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OCEANOGRAPHY OF LONG ISLAND SOUND, 1952–1954[1]

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OCEANOGRAPHY OF LONG ISLAND SOUND, 1952–1954

VI. BIOLOGY OF *ACARTIA CLAUSI* AND *A. TONSA*[1]

By

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[1] This paper represents the major portion of a dissertation presented to the Faculty of the Graduate School of Yale University in candidacy for the degree of Doctor of Philosophy.

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ABSTRACT

Descriptive data have been supplemented with comparative laboratory studies to determine as precisely as possible the effect of environment on *Acartia clausi* and *A. tonsa*. Developmental stages are described and the characters used to distinguish between them are discussed.

The Sound appears to be a marginal area for both species. *A. clausi* is dominant in winter and spring and *A. tonsa* is an important constituent of the zooplankton in summer and fall, but twice each year both species can be taken in the same plankton tow. During most of the year, males of both species are less abundant than females. Probably the males and certainly the developmental stages are affected by changes in the environment before the females. At least four generations of *clausi* and probably four generations of *tonsa* are produced each year. Whereas *tonsa* develops from egg to adult in three to four weeks during summer, *clausi* requires over a month for comparable development during the cooler months. For both species, the adult life is a month or less during much of the year, but in winter it is prolonged. Both species attain greatest size in winter and are smallest in summer.

Laboratory experiments demonstrate that light controls vertical migration but does not affect respiratory or grazing rates. Temperature was found to have a profound effect on metabolism and activity. Vertical migrations of *tonsa* are retarded by low temperatures, and a thermocline can limit the vertical migration of *clausi* when surface waters have warmed to a critical level (16 to 18° C). At low temperatures, *clausi* is more active and has a higher respiratory rate than *tonsa*.

Evidence for seasonal adjustment of metabolism, particularly for *clausi*, was found. The amount of food available and perhaps the reproductive state of the animals can also influence respiration. Temperature, the kind and amount of food, and the physiological state of the food culture affect feeding rates. Food selection has been demonstrated for both species; adult *clausi* and *tonsa* may have different food preferences in summer.

Respiratory and filtering rates were used to compare the relative efficiencies of each species under different temperature conditions. Adult *clausi* appears to be more successful in laboratory experiments under both winter and summer temperature conditions, but the total amount of food available in the natural environment, as indicated by chlorophyll analyses, appears to be sufficient to support a large population of either species in summer. However, grazing was relatively inefficient when the food organisms consisted of naked flagellates and other nannoplankton. These organisms were abundant in summer, so that food limitation was a possibility.

Evidence from Tisbury Great Pond suggests a rigid temperature control of seasonal distribution for these species. In Long Island Sound, temperature appears to control the dominance of *clausi* and *tonsa* in a more subtle manner. Classical competition theory is used to interpret the distribution of the Sound populations. During periods of coexistence, temperature keeps the ecological niches separated. However, twice a year the niches coincide, and competition, probably between the younger stages, eliminates the species less well adapted to prevailing conditions.

Data accumulated in this study have been used to interpret seasonal distribution of *Acartia* in other localities.

Daily zooplankton production of a population dominated by *Acartia* is estimated to be 16.6% under favorable conditions.

INTRODUCTION

Pelagic copepods constituted the major portion of the Long Island Sound zooplankton taken in routine hauls with the Clarke-Bumpus plankton sampler. Of the copepods, two species of *Acartia* predominated during most of the year. *A. clausi* was present throughout winter and spring and disappeared in July, while *A. tonsa* was most abundant from July to December or January, although some individuals lingered well into spring. Deevey (1948) observed a similar seasonal cycle for these species in Tisbury Great Pond, but there the period of existence for each was somewhat shorter and terminated more abruptly. Her data suggested a rigid temperature control; *clausi* apparently could not tolerate temperatures much over 20° C, and *tonsa* did not appear until temperatures reached 20°. However, in Long Island Sound the populations of *tonsa* survived the coldest months, only to disappear in spring after the water temperatures had begun to rise again.

If temperature is the factor that controls the seasonal distribution

of these species in the Sound, it may also control their geographical distribution. Both have been found in estuarine and coastal waters over much of the world, and occasionally they have been observed as part of the oceanic plankton. Although *clausi* has been reported from Lat. 50° S to 80° N and within 5° of the Equator in all major oceans, off the east coast of North America this species is more successful in the cooler waters (Sewell, 1948). Bigelow and Sears (1939) found that it was confined to coastal water south of Cape Cod; to the north, however, it might occur offshore as well. On the other hand, *tonsa* is largely restricted to a band of tropical, subtropical and warm temperate waters around the earth. While this species does penetrate the high latitudes in European waters, it is confined to warmer estuarine conditions. For instance, it is found in the Baltic and Gulf of Finland but not off the coast of Norway at comparable latitudes. On the east coast of the United States, Cape Cod may be a barrier to this form since, to the north, it has been found only in Plymouth Harbor (Wheeler, 1901); Bigelow (1926) did not report it from the Gulf of Maine.

Thus, Long Island Sound appears to be a marginal area for both *tonsa* and *clausi*, a region which is ideal for study of the environmental and biological interrelations that govern their distribution.

ACKNOWLEDGMENTS

I should like to thank Gordon A. Riley and other members of the Bingham Laboratory for their direction and help. Constructive criticism of this manuscript by Gordon A. Riley, Georgiana B. Deevey, John L. Brooks, and Daniel Merriman is greatly appreciated. Special thanks are extended to G. E. Hutchinson for his interest and helpful suggestions and to J. S. Nicholas and the Departments of Zoology and Botany for laboratory facilities. S. C. Shen, E. J. Boell, Morris Foster, and T. H. Waterman have given valuable assistance with physiological equipment and techniques, and Georgiana B. Deevey furnished some of the zooplankton estimates. James Roach and George Martin have been most helpful in acquiring and constructing apparatus. Jack Fu kindly assisted in the preparation of several figures.

The field work was carried out from the U. S. Fish and Wildlife Service vessel SHANG WHEELER, out of Milford, Connecticut. Thanks are extended to Victor Loosanoff, director of the Milford Laboratory, and to Herman R. Glas, skipper of the SHANG WHEELER, for their cooperation.

Finally, this study would have been impossible without the understanding, encouragement and assistance of my wife, Shirley Conover.

COMPARATIVE DEVELOPMENT OF *A. CLAUSI* AND *A. TONSA*

In order to understand as clearly as possible the relationships between environment and zooplankton distribution in the Sound, it was necessary to obtain a detailed analysis of the seasonal variation in numbers of all the developmental stages. Grandori (1912) has described the copepodid stages of *Acartia clausi* and Oberg (1906) has given the only account of naupliar development within the genus. Since the descriptions by these authors were inadequate to separate the nauplii and younger copepodid stages of *clausi* and *tonsa*, it was essential at the beginning of this study to find reliable specific characters that could be employed for rapid identification of any developmental stage under low magnification.

Methods. Several previous workers have reared the younger stages of marine copepods from eggs obtained from captured females or from fresh-caught plankton tows. However, few if any marine calanoid copepods have been cultured successfully, and our attempts to establish laboratory cultures of *clausi* and *tonsa* met with similar failure. A few copepods were maintained in the laboratory for as long as six weeks, but no molting was observed, and when eggs were laid by apparently mature females, they failed to develop as far as the first naupliar stage. Alternatively, the developmental stages were described from preserved material.

With the aid of descriptions by Grandori and by Oberg, nauplii and copepodids of each species were sorted from the No. 10 net plankton taken during a period of the year when only one species of adult was present. These were grouped into the six naupliar and six copepodid stages and were permanently mounted in glycerine jelly. Each stage was examined for uniformity and then the same stages of each species were compared to determine if useful specific differences existed. Finally, groups of younger stages, taken from tows obtained during periods when the two species were likely to coexist, were examined to determine whether the specific characters observed could be used to separate the juveniles.

Naupliar Stages. The nauplius of the *Acartia* is relatively unspecialized compared with nauplii of other calanoid genera. Because there are so few distinct morphological characteristics, distinguishing between the two species might have been difficult. While stages I and II showed no differences which could be employed for low magnification counts, at least one clear-cut difference could be used to separate stages III–VI.

Stage I, less than 0.1 mm long, showed little morphological resemblance to the adult (Figs. 1A, 1B). However, rudiments of the first antennae (a), second antennae (b), and mandibles (c) were present. After the first molt, the nauplius increased slightly in size while the second antennae and mandibles acquired certain specializations; to a taxonomist, the number and character of the short bristles on the ventral posterior region might be useful (Figs. 1C, 1D). In stage III, the primordia of the first maxillae (d) had appeared, but more important was the single pair of stout spines on the extreme posterior of what is destined to become the adult abdomen; on the *clausi* specimens (Fig. 1E) these spines were longer and stouter than those on the *tonsa* nauplii (Fig. 1F). By stage IV a second pair of stout spines had been added ventral to the first pair (Figs. 1G, 1H). The difference between the first pair of spines in stage IV was, if anything, more exaggerated than in stage III. In stage V (Figs. 2A, 2B), the rudiments of two additional thoracic appendages, the second maxillae (e) and maxillipeds (f), appeared, while the relationship between the posterior spines remained essentially unchanged. In stages IV and V, the difference in the dorsal, most posterior pair of spines was probably more pronounced in lateral view (Figs. 3A, 3B, 3C, 3D) than in either dorsal or ventral views. In stage VI, the first indication of swimming legs (g and h) became apparent, and the posterior spines were still distinguishing characteristics (Figs. 2C, 2D, 3E, 3F).

Although it was not possible to distinguish between *clausi* and *tonsa* before stage III, the inability to separate the first two stages did not appear to be an important handicap in the present investigation. Sverdrup, *et al.* (1942) gave 0.158 mm as the average aperture size for No. 10 bolting silk. The nets used in this investigation were not measured, but even allowing for a certain diminution of the

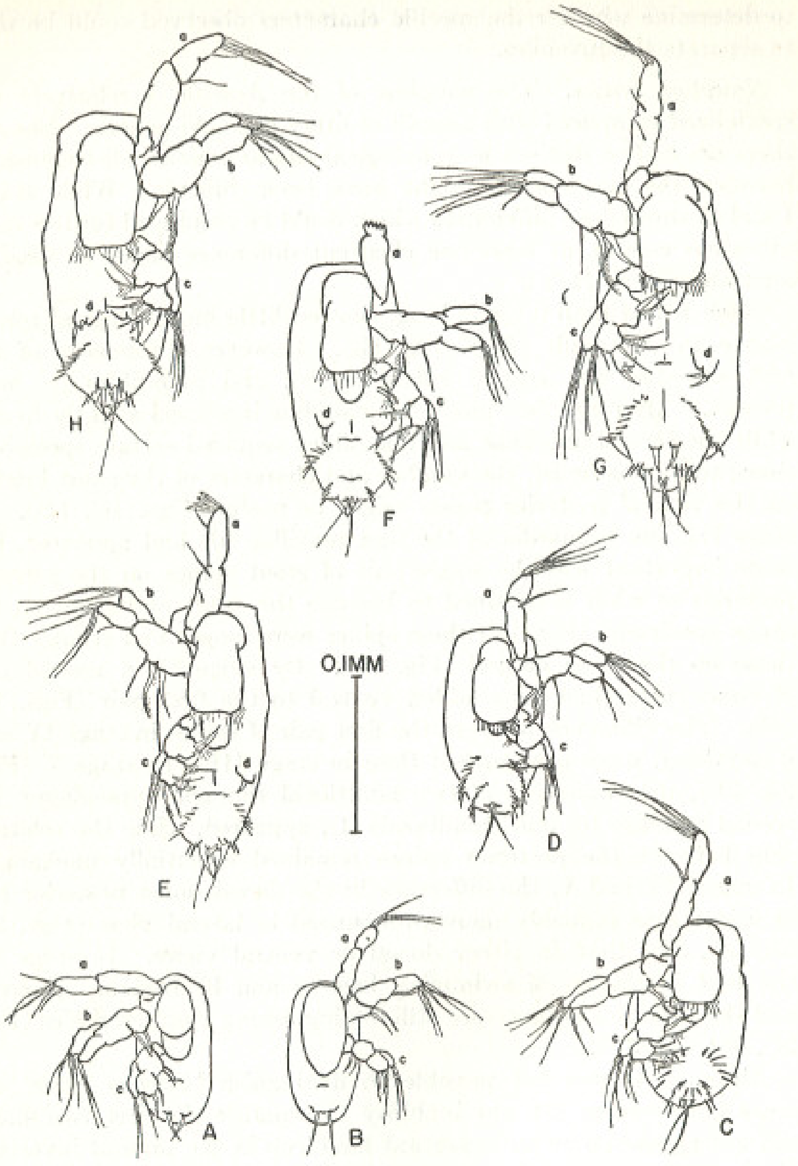

Figure 1. Naupliar stages I, II, III and IV. A, *clausi* stage I; B, *tonsa* stage I; C, *clausi* stage II; D, *tonsa* stage II; E, *clausi* stage III; F, *tonsa* stage III; G, *clausi* stage IV; H, *tonsa* stage IV. Key to naupliar appendages shown in Figs. 1–3. a, first antenna; b, second antenna; c, mandible; d, first maxilla; e, second maxilla; f, maxilliped; g, first swimming leg; h, second swimming leg.

