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THE ZOOPLANKTON OF TISBURY GREAT POND

BY GEORGIANA BAXTER DEEVEY
Woods Hole Oceanographic Institution

Issued June, 1948

New Haven, Conn., U. S. A.

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BY GEORGIANA BAXTER DEEVEY[2]

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CONTENTS

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ABSTRACT

The purpose of this paper is to report the seasonal cycle of the zooplankton of Tisbury Great Pond and the effects of the wide range of temperature and salinity on the organisms. Zooplankton samples were taken usually at weekly intervals from May 20, 1945 to September 2, 1946. The majority of the samples were taken with a Clarke-Bumpus plankton sampler and a No. 10 net, but for a few only the net was used; since all the tows were made over the same course, quantitative estimates of the number of zooplankton per cubic meter have been made for the qualitative samples. The beach which separates the pond from the sea is opened at periodic intervals, so that during the year the salinity varies from less than 1 to 31°/₀₀ at the surface. The temperature varies from 0° to over 25° C.

The zooplankton is composed of several species of copepods, rotifers, *Podon polyphemoides*, larval forms of barnacles, gastropods, lamellibranchs, and polychaetes, and adventitious forms. *Acartia clausii* Giesbrecht was the dominant copepod during the first half of the year, disappearing at the beginning of July when the temperature reached 24° C. *Acartia tonsa* Dana appeared in June and was dominant throughout the summer. During both summers a sudden rise in salinity coincided with a marked decrease in numbers of this species. *Eurytemora hirundoides* (Nordquist) occurred during the period when *A. clausii* was dominant. These three species produced two generations a year in the pond. The rotifer *Synchaeta littoralis* Rousselet occurred erratically throughout the year, attaining its greatest maximum in May. The cladoceran *Podon polyphemoides* (Leuckart), which is extremely euryhaline but only moderately eurythermal, was present only during May and June while the temperature was rising from 12° to 24° C.

All the organisms living in the pond for any length of time are fairly euryhaline. The temperature is therefore more important in limiting the periods of their occurrence. The range of salinity bars the littoral forms that would occur in greater abundance if the pond were always open, as in estuarine situations. The members of the zooplankton are grouped according to the degree of their temperature and salinity tolerances.

Phytoplankton counts showed that diatoms were numerous throughout the year while flagellates and dinoflagellates were most abundant during the summer months. There were two pronounced maxima, a January diatom maximum and an August maximum of flagellates.

The total zooplankton counts showed a seasonal cycle with a single late spring maximum. Almost no zooplankton was present during the fall months; from January to March there was a barely perceptible increase in quantity, but from March to August the various species attained maximum numbers. There is no direct correlation between the abundance of the zooplankton and the temperature, the salinity, or the total numbers of phytoplankton.

INTRODUCTION

The primary objective of this paper is to report the seasonal changes in the zooplankton of Tisbury Great Pond. This is a shallow brackish water pond, separated from the sea by a narrow beach, on the southern shore of Marthas Vineyard, Massachusetts. The salinity of the pond varies greatly, due to the periodic opening of the beach. This is done intentionally in order to maintain an adequate salinity for oyster culture. Because of this the pond presents a specialized type of environment, and it was of interest to discover what planktonic organisms are capable of surviving under these extreme conditions. During the year the temperature range is also considerable. Therefore, the secondary objective was to determine the effects of the wide variations of salinity and temperature on the zooplankton population.

Tisbury Great Pond differs from an estuary in that it is open to the sea for only limited periods of time. During these intervals littoral organisms, mainly copepods, enter the pond. Usually within a month's time the opening has filled with sand, so that the pond is once more cut off from tidal action. As the salinity decreases the adventitious forms that are unable to withstand the lower salinities disappear. Only euryhaline organisms are capable of living in the pond for any length of time. The zooplankton population consists, therefore, of brackish water species, neritic organisms, and the larval forms of adults adapted to these conditions.

The zooplankton tows were made by Willard Huntington as part of the collection of samples and data for the Woods Hole Oceanographic Institution project concerned with the study of salt ponds under the direction of George L. Clarke. This was a cooperative investigation. The results of the analysis of the oysters will be published later by Yvette H. Edmondson. Phytoplankton counts, covering the twelve month period from September 1945 to September 1946, were made by Mary Goffin. This material will not be published separately, and therefore a brief summary of the phytoplankton is included in this paper in order to complete the picture of the plankton and to compare the seasonal abundance of the phytoplankton and the zooplankton.

ACKNOWLEDGMENTS

I am indebted to George L. Clarke for suggesting this problem, for the privilege of examining this material, and for making it possible for me to carry out the work at the Woods Hole Oceanographic Institution and later at the Bingham Oceanographic Laboratory. Grateful acknowledgment is also due to my co-workers, especially to Y. H. Edmondson for sharing with me the data for temperature, salinity, and phytoplankton and to W. T. Edmondson for the identification of the rotifers. I am extremely grateful to Daniel Merriman, Director of the Bingham Oceanographic Laboratory, for granting me the facilities of the laboratory. For their advice and very helpful criticism of the manuscript, I am indebted to Ernest F. Thompson, G. L. Clarke, and my husband, Edward S. Deevey, Jr.

METHODS

The Clarke-Bumpus plankton sampler (Clarke and Bumpus, 1940) was used in making the zooplankton tows. These were taken usually at weekly intervals from May 20, 1945 to September 2, 1946. The tows were made in the vicinity of the oyster beds between two landmarks on the southwestern shore of the pond. The first several tows were made with a No. 2 silk net, but from June 18, 1945 onward a No. 10 silk net was used. Few samples could be obtained in midwinter as the pond was frozen over for part of December, January, and February. The quantitative data cover the period from August 31 to December 2, 1945; then there was a long break in midwinter, and although samples were obtained on January 6 and February 10, 1946, unfortunately the number of revolutions was not recorded. The quantitative data continue from March 10 to July 7, 1946, when the sampler was returned to Woods Hole. The remaining 1946 summer samples were taken with a No. 10 net. Since all the tows were made over the same course, quantitative estimates for the qualitative samples have been obtained by averaging the number of revolutions recorded for the quantitative samples. The average number of revolutions, 328.2, and its standard deviation of 165.5, provide a quantitative "belt of confidence" for the qualitative samples. From this the approximate number of organisms per cubic meter can be estimated.

One to four counts were made on each sample, the number depending largely on the quantity and variety of organisms present. As a rule at least 500 organisms were counted, except in the case of the extremely scanty fall samples, where on one occasion, for example, 40 per cent of the total sample yielded only 36 organisms.

It has been impossible to identify the copepod nauplii while making the counts. In the later sections, where the developmental stages of the most important copepods are considered, the nauplii are assumed to belong to the currently dominant species. There can be little doubt of the identity of the great majority of nauplii in each case since only one species was abundant at any one time.

SALINITY AND TEMPERATURE

Fig. 1 gives the temperature and salinity data for the period covered by the samples. These data are for the surface temperatures and salinities only, since the tows were made just below the surface. Hydrometer readings were made whenever samples were collected and these have been converted to salinity readings by means of Knudsen's tables. The times when the beach was opened are indicated by arrows in Fig. 1; in 1945 this occurred on May 17, August 12–13, and December 10, and in 1946 on March 11, in late June and in late August. The extreme range of salinity at the surface during the period studied is from less than 1 to 31°/₀₀. The salinity varied from the surface to the bottom at around eight or nine feet, the lower layers always being more saline. The water was mixed when the beach was opened; as the pond closed the less saline water was found at the surface. Extreme differences in salinity resulted in mid-December when the pond was frozen and the beach was opened; at five feet the salinity was 26.05°/₀₀, while the surface layer was fresh.

The temperature cycle of the pond showed a range of from 0° to over 25° C. at the surface. From December through February the temperature varied between 0° and 6° C.; during March and April a slow rise occurred, followed by an abrupt increase in May. By late June the temperature reached 24° C. and until mid-September it oscillated between 20° and 25° C. Early in October the temperature dropped rapidly, then continued to decrease more slowly to the minimum. Only slight thermal stratification occurred.

THE SEASONAL CYCLE OF THE ZOOPLANKTON

The zooplankton of Tisbury Great Pond is composed of the following elements: (1) The copepod population, of which *Acartia* is the dominant genus. (2) Sporadic maxima of larval forms, which include barnacle nauplii and cyprids, gastropod and lamellibranch veligers, and polychaete larvae. (3) A rotifer population, consisting of two species of *Synchaeta*. (4) A late spring population of the cladoceran *Podon polyphemoides*. (5) Forms entering the pond accidentally when the beach was opened. Of these *Sagitta* appeared in greatest quantity

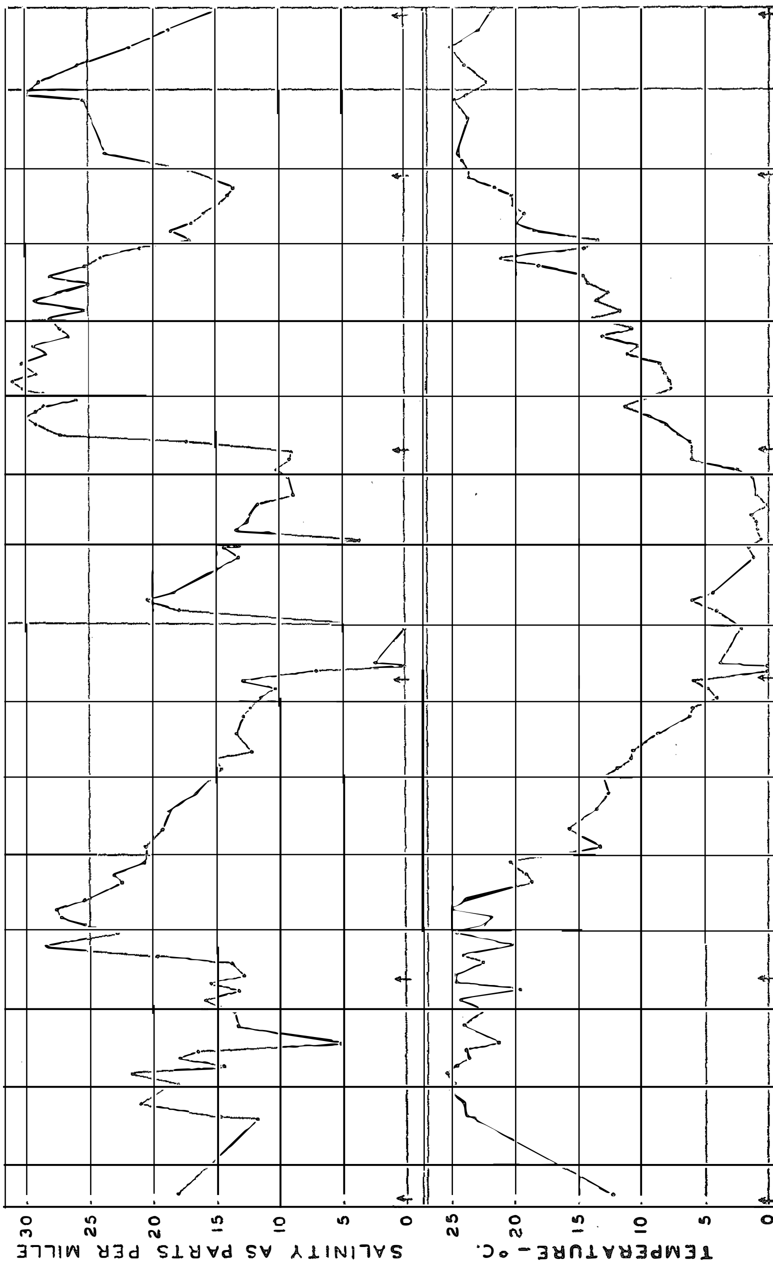

Figure 1. The temperature and salinity of the surface layers of Tisbury Great Pond from May 20, 1945 to September 2, 1946.

