, five minutes subsurface) at a speed of $1\frac{1}{2}$ knots were made usually at monthly intervals at the various stations. During the summer of 1929 samples were collected at depths down to 15 fathoms, but starting in January 1930 the regular 10 minute tow sampled only the upper few meters. Samples thus collected obviously cannot yield a complete picture of the zooplankton population. The total water column was not sampled and so the data obtained apply only to the surface and subsurface forms. Also, since a fine meshed net was not used,

only the larger forms were caught in their true proportion. The nauplii and early copepodid stages of copepods and small species such as *Oithona* spp. and *Paracalanus crassirostris* were retained only after the net was clogged with larger forms. Small specimens were frequently found in the samples, so the species list is probably essentially correct; however, hauls made with a fine meshed net in these waters would undoubtedly show that the smaller species are of greater importance than they appear to be from this collection of samples.

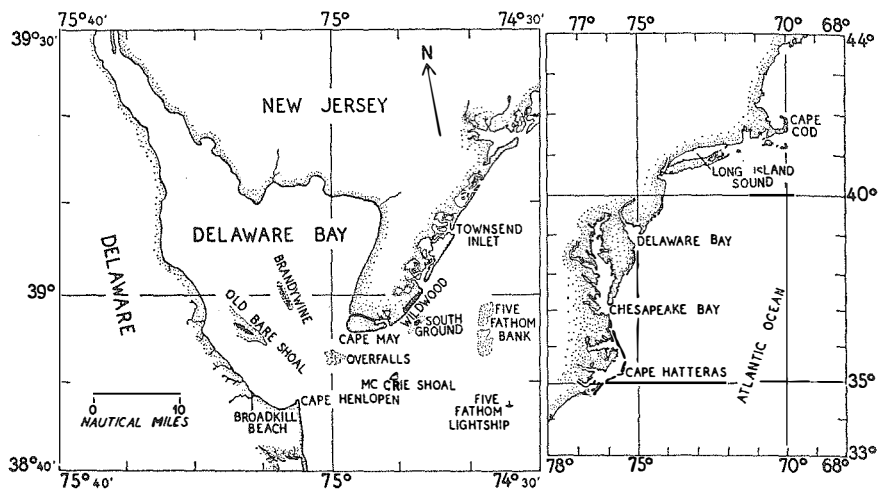


Figure 1. Left: Station locations in and outside Delaware Bay. Right: Location of Delaware Bay relative to other areas where plankton studies have been made.

A number of stations that were visited regularly were chosen for study (see Fig. 1). The stations outside the Bay are Five Fathom Bank, west of Five Fathom Lightship, McCries Shoal, and South Ground. Samples were collected at the traps off Wildwood, N. J. from December 1930 through March 1933, but hauls were made usually at monthly intervals at some or all of the other stations outside the Bay from the summer of 1929 to the summer of 1933. Occasional hauls were made off Townsend Inlet.

The stations selected in the Bay are in the central to lower part and include those off Broadkill Beach, east of Brandywine Shoal, and Old Bare Shoal. Samples were obtained regularly at these stations from January 1930 through September 1933. The stations at the mouth of the Bay were not visited consecutively over a long period. Samples were collected at Overfalls Shoal during the summer of 1929 and the winter and spring of 1930 and 1931. There were several cruises, largely to the stations in the Bay, in June, September and November 1934. In 1935 there were cruises in February, March, May and June both in the Bay and outside. However, due to the fragmentary

nature of these data, the samples obtained in 1934 and 1935 have not been considered unless the species composition was of especial interest. Consecutive monthly data are available from January 1930 through July 1933.

The samples were studied by the usual methods. Counts were made of known fractions of the total sample in order to obtain the percentage composition and estimates of the numbers per 10 minute tow. The remainder of the sample was examined for rarer species. Determinations of total displacement volumes were made on many, but not all, of the samples for the period from January 1930 through July 1933. After any Scyphomedusae had been removed, the samples were strained on a piece of No. 2 silk and then placed on sheets of absorbent paper to drain off excess water. In 10-30 minutes, when the excess water was removed, the zooplankton was added to a known volume of water to obtain the displacement volume.

Length measurements, from the top of the head to the base of the caudal rami, were made on a number of species of copepods in order to study size variations during the year. Some of these data will be included in this report, since the annual variations in length aid in estimating the number of generations of a species during the year. Most of this material, however, is included in the accompanying report (Deevey, 1960) which deals exclusively with annual size variations in copepods.

TEMPERATURE AND SALINITY

Fig. 2 shows the average surface water temperatures for the days when samples were collected from May 1929 through July 1933. The range in the Bay, where it usually varied from less than 2°C in the winter to 24° or 25° in the summer, was more extreme than that outside the Bay, where temperatures ranged from over 2° to approximately 22°, but the cycles varied considerably from year to year. The temperatures recorded in 1930 and 1931 exhibited a similar seasonal range, but the winters of 1932 and 1933 were more moderate, especially outside the Bay. For 1932 the lowest temperatures were noted in March instead of in January and February, and summer temperatures outside the Bay did not exceed 20°C. Comparison of the annual cycles shows that temperatures were similar only in March and in September or October. Except in 1932, by March the Bay waters had warmed to the same degree as the waters outside, and from then until fall temperatures were higher in the Bay. In early fall the Bay waters cooled more rapidly than the waters outside and remained cooler until the following March.

It is important to emphasize the temperature conditions found throughout the middle Atlantic coastal waters, since they aid in explaining the seasonal distribution and species composition of the zooplankton. Parr (1933), in his analysis of seasonal temperature changes in the shallow waters of the Atlantic coast of the United States, found that in the region between Cape Cod and

Cape Hatteras there is a wide annual range without any of the abrupt short term fluctuations which he believed form a temperature barrier. At Nantucket Shoal off Cape Cod, abrupt deviations from the annual cycle occur, especially in summer, whereas similar sudden fluctuations in temperature are found off Cape Hatteras in winter (see Parr, fig. 24). Thus, in winter when no temperature barrier exists off Cape Cod, boreal forms may spread southward, theoretically as far as Cape Hatteras. Opposite conditions are found during summer

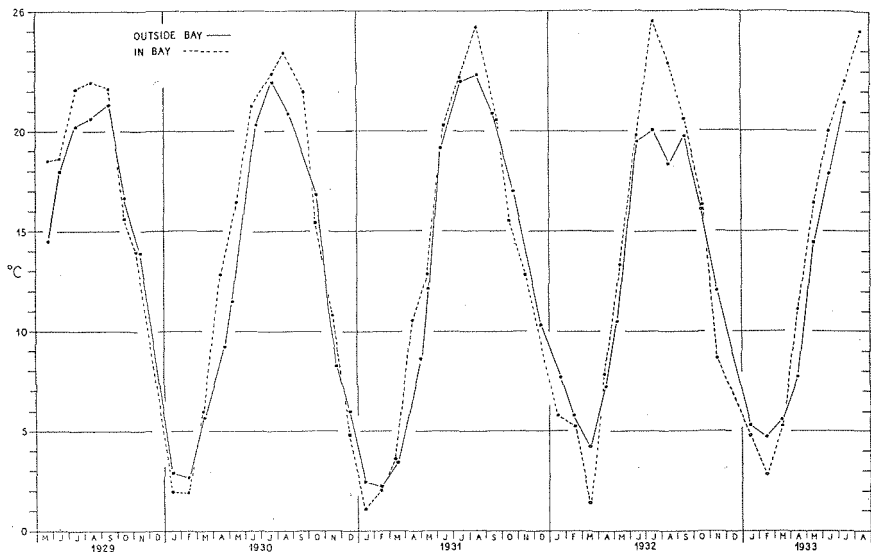


Figure 2. Average surface temperatures at the stations in and outside Delaware Bay on the dates when samples were obtained, from May 1929 through August 1933.

when there is no barrier off Cape Hatteras and southern species penetrate more northern coastal waters.

Extensive salinity data are not available, but a number of determinations were made from 1929 to 1931. Outside the Bay it varied from a minimum of 30 ‰ off Wildwood Beach, N.J. to a maximum of 32.88 ‰ at Five Fathom Bank and South Ground. In the Bay at Old Bare Shoal it ranged from 24.9–32.25 ‰, while east of Brandywine Shoal the range noted was 23.04–30.39 ‰. Off Broadkill Beach a similar range was recorded, 22.8–31.2 ‰. At the mouth of the Bay off Cape Henlopen the salinity varied from 24.5–31.8 ‰. Thus the salinity was over 30 ‰ at the stations outside the Bay while the range at the mouth of the Bay and at the stations inside was such as to exclude ordinarily from the Bay some of the neritic species common in the outside waters.

TOTAL ZOOPLANKTON

The mean monthly total displacement volumes are shown in Fig. 3. Outside the Bay, maximal volumes were found in summer and in late fall and early winter. Usually volumes were relatively high in January and decreased to the lowest annual values during the period from February to May. In 1930 and 1931 there was a secondary maximum in March, but in 1932 and 1933 minimal volumes were noted during this month. The yearly cycle was similar

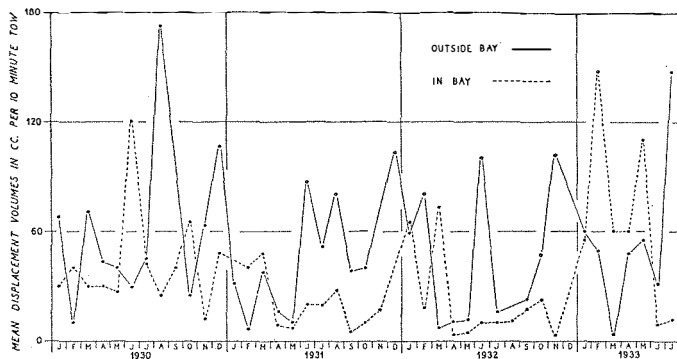


Figure 3. Mean monthly total zooplankton displacement volumes, in cc/10 minute tow, obtained at the stations in and outside Delaware Bay, from January 1930 through July 1933.

in 1930 and 1931, but maximal quantities were greater in 1930. For 1932 large volumes were found in January and February, June and November, but the total quantity of zooplankton was small during the rest of the year compared with the volumes recorded for 1930 and 1931. As previously noted, 1932 was a year of moderate temperatures: a relatively warm winter was followed by a cool summer (see Fig. 2), and this had a significant effect on the zooplankton. The volumes obtained during the first half of 1933 were as large as those recorded for 1930. The second highest mean monthly volume found during the 3½ year period was obtained in July 1933.

The volumes recorded in the Bay were in general smaller than those obtained outside, although large volumes were recorded for individual months in 1930 and 1933. This is reasonable, since the dominant species are smaller than those outside and the meter net undoubtedly retained a smaller proportion of the total number present. In general the volumes were relatively high during winter, but the annual cycle was not as consistent from year to year as that at the stations outside. In 1931 and 1932 only small volumes of zooplankton were found from April to the end of the year, although somewhat larger volumes were obtained in late summer or early fall. In 1930 and

1933 large volumes were noted from January to May or June, and there was no April–May minimum as in 1931 and 1932.

Table I lists the mean annual volumes for 1930–1932; the 1933 figures are means for the months January–July. Larger quantities of zooplankton were found in 1930 and 1933 than in 1931 and 1932, both in and outside the Bay. Mean volumes from the stations in the Bay were at most half as large in 1931 and 1932 as in the other two years, and also they were less than half as large as the volumes obtained outside the Bay during the same years.

The average volumes recorded by Bigelow and Sears (1939: table on p. 200, figs. 2–10) for the waters over the continental shelf are considerably larger than those found in the Delaware Bay region during the same period. Their data, based on 20 minute hauls, primarily oblique, made with meter or $\frac{1}{2}$ meter nets between February and July 1929–1932, show considerable variability. Although they found very small quantities of zooplankton off Delaware Bay from April to July 1929, their 1930–1932 volumes for this region were, except for June 1932, appreciably larger than those here recorded for the stations outside Delaware Bay. This may be explained in part by the preponderance of small species in the inshore waters and by the fact that the Delaware Bay samples were obtained by horizontal rather than oblique tows.

TABLE I. MEAN ANNUAL ZOOPLANKTON DISPLACEMENT VOLUMES, IN CC PER 10 MINUTE TOW, FROM THE STATIONS IN AND OUTSIDE DELAWARE BAY.

	In Bay	Outside
1930.....	42.4	61.2
1931.....	20.25	45.6
1932.....	21.7	45.6
1933.....	64.7	56.3

The mean monthly total numbers per 10 minute tow are shown in Fig. 4. The annual cycle in numbers was essentially similar to the cycle in total volumes. In general, outside the Bay maximal numbers were found in summer and late fall or early winter whereas minimal numbers were recorded for late winter or spring. In 1930 and 1931 numbers were maximal in August and December and minimal in February, May or June, and October. The data obtained for 1932 varied in that high numbers were found only during the colder months, in February and November, and numbers were unusually small from spring to early fall. During the first half of 1933 minimal numbers were found in March, but from April to July exceptionally large numbers of zooplankton were present.

The seasonal cycle in the Bay differed from that found outside. In 1930 and 1931 numbers were maximal in early summer and October or November and minimal in the spring and late summer or early fall. As was the case outside

the Bay, the data obtained for 1932 varied considerably from those for the two previous years. Total numbers were relatively large only from January through March and in September. In 1933 unusually large numbers were recorded from January through May, with maxima in February and May, but then an abrupt decrease occurred and only small numbers were noted for June and July.

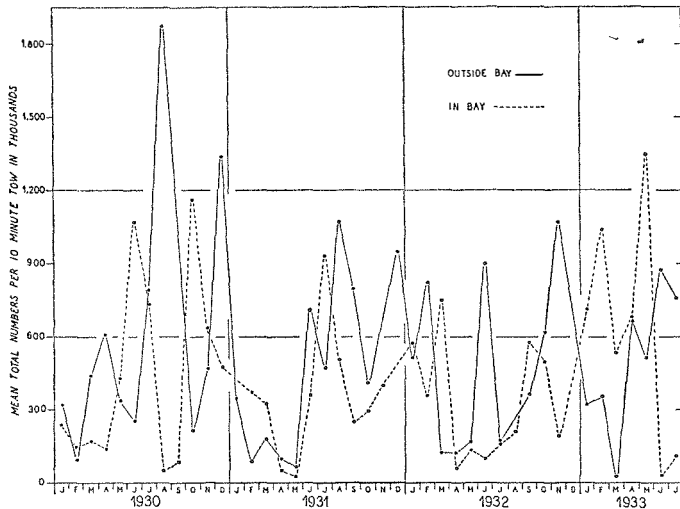


Figure 4. Mean monthly total numbers of zooplankton per 10 minute tow (in thousands) at the stations in and outside Delaware Bay, from January 1930 through July 1933.

The seasonal cycle in total numbers thus varied rather widely during the $3\frac{1}{2}$ year period studied. The largest numbers were found in 1930 outside the Bay and in 1930 and 1933 in the Bay. In 1931 and 1932 the total quantity of zooplankton, both in numbers and volumes, was smaller throughout the region. Thus, despite differences in the seasonal cycle of abundance, the relative quantity of zooplankton varied similarly from year to year both outside and in Delaware Bay.

COMPOSITION OF THE ZOOPLANKTON

Figs. 5 and 6 show the percentage composition by count of the major groups found in and outside the Bay, respectively, from 1930 to 1933. Copepods were by far the dominant organisms for the greater part of the year. In the Bay other important groups included the larvae of bottom invertebrates, fish eggs, and hydromedusae, but chaetognaths, siphonophores and *Noctiluca* sp. occurred occasionally in significant quantities. During the fall of 1930

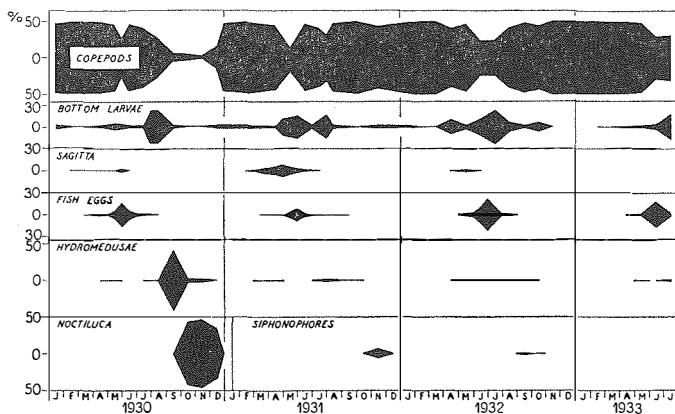


Figure 5. Relative percentages, by count, of the major groups of zooplankton organisms found at the stations in Delaware Bay, from January 1930 through July 1933.

hydromedusae and later *Noctiluca* sp. were so numerous in the Bay that the proportion of total copepods dropped to less than 10%. In late fall of 1931 and 1932, siphonophores entered the Bay in appreciable numbers. Outside the Bay the species composition was more varied; the same general groups were abundant, but tunicates and Cladocera were also numerous seasonally. Bottom larvae were more abundant in the Bay, but chaetognaths and hydromedusae were found in greater numbers outside.

Centropages typicus was the dominant copepod in the surface waters outside the Bay while *Acartia tonsa* was most numerous inside. *Sagitta elegans* and *S. serratodentata* were the important chaetognaths and *Penilia avirostris* was the only cladoceran that occurred in numbers every year. *Doliolum nationalis* and *Oikopleura dioica* were seasonally the commonest tunicates, although *Thalia democratica* was noted occasionally and in September 1934 little else was present in the samples. Table II lists the species of copepods while Table III gives the other zooplankton species, exclusive of copepods and larval forms. The limits of its period of occurrence are given for each species. In most instances, forms that appeared seasonally were not present for exactly the same months year after year. *Acartia clausi*, for example, was found from March to June in 1930 and from February to May in 1931–1933; the limits of its period of occurrence are therefore given as February–June. In the case of a warm water species, whose appearance was more sporadic, the period of occurrence given indicates only the time of year when it might be found. For example, *Corycaeus amazonicus*, listed as occurring between August and December, was recorded for August 1929, October and December 1930, and September–November 1932.

In general, during the first half of the year the zooplankton population

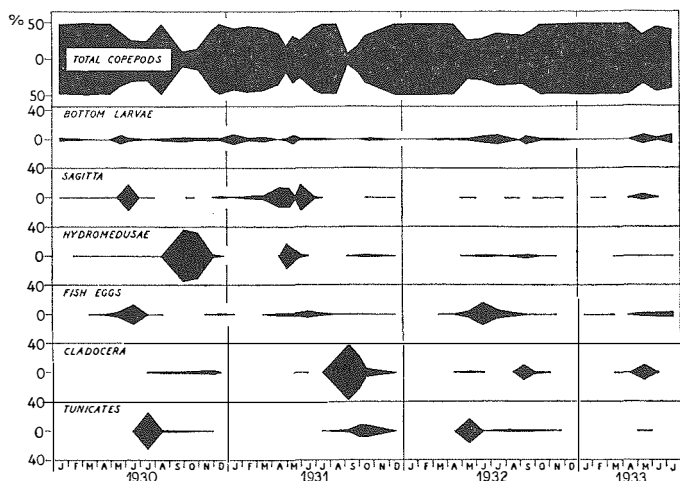


Figure 6. Relative percentages, by count, of the major groups of zooplankton organisms found at the stations outside Delaware Bay, from January 1930 through July 1933.

consisted almost entirely of boreal-temperate species whereas during the second half a variety of warm water forms was present. The two most important year-round species, *Acartia tonsa* in the Bay and *Centropages typicus* outside, may be considered typical members of the zooplankton population of the coastal waters of the middle Atlantic states.

TABLE II. SPECIES OF COPEPODS AND LIMITS OF PERIODS OF OCCURRENCE IN THE DELAWARE BAY REGION, MAY 1929 THROUGH JULY 1933.

Species	Period of Occurrence
<i>Acartia clausi</i>	February-June
<i>A. danae</i>	August 1929. Outside Bay
<i>A. longiremis</i>	January-May 1931. Outside Bay primarily
<i>A. tonsa</i>	Year-round. Sometimes absent in April
<i>Alteutha depressa</i>	Between February and June. In Bay primarily
<i>Anomalocera pattersoni</i>	June, October 1929
<i>Calanus finmarchicus</i>	January-August
<i>C. minor</i>	Between July and January. Outside Bay
<i>Caligus</i> spp.	Between July and September
<i>Calocalanus pavo</i>	August 1929. Outside Bay
<i>Candacia armata</i>	Between July and December. Outside Bay
<i>Centropages bradyi</i>	July 1929. Outside Bay
<i>C. furcatus</i>	September-November 1930
<i>C. hamatus</i>	Year-round 1932. Absent late summer or early fall of other years

(cont.)

TABLE II. (cont.)

Species	Period of Occurrence
<i>C. typicus</i>	Year-round
<i>Clytemnestra rostrata</i>	July 1929; Jan., Mar., Dec. 1930; Jan.-Mar. 1931; June, Aug., Nov. 1932. Outside Bay
<i>Copilia mirabilis</i>	August 1929. Outside Bay
<i>Corycaeus amazonicus</i>	Between Aug. and Dec., except 1931. Outside Bay
<i>C. americanus</i>	Between Oct. and Feb., except 1931. Outside Bay
<i>C. giesbrechti</i>	Between Aug. and Nov., except 1931. Outside Bay
<i>C. latus</i>	August 1929. Outside Bay
<i>C. speciosus</i>	August 1929. Outside Bay
<i>Eucalanus attenuatus</i>	December 1930. Outside Bay
<i>E. pileatus-subcrassus</i>	July-December. Outside Bay primarily
<i>Euchaeta marina</i>	November 1930. Outside Bay
<i>Euterpina acutifrons</i>	Between October and December 1930, 1932
<i>Eurytemora affinis</i>	Between March and May. In Bay
<i>E. americana</i>	June 1929; Jan., May 1930; May 1931. In Bay
<i>Farranula carinata</i>	Aug.-Sept. 1929; Sept. 1932. Outside Bay
<i>Labidocera aestiva</i>	Between May and January
<i>Lerneae</i> sp.	August 1932. In Bay
<i>Mecynocera clausi</i>	July 1929; Aug. 1932; Jan. 1933. Outside Bay
<i>Metridia lucens</i>	May 1930; July, Aug. 1932. Outside Bay
<i>Monstrilla</i> sp.	July 1931. In Bay
<i>Mycicola major</i>	September 1931. Outside Bay
<i>Oithona brevicornis</i>	Between May and November. In Bay
<i>O. plumifera</i>	September-December 1930, 1932. Outside Bay
<i>O. similis</i>	Year-round, but not noted in September
<i>O. spinirostris</i>	Between December and August
<i>Oncaea media</i>	Aug. 1929; Nov., Dec. 1930; Sept., Nov. 1932. Outside Bay
<i>O. venusta</i>	Between August and December. Outside Bay
<i>Paracalanus crassirostris</i>	Occasional throughout year
<i>P. parvus</i>	Year-round, spring minimum. Outside Bay primarily
<i>Pseudocalanus minutus</i>	Year-round 1930, 1932; missing late summer to early fall of other years
<i>Pseudodiaptomus coronatus</i>	Usually year-round, spring minimum. In Bay primarily
<i>Rhincalanus nasutus</i>	Feb., Dec. 1930; Mar. 1931, 1932. Outside Bay
<i>Sapphirina</i> sp.	November 1932. Outside Bay
<i>Scolecithrix danae</i>	November 1930. Outside Bay
<i>Temora longicornis</i>	Jan.-June, Oct.-Dec. 1930; Jan.-Aug. 1931; April-July 1932, 1933
<i>T. stylifera</i>	Between July and Nov., except 1931. Outside Bay
<i>T. turbinata</i>	Between Oct. and Dec. 1930, 1932. Outside Bay
<i>Tortanus discaudatus</i>	May, June 1929; May 1932. Outside Bay
Unidentified cyclopoids	July, Nov. 1929; Nov. 1930; Sept., Nov. 1932; Jan.-Feb. 1933
Unidentified harpacticoids	Occasional throughout year

TABLE III. SPECIES LIST AND LIMITS OF PERIODS OF OCCURRENCE OF ZOOPLANKTON ORGANISMS OTHER THAN COPEPODA AND LARVAL FORMS IN THE DELAWARE BAY REGION, MAY 1929 THROUGH JULY 1933.