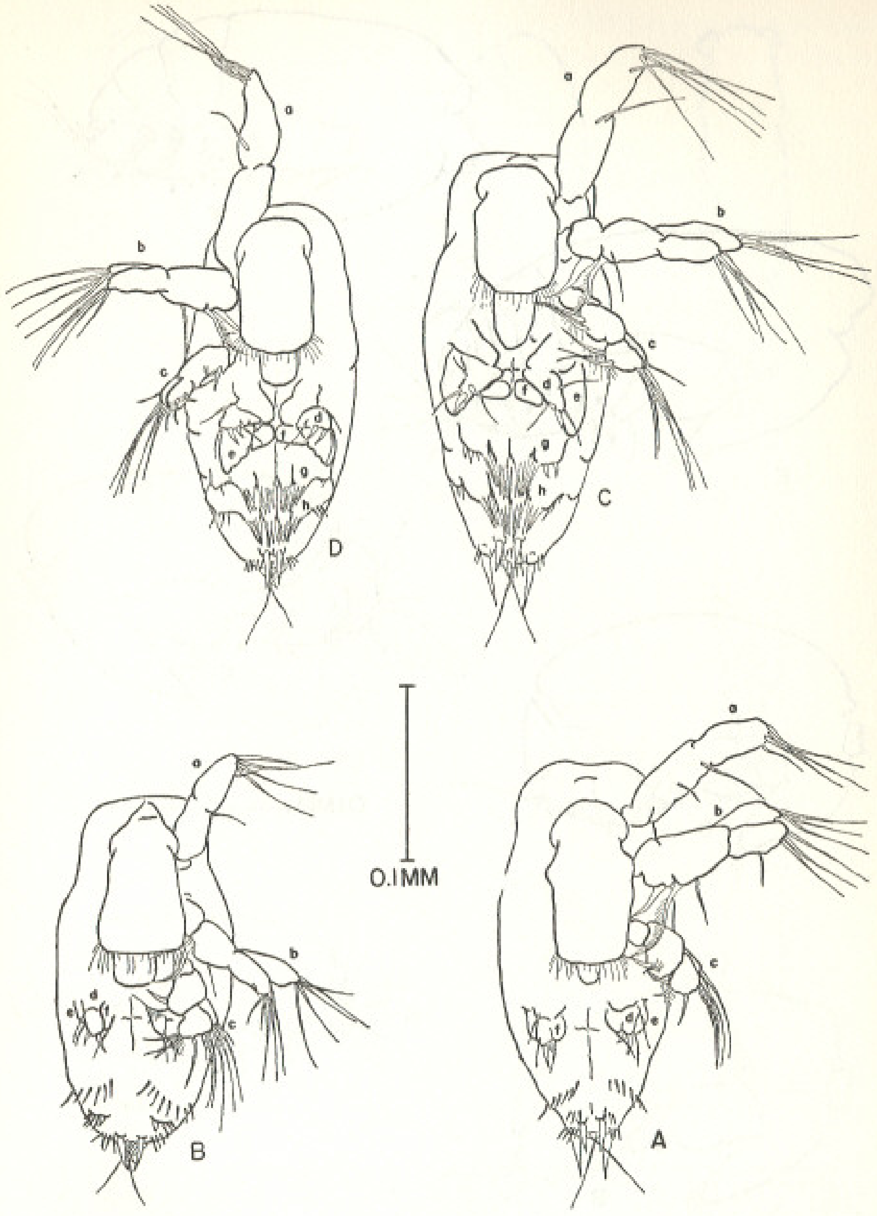

Figure 2. Naupliar stages V and VI. A, *clausi* stage V; B, *tonsa* stage V; C, *clausi* stage VI; D, *tonsa* stage VI. See Key in Fig. 1.

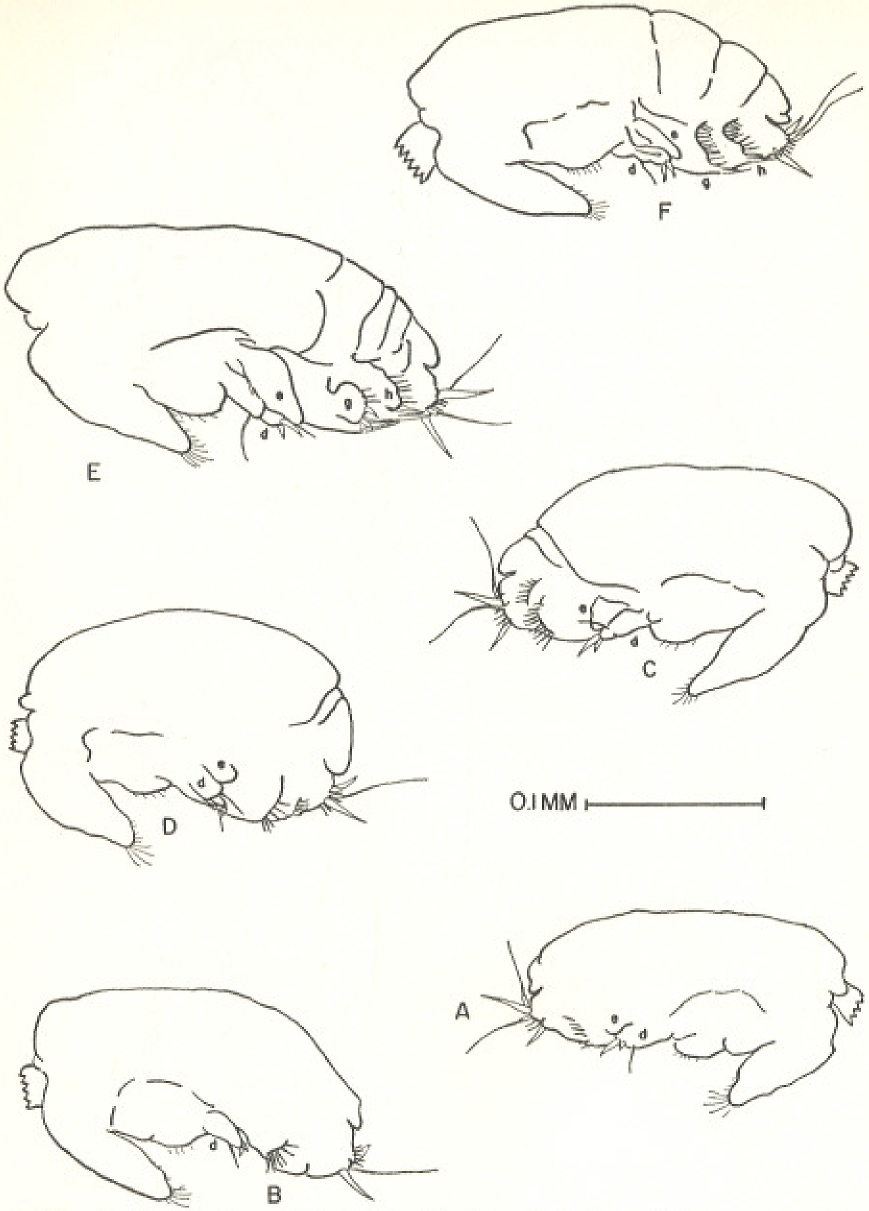

Figure 3. Naupliar stages IV, V and VI in side view. A, *clausi* stage IV; B, *tonsa* stage IV; C, *clausi* stage V; D, *tonsa* stage V; E, *clausi* stage VI; F, *tonsa* stage VI. See Key in Fig. 1.

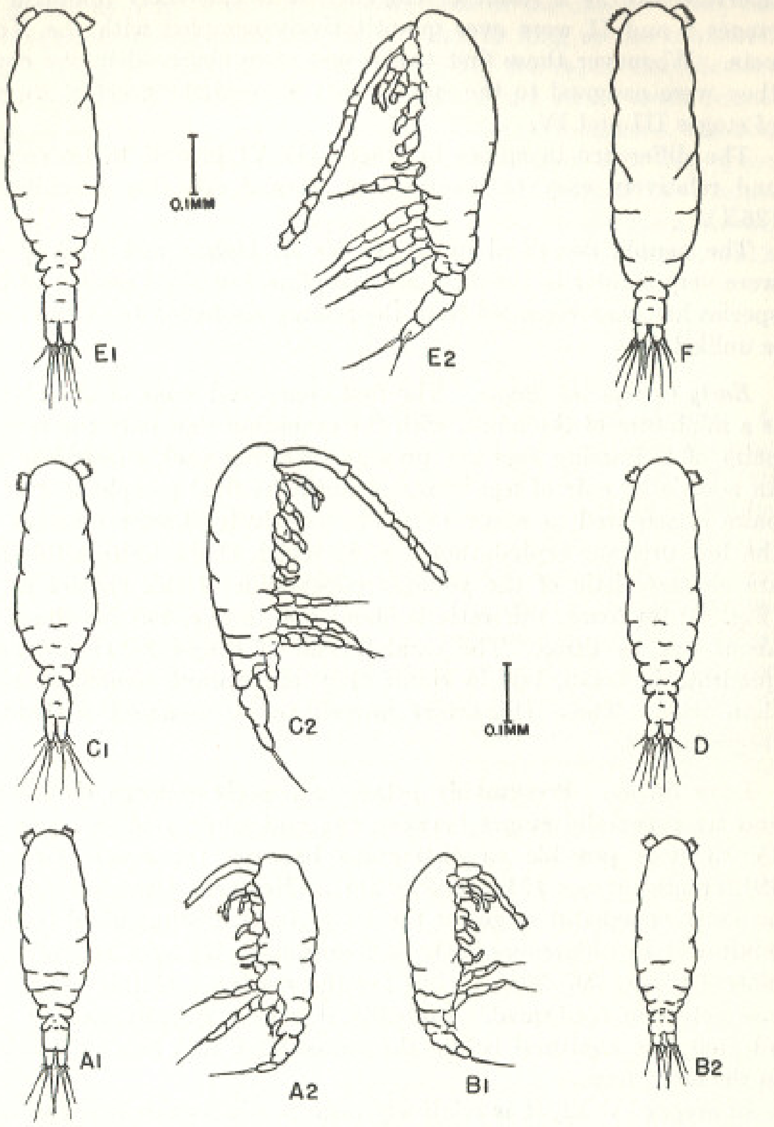

Figure 4. First three copepodid stages of *Acartia clausi* and *A. tonsa*. A1, dorsal view stage I *clausi;* A2, side view stage I *clausi;* B1, dorsal view stage I *tonsa;* B2, side view stage I *tonsa;* C1, dorsal view stage II *clausi;* C2, side view stage II *clausi;* D, dorsal view stage II *tonsa;* E1, dorsal view stage III *clausi;* E2, side view stage III *clausi;* F, dorsal view stage III *tonsa.*

aperture size as a result of clogging, it is extremely doubtful that stages I and II were ever quantitatively sampled with the No. 10 nets. Whenever these first two stages were observed in the counts, they were assigned to the species that showed the greatest numbers of stages III and IV.

The difference in spines in stages III–VI proved to be constant and relatively easy to ascertain at normal counting magnification (36X).

The nauplii described by Oberg for *A. bifilosa* and *A. longiremis* were very similar to the *A. clausi* nauplius, but since neither of these species has been recorded from the Sound, confusion from this source is unlikely.

Early Copepodid Stages. The first copepodid stage of all calanoids is a miniature of the adult, with the exception that only the first two pairs of swimming legs are present. During each succeeding molt an additional pair of legs is added until the final complement of five pairs is acquired at stage IV. The relatively shorter urosome and the low urosome-cephalothorax ratio which characterize adult *tonsa* are characteristic of the younger copepodids of this species as well (Fig. 4); for *tonsa*, this ratio is about one to five, but for *clausi* it is about one to three. The caudal rami of stages I–III are nearly quadrate in *tonsa*, but in *clausi* they are always somewhat longer than wide. These characters proved to be constant without intergradations.

Later Stages. Presumably pelagic copepods undergo six naupliar and six copepodid stages between egg and adult, and in copepodids IV–VI it is possible to distinguish between the sexes (Grandori, 1912: plate 10; figs. 171–176, 205–211). However, Grandori described an extra copepodid stage for the male *clausi*, distinguished from the adult only by differences in the fifth swimming leg (*cf.* Grandori, 1912: plate 10; figs. 207–208). Thus far the existence of this extra stage has not been confirmed. Probably it was a recently molted stage VI that was captured before the exoskeleton had become hardened in the adult form.

In stages IV–VI, it is relatively easy to distinguish between *clausi* and *tonsa*. In Long Island Sound, *tonsa* is always larger than *clausi* in the later stages, and the urosome is shorter in relation to the cephalothorax. The most lateral caudal bristle on each ramus is as heavy and nearly as long as the four middle ones in the case of *tonsa*, but it is definitely thinner and only about half as long as the others for *clausi*. This difference is particularly useful for rapid identification of the males. The fifth swimming legs of the adult *tonsa* female are characterized by a proximal swelling of the end segment, tapering to a coarse toothed central portion and terminating in a thin spine. The fifth legs are symmetrical and are not as described by Wheeler (1901) and figured by Wilson (1932). The *clausi* female has a shorter, less specialized end segment on the fifth leg (see Grandori, 1912: plate 10; fig. 211).