TABLE 1. Seasonal Cycle of Abundance of the Major Elements of the Zooplankton of Tisbury Great Pond. Semiquantitative, as Number per Cubic Meter. x: 1–100; xx: 101–1,000; xxx: 1,001–10,000; xxxx: 10,001–100,000; xxxxx: 100,001–1,000,000.

	1945							1946							
	June	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
Acartia clausii	xxx	x	—	—	x	x	—	x	x	xx	xxx	xxxx	xxxx	xx	—
Acartia tonsa	xxxx	xxxx	xxxx	xx	—	—	—	x	—	—	—	—	x	xxx	xxx
Eurytemora hirundoides	xx	x	—	—	—	x	—	xx	xx	xxx	xx	xx	xx	x	—
Centropages hamatus	x	x	—	—	—	—	—	x	x	x	x	x	x	x	—
Oithona brevicornis	—	—	—	—	—	—	—	—	—	x	x	x	xx	xx	xx
Harpacticoids	x	x	x	x	x	x	—	x	—	xx	xx	x	xx	xx	x
Copepod Nauplii	xxx	xxxx	xxxx	xxx	xx	xx	x	xx	xx	xxxx	xxx	xxxx	xxxx	xxxx	xxx
Podon polyphemoides	xxx	—	—	—	—	—	—	—	—	—	—	xxx	xxx	—	—
Barnacle larvae	x	x	x	x	—	x	x	x	x	x	xx	xxx	xxx	x	x
Polychaete larvae	xx	x	xx	xx	x	xx	x	—	x	x	xxxx	xxxx	xx	xx	xx
Gastropod veligers	xxx	x	x	xx	xx	x	—	—	x	x	x	xxx	xxxx	xxx	xx
Lamellibranch veligers	x	xxx	xx	xx	xx	xxx	xx	—	—	—	x	xxx	xxx	xxx	xx
Synchaeta littoralis	—	—	x	xx	—	—	x	xx	xxx	xxx	xxx	xxxxx	xxx	xx	x
Synchaeta sp.	—	—	—	—	—	xx	xx	x	x	—	—	—	—	—	—
Aver. Surface Temperature (° C.)	—	23.9	22.9	21.6	14.15	9.9	2.97	3.46	0.91	7.33	9.72	15.0	20.1	24.3	23.8
Surface Salinity Range (°/₀₀)	11.7–21.9	5.2–21.6	12.8–28.4	20.5–27.6	16.7–20.5	12.2–15.0	0–12.8	13.2–20.3	3.6–13.3	9.0–29.9	26.7–31.0	25.0–29.2	13.7–18.4	17.0–29.8	18.5–28.9

on one occasion, but several littoral copepods also belong in this category. Table I summarizes, semiquantitatively, the seasonal abundance of the various organisms and also gives the average monthly surface temperature and the surface salinity range in parts per mille.

THE COPEPOD POPULATION

Acartia tonsa Dana

Appeared in mid-June 1945, late June 1946
Disappeared in September
Temperature range: 19.6°–25.4° C.
Extreme salinities from both summers: 5.2–29.8°/oo

Acartia tonsa is the most abundant copepod in Tisbury Great Pond during the summer months. This is a littoral form capable of living in waters of relatively low salinities. In Chesapeake Bay, Davis (1944) found it in water with a chlorinity of 0.4°/oo as well as in water with a chlorinity approaching that of the ocean. Bigelow and Sears (1939) considered it probably an indicator of coast water. Cape Cod forms the northern boundary of this species (Bigelow, 1926). It is abundant in the Woods Hole region, both in brackish ponds and in the open water off Marthas Vineyard (Wilson, 1932a; Sharpe, 1910; Clarke and Zinn, 1937). *Acartia tonsa* has also been reported abundant in the

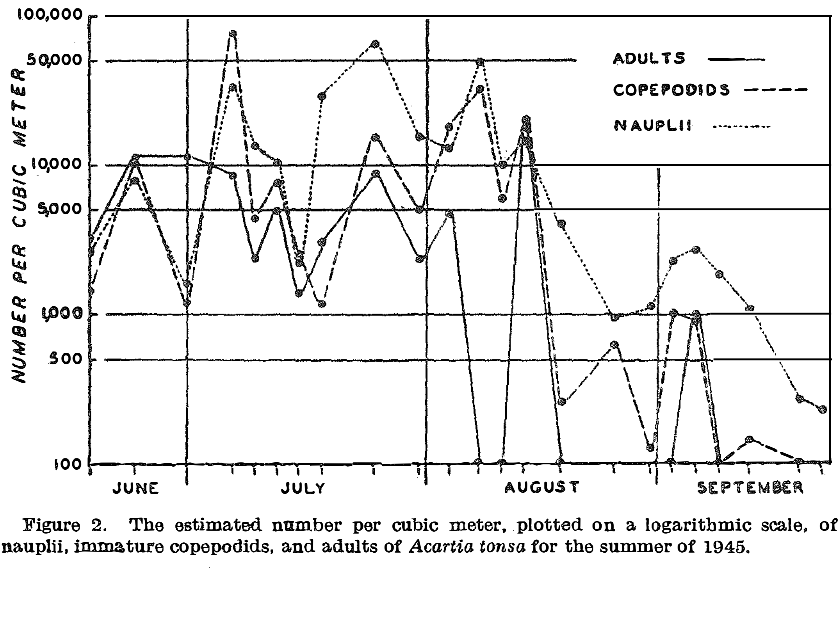

Figure 2. The estimated number per cubic meter, plotted on a logarithmic scale, of nauplii, immature copepodids, and adults of *Acartia tonsa* for the summer of 1945.

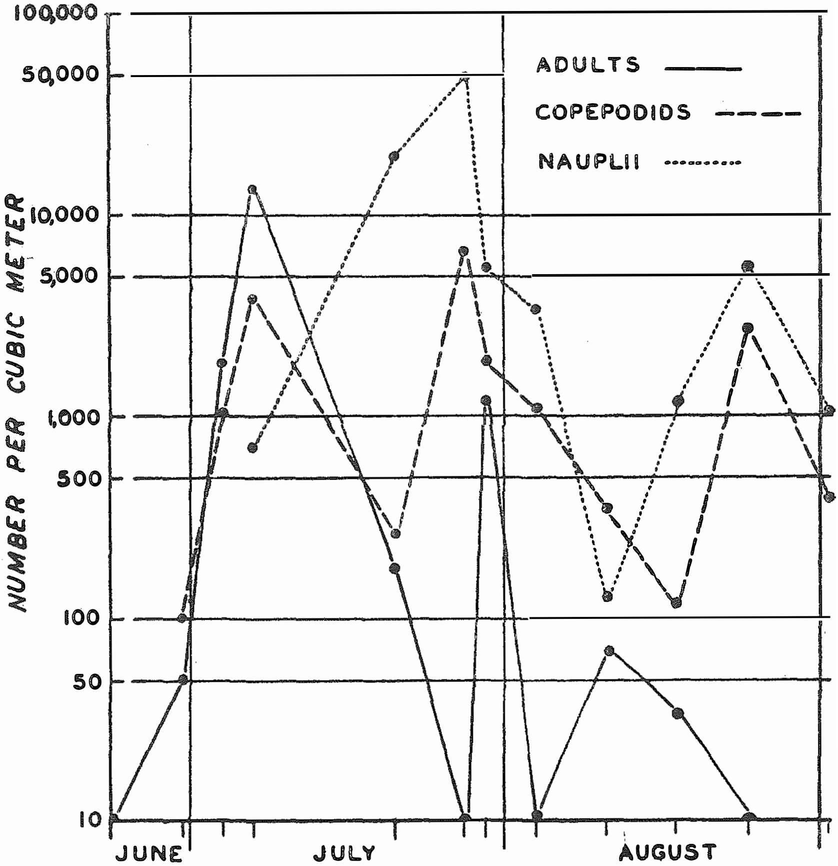

Figure 3. The estimated number per cubic meter, plotted on a logarithmic scale, of nauplii, immature copepodids, and adults of *Acartia tonsa* for the summer of 1946.

bays in San Diego, California by Esterly (1905), from the Louisiana coast by Foster (1904), and from Long Island bays (Tressler and Bere, 1939). Fish (1925) listed *A. tonsa* as one of the two most typical summer copepods in Woods Hole Harbor.

Figs. 2 and 3 give in graphical form the estimated numbers per cubic meter, plotted on a logarithmic scale, of nauplii, copepodids, and adults of *Acartia tonsa* for the summers of 1945 and 1946 in Tisbury Great Pond. In Fig. 2, two major maxima of adults are apparent, one in late June to early July and the other in mid-August. Each of these was followed by a secondary maximum, one in late July and the other in early September. Bursts of nauplii produced by the adults were evident throughout July and early August. Immediately following the mid-August adult maximum, however, there was a sudden drastic reduction in numbers of the *Acartia* population. The total number of all stages from nauplius to adult dropped from 55,000 on August 14 to about 4,000 per cubic meter on August 19. Nauplii were not produced in any quantity by the adults maturing in mid-August, and after the small peak of adults in early September, mature *Acartia tonsa* disappeared from the samples. Copepodids remained in small numbers until early October, and a few adult females were observed in early January 1946, but no more *A. tonsa* were found until the following June.

During the summer of 1946 (see Fig. 3), *A. tonsa* was not as successful as in 1945. The first adult maximum occurred in early July and was followed by a peak of nauplii and then a secondary adult maximum in late July, but between July 28–30 there was, once again, a sharp drop in numbers of the total *Acartia* population, including adults, copepodids, and nauplii, from 55,000 to a little over 8,000 per cubic meter. The latter number was not exceeded for the rest of the summer, nor did the second major maximum of adults materialize in the samples, although the small numbers of adults found in mid-August may represent the survivors of this group. It is possible, also, that a maximum of adults may have occurred in September, but the data stopped on September 2 and on that day the stock of *A. tonsa* was very low in numbers.