Species	Period of Occurrence
Cladocera	
<i>Evadne nordmanni</i>	March, May-July. Outside Bay
<i>E. spinifera</i>	August-September 1929. Outside Bay
<i>E. tergestina</i>	July-October. Outside Bay
<i>Penilia avirostris</i>	July-November. Outside Bay primarily
<i>Podon intermedius</i>	August 1929; September-October 1931. Outside Bay
<i>P. polyphemoides</i>	May-June 1929; July 1932
Ostracoda	
<i>Euconchoecia chierchiae</i>	November 1932. Outside Bay
Isopoda	
<i>Edotea montosa</i>	May-June 1930. In Bay
Unidentified	July 1929; March, September 1932
Decapoda	
<i>Lucifer faxoni</i>	August-December. Outside Bay primarily
Tunicata	
<i>Dolioletta gegenbauri</i>	October-November 1932. Outside Bay
<i>Doliolum nationalis</i>	July-November. Outside Bay
<i>Fritillaria borealis</i>	April-May 1932; May 1933. Outside Bay
<i>Oikopleura dioica</i>	July-November. Outside Bay primarily
<i>O. labradoriensis</i>	May 1932 and 1933
<i>O. longicauda</i>	August-September 1929. Outside Bay
<i>Salpa fusiformis</i>	November 1930. Outside Bay
<i>Thalia democratica</i>	Aug. 1931; July 1932; Sept. 1934. Outside Bay
Chaetognatha	
<i>Sagitta elegans</i>	January-August
<i>S. enflata</i>	July-December. Outside Bay primarily
<i>S. helenae</i>	November 1932. Outside Bay
<i>S. hispida</i>	October 1932-January 1933. Outside Bay
<i>S. minima</i>	November 1932. Outside Bay
<i>S. serratodentata</i>	Year-round, but not noted in March. Outside Bay primarily
Pteropoda	
<i>Clione limacina</i>	July 1929; May 1930; May, July, Aug. 1932
<i>C. gracilis</i> (?)	September 1932. In Bay
Unidentified gymnosomes	June, July, November 1932. Outside Bay
<i>Creseis virgula</i>	Aug. 1929; Sept. 1931; July, Sept. 1932. Outside Bay
<i>Limacina retroversa</i>	April-July
Heteropoda	
<i>Oxygyrus keraudreni</i>	August 1929; Oct.-Nov. 1930. Outside Bay
Polychaeta	
<i>Autolytus</i> sp.	Jan., Apr.-June, Aug.-Oct. Sporadic
<i>Tomopteris</i> sp.	July 1931; March-May 1932

(cont.)

TABLE III. (cont.)

Species	Period of Occurrence
Coelenterata	
Hydromedusae	Year-round, but not noted in January
<i>Aglantha digitale</i>	February-June
<i>Hybocodon prolifer</i>	February, April
<i>Rathkea octopunctata</i>	May
<i>Obelia</i> sp.	April-July
<i>Stomatoca dinema</i>	August
<i>Nemopsis bachei</i>	June, August-November
<i>Bougainvillea carolinensis</i>	July, September-November
<i>Liripe</i> sp.	September-November
Siphonophora	
<i>Muggiaea kochii</i>	July-January
Agalmids	July 1929; March, August-November 1932
Other siphonophores	August-December
Protozoa	
<i>Acanthometron</i> sp.	August 1929. Outside Bay
<i>Noctiluca</i> sp.	October-December 1930. In Bay primarily
Fish Eggs	Year-round, but not noted in October
Fish Larvae	Year-round, but not noted in February

Copepods

At least 56 different copepods have been recorded, several of which have not been identified to species. Six species were especially abundant, three in and three outside the Bay. In the Bay (see Fig. 7) *Acartia tonsa* was dominant in the surface waters, with *Centropages hamatus* and *Pseudodiaptomus coronatus* second in importance. On occasion during the colder months, *Centropages typicus* entered the Bay in numbers but was unable to maintain itself there due to the lower salinity. Other important forms were *Pseudocalanus minutus*, *Labidocera aestiva*, *Acartia clausi*, *Oithona* spp., *Temora longicornis* and *Paracalanus parvus*. In the surface waters outside the Bay (see Fig. 8) *Centropages typicus* was unquestionably the dominant form, present every month of every year studied, while *Paracalanus parvus* and *Pseudocalanus minutus* were seasonally the next abundant species. *Acartia tonsa*, *Centropages hamatus*, *Calanus finmarchicus*, *Oithona* spp. and *Labidocera aestiva* were of lesser importance. No other species occurred consistently in significant numbers.

At the mouth of the Bay, off Cape May or Cape Henlopen or Overfalls Shoal, the three most important Bay species were usually predominant, although occasionally in winter and spring *Pseudocalanus minutus* and *Centropages typicus* were abundant. North of the mouth of the Bay at the traps off Wild-

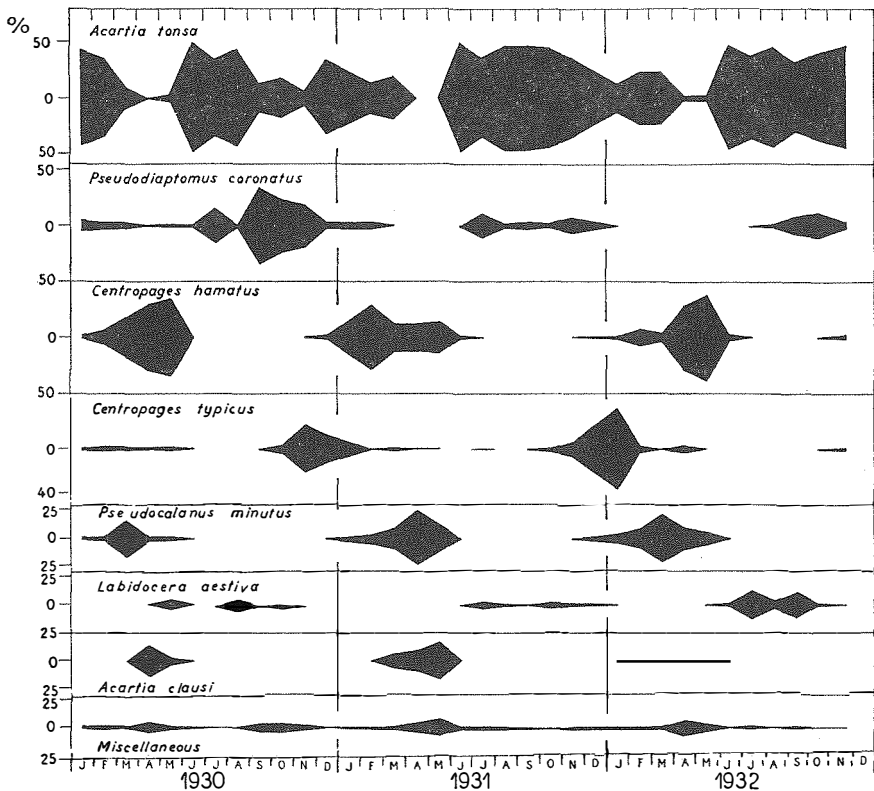


Figure 7. Relative percentages, by count, of the species of copepods found at the stations in Delaware Bay, from January 1930 through December 1932.

wood, an inshore station, *C. typicus* and *A. tonsa* were the dominant species; *C. hamatus* and *P. minutus* were abundant in winter and spring whereas *P. coronatus* and *L. aestiva* were fairly numerous in the fall.

Centropages typicus Krøyer

This is one of the most important forms over the continental shelf from Cape Cod to Chesapeake Bay (Bigelow and Sears, 1939); it also occurs in the Gulf of Maine but has not been recorded north of St. Andrews, New Brunswick (Bigelow, 1926). It is a neritic species, rare outside the continental shelf (Clarke, 1940), but at least off southern New England it does not tolerate salinities lower than $c30\text{‰}$; thus it is predominant only in open coastal waters where it is primarily a surface form (Bigelow, 1926; Deevey, 1952a). The southern limits of its abundance are not known; it may not extend south

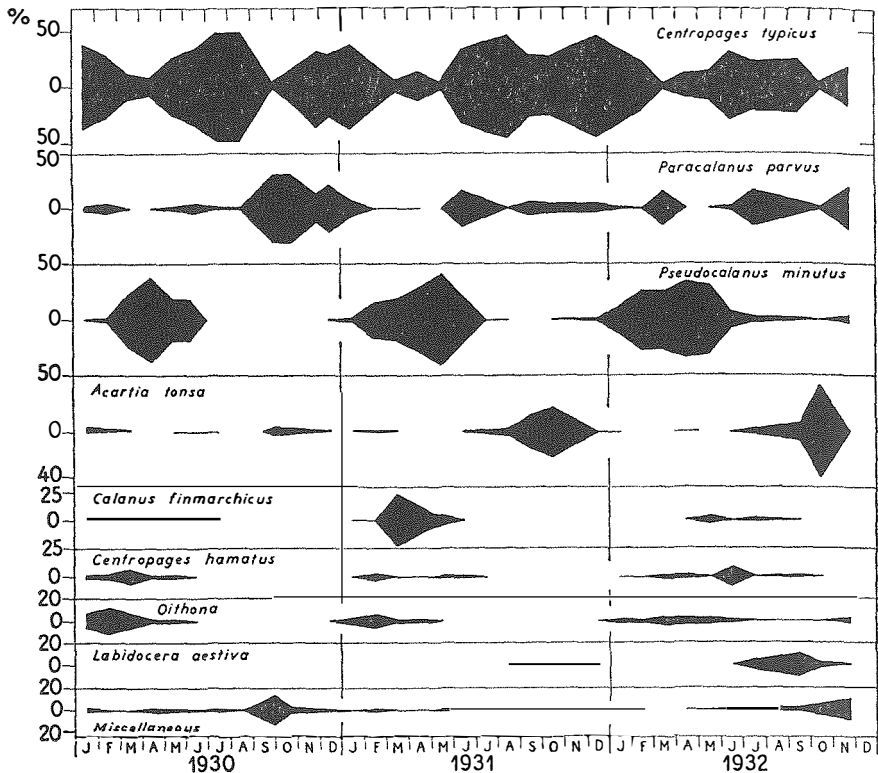


Figure 8. Relative percentages, by count, of the species of copepods found at the stations outside Delaware Bay, from January 1930 through December 1932.

of Cape Hatteras, although Sutcliffe (1950) noted its presence in late winter and spring at Beaufort, North Carolina, and Foster (1904) recorded it from the Louisiana coast. However, unpublished data from the Gulf of Mexico indicate that in these waters *C. furcatus* replaces *C. typicus*. The recorded temperature range of *C. typicus* is 1–24°C (Bigelow, 1926; Deevey, 1952b); in the Delaware Bay region a range of 0–28.35°C was noted.

Comparison of Fig. 9, which gives the total numbers of *C. typicus*, with Fig. 4, which shows the total numbers of zooplankton, reveals the importance of *C. typicus* in the surface waters outside the Bay. No other species occurred in comparable numbers. In general it was most abundant in summer and winter, with minimal numbers during late winter or spring and in the fall. The spring minimum has also been observed over the continental shelf (Bigelow and Sears, 1939) and in Block Island Sound (Deevey, 1952a, 1952b). In 1932, a year of moderate temperatures, *C. typicus* was much less abundant, especially during the summer.

Data obtained from the variations in size and the relative percentages of adults and copepodids indicate that spawning, though possibly more or less continuous, occurred primarily in January or February, in April, during the summer, and in October; and at least five to six generations were produced per year. The data for 1931 are presented in Fig. 10, which shows the relative percentages of stages III–VI as well as the length distribution of stage IV–VI *C. typicus* for representative months plotted as number of individuals measured. Stage III individuals were taken in quantity only in winter and spring; presumably they were too small to be retained by the net during the warmer

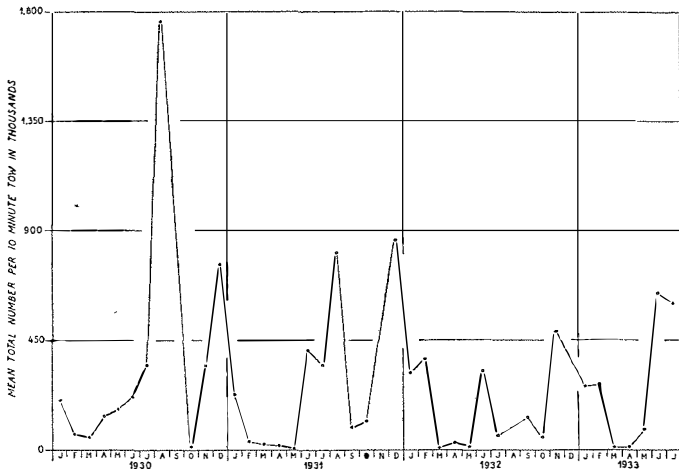


Figure 9. Mean total numbers of *Centropages typicus* per 10 minute tow (in thousands) obtained at the stations outside Delaware Bay, from January 1930 through July 1933.

months. The adult length range was similar from January to April or May during the other years studied, but in 1931 the adults were unusually small in January and February and exceptionally large in April. There was a complete or nearly complete break in length range of females and males between February and April, April and June, June and July, August and October, and October and February 1932 (see Fig. 10). The length range did not vary widely during the summer, but weekly data obtained from June to August 1929 showed that larger females (1.5–1.8 mm) occurred in June; by mid-July the length range was 1.2–1.5 mm, and in August larger females appeared again, the majority 1.5–1.6 mm long. Probably there were several rapidly developing generations during the warmer months. The percentage data shown in Fig. 10 are inadequate, since monthly horizontal tows cannot yield sufficient information, but it is evident that adults were relatively more numerous in February, April, and from July to October. Although only small percentages of adults were noted for June, the length distribution indicates that individuals spawned

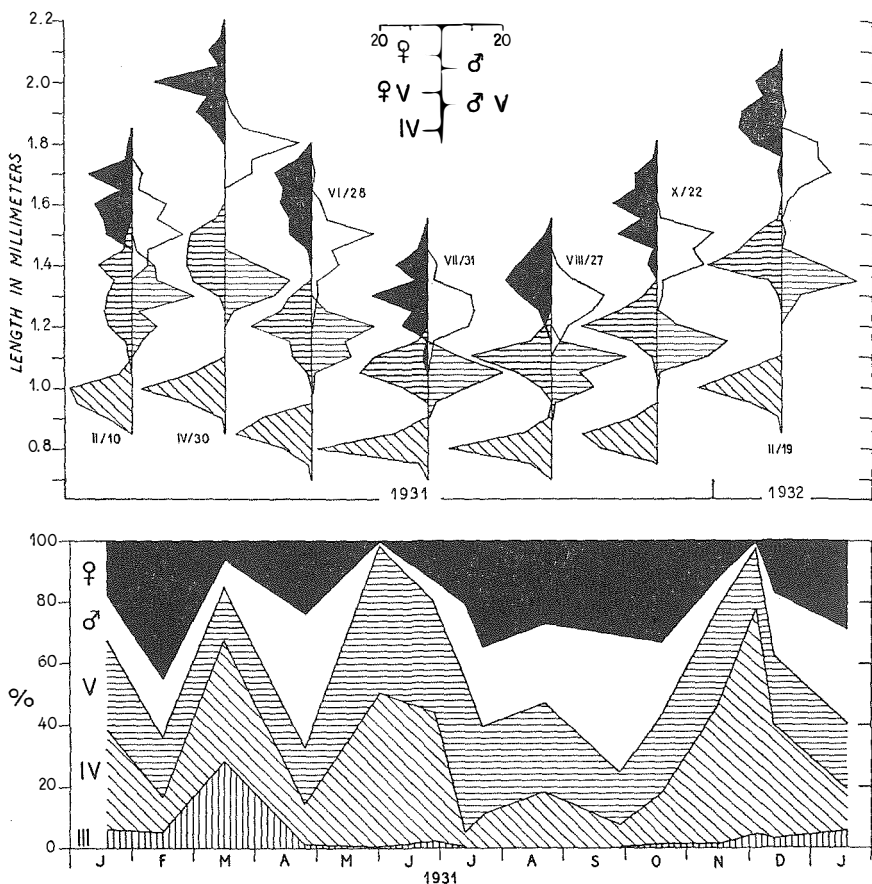


Figure 10. Top: Length distribution, by number, of stages IV-VI *Centropages typicus* on selected dates, from February 1931 through February 1932. In every case 50 specimens of each stage were measured. Bottom: Relative percentages, by count, of stages III-VI *C. typicus* in 1931.

in April had matured and in turn had produced the small July generation. Twice during the year, in late spring and late fall of 1929-1931, few adults were found and the *C. typicus* population was represented almost entirely by immature stages. Apparently adults do not live longer than several months, possibly up to four months in the winter but to no more than two months in the summer.

Centropages hamatus (Lilljeborg)

This is a relatively euryhaline boreal and temperate species which occurs primarily in sheltered or inshore waters. On the eastern American coast its range extends from the Straits of Belle Isle (Pinhey, 1926) to the Gulf of

Mexico. At Beaufort, N.C. it was recorded from December to April (Sutcliffe, 1950). A similar period of occurrence was noted by Grice (1956) for Alligator Harbor, Florida, where *C. hamatus* was found from November to April over a temperature range of 9.0–22.3°C. For Delaware Bay the range noted was –0.65 to 23.9°C.

C. hamatus was much more abundant in the surface waters of Delaware Bay than it was outside (see Figs. 7, 8). The mean total numbers found in the Bay are shown in Fig. 11. In general it was most numerous from February to May and occurred in greatest numbers in 1933. In 1930 it was present from January to July and in December, but it was recorded throughout the year in 1932, and in 1931 it was absent only in October. From June onward, as the temperatures in the Bay exceeded those outside, *C. hamatus* was more numerous outside, where the largest numbers noted were 100,000/10 minute tow in June 1932 and 1933.

C. hamatus exhibited a marked variation in size during the year. The length distributions of males and females on selected dates are shown in Fig. 12. The largest adults were found from January to April and the smallest during the summer. Usually adults of intermediate size were noted for May. In 1930 there was an abrupt decrease in size between March and April whereas in

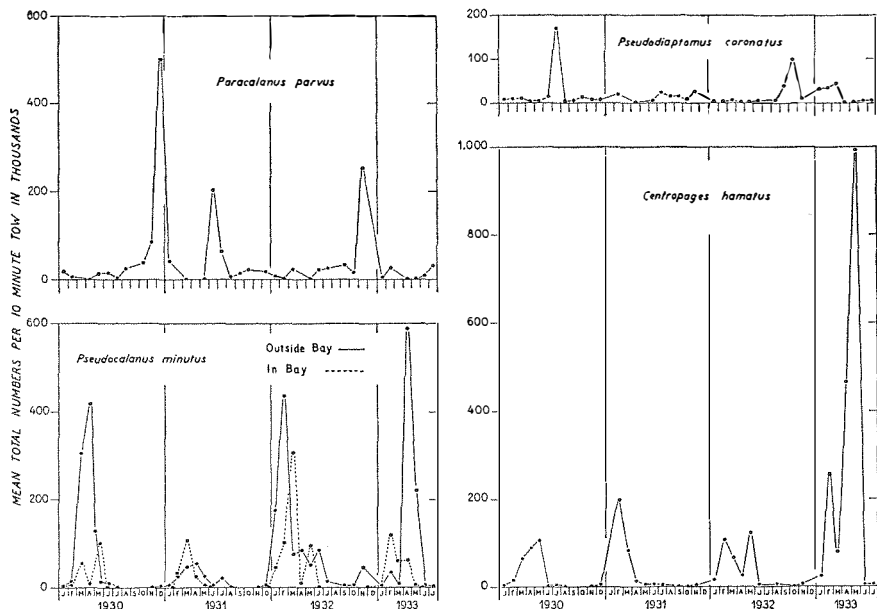


Figure 11. Mean total numbers per 10 minute tow (in thousands) of *Paracalanus parvus* outside the Bay, *Pseudodiaptomus coronatus* and *Centropages hamatus* in the Bay, and *Pseudocalanus minutus*, from January 1930 through July 1933. All drawn to same scale.

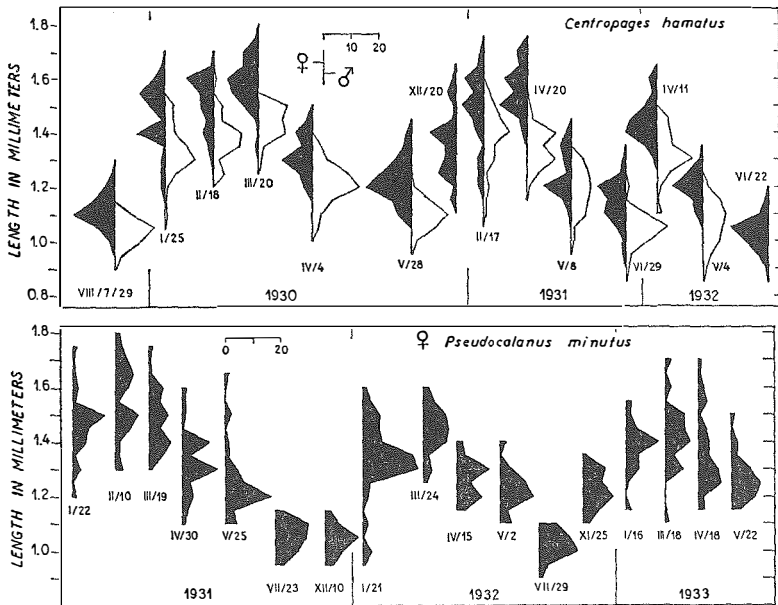


Figure 12. Length distributions, plotted as number measured, of female and male *Centropages hamatus* in the Bay and of female *Pseudocalanus minutus* outside the Bay on selected dates.

1931 to 1933 this sudden decrease occurred between April and May. These data together with those for the relative percentages of immature stages and adults show that there were at least three generations during the year, spawning occurring primarily from January to March, in late May, and from late June to July. Females with spermatophores were noted every month from January to July. During summer and fall the occasional specimens obtained were adults, small in size. In late fall, late-stage copepodids appeared, and by December 1930 or January 1931 and 1932 large adults were present and total numbers were increasing. There was evidence of spawning at this time, but the data are not sufficient to show a separate January generation, since in January *C. hamatus* was less numerous in the Bay than it was outside. By March of each year the relative percentages of adults were high and spawning undoubtedly occurred. In February and April of each year, stages III–V were relatively most numerous. Stage III copepodids were found only from February to May and, as in the case of *C. typicus*, presumably they were too small by June to be retained by the net. By April 1930 and May 1931–1933 (see Fig. 12) intermediate-sized adults appeared and must have produced the late June–July generation of small adults. In June the center of abundance shifted from the Bay to the surface waters outside, but evidence for the small generation in the Bay was obtained for August 1929 and late June 1932.

Pseudocalanus minutus (Krøyer)

P. minutus, an arctic to temperate neritic and euryhaline species, recorded on the American Atlantic coast from the Straits of Belle Isle to just north of Cape Hatteras, was an important winter to spring form both outside and in the Bay (see Figs. 7, 8), although it was more abundant and occurred for a longer period outside the Bay. The mean total numbers recorded for *P. minutus* are shown in Fig. 11. In 1930 and 1932 it was present in the surface waters outside the Bay throughout the year; in 1931 it disappeared in July and reappeared in December. Maximal numbers were found in March and April 1930, April 1931 and 1933, and February 1932. In the Bay it occurred from January to July in 1930 and 1931 and from January to May in 1932 and 1933. It was most numerous in March and May 1930 and 1932, March 1931, and February 1933. The temperature range noted was identical with that of *Centropages hamatus*, -0.65 to 23.9°C .

Reproduction was probably more or less continuous during winter and spring since females with eggs were noted every month from January to June. Fig. 12 shows the length distribution of females on selected dates. The annual cycle in length variations is similar to that of *C. hamatus*, and it is probable that spawning periods also occurred concurrently. The greatest mean length was found for January to March. Intermediate-sized adults were present in April and May and small adults were noted from June into the fall. In 1931 females were the same size in December and in July, but in 1932 there was a complete break in size between July and November (see Fig. 12). Thus the available data suggest winter, spring and early summer generations outside the Bay. Possibly, between late November and March, two generations were produced, but if so the data are inadequate to separate them. In the Bay only the winter and spring generations were found.