SEASONAL DISTRIBUTION OF *A. CLAUSI* AND *A. TONSA* BASED ON PRESERVED MATERIAL

Annual Variation in Total Numbers of Young and Adults. As mentioned earlier, these two species have a definite seasonal distribution in the Sound. Fig. 5 shows the distribution of all stages of both species. *A. clausi* first appeared in late November or early December 1952, reached maxima in May of both 1952 and 1953, and disappeared in July or early August. *A. tonsa* appeared in June each year, rose rapidly to its midsummer maximum in August, and then decreased more or less steadily throughout fall and winter. A small April peak occurred in both years, after which *tonsa* disappeared for over a month. Apparently this April increase reflected the superabundance of food available to all zooplankton organisms during the spring flowering. The significance of this rise followed by the abrupt disappearance of *tonsa* will be discussed later.

Neither species was as successful in 1953 as in 1952. The maximum number of *clausi* during 1952 was 102,100/m^3 on May 21, and the numbers remained well above 50,000 during the following month. In 1953, the *clausi* peak on May 18 was only 61,800, after which the numbers fell off in two weeks to less than half this figure. In 1952, *tonsa* reached its peak of 82,000 on August 19 and the population remained quite high until September 16. In 1953, a maximum of 46,000 occurred on August 5, but one week later the total number had fallen to only 15,500. It is possible that a higher count might have been recorded after August 18, the date when analyses were terminated. However, displacement volumes were measured throughout summer and fall of 1953. While displacement volumes reveal nothing about the abundance of a particular organism, it seems

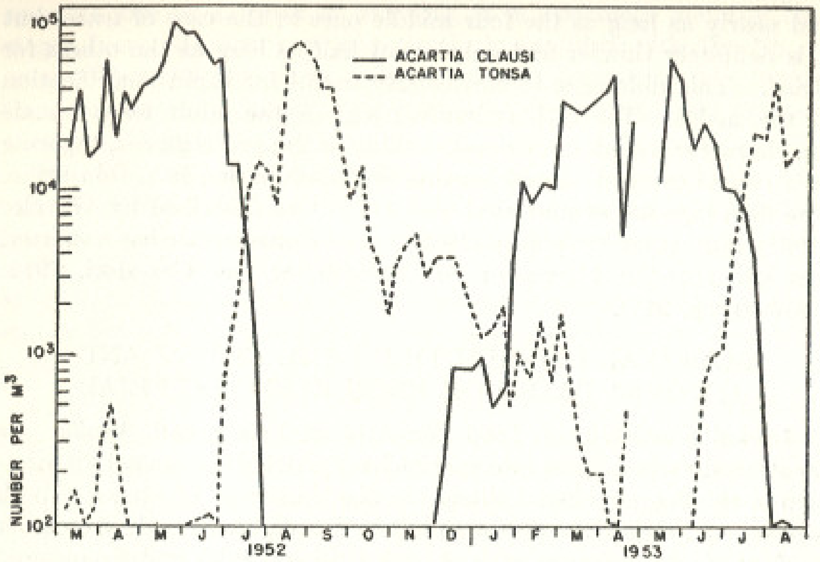

Figure 5. Seasonal distribution of all stages of both species plotted on log scale, No. 10 net.

probable that a late August or early September increase in *tonsa* would be reflected in higher volumes of total plankton. On the contrary, after August 18, volumes of plankton fell away sharply to less than half the August 5 figure of 1.53 cc/m³.

Cell counts and chlorophyll values were lower in spring and early summer of 1953 than they were during the same period of 1952, perhaps accounting for lower numbers of *clausi* in 1953. On the other hand, there was more food available in the late summer of 1953. The major difference in the biological environment of these two species for the two years was not so much the amount of food available as the type of food. There were striking differences in the species composition of the phytoplankton between the two years (see S. M. Conover's paper, PHYTOPLANKTON, in this volume), the quantity of diatoms and other larger phytoplankton elements being greater in 1952. Experimental evidence on food preferences, which will be introduced later, provides a possible explanation for the larger standing crop of zooplankton in 1952.

Seasonal Distribution of Adults. The sex ratio of adult copepods varies considerably in different species and from season to season.

Marshall (1949) found that male *Centropages hamatus* and *Temora longicornis* outnumbered females in Loch Striven whereas females of *Pseudocalanus minutus*, *Paracalanus parvus*, *Microcalanus pygmaeus*, *Acartia clausi*, and *Oithona similis* were more abundant than males during at least part of the year. In that body of water, *clausi* in particular showed a marked seasonal variation in sex ratio; during winter the males constituted only 7.7% of the total adult population of this species, whereas in summer the males often outnumbered the females.

This striking variability in sex ratio does not necessarily reflect differences in actual numbers of the sexes produced. Marshall has shown that, for copepodid stages IV and V, the number of males and females of the seven species mentioned above was nearly equal. Probably variation in the proportion of males to females is dependent on differences in the life span of the adults. If the adult life span of one sex of a certain species is shorter than that of the other, the explanation for the phenomenon may be found in differential success in utilizing the environment. In some species of copepods, notably *Euchaeta norvegica* (Sars, 1903; Nicholls, 1934), the male's reduced mouth parts must be a factor in his longevity. Marshall, in her study of Loch Striven copepods, found an average of less food in the intestines of the males. In the Sound, males of both *clausi* and *tonsa* usually showed less gut contents than females. Respiration and grazing experiments with *tonsa* suggest that the female is more efficient than the male under temperature conditions approximating the natural environment (20° C).

If we assume that the males of certain species are not as efficient as the females, then unfavorable environmental conditions should affect the males first. In the Sound, during periods of low abundance or decreasing numbers, females of each species were more plentiful than the corresponding males (Fig. 6). In the case of *tonsa*, the males and females were about equal in numbers on August 26, one week after the highest 1952 total was recorded for this species, but during the next two weeks the number of adult females increased while the total of all stages (see Fig. 5), particularly that of the adult males, declined (Fig. 6A). With regard to *clausi*, maximum numbers of adults occurred in April 1952, with males actually outnumbering females on April 21. Both sexes then decreased sharply in abundance, but the males declined in numbers even more precipitously

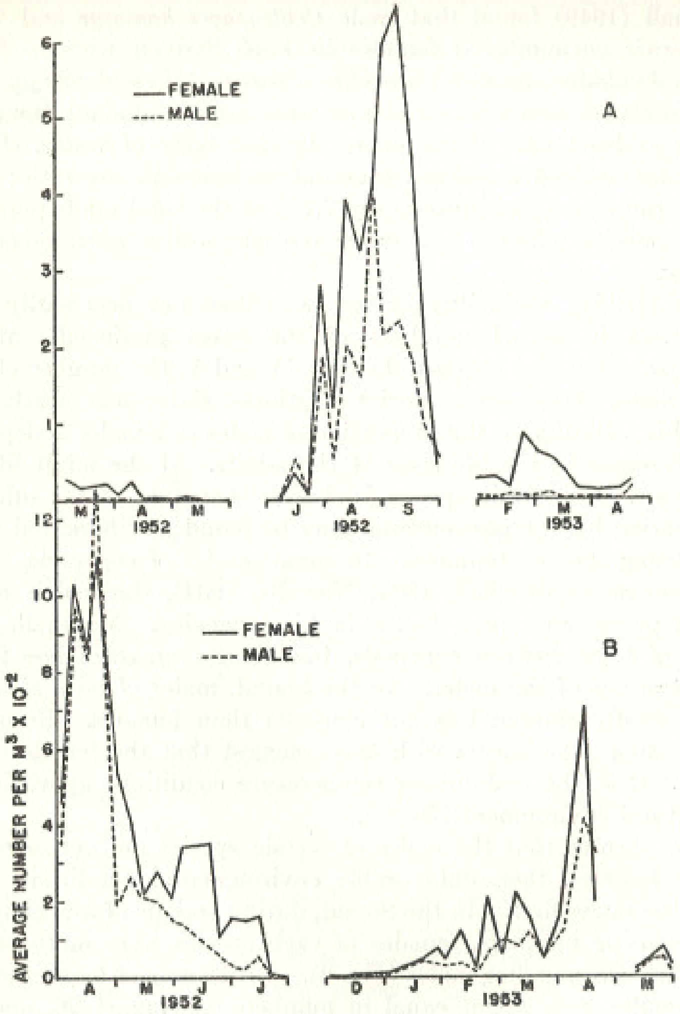

Figure 6. Seasonal distribution of males and females. No. 2 net. A, *tonsa;* B, *clausi.*

than the females (Fig. 6B). Through the rest of the spring, the females outnumbered the males. Total numbers of *clausi* continued to increase during most of May to a maximum on May 21 which consisted largely of nauplii and young stages (see Fig. 5). It is concluded that mid-April rather than May was actually the period

of optimal conditions for *clausi* despite the high total numbers in May.

In 1953 the number of males did not approach the level of abundance found for females. Since the spring totals were considerably lower in 1953 than in 1952, it is suggested that optimal conditions for production of *clausi* were never attained in 1953.

Distribution of Different Stages during Transition Periods. Twice a year in the Sound, once in early summer and again in early winter, both species are taken in the same tow in more or less equal numbers. The distribution of all developmental stages during these important transition periods was investigated. Because development of these copepods is relatively rapid and since breeding is nonsynchronous, it was found necessary to lump together certain developmental stages in order to produce a clearer picture. All nauplii were treated as a unit and the copepodids were grouped into three units consisting of stages I–II–III, stages IV–V, and stage VI. To minimize sampling errors due to nonrandom distribution, the data are presented as percent of total numbers of zooplankton captured. Figs. 7 and 8 show graphically the summer transitions for 1952 and 1953.

Despite certain minor discrepancies in the distribution between the two years, it seems probable that unfavorable environmental conditions affect the younger developmental stages of *clausi* sooner than the adults. The nauplii were completely gone by the end of July, although they persisted slightly longer in 1952 than in 1953. Copepodid stages I–II–III disappeared in the latter part of July about a week earlier than stages IV–V. The adults, last to disappear, were still present in low abundance in August and were taken later in 1953 than in 1952.

A. tonsa nauplii first appeared in early June of both years while the population was still dominated by *clausi;* a few *tonsa* adults, the initial breeding stock, were also found through most of June. In 1953, copepodid stages I–II–III appeared in early June, whereas in 1952 they appeared rather abruptly in July. Stages IV–V rose significantly in numbers shortly after the younger stages started to increase, and by the fourth week in July, the first summer generation adults appeared in both 1952 and 1953.

Breeding was certainly not spontaneous and development was rather irregular, but nonetheless it was possible to ascertain the approximate length of time required for the development of the first

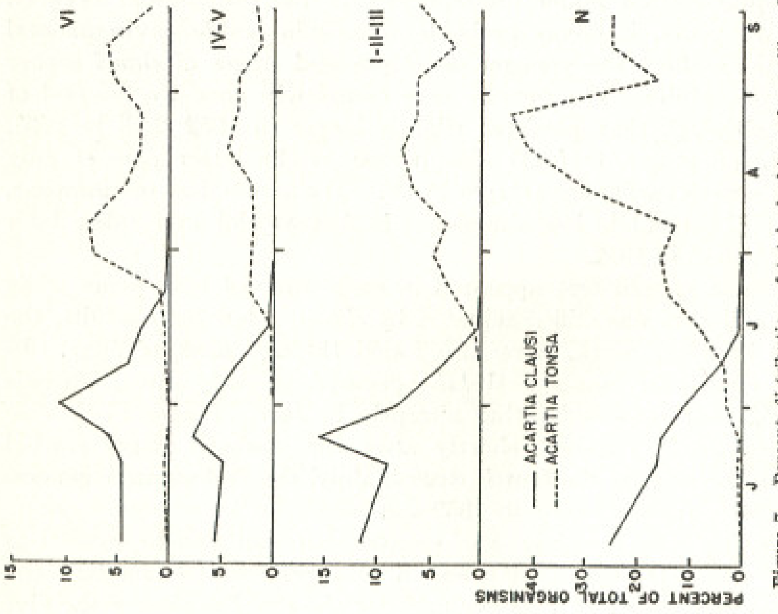

Figure 7. Percent distribution of total plankton of nauplii and copepodid stages during the summer transition period, 1952. No. 10 net.