The cause of the abrupt decimation of the *A. tonsa* population is not clearly apparent, but on both occasions the marked diminution in numbers coincided with a sudden increase in the salinity. Fig. 4 shows in graphical form on a logarithmic scale the total numbers of copepodids and adults plotted together with the surface salinity readings for the summer of 1945; the arrow indicates the date the beach was opened. In this case the total numbers of copepodids and adults dropped from about 40,000 on August 14 to 250 per cubic meter on August 19. The beach was opened on August 12–13, but there was a time lag before the change in salinity showed up in the hydrometer readings. According to the readings, the salinity on August 19 was 14.0°/₀₀, and the drastic rise in salinity occurred between then and August 22, with the maximum salinity of 28.5°/₀₀ on August 26. Un-

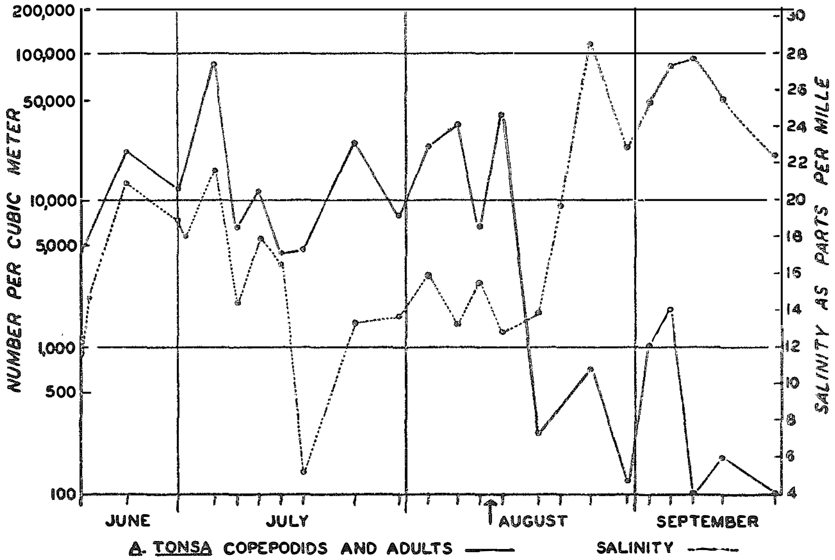

Figure 4. The total number per cubic meter, on a logarithmic scale, of copepodids and adults of *Acartia tonsa* plotted with the surface salinity for the summer of 1945.

questionably the salinity at the deeper levels was much greater than at the surface. It is also probable that the *Acartia* came in contact with a layer of this much more saline water before the hydrometer registered the change at the surface and that this may have been the cause of the drastic reduction in numbers of the population. As an alternative it is perhaps possible that tidal currents may have dispersed the population on this occasion, but this would not apply to the 1946 decrease.

In 1946 the circumstances were different. Fig. 5 gives in graphical form on a logarithmic scale the total numbers of adults and copepodids plotted with the surface salinity. In 1946 fewer numbers of adults and copepodids were found, and so the total numbers of *Acartia* of all stages including nauplii are also shown. During this summer the beach was opened at the end of June and again at the end of August, as indicated by arrows in Fig. 5. In this case *A. tonsa* appeared immediately after the opening of the beach at the end of June. The salinity had been rising from 13.5°/₀₀ in the latter part of June to 25.5°/₀₀ on July 28. During the next two days, within which time the marked decrease in total numbers of *Acartia* occurred, the salinity rose

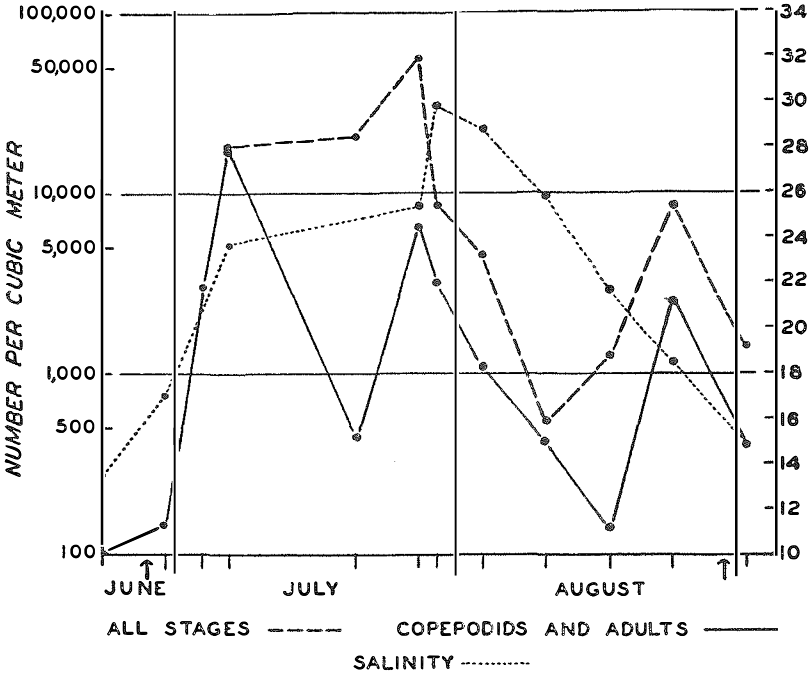

Figure 5. The total number per cubic meter, on a logarithmic scale, of all stages and of copepodids and adults of *Acartia tonsa* plotted with the surface salinity for the summer of 1946.

to 29.85°/₀₀. It is impossible to prove from these data whether this increase is sufficiently abrupt to cause such a sudden drop in numbers of *Acartia*. If these changes in salinity are concerned in the equally drastic diminution of the *A. tonsa* population, it is apparent that only the most abrupt increases at the higher salinity levels can be responsible. A steep drop in salinity in 1945 (see Fig. 4) did not affect the numbers of *Acartia*, nor did sharp rises in salinity which occurred over a week's time. However, the coincidence of an abrupt rise in salinity with a drastic reduction in numbers of *Acartia tonsa*, occurring twice, seems too great to be fortuitous. The evidence indicates that although *A. tonsa* has a wide salinity tolerance it may not be sufficiently heteroeuryhaline to withstand a sudden change in salinity.

In 1946, due to the fact that *A. tonsa* was found in numbers only during the month of July, adults of the midsummer maximum did not appear in appreciable quantity, but in 1945 two months elapsed before the sudden mortality of *Acartia* occurred. Judging from the data for this latter period (see Fig. 2), *A. tonsa* produced one generation during the summer. During the period studied, two generations a year were produced, the first maturing in late June and early July and the second in mid-August. The length of time intervening between the two major maxima of adults was six to seven weeks in summer, from late June-early July to mid-August. A similar interval occurred between the two secondary adult maxima in late July and early September; the late July group probably represents a second brood of the parents of the early July maximum. Six to seven weeks is a reasonable time interval for the development of *Acartia* at temperatures ranging between 20° and 25° C., and is within the time range obtained for other calanoid copepods. The developmental period of *Calanus finmarchicus* varies considerably, with temperature as an important factor, from one month in the laboratory (Nicholls, 1933) to three months in the Norwegian Sea (Ruud, 1929). In the Gulf of Maine 2½ months are necessary for its development from egg to spawning adult (Fish, 1936a). Clarke and Zinn (1937) also gave 2½ months as the approximate interval between the spring and summer generations of *Calanus* off Marthas Vineyard. *Pseudocalanus minutus* has a developmental period of approximately two months in the Gulf of Maine (Fish, 1936b). It is a fair assumption that no more than six or seven weeks should be required for the development of *A. tonsa* under summer conditions.

Less can be said conclusively about the origin and development of the generation reaching maturity in late June and early July. It is not inconceivable, since such is apparently the case with *Calanus*, that offspring of the August maximum overwinter in late copepodid stages to form the first generation the following year. But we lose sight of *A. tonsa* until it appears in numbers in late June. During the spring, however, immature stages may have been overlooked, due to the presence in numbers of *A. clausii*. It is also possible that *A. tonsa* may not have overwintered in the pond from 1945 to 1946, and that this species returned after the opening of the beach late in June 1946. On the other hand, in the spring of 1945 *A. tonsa* did not appear until about a month after the beach was opened in May.

Acartia clausii Giesbrecht

Appeared in early copepodid stages in October
Disappeared in early July
Maxima in mid-April and June
Temperature range: 0°–24° C.
Extreme salinities: less than 1–31°/oo

Acartia clausii is a northern species and has a lower temperature range than *A. tonsa.* From Cape Cod south it is strictly neritic (Bigelow and Sears, 1939), but in more northern waters it occurs farther out from the coast. It is widespread over the Gulf of Maine, although more numerous in shallow waters (Bigelow, 1926). In reporting the Port Erin plankton investigations, Johnstone, Scott and Chadwick (1924) listed *A. clausii* as a North Atlantic oceánic species. Wiborg (1940), in his study of the zooplankton of Oslo Fjord, also considered it dependent on Atlantic water to a certain extent. On the other hand, Gurney (1928–1929) referred to *A. clausii* as a littoral and brackish water form. It was found to be the dominant species in l'Etang de Thau, a pond connected with the Mediterranean (Fatemi, 1938) and also in the Thames estuary (Wells, 1938). In 1932 Wilson (1932b) reported it the dominant copepod in Chesapeake Bay throughout the year. More recently Davis (1944) found *A. tonsa* more numerous than *A. clausii* in the Bay, although Wilson had not found *A. tonsa* there. Davis was not specific about the dates when his samples were collected, but he said that most of them were obtained in August 1942, and some at other times, especially during the winter months of 1942–1943. From this it is impossible to tell whether the greater abundance of *A. tonsa* is seasonal, or whether *A. tonsa* is now the dominant form during the entire year. In any event, *A. tonsa* has only recently appeared in Chesapeake Bay to equal or exceed *A. clausii* in numbers.

From October to March only a few *Acartia clausii* were found in Tisbury Great Pond. During the fall months, small numbers of early copepodid stages were observed. Specimens examined from a late November sample proved to be at Stages III and V as described by Grandori (1912). By early January 1946 a few adults were also present. From then until late March *A. clausii* was well outnumbered by rotifers and *Eurytemora hirundoides,* the only organisms to increase in numbers during the early months of the year.

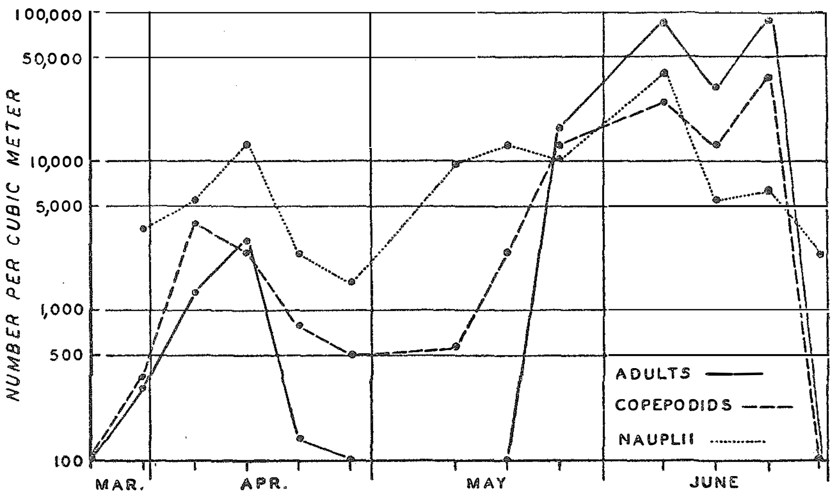

Figure 6. **The number per cubic meter, on a logarithmic scale, of nauplii, copepodids, and adults of *Acartia clausii* for the spring of 1946.**

Fig. 6 gives in graphical form, plotted on a logarithmic scale, the age structure of the *Acartia clausii* population during the period from late March to the end of June. Two maxima of adults were apparent, the first in mid-April and the second in June. The first spring generation consisted of relatively small numbers, only about 3,000 adults per cubic meter, compared with the later June generation. This may be partly due to the predatory activities of the hydromedusae and sagittae that were present in the pond during April. Fatemi (1938) also noticed a decrease in the number of *Acartia* coincident with the presence of hydromedusae. *A. clausii* was most abundant throughout June, but a week before its disappearance the highest count of 86,000 adults per cubic meter was obtained. About 122,000 *Acartia* per cubic meter, including immature copepodids and adults, virtually disappeared in a week's time. Between June 23 and June 30, when the samples were taken, the beach was opened again, but this cannot be entirely responsible for the disappearance of the *Acartia clausii* population, since *A. clausii* vanished on July 2 the previous summer, although the beach was not opened at that time. In 1946 a few adult *A. clausii* were present until July 4.