Acartia tonsa Dana

On the North American coast this euryhaline eurythermal species occurs from Miramichi Bay on the Gulf of St. Lawrence (Willey, 1923) to Biscayne Bay, Florida and the Gulf of Mexico, primarily in sheltered waters where it is a dominant species. The greatest recorded salinity range, $4.6-35.4$ ‰, was noted by Sutcliffe (1950) in Bogue and Pamlico Sounds, North Carolina, where *A. tonsa* is dominant. In Delaware Bay it was present at temperatures ranging from -0.65 to 28.35°C ; Grice (1956) has recorded a range of $9.0-31.8^{\circ}$ for *A. tonsa* in Alligator Harbor and Woodmansee (1958) a range of $15.6-32.0^{\circ}$ in Biscayne Bay, Florida; obviously, this species has an exceptionally wide temperature range.

In Delaware Bay it was unquestionably the most important species, and it was also numerous on occasion outside the Bay (see Figs. 7, 8). Fig. 13 shows the mean total numbers taken in the Bay. As in the case of *Centropages typicus*,

A. tonsa was present the year around, with a spring minimum. In 1931 and 1933 it was not observed in April. In 1930 and 1931 maximal numbers were found in June and July, but in 1932 it was most numerous in late summer and fall; secondary maxima occurred during winter. Hydromedusae and ctenophores were abundant in the late summer and fall of 1930 and may have brought about the decrease in its numbers at this time. *A. tonsa* was relatively abundant during the fall of 1931 and 1932.

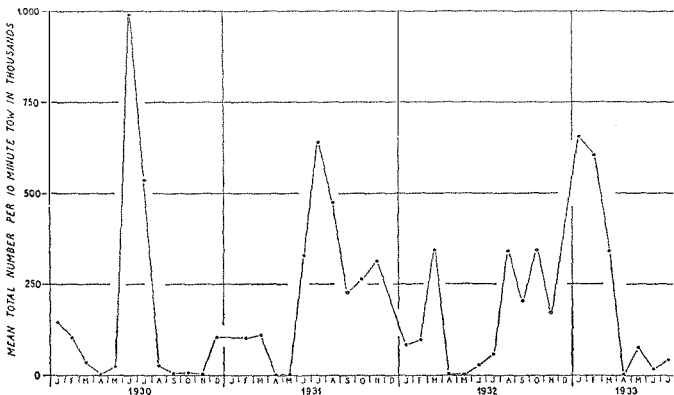


Figure 13. Mean total numbers per 10 minute tow (in thousands) of *Acartia tonsa* in Delaware Bay, from January 1930 through July 1933.

The length ranges of males and females on selected dates as well as the relative percentages of adults and immature stages of *A. tonsa* and *Pseudodiaptomus coronatus* are shown in Fig. 14. The percentage data illustrated for *A. tonsa* cover the period from late May 1931 to June 1932 and serve only to give a general picture of the seasonal cycle, since monthly horizontal tows cannot yield adequate information. The preponderance of adults during the summer months may be explained by the fact that *A. tonsa* was smaller at this time and that the immature stages were less readily retained by the net. The percentage and length range data together suggest that probably four generations were produced at approximately monthly intervals between May and September; in 1932, for example, the length range data indicate separate broods of adults in June, July, August and September (see Fig. 14). For 1931 the percentage data show relatively numerous adults in early October, high percentages of immature stages from November to January, and increasing numbers of adults in March. The offspring of the fall generation apparently develop slowly during the winter. In March 1932, total numbers of adults had increased to 250,000/10 minute tow, but by mid-April the total numbers of all stages had decreased to 2250; in May the numbers were still minimal and the *A. tonsa* population was represented almost entirely by immature stages.

Adults that matured during the winter apparently die at the time of the spring minimum, since in 1931 and 1932 there was a sharp break in the size of the March or April adults compared to those present in June. The virtual absence of *A. tonsa* in April and May may be partially explained by the fact that the net would not have caught the early stages. However, this species also occurs in minimal numbers in spring in Long Island Sound (Conover, 1956; Deevey, 1956), where more extensive sampling of the entire water column with finer-meshed nets has shown that the *A. tonsa* population is at its lowest ebb at this time. Thus it is probable that there were at least five to six generations per year in Delaware Bay: three to four rapidly developing generations during summer, a fall generation, and a winter generation. Since the length range remained similar from January to March and since abrupt changes in the percentage composition of the population were not noted, there is no evidence for separate generations in early and late winter. In Long Island Sound, Conover (1956) recognized four generations per year between June and March: in late July, September, late October, and December to January. This cycle differs from that suggested for Delaware Bay only in that one or two generations more are postulated for the summer months in the Bay. Although winter temperatures appear to be fairly similar in these two bodies

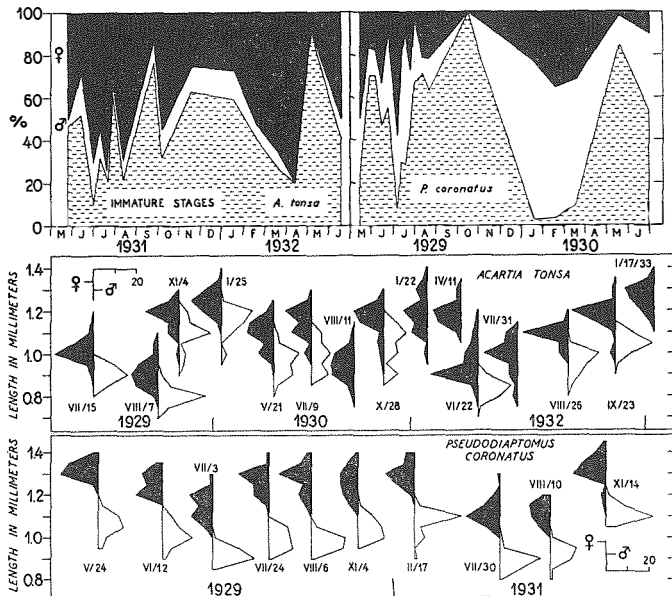


Figure 14. Top: The relative percentages of females, males and immature stages of *Acartia tonsa* from May 1931 through June 1932 and of *Pseudodiaptomus coronatus* from May 1929 through June 1930. Bottom: Length distributions, plotted as number measured, of female and male *A. tonsa* and *P. coronatus* on selected dates.

of water, the summer temperatures recorded for the periods studied were slightly higher in the surface waters of Delaware Bay than in Long Island Sound (cf. Fig. 2 with Riley, 1956; fig. 1), and this may explain the apparently more rapidly developing generations in the Bay. In Biscayne Bay, Woodmansee (1958) found about 11 generations/year at mean temperatures ranging from 20.6 to 30.6°C.

Pseudodiaptomus coronatus Williams

This euryhaline species, recorded from Miramichi estuary on the Gulf of St. Lawrence to the Gulf of Mexico, occurred primarily from summer to winter in Delaware Bay (see Fig. 7) and was rarely found at the stations outside. It was obtained in highest numbers at Overfalls Shoal at the mouth of the Bay during the summer of 1929, when maximal numbers of nearly $2\frac{1}{2}$ million per 10 minute tow were recorded in late June. Its cycle of abundance varied from year to year, but it always occurred in minimal numbers in April and May (see Fig. 11). Thus its seasonal cycle was similar to that of *Acartia tonsa* and *Centropages typicus*. Its recorded temperature range was -0.65 to 25.3°C in Delaware Bay; Grice (1956) noted a range of 13.0-31.8°C for it in Alligator Harbor, Florida.

Females with egg sacs were observed every month from late May to November, but not during any one year, so reproduction probably occurs fairly continuously during this period. There is some evidence that the females prefer deeper waters; frequently few females were found at the surface when males and immature stages were present. Possibly the major part of the *P. coronatus* population remained well below the surface; this would explain why the total numbers found from 1930 to 1933 were so small compared with those obtained in 1929 when hauls were made at various depths. Data obtained from the relative percentages of adults and immature stages for May 1929 to June 1930 (see Fig. 14) indicate that probably five generations were produced during the year. Spawning occurred primarily in late May, early July, and mid-August, with secondary periods in mid-June and late July. By mid-October only immature stages were found, but in November males as well as females with egg sacs were present, the progeny of this group maturing during the period from January to March 1930. Spawning again occurred in February or March. During April and May, *P. coronatus* virtually disappeared; by late May the majority of specimens were immature, but females with spermatophores and egg sacs were present. By June more adults had matured.

P. coronatus did not vary greatly in size during the year (see Fig. 14). There was an incomplete break in length range between late May and early July and between early July and August 1929. In 1931 there was also a break in size between winter and summer and between August and November. These fragmentary data bear out the suggested cycle of generations.

Paracalanus

P. parvus (Claus) is a cosmopolitan, tropical and temperate, oceanic and neritic species whose range on the North American Atlantic coast extends southward from the Gulf of Maine. Although this species has been recorded at salinities ranging from 19.33–40.0 ‰ (Bigelow, 1926) and from 14.8–35.1 ‰ (Woodmansee, 1958), it is not an important form in the coastal waters of southern New England. It has been recorded from Woods Hole, Massachusetts (Fish, 1925; Clarke and Zinn, 1937), but it does not occur in Long Island Sound (Deevey, 1956), and no more than 1,000/m³ have been taken in Block Island Sound (Deevey, 1952a). Large volumes of this species were found on relatively rare occasions over the continental shelf from Cape Cod to Chesapeake Bay (Bigelow and Sears, 1939), so *P. parvus* may not be as abundant in this general region as it probably is farther south. In the Delaware Bay region it occurs in numbers only outside the Bay, although it was sometimes observed at stations in the Bay (see Fig. 8).

In general its seasonal cycle resembled that of *Acartia tonsa*, since minimal numbers were found in the spring (see Fig. 11). It was most abundant in December 1930 (500,000/10 minute tow), in June 1931 (200,000/10 minute tow), and November 1932 (250,000/10 minute tow). During most of the period studied, mean total numbers did not exceed 25,000/10 minute tow, but it may have been more numerous than these figures indicate, since a smaller proportion of the total numbers would have been caught because of its relatively small size. Length measurements were not made on this species, and not enough data are available to discuss the number of generations per year. The temperature range noted was 0.85–25.3°C.

P. crassirostris Dahl was noted on numerous occasions, especially from summer to winter, both in and outside the Bay, but it was too small to be taken unless the net were clogged. It is an important form in Long Island Sound (Deevey, 1956) where it occurs for the greater part of the year, with a spring minimum; it may also prove to be numerous in the Delaware Bay region, where it was present at temperatures of 1.95–26.65°C.

Labidocera aestiva Wheeler

L. aestiva is an American species, known from the Gulf of St. Lawrence to the Gulf of Mexico. It is the largest euryhaline copepod found in open inshore and sheltered less saline waters along the northeast Atlantic coast. Although it occurs regularly from early summer to early winter from Cape Cod to Chesapeake Bay, it has not been recorded as abundant or as a dominant species of any area yet studied. Few quantitative data are available; the highest total number obtained in Long Island Sound (Deevey, 1956) was 920/m³ in September, but usually fewer than 100/m³ were taken. In Alligator Harbor, Florida, where this species occurred from April to September and in De-

ember, the highest number, 1,990/m³, was recorded for mid-September (Grice, 1956). In the Delaware Bay region adults were found at temperatures of 12.8–26.65°C, but immature stages were noted at temperatures down to 5.85°; in Alligator Harbor the recorded range was 11.5–31.8°.

L. aestiva was found in and outside Delaware Bay (see Figs. 7, 8), on occasion constituting 25 % of the total population. As a rule, it appeared first and was more numerous in the Bay, but later in the summer it was more abundant outside. Usually it was found in the Bay in May and outside by June, where it occurred until November to January. Except for 1930, when 37,000/10 minute tow were obtained in the Bay during May, highest numbers were found from July to October. The highest total recorded was 64,000/10 minute tow for September 1932.

Since the center of abundance usually shifted from the Bay to the waters outside during the summer and since it is not known whether these were separate populations, the data for the number of generations are fragmentary. Also, immature stages were predominant in the surface waters during most of the period studied. However, there were indications that spawning may have occurred in late spring, summer and fall in the Bay and in summer and fall outside. The seasonal cycle in the Bay is best illustrated by the length range data for 1930 (see Fig. 15), when the relative percentages of adults were fairly high in late May, late July and late October. The late May adults must have produced the individuals that matured in late July; the relative

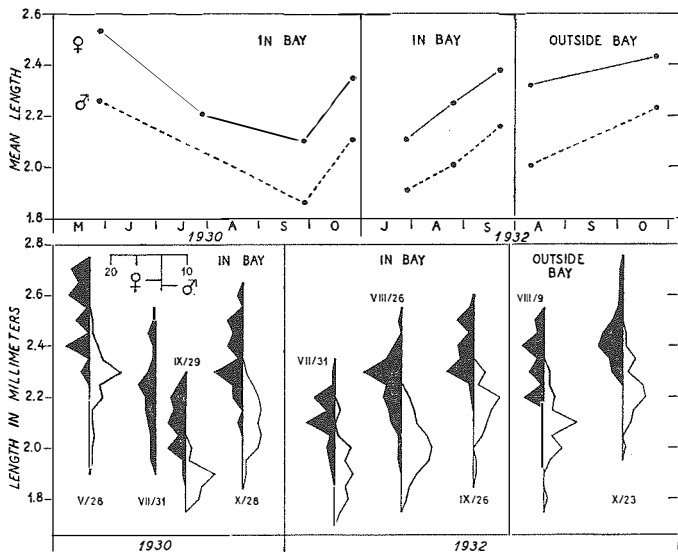


Figure 15. Variations in length of *Labidocera aestiva*. Top: Mean lengths of females and males. Bottom: Length distributions of females and males on the same dates.

percentages of adults were high from late July to late August 1931 and 1932, so spawning must be fairly continuous during the summer. The relatively small adults found in late September 1930 (see Fig. 15) were probably spawned in late July or early August whereas the larger late October adults may have been produced later in the summer. Presumably the offspring of the fall generation do not mature until the following year. Length measurements of adults obtained for late July to late September 1932 show a monthly increase in size as well as an almost complete break in size between the late July and late September females. Outside the Bay the relative percentages of adults were high from late July to early August and in September to October 1929 and 1932. Between early August and late October 1932 (see Fig. 15) there was a slight increase in size, the length range data thus indicating the probability of two generations.

Calanus finmarchicus (Gunner)

Although this is one of the most important species over the continental shelf from Cape Cod to Chesapeake Bay, where it was most abundant from April to early August (Bigelow and Sears, 1939), outside Delaware Bay it usually occurred in relatively small numbers from January to July or August (see Fig. 8). Largest numbers were found for April, May and July 1930, and for March and April 1931 when the highest recorded number (148,000/10 minute tow) was obtained at Five Fathom Bank. In 1932 it was less numerous and did not appear until March; in 1933 numbers were maximal in May. It was recorded occasionally, though never in abundance, in the Bay. Females were noted for March through May and for July and August, but most of the individuals observed were immature. Presumably *Calanus* spreads down the coast in the winter from its center of abundance north and east of this region.

C. helgolandicus was not observed at any time during the period studied.

Acartia clausi Giesbrecht

On the American coast this boreal-temperate species has been recorded from the St. Lawrence River to Cape Hatteras. Bigelow (1926) found it widespread over the Gulf of Maine, but south of Cape Cod it is confined to less saline or inshore waters, since it was recorded only once over the continental shelf (Bigelow and Sears, 1939). In sheltered waters off southern New England, such as Long Island Sound (Conover, 1956; Deevey, 1956), it is a dominant winter to spring species. Although Wilson (1932a) reported that *A. clausi* was the dominant species in Chesapeake Bay in 1915 to 1916 and 1920 to 1921, Davis (1944) later found *A. tonsa* more abundant there. Since by 1930 *A. tonsa* was dominant at least in the surface waters of Delaware Bay, it may be that this species is replacing *A. clausi* at the southern limits

of the latter's range. *A. clausi* has a wide salinity and temperature tolerance; in Tisbury Great Pond, Massachusetts (Deevey, 1948) it was present at salinities ranging from less than 1 to 31 ‰ and at temperatures of 0–24°C.

In Delaware Bay *A. clausi* occurred regularly from February or March to May or June and was most abundant during the period of *A. tonsa*'s seasonal minimum (see Fig. 7). As a rule numbers did not exceed 40,000 at any station and were usually less than 10,000/10 minute tow; however, for April and May 1933, up to 210,000/10 minute tow were recorded, so considerable fluctuation in numbers may occur from year to year.

Temora longicornis Müller

This is a boreal-temperate euryhaline neritic species whose range on the American coast extends from the Straits of Belle Isle (Pinhey, 1926) south to Cape Hatteras. *T. longicornis* is widespread over the Gulf of Maine (Bigelow, 1926) and has been found out to the edge of the continental shelf south of Cape Cod (Bigelow and Sears, 1939), although it was more numerous inshore. In Block Island Sound it occurred for most of the year, in largest numbers in late spring or early summer, but in Long Island Sound where summer temperatures are higher it was found from November to early August.

On the basis of these collections, *T. longicornis* was not an important species in the surface waters of the Delaware Bay region. In 1930 and 1931 it was found from January or February to July or August, more consistently outside the Bay, but in 1932 and 1933 it was present only from April to July. Largest numbers were obtained in June and July 1929, usually at depths of four fathoms or more, outside and at the mouth of the Bay. Evidence that by early summer *Temora* prefers the deeper levels was obtained on a number of occasions. In mid-June 1929 over 780,000/10 minute tow were taken at 4–5 fathoms depth at Five Fathom Bank while the surface tow yielded only 6,000. Similarly, on July 1, 309,000/10 minute tow were obtained at 5–6 fathoms depth west of Five Fathom Lightship, but only 2,400 were collected at the surface. This preference for deeper waters, at least during the warmer months, suggests that *Temora* may have been more abundant in these waters than is indicated by the surface samples collected from 1930–1933.

Oithona

Species of *Oithona* were present throughout the year. These include in particular *O. similis* Claus and *O. spinirostris* Claus. *O. brevicornis* Giesbrecht was noted occasionally, usually in the Bay, and in all probability it was numerous there. *O. plumifera* Baird appeared in the fall of 1930 and 1932 with other warm water forms. All of these species, especially *O. brevicornis*, are too small to have been retained by the net in their true proportion. In other areas, such

as the Gulf of Maine (Fish, 1936), *O. similis* is of considerable importance. In Block Island Sound (Deevey, 1952a) it occurred throughout the year in greater numbers than any other copepod.

In the Delaware Bay region, species of *Oithona* were most numerous the first half of the year (see Fig. 8), especially outside the Bay. *O. similis* occurred for the greater part of the year, but it was not taken consistently in summer and fall. *O. spinirostris* was found primarily outside the Bay from January or February to early summer, although it remained until August during the cooler summer of 1932. *Oithona* spp. were undoubtedly far more abundant than this survey indicates.

Other Copepods

The remaining copepods include: 1) warm water forms which occurred primarily outside the Bay in summer and fall; 2) relatively rare boreal or temperate species; 3) brackish-water species; and 4) parasitic forms. The periods of occurrence of these species are listed in Table II.

The southern forms recorded were *Acartia danae*, *Calanus minor*, *Calocalanus pavo*, *Centropages bradyi*, *C. furcatus*, *Clytemnestra rostrata*, *Corycaeus americanus*, *C. amazonicus*, *C. giesbrechti*, *C. latus*, *C. speciosus*, *Copilia mirabilis*, *Eucalanus attenuatus*, *E. pileatus-subcrassus*, *Euchaeta marina*, *Euterpina acutifrons*, *Farranula carinata*, *Mecynocera clausi*, *Oithona plumifera*, *Oncaea media*, *O. venusta*, *Sapphirina* sp., *Temora stylifera*, *T. turbinata*, and *Scolecithrix danae*. Some of these, *Acartia danae*, *Calocalanus pavo*, *Centropages bradyi*, *Copilia mirabilis*, *Corycaeus latus* and *C. speciosus* were found only during July or August 1929. *Centropages furcatus*, *Eucalanus attenuatus*, *Euchaeta marina* and *Scolecithrix danae* were observed only in the fall of 1930. *Calanus minor* and *Oncaea venusta* were the only warm water copepods recorded in the fall of 1931. The southern forms that appeared most consistently were corycaeids and oncaeids, *Calanus minor*, *Eucalanus pileatus-subcrassus* and *Temora stylifera*.

Oncaea media and *Euterpina acutifrons* may not have been previously recorded north of Cape Hatteras, since they are not listed by Wilson (1932a, 1932b) or by Bigelow and Sears (1939). *Centropages furcatus* was noted as an offshore stray south of the Delaware Bay region (Bigelow and Sears); its occurrence from late September to November 1930 in and outside the Bay is probably the northernmost record for this species. Most of the other warm water forms listed have been recorded north of Cape Hatteras, but in the case of the corycaeids, confusion has arisen due to faulty identification. *Corycaeus amazonicus* F. Dahl and *C. americanus* M. S. Wilson occurred most commonly in the Bay region, but the latter was found later in the winter, being present in January and February 1933; on the other hand, *C. amazonicus* was not recorded after December. These two species have been found together in

inshore waters of the Gulf of Mexico and at Beaufort, North Carolina (M. S. Wilson, 1949). According to M. S. Wilson, the species listed by C. B. Wilson (1932a) from Chesapeake Bay as *C. lubbocki* Giesbrecht was *C. americanus*; thus the distribution of this species was known to extend from the Gulf of Mexico to Chesapeake Bay; on the other hand, *C. amazonicus* has not been recorded north of Cape Hatteras until now. *C. giesbrechti* F. Dahl may not have been noted on this coast previously, but it was fairly common in the Bay region, occurring during the period from August to November. A re-examination of the October 1949 sample from Block Island Sound (Deevey, 1952a) yielded the following species of corycaeids: *C. clausi* F. Dahl, *C. speciosus* Dana, *C. amazonicus*, *C. americanus*, and *C. giesbrechti*. Thus the range of the last three species extends north almost to Cape Cod. *C. latus* Dana, found only in August 1929 outside Delaware Bay, has apparently not been recorded from the Atlantic coast north of Cape Hatteras.

Several boreal or temperate species were occasionally observed. *Anomalocera pattersonii* Templeton was noted only in June and October 1929, and *Metridia lucens* Boeck was found in May 1930 and July and August 1932; these are primarily offshore boreal species, but according to Bigelow and Sears, *M. lucens* is more common than *A. pattersonii* over the continental shelf south of Cape Cod. *Candacia armata* (Boeck), an offshore temperate copepod, occurred every summer or fall from 1929-1932, the highest numbers (10,200/10 minute tow) being obtained at Five Fathom Bank in August 1929. *Acartia longiremis* (Lilljeborg) was found only from January to May 1931. Although Wilson (1932a) reported that this species was abundant in Chesapeake Bay in 1915 to 1916 and 1920 to 1921, by 1930 it was not a regular member of the plankton of the Delaware Bay region unless it was confined to the deeper waters. *Tortanus discaudatus* (Thompson and Scott), a North American boreal euryhaline species, has never been found numerous south or west of southern New England. Its occurrence in late spring 1929 and 1932 outside and at the mouth of Delaware Bay may be the southernmost record for this species, since it was not listed for Chesapeake Bay or for the continental shelf south of Cape Cod.

Two brackish water copepods, both species of *Eurytemora*, were found in the Bay. *E. americana* Williams, known only from Cape Cod to Chesapeake Bay, was obtained in January, May and June. The other species, previously identified as *E. hirundoides* from Tisbury Great Pond (Deevey, 1948), is probably a variety of *E. affinis* according to M. S. Wilson, who has recently examined specimens from the above mentioned locality. *E. affinis* occurred in the spring from March to May.

Parasitic copepods were obtained on rare occasions. Species of *Caligus* were noted at various times from July to September 1931-1933. *Mycicola major* (Williams) was taken in September 1931 and *Monstrilla* sp. was observed in July 1931.

Cladocera

An interesting variety of marine Cladocera was found: *Penilia avirostris* Dana, *Evadne nordmanni* Loven, *E. spinifera* Müller, *E. tergestina* Claus, *Podon intermedius* Lilljeborg, and *P. polyphemoides* (Leuckart). *Daphnia* sp. was also noted outside the Bay for February 1931. Although most of these species are known to be euryhaline, the Cladocera were numerous only outside the Bay (see Fig. 6) and were rarely found at the stations inside. Since these are small species, probably only a fraction of the total number was retained by the meter net.