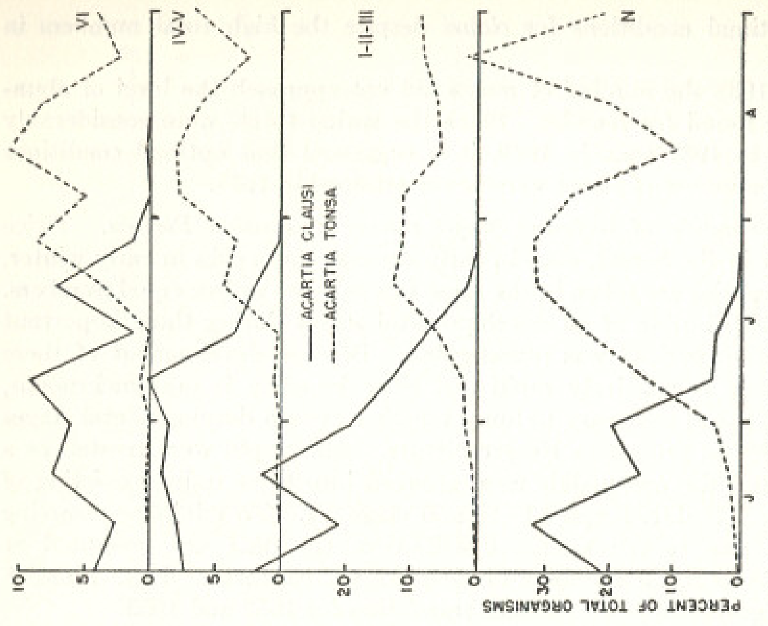

Figure 8. Percent distribution of total plankton of nauplii and copepodid stages during the summer transition period, 1953. No. 10 net.

generation of *tonsa*. Since the first major accumulation of nauplii found during the week of July 1–8 was followed by an initial maximum of adults in late July, it is postulated that complete development under the environmental conditions of the Sound took place in three to four weeks. The data of Marshall (1949) and Digby (1950) suggest four to five weeks as the length of a summer generation of *A. clausi* in British waters, and Nicholls (1933) reported 28 days as the maximum period of development for the much larger *Calanus finmarchicus* in the Clyde Sea area during spring. Considering that Long Island Sound temperatures during July and August are at least 5° C warmer than the maximum summer temperatures in British waters, a three to four week development of *tonsa* from egg to adult seems reasonable.

As would be expected, the winter transition was more gradual and the data clearly suggest that conditions became unsatisfactory for continuous development of the younger stages of *tonsa* (Figs. 9, 10). During December and January, stages I–II–III disappeared progressively from the plankton, despite the fact that a few nauplii were produced throughout the winter. From November through February the total numbers of stages IV, V, and VI did not change significantly (Fig. 9), although a sharp increase in the percentage of adults was recorded in late December (Fig. 10). This peak was unquestionably an artifact which resulted from the final elimination of lingering summer populations of other species before winter forms had become well established. Thus, for a short period the percentage of the more resistant *tonsa* was disproportionately high. The relative uniformity in numbers of later copepodids indicates little recruitment from younger stages. In fact, there was probably little molting at any level.

During winter many of the older stages of *tonsa*, even stages IV and V, were host to a stalked protozoan, while at other times of the year only an occasional large and probably senile adult was found infected. If it is assumed that the incidence of infection will increase with the length of time an individual has been in the water, this observation lends further support to the theory that the *tonsa* population is in a steady state during the cold months.

The behavior of either species could not be determined during the spring flowering, since clogging of the No. 10 net with phytoplankton was so great that quantitative sampling was impossible. Comparison

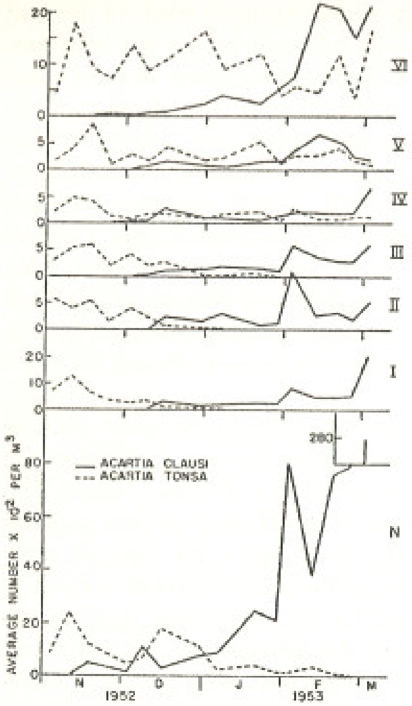

Figure 9. Distribution of nauplii and copepodid stages during the winter transition period, 1952–1953. No. 10 net.

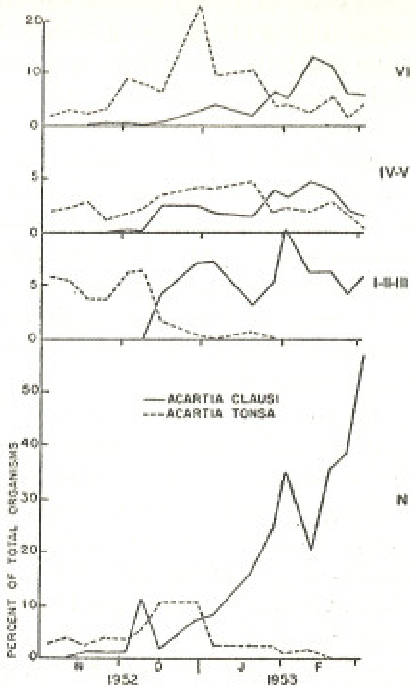

Figure 10. Percent distribution of total plankton of nauplii and copepodid stages during the winter transition period, 1952–1953. No. 10 net.

of preflowering and postflowering data showed higher numbers of *tonsa* copepodids and nauplii in the latter period.

The development of the *clausi* population during winter was gradual and rather irregular. The length of the first generation was undoubtedly longer, perhaps twice as long as the summer estimate of three to four weeks for *tonsa*. Possibly the small but distinct rise in naupliar numbers in early December produced some of the *clausi* adults that matured in late January and early February just prior to the spring flowering. In any case, the abundance of food during the flowering unquestionably set off the great breeding activity as indicated by the nearly fourfold increase in numbers of nauplii between February 24 and March 2. In a few weeks the entire population rose to the high springtime level shown in Fig. 5.

Examination of the gonads of mature females of both species to determine the effect of environmental changes on the reproductive potential of the breeding stock showed that there were always some females capable of oviposition. The number of eggs in the ovary and ducts was not related to the number of nauplii taken in No. 10 net hauls. While no attempt was made to distinguish between the eggs of the various species of copepods found in the Sound, the number of eggs of all species relative to the number of nauplii was greatest in spring and least in summer. The environment surely has some effect on the breeding cycles of adults, but its influence on the eggs and young may have been greater, through control of survival rate and speed of development.

Number of Generations. Digby (1950) postulated at least five generations of *A. clausi* in the waters off Plymouth, England. The data of Marshall (1949) suggest perhaps four generations of this species in Loch Striven. While *clausi* is a year-round inhabitant of these British waters, both authors found that the last generation, produced late in the fall, was not very successful, so that overwintering populations were small.

On this side of the Atlantic, in Tisbury Great Pond, Deevey (1948) found two distinct generations of *clausi* in 1945 and 1946, one of which matured in April and the other in late May and June. Especially notable is the fact that almost no adults of this species were observed from late April to late May. Deevey also noted four generations of *tonsa* in 1945 and three in 1946, but it is possible that a fourth brood matured in the latter year after September 2, when her survey was terminated.

The number of generations of each species of *Acartia* in the Sound was estimated from the distribution of nauplii and adults (Fig. 11). The data are presented on a log plot since this form of presentation minimizes nonsignificant differences in numbers between nauplii and adults and facilitates comparison. The nauplii of each generation are designated by Roman numerals and the corresponding adults in Arabic.

An estimate of four generations a year was obtained using data from 1953 (Fig. 11B) supplemented by the information recorded from 1952 (Fig. 11A). Adults noted about December 1, 1952 have been designated 0. Some of the offspring (I) of this primary breeding stock reached maturity in February and were designated 1. The

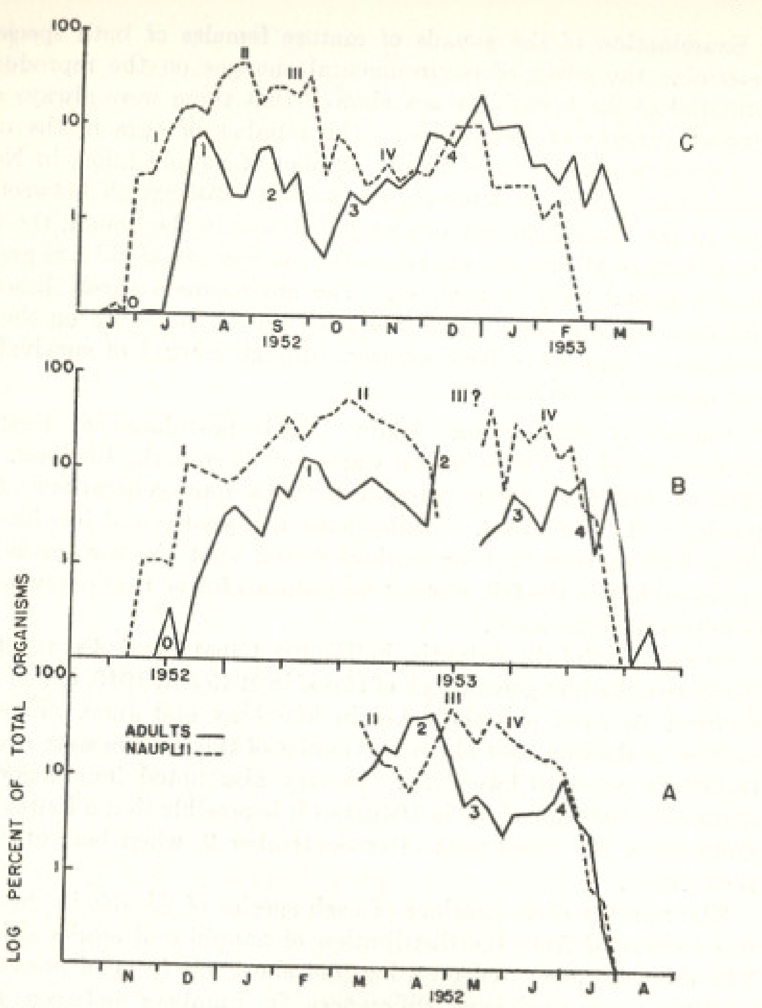

Figure 11. Seasonal distribution in percent of total organisms of adults and nauplii. A, *clausi* 1952; B, *clausi* 1953; C, *tonsa* 1952–1953. No. 10 net.

precise designation of adults 1 is complicated by subsidiary peaks in December and January, but a second naupliar peak II was undoubtedly produced by these adults. Adults 2 matured in April of both 1952 and 1953 and probably produced nauplii III, although a gap in the 1953 data makes the exact date of origin of this generation questionable. Generation 3 adults matured slightly later and were

probably more successful in 1953 than in 1952. Naupliar peak IV, appearing in late May and early June of both years, gave rise to adults 4 which lingered into the summer. Considering the observations of Digby (1950) and Marshall (1949), four generations of *clausi* per year in the Sound are not unreasonable.

The discrepancy between Deevey's observations on *clausi* in Tisbury Great Pond and ours in Long Island Sound is not easily resolved. Tisbury Great Pond, by comparison with the Sound, is such a small body of water and is subject to such extreme variations in temperature, salinity, and probably other ecological factors, that unassessed variables may complicate the picture. As mentioned previously, Deevey observed no adult *clausi* in Tisbury Great Pond for over a month during April and May, whereas in the Sound, these same months are extremely favorable for continuous development. According to Deevey's interpretation, a generation of *clausi* in Tisbury Great Pond would require eight to ten weeks for development from egg to adult; this would seem to be an unusually long life cycle, particulary since the temperature range of approximately 12° to 18° C during this period is clearly favorable for Sound *clausi*.

As in the case of *clausi*, there were probably four generations of *tonsa* annually in the Sound, produced in the period from June through March. In Fig. 11C, the development of the first two generations is clear enough; however, on September 23, a secondary peak of adults appeared which must have produced some of nauplii III. After mid-October, the percentage of *tonsa* in the tows increased while totals of all species were decreasing, suggesting that *tonsa* was more resistant to fall and winter conditions than other summer zooplankton forms. In any event, adult peak 3 appears to be significant. The designation IV applies to low levels of nauplii produced through the cooler months. Possibly a few of the early IV nauplii matured so as to produce an overwintering population which consisted of both adults 3 and 4.

Comparing the Sound with Tisbury Great Pond, it appears that the same number of broods of *tonsa* are produced, but the periods of occurrence are somewhat different, probably due to differences in seasonally controlled environmental conditions resulting from the size discrepancy between the two bodies of water.

Seasonal Variation in Size. The literature on size variation in copepods has been reviewed by Sewell (1948), and it will be necessary to mention only briefly here some of the more pertinent work. Bogorov (1934) noted that the largest *Calanus finmarchicus* developed in the spring and he concluded that it was the temperature at which the copepod developed that determined its size. On the other hand, Digby (1950) and Marshall, *et al.* (1934) found that the largest copepods developed during periods of abundant food. Difference in the density of the environment may explain the large size of the North Sea population and the smaller estuarine populations of *A. clausi* described by Gurney (1931). Certainly, the large size of *A. clausi* in the Adriatic is primarily dependent on the density of those warm waters (Sewell, 1948). In Block Island Sound, Deevey (1952a) noted that *Centropages typicus* increased in size during the winter to a maximum length in early spring. In Tisbury Great Pond, she observed that both *clausi* and *tonsa* of the first generation were larger than those of subsequent generations of the same year (Deevey, 1948).