In this instance the evidence indicates that temperature was the deciding factor, limiting the period of occurrence of *A. clausii* in the surface layers of Tisbury Great Pond. During the early spring an abrupt rise in salinity from 9.0 to 29.9°/₀₀ did not have an adverse effect on this species. At the time of the April maximum the temperature was 8.6° C., and the salinity was 30.3°/₀₀. In June, while *A. clausii* was present in large numbers, the temperature varied between 20° and 21.7° C., and the salinity between 13.5 and 20°/₀₀. It is evident that *Acartia clausii* has a wide temperature and salinity tolerance. However, temperatures approaching and exceeding 24° C. may have a deleterious effect on the population. Both in 1945 and in 1946 the temperature had reached this point when *Acartia clausii* disappeared.

A. clausii had two generations during the year. The time interval between the mid-April maximum and the June maximum is eight to ten weeks, and therefore this is the length of time required for the spawning and development of the late spring generation. As in the case of the first generation of *A. tonsa*, the origin and the length of the developmental period of the first generation of *A. clausii* are not fully evident in these data, but the appearance of young copepodids in the fall suggests that a few offspring of the June maximum may have survived the summer, perhaps at or near the bottom of the pond. A slow development of these individuals is also indicated. If these copepodids are the offspring of the previous June maximum, the length of the developmental period was about ten months at most. The present data do not offer sufficient evidence to prove whether young stages of *A. clausii* and *A. tonsa* survive periods of adverse conditions in small numbers, or where this may occur. However, this cyclic alternation of *A. clausii* during the spring months and *A. tonsa* during the summer, observed for two successive spring and summer seasons, is probably a yearly occurrence in Tisbury Great Pond, at least under present conditions. If the pond were allowed to remain closed for an extended period it would be interesting to learn how long each population could maintain itself at extremely low salinities.

Eurytemora hirundoides (Nordquist)

Appeared in early copepodid stages in November
Disappeared in early July
Temperature range: 0°–24° C.
Extreme salinities: less than 1–31°/₀₀

E. hirundoides is common in brackish and fresh ponds in the Woods Hole area, although it occasionally appears in waters of higher salinity.

Fish (1925) reported its occurrence in Woods Hole harbor during the spring months, and Davis (1943) found it in Chesapeake Bay under widely varying conditions of temperature and salinity. It is scarce in the Thames estuary (Wells, 1938) and in Oslo Fjord (Wiborg, 1940), although Sars (1903) found it in both brackish and salt water on the Norwegian coast. That it is predominantly a brackish water form is evidenced by the fact that it was not taken by Bigelow (1926) in the Gulf of Maine or by Bigelow and Sears (1939) in their study of the coastal waters from Cape Cod to Cape Hatteras.

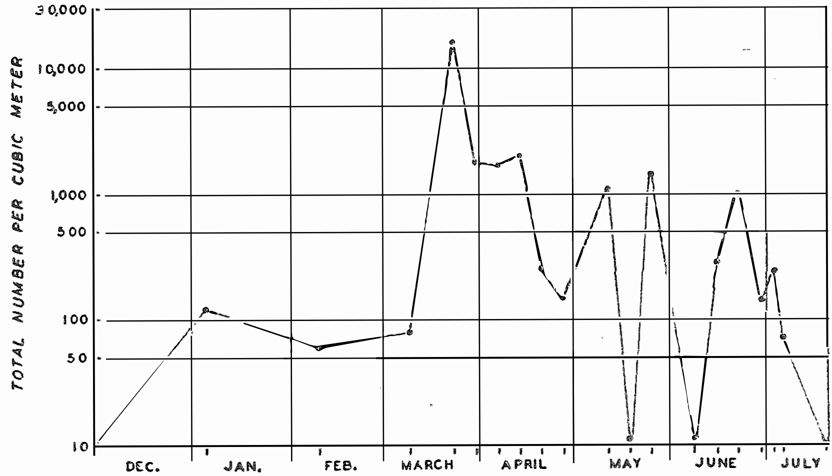

Figure 7. The total number per cubic meter, on a logarithmic scale, of copepodids and adults of *Eurytemora hirundoides* from January to July 1946.

Considering its salinity preferences it is surprising that *E. hirundoides* is not a more dominant form in Tisbury Great Pond. Possibly the sudden increases in salinity when the beach is opened have an adverse effect on it, but this is not borne out by the data, for the largest number recorded, nearly 17,000 per cubic meter, occurred coincident with a sharp rise in salinity from 9 to 30°/₀₀. Another possibility is that *Acartia clausii* and the other organisms abundant during the spring months may offer too much competition.

E. hirundoides was found in the pond throughout the period during which *A. clausii* was present, but it was much less abundant than *Acartia* except for the early months of the year. Fig. 7 gives in graphical form the total number of adults and copepodids of *Eurytemora* per cubic meter, plotted on a logarithmic scale, for the period of its occurrence. In early January 1946, copepodid stages II to V were present. In early March adults began to appear, and by late March many young copepodids at stages I to III were also observed. Thereafter the numbers declined rapidly as *Acartia clausii* increased in abundance. During the first half of April adults and maturing copepodids were predominant, but throughout the latter half of this month and during May a succession of copepodid stages occurred. The later stages of development passed through during early June culminated in a maximum of adults shortly before the end of this month. In mid-June 1945 *E. hirundoides* attained a similar maximum of adults. Adults continued to occur until early July in 1945 and in 1946 and then, like *Acartia clausii, Eurytemora hirundoides* vanished from the samples.

The data show that in Tisbury Great Pond *E. hirundoides* produced two generations a year synchronous with those of *Acartia clausii,* which it so closely paralleled in period of occurrence. The reproductive activity of the early generation extended from early March to early April, while the adults of the June maximum produced no offspring that were immediately apparent in the samples. The length of time necessary for the development of the June generation was approximately 2½ months. As in the case of *Acartia clausii,* the higher summer temperatures must be responsible for the disappearance of *Eurytemora hirundoides* early in July.

Size Range of the Generations of *Acartia* and *Eurytemora*

It has been noted, especially with regard to *Calanus finmarchicus,* that the size range of the several generations produced throughout the the year varies. Bogorov (1934) and Marshall, Nicholls, and Orr (1934), for example, found that the largest adults of *Calanus* appeared in the spring generation that was spawned at the lowest temperatures. The greater size was not correlated with the length of the developmental period. On the other hand, Clarke and Zinn (1937) reported that the *Calanus* spawned in June and maturing the following January and February were larger than those developing during the early months of the year. An intensive study of the variation in size of *A. tonsa, A. clausii,* and *E. hirundoides* has not been made, but random measurements of males and females from the two generations of each species indicate that the adults of the first generation attained a slightly larger size than their offspring of the second generation. In Table II the length range of individuals of each generation of the three species is tabulated; the length range of each species as given by Wilson (1932a) is included for comparison. Approximately 50 specimens of *E. hirundoides* and 300 specimens of each species of *Acartia* were measured. In the case of these three species the individuals developing at lower temperatures and at a slow rate attained slightly greater size. It is also of interest to note that some individuals of *E. hirundoides*, a brackish water form, were larger than the maximum recorded by Wilson, while the majority of the specimens of *Acartia* that were measured were below the minimum recorded length.

TABLE II. VARIATION IN LENGTH, IN MILLIMETERS, BETWEEN INDIVIDUALS OF THE FIRST AND SECOND GENERATIONS OF *Acartia clausii*, *A. tonsa*, AND *Eurytemora hirundoides*

	A. clausii	*A. tonsa*	*E. hirundoides*
First Generation			
Female	1.0–1.2	0.95–1.2	1.1–1.4
Male	0.9–1.05	0.85–1.0	0.9–1.25
Second Generation			
Female	0.9–1.1	0.85–1.0	0.9–1.1
Male	0.8–1.0	0.80–0.9	0.8–0.95
Reported Length (Wilson, 1932a)			
Female	1.15–1.25	1.25–1.5	1.0–1.25
Male	1.0–1.1	1.0–1.15	0.9–1.0

Oithona brevicornis Giesbrecht

Extreme salinities: 13.5–31‰

Oithona brevicornis is the only cyclopoid copepod that was found in any numbers in Tisbury Great Pond. During the period studied it entered the pond and became established there. It first appeared during the latter part of March 1946, shortly after the beach was opened, and was present until the end of the observations in early September. The total numbers of *O. brevicornis* per cubic meter for this period are shown in graphical form in Fig. 8. A small maximum in April was followed by a much higher peak in June. Two smaller maxima occurred in late July and late August. Females with egg sacs were observed in April, June, late July, and late August to early September. This indicates, but does not prove, four generations during this time, with a two month interval as the developmental period

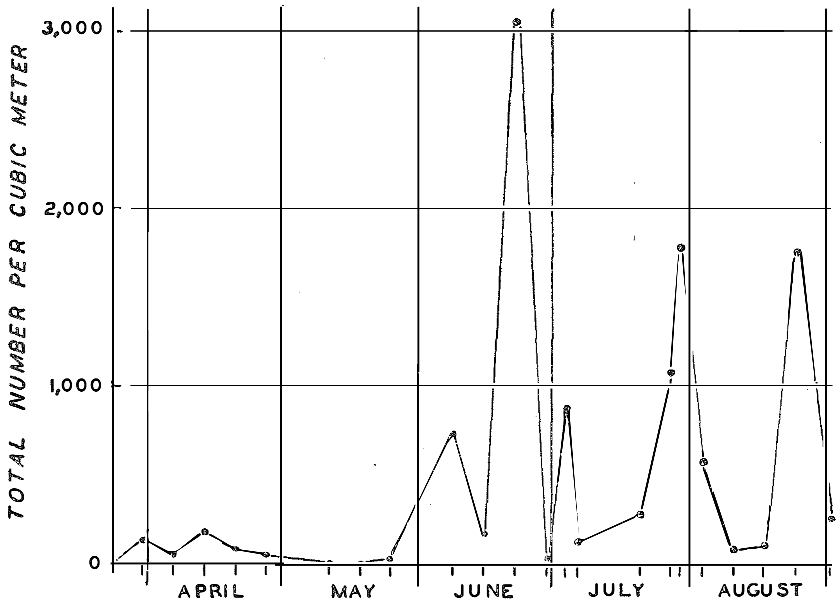

Figure 8. The total number per cubic meter of *Oithona brevicornis* from April through August 1946.

for the June maximum, while the last two generations were about a month apart.

Oithona brevicornis is an exceptionally small copepod, males and females averaging around 0.5 mm. in length, although occasional females 0.6 mm. long were encountered. Nearly all the individuals counted were adults, none smaller than 0.4 mm. in length being observed. A month is probably not too short a time for the development of this species in summer at temperatures ranging between 22° and 25° C., since Fish (1936c) gave six weeks as the interval between generations of *Oithona similis,* a larger species, during the summer in the Gulf of Maine.

Due to the fact that *Oithona brevicornis* did not become a member of the pond fauna until relatively late in the period under investigation, it would be misleading to give the known dates of its occurrence as limiting its seasonal appearance. The known temperature range, 7.7° to 25.2° C., also cannot represent the true limits of its tolerance. However, this species has withstood variations in salinity from 13.5 to 31°/₀₀. Wilson (1932b) also reported a wide salinity range for *Oithona* *brevicornis* in Chesapeake Bay, where the average salinity was less than 10°/₀₀ at some of the stations where it was found. *O. brevicornis* was widely distributed throughout the Bay during the entire year and ranked third in abundance after the two species of *Acartia, A. clausii* and *A. longiremus*. *O. brevicornis* is apparently both a neritic and a brackish water species.