Penilia occurred consistently from July or August to October or November every year and was the most abundant cladoceran (see Fig. 16). Highest numbers of over 800,000/10 minute tow at individual stations were obtained

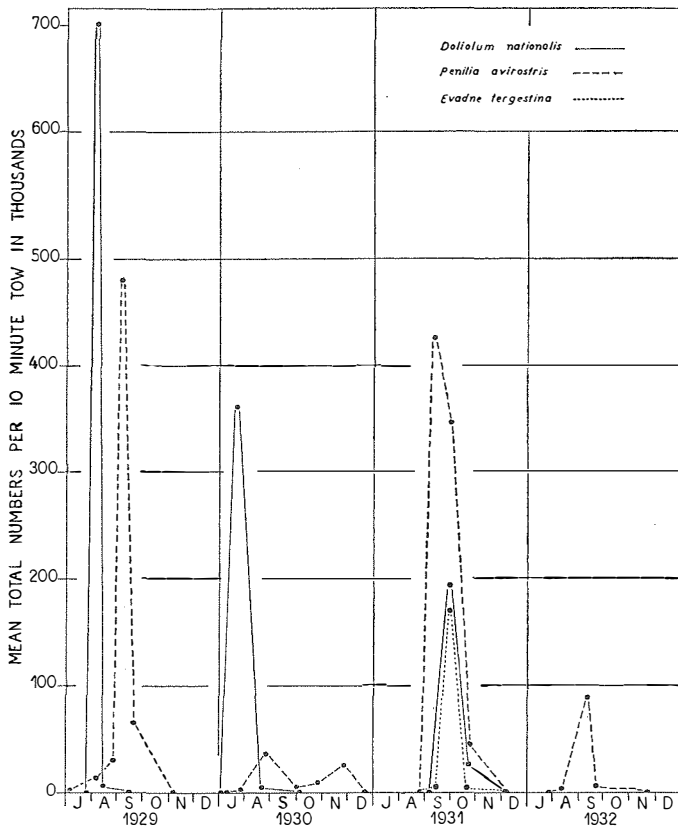


Figure 16. Mean total numbers per 10 minute tow (in thousands) of *Doliolum nationalis*, *Penilia avirostris*, and *Evadne tergestina*, from July to December, 1929-1932.

in September 1929 and 1931. A similar period of occurrence has been found in Long Island Sound and Block Island Sound. On this coast it has not been recorded farther north than these localities and Woods Hole, Massachusetts (Lochhead, 1954). The distribution and biology of this species have been discussed by Della Croce (1958) and Lochhead.

Evadne spinifera and *E. tergestina* are warm water forms. *E. spinifera* was found only in August and September 1929, but *E. tergestina* occurred at some time between July and October each year. According to Baker (1938), the latter species is more or less limited to equatorial regions. It occurs in the Gulf of Mexico, but although Fish (1925) found it at Woods Hole, Massachusetts, it was not observed in Long Island Sound or Block Island Sound. *E. tergestina* was most numerous in September 1931 when mean numbers of nearly 170,000/10 minute tow were obtained (see Fig. 16).

E. nordmanni occurred during the period from May to July outside the Bay each year except 1930. This species is relatively numerous in Block Island Sound and Long Island Sound, but Delaware Bay may be the southernmost region from which it has been recorded on the Atlantic coast. It was most abundant in June 1929, when highest numbers of over 500,000/10 minute tow were obtained at Five Fathom Bank. Only small numbers were found during the rest of the period studied.

Podon polyphemoides was noted only from May to July 1929 and in July 1932 whereas *P. intermedius* was found in August 1929 and September and October 1931. The geographical distribution of *P. polyphemoides* is similar to that of *E. nordmanni*, except that Sutcliffe (1950) has recorded *P. polyphemoides* for Pamlico Sound, North Carolina.

Tunicates

Pelagic tunicates occurred seasonally in appreciable numbers outside the Bay (see Fig. 6). The following species were obtained: *Fritillaria borealis* Lohmann, *Oikopleura dioica* Fol, *O. labradoriensis* Lohmann, *O. longicauda* Vogt, *Doliolum nationalis* Borgert, *Dolioletta gegenbauri* (Uljanin), *Salpa fusiformis* Cuvier, and *Thalia democratica* (Forskål). *Fritillaria borealis* was found only in April and May 1932 and May 1933; in early May 1932 over 270,000/10 minute tow were taken at Five Fathom Bank. *Oikopleura labradoriensis* was also noted for May 1932 and 1933, but it was not numerous. The warm water forms occurred during the period from July to November. *O. longicauda* was observed in August and September 1929, although its presence may have been overlooked on other occasions, and *Salpa fusiformis* was found only in November 1930. *Thalia democratica* appeared infrequently, in August 1931, July 1932 and September 1934, but on the latter date it was exceedingly abundant; the 10 minute tow at McCries Shoal yielded 11 quarts of *Thalia* while over a bushel was obtained at South Ground. Over

90 % of the specimens were aggregated zooids, but a few solitary zooids were present. Since only a quart was saved from each of these samples, the number per 10 minute tow could not be estimated.

Oikopleura dioica and *Doliolum nationalis* were the two tunicates which appeared regularly each summer or fall, usually during the same period. *Doliolletta gegenbauri* was found only in October and November 1932. *O. dioica* occurred from July to September 1929 and 1932, July to October 1930, and August to November 1931. Estimated numbers were small, but this is a small species and undoubtedly was fairly abundant. The highest mean number, 38,850/10 minute tow, was obtained in October 1931. *D. nationalis* was found from July to September 1929 and 1932, July and August 1930, and September and October 1931. Fewer were noted in 1932, but from 1929-1931 maximal numbers of over 400,000 to over 800,000/10 minute tow were taken at individual stations. Fig. 16 shows the mean total numbers obtained. The doliolids and salps occurred only at the mouth and outside the Bay, but appendicularians were also found in the Bay.

Coelenterates

Hydromedusae were taken during the greater part of the year, in largest numbers in spring or fall (see Figs. 5, 6). They were especially abundant in the fall of 1930 when the highest number (156,700/10 minute tow) was obtained at South Ground in late October. The maximal number recorded for the Bay, 68,400/10 minute tow, was found off Broadkill Creek in late September. Not all the species were identified. The winter to spring species included *Aglantha digitale*, an arctic-boreal form, and *Hybocodon prolifer*. *A. digitale* was most numerous in 1930, when it occurred from February to June. *Rathkea octopunctata* was noted in the spring, and *Obelia* sp. from April to July. *Stomatoca dinema* was observed only in the summer. Species present during summer and fall included *Nemopsis bachei* and *Bougainvillea* sp., probably *B. carolinensis*; these forms were found from June or July to November. *Liriope* spp. occurred from September to November. At least two species were present, and these were tentatively identified as *L. scutigera* and *L. catharinensis*.

Siphonophores were obtained on occasion during the second half of the year; they were most numerous from September to December in 1931 and 1932. In November 1931, 44,000/10 minute tow were taken in the Bay at Old Bare Shoal, but in 1932 the highest number (20,400) was found outside the Bay off Townsend Inlet. *Muggiaea kochii* was the commonest form and in various years it was noted at some time during the period from July to January. Agalmids were noted for July 1929 and for March, August, September and November 1932. Other siphonophores were represented by fragments such as floats, bracts, bells, etc., which were not identified; these appeared from August to December.

Chaetognaths

Chaetognaths were more numerous in 1930 and 1931 than in 1932 and 1933 (see Figs. 5, 6). *Sagitta elegans*, *S. serratodentata*, and *S. enflata* occurred regularly every year. Three other species appeared briefly outside the Bay: *S. hispida* in October and November 1932 and January 1933 and *S. helena* and *S. minima* in November 1932. *S. hispida* and *S. helena* are common on the west coast of Florida (Pierce, 1951), and the latter species also occurs over the continental shelf off North Carolina (Pierce, 1953) although the former was not recorded there. Pierce found *S. minima* most abundant at the outer edge of the continental shelf. Apparently there is no previous record for the occurrence of these three species north of Cape Hatteras.

S. enflata, a cosmopolitan warm water species, was found every year at some time during the period from July to December, but most frequently in the fall. It was present for the longest period, August to December, in 1930 outside the Bay. On rare occasions, in November 1931 and October 1932, it was found in the Bay as well as outside. Maximal numbers obtained for each year ranged from 330 to 1,800/10 minute tow. Length measurements were made on only two occasions: in August 1929 the mean length of stage III individuals was 14.1 mm and in November 1932 it was 18.44 mm. In the Delaware Bay region *S. enflata* is a warm water stray.

S. elegans occurred almost entirely during the first half of the year, although it was present in August of 1929 and 1932. According to Bigelow and Sears (1939) it was found in June 1929-1932 at their inshore stations down to the offing of Chesapeake Bay, but at least in 1929 it had disappeared from this region by July. Large volumes of *S. elegans* were not obtained south of Chesapeake Bay, although Sutcliffe (1950) has recorded its presence just north of Cape Hatteras. Russell (1932) suggested that successful reproduction may not occur at temperatures over 14°C whereas Bigelow and Sears thought that 18 to 20° might represent its upper limit for survival. In the Delaware Bay region, no mature *S. elegans* were found in the surface waters when the temperature rose above 17°C, although immature stages might still be present. It is probable that this species spreads south from the Cape Cod area along the middle Atlantic coast in winter and spring, dying out at the southern limits of its range each year.

S. elegans was more numerous and occurred for a longer period outside than in the Bay. In 1930 and 1931 it was relatively abundant, but few were found in 1932. Only small numbers were found in 1933 also, except in late May, when the highest mean numbers (> 32,000/10 minute tow) were taken outside the Bay.

An analysis was made of the populations obtained in 1930 and 1931. Specimens were stained with a dilute solution of alum carmine in order to differentiate the three maturity stages as described by Russell (1932). Length

measurements exclude the caudal fin and are given to the nearest millimeter. The data obtained for 1930 in the Bay and for 1931 outside the Bay are presented in Fig. 17. The histograms show the length ranges of the stages plotted against the number measured; the areas represent roughly the relative proportions of the three stages on any given date. In 1930 (see Fig. 17) there were two spawning periods in the Bay, in February–March and in May; the mean length of stage III individuals decreased from 20.1 mm in March to 15.4 mm in May. In 1931 there was evidence for only the March period in the Bay, but outside the Bay both mature sagittae and eggs were present in the surface waters from February to late May, indicating that spawning

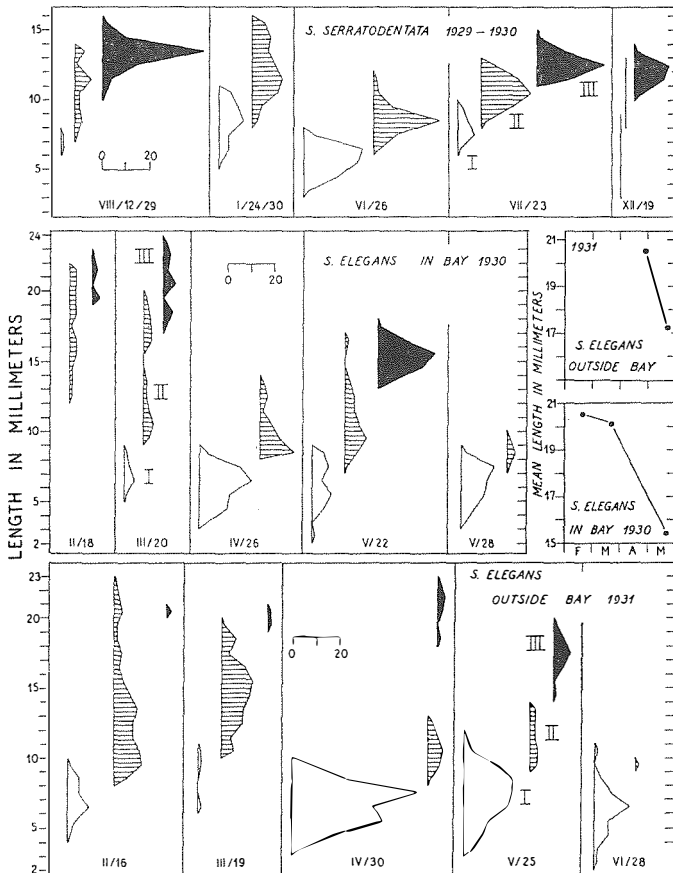


Figure 17. Length distributions for selected dates of the three maturity stages plotted against the number measured: *Sagitta serratodentata* from 1929-1930 (top); *S. elegans* in the Bay in 1930 (middle); and *S. elegans* outside the Bay in 1931 (bottom). The two small figures show the variations in mean length of stage III *S. elegans*.

was apparently more or less continuous there. Relatively large stage III sagittae were found from February to the end of April (see Fig. 17) at temperatures up to 8.6°C; in May smaller stage III individuals appeared. Mean lengths ranged from 20.5 mm at the end of April to 17.2 mm in late May. In general, at temperatures of 2.2–8.6°C, mean lengths of over 20 mm were obtained, but in May and early June, at temperatures of 14.0 to 16.65°C, the mean lengths ranged from 14.9 to 18.3 mm.

S. serratodentata was found during the greater part of the year, though never in March; these data are fragmentary, however, since as a rule it was fairly abundant only in July and August and November or December. Usually only occasional specimens were recorded for other times of year. The highest number, 15,000/10 minute tow, was obtained west of Five Fathom Lightship in December 1930. *S. serratodentata* occurred primarily outside the Bay, but it was recorded for the Bay in May 1930 and from August to October 1932. Stage III individuals were numerous only in July and August 1929, July and December 1930, and November 1932. Individuals observed at other times were almost entirely at stage I or II, although several stage III sagittae were recorded for December 1931, May 1932 and February 1933. The annual cycle as observed in the surface waters outside the Bay from August 1929 to December 1930 is shown in Fig. 17. In January the range in length of stage II individuals was exceptionally wide, from 8.5 to 15.5 mm (see Fig. 17), but it is not known whether these sagittae developed into a large-sized generation that remained at deeper levels or whether they were unable to survive the winter cold. The several adults found in February 1933 and May 1932 were 14.5 mm long; for July and August mean lengths ranged from 12.4 to 13.5 mm and for November and December from 11.9 to 12.3 mm. Thus spawning probably occurred in summer and late fall, but because of the absence of mature sagittae in the surface waters during winter and spring, there is no evidence for a winter or spring generation in the Delaware Bay region. According to Bigelow and Sears, *S. serratodentata* is more abundant offshore than inshore in these latitudes; it is probable that the population of the Delaware Bay region is continually renewed from offshore waters.

The Larvae of Bottom Invertebrates

Larval forms occurred throughout the year but constituted a higher proportion of the zooplankton population in the Bay than outside (see Figs. 5, 6). The majority of those obtained were crustacean larvae, since they were large enough to be retained by the net. Smaller organisms such as cyphonautes larvae or lamellibranch veligers were captured only when the net was clogged. Table IV lists the species and the months when they were observed from 1929 to 1933. The period of occurrence of each form for each year is not given; instead the data have been consolidated to show concisely the months

TABLE IV. CHECKLIST AND PERIODS OF OCCURRENCE OF THE LARVAE OF BOTTOM INVERTEBRATES, AS NOTED FROM 1929 TO 1933.

CRUSTACEA	J	F	M	A	M	J	J	A	S	O	N	D
Zoeae:												
<i>Callinectes sapidus</i>	-	-	-	-	x	x	x	x	x	x	-	-
<i>Cancer irroratus</i>	-	-	-	x	x	x	-	-	-	-	-	-
<i>Carcinides moenas</i>	-	-	-	-	-	x	x	x	-	-	-	-
<i>Libinia</i> sp.	-	-	-	-	-	-	x	x	x	x	-	-
<i>Neopanope texana sayi</i>	-	-	-	-	-	x	x	x	x	x	-	-
<i>Pinnixa chaetoptera</i>	-	-	-	-	-	-	x	x	x	x	-	-
<i>P. sayana</i>	-	-	-	-	-	-	x	x	x	x	-	-
<i>Pinnotheres maculatus</i>	-	-	-	-	-	-	x	x	x	x	-	-
<i>P. ostreum</i>	-	-	-	-	-	x	x	-	-	x	-	-
Unidentified	-	-	-	-	-	x	x	-	-	-	-	-
Megalops larvae	-	-	-	-	x	x	x	x	x	x	-	-
<i>Eupagurus</i> sp.	-	-	-	-	x	x	x	x	x	x	-	-
<i>Emerita talpoida</i>	-	-	-	-	-	-	x	-	x	x	-	-
<i>Crago septemspinosus</i>	-	x	x	x	x	x	x	x	x	x	x	x
<i>Callinassa</i> (?) sp.	x	-	x	-	-	-	x	x	x	x	-	-
Glaucothöe larvae	-	-	-	-	-	x	x	-	-	x	-	-
Cumacean larvae	x	x	x	x	x	x	x	-	x	x	-	x
Barnacle nauplii	x	x	x	x	x	x	x	x	x	x	x	x
Barnacle cyprids	x	x	x	x	x	x	x	x	x	x	x	x
Mysid larvae	x	x	x	x	x	x	x	x	x	x	x	x
<i>Naushonia crangonides</i>	-	-	-	-	-	-	-	x	x	x	-	-
<i>Paleomonetes</i> sp.	-	-	-	-	-	x	x	x	x	-	-	-
Porcellanid larvae	-	-	-	-	-	x	x	x	x	x	-	-
Stomatopod antizoeae	-	-	-	-	-	x	x	x	x	-	-	-
Stomatopod pseudozoeae	-	-	-	-	-	-	x	-	-	-	-	-
<i>Upogebia</i> sp.	-	-	-	-	-	-	x	x	-	x	-	-
Larval isopods	x	x	x	-	x	x	x	x	x	x	-	-
Larval gammarids	-	x	-	-	x	x	x	x	x	x	-	-
Hyperiid amphipods	x	x	x	x	x	x	x	x	x	x	x	x
<i>Hippolyte</i> (?) sp.	-	-	-	x	-	-	-	-	-	-	-	-
Unidentified larvae	-	x	x	x	x	x	x	x	x	x	x	x
OTHER FORMS												
Polychaete larvae	x	x	x	x	x	x	x	x	x	x	x	x
Echinoderm larvae	-	-	x	x	x	x	-	-	-	x	x	-
Cyphonautes larvae	-	-	-	-	-	-	x	-	x	x	-	-
Lamellibranch veligers	x	x	x	x	x	x	x	x	x	x	x	x
Gastropod veligers	x	x	x	x	x	x	x	x	x	x	x	x
Squid larvae	-	-	-	-	-	-	-	x	x	-	-	-

when the various species were observed over the four year period. For example, *Callinectes* zoeae were found only between May and October. None of those checked for every month of the year occurred consistently during each month of each year. Zoeae were most numerous from May to September; the highest

number obtained (272,800/10 minute tow) was taken in the Bay east of Brandywine Shoal in July 1931; the next highest number (123,600/10 minute tow) was found outside the Bay at South Ground in July 1933. Other crustacean larvae occurred throughout the year; these were usually most numerous during the warmer months, although *Balanus* larvae were sometimes fairly plentiful in November or December, as in December 1930 when up to 22,000 were recorded in the Bay east of Brandywine Shoal. The highest numbers of crustacean larvae, excluding zoeae, 74,400 in July 1931 and 80,400 in October 1932, were also obtained east of Brandywine Shoal. Outside the Bay the maximum number (76,800/10 minute tow) was found at South Ground in July 1933.

Other Forms

Fish eggs were most abundant from May to July (see Figs. 5, 6), although they were found from late winter to late summer and sometimes in the late fall. The highest numbers recorded for individual stations outside the Bay were taken off Townsend Inlet (263,000/10 minute tow) in June 1932 and at McCries Shoal (255,000) in June 1933. The next highest numbers (118,000/10 minute tow) were obtained off Cape May in late May 1930. At Brandywine and Old Bare Shoal, numbers exceeding 40,000 were recorded only in late May 1930 and June 1932. Fish larvae were relatively rare; the highest numbers found were 6,000/10 minute tow off Cape May in late May 1930 and 7,200 at McCries Shoal in July 1933.

Two protozoans were briefly abundant. Radiolaria of the genus *Acanthometron* were exceedingly numerous in late August 1929, when over 7,000,000/10 minute tow were obtained west of Five Fathom Lightship. *Noctiluca* sp., noted outside the Bay in October, was plentiful in the Bay from October to December 1930 (see Fig. 5); it was most abundant in the Bay in late October off Broadkill Creek when over 2,000,000/10 minute tow were taken; on this occasion it constituted 96% of the sample.

The pelagic polychaete *Tomopteris* sp. was observed infrequently, in July 1931 and in March and April 1932 outside and at the mouth of the Bay. *Autolytus* sp. occurred on a number of occasions outside and in the Bay; during the period studied it was noted in January, March to June, and from August to October.

The isopod *Edotea montosa* was found in the Bay in May and June 1930. Unidentified isopods were observed in July 1929 and in March and September 1932 outside the Bay. The warm water pelagic ostracod *Euconchoecia chierciae* Müller was noted only in November 1932 outside the Bay. Another warm water form, the penaeid *Lucifer faxoni* Borradaile, appeared outside the Bay each year in late summer or fall: in August 1929, August and October 1930, and December 1931; in September and October 1932 it was also present in

the Bay, 1,200/10 minute tow being recorded from east of Brandywine Shoal in mid-October.

The remaining groups to be briefly mentioned are the pteropods and heteropods. The small atlantid, *Oxygyrus keraudreni* Rang, noted in August 1929 and in October and November 1930 outside the Bay, was the only heteropod found. The pteropods included the boreal species, *Clione limacina* and *Limacina retroversa*, and the warm water form *Creseis virgula*. In addition, unidentified larval gymnosomes were recorded in June and November 1932 outside the Bay. *C. virgula* was taken outside the Bay in August 1929, September 1931, and July and September 1932; in August 1929, 1,200/10 minute tow were obtained west of Five Fathom Lightship and in late September 1931, 4,000 were recorded from Five Fathom Bank. *C. limacina* and *L. retroversa* often occurred together, although the latter was taken more frequently. Both were found primarily outside the Bay. *C. limacina* was noted in July 1929, May and September 1930, and May, July and August 1932; usually only stray specimens were taken, but 400/10 minute tow were obtained in late July 1932 from McCries Shoal. *L. retroversa* occurred between April and July every year: in July 1929, May and June 1930, May and July 1931, and April and May 1932 and 1933; the highest numbers (1,000/10 minute tow) were obtained in April 1930 at Five Fathom Bank. According to Bigelow and Sears, *C. limacina* was usually most widespread over the continental shelf from May to July, and the highest average monthly volumes of *L. retroversa* were obtained for May 1929-1931. Thus the period of occurrence of these two species in the Delaware Bay region agrees with their findings concerning the seasonal distribution of these forms over the continental shelf.

DISCUSSION

Temperature Ranges, Geographic Ranges and Seasonal Occurrence of Copepods

Between Cape Cod and Cape Hatteras in the open coastal waters of the middle Atlantic states there is an exceptionally wide annual range in temperature. This is well shown by Parr's (1933) analysis, in which he found a mean range of about 20°C at Five Fathom Bank compared with mean ranges of 11-12° at Cape Hatteras and in the Gulf of Maine and of 15-16° at Nantucket Shoal off Cape Cod. In sheltered waters the annual range is invariably wider. The extremes of temperature noted in Delaware Bay during the period studied, -0.65 to 28.35°C, almost equal the temperature range found over 40° or more of latitude. Because of this it is of interest to compare the seasonal occurrences of important species with their temperature and geographic ranges.

Few of the zooplankton organisms occurring in the Delaware Bay region are present throughout the year. Only four copepods, *Acartia tonsa* and *Pseudo-*

diaptomus coronatus in the Bay and *Centropages typicus* and *Paracalanus parvus* outside, may be considered year-round or virtually year-round species. All of these have a spring minimum. The great majority of the organisms appeared seasonally. Thus the important winter-spring species are *Pseudocalanus minutus*, *Centropages hamatus*, *Calanus finmarchicus*, *Acartia clausi*, and probably *Temora longicornis*; on the other hand, *Labidocera aestiva* was the only summer-fall species of any importance. The species of *Oithona* were not adequately sampled by the net used and may later prove to be far more abundant than this survey indicates.