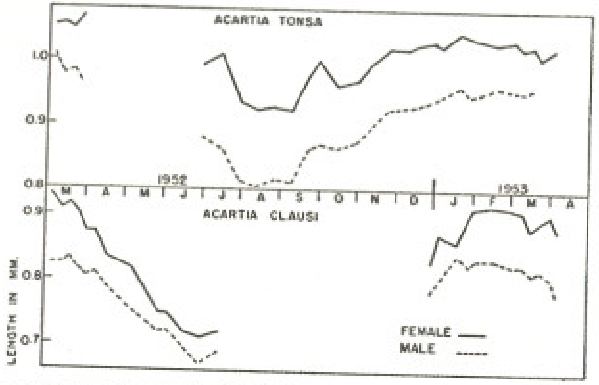

Figure 12. Seasonal variation in length of adults as determined by length of cephalothorax.

In our study, measurements were made on the length of each sex and species of *Acartia* collected from the Sound during an entire year (Fig. 12). From March to June 1952, the size of both male and female *clausi* decreased more than 0.2 mm, and in early winter 1953 a rather abrupt increase was noted. In the case of *tonsa*, the sharp decrease in length in July was followed by a gradual increase through fall and winter to its largest size in early spring. The occurrence of the largest specimens of each species was better correlated with the winter temperature minimum and consequently high density than with the spring phytoplankton peak.

Since previous workers have delineated different broods on the basis of size, a similar procedure was followed for *clausi* and *tonsa* of Long Island Sound. Referring to the 1952 data, the decrease in size of the *clausi* females, from over 0.9 mm in late March to 0.84 mm by mid-April, corresponded to the burst of adults designated 2 (Fig. 11A). Another decrease in size corresponded with adults 3 appearing in May. Finally, the small size of the late June and July individuals appeared to confirm a fourth generation of adults.

As for *tonsa*, the maturation of generation 1 about July 29 (see Fig. 11C) coincided precisely with the significant decrease in length shown in Fig. 12. The second brood of adults matured about the first week of September, but no apparent change in size occurred until September 23, when a group of rather large individuals appeared. This sudden increase in size corresponded exactly with the subsidiary maximum mentioned in the previous section. Either our determination of generation 2, as originally defined, is in error and should be disregarded, or else an extra generation developed just after the maximum of adults 2. Certainly two weeks would be an exceedingly short development period, and, moreover, the peak of September 9 was greater in total numbers than that of September 23. Possibly brood 2 actually split into early and late sections. In that event, the early maximum might represent a group which developed more rapidly in inshore waters (slightly lower salinity and higher temperature) while the subsidiary maximum might represent those which developed more slowly under offshore conditions. Worthy of mention in this regard was the moderate chlorophyll peak observed in the inshore waters about the first week in September and a similar peak at the offshore stations two weeks later on the 23rd.

The third brood of *tonsa* must have matured over a period of several weeks. The gradual increase in size during fall and early winter suggests a slow but continuous recruitment of organisms developing under a variety of temperature and food conditions.

To determine as precisely as possible the age structure and behavior of these different broods, a series of frequency diagrams for adult females of both species has been prepared (Fig. 13).

A single brood should be characterized by a histogram that closely approximates the normal curve, with the majority of individuals falling into rather narrow size limits. On March 5, 1952, the size distribution for *clausi* was quite uniform, with the majority of individuals falling between 0.91 and 0.95 mm; these animals could have been remnants of generation 1 (see Fig. 11). In the succeeding weeks, smaller individuals appeared until on April 2 a reasonably homogeneous group was found with a mode about 0.87 mm. This histogram probably represents adults of generation 2. During the next few weeks, several size categories were found, so that precise delineation of generation 3 was difficult. On April 9 a small group of animals (0.82 to 0.84 mm) appeared which could be followed through to May 8, but the histogram for May 24 fitted the theoretical criteria for normality better and was therefore considered typical of brood 3. The narrow spread and smaller mean of the histogram for July 1 suggests that these individuals constituted a definite fourth brood.

It is also possible to obtain an estimate of the length of adult life from these data. If the few large specimens found in mid-April tows are considered members of brood 1, which developed during the winter, the adult life of this early spring generation must have been a month or more. Some members of brood 2 were still present on May 8, approximately a month after they first appeared. Females of generation 3, which were noted on May 24, in all probability had nearly disappeared by July 1, despite the apparent bimodality of the July 15 distribution. Thus one month was about the maximum life span for an adult female *clausi* during the spring, but undoubtedly the life span was considerably longer during the winter.

Referring to the data on *tonsa*, a striking drop in size was apparent during the latter part of July in 1952; the larger females taken on the 15th probably represented remnants of the breeding stock 0, whereas the smaller ones obtained on the 29th represented generation 1. There was no further change in the size structure of the population until September 23, when the group of large individuals of enigmatic origin appeared distinct from those found on September 9 (brood 2). The platykurtic nature of the frequency diagrams during the cooler months of the year, for *clausi* as well as *tonsa*, lends confirmation to the theory that breeding and development is retarded and somewhat erratic during the winter.

One other point is suggested by the size data. The adult *tonsa* taken on July 15, 1952 were actually about the same size as those observed the following spring, March 16, 1953, the mean lengths being 1.009 mm with a standard deviation of 0.0318 and 1.022 mm with a standard deviation of 0.0555. Although these broods are not

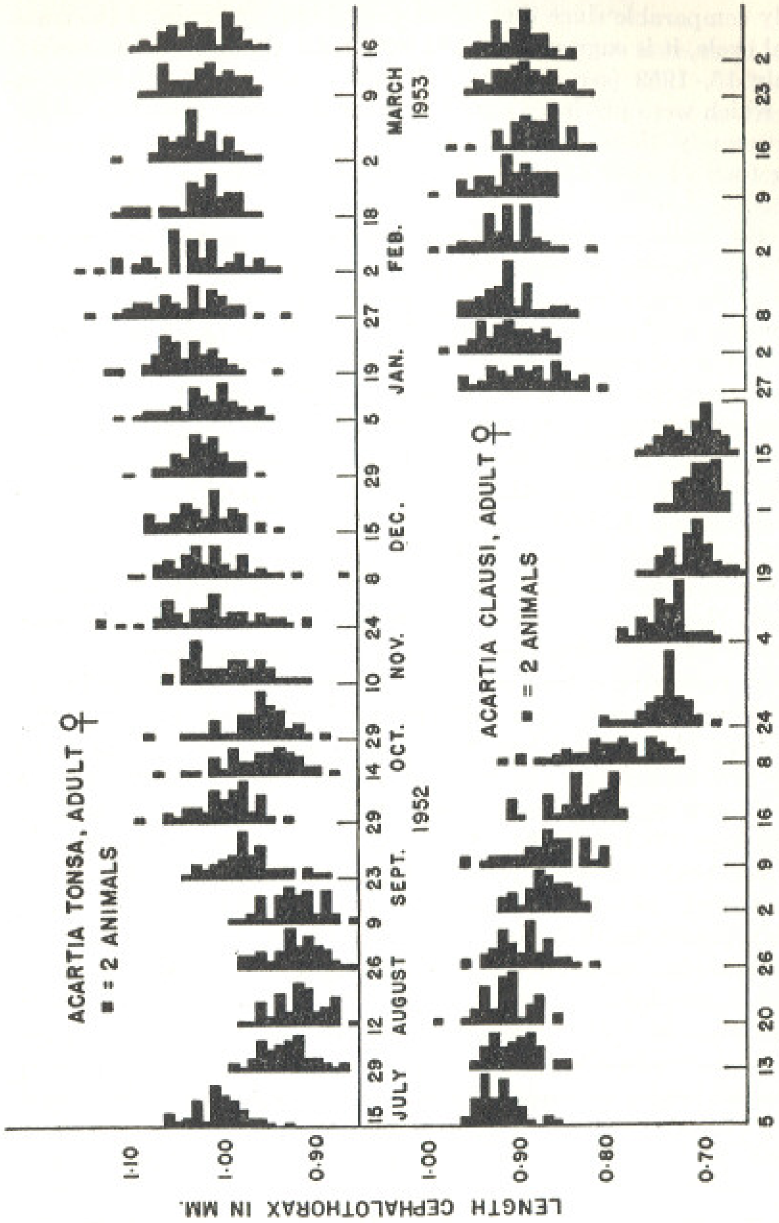

Figure 13. Size distribution of adult female *clausi* and *tonsa* at different times of the year, 1952–1953.

strictly comparable since they developed at opposite ends of the same annual cycle, it is suggested that at least some of the adults measured on July 15, 1952 (see Fig. 12) belonged to the same generation as those which were produced earlier, during the cooler months of 1952. Unfortunately there were not enough adult females in the early spring tows of 1952 to make statistical confirmation of this theory possible.

On the basis of 1952–1953 measurements, summer and winter *clausi* were clearly different broods, but no measurements were obtained of the first *clausi* which appeared in the fall of 1952. In 1953, measurements of random samples taken on July 22 and November 11 indicate that some spring *clausi* might have survived until fall. While the mean lengths of these two samplings, 0.732 and 0.761 mm, were significantly different statistically, a frequency diagram for the November date suggests that more than one brood was represented; at least half of the measurements fell within the size limits of the July sample and the rest were definitely larger.

If a population is to survive unfavorable seasonal conditions, some means of maintaining a breeding stock must exist. In marine copepods there is no direct evidence for "resting" eggs as in some freshwater forms. While immigration from other regions is a possible means of supplying a breeding stock, in this case it seems unlikely. The pattern of circulation for the Sound is such that bottom water enters from Block Island Sound and moves west at an average speed of only half a kilometer per day. Moreover, Deevey (1952a, 1952b) found *Acartia* spp. a minor element in Block Island Sound, and *tonsa* often appeared in Long Island Sound first. Possibly *clausi* and *tonsa* never disappear completely from the water column but merely become scarce enough to remain unnoticed; however, the breeding stock always appeared suddenly and in considerable quantity. Or possibly a few organisms survived unfavorable conditions in low abundance in some unsampled area. In this regard, it is worth mentioning that Howard Sanders (personal communication) found *clausi* in a good state of preservation in bottom samples collected on June 30, 1953, a date when *tonsa* was increasing in numbers and *clausi* was decreasing (see Fig. 5).

COMPARATIVE PHYSIOLOGY

Thus far, differences in seasonal distribution have been emphasized, and generalizations have been made concerning the relationships of the organisms to seasonally determined variables such as temperature and food. In the following sections, the effect of certain ecological factors is investigated, usually under controlled laboratory conditions, in order to learn more about the mechanism of environmental control over the copepods.

At least five oceanographic parameters which might affect a marine animal show marked seasonal variation in Long Island Sound, namely, dissolved oxygen, salinity, light, temperature, and the amount of phytoplankton, but the first two probably have little influence on the local zooplankton fauna. Marshall, *et al.* (1935) found that respiration in *Calanus finmarchicus* was independent of oxygen concentration above 3 ml/l. Although no experiments have been performed to test the effect of oxygen concentration on Sound copepods, there is no evidence that variation in oxygen concentration within the range observed in nature affects their metabolism. In the Sound, the waters just above bottom may fall below 3 ml/l in late summer, but through most of the water column oxygen concentrations remained well above 50% saturation. Nor should seasonal changes in salinity have a noticeable effect on *clausi* and *tonsa*. Both are extremely euryhaline copepods. Davis (1944) found *tonsa* in Chesapeake Bay waters that varied in chlorinity from 0.4 to nearly 19‰; Sewell (1948) gave 0–36‰ as the salinity range for *clausi*. Marshall, *et al.* (1935) noted that respiratory rates of *C. finmarchicus* remained unchanged with a 20% dilution of sea water. If the relatively stenohaline *C. finmarchicus* could withstand a 20% dilution of its environment over the course of a few days without any obvious change in metabolism, certainly the euryhaline *clausi* and *tonsa* should not be seriously affected by a 6–8% dilution of Long Island Sound over a period of several months. On several occasions, Deevey (1948) noted a sudden decrease in the numbers of *tonsa* accompanying a sharp rise in salinity when Tisbury Great Pond was opened to the sea. However, her evidence did not indicate whether the population was actually harmed by the increased salt content or simply diluted by the outside water. In any event, the minor seasonal fluctuations in the Sound are considered a doubtful determinant of the behavior of *clausi* and *tonsa*. For these reasons, major attention has been devoted to study of the effect of light, temperature, and kind and abundance of food. Most of the experiments were designed to compare the effects of the different variables on the two species.

Light Responses

A. tonsa and *A. clausi*, like many other zooplankters, undergo diurnal migration in the sea. This behavior has been duplicated in the laboratory with natural and artificial illumination (Schallek, 1942). A preliminary experiment was performed on October 10, 1952 to see whether Sound *tonsa* behaved as predicted. Two large graduated cylinders filled with sea water were placed in a window and shielded from direct sunlight. Some *tonsa* were added to each cylinder, and the one designated B was hooded to keep out the light. Counts were made at four levels in the cylinders at approximately three hour intervals for an entire day. The results are presented in Table I.