Other Copepods

The copepods included under this heading are only those which may be considered as living in the pond. The adventitious species are listed with other accidental visitors. *Centropages hamatus* is the only other calanoid copepod that was found for an extended period of time. This is a littoral species that penetrates estuarine situations. It has been reported from the Thames estuary (Wells, 1938), from the Norfolk estuaries (Gurney, 1928–1929), and from the brackish pond connected with the Mediterranean that was studied by Fatemi (1938). In Oslo Fjord *C. hamatus* is the most important copepod in the innermost part of the fjord, occurring in maximum numbers in summer (Wiborg, 1940). It is characteristic of winter plankton in Woods Hole harbor (Fish, 1925) but has been found most abundant in June and July off Marthas Vineyard (Clarke and Zinn, 1937).

Centropages hamatus first appeared in early January 1946 and occurred fairly consistently in small numbers until early July. A small maximum was found in April, while another was observed in early July. During the period of its occurrence it experienced the same range of temperature and salinity as *Acartia clausii* and *Eurytemora hirundoides*. That it remained for so long a period is proof of its ability to withstand greatly varying salinities and temperatures.

It is questionable whether *Paracalanus crassirostris* Dahl should be considered a member of the pond fauna or an adventitious form. It was found in the samples during the latter half of March, most of April, and in August, 1946. However, it is of interest to note its presence, since this species is not listed by Wilson (1932a) and may not have been reported from this region before. Its relative, *Paracalanus parvus*, has been recorded from the Gulf of Maine to Chesapeake Bay. *P. crassirostris* is reputedly the smallest calanoid, adult females measuring about 0.5 mm. in length, and this may be one reason why it has not been observed. Davis (1944) has described *Paracalanus crassirostris* Dahl var. *nudus* Davis from Chesapeake Bay. His specimens differed from all descriptions of *P. crassirostris* in having a less well developed spiny armature on the rami of the swimming legs, the second legs being entirely bare. The specimens of *P. crassirostris* found in Tisbury Great Pond agree in all respects with Gurney's (1927) description of this species from specimens obtained from the Suez Canal, and therefore are not similar to the variation of this species described by Davis. Only adult females were found in Tisbury Great Pond.

Aside from *Oithona brevicornis*, two other species of cyclopoid copepods were found in the pond. *Halicyclops magniceps* (Lilljeborg) is definitely a brackish water form (Gurney, 1928–1929), which occurred sporadically throughout the year, with maximum numbers in late June. Females with egg sacs were observed in June, July, and August, immature stages in September and November, and females in January. In late June and early July 1946, males, females, and immature stages were present.

One male specimen of *Myicola major* (Williams) was found in the plankton in late July 1945. This record is of interest, since, according to Wilson (1932a), this species has heretofore been found only in the mantle cavities of *Mya arenaria*, *Venus mercenaria*, and *Mactra solidissima* in Narragansett Bay.

A number of harpacticoid copepods, not all of which have been identified, occur in Tisbury Great Pond. Table III lists the species and the known times of their occurrence. Many of these undoubtedly were present at other times, but since it was always necessary to dissect most of these species in order to identify them a complete study has not been made. *Tachidius brevicornis* Lilljeborg, a brackish water species, and *Harpacticus tenellus* Sars were the harpacticoids noted most frequently. *T. brevicornis* was most abundant during the spring, while *H. tenellus* was fairly common especially during the summer months. *Parategastes sphaericus* (Claus) is strikingly different in appearance from other harpacticoids, and therefore it is certain that this species occurred only during July and August of both summers. Fish (1925) also found this a common summer form in Woods Hole harbor.

TABLE III. KNOWN TIMES OF OCCURRENCE OF HARPACTICOIDS IN TISBURY GREAT POND

	1945							1946							
	June	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
Tachidius brevicornis	x	x	—	—	—	x	—	x	—	x	x	x	—	—	—
Harpacticus tenellus	—	x	x	x	—	x	—	x	—	x	—	x	x	x	x
Parategastes sphaericus	—	x	x	—	—	—	—	—	—	—	—	—	—	x	x
Ectinosoma curticorne	—	—	—	—	—	—	—	x	—	—	x	—	—	—	—
Dactylopusia brevicornis	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
Dactylopusia vulgaris	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
Microsetella norwegica	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—
Amphiascus pallidus	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—
Mesochra pygmaea	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—

Larval Forms

Barnacle Nauplii and Cyprids

Balanus balanoides: March–April
Balanus crenatus: latter half of April–early July
Balanus eburneus (?): late July–September 1946; November, 1945

Adult barnacles apparently do not occur in abundance in the vicinity where the plankton tows were made, since neither nauplii nor cyprids were taken in any great quantity. According to Fish (1925), identification of the nauplii of the species found in the Woods Hole region is facilitated by the fact that they have different breeding periods: *Balanus balanoides* larvae occur from December to April, *B. crenatus* larvae in July, and *B. eburneus* larvae from August to October. He found *Chthamalus stellatus* larvae in late July or early August, within the period for *B. eburneus.*

The identification of acorn barnacle nauplii would not be difficult were it not for the paucity of published accounts of the developmental stages of the various species. The naupliar stages of *B. crenatus* have been studied by Herz (1933), while those of *B. balanoides, Chthamalus stellatus,* and *Verruca stroemia* have been worked out by Bassindale (1936). These papers serve to emphasize the differences between the various species in shape, size, and relative proportions, as well as in the setation of the antennules, antennae, and mandibles. However, judging from the Tisbury Great Pond material, variations in the size and setation of *B. balanoides* nauplii are slightly greater than Bassindale found them to be.

Nauplii and cyprids of *Balanus balanoides* were found from late March to the end of April but were most abundant during the first half of April. The larger nauplii were intermediate in size and setation between two of Bassindale's stages. This would be expected if the number of instars is not fixed. The length of the cyprid varied considerably also, from 0.8 to 1.25 mm., although the majority agreed closely with Bassindale's figure of 0.94 mm. This variation in the size of the cyprid gives evidence of a range in size and possibly in number of instars of the naupliar stages.

Balanus crenatus nauplii appeared during the latter half of April and were present until the end of June. Cyprids were first found during the second week of May and continued to appear until early July. The nauplii of *B. crenatus* occurred in greater numbers than those of the other species. Two maxima of nauplii were observed, one in mid-May and the other in the latter half of June. On both occasions approximately 3,000 per cubic meter were present. In contrast with *B. balanoides*, *B. crenatus* larvae showed only slight variation in size and setation from the description of the developmental stages given by Herz. During the period when *B. crenatus* larvae were present the temperature rose from 10° to 24° C., a greater range than that experienced by Herz's specimens.

From late July until early September, when the data stopped, nauplii of another species of *Balanus* were found. A few were also observed in November 1945. Presumably these were the nauplii of *Balanus eburneus*, since this is the time of year when this species breeds. These were never numerous; the highest number of 200 per cubic meter occurred in late July.

Aside from these forms, small cyprids appeared sporadically throughout the year. The majority of these were found from November to March, but occasional specimens were seen in April, June, and July. No nauplii appeared that could belong to the same species as these cyprids. The cyprids measured 0.4 mm. long by 0.25 mm. wide; of the barnacle larvae whose dimensions are known, only *Chthamalus stellatus* has a cyprid as small as this. It is probable that these are cyprids of *Chthamalus*, since *C. fragilis* and possibly *C. stellatus* occur in the Woods Hole region.

Gastropod Veligers

Table I shows that gastropod veligers were most abundant from May through July, with maximum numbers in June. No attempt has been made to identify them. According to Fish (1925), the bulk of planktonic gastropod larvae undoubtedly belong to the group of gastropods which discharge their eggs directly into the sea water. He found the eggs and larvae of *Littorina litorea* numerous from March to July, while those of *Lacuna vincta* were abundant in February also. Gastropod eggs were scarce in Tisbury Great Pond, only a few being observed in early March. Few gastropod veligers were present in April, but in May the numbers began to rise; the highest number of about 37,000 per cubic meter occurred in the latter part of June. A much smaller maximum appeared in late July. Gastropod veligers declined in abundance during the fall months of 1945, and none were found from December through February.

Lamellibranch Veligers

Table IV shows the period of occurrence in 1946 of the lamellibranch veligers which could be identified by means of Stafford's (1912) descriptions and plates. *Mytilus edulis* veligers appeared infrequently and in small numbers, and therefore the period when they were observed is shorter than has been reported. Fish (1925) found these veligers in Woods Hole harbor from early June until late in the fall. The veligers of *Mya arenaria* were the dominant type in Tisbury Great Pond from late April into June and continued to appear throughout the summer. The veligers of *Venus mercenaria* were most abundant in late July and early August. None of these veligers could be identified in making the counts, and so quantitative estimates of their seasonal abundance cannot be given. However, at the end of July, *Venus* was by far the dominant form among the more than 10,000 veligers per cubic meter that were found at this time. Unfortunately the veligers in the 1945 fall samples were not sufficiently well preserved to allow their identification, but it is probable that *Venus* and *Mya* veligers were present. Only early veligers appeared during this period; possibly they were dead when caught by the net and this, too, may explain the distortion of the specimens.

TABLE IV. Period of Occurrance of Lamellibranch Veligers in 1946

	April	*May*	*June*	*July*	*August*
Mya arenaria	x	x	x	x	x
Mytilus edulis	x	x	x	—	—
Venus mercenaria	—	—	x	x	x
Ostrea virginica	—	—	x	x	x

Due to the greater development of the left umbo, it was possible to identify all but the earliest veligers of *Ostrea virginica* when making the counts. The asymmetry of the umbones was evident in specimens only 0.1 mm. in length. In 1945, the first oyster veliger was detected on June 24, but two weeks elapsed before significant numbers of these veligers appeared. During this summer only one maximum occurred on July 12, when nearly 15,000 per cubic meter were present. *Ostrea* veligers continued to be present in small numbers until mid-August. Since samples were taken every three days or so during the summer of 1945 it is unlikely that a maximum was missed, but it is surprising that only this one good-sized brood of veligers occurred.

In 1946, a few veligers, probably young stages of *Ostrea,* were found on June 23. Later stages were present throughout July and August, but fewer were counted than in 1945. A small peak of veligers appeared in early July and a larger one of about 9,000 per cubic meter occurred at the end of July. Since no samples were taken between July 7–21, more veligers may have been present during this period.

The numbers of oyster veligers noted during both summers are small, but spawning may have been much more extensive than the figures given would indicate. Loosanoff (1932), who studied the distribution of oyster larvae in relation to currents and depth, found that the veligers remain on the bottom during most of their existence, swimming only when the current velocity is least. Probably the number of oyster veligers taken by the plankton sampler is only a small proportion of the numbers present between the surface and the bottom of the pond.

Judging from the times of appearance of the veligers, spawning did not occur in any intensity until the temperature of the water had reached 24° C. It is known that spawning may occur over a wide range of temperature, from 16.6° to 28° C. in Long Island Sound (Loosanoff and Engle, 1940). According to Medcof (1939), a rise in temperature when the oysters are ripe is more important than the actual temperature. Since the temperatures rose fairly steeply throughout June of both years and since the ages of the observed veligers are not known it is impossible to state with exactitude the times when spawning began.

Polychaete Larvae

Polychaete larvae occurred sporadically throughout the year, attaining maximum numbers in April and May (see Table I). Fig. 9 gives the quantitative data for 1946 in graphical form, plotted on a logarithmic scale. This shows the two major maxima which were found in April and May. Only *Synchaeta* and *Acartia* appeared in greater numbers during the year. In 1945, small maxima of polychaete larvae were observed every month from June to December, the largest number of about 1,700 per cubic meter occurring at the end of November.