It is a common observation that in the northern hemisphere at the northern limits of its range a species appears during summer and fall and at its southern limits from winter to spring. Where conditions are optimal the year around it should occur throughout the year. Just north of an area of optimal conditions a species may survive the winter in considerable numbers and have a spring minimum. At the southern border of its optimal range a species may occur during summer and disappear in early fall. Thus, as a species approaches the outer limits of its range the length of its period of annual occurrence decreases, from $\frac{3}{4}$ to $\frac{1}{2}$ year or less. An annual occurrence of several months probably marks the outer limits of the normal range throughout which reproduction is possible, and beyond these areas a species might be recorded as a stray. *Acartia clausi*, for example, is a dominant species for half of the year in Long Island Sound, but in the surface waters of Delaware Bay it was found for only 3-4 months.

A species' range may be telescoped seasonally or geographically by one or more of a number of limiting factors such as competition with other species, food, temperature, salinity or other hydrographic conditions. Although it is not possible at present to assess most of these factors, sufficient temperature data are available to show the ranges of temperature over which breeding may occur together with the extreme range as now known. Fig. 18 presents these data for a number of the species found in the Delaware Bay region, including two species, *Euterpina acutifrons* and *Centropages furcatus*, which occurred there as strays but which are common south of Cape Hatteras. The sources of these data are largely the studies carried out in American waters. The below-zero ranges of *Calanus finmarchicus*, *Pseudocalanus minutus* and *Oithona similis* were obtained from Ussing's (1938) investigation of East Greenland fjords. The lower limit (6°C) of the breeding range of *Paracalanus parvus*, established from Digby's (1950) study of English Channel copepods, agrees with the lowest temperature at which this species was probably spawning outside Delaware Bay. The upper limit of 31.8° shown for *Pseudodiaptomus coronatus*, *Labidocera aestiva*, *Oithona brevicornis*, *Euterpina acutifrons* and *Centropages furcatus* was obtained from Grice's (1956) data for Alligator Harbor, Florida; the 32° limit of *Acartia tonsa* and *Paracalanus parvus* is from Woodmansee's (1958) data. The other limits given for the various

species were taken from the Delaware Bay data or from reports on Block Island Sound (Deevey, 1952a, 1952b), Long Island Sound (Conover, 1956; Deevey, 1956), and Tisbury Great Pond, Massachusetts (Deevey, 1948). The lower limits of the breeding ranges of *Oithona brevicornis*, *Euterpina acutifrons* and *Centropages furcatus* were set rather arbitrarily, there being no definite evidence of reproduction at temperatures lower than 10, 15, and 20° respectively.

Fig. 18 shows that three species, *Acartia tonsa*, *Pseudodiaptomus coronatus*, and *Paracalanus parvus*, have breeding ranges of over 25°C. *Centropages typicus* is next with a range of 24°. The other species, with the exception of *Centropages furcatus*, have breeding ranges varying from 17 to 22°. These extreme ranges may be considered as representing the potentialities of the various species. Although the boreal-temperate species may be exposed to the full extent of their ranges every year in the coastal waters of southern New England and the Middle Atlantic states, the tropical-temperate species such as *Acartia tonsa* would not often be subjected to a range of 0–30° in a single

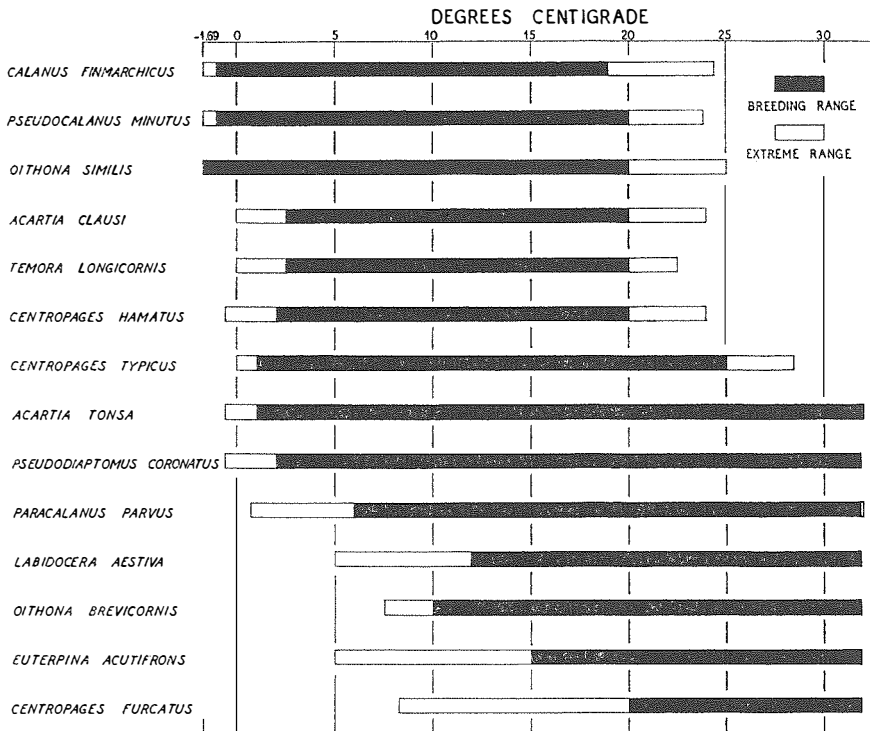


Figure 18. Known temperature ranges of 14 copepods found in the Delaware Bay region. The breeding ranges are shown in black.

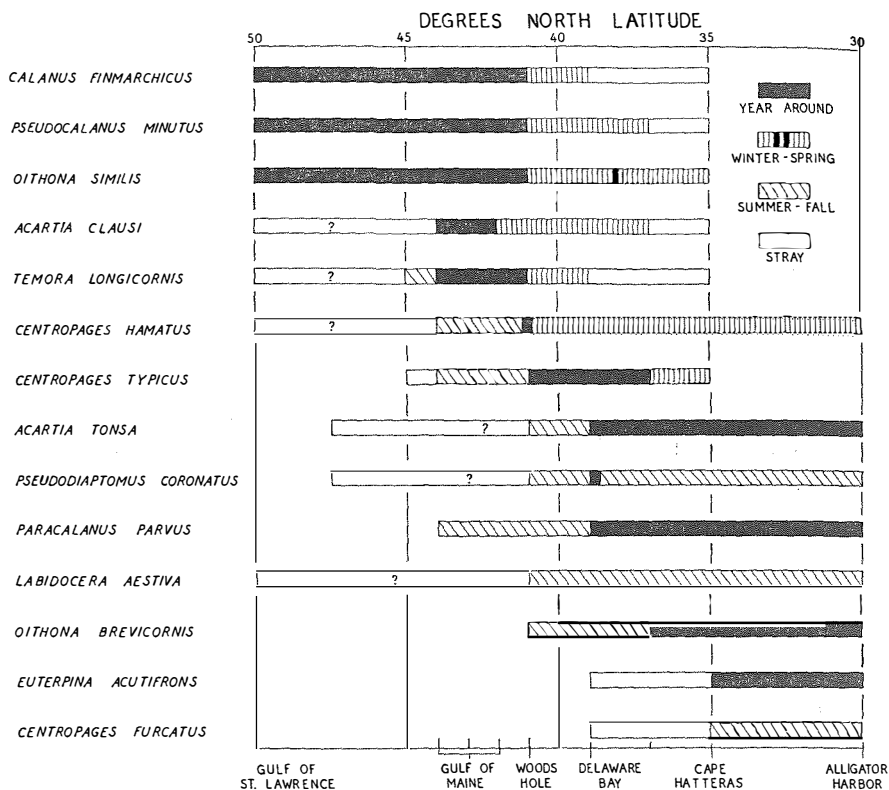


Figure 19. The latitudinal and seasonal occurrence in eastern American waters of the same copepods listed in Fig. 18.

locality. Since summer temperatures in the Delaware Bay region may reach or exceed 25° , the only species capable of occurring throughout the year are the warmer water forms which can reproduce as well as survive during the colder months. During cooler summers, as that of 1932, boreal-temperate species such as *Centropages hamatus* and *Pseudocalanus minutus* may occur in small numbers throughout the second half of the year. So far as can be ascertained at present, the upper limit of the breeding ranges of all the boreal-temperate species shown in Fig. 18 is approximately 20°C .

The seasonal and latitudinal distributions of the copepods listed in Fig. 18 are presented in Fig. 19, which shows the ranges of these species on the American Atlantic coast from 50°N Lat. (the approximate latitude of the Gulf of St. Lawrence, the St. Lawrence River and Newfoundland) to Cape Hatteras. Since no comprehensive survey has been made of the zooplankton south of Cape Hatteras on the Atlantic coast, Grice's (1956) data for the copepods of

Alligator Harbor on the Gulf of Mexico have been used to extend the known ranges of some of the species to 30°N Lat. Information about distributions near Cape Hatteras was obtained from Sutcliffe's (1950) study of the zooplankton at Beaufort, North Carolina.

It is more difficult to establish seasonal and geographic boundaries than temperature limits since the former are subject to somewhat more fluctuation than temperature limits, but the available data suggest the ranges shown in Fig. 19. Further investigation should expand or contract some of the limits. The coastal waters of southern New England, at 41°N Lat., include four areas (Woods Hole, Massachusetts; Narragansett Bay, Rhode Island; Block Island Sound; and Long Island Sound) where plankton investigations have been made, and on a latitudinal graph it is impossible to differentiate between them. In these localities the seasonal cycles of the boreal-temperate species vary; *Temora longicornis* and *Pseudocalanus minutus*, for example, may occur throughout the year in Block Island Sound where the annual temperature range is approximately 0–20°C, whereas in Long Island Sound where summer temperatures usually exceed 20° they are present during winter and spring. Therefore, these species are considered year-round down to 41°N Lat. and winter-spring species south of this latitude.

Comparison of the temperature ranges with the seasonal and latitudinal distributions shows that in a number of cases temperature is not the limiting factor. In general, however, on the American Atlantic coast the distributions of the boreal-temperate species conform to their temperature ranges. Three of these copepods, *Calanus finmarchicus*, *Pseudocalanus minutus*, and *Oithona similis*, are able to live the year around within the Arctic circle. The geographic ranges of all three extend south to Cape Hatteras; *Calanus* and *Pseudocalanus* are recorded as winter-spring species down to Delaware Bay and Chesapeake Bay, respectively; *O. similis*, with the widest temperature range, is a winter-spring species at Cape Hatteras (Sutcliffe, 1950), and further investigation should show that its range extends south of this point.

Four species have been recorded from as far north as approximately 50°N Lat. (see Fig. 19), but their seasonal occurrence north of the Gulf of Maine is not known. Only three of these, *Acartia clausi*, *Temora longicornis*, and *Centropages hamatus*, may be classed as colder water species. *Acartia clausi* and *Temora longicornis* appear to have limited seasonal and geographical distributions, both occurring as strays as far south as Cape Hatteras. *A. clausi* has a limited year-round range, the Gulf of Maine (Bigelow, 1926); its seasonal distribution south of Cape Cod in waters where summer temperatures don't exceed 20°C is apparently governed by factors other than temperature, such as competition with associated species. According to the available data, *C. hamatus* has the most limited year-round range; it was present in Block Island Sound at all times of year and was noted the year around in Narragansett Bay by Williams (1907), but in the Gulf of Maine (Bigelow, 1926) it occurred

primarily from late summer to winter. South of Cape Cod it is a winter-spring species. However, *C. hamatus* is exceptional in its wide latitudinal distribution; it is the only colder water form that has extended its range to inshore waters of the Gulf of Mexico, where at some stage of its life history it must survive temperatures exceeding 30°C.

On the eastern Atlantic coast the temperature cycles are such that the colder water species may be found throughout the year in the Gulf of Maine where the annual range is 0–15°C, during most of the year in the coastal waters of southern New England such as Block Island Sound where the range is 0–20°, and during winter and spring in the waters of the middle Atlantic states where there may be an annual range of 0–25°. At Cape Hatteras and south of this region, where the mean temperature range is 15–27°C according to Parr (1933), these species might on occasion be recorded as strays. *Oithona similis*, a winter-spring species at Beaufort, might be expected to occur down to Cape Canaveral or as far south as part of the annual cycle includes temperatures as low as 10–15°.

Despite a breeding range of 1 to 25°C, the known latitudinal range of *Centropages typicus* is more limited than that of any of the other species discussed here (see Figs. 18, 19). It is not known whether it occurs on the Atlantic coast south of Cape Hatteras, but in those waters competition with tropical species might be an important factor. *C. typicus* thrives in open coastal waters over the continental shelf between Cape Cod and Chesapeake Bay. In southern New England waters it is not abundant at salinities below 30‰, and this may explain its limited occurrence at Beaufort, North Carolina.

Acartia tonsa and *Pseudodiaptomus coronatus* have not only the widest temperature ranges but a wide latitudinal distribution. North of Cape Cod their seasonal occurrence has not been observed. Both are summer to winter forms in inshore coastal waters of southern New England, although Williams (1907) noted that *P. coronatus* was present throughout the year in Narragansett Bay; both are found virtually the year around in Delaware Bay. *A. tonsa* occurs throughout the year where the annual temperature ranges are 0–25° (Delaware Bay), 5.0–29.4° (Beaufort), 9.0–31.8° (Alligator Harbor), and 15.6–32.0° (Biscayne Bay). The seasonal distribution of *P. coronatus* is less regular and obviously is not limited by temperature; it was found in spring and fall at Beaufort, from March to December in Alligator Harbor, and from October to December in Biscayne Bay. The reasons for its limited seasonal occurrence are not known. *Paracalanus parvus* has almost as wide a temperature range as *A. tonsa*, which it parallels in latitudinal and seasonal distribution, although north of Cape Hatteras it is found in open coastal waters whereas *A. tonsa* is abundant only in sheltered areas throughout its known range in American waters.

Labidocera aestiva is a problematical species. Despite its wide latitudinal range and a breeding range of at least 12.0–31.8°, it occurs as a summer or

spring-to-fall form from Cape Cod to the Gulf of Mexico. Possibly, since there is no evidence of spawning at temperatures below 12°C, it is north of its optimal range throughout eastern North American waters; however, Fleminger (1957) has reported that it is characteristic of the northern temperate coastal area of the Gulf of Mexico. Of the remaining warmer water forms, *Oithona brevicornis* is found at least as a summer-fall species from Cape Cod to Delaware Bay and occurs throughout the year from Chesapeake Bay south. Its presence from spring to summer in Tisbury Great Pond indicates a lowest breeding temperature of 10°C, but partly because of its small size this species has not been fully studied. *Euterpina acutifrons* and *Centropages furcatus* represent warm water strays in the Delaware Bay region. *Euterpina* is found throughout the year south of Cape Hatteras whereas *C. furcatus*, a summer-fall species at Beaufort and a spring-summer form at Alligator Harbor, apparently needs temperatures of 20° and higher for its year-round range. It must be noted, however, that *C. furcatus* may be a relatively stenohaline as well as stenothermal species and its limited occurrence at both Beaufort and Alligator Harbor may be related to salinity changes as well as to temperature. It was present at high temperatures and salinities at Beaufort (Sutcliffe, 1950), and at Alligator Harbor it was not found at salinities lower than 29 ‰ (Grice, 1956).

A glance at the seasonal and latitudinal distribution of the copepods (Fig. 19) shows that in general the year-round ranges of the colder water species stop at Cape Cod. Warmer water forms such as *Acartia tonsa* and *Paracalanus parvus* have extended their year-round ranges at least as far north as Delaware Bay, and temperature alone (see Fig. 18) should not prevent their occurrence throughout the year in southern New England waters. *Centropages typicus* is the only species here considered that may be found the year around in the coastal waters between Cape Cod and Chesapeake Bay and possibly Cape Hatteras. There is at present no explanation for the limited seasonal occurrence of the two species with the widest latitudinal distribution, *Centropages hamatus* and *Labidocera aestiva*. The colder water forms are primarily limited in their distribution by temperature and secondarily by competition with other species. Species like *Acartia tonsa* appear to be limited in their seasonal distribution more by the presence of dominant colder water species, such as *A. clausi*, than by temperature.

It is probable that there is intensive biological competition among species existing near the limits of their temperature or geographic ranges. This is most evident in the case of the two species of *Acartia*; *A. clausi* and *A. tonsa* are dominant for equal parts of the year in Long Island Sound, but in Delaware Bay, where winter temperatures are certainly within its range, *A. clausi* was numerous only in the spring at the time of *A. tonsa*'s annual minimum. The seasonal periodicity of most of the species in southern New England waters and in the Delaware Bay region as winter-spring or summer-fall forms, present

during rising or falling temperatures over the same range, indicates that competition as well as temperature is a major factor limiting seasonal and possibly geographic distribution. In relatively open waters, such as Block Island Sound, hydrographic conditions may be important; here, for example, the influx of Gulf Stream waters and species in late summer and fall may modify greatly the seasonal patterns of the endemic species. Food is apparently not of major importance in eastern American waters as it is, for example, in Loch Striven (Marshall, 1949), where the cycles of abundance of the copepods definitely appear to be related to periods of diatom maxima.

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Зоопланктон поверхностных вод Делаверского Залива.

Краткий обзор.

Пробы зоопланктона, на которых основано это исследование, были собраны от 1929 до 1935 года на многочисленных станциях нижней части Делаверского Залива и в морских водах перед Заливом горизонтальным буксированием метровой крупной шелковой сети Но 2 и 10, длившимся 5 минут в поверхностном слое воды и 5 минут в подповерхностном слое. Последовательные месячные данные включающие собранные виды, сметные количества и объемы измещения для каждого 10 минутного буксирования имеются от января 1930 до конца Июля 1933 года. В общем максимальное число и объем вне Залива было летом и поздней осенью или ранней зимой, минимальное поздней зимой или весной, В Заливе общая величина за годовой цикл была менее регулярна: обыкновенно минимум был весной, а максимум ранним летом, осенью или зимой. Несмотря на различия в сезонных циклах относительное количество зоопланктона колебалось соответственно с года на год вне Залива и в самом Заливе. Общие числа объемов в Заливе и вне его были значительно выше в 1930 и 1933 году, чем в 1931 и 1932.

Копеподы были значительно преобладающими организмами. Из других групп важных в Заливе были личинки донных безпозвоночных, хэтогнаты, яйца рыб и гидромедузы. Вне Залива кроме этих групп обильными в сезонное время были кладоцеры и туникаты. Все виды перечислены в таблицах с указанием периодов их присутствия. 56 видов копепод зарегистрированы.

В Заливе *Acartia tonsa* преобладали, а *Centropages hamatus* и *Pseudodiaptomus coronatus* занимали второе место по важности. Вне Залива *Centropages typicus* преобладал, а *Paracalanus parvus* и *Pseudocalanus minutus* по обилию занимали второе место. Сезонные циклы были приняты в соображение для всех важных видов. 6 видов Кладоцер зарегистрировано, из которых сезонно преобладающими были *Penilia avirostris*. 8 видов пелагических Туникат были найдены вне Залива. Из них *Oikopleura dioica* и *Doliolum nationalis* появлялись каждым летом и осенью. Из Хэтогнат регулярно присутствовали *Sagitta elegans*, *S. serratodentata* и *S. inflata*. Личинки, преимущественно Ракообразных, были более обильны в Заливе, чем вне его. Яйца рыб были наиболее многочисленны от Мая до Июля. Два вида Простейших, *Acanthomaton sp.* и *Noctiluca sp.* были на короткое время чрезвычайно обильны. Другие группы, представители которых иногда встречаются, включают пелагических полихэт, изопод, остракод *Euconchoecia chierchiae*, пенеид *Lucifer faxoni*, гетеропод *Oxygurus keraudreni* и птероподы *Clione limacina*, *Limacina retroversa* и *Creseis virgula*.

Вследствие широких пределов колебания годовой температуры в районе Делаверского Залива, приблизительно от 0° до 25°C., не многие организмы встречаются в течении всего года. 4 вида Копепод, *Acartia tonsa*, *Pseudodiaptomus coronatus*, *Centropages typicus* и *Paracalanus parvus*, являются круглогодичными. Установленные пределы температурных колебаний, включающие периоды размножения, а так же и зарегистрированные крайние пределы даны для 14 видов Копепод и сопоставлены с установленным географическим распространением и сезонным появлением этих видов между 50° и 30° Северной широты. *Acartia tonsa* и *Pseudodiaptomus coronatus* размножаются в самых широких пределах температуры, включающих 31°C., *Paracalanus parvus* и *Centropages typicus* от 24° размножаются в пределах включающих от 24° до 26°C. Виды более холодных вод, *Pseudocalanus minutus*, *Temora longicornis* и *Acartia clausi* повидному не размножаются при температурах превышающих 20°C. Их широтное и сезонное появление по видимому ограничено главным образом температурой и до известной степени соревнованием с соевыми видами. Виды более теплых вод, способные размножаться в необычайно широких пределах температуры, примером которых служит *Acartia tonsa*, вероятно ограничены в их сезонном появлении в северной части их района соревнованием с видами преобладающими в более холодных водах. В районе нами исследованном другие факторы вроде гидрографических условий или пищи по видимому не имеют большого значения в ограничении сезонных и широтных пределов.

*Relative Effects of Temperature and Food on
Seasonal Variations in Length of Marine Copepods
in some Eastern American and
Western European Waters*

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ABSTRACT

All the common marine copepods of temperate to boreal regions that have been studied for at least the greater part of a year exhibit marked seasonal variations in adult size. The annual pattern of length variations differs in western European and eastern American waters, and the same species exhibits dissimilar patterns in different localities. Temperature and food have been assumed to be important factors in influencing size variations. Therefore, using both original and published data, their relative effects have been assessed for several widely differing regions.

Simple, partial and multiple correlation coefficients have been calculated for length, temperature and phytoplankton data from Long Island Sound, the western Mediterranean, and Loch Striven. For these waters the annual length cycles of the copepods have been calculated from the temperature and phytoplankton data for comparison with the observed length cycles; good agreement was found in each case between the calculated and observed length variations. Length-temperature correlation coefficients have also been calculated for regions lacking corresponding phytoplankton data, including the Delaware Bay region, Block Island Sound, the English Channel, the North Sea and the Kattegat, and Woods Hole, Massachusetts.

These data show that the relative effects of temperature and food on the seasonal length variations of marine copepods vary, depending on the extent of the annual temperature range and on the quantity of phytoplankton present during the year. Significant negative correlations between length and temperature at the time of sampling were obtained for all waters with an annual mean temperature range of 14°C or more. Conversely, when the range was 14°C or less, significant positive correlations were found between length and mean quantity of phytoplankton of the month previous to sampling, which represents food conditions during development. Every species from every locality investigated gave significant negative correlations between length and the mean temperature of the previous month.

In Long Island Sound, with a mean range of about 20°C, temperature is the important factor influencing seasonal size variations. In the western Mediterranean (mean range, 13-14°C) and in Loch Striven (mean range, 7-8°C) both the temperature and the quantity of phytoplankton available during development determine the relative sizes of successive generations. Also, comparison of the length and temperature data for two representative species, *Pseudocalanus minutus* and *Acartia tonsa*, shows that the effects of temperature on size may vary with the species, depending on the extent of its temperature range.

INTRODUCTION

Length variations, whether they occur seasonally, geographically or concurrently in one locality at the same or different depths, have been observed for many species of copepods. Sewell (1948) and Marshall and Orr (1955) have discussed this problem and have reviewed data for both marine and freshwater copepods. For the coastal waters of temperate and boreal regions of the northern hemisphere, seasonal variations in size have been noted for all the common species that have been studied for at least the greater part of a year. These variations have been largely attributed to the differing conditions of temperature, food and other environmental factors encountered by successive generations during a year. In any given locality, although there may be minor variations, all species show the same general pattern of size changes, but the same species may exhibit dissimilar cycles in different regions. That temperature is an important factor was demonstrated by Coker (1933) who found an inverse correlation between temperature and mean length when the freshwater species *Cyclops vernalis* Fischer was reared at different constant temperatures. Under natural conditions, however, maximal length may not necessarily be found at times of minimal temperature.