TABLE I. Vertical Distribution of *Acartia tonsa* in Response to Variation in Amount of Natural Light

	Number of animals at each level at different times of day								
	0900	*1200*	*1500*	*1800*	*2100*	*0000*	*0300*	*0600*	*0900*
Vessel A (uncovered) Depth									
1 (surface)	4	4	14	19	20	14	24	11	12
2 (intermediate)	5	2	1	5	10	9	5	10	12
3 (intermediate)	2	5	2	3	3	9	1	1	1
4 (bottom)	2	4	0	3	2	2	1	1	4
Vessel B (covered) Depth									
1 (surface)	0	15	6	18	12	11	14	18	15
2 (intermediate)	13	9	16	12	12	14	10	16	9
3 (intermediate)	8	11	9	11	14	1	6	4	7
4 (bottom)	11	7	8	2	3	3	7	2	6

The copepods in the dark cylinder (B) maintained a relatively unchanged distribution, with greatest concentrations in the upper layers. No innate rhythm of migration in the absence of light was observed. In cylinder (A), exposed to daily changes in light, the greatest numbers were noted in the surface layers between 1800 and 0300, the hours of darkness. At 1500 there were some animals in the upper layers; perhaps due to shorter day length at this time of year, there was sufficient diminution of light to start some organisms on their upward migrations. Twelve animals were still lingering in the surface waters by 0900 the next morning, but the majority had descended to the bottom. Organisms directly on the bottom could

not be counted; hence bottom counts were made on only those organisms swimming in the bottom one inch of water.

Although copepods remain in deeper water during the day, some species, including *clausi* and *tonsa*, are attracted to direct light. When light has directionality, it strikes only one region of the photoreceptor and the copepod swims towards the source. But if the light is made diffuse, as by passing through a quantity of water, it strikes the photoreceptor from several directions simultaneously; under these conditions the animal ceases to swim and sinks to the bottom of a vessel or to some threshold level in the sea (Schallek, 1942).

Effect of Temperature on Light Responses. Because seasonal temperature changes appear to play an important rôle in the control of *Acartia* populations, an experiment was designed to compare light reactions of both *clausi* and *tonsa* at different temperatures. Four 2000 ml graduated cylinders were filled with sea water to the two liter mark. Fifty *clausi* were added to two of these cylinders and fifty *tonsa* to the other two. One cylinder containing *clausi* and one *tonsa* were placed at 15° C; similar tubes were placed at 4° C; all tubes were allowed to equilibrate several hours in darkness. Observations were made as follows: after five minutes of direct overhead illumination; after five minutes of diffuse illumination following two hours for re-equilibration; and after a two hour period of darkness. Diffuse light was produced by placing several thicknesses of rice paper over the cylinder; although no single point of illumination was present, the light intensity was not uniform from all directions. Distribution was ascertained by rapid counts of the organisms observed in 200 ml of water at four levels in each cylinder; the general abundance in the intervening regions was also noted.

Comparison of the results showed no essential difference in the responses of *clausi* and *tonsa* to direct light at 15° (Fig. 14). On the other hand, at 4° less than half as many *tonsa* were attracted to the light while the response of *clausi* was about the same as at 15° C. Examination of the 4° cylinder containing *tonsa* showed that many were dead or dormant on the bottom, but when the tube was warmed to 15°, a normal response to direct light could be elicited.

Diffuse light at 15° appeared to provoke a different response from each species. When the light was turned on, most of the *clausi* ceased to swim and, with head up and antennae outspread, sank toward the bottom. A few aberrant animals started to sink but then swam upward for a short time, thus remaining more or less in one region. Although some *tonsa* started to sink immediately, a large percentage swam upward toward the area of most intense illumination. At 4° most individuals of both species underwent the sinking reaction under the influence of diffuse light.

In darkness at 15°, both species tended to congregate in the upper waters as they did in the experiment discussed previously (see Table I). Again at 4°, the *tonsa* response was much weaker; few animals apparently made an upward migration in the dark. Thus temperatures approaching winter levels in Long Island Sound might produce in the two species different reaction to light and, consequently, different vertical distribution.

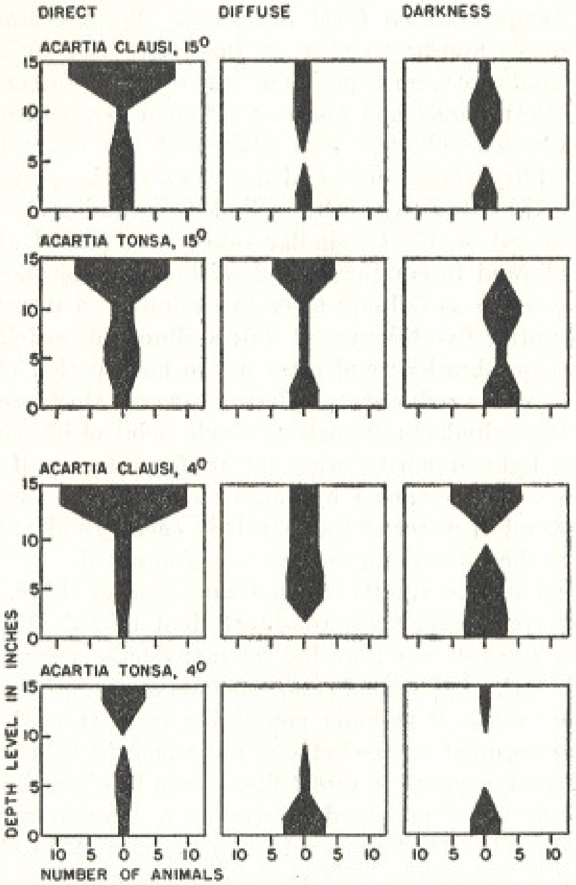

Figure 14. Vertical distribution under laboratory conditions in response to direct light, diffuse light, and complete darkness at two different temperatures.

Vertical Distribution in the Sound. On the basis of this and other experiments in which temperature was a factor, a study was made of the vertical distribution of the copepods throughout the year, paying particular attention to the distribution in relation to the thermocline when present. Periodic tows with the Clarke-Bumpus sampler and No. 2 bolting silk nets were made at two depths, one in the upper five meters, which was intended to sample the water above the thermocline, and the other near the bottom. In conjunction with these tows, a bathythermograph trace was usually obtained to establish the temperature distribution within the water column.

Before comparison of the vertical distribution of animals and temperature could be made, the depth of the tow had to be ascertained. The approximate depth at which the plankton sampler was operating was estimated from the amount of towing wire and the wire angle, using a correction for curvature of the wire. The correction was derived from statistical examination of cases in which the weight on the end of the wire dragged bottom at known depths.

The results of these tows, taken at intervals from April 1953 through July 1954, have been plotted in Fig. 15. The histograms represent the percentage of adults and copepodids of each species in the total plankton. The base of each histogram indicates the temperature at which the sample was taken. The histograms are arranged so that surface tows run toward the top of the illustration and the deep tows toward the bottom. The heavy horizontal line approximates the position of the thermocline during the spring and summer months. Actually, this figure represents the top of the thermocline. The bathythermograph record was read at intervals of 2.5 m; when the depth interval showing the greatest gradient was located, the higher temperature was used as the thermocline temperature.

In the spring of 1953 the greater percentage of adult *clausi* remained in the cooler waters beneath the thermocline during the day. On the basis of actual numbers per cubic meter the difference in concentration between surface and deeper waters was even more exaggerated. Night tows in the early spring indicated no restriction of vertical migration by the thermocline, but in June there were fewer adult animals in surface waters at night, suggesting that the thermocline serves as a kind of barrier when the surface waters have warmed to

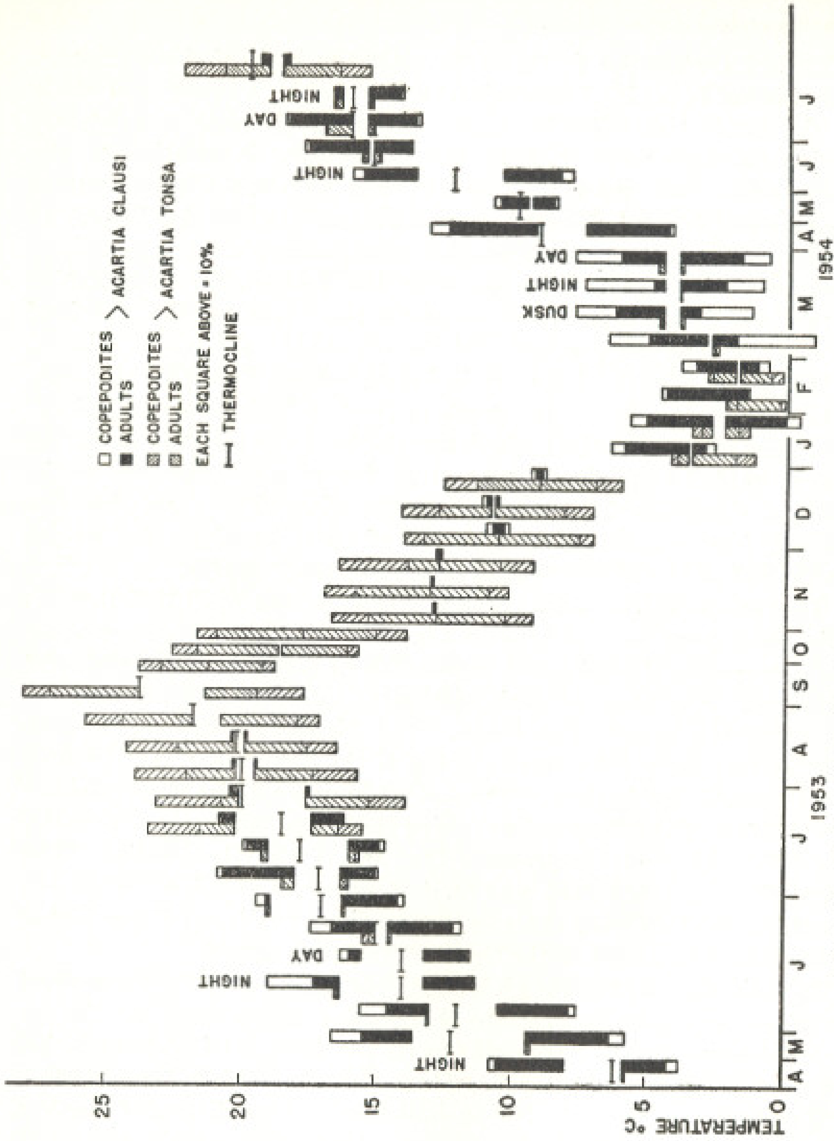

Figure 15. Vertical distribution of the *Acartia*, percent total plankton. See text, p. 187.

some critical level (16° to 18° C). Throughout this period the developmental stages of *clausi* remained more abundant in surface waters both day and night. By July the adults as well as the copepodids were more frequently observed in the upper waters regardless of the time of day. Perhaps when the bottom waters become warmed beyond a certain point, they no longer serve as a refuge for *clausi*. At this stage in the seasonal cycle, the marked decline in total numbers of *clausi* began and the younger stages particularly became scarce in the plankton (see Fig. 5).

In the summer of 1953, the daytime surface tows almost always contained more *tonsa* than deep tows. *A. tonsa* has been seen actually struggling against the surface film on a bright day when there was no wave action (Shirley Conover and Howard Sanders, personal communication). Though light from the sky would normally be scattered by wave action, it is possible that the rays of the sun are sufficiently direct on a calm day to cause a phototactic response. Moreover, in the laboratory, *tonsa* responded to differences in light intensity even though the light was not directional (see Fig. 14). Thus, if the summer sun is fairly bright and the water surface relatively smooth, significant numbers of *tonsa* might collect in the surface waters during the day.

From mid-September to mid-December the water column was subject to more or less complete mixing and the percent distribution of both species was about the same. Cold spells in December and January lowered the water temperature to below 4° C, where it remained for over two months. During this time, the number of *tonsa* decreased gradually while *clausi* became increasingly important in the plankton. The most interesting feature of the cold water samples was the greater concentration of *tonsa* in deep water. Although no information on the nocturnal behavior of these species was obtained during this period, the laboratory behavior of *tonsa* (see Fig. 14) was in complete agreement with the winter field observations.

Data collected during the spring and early summer of 1954 proved to contradict somewhat the results obtained during this period in the previous year. On March 30 tows were taken in the evening and at night, and on March 31 during daylight. The highest percentages of *clausi* adults were found in surface waters at dusk and in bottom waters during the day; however, the number of adults in the surface sample at night was low, perhaps due to the meteorological conditions at the time. The average wind speed on these dates at New Haven was over 10 mph, with gusts over 20 mph, and it is probable that the wind speed at sea was even greater. Under such conditions there may have been sufficient instability in the water column to disturb the normal plankton distribution. Moreover, the night tow of March 30 was taken during a severe snow squall; Schouteden (after Cushing, 1951) found that sudden rain or hail drove Crustacea to lower levels at night.