A number of different species were present, but it has been impossible to identify them properly. The dominant forms were spionid larvae. The April maximum consisted almost entirely of so-called spionid "metatrochophores." Species of *Polydora* were undoubtedly present,

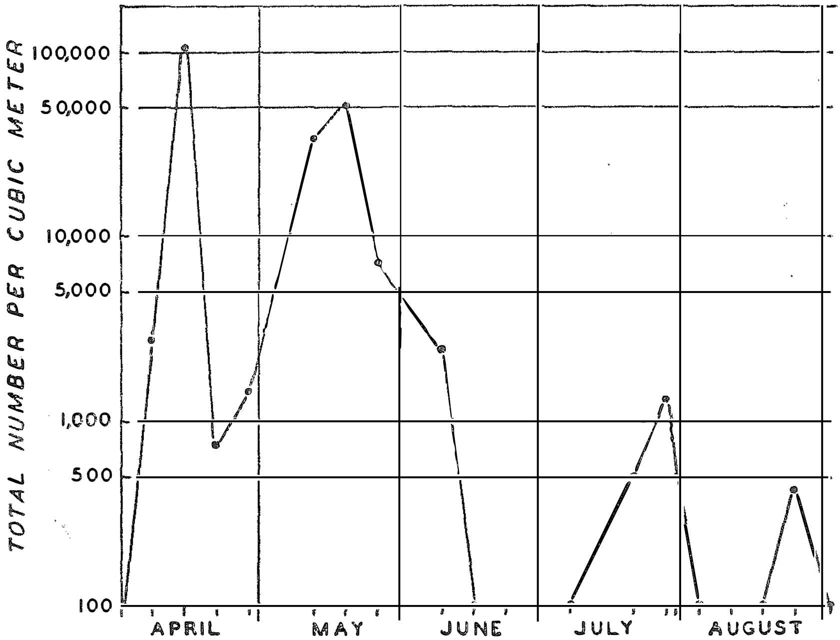

Figure 9. The total number per cubic meter, on a logarithmic scale, of polychaete larvae from April through August 1946.

since some later stages of spionid larvae appeared identical in morphology and pigmentation to Thorson's (1946, fig. 42) figure of *Polydora ciliata* Johnst. Another larva, which occurred in limited numbers in April and May, is probably *Nereis pelagica* Linn., as it is similar to Thorson's (1946, fig. 29) and to D. P. Wilson's (1932) figures of this species. Other larval forms probably include species of *Nephthys* and possibly of *Mystides*.

The Rotifer Population

Synchaeta littoralis: present throughout year.
Temperature range: 0°–25° C.
Extreme salinities: less than 1–31°/oo

Synchaeta sp.: late October 1945 to February 1946
Temperature range: 0°–13° C.
Extreme salinities: less than 1–20.3°/oo

The rotifer population consisted of two species of which *Synchaeta*

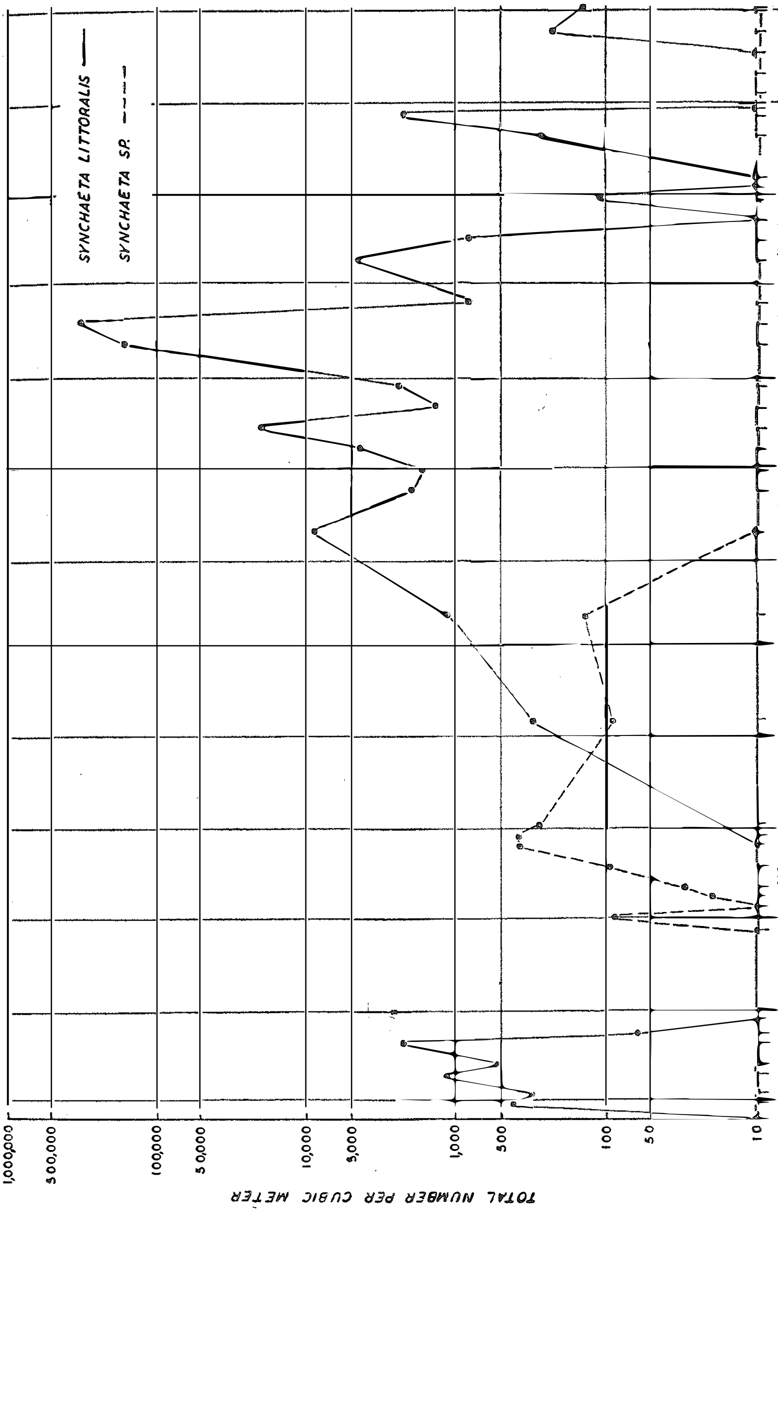

Figure 10. The total numbers per cubic meter, on a logarithmic scale, of *Synchaeta littoralis* and *Synchaeta* sp. from September 1945 through August 1946.

littoralis Rousselet was by far the dominant form. According to Rousselet (1902), who described *S. littoralis* from brackish water on the English and Scottish coasts, this species prefers the warmer spring months but is erratic in its appearance. This was found to be the case in Tisbury Great Pond.

The total numbers per cubic meter of the two species of *Synchaeta*, plotted on a logarithmic scale, are given in graphical form in Fig. 10. This shows that the greatest numbers of *S. littoralis* appeared from March to May. In mid-May this species attained a higher maximum than any other member of the zooplankton at any time during the year, when 315,000 per cubic meter were present. During the period when this greatest rise in numbers occurred the temperature rose from about 11° to 14.7° C. The salinity was relatively high at this time, ranging between 25 and 29°/₀₀. However, the appearance of *S. littoralis* at all times of year provides proof that it is both widely euryhaline and eurythermal. *Synchaeta* sp., on the other hand, preferred the late fall to winter months and was never abundant.

Podon polyphemoides (Leuckart)

Fairly abundant May–June
Temperature range: 11°–24° C.
Extreme salinities: 13.7–29.2°/₀₀.

Podon polyphemoides appeared in numbers in Tisbury Great Pond only during May and June. Several specimens were observed in March, but no more were seen until late April. Fig. 11, which gives the total number per cubic meter in graphical form, shows clearly the abrupt rise and fall in numbers of the *Podon* population. The highest maximum was reached in the third week of June. This was followed by such a sudden decrease in numbers that by the end of the month *Podon* had virtually disappeared. The picture was the same in 1945, although the estimated numbers were not as great; since a No. 2 net was used for the May sample the smaller individuals were not retained. As in 1946, by July 1 few *Podon* remained and the sample contained dead specimens.

Podon polyphemoides is predominantly a neritic cladoceran, extraordinarily euryhaline and moderately eurythermal. It is a cold water form and, according to Baker (1938), it is virtually absent from about Lat. 40° N. to Lat. 20° S. On the Northeast Atlantic coast of the

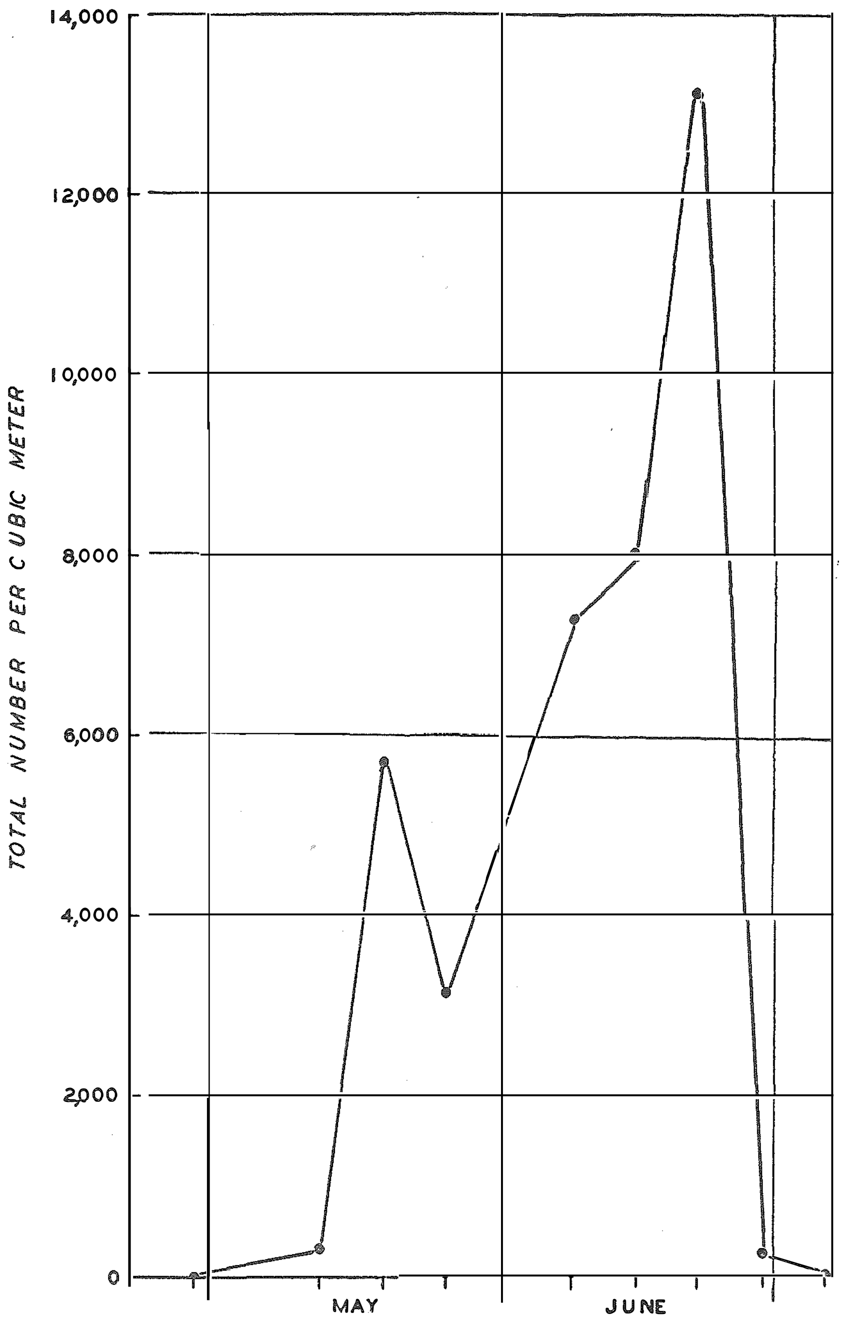

Figure 11. The total number per cubic meter of *Podon polyphemoides* for May and June 1946.