The pattern of the annual cycle of copepod length variations observed in coastal waters of the northeastern United States differs from that found in

western European waters. In eastern American waters, almost without exception, greatest size is attained in winter and smallest size in summer (Clarke and Zinn, 1937; Deevey, 1952; R. Conover, 1956); but in Loch Striven (Marshall, *et al.*, 1934; Marshall, 1949), in the English Channel (Bogorov, 1934; Digby, 1950), in the North Sea and the Kattegat (Adler and Jespersen, 1920), maximal size is found in spring and minimal size in winter or from summer to winter; in the waters of western Norway, maximal size may occur in spring or from spring to summer (Wiborg, 1954). Between these European and American waters there are marked differences in: (1) the extent of the annual temperature range, which is much greater in the coastal waters of the northeastern United States, and (2) the time of the "spring" phytoplankton bloom. In Loch Striven, for example, the major bloom occurs in March–April, and in the Norwegian Sea (Halldal, 1953) a single bloom starts in April and reaches its maximum in July–August; on the other hand, in the American waters studied, at least in Block Island Sound (Riley, 1952) and Long Island Sound (S. Conover, 1956), the major diatom maximum is found in February–March when temperatures are minimal.

The purpose of this report is to present statistical analyses of data on temperature, phytoplankton, and copepod length, and to show how the effects of temperature and food on the size of the common marine calanoid copepods vary depending upon the extent of the annual temperature range and according to the phytoplankton cycle. Both original and published data are used. The original data include the annual length cycles of six species of copepods from the Delaware Bay region, of two species from Long Island Sound, and of one species from the western Mediterranean; some hitherto unpublished measurements from Block Island Sound are also used. For comparison, there are data on length published by Marshall, *et al.* (1934) and Marshall (1949) for Loch Striven, by Digby (1950) for the English Channel, by Adler and Jespersen (1920) for the North Sea and the Kattegat, by Clarke and Zinn (1937) for Woods Hole, Massachusetts, and by R. Conover (1956) for Long Island Sound. For some of these localities only the figures for mean or median lengths and temperatures are available, but for Loch Striven, Long Island Sound and the western Mediterranean there are complete sets of data. There are therefore several quite diverse bodies of water where the effects of the temperature and phytoplankton cycles on the annual size variations of copepods may be assessed.

Species considered in this report:

Acartia clausi Giesbrecht
Acartia tonsa Dana
Calanus finmarchicus (Gunner)
Centropages hamatus (Lilljeborg)
Centropages typicus Krøyer
Labidocera aestiva Wheeler

Microcalanus pygmaeus (G. O. Sars)
Paracalanus parvus (Claus)
Pseudocalanus minutus (Krøyer)
 = *P. elongatus* Boeck
Pseudodiaptomus coronatus Williams
Temora longicornis Müller

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METHODS

During a survey of the zooplankton of the Delaware Bay region, length measurements were made on the copepods that occurred regularly from year to year. These include *Centropages typicus*, *Pseudocalanus minutus*, *Labidocera aestiva*, *Acartia tonsa*, *Pseudodiaptomus coronatus* and *Centropages hamatus*. From 25 to 50 or more measurements, from the top of the head to the base of the caudal rami, were made on these copepods whenever they were sufficiently numerous in the samples collected from May 1929 through July 1933. The temperature cycle and other pertinent data concerning these samples and the species measured are contained in the accompanying report in this issue (Deevey, 1960).

Length measurements of female *C. typicus* from the western Mediterranean were obtained in August 1957 during a visit to the Laboratorio Costero de Investigaciones Pesqueras at Grao, Castellón, Spain. Zooplankton samples, in the custody of M. Durán, had been collected at weekly intervals for a number of years, but due to limited time, measurements were made on female *C. typicus* for only two years, from January 1955 to January 1957. Cephalothorax length, length to base of caudal rami, and total length were measured on 1,188 females from 28 samples. Both temperature and phytoplankton data are available and have been published for the period from January 1955 to June 1956 (Margalef, *et al.*, 1957: tables II, IV).

Including R. Conover's (1956) cephalothorax measurements of *Acartia clausi* and *A. tonsa*, there are mean length data for four Long Island Sound species for the period from March 1952 to May 1953. Measurements of cephalothorax length were made on females of *Pseudocalanus minutus* and *Temora longicornis*. Whenever possible, 50 specimens were measured to obtain each mean length. Weekly data for phytoplankton (given as chlorophyll in micrograms/liter) and for temperatures are on file in the Bingham Oceanographic Laboratory; these data have also been figured by Riley (1956: figs. 1, 2) and by Riley and S. Conover (1956: figs. 2, 3). S. Conover (1956:

figs. 1, 4) has compared the phytoplankton cycles obtained from cell counts and chlorophyll analyses.

Since my length measurements for the Delaware Bay region and Block Island Sound were made from the top of the head to the base of the caudal rami and since other workers have used either cephalothorax length or total length, these three measurements have been made on 50 or more specimens of five of the species studied in order to obtain ratios for converting length to caudal rami to cephalothorax or total length. Table I lists the percentage ratios of mean cephalothorax length and of mean length from head to base of caudal rami to mean total length; it also gives factors for converting length from head to base of caudal rami to cephalothorax length and to total length. These figures facilitate comparison of the length ranges of these five species from the Delaware Bay region and Block Island Sound with their length ranges recorded from other localities.

TABLE I. PERCENTAGE RATIOS FOR CONVERTING TOTAL LENGTH TO CEPHALOTHORAX LENGTH (CEPH.) AND TO LENGTH FROM HEAD TO BASE OF CAUDAL RAMI (C. R.), AND FACTORS FOR CONVERTING C. R. TO CEPH. AND TO TOTAL LENGTH.

Species	Number Measured	Percent of Total		Conversion Factors	
		Ceph.	C. R.	Ceph. =	Total =
<i>Pseudocalanus minutus</i> female..	100	68.4	92.7	.74 C.R.	1.08 C.R.
<i>Centropages typicus</i> female.....	1,038	70.6	92.7	.76 C.R.	1.08 C.R.
<i>Centropages hamatus</i> female ...	50	69.7	91.4	.76 C.R.	1.09 C.R.
male	50	70.5	90.3	.78 C.R.	1.107 C.R.
<i>Acartia tonsa</i> female	50	78.3	92.8	.84 C.R.	1.077 C.R.
<i>Temora longicornis</i> female	50	64.3	83.6	.77 C.R.	1.196 C.R.

Simple correlation coefficients have been calculated for the length-temperature data from the Delaware Bay region, Block Island Sound, Woods Hole, the English Channel, the North Sea and the Kattegat. Simple, partial, and multiple correlations have been obtained for length-temperature-phytoplankton data from Loch Striven, Long Island Sound and the western Mediterranean. From the regression coefficients and from the means and standard deviations for length, temperature and phytoplankton, the annual length cycles of copepods from these three regions have been calculated for comparison with the observed cycles. In most instances, correlation coefficients were calculated using not only the temperature and phytoplankton of the day of sampling but also the mean temperature and phytoplankton of the month prior to sampling in order to ascertain whether the temperature and food conditions encountered during growth influenced the ultimate size of the individuals. This was done on the assumption that the majority of specimens measured for any given date would have matured during the previous month and that

a month is the approximate or at least minimal developmental period for most of the smaller marine calanoid copepods. Although the length of the developmental period may vary with both the species and the locality, two months should represent the maximum period necessary for most of the species here considered.

For a number of reasons, not all of the available data lend themselves to this type of analysis. If the depth of the water column is too great, then varying temperatures from top to bottom as well as the vertical migrations of the copepods may complicate the results. This is the case, for example, with Wiborg's (1954) measurements of *Pseudocalanus elongatus* and other species from Norwegian waters. The mean annual temperature range of the 200 m water column sampled was on occasion less, especially in summer, than the range within the column. Moreover, the vertical distribution of the copepods varied during the year, the major part of the population sometimes being above and sometimes below 50 m. Also, if the length of the developmental period is long, the relationship of adult size to temperature and food is difficult to assess. This applies, for example, to Comita and Anderson's (1959) data for the freshwater species *Diatomus ashlandi* in Lake Washington. This species had only one distinct breeding period during the year, most of the adults appearing in late fall, presumably having developed from eggs hatched the previous winter. Data from Arctic waters also do not appear to be suitable for this type of analysis. The developmental cycle of copepods differs in marine and freshwater Arctic environments. In an Arctic lake, Comita (1956) found that *Limnocalanus johanseni* overwinters in the egg and that the entire development to adult occurs in July and August. In this case the annual cycle is too compressed to yield sufficient data for length-temperature-phytoplankton correlations. For East Greenland waters, Digby (1953, 1954) also found that the copepods have one generation a year. All stages were present throughout the year; the major part of development of species such as *Calanus finmarchicus* and *Pseudocalanus minutus* occurred in summer and fall, but during the winter, at a temperature of -1.77°C , some development was probably proceeding slowly. An analysis of Digby's data is not presented because of the long developmental period and also because the data are confused by the vertical migrations of the copepods.

DELAWARE BAY REGION

Zooplankton samples were collected with a meter net of fairly coarse mesh at monthly intervals from May 1929 through July 1933 at a number of stations in the lower and central part of the Bay and in the coastal waters outside, in particular at Five Fathom Bank, west of Five Fathom Lightship, at South Ground, and McCries Shoal (Deevey, 1960: fig. 1). This region is characterized by a wide annual temperature range (Parr, 1933: figs. 21,

24, 28; Deevey, 1960: fig. 2). There is a mean range of about 20°C outside at Five Fathom Bank and up to 25°C in the Bay. During the period studied, the extremes in temperature noted in the Bay were -0.65° and 28.35°C , outside 0.85° and 24.45°C . Compared with temperature cycles of other areas where length measurements of copepods have been made, the Delaware Bay region has an exceptionally wide range.

In this region all of the species were large in winter and small in summer, although the extent of the seasonal length range varied with the species. The

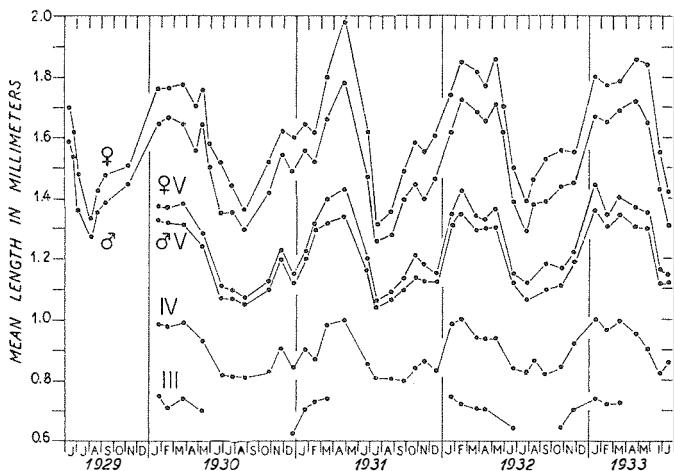


Figure 1. Variations in mean length from top of head to base of caudal rami of stages III to VI *Centropages typicus* from the stations outside Delaware Bay, June 1929 through July 1933.

temperate-to-boreal species showed more striking annual size changes than the species with wider temperature ranges. *Centropages typicus*, the dominant form in the surface waters outside the Bay, was present throughout the year and produced at least five to six generations annually. Fig. 1 illustrates the variations in mean length of stages III–VI of *C. typicus* from the outside stations from June 1929 through July 1933. Fifty specimens were measured to obtain each mean, except for April 1933 when not enough males were caught. Stage III individuals were taken in quantity only in winter and spring; presumably they were too small to be retained by the net during the rest of the year. The largest adults were found from January to May, the smallest in July and August. All the stages measured were large or small on the same dates. There was no time lag between maximal lengths of the copepodid stages, such as that noted for the more slowly developing *Diaptomus ashlandi* in Lake Washington (Comita and Anderson, 1959). The extreme range in length noted for females was 1.1–2.15 mm (:0.84–1.63 mm cephalothorax length) and for males 1.15–1.9 mm. Similar length variations have been recorded for

C. typicus from Block Island Sound (Deevey, 1952a), but there the range in mean length was not as great as that in Delaware waters.

Fig. 2 shows the variations in mean length of male and female *Centropages hamatus*, an important form in the Bay, and of female *Pseudocalanus minutus*, which occurred both in and outside the Bay. These are boreal species whose temperature ranges are exceeded by summer temperatures in this region. Both were abundant in winter and spring and produced at least three generations during the first half of the year. Although a few specimens of each species

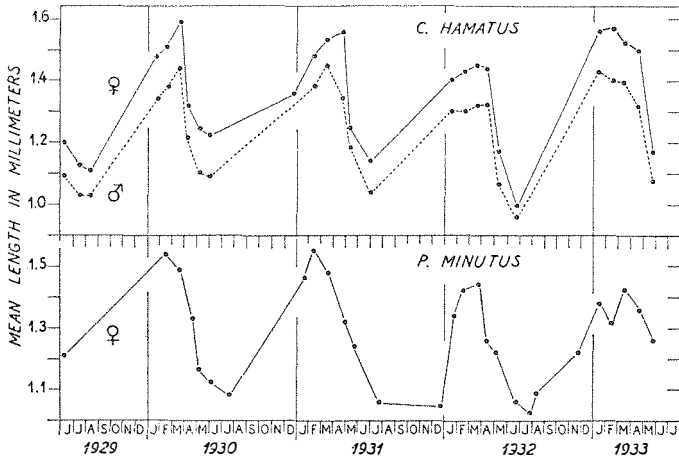


Figure 2. Variations in mean length from top of head to base of caudal rami of female and male *Centropages hamatus* in the Bay and of female *Pseudocalanus minutus* outside Delaware Bay, June 1929 to May 1933.

might be found in the samples collected in summer and fall, usually not enough were present to allow mean length determinations. *C. hamatus* and *P. minutus* showed marked seasonal variations in size, being largest in winter, of intermediate size in spring, and smallest in summer. The extreme range in length from head to base of caudal rami noted for female *C. hamatus* was 0.9–1.75 mm (:0.684–1.33 mm cephalothorax length) and for female *P. minutus* 0.9–1.8 mm (:0.67–1.33 mm cephalothorax length).

Acartia tonsa, the dominant Bay species, and *Pseudodiaptomus coronatus* occurred virtually throughout the year in the Bay. The length variations of male and female *A. tonsa* and *P. coronatus* from May 1929 through July 1933 are shown in Fig. 3. These species were generally larger in winter and smaller in summer, but their seasonal cycles are not as striking as those of *P. minutus*, *C. typicus*, and *C. hamatus*. *A. tonsa* and *P. coronatus* have wider known temperature ranges than any other species found in the Delaware Bay region (see Deevey, 1960). Both are able to breed over a range of at least

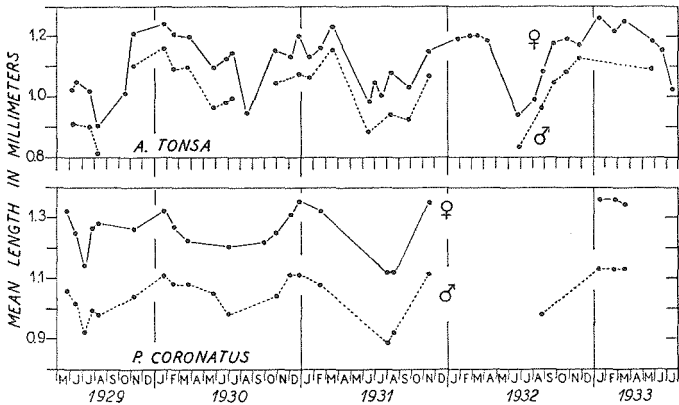


Figure 3. Variations in mean length from top of head to base of caudal rami of female and male *Acartia tonsa* and *Pseudodiaptomus coronatus* in Delaware Bay, May 1929 to July 1933.

30°C. The extreme length range observed for female *A. tonsa* in the Bay was 0.85–1.35 mm (:0.714–1.134 mm cephalothorax length) and outside the Bay 0.9–1.4 mm (:0.756–1.176 mm cephalothorax length). Usually the mean length of the population outside was slightly greater than that inside. For *P. coronatus* in the Bay an extreme range of 1.05–1.45 mm was noted for females and of 0.8–1.2 mm for males.

Labidocera aestiva is a summer-fall species which was found both in and outside the Bay. The data for this species are more fragmentary, since adults

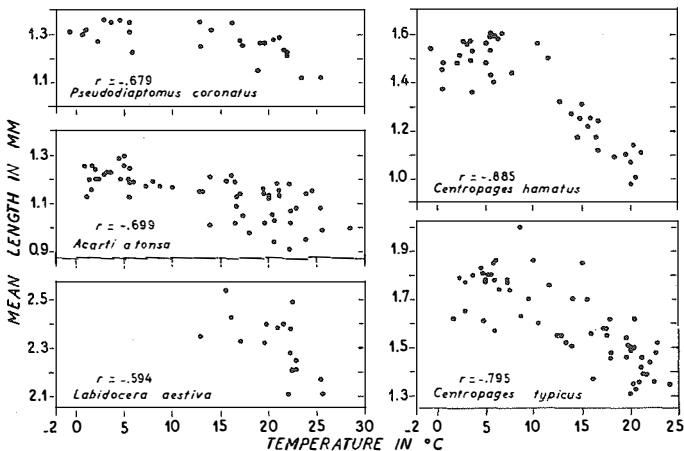


Figure 4. Dot diagrams showing mean lengths from top of head to base of caudal rami plotted against temperature at sampling of female *P. coronatus*, *A. tonsa*, *L. aestiva*, *C. hamatus* and *C. typicus* from the Delaware Bay region, together with the correlation coefficients obtained from these data.

were usually not sufficiently numerous in the surface waters, even when immature stages were abundant. However, between late May and October of the several years studied, 17 mean length determinations each of females and males were obtained, and in general smaller size was found at higher temperatures. The extreme length range of females was 1.9–2.7 mm, of males 1.65–2.5 mm.

Dot diagrams showing the mean lengths from head to base of caudal rami for females of five of these species plotted against temperature at the time of sampling are presented in Fig. 4 together with the correlation coefficients obtained from these data. In Table II are listed all the correlation coefficients for mean length against temperature calculated for copepods from the Delaware Bay region. In all instances significant negative correlations were found between length and temperature at sampling as well as between length and the mean temperature of the month previous to sampling. Only in the case of *L. aestiva* was the latter correlation appreciably greater (see Table II). This may be explained by the fact that it is a larger copepod than the others, requiring probably at least two months for development; therefore the mean temperature of the month prior to sampling would approach more closely the temperatures occurring during its growth. For the smaller and more rapidly developing species, the constantly changing temperatures apparently exert a continuous effect on development, so that temperatures for the day of sampling

TABLE II. CORRELATION COEFFICIENTS FOR MEAN LENGTH WITH TEMPERATURE AT SAMPLING AND TEMPERATURE AVERAGED FOR PREVIOUS MONTH OBTAINED FOR COPEPODS FROM THE DELAWARE BAY REGION.

Species	No. of Pairs	Length vs. Temp. at Sampling	No. of Pairs	Length vs. Temp. of Previous Mo.
<i>Centropages typicus</i> females ...	61	-.795	37	-.874
males	41	-.835	36	-.885
Stage IV	38	-.804	—	—
<i>Centropages hamatus</i> all females	46	-.885	—	—
females, in Bay	31	-.876	31	-.914
males, in Bay	24	-.915	—	—
<i>Pseudocalanus minutus</i> females	37	-.868	29	-.855
males	17	-.689	—	—
<i>Acartia tonsa</i> all females	59	-.699	46	-.631
females, in Bay	42	-.723	37	-.691
males, in Bay	24	-.728	23	-.638
<i>Pseudodiaptomus coronatus</i> all				
females	27	-.679	—	—
females, in Bay	23	-.726	19	-.672
males, in Bay	23	-.887	20	-.822
<i>Labidocera aestiva</i> females ...	17	-.594	17	-.775
males	17	-.573	17	-.730

yield as high negative correlations with length as do temperatures of the previous month, even though these latter presumably represent more exactly the conditions pertaining during development. For the three important Bay species, *C. hamatus*, *A. tonsa* and *P. coronatus*, measurements had been obtained from samples collected both in and outside the Bay. Since lower salinities in the Bay might affect size, correlation coefficients were also calculated for these species excluding all outside-the-Bay data, but no significant differences were noted (see Table II). In the Delaware Bay region the wide annual temperature range appears to be of prime importance in influencing the seasonal variations in size of copepods.

LONG ISLAND SOUND

The annual pattern of variations in copepod length observed for Long Island Sound is similar to that for the Delaware Bay region, although no one species is abundant or dominant for the greater part of a year. Winter-spring species are succeeded by predominantly summer-fall species. The mean annual temperature range is about 20°C. For these waters there are comparable data for mean cephalothorax length, temperature and phytoplankton for females of four of the common species: *Temora longicornis*, *Pseudocalanus minutus*, *Acartia clausi* and *A. tonsa*. R. Conover's (1956) determinations of mean length have been used for the two species of *Acartia*. Whereas *A. clausi*, *P. minutus* and *T. longicornis* are winter-spring species, *A. tonsa* is the dominant summer-fall form although it is present for most of the year (Deevey, 1956). The length, temperature and phytoplankton data used in the calculations for *T. longicornis* and *P. minutus* are contained in Tables III and IV, respectively.

Simple, partial and multiple correlation coefficients have been calculated from the temperature and phytoplankton data for the day of sampling and also averaged for the previous month (Table V). All four species show highly significant negative correlations between length and temperature but no significant correlation between length and quantity of phytoplankton. The results are similar whether the temperature and phytoplankton data for the day of sampling are used or whether these are averaged for the month prior to sampling. The partial correlations shown in Table V demonstrate clearly that temperature is a more important factor than the quantity of phytoplankton in influencing the seasonal variations in copepod length in Long Island Sound.

From the regression coefficients and from the means and standard deviations for length, temperature and chlorophyll, the annual length cycles of three of these species have been calculated for comparison with the observed lengths. The multiple correlation coefficients given in Table V indicate in each instance a high correlation between the observed and calculated lengths. Fig. 5

TABLE III. FEMALE *Temora longicornis* FROM LONG ISLAND SOUND. MEAN CEPHALOTHORAX LENGTHS FOR 50 INDIVIDUALS IN MM WITH MEAN TEMPERATURES IN °C AND MEAN CHLOROPHYLL IN MICROGRAMS/LITER FOR DAY OF SAMPLING AND AVERAGED FOR PREVIOUS MONTH.

Date	Ceph. Length	Temp. at Sampling	Temp. of Previous Mo.	Chlor. at Sampling	Chlor. of Previous Mo.
III/5/52	1.16	1.94	-	10.40	-
III/20	1.13	3.13	-	9.00	-
IV/2	1.10	5.00	2.90	5.60	9.30
IV/9	1.16	5.00	3.65	4.40	8.10
IV/16	1.17	6.60	4.20	7.90	6.50
V/897	8.40	6.75	4.30	5.95
V/2190	10.50	8.65	4.70	5.75
VI/480	14.40	10.25	4.10	7.20
VI/1965	16.50	13.00	9.00	6.74
VII/163	17.90	15.36	7.80	6.63
VII/1566	21.60	16.94	6.00	7.06
I/5/53	1.00	5.00	6.82	4.30	4.08
I/19	1.13	4.00	4.32	6.40	4.80
I/27	1.11	3.50	4.14	6.30	5.23
II/2	1.15	3.40	4.01	4.20	5.70
II/10	1.14	3.20	4.62	2.70	5.50
II/18	1.16	2.80	3.70	5.80	5.15
II/24	1.18	3.40	3.20	5.00	4.75
III/2	1.16	3.25	3.24	13.30	5.30
III/9	1.19	2.90	3.12	29.30	8.90
III/16	1.17	3.64	3.07	22.40	14.04
III/23	1.20	5.20	3.26	6.90	18.00
IV/2	1.13	5.40	3.70	5.90	19.24
IV/20	1.05	6.50	5.80	3.00	6.30
V/1392	9.74	7.65	5.50	5.02
VI/171	11.94	10.91	4.00	5.05

presents the calculated and observed length cycles of female *T. longicornis*; the cycle was calculated from both temperature and phytoplankton data for the day of sampling (Fig. 5 B) and from these data averaged for the previous month (Fig. 5 A). For both sets of calculations the agreement with the observed cycle is good and there is no significant difference between the two, but the fit is slightly better for early winter and spring when the data for the previous month are used (see Fig. 5 A). For *P. minutus* females, the length cycle was calculated using only the temperature and phytoplankton of the day of sampling; the observed and calculated cycles are shown in Fig. 6. In this case, also, the calculated lengths closely follow the observed lengths. In Fig. 7 the length cycles calculated for female *A. clausi* are compared with R. Conover's observed lengths. For this species, lengths were calculated from data of the day of sampling (Fig. 7 B) and also from data averaged for the month previous

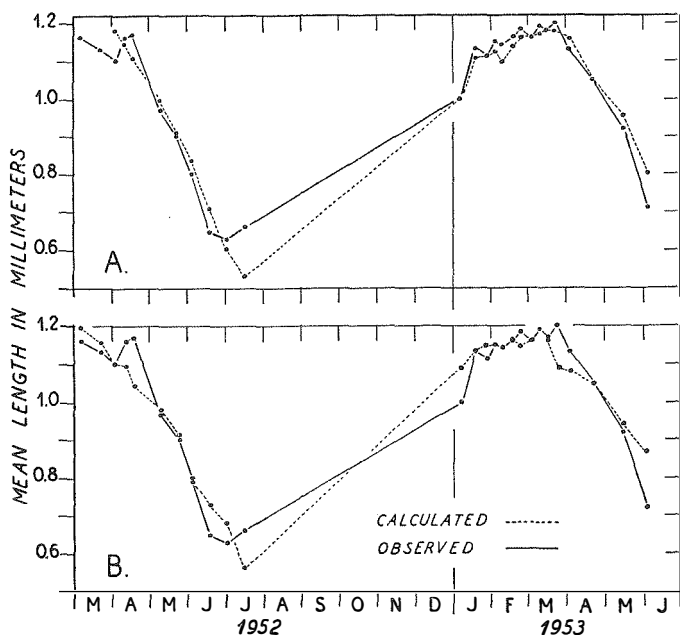


Figure 5. The calculated and observed mean cephalothorax length cycles of female *Temora longicornis* in Long Island Sound, March 1952 to June 1953. *A* Calculated lengths based on mean temperature and chlorophyll of the month previous to sampling. *B* Calculated lengths based on the temperature and chlorophyll of the day of sampling.