Subsequent observations might also be explained by weather conditions. Rather high numbers of *clausi* were taken at the surface in daytime on April 27 when moderately strong easterly winds were recorded. In the Sound, a sizable swell develops with an easterly wind, and since the thermocline was not particularly strong at this time, considerable mixing of surface and deeper waters may be assumed.

Comparison of the hydrographic data for the spring and summer of 1953 and 1954 showed a higher degree of stability in the former year. In 1953, a reasonably strong thermocline existed, frequently extending down 10 m or more at the deep stations; the temperature difference between surface and bottom in spring and early summer averaged about 3° C and was often considerably greater. In 1954, the vertical temperature difference resulted principally from short term surface warming in the upper 2–3 m and a sharp thermocline was infrequently observed. The BT trace often showed several steps between surface and bottom. On May 10 and July 22, so-called surface tows appeared to be below the thermocline, although they were taken at 5 and 4 m respectively. On both dates, the vertical temperature gradient was small and principally in the upper surface layer. If stability conditions comparable to the previous year had existed, these tows would have sampled the warmer epithalassa.

Though the evidence is inconclusive, the vertical distribution of *clausi* at least appears to be affected by the degree of stability of the water mass and the presence of a thermocline.

Response of A. clausi *to an Experimental Thermocline.* To supplement field observations, an experiment was designed to study the effect of an experimental thermocline on *clausi.* Four two liter graduates were filled with sea water and 50 *clausi* were added to each. Two graduates, designated 1 and 2 in later discussion, were partially submerged in a constant temperature bath of about 13° C, with the upper half exposed to room temperature (18–20°). Within a few hours, examination of the temperature distribution in these cylinders showed that a definite thermocline had developed. The other cylinders, 3 and 4, were completely exposed to constant temperature equal to about that of the bath (13°). Cylinders 2 and 4 were hooded to keep out the light while 1 and 3 were exposed to periods of night and day. Distribution was checked in the manner mentioned previously (p. 185), and the temperature at each level was recorded after each count. The histograms in Figs. 16A and 16B represent observations at about 0100 and 1100 respectively. Histograms I and II represent the distributions observed in cylinder 1, with thermocline and natural light conditions; III and IV, results from cylinder 2, with thermocline and constant darkness; V and VI, results from cylinder 3, with uniform temperature and natural light; VII and VIII, results from cylinder 4, with uniform temperature and constant darkness. The vertical row containing histograms I, III, V and VII gives the distributions before illumination, and similarly II, IV, VI and VIII give the results after five minutes of exposure to direct overhead light. Thus each horizontal row contains observations on a single cylinder and each vertical row indicates identical observations on each of the four graduates. The small graphs in the middle give the temperature distribution in each cylinder at the time of observation.

The animals kept at uniform temperatures in cylinders 3 and 4 behaved as expected (see Fig. 14, Table I); at night or in darkness, they gathered in the upper waters, and they demonstrated a strong phototactic response to direct light at any time of day. However, in cylinders 1 and 2, which contained the artificial thermocline, few animals were found in the upper water under any conditions. Even direct illumination did not induce the copepods to cross the thermocline, but instead most of them congregated near the middle of the cylinder right at the thermocline.

Obviously the experimental thermocline used here has been greatly compressed; that is, a vertical temperature difference that normally extends throughout a column of water 15–20 m deep has been produced in a graduated cylinder only 15 inches deep. Thus the observed response of the organisms is probably greatly exaggerated. Nonetheless, this experiment seems to indicate that a strong vertical

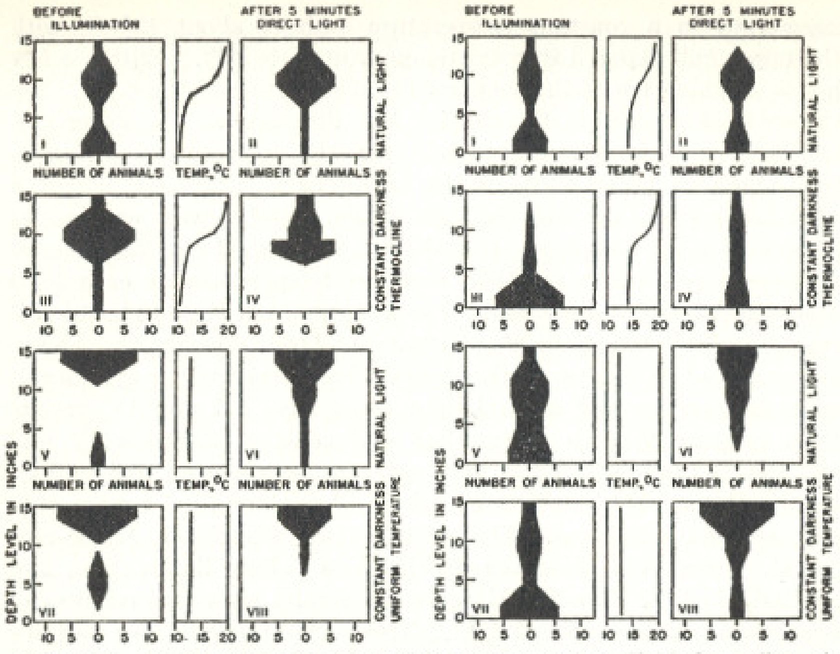

Figure 16. Vertical distribution of *clausi* in response to an artificial thermocline. A (left), night; B (right), day. See text, p. 191.

stratification might closet one or more species into a separate compartment within what is often considered a homogeneous environment.

It is clear that the thermocline *per se* does not present an invisible barrier through which no animal can penetrate. Moreover, different planktonic organisms have widely different ranges of temperature tolerance. Cushing (1951) summarized the probable situation adequately in stating: "It is a possibility that a homogeneous group of animals (stage, sex or brood of a species) has a temperature range, beyond the extremes of which the animal does not appear; a thermocline near the limits of this range will be obviously more effective in modifying migration than one in the center of the range." The behavior of *clausi* would seem to be in agreement with this interpretation. When temperature above the thermocline remains below 15–16° C, at least some animals can cross it, but there is evidence that diurnal migration is restricted by a thermocline as the temperature of the surface water rises. Under these conditions, *clausi* becomes partially isolated from a section of its environment.

Response to Colored Light. Lumer (1932) noted that four species of *Cladocera* showed a higher degree of stimulation by red-orange light than by any other color. More recently, Smith and Baylor (1953) found that *Daphnia* swam toward or parallel to a beam of red light but swam perpendicular to or down from a beam of green or blue light. These authors also found that *Daphnia*, when cooled, lost their response to blue light and swam only the red "dance," with the principal vector in the vertical; however, by increasing the light intensity Smith and Baylor could cause downward swimming again. Experiments on both species of *Acartia* with various monochromatic filters under different temperature conditions showed that their response to visible light was essentially the same at either end of the spectrum. The result, therefore, was negative.

The principal difficulty with light experiments on these two species has been the lack of any criteria for orientation other than by attraction or movement toward light. Spooner (1934) noted that *Acartia clausi* was phototactic but that its movement toward light was completely unoriented. Our observations also indicate little orientation of the body to light, but the movement toward light was usually zig-zag, with a constant angle to the beam of light. Both species were attracted in the same manner to each of the different filters regardless of temperature, but the degree of attraction of *tonsa* was several times greater (*i.e.*, more animals appeared at the light) at 16° than at 4° C. In an earlier experiment, the apparent sluggishness of *tonsa* at low temperatures was demonstrated; however, this experiment suggests that such behavior resulted from a narcotization of the organism rather than from an actual physiological change brought about by lower temperature.

Oxygen Consumption by *clausi* and *tonsa*

If temperature affects activity, as indicated by preceding experiments, then some measureable indicator of physiological activity, such as oxygen consumption, may be affected also. However, finding a suitable method for respiratory measurement has presented a problem. Although some extremely sensitive monometric equipment has been developed in recent years, in almost every case increased sensitivity has been attained by reduction of the volume of the apparatus. To be sure, a copepod is a small creature and does not use much oxygen, but it is an extremely active one. Zeuthen

(1947), using the Cartesian Diver for respiratory measurements with *Centropages hamatus*, found a steady decline in oxygen utilization accompanied by a visible decrease in activity over a 10–12 hour period. Marshall, *et al.* (1935) used the Winkler method for similar studies on *Calanus finmarchicus*, and when the data for both experiments were converted to comparable units, Zeuthen's results were approximately 25% lower than those of Marshall and co-workers. Since Zeuthen used a smaller animal of a different species, differences in oxygen utilization might be expected. It is also possible that the oxygen bottle method caused more initial disturbance than the "diver," but present investigations indicate that healthy copepods do not become less active with time. In Zeuthen's experiment, *C. hamatus* was confined to a volume of water only a few times greater than its own volume; perhaps his values should be considered with reservation since they were obtained under such highly unnatural conditions.

Methods. Two means of measuring oxygen consumption have been employed here. Some measurements were made with the Warburg constant volume type respirometer, but this equipment had two major disadvantages: it was possible to run respiration studies at only one temperature at a time; and an inconvenient amount of material was required to obtain significant results, even with the 5 ml flasks. Hence this technique was used only as a check on the second method. More satisfactory results were obtained with a modification of the water bottle method employed by Marshall, *et al.* (1935) and later by Riley and Gorgy (1948). Glass-stoppered bottles of approximately 35 ml volume were filled with sea water, and to these were added 50 *clausi* or *tonsa*. Berkefeld filtered sea water of known oxygen content was then added to the bottles by flushing three times, using a siphon arrangement; a bolting silk screen over the outflow siphon prevented escape of the animals. By means of neutral dyes, it was found that the rate of flow through the experimental bottle could be adjusted to give complete flushing with about 100 ml of water. Controls were prepared in exactly the same manner except that no copepods were added. Both experimental and control bottles were then immersed in constant temperature baths from 4 to 12 hours, depending on the temperature. Simultaneous measurements of oxygen utilization at several temperatures were obtained by the use of different constant temperature baths which were simply large

wash tubs fitted with compressed air stirrers and thermoregulators. All baths were kept in a constant temperature room at about 4 to 5° C, and therefore they could be adjusted to any higher temperature. The temperatures employed were usually 5, 10, 15, 20, and sometimes 25°. At the end of each experiment, the oxygen content of the experimental and control bottles was measured by the Winkler method, modified for use with the 35 ml volume; the oxygen consumption by the copepods was obtained from the difference between the two. Winkler titrations were made with a self-filling 10 ml burette graduated in fiftieths of a milliliter. By dividing drops, as little as 0.01 ml of thiosulfate could be added at a time.

Although the titrations were carried out with great care, certain undetermined sources of error were introduced. Thompson and Robinson (1939) found that the loss of volatile iodine could be significant when small volumes were titrated. As a check on the accuracy of our analytical procedure, 20 replicate samples of sea water were prepared and titrated in the usual manner. One series gave a mean titer of 5.8185 ml/l oxygen uncorrected with a standard deviation of 0.02439, while a second series gave 5.7895 and 0.01792 respectively. Using the second series, a difference of 0.36 ml oxygen per bottle between experimental and control bottles would limit the error to 10% in 68 experiments out of 100. Although a titer difference of 1.08 ml oxygen per bottle would practically insure an error of 10% or less, it was impossible to assure a difference of over 1.00, particularly at low temperatures, without making the experimental technique impractically tedious. However, a titer difference of 0.36 ml per bottle was usually obtained; in the comparative experiments, analytical errors were probably systematic.

The copepods used in these experiments were obtained with a coarse tow net on the day preceding the experiment. They were diluted several times in the laboratory with raw sea water and then placed at a constant temperature of 4 or 13° C depending on the season. Unless the animals were to be kept longer than overnight, they were not fed. Animals of the desired sex and species were isolated from the diluted samples with the low power of a dissecting microscope and placed directly in the experimental bottle. After the experiment, the Winkler reagents were added directly to the containers before the animals were removed. Care was taken to avoid the loss of animals during the addition of Winkler reagents or in titration. The animals were then counted and the length of the cephalothorax was measured with an ocular micrometer. Although there was some shrinkage with this Winkler "preservation," the error was less than 3%.

After the experiment was set up, a portion of each tow was preserved in formalin for later analysis of size and weight. For dry weight determinations, a thousand copepods, usually of one sex and species, were sorted from the preserved tows with the aid of a dissecting microscope. A random sample of 50 was measured with an ocular micrometer before desiccation so that a correction could be applied in the event that those used for respiratory experiments differed in size from those weighed. Since both weighed and experimental animals usually came from the same tow, such differences were not great. Once isolated and measured, the copepods were removed to a fine-pore filtering crucible which served as a weighing container. After several washings with distilled water to remove the soluble contaminants, the animals were dried in air at about 80° C overnight, or until constant weight was obtained. Before weighing, the crucibles were allowed to cool in a calcium sulphate desiccator of standard design.

Pilot Experiments. Before comparative studies of these two species were begun, several pilot experiments were run to establish a reasonable experimental procedure. There was no essential difference in oxygen consumption when the same number of copepods was placed in bottles of different sizes, nor was there a difference in the respiration of different numbers of copepods in bottles of the same volume. When the water bottle method was checked against the Warburg procedure, fair agreement was obtained.