United States *P. polyphemoides* has been definitely recorded as far south as New Haven Harbor in Long Island Sound (Fish, 1925), although Bigelow and Sears (1939) reported *Podon*, species not given, as present between the offings of Marthas Vineyard and Chesapeake Bay.

Baker stated that *P. polyphemoides* has been known to withstand sudden extreme changes in salinity, from 1.05 to 35.1°/₀₀. Therefore the variations in the salinity of Tisbury Great Pond were well within its range.

However, the thermal preferences of *Podon* explain, at least in part, the period of its occurrence in the pond. Baker gave its optimal thermal range as 10° to 15° or 16° C., although it has been recorded at temperatures as low as 2.46° C. and as high as 19.8° C. During May the temperature rises rapidly in Tisbury Great Pond from about 11° C. to over 20° C., so that the period of optimum temperatures is short indeed. During the latter part of June when *Podon* was most abundant, the temperature was 21.7° C. This is probably the highest temperature at which *P. polyphemoides* has been recorded in numbers. *Podon* appeared when the temperature was about 11° C. and disappeared both summers at the beginning of July when the temperature exceeded 24° C. It seems obvious that temperatures in the vicinity of 24° C. are lethal to the population of *Podon polyphemoides*.

Forms Entering the Pond Accidentally

Chaetognaths are the most important organisms in this category in that they were fairly numerous for a short period, but several littoral copepods also appeared in small numbers after the opening of the beach. Table V lists the species and shows the months when they occurred.

Temora longicornis (Müller) and *Tortanus discaudatus* (Thompson and Scott) were found consistently in the samples during the period of their occurrence, while the other two calanoids appeared much more infrequently. These species were present only while the salinity was relatively high, between 25 and 31°/₀₀. Although Bigelow (1926) recorded a wide temperature and salinity tolerance for *Temora longicornis*, this species has not proved itself to be more than moderately euryhaline and eurythermal in Tisbury Great Pond. *Oithona similis* Claus entered the pond nearly every time the beach was opened during the period studied but never became established there. *Eurytemora herdmani* Thompson and Scott, not listed in Table V, was found on only one occasion immediately after the opening of the beach in May 1945.

TABLE V. TIMES OF OCCURRENCE OF ADVENTITIOUS FORMS

	1945		1946				
	June	*Sept.*	*Mar.*	*Apr.*	*May*	*June*	*July*
Temora longicornis	—	—	—	x	x	—	x
Tortanus discaudatus	—	—	x	x	x	—	—
Pseudocalanus minutus	—	—	—	x	x	—	—
Pseudodiaptomus coronatus	—	x	x	—	—	—	—
Oithona similis	x	x	x	x	x	—	x
Sagitta sp.	—	—	x	x	—	—	—

The Chaetognaths were most abundant in mid-April when 2,300 per cubic meter were present. These belong to the genus *Sagitta*, but the species has not been determined, since all the specimens were immature. They may be *S. elegans*, since Clarke and Zinn (1937) and Bigelow and Sears (1939) reported swarms of this species off Marthas Vineyard in April or May. The sagittae did not remain in the pond but disappeared rapidly.

THE PHYTOPLANKTON

The phytoplankton counts include the period from September 13, 1945 to September 2, 1946. Fig. 12 gives the total phytoplankton as cells per liter as well as the total zooplankton in numbers per cubic meter. Table VI shows, semiquantitatively, the seasonal abundance of the diatoms, dinoflagellates, and flagellates that occurred in greatest numbers. From this it is apparent that diatoms were present throughout the year, while flagellates and dinoflagellates were most abundant during the summer months. The highest maximum of diatoms occurred in January when a count of 350,000 cells per liter was obtained. Large numbers were also present in February, during the latter half of May, and from September to December. The dinoflagellates were most abundant in late April, late June, and late July. In mid-August *Euglena* occurred in greater numbers than any other organism during the year, when 855,000 cells per liter were present.

In general, the cycle of the phytoplankton of Tisbury Great Pond differs from that of oceanic areas in that diatoms are fairly abundant throughout the year, with only one pronounced maximum in January.

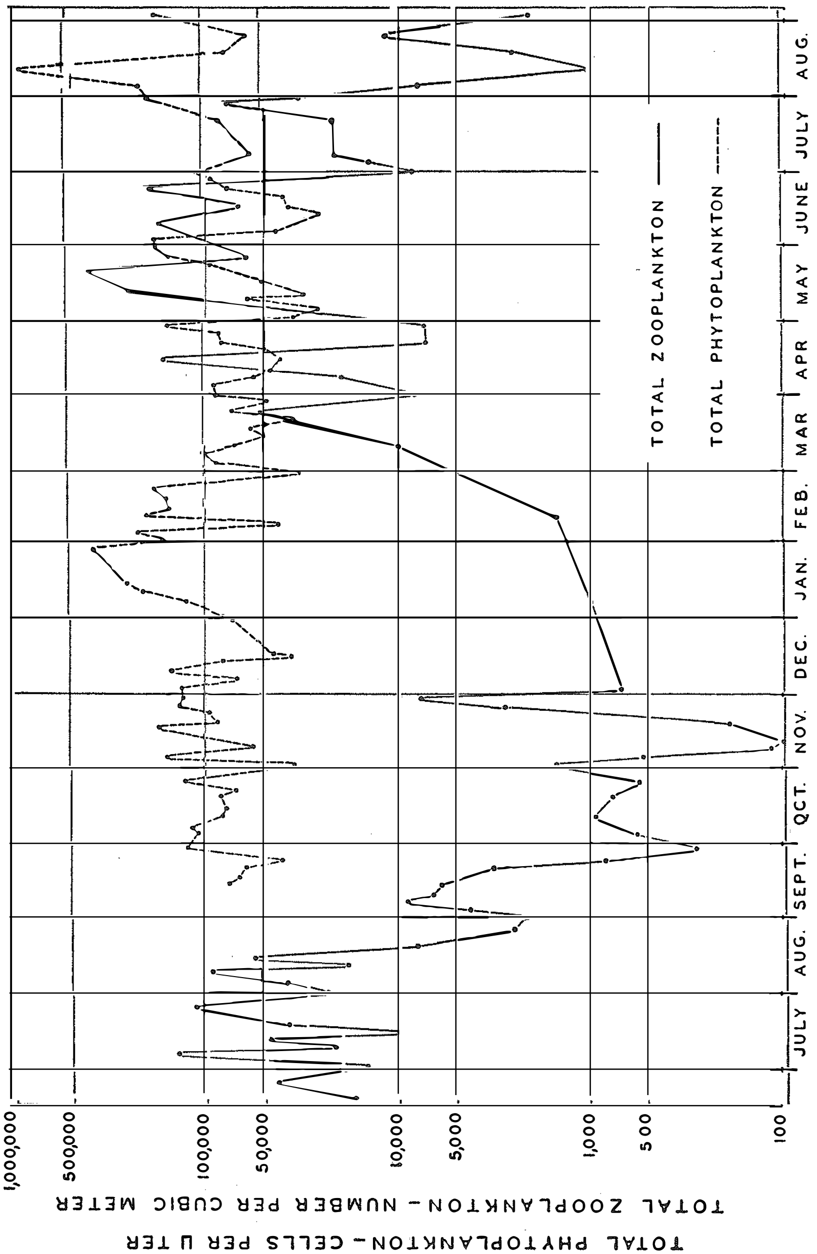

Figure 12. The total numbers of phytoplankton as cells per liter from September 1945 to September 1946 and the total numbers of zooplankton per cubic meter from June 1945 to September 1946.

TABLE VI. SEASONAL CYCLE OF ABUNDANCE OF THE MAJOR ELEMENTS OF THE PHYTOPLANKTON
x: 1,000–10,000; xx: 10,001–100,000; xxx: 100,001–1,000,000. SEMIQUANTITATIVE, AS CELLS PER LITER.

	1945				1946							
	Sept.	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
DIATOMS:												
Skeletonema	xx	xx	xx	xx	xxx	xx	xx	x	x	—	—	x
Navicula	x	x	x	x	x	x	xx	x	x	x	x	x
Nitschia	x	x	x	—	—	xx	x	x	x	—	x	x
Melosira	xx	xx	xx	xx	xx	x	xx	xx	x	x	x	—
Lichmophora	x	xx	x	—	—	—	—	—	—	—	x	x
Chaetoceros	—	—	—	—	—	xx	x	x	xx	xx	xx	x
Pleurosigma	—	x	—	—	—	—	x	x	x	—	—	—
DINOFLAGELLATES:												
Peridinium	—	—	—	x	x	x	—	—	x	x	—	xx
Prorocentrum micans	—	—	—	—	—	—	—	—	—	xx	xx	xx
Dinophysis	—	—	—	—	—	—	—	—	—	x	—	—
Gymnodinium	—	—	—	—	—	—	—	xx	—	x	xx	xx
FLAGELLATES:												
Eutreptia	x	x	xx	x	—	—	—	—	—	—	x	xx
Euglena	—	—	—	—	—	—	—	—	—	—	x	xxx

DISCUSSION AND CONCLUSIONS

The Composition of the Zooplankton Population

Most of the zooplankton organisms of Tisbury Great Pond live a precarious existence. To survive successfully throughout the year under present conditions, each species must be able to tolerate and to thrive on extremes of salinity and temperature. Except for accidental visitors, the organisms living in the pond are both euryhaline and eurythermal, at least to a considerable extent. Environmental conditions are far more rigorous than those of any oceanic area. For this reason it is of interest to know what species are capable of living in Tisbury Great Pond as well as the degree to which they are acclimated to its conditions.

In general, several categories of organisms occur:

1. Extremely euryhaline and eurythermal species, present at all seasons. None of the calanoid copepods belong in this group, and it is questionable whether any harpacticoids do, since they rarely occurred in numbers in the plankton samples. *Halicyclops magniceps* appeared erratically throughout the year and probably belongs in this category, as does *Synchaeta littoralis.* Both of these have long been known as brackish water species.

2. Fairly euryhaline and eurythermal species surviving unfavorable conditions either as resting stages or in small numbers. As stated, this category includes forms for which either the salinity or the temperature range is too great or the change of either too abrupt. The majority of the zooplankton living in the pond with any degree of permanence should fall in this general group, but it is extremely difficult to draw hard and fast lines for them. Because of the special conditions in Tisbury Great Pond, due to the periodic opening of the beach, any organism surviving in the pond for any length of time must be fairly euryhaline; this implies a wide salinity range a bit short of complete euryhalinity.

The organisms most affected by temperature are *Acartia clausii*, *A. tonsa*, *Eurytemora hirundoides*, and *Centropages hamatus*. *Acartia clausii* disappeared from the samples when the temperature rose to about 24° C., while *A. tonsa* was not found until the temperature was about 20° C. and was abundant only during the period when the temperature varied between 20° and 25° C. This implies that *A. tonsa* has an exceptionally narrow temperature range, but the fact that it has been taken in numbers in January in Long Island Sound proves that a factor other than temperature is responsible for its limited period of abundance in the pond. Both *Eurytemora hirundoides* and *Centropages hamatus* are winter-to-late-spring forms with a temperature range similar to that of *Acartia clausii.* Both of these species may be considered members of the pond fauna, and not adventitious species, although *Centropages hamatus* in particular was never abundant. It is perhaps possible that the competition of the other organisms occurring during the spring months was too great for either *E. hirundoides* or *C. hamatus* to become fully established.