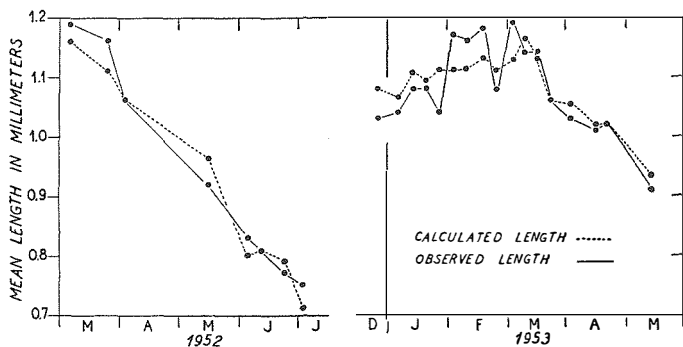


Figure 6. The calculated and observed mean cephalothorax length cycles of female *Pseudocalanus minutus* in Long Island Sound from March 1952 to May 1953. Calculated lengths based on the temperature and chlorophyll of the day of sampling.

TABLE IV. FEMALE *Pseudocalanus minutus* FROM LONG ISLAND SOUND. MEAN CEPHALOTHORAX LENGTHS IN MM, MEAN TEMPERATURES IN °C, AND CHLOROPHYLL IN MICROGRAMS/LITER.

Date	No. Measured	Mean Lengths	Temperature	Chlorophyll
III/5/52	50	1.19	1.94	10.40
III/26	33	1.16	3.60	6.90
IV/2	50	1.06	5.00	5.60
V/14	36	.92	8.70	7.30
VI/4	50	.83	14.40	4.10
VI/11	22	.81	14.60	12.40
VI/24	27	.77	14.90	7.40
VII/1	26	.75	17.90	7.80
XII/29	50	1.03	4.50	5.20
I/5/53	50	1.04	5.00	4.30
I/13	50	1.08	3.55	5.00
I/19	50	1.08	4.00	6.40
I/27	100	1.04	3.50	6.30
II/2	50	1.17	3.37	4.20
II/10	50	1.16	3.18	2.70
II/18	50	1.18	2.80	5.80
II/24	100	1.08	3.40	5.00
III/2	50	1.19	3.25	13.30
III/9	50	1.14	2.90	29.30
III/16	50	1.14	3.64	22.40
III/23	50	1.06	5.20	6.90
IV/2	50	1.03	5.40	5.90
IV/15	25	1.01	6.70	6.10
IV/20	50	1.02	6.50	3.00
V/13	50	.91	9.74	5.50

to sampling (Fig. 7 A). Although there is no significant difference between the two, the *A. clausi* lengths calculated from the data of the sampling date follow the observed lengths somewhat more closely than do the lengths calculated from data of the previous month. Actually, for *A. clausi*, calculations based only on the temperature of the day of sampling follow the observed lengths as closely as the lengths calculated from the phytoplankton and temperature (Fig. 7 B).

Thus in Long Island Sound, where there is a wide temperature range, the seasonal size variations of the calanoid copepods are closely associated with the annual temperature cycle. The quantity of phytoplankton present during development has little effect on the ultimate size of the individuals. A glance at Tables III and IV shows that both *T. longicornis* and *P. minutus* had increased in size well before the phytoplankton bloom. Also, as was found for the Delaware Bay region, the significant negative correlations between length and temperature were not and indeed could not be significantly increased by averaging the temperatures of the preceding month, which presumably rep-

TABLE V. SIMPLE, PARTIAL AND MULTIPLE CORRELATION COEFFICIENTS FOR MEAN LENGTH WITH THE TEMPERATURE AND CHLOROPHYLL OF THE DAY OF SAMPLING AND AVERAGED FOR THE PREVIOUS MONTH OBTAINED FOR COPEPODS FROM LONG ISLAND SOUND. x: LENGTH; y: TEMPERATURE; z: CHLOROPHYLL.

Species	No. of Pairs	r_{xy}	r_{xz}	r_{yz}	$r_{xy \cdot z}$	$r_{xz \cdot y}$	$R_{x \cdot yz}$
<i>P. minutus</i>							
Day of Sampling	25	-.957	.178	-.111	-.958	.249	.959
Av. of Previous Mo. . .	24	-.911	.062	-	-	-	-
<i>T. longicornis</i>							
Day of Sampling	26	-.945	.248	-.219	-.942	.128	.947
Av. of Previous Mo. . .	24	-.970	.267	-.249	-.968	.108	.971
<i>A. clausi</i>							
Day of Sampling	24	-.950	.272	-.261	-.946	.083	.950
Av. of Previous Mo. . .	21	-.927	.307	-.357	-.919	-.068	.918
<i>A. tonsa</i>							
Day of Sampling	28	-.874	.228	-.356	-.871	-.183	-
Av. of Previous Mo. . .	25	-.844	.191	-	-	-	-

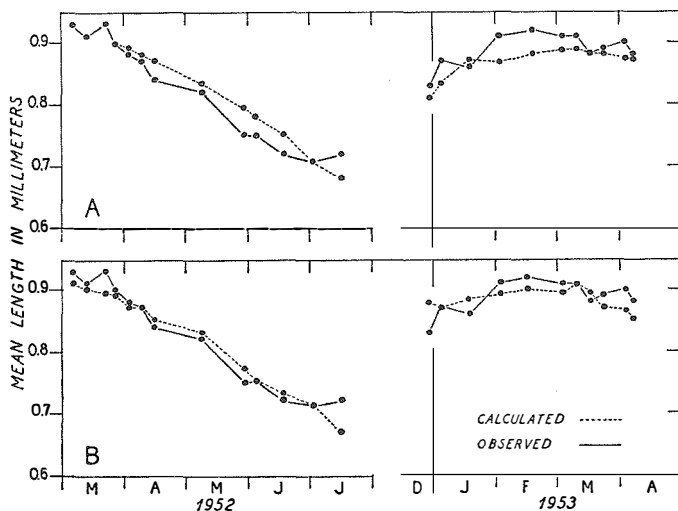


Figure 7. R. Conover's (1956) observed mean cephalothorax length cycles of female *Acartia clausi* compared with: *A* lengths calculated from the mean temperature and chlorophyll of the month previous to sampling; *B* lengths calculated from the temperature and chlorophyll of the day of sampling.

resent temperature conditions obtaining during the growth of the copepods. It should be noted, however, that at no time during the period studied were the quantities of phytoplankton minimal for copepod growth and reproduction (see Tables III, IV). Since sufficient food was always available, phytoplankton was not a limiting factor. Unfortunately, there are no data for waters with a wide temperature range and limited amounts of phytoplankton.

CENTROPAGES TYPICUS IN THE WESTERN MEDITERRANEAN

C. typicus is the dominant winter-spring species in the coastal waters near Castellón, Spain. It is numerous from November or December to July and is usually present in small numbers in late summer and early fall. In general the largest size was attained in March and the smallest from summer into fall, but in January 1955 the individuals were also quite small. The annual temperature range in these waters is 13–14°C. The extreme temperatures recorded during the two year period were 27.3°C in August 1955 and 10.3°C in February 1956. Fig. 8 compares the seasonal cycle in mean cephalothorax length in the western Mediterranean with the annual cycles of female *C. typicus* in the Delaware Bay region (Deevey, 1960) and in Block Island Sound (Deevey, 1952a). Although the pattern of the cycles is similar, the Mediterranean *C. typicus* is noticeably smaller than the American and was also smaller at comparable temperatures. Of the three localities, the annual range in mean length is greatest for the Delaware Bay region, which has the widest temperature range, and least for the western Mediterranean with the narrowest range.

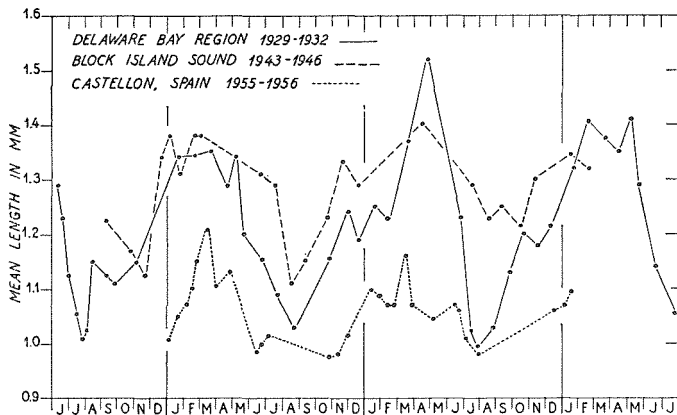


Figure 8. Seasonal mean cephalothorax length variations of female *Centropages typicus* from the western Mediterranean in 1955–1956 compared with those of female *C. typicus* in the Delaware Bay region (Deevey, 1960) and in Block Island Sound (Deevey, 1952a).

TABLE VI. FEMALE *Centropages typicus* FROM CASTELLÓN, SPAIN. MEAN CEPHALOTHORAX LENGTHS IN MM WITH MEAN TEMPERATURES IN °C AND MEAN HARVEY UNITS OF PIGMENT/LITER FOR DAY OF SAMPLING AND AVERAGED FOR PREVIOUS FOUR WEEKS.

Date	Number Measured	Ceph. Length	Temp. at Sampling	Temp. of Previous Mo.	H.U. at Sampling	H.U. of Previous Mo.
I/5/55	25	1.01	16.00	-	1.01	-
I/20	50	1.05	16.00	-	1.33	-
II/4	50	1.07	14.90	15.42	1.81	2.19
II/15	25	1.10	14.00	14.80	2.71	2.34
II/22	51	1.15	13.90	14.40	5.23	2.48
III/15	25	1.21	13.30	13.70	5.12	6.59
III/30	25	1.10	14.00	13.95	2.50	3.45
IV/22 & 29	50	1.13	17.10	15.42	1.21	1.65
VI/18	25	.99	23.30	20.76	.63	.96
VI/25	50	1.00	22.10	21.63	.63	.96
VII/7	25	1.02	25.10	21.82	1.32	.83
X/28	30	.98	21.10	22.95	1.64	1.20
XI/11	30	.99	19.50	21.83	.78	1.07
XI/30	50	1.02	18.00	19.45	2.50	1.63
I/13/56	53	1.10	14.00	14.70	2.61	2.58
I/31	52	1.09	14.00	14.30	2.62	3.19
II/13	50	1.07	12.50	13.87	2.50	2.97
II/22	50	1.07	12.80	13.40	4.04	3.04
III/14	50	1.16	14.00	12.40	1.04	2.28
III/27	50	1.07	13.50	12.90	2.67	1.56
V/3	50	1.04	15.30	14.85	1.90	1.59
VI/13	51	1.07	19.40	19.14	2.10	1.93
VI/21	53	1.06	21.10	19.84	.98	2.11
VII/6	51	1.01	20.50	21.15	.90	1.52
VII/31	52	.98	25.20	24.06	1.86	1.31
XII/18	28	1.06	15.70	15.97	1.50	2.10
I/3/57	51	1.07	-	15.60	-	1.55
I/13	51	1.10	-	15.30	-	1.66

It is of interest to note that in June and early July 1956 the Mediterranean specimens showed a secondary length maximum (see Fig. 8) that was more apparent in the total lengths than in the cephalothorax lengths. These specimens had an appreciably different cephalothorax to total length ratio, 0.670, compared with the ratio of 0.706 obtained from all others measured (see Table I); according to M. Durán (personal communication), they provide evidence for an influx at this time of offshore waters, presumably of northern Mediterranean origin. In 1956 there was also a spring maximum of more oceanic types of diatoms (Margalef, *et al.*, 1957). Therefore, in considering the seasonal cycle of *C. typicus* at Castellón it would probably be better to ignore this June maximum since it was caused by a biometrically different offshore population;

TABLE VII. SIMPLE, PARTIAL AND MULTIPLE CORRELATION COEFFICIENTS FOR MEAN LENGTH WITH THE TEMPERATURE AND PHYTOPLANKTON OF THE DAY OF SAMPLING AND AVERAGED FOR THE PREVIOUS FOUR WEEKS OBTAINED WITH 26 PAIRS OF DATA FOR FEMALE *Centropages typicus* FROM CASTELLÓN, SPAIN. x: LENGTH; y: TEMPERATURE; z: PHYTOPLANKTON.

	r_{xy}	r_{xz}	r_{yz}	$r_{xy \cdot z}$	$r_{xz \cdot y}$	$R_{x \cdot yz}$
Day of Sampling	-.701	.634	-.581	-.528	.390	.754
Av. of Previous Mo.	-.811	.745	-.592	-.688	.562	.899

however, these figures were included in the calculations. The mean lengths obtained for 1955 should represent the cycle of the coastal population.

Mean cephalothorax lengths, temperatures, and the quantity of phytoplankton (in Harvey units of pigment/liter) for the day of sampling and averaged for the four weeks previous are presented in Table VI. The correlation coefficients calculated from these data are listed in Table VII. Significant negative correlations between length and temperature and significant positive correlations between length and phytoplankton were obtained for both the temperature and phytoplankton data of the sampling date and of the previous month. The latter correlations, however, were somewhat higher than the former (see Table VII). Lengths calculated from both sets of data are compared with the observed lengths in Fig. 9. There is no significant dif-

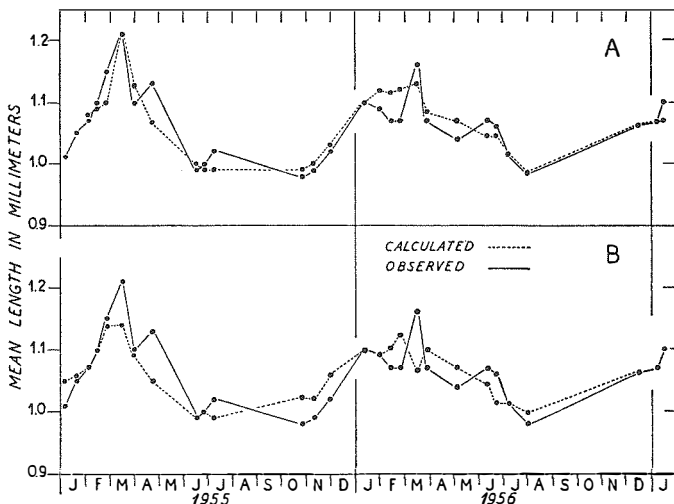


Figure 9. Observed variations in mean cephalothorax length of female *C. typicus* from the western Mediterranean compared with the length cycles calculated from: *A* the mean temperature and phytoplankton of the month prior to sampling; *B* the temperature and phytoplankton of the day of sampling.

ference between the two. Both closely follow the observed cycle, but as is indicated by the multiple correlation of 0.899, the fit is better for the temperature and phytoplankton data of the previous month (Fig. 9 A) than it is for the data taken at the time of sampling (Fig. 9 B).

In the localities thus far considered, maximal copepod size has usually coincided with periods of minimal temperature; therefore, significant negative correlations have been obtained between length and temperature at sampling as well as between length and the mean temperature of the previous month. Also, maximal length has usually been found at the same time of year as the major phytoplankton bloom, but for Long Island Sound no correlation was found between length and phytoplankton whereas a significant correlation was obtained for the Castellón region. This may be due to the fact that in the latter locality the temperature range is not as wide and the quantity of phytoplankton is usually considerably less than in Long Island Sound. Therefore temperature and the relative quantity of phytoplankton appear to be equally important in influencing seasonal length variations of *C. typicus* in the waters near Castellón. In 1955 the major phytoplankton bloom occurred between January and March and the total quantity was low during the rest of the year. In 1956 the cycle was less regular, since a small winter bloom was followed by small blooms in May and November. During both years the variations in length of *C. typicus* reflected both the phytoplankton and the temperature cycles (see Fig. 9).

LOCH STRIVEN

Data published by Marshall (1949) and by Marshall, *et al.*, (1934) for copepods of Loch Striven have been used to assess the relative effects of temperature and food on the annual size variations. The weekly temperatures and numbers of diatoms in 20 cc of sea water are listed by Marshall, *et al.* (1934, table IV). Loch Striven has a fairly narrow mean temperature range of 8–9°C. In 1933 the extreme range at 0 m was 4.5–16.4°C and at 30 m 6.37–12.98°C. Winter temperatures are not as low and summer temperatures are much lower than comparable data for the American waters considered. In 1933 the major diatom bloom occurred from late March to early April and was followed by smaller blooms in May, July and late summer. Only small numbers of diatoms were found during the winter. Adults of only three species of calanoid copepods, *Calanus finmarchicus*, *Pseudocalanus minutus*, and *Microcalanus pygmaeus*, were present during the winter in sufficient numbers for measuring, although a few female *Acartia clausi* were found in January and early February. *A. clausi* then disappeared until April, when adult *Centropages hamatus* and *Temora longicornis* also appeared. Since winter temperatures were not too low for these species, their absence during this period must have been due to other factors, possibly food. The seasonal cycle of

TABLE VIII. SIMPLE, PARTIAL AND MULTIPLE CORRELATION COEFFICIENTS FOR MEDIAN LENGTH WITH THE TEMPERATURE AND NUMBER OF DIATOMS IN 20 CC OF SEA WATER FOR THE DAY OF SAMPLING AND AVERAGED FOR THE PREVIOUS MONTH OBTAINED FOR COPEPODS FROM LOCH STRIVEN.
 x: LENGTH; y: TEMPERATURE; z: DIATOMS.

Species	No. of Pairs	r_{xy}	r_{xz}	r_{yz}	$r_{xy \cdot z}$	$r_{xz \cdot y}$	$R_{x \cdot yz}$
<i>P. minutus</i> females							
Day of Sampling	31	-.507	.203	-.199	-	-	-
Av. of Previous Mo.	29	-.689	.731	-.378	-.653	.701	.856
Stage III							
Day of Sampling	29	-.599	.291	-	-	-	-
<i>A. clausi</i> females							
Day of Sampling	21	-.443	.261	-	-	-	-
Av. of Previous Mo.	20	-.733	.581	-.368	-.686	.492	.805
<i>M. pygmaeus</i> females							
Day of Sampling	31	-.611	-	-	-	-	-
Av. of Previous Mo.	29	-.841	.549	-.378	-.819	.461	.904
<i>C. finmarchicus</i> females							
Day of Sampling	28	-.246	-.011	-.199	-	-	-
Av. of Previous Mo.	26	-.449	.614	-.485	-.219	.507	.637
Stage III							
Day of Sampling	22	-.854	.388	-	-	-	-
Stage I							
Day of Sampling	19	-.850	.594	-	-	-	-
<i>C. hamatus</i> females							
Day of Sampling	21	-.911	.068	-	-	-	-
Av. of Previous Mo.	21	-.912	.537	-.661	-	-	-

female *C. finmarchicus* and *P. minutus* showed small size in winter, an abrupt increase to maximal size in April, and then a gradual decrease during the summer months. *M. pygmaeus* was also largest in April, but the size changes were much less striking than those of the other species. The few *A. clausi* present in the winter were small, and maximal size in April was followed by decreasing length into the summer. *C. hamatus* and *T. longicornis* were also large in April and then decreased in length.

Table VIII lists the correlation coefficients obtained for Loch Striven copepods from the data for median length with the temperature and phytoplankton for the day of sampling and averaged for the previous month. In all instances significant simple correlations were found between length and temperature or number of diatoms averaged for the preceding month. Only Stage I *C. finmarchicus*, the youngest stage analyzed, gave a significant correlation between length and phytoplankton of the sampling date, but the females of all five species yielded significant correlations between length and

number of diatoms averaged for the previous month. Stage I and III *C. finmarchicus* and female *C. hamatus* gave high negative correlations between length and temperature at sampling; this was to be expected since these forms did not appear until the time of the spring bloom and then decreased in length into the summer; they were therefore larger at lower temperatures and smaller at higher temperatures. For all species, however, significant negative correlations were found between length and mean temperature of the previous month.

P. minutus females gave the highest partial correlations with both temperature and number of diatoms of the month prior to sampling (see Table VIII). *C. finmarchicus* females gave the lowest correlation with temperature and *M. pygmaeus* females the highest. The length cycles of the females of four species were calculated from the temperature and phytoplankton data of the month previous to sampling for comparison with the median lengths recorded

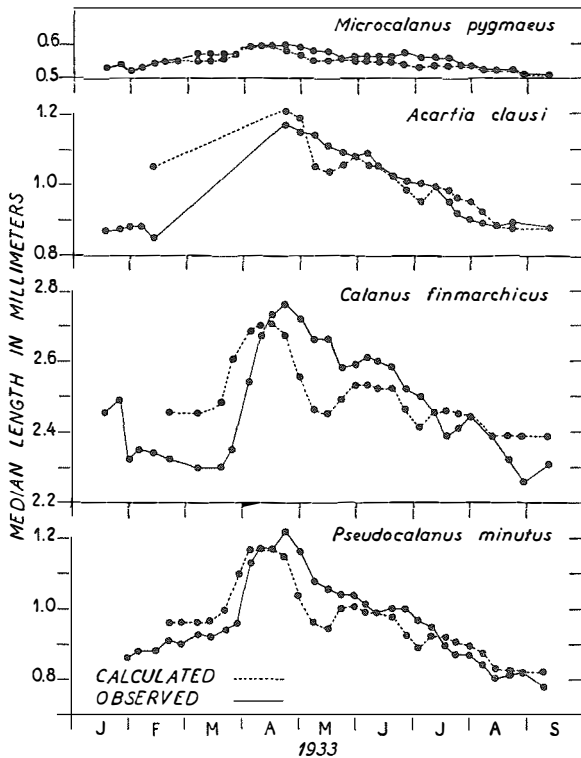


Figure 10. Observed seasonal variations in median length of female *M. pygmaeus*, *A. clausi* and *P. minutus* (Marshall 1949) and of *C. finmarchicus* (Marshall, *et al.*, 1934) in Loch Striven in 1933 compared with length cycles calculated for these species from the mean temperature and number of diatoms of the month previous to sampling.

by Marshall (1949) and Marshall, *et al.* (1934), and these are presented in Fig. 10. For all species the multiple correlations are significant (see Table VIII) and the calculated lengths show the same general pattern as the observed lengths. The agreement between the two is good in the case of *P. minutus*. *M. pygmaeus* females showed only slight variation in length during the year. For *A. clausi* females, few data were available for the winter months, but the April to September data are in fair agreement. The arbitrary choice of a month as the developmental period for all species can be expected to yield good results only when a species is breeding more or less continuously, so that the majority of specimens measured on any date should have developed during the previous month. If a species has definite breeding periods, or if the length of the developmental period varies during the year, as it may, particularly in the case of *C. finmarchicus*, or if females measured on any occasion are several months old at this time, the average temperature and phytoplankton of the month previous to sampling may bear little relation to the conditions under which the individuals matured. Everything considered, the agreement between the observed and calculated lengths is good. Thus in Loch Striven, where there is a narrow temperature range and a pronounced spring flowering, the annual pattern of copepod length variations reflects the phytoplankton and temperature cycles. As in Long Island Sound and in the western Mediterranean, maximal copepod size was found during the same period as the major diatom bloom, but unlike the other localities considered, this was not at times of minimal temperatures. In Loch Striven the relative sizes of successive generations are probably determined largely by temperature and by the quantity of phytoplankton available during development.

LENGTH-TEMPERATURE DATA FROM OTHER REGIONS

Length-temperature data are available for the English Channel, the North Sea and the Kattegat, and for Woods Hole, Massachusetts. Also, there are data for several species of copepods from Block Island Sound; some of these data have been published, but the correlation coefficients here presented have been calculated by using all mean length data from the 1943-1946 and 1949 surveys (Deevey, 1952a, 1952b). The correlation coefficients obtained for these localities are listed in Table IX. For all the European waters, with the exception of *T. longicornis* in the North Sea, the correlation between length and temperature was increased appreciably when the average temperature of the month prior to sampling was used. For Block Island Sound and Woods Hole, high negative correlations were obtained for length versus temperature at sampling, and at least in the case of *C. typicus* in Block Island Sound the correlation was not noticeably greater when temperatures of the previous

TABLE IX. CORRELATION COEFFICIENTS FOR MEAN OR MEDIAN LENGTHS WITH TEMPERATURE AT SAMPLING AND AVERAGED FOR THE PREVIOUS MONTH OBTAINED FOR SEVERAL COPEPODS FROM THE ENGLISH CHANNEL, THE KATTEGAT, THE NORTH SEA, AND SOUTHERN NEW ENGLAND WATERS.

	No. of Pairs	Length vs. Temp. at Sampling	No. of Pairs	Length vs. Temp. of Previous Mo.
English Channel (Digby, 1950)				
<i>Pseudocalanus elongatus</i> fem.	21	-.421	20	-.660
<i>Acartia clausi</i> females	18	-.329	17	-.654
<i>Paracalanus parvus</i> females	19	-.449	18	-.630
North Sea (Adler and Jespersen, 1920)				
<i>Pseudocalanus elongatus</i> fem.	49	-.526	45	-.729
<i>Temora longicornis</i> females..	47	-.605	45	-.607
Kattegat (Adler and Jespersen)				
<i>Pseudocalanus elongatus</i> fem.	44	-.655	43	-.739
Woods Hole, Mass. (Clarke and Zinn, 1937)				
<i>Calanus finmarchicus</i> females	15	-.876	-	-
Block Island Sound				
<i>Centropages typicus</i> females..	23	-.700	22	-.734
<i>Centropages typicus</i> males . . .	22	-.705	21	-.731
<i>Centropages hamatus</i> females	19	-.811	-	-
<i>Pseudocalanus minutus</i> fem..	16	-.788	-	-

month were averaged (see Table IX). This was also the case for the species studied from Long Island Sound and the Delaware Bay region.

It should be noted that although Digby (1950) and Adler and Jespersen (1920) referred to their *Pseudocalanus* as *P. elongatus* Boeck (see Table IX), this is usually considered synonymous with *P. minutus* (Krøyer). Wiborg (1954, 1955) believes they are different species, separating them on the basis of size, shape of body and length of the second antenna, *P. elongatus* being the smaller neritic species. In this instance size is not an ideal criterion, since the length ranges of the two appear to overlap completely. The largest Loch Striven *Pseudocalanus*, which Marshall (1949) identified as *P. minutus* but which Wiborg (1954: 127) has referred to as *P. elongatus*, were as large as the largest *P. minutus* recorded by Wiborg (1955) from the Norwegian Sea. Both had mean or median cephalothorax lengths of 1.2 mm. In this report the two are considered synonymous.

For the North Sea and the Kattegat, Adler and Jespersen tabulated mean length data for *P. elongatus*, *T. longicornis* and *C. finmarchicus*. At Horn Reef in the North Sea, weekly samples were collected during 1913; for Anholt Knob in the Kattegat, mean monthly cephalothorax lengths for January 1911 to September 1914 were listed with mean monthly temperatures at

10 m depth. Correlation coefficients were calculated for *P. elongatus* from both localities and for *T. longicornis* from the North Sea. The mean lengths for *T. longicornis* from the Kattegat and for *C. finmarchicus* from both areas were based on few measurements. For the North Sea in 1913, the mean temperatures listed gave an annual range of 13°C, but the mean range recorded for the Kattegat, greater than that noted in any of the European waters here considered, varied from 14.7° to 16.1°C during the four year period. In this respect the data from the Kattegat serve as a link between the colder European waters and American waters such as Block Island Sound, where the mean annual range is 17–18°C. The data for *P. elongatus* from the Kattegat gave a higher negative correlation, -0.655 , between length and temperature at sampling (see Table IX) than was obtained for any of the copepods that were found during the greater part of the year in other northwestern European localities. In the North Sea and the Kattegat, the major flowering occurs in the spring, and this is reflected in the seasonal size variations of *P. elongatus*. In the North Sea, as in Loch Striven, maximal size was found in the spring, *Pseudocalanus* being small during the rest of the year; in the Kattegat, however, the annual length cycle approached that noted for American waters: maximal size in April decreasing to minimal size in late summer and early fall, then increasing in size during fall and winter to the spring maximum. This pattern of maximal and minimal size lags a month or so behind the length cycle noted in American waters where the temperature range is slightly wider.

The annual length cycle of *T. longicornis* in the North Sea varied from that of *P. elongatus* in that there was a second length increase in November followed by decreased size in December. Since *T. longicornis* was small in summer and winter and then increased in size in both spring and fall when temperatures were rising and falling, respectively, the correlation coefficient for length versus mean temperature of the previous month, -0.607 (listed for this species in Table IX), is similar to that of -0.605 obtained for length with temperature at sampling. This is the only species that showed this secondary late fall length maximum. There is also a suggestion of a fall length increase in Digby's (1950) measurements of *T. longicornis* from the English Channel and in Adler and Jespersen's data for the Kattegat, but in these waters it was scarce during the fall months and few measurements were made. Such minor variations in the annual length cycle may be related to differences in the breeding cycles or to seasonal differences in the food or feeding requirements of the species (see Marshall, 1949; Marshall and Orr, 1955).

In the English Channel, as in these other European waters, the major diatom bloom occurs in the spring. In 1947 when Digby's data were collected there was an annual temperature range of 11–12°C. The seasonal length cycle of the smaller copepods followed the same pattern as that in Loch Striven; maximal length was found in the spring, and during the rest of the year the

copepods were relatively small. Using Digby's (1950) median length measurements, correlation coefficients were calculated for three calanoids that were taken during the greater part of the year. All yielded significant negative correlations between length and the average temperature of the month previous to sampling (see Table IX). It is evident that in the waters off Plymouth, England and in the North Sea and the Kattegat both the temperature and the quantity of phytoplankton available during development influence the relative size of adult copepods.

That food is a more important factor in these European waters than in the American waters studied is borne out by comparison of dry weight and length cycles. In the English Channel (Bogorov, 1934) and in Loch Striven (Marshall, *et al.*, 1934) there is a correlation between the dry weight and median length cycles of *Calanus finmarchicus* and the relative quantities of phytoplankton available during the year. In Block Island Sound, on the other hand, although the wet weights of *Centropages typicus* showed a good correlation with mean length, the dry weights did not (Deevey, 1952a). In some instances larger size meant only a higher water content. *C. typicus* increased in size with decreasing temperatures, but not necessarily at times of increased quantities of food.

DISCUSSION

The reactions of the same species to a variety of temperature and food conditions is exemplified by *Pseudocalanus minutus* (: *P. elongatus*), the one copepod for which there is a large body of data from a number of localities. These data show that the relative effects of temperature and quantity of phytoplankton vary widely in different waters and that annual patterns of size variations reflect local conditions. In East Greenland waters, where there is a minimal temperature range and where copepods produce but one generation a year, both Digby (1953, 1954) and Ussing (1938) found that adult female *Pseudocalanus* varied little in size, although the relative sizes of immature stages were related to the annual phytoplankton bloom. In Loch Striven, with a narrow temperature range and with the major diatom flowering in the spring, the temperature and the quantity of phytoplankton present during development are both important in determining the size of the adult; here the seasonal cycle is characterized by maximal size in spring and relatively small size during the rest of the year. Conditions are similar in the North Sea and in the English Channel. In the Kattegat, which has a somewhat wider temperature range, the annual pattern of length variations approached that found in American waters. In Block Island Sound, Long Island Sound and the Delaware Bay region there is a wide temperature range, and temperature is the most important known factor influencing seasonal variations in size. This has been shown for Long Island Sound in particular, where the partial correlation be-

tween length and temperature was exceptionally high, -0.958 , and where there was no correlation between length and chlorophyll. In Long Island Sound, *Pseudocalanus* increased in size well before the phytoplankton bloom and was smallest when more than adequate quantities of phytoplankton were present (see Table V). However, in Long Island Sound the quantity of phytoplankton was never minimal for copepod growth and reproduction; if it were, this might be reflected in the seasonal length cycle.

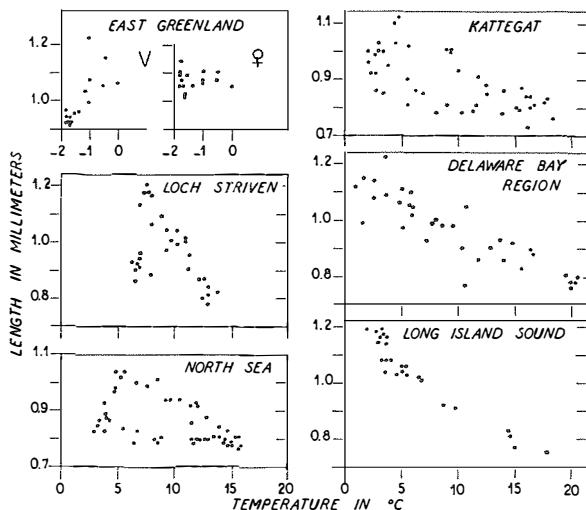


Figure 11. Dot diagrams of *Pseudocalanus* cephalothorax lengths plotted against temperature at sampling for stage V females and adult females in East Greenland waters (Digby, 1953, 1954), and for adult females in Loch Striven (Marshall, 1949), the North Sea and the Kattegat (Adler and Jespersen, 1920), the Delaware Bay region, and Long Island Sound. Digby's and Marshall's data are for median lengths, the others are mean lengths. Except for the East Greenland data, all are drawn to the same temperature scale.

The differing reactions of *Pseudocalanus* to the temperature ranges of these various regions are illustrated in Fig. 11, which shows dot diagrams of female mean or median length plotted against temperature at sampling; included are Digby's (1953, 1954) data for both stage V and adult females from East Greenland waters, Marshall's (1949) data for Loch Striven, Adler and Jespersen's (1920) measurements from the North Sea and the Kattegat, and the data from the Delaware Bay region and Long Island Sound. These diagrams show that the negative correlation between length and temperature at sampling increases with an increasing temperature range. In East Greenland waters, as already noted, adult females varied little in size, but stage V females were small in winter and larger from late spring to early fall during the period of the phytoplankton bloom. Since maximal lengths were found at the time of

the spring diatom bloom, the effect of the bloom is clearly discernible in the Loch Striven and North Sea diagrams; small size in winter was followed by an abrupt increase to maximal size in spring, after which there was a gradual decrease to minimal size in late summer and early fall. The Kattegat diagram may similarly be read clockwise, with maximal lengths in the spring, but the effect of the spring bloom is not as strikingly apparent; here the temperature range was wider, and during the winter *Pseudocalanus* gradually increased in length up to the spring maximum. In the Delaware Bay region and Long Island Sound, where the annual temperature range was about 20°C , the mean lengths of *Pseudocalanus* females were invariably greater in the winter (see Fig. 11). Comparison of the Kattegat and Long Island Sound diagrams shows that *Pseudocalanus* was present over the same temperature range in the two localities. Females were not sufficiently numerous for measuring at the highest Long Island Sound temperatures. The much more pronounced effect of temperature in Long Island Sound may be attributed to the more steeply rising temperatures of these waters, where summer temperatures appear to be too high for this species.

The European data for *Pseudocalanus* include only the more northern waters, where the major diatom bloom occurs in the spring. The seasonal cycle of *Centropages typicus* in the western Mediterranean illustrates the annual pattern of length variations found in waters where the temperature range ($13\text{--}14^{\circ}\text{C}$) is not as wide as that in the American waters studied but where the temperature and phytoplankton cycles are in direct opposition; the major bloom occurs in the winter when temperatures are minimal. In this case maximal size was also found in the winter and significant correlations were obtained between length and temperature and between length and phytoplankton. Thus the several regions (Loch Striven, the western Mediterranean, and Long

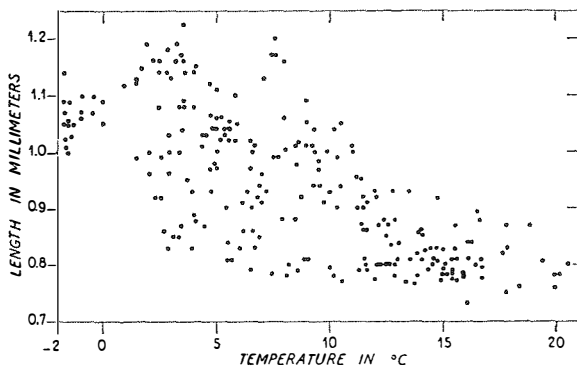


Figure 12. Dot diagram showing mean or median cephalothorax lengths of female *Pseudocalanus* plotted against temperature at sampling, including the data shown in Fig. 11 (except for Digby's stage V females from East Greenland) and data from the English Channel (Digby, 1950) and Block Island Sound.

Island Sound) for which there are both temperature and phytoplankton data demonstrate clearly that temperature and food are important factors governing the annual size variations of marine copepods and that their relative effects vary widely in different localities.

It is instructive to plot together all length-temperature data for representative species. Fig. 12 presents the adult female *Pseudocalanus* mean or median lengths plotted against temperature at sampling; it includes data from all the localities shown in Fig. 11 and from the English Channel (Digby, 1950) and Block Island Sound as well. Fig. 12 shows that at temperatures above 11°C this species was always small (mean cephalothorax lengths, 0.75–0.9 mm), but throughout the range of about 2–10°C there was wide variation in adult size, and this must be due largely to varying quantities of food available during growth. The East Greenland specimens had a narrow median size range, about 1.0–1.1 mm; despite minimal food conditions for the greater part of the year they were not small, nor were they as large as some from other localities and higher temperatures. Wiborg (1955) has noted that females were somewhat smaller in the Greenland Sea than in the temperate area of the Norwegian Sea. Thus it was always relatively large at sub-zero temperatures and always small at temperatures over 11°C, but over a range of 2–10°C, food or other factors may limit size. These data cover the entire temperature range of this species. Excluding Digby's (1954) measurements for East Greenland, where he found exceptionally large specimens which may be a different species, *Calanus finmarchicus* presents a similar picture at temperatures above 0°C: a wide range in length at temperatures up to 10–11°C and small size at higher temperatures.

For comparison with *Pseudocalanus*, the length-temperature data for female *Acartia tonsa* are illustrated in Fig. 13, drawn to the same scale as Fig. 12. *A. tonsa* has a breeding range of at least 30°C, but there are no data for the upper part of its range. It is a dominant species in inshore waters of the Gulf of Mexico (Grice, 1956) and southern Florida (Woodmansee, 1958), and

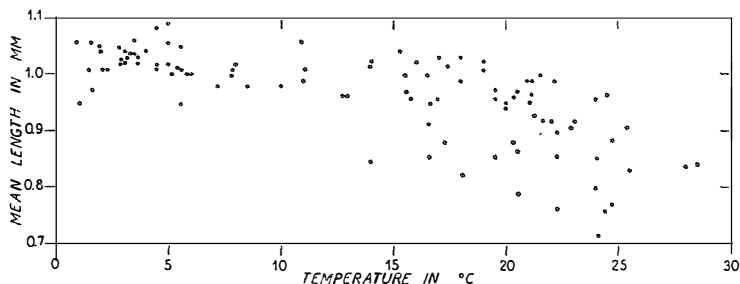


Figure 13. Dot diagram showing mean cephalothorax lengths of female *Acartia tonsa* plotted against temperature at sampling, including data from Long Island Sound (R. Conover, 1956), Block Island Sound, Delaware Bay and Tisbury Great Pond, Massachusetts.

measurements from such localities would fill this need. The data shown in Fig. 13 are from Long Island Sound (R. Conover, 1956), Block Island Sound, Delaware Bay and Tisbury Great Pond, Massachusetts (Deevey, 1948). *A. tonsa* was large up to 14°C and usually smaller at higher temperatures. This species obviously does not exhibit the wide seasonal variations in length shown by the boreal species, such as *P. minutus*. If sufficient data were available, presumably *Pseudodiaptomus coronatus* would yield a similar pattern since this species has the same temperature range as *A. tonsa* and showed even less seasonal length variation in Delaware Bay (see Figs. 3, 4).

The other common copepods considered in this report have length-temperature patterns intermediate between those shown for *P. minutus* and *A. tonsa*. These patterns indicate that whereas temperature or some factor associated with temperature is important in influencing seasonal size variations of copepods, the effects vary with the species. The species with narrower temperature ranges show greater seasonal variations in length. The known temperature ranges of the species here considered are discussed in the Delaware Bay report in this issue (Deevey, 1960: fig. 18).

In general it may be noted that the seasonal length cycles of the common marine calanoid copepods may be roughly correlated with latitude. All of the species here considered attained maximal size at approximately the same time of year as the major phytoplankton bloom, and this in temperate to boreal regions occurs with increasing light intensity after the darkest time of year. At Station M in the Norwegian Sea at Lat. 66°N there is a single phytoplankton maximum starting in April, with maximal quantities in July (Halldal, 1953). Stage V and female *Calanus finmarchicus* (Wiborg, 1954; Østvedt, 1955) were largest during this period. Between Lat. 50–56°N in Loch Striven and the English Channel the bloom occurs at some time from late March to May, and maximal copepod size is found during the April–May period (Marshall, 1949; Bogorov, 1934; Digby, 1950). Long Island Sound,

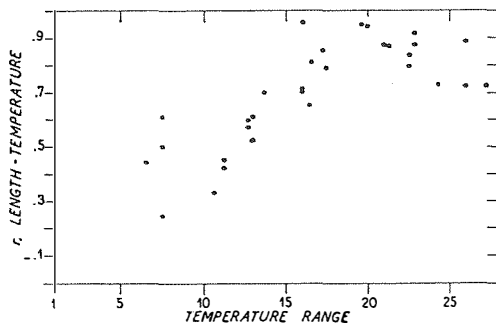


Figure 14. Correlation coefficients for adult copepod length versus temperature at sampling plotted against the temperature range of each set of data.

Block Island Sound and Castellón, Spain are at Lat. 40–41°N, and in these regions the major phytoplankton maximum is found in February to March, as is maximal copepod size. At this latitude there may be a correlation between length and phytoplankton, as in the case of *Centropages typicus* in the western Mediterranean, or there may not be, as in Long Island Sound, depending on the extent of the temperature range and the quantity of phytoplankton present during the year. At higher latitudes where annual temperature ranges are narrower, one would expect, as was found for Loch Striven, a correlation between phytoplankton and length cycles.

In Fig. 14 the correlation coefficients obtained for adult copepod length versus temperature at sampling are plotted against the temperature range of each set of data. The coefficient obtained for *Centropages hamatus* from Loch Striven is excluded, since this species was not adequately represented for a sufficient period during the year. Fig. 14 shows high negative correlations between length and temperature at sampling when the temperature range was 14°C or more. However, without exception, every species from every locality listed in Tables II, V, VII, VIII and IX yielded a significant negative correlation between length and the mean temperature of the month previous to sampling. Although less phytoplankton data are available, these are presented in Fig. 15, which shows the correlation coefficients for length versus mean quantity of phytoplankton of the month previous to sampling plotted against the temperature range of each set of data. Fig. 15 indicates that the effect of food on size increases when the temperature range is narrower. For Loch Striven and the Spanish coastal waters, where the temperature range was 14°C or less, significant positive correlations were found between length and phytoplankton, but in Long Island Sound, little correlation was noted. Theoretically, therefore, phytoplankton should be an important factor governing

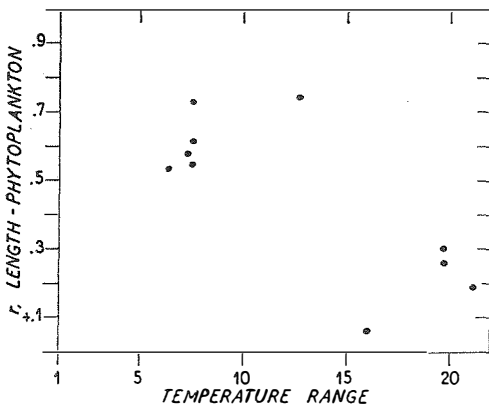


Figure 15. Correlation coefficients for length versus the mean phytoplankton of the month previous to sampling plotted against the temperature range of each set of data.

size variations in the Arctic, as suggested by Digby (1954) and Ussing (1938); it should also be a factor in equatorial waters or other regions where the temperature range is slight. Whether or not this is true might best be determined in warmer waters, since low temperatures greatly extend the developmental period.

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Георгиана Б. Дивей

Влияние температуры и пищи на сезонные вариации длины морских Копепод в некоторых Восточно-Американских и Западно-Европейских водах.

Краткий Обзор.

Все обыкновенные морские Копеподы умеренных и северных областей подвергнутые исследованию в течении большей части года, проявляли заметные сезонные колебания в зрелом возрасте. Годовой паблон вариаций длины различен в западно-европейских и восточно-американских водах. Принято что температура и пища являются важными факторами влияющими на вариации величины. По этому принимая во внимание как опубликованные, так и оригинальные данные, их относительное влияние было определено для нескольких широко разбросанных областей.

Простые, частичные и множественные коэффициенты корреляции были высчитаны по данным длины, температуры и фитопланктона в Проливе Лонг Исланд, в западной части Средиземного моря и в Лох Стривене. Для этих вод годовые циклы длины Копепод были высчитаны по данным температуры и фитопланктона для сравнения с наблюдаемыми годовыми вариациями длины, что установило их вполне удовлетворительную согласованность. Коэффициенты корреляции длины с температурой были тоже подсчитаны для областей не имевших соответственных данных по фитопланктону и включавших Делаверский Залив, Пролив Блок Исланд, Английский Пролив, Северное море, Каттегат и Вудс Хол, Массачусетс.

Эти данные показывают что относительное влияние температуры и пищи на сезонные вариации длины морских Копепод варьирует в зависимости от размера годовой вариации температур и от годового количества фитопланктона. Значительные отрицательные корреляции между длиной и температурой во время сбора проб были найдены во всех водах с годовой средней температурой в 14°C. или еще выше. Наоборот, когда температура была ниже 14°C. значительная положительная корреляция была найдена между длиной и средним количеством фитопланктона за месяц предшествующий сбору и представляющим пищевые условия во время развития. Каждый вид из каждой исследованной местности дал важные отрицательные корреляции между длиной и средней температурой предшествующего месяца.

В Проливе Лонг Исланд, где средняя температура приблизительно равна 20°C. температура является важным фактором влияющим на величину сезонных вариаций. В западной части Средиземного моря, с средней температурой от 13° до 14°C., и в Лох Стривене с средней температурой от 7° до 8°C. и температура и количество фитопланктона в период развития обуславливают относительные размеры последовательных поколений. Сравнение данных длины и температуры для двух представительных видов, *Pseudocalanus minutus* и *Acartia tonsa*, показывает что влияние температуры на длину может отличаться в одном виде от ее влияния, в другом виде в зависимости от их предельных температурных амплитуд.