Despite the fact that *Acartia tonsa* has a wide salinity range, a steep rise in salinity during both summers coincided with an abrupt decrease in numbers of the population. Since this occurred during its period of optimum temperatures, it seems to indicate that *A. tonsa* is not sufficiently heteroeuryhaline to withstand readily a sudden rise in salinity, although it is tolerant to great variations in salinity when the change occurs gradually. The problem of the true limits of tolerance of *A. tonsa* to varying temperatures and salinities cannot be resolved with the available data.

3. Extremely euryhaline and moderately eurythermal species. *Podon polyphemoides* is the only member of this category. Its thermal range is more limited than that of the other organisms mentioned, since it appeared at about 12° C. and disappeared as the temperature rose to 24° C.

4. Larval forms, presumably of adult species that live in the pond and are adapted to its conditions. The three species of *Balanus* nauplii found, for example, are the young of barnacles suited to this environment. Since these organisms occur in the plankton only during their larval stages, they cannot be considered permanent members of the zooplankton and therefore require a separate category.

5. Adventitious species. This could include both neritic and oceanic forms, but only predominantly neritic species were brought into the pond when the beach was opened. The sagittae belong in this category. Undoubtedly the littoral copepods *Tortanus discaudatus, Temora longicornis*, *Pseudocalanus minutus*, and *Oithona similis* may be included here, since none of these species became established in the pond. It is probable that *Paracalanus crassirostris* is a member of this group.

Oithona brevicornis is an adventitious species that has proved itself capable of surviving and reproducing in this environment. That this is so is shown by its continuous presence in the pond during the last half year of the observations, and also by the appearance of maximum numbers of adults after the pond was closed.

In conclusion, almost no members of the zooplankton community are capable of living in the surface layers of Tisbury Great Pond throughout the year. The rotifers are the only forms that appear at all seasons. Temperature is the more important factor limiting the periods of occurrence of the majority of organisms living in the pond, since they must, of necessity, be fairly euryhaline in order to survive there. On the other hand, the range of salinity is a significant factor, in that it bars from the pond the littoral forms that would appear in greater abundance if the outlet were always open, as in estuarine situations. In contrast with oceanic areas, the pond is poor in numbers of species of calanoid copepods, because few calanoids are capable of tolerating such a range of salinity.

The Seasonal Cycle of the Total Zooplankton

The cycle of the total zooplankton in numbers per cubic meter is shown in Fig. 12, which also portrays the total phytoplankton as cells per liter. The seasonal change in numbers of the zooplankton was pronounced. During the period from late August to January, copepods virtually disappeared from the samples and almost no zooplankton was present, except for occasional bursts of *Synchaeta*, polychaete larvae and veligers. In early January a few copepods appeared, rotifers were increasing in numbers, and a few barnacle larvae were present. The quantity rose barely perceptibly to March, when *Synchaeta* and *Eurytemora* produced a maximum. The mid-April maximum was due largely to polychaete larvae with rotifers second in numbers and copepods a poor third. The May peak was predominantly *Synchaeta*, with polychaete larvae and *Acarta clausii* contributing in appreciable numbers. During June, *A. clausii* occurred in greatest abundance, with gastropod veligers numerically second. *A. clausii* disappeared in early July as *A. tonsa* appeared abruptly with its maximum at this time. The data for the two summers show clearly how the sudden decrease in the *A. tonsa* population left low numbers of zooplankton in the pond.

Essentially, therefore, there was but a single maximum in the zooplankton, although this covered the period from March to July or August. This cycle of the zooplankton is obviously not correlated directly with temperature, even though temperature must be one of the most important factors. The numbers began to increase gradually in January when temperatures were minimal and the pond frozen. A barely perceptible rise in numbers continued to March, but during this and the succeeding months to July or August, when the temperature had reached its highest point, maximum followed maximum. From this time to December there was an impoverishment of the zooplankton. The temperature was high at least until mid-September, but no autumn maximum occurred. Since the numbers were low while the temperature was falling and high while it was rising, the correlation coefficient between total zooplankton and temperature is close to zero. On the other hand, the correlation coefficient between total copepods and temperature is barely significant, 0.282, because the two species of *Acartia* attained their maximum numbers when the temperature was above 20° C.

The lack of a linear correlation between zooplankton and temperature may be explained by the fact that the real relationship between numerical abundance of organisms and temperature is complex. When the total numbers of copepods per cubic meter are plotted against temperature, as in Fig. 13, the result is a wide scattering of points. However, a dot diagram prepared for a single species, such as that shown in Fig. 14 for *Acartia clausii*, takes the form of a curve with a rising and a falling limb. This means that the numbers increase as the temperature rises to an optimum and then decrease as the temperature continues to mount. If the total zooplankton consists of organisms with similar temperature curves, obviously no straight-line correlation between zooplankton and temperature can exist.

That an abundance of food was available to the zooplankton throughout the year is evidenced by the phytoplankton counts shown in Fig. 12. Diatoms were abundant for the greater part of the year, while flagellates and dinoflagellates were maximal during the summer months. The phytoplankton shows but two pronounced peaks, the January diatom maximum and the August maximum largely made up of *Euglena*. There was no pronounced autumn diatom maximum, but diatoms were plentiful during the fall months. In this case, also, there is no direct correlation between the total zooplankton and the total phytoplankton, the coefficient obtained being negative but insignifi-

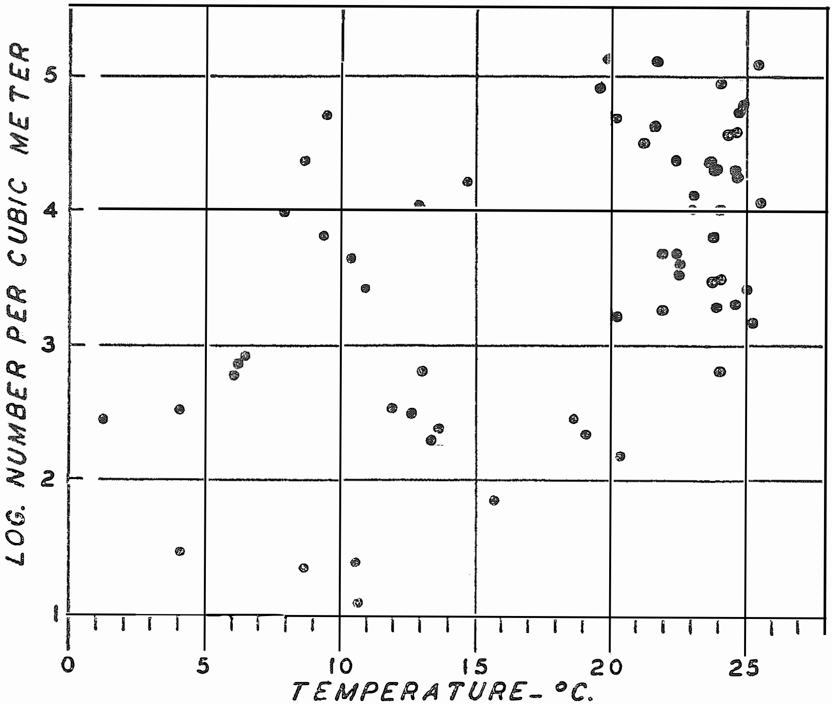

Figure 13. The relation between the total number of copepods of all stages, plotted on a logarithmic scale, and temperature.

cant. It is true that the zooplankton began to increase to a maximum after the January diatom maximum, but it decreased after the August peak. Phytoplankton was always abundant, while the zooplankton was never so plentiful as to give evidence of any appreciable "grazing" of the phytoplankton.

Neither zooplankton nor phytoplankton shows any correlation with salinity. This is not surprising, since all the organisms occurring in any numbers in the pond are fairly euryhaline. The variability of the salinity may act as a complicating factor, reducing the intelligibility of the other relationships. It has already been noted that at least one dominant species, *Acartia tonsa*, may not be sufficiently heteroeury-haline to withstand successfully the rapid increase in salinity attendant upon the opening of the beach. In this case, also, there is no simple correlation, since, although the numbers decrease with rising salinity,

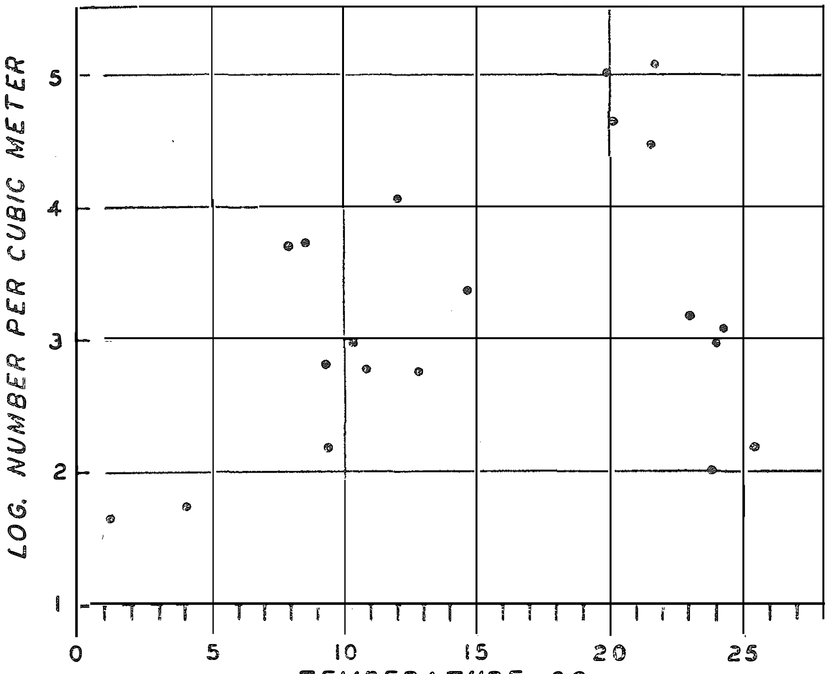

Figure 14. The relation between the total number of copepodids and adults of *Acartia clausii*, plotted on a logarithmic scale, and temperature.

they fail to increase as the salinity falls. Perhaps the opening of the beach in August of both summers may be in part concerned in the paucity in numbers of zooplankton during the fall months.

From the foregoing paragraphs it is evident that the zooplankton had a pronounced seasonal cycle with a single late spring maximum, and that its abundance was not directly related to the temperature or the salinity or the phytoplankton. The effect of temperature on the zooplankton population was marked, for the zooplankton increased in numbers as the temperature rose, but when maximum temperatures were reached the zooplankton decreased in abundance. That the real relationship between the temperature and the total quantity of organisms is complex is shown by the temperature curves of individual species. Any effects of the varying salinity, however, were not clearly reflected in the abundance of the total zooplankton, since the latter increased or decreased regardless of salinity conditions. There is one exception to this, for it has been shown that the rising salinities, through their possible effect on the dominant summer species, may have been involved in the diminution in numbers of the total zooplankton that occurred in August. The phytoplankton, on the other hand, showed no relationship with the zooplankton, since it was always abundant regardless of whether the zooplankton was increasing or decreasing in numbers. Presumably because the zooplankton consisted of organisms with widely varying requirements in these respects, the total number of zooplankton showed no direct relationships with temperature, salinity, or total phytoplankton.

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