In order to determine if oxygen was used by the copepods at a constant rate, replicate experimental and control bottles were prepared and placed simultaneously in a constant temperature bath. Oxygen determinations were then made after different time intervals. When bottles were removed at four hour intervals (Fig. 17A), *clausi* appeared to have an initially higher oxygen consumption which leveled off to a constant rate after 12 hours. When the time interval between oxygen determinations was shortened to two hours, the leveling off occurred much earlier (Fig. 17B). In this case, the observations suggest that the initially high period of oxygen uptake was followed by a short recuperation period in which oxygen utilization was less than "normal." A similar experiment with *tonsa* gave high initial oxygen consumption rates with a level period between 6 and 16 hours; after 16 hours the rate of oxygen uptake decreased again.

Because bacteria could not be eliminated as a possible source of error in respiratory experiments, comparison of the growth rates of bacteria in experimental and control vessels was made. Below 15° C no significant bacterial growth occurred over the normal experimental period, but at higher temperatures results were somewhat variable. However, an error greater than 10% occurred only once. In these experiments, it was necessary to assume that the growth of those suspended bacteria which can multiply on the sea water agar provided an index to the growth of all bacteria in the bottle. If this assumption is correct, bacterial respiration would seem to be of minor importance under the conditions employed in these experiments, and even if this assumption is not correct, errors due to bacterial respiration should cancel out in the comparative studies.

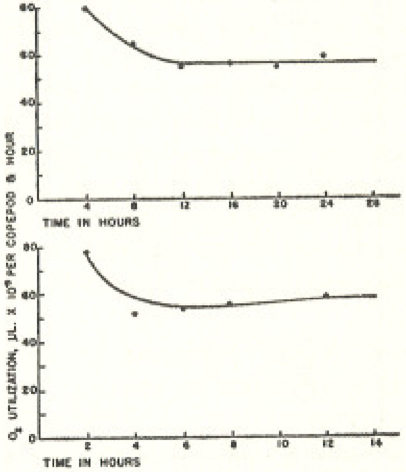

Figure 17. Oxygen consumption of *clausi* at 15° C plotted against time. A (top), Bottles removed at four hour intervals; B (bottom), Bottles removed at two hour intervals.

Effect of Light on Respiration. Marshall, *et al.* (1935) found that the oxygen consumption of *Calanus finmarchicus* increased up to 50% when exposed to natural light, but when the copepods were placed in bottles suspended in the sea, this stimulatory effect was not present below 0.5 m. Artificial light had no effect on respiration. In the Sargasso Sea, Riley and Gorgy (1948) found that respiration of zooplankton in light bottles was 16% higher than that of similar specimens in dark bottles. Klugh (1929, 1930) has shown that the ultraviolet component of daylight is harmful to a number of marine animals. It is probable that the high respiratory rate observed for animals exposed to natural light represents an injury response.

Several experiments were run to determine if artificial light affected the respiratory physiology of *clausi* and *tonsa*. Light was provided by a single 20 watt fluorescent tube, shielded by a parabolic reflector and suspended about 16 to 18 inches above the experimental vessels. In one experiment with *tonsa*, run at five different temperatures, only at 25° C were both light bottle values higher than the dark ones (Fig. 18). At the beginning and end of this experiment, aliquots were taken for determination of bacterial numbers. When the bacterial respiration component was deducted, the values for the light bottles were not different from the dark bottle values. In another experiment, designed expressly to test the effect of light on *clausi*, six replications were run in the dark and six in the light at 15° C. The mean respiratory rates were 0.039 0 µl per copepod and

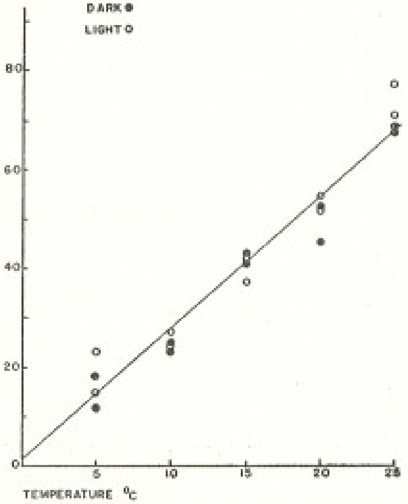

Figure 18. Oxygen consumption of *tonsa* in the light and in the dark plotted against temperature.

hour in the light and 0.0368 µl in the dark. The difference between the means was not statistically significant.

No experiments were performed with direct or diffuse sunlight. Klugh (1930) found that *clausi* was more resistant to ultraviolet radiation than *Calanus finmarchicus*. Since ultraviolet radiation would be quickly absorbed by the surface waters of Long Island Sound, the light conditions at a few feet below the surface are probably similar to the artificial conditions used in our experiments. Therefore, any lethal effect of light on the two species of *Acartia* must be of minor importance.

Effect of Temperature on Respiration. It has long been recognized that an increase in temperature will speed up a biological as well as a chemical reaction, but the basic laws of temperature coefficients, such as Berthelot's exponential formula and the Van't Hoff-Arrhenius law, designed to predict the behavior of chemical reactions, do not apply in many biological cases (Bělehrádek, 1930). Nevertheless, the simplified version of Van't Hoff's law,

$$(K_t + 10)/K_t = Q_{10} = 2 \text{ to } 3, \tag{1}$$

has had many biological applications. However, respiration data need not be referred to some coefficient of temperature such as Q_{10} to be useful to the ecologist.

Scholander, *et al.* (1953) used the term "MT curve" to describe oxygen uptake at a graded series of temperatures. Such data have been used previously to describe seasonal or climatic adaptation of cold-blooded animals. Wells (1935a, 1935b) found that *Fundulus parvipinnis* adjusted its metabolism to different environmental conditions. Fox and Wingfield (1937) compared two species of prawns from Swedish and British waters and found the respiratory curve of *Pandalus montagui* displaced upward in the colder environment. Arctic lamellibranchs had approximately the same respiratory rate at 5° C which was shown by Mediterranean forms at 15° C (Spärck, 1936). Essentially the same sort of climatic adaptation was recorded by Thorson (1936) for different generic pairs of bivalve mollusks in arctic and warmer waters. Scholander, *et al.* (1953), comparing the respiratory metabolism of poikilothermic animals from Point Barrow, Alaska and Barro Colorado, Canal Zone, found adaptation in aquatic forms such as fish and Crustacea.

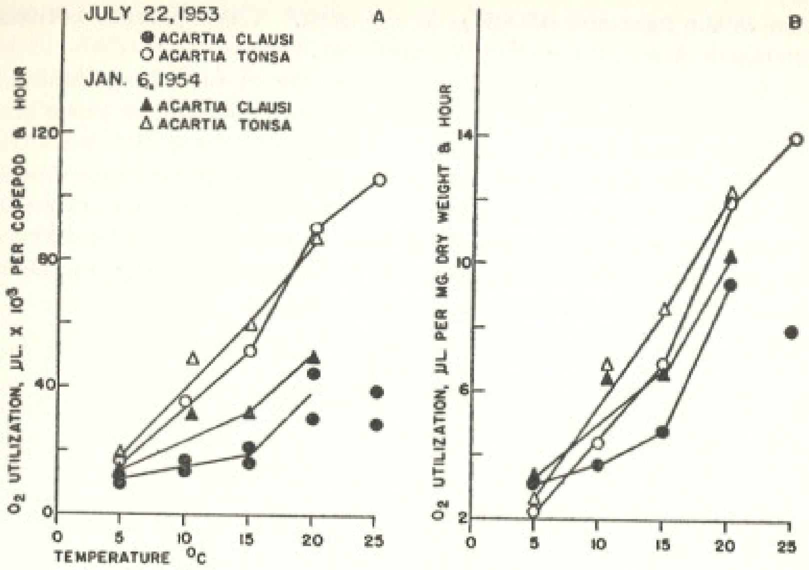

Figure 19. Respiratory rates on two different dates, one in summer and one in winter, plotted against temperature. A, Oxygen consumption in μl per copepod and hour; B, Oxygen consumption in μl per mg dry weight and hour.

Since the two species of *Acartia* in Long Island Sound have different seasonal and regional distributions, variations in oxygen consumption rates with temperature might prove useful to establish their environmental relationships. The amount of oxygen used in μl per copepod can be plotted directly with temperature (Fig. 19A), but since there is a significant difference in size between *clausi* and *tonsa*, a better comparison is obtained by converting oxygen values to common units (Fig. 19B). Milligrams dry weight was chosen because it was relatively easy to measure accurately and because it produced less distortion of the curves than any other measurement of volume or mass tried.

It is apparent in Figs. 19A and 19B that oxygen consumption was not necessarily related to temperature by a straight line, particularly in the case of *clausi*. Experiments from other times of the year indicated that the *tonsa* curve was nearly always linear while the *clausi* curve often showed an increasing Q_{10} between 15 and 20° C. This latter feature was more marked during the cooler months of the year than during the summer although Fig. 19 might appear to indicate otherwise. However, the *clausi* curves for July 1954 did not show a significant trend towards nonlinearity. The significant decrease in respiratory rate of *clausi* on July 22, 1953 between 20 and 25° C was almost certainly an injury response, suggesting that 25° is near the lethal temperature for this species.

Previously, Marshall, *et al.* (1935) and Clarke and Bonnet (1939) had found that the respiratory curves of different stages of *Calanus finmarchicus* were nonlinear. Gauld and Raymont (1953) measured the increase in respiratory rate with temperature for *Temora longicornis*, *Acartia clausi*, and *Centropages hamatus*. *Temora* showed a distinct nonlinearity, with the respiratory rates nearly doubling between 10 and 20° C. Their curve for *clausi* was similar to those shown in Fig. 19, but it was displaced upward. The English Channel *clausi* appeared larger than those used in our experiments, but no correction for weight could be made for comparative purposes. The curve for *C. hamatus*, though based on incomplete data, resembled that given in Fig. 19 for *tonsa;* respiration appeared to increase linearly with temperature, although their curve for *Centropages* showed some tendency toward a decreasing Q_{10} around 20°.

The curves for the two species of *Acartia* also appear to be different in character. If each curve is extended to the left (Fig. 19A), the *clausi* curve would intersect the ordinate considerably above zero while the *tonsa* plot would pass near or through the origin. At low temperatures, the respiratory rate for *clausi* was actually higher than that for *tonsa* (Fig. 19B).

Zeuthen (1947) has pointed out that, at least under uniform conditions, the respiratory rate is a reflection of the animal's activity. Earlier experiments and observations on light responses showed that *tonsa* was definitely sluggish at low temperatures; the respiratory measurements confirm a low level of activity for *tonsa* when the temperature is low. In theory, the flat respiratory-temperature curve for *clausi* would indicate a considerable degree of eurythermy; that is, an increase or decrease in temperature over a considerable range would not seriously alter the metabolism of the animal. On the other hand, the curve for *tonsa* indicates a more stenothermal animal; *tonsa* cannot exert an appreciable degree of control over its body metabolism independent of temperature.

Seasonal Adaptation. Marshall, *et al.* (1935) found that oxygen utilization could vary as much as 0.2 ml per 1000 animals per hour in *Calanus finmarchicus.* There appeared to be no relation to size, and they found no difference between winter and summer populations. However, when comparison of winter and summer populations of stage V *Calanus* was made on a weight basis, the winter population had a higher oxygen uptake at a given temperature than the heavier summer population (Riley, *et al.*, 1949).

Since both species of *Acartia* inhabit such a wide range of temperatures, seasonal adaptation in their respiratory metabolism might be expected. July 22 and January 6 (Fig. 19) represent the approximate temperature extremes at which the two species coexist. While the curves for *tonsa* on these two dates were similar, the slope of the January curve for *clausi* was probably significantly greater than that observed in July. Additional winter experiments confirmed this relationship although the data might suggest that by the end of winter the few *tonsa* remaining had made slight physiological adjustments so that their respiratory curve, if continued toward the left, would no longer pass through zero.

These two species appear somewhat similar in their relative environmental relationships to the common sand crab *Emerita talpoida* and the beach flea *Talorchestia megalopthalma* studied by Edwards and Irving (1943a, 1943b). Like *A. clausi,* the sand crab was active during the cold months and could readily adjust its metabolism to different temperature conditions; similar to *tonsa,* the beach flea, which hibernates in winter, could make no such alteration.

Further evidence of physiological adaptation by *clausi* was illustrated in heat tolerance experiments. Animals kept at 25° C on May 22, 1953 were largely moribund at the end of four hours; two months later the copepods still appeared active and healthy after eight hours at the same temperature even though the oxygen uptake values indicated that some injury may have occurred (Fig. 19).

Oxygen Consumption and Reproduction. During the summer of 1953 a progressive decrease in the respiration rate of *tonsa* was noted that could not be explained merely on the basis of decreasing size. When the oxygen consumption data from four experiments during July and August were converted to µl per milligram dry weight of copepods and a regression line was fitted to the points obtained, a progressive drop in slope from 0.59 on July 22 to 0.50 on August 19 was revealed (Fig. 20). Although transformation displaced the curve for July 29 somewhat higher than the remaining three, the slope was between the 0.59 recorded for July 22 and the 0.53 value for August 5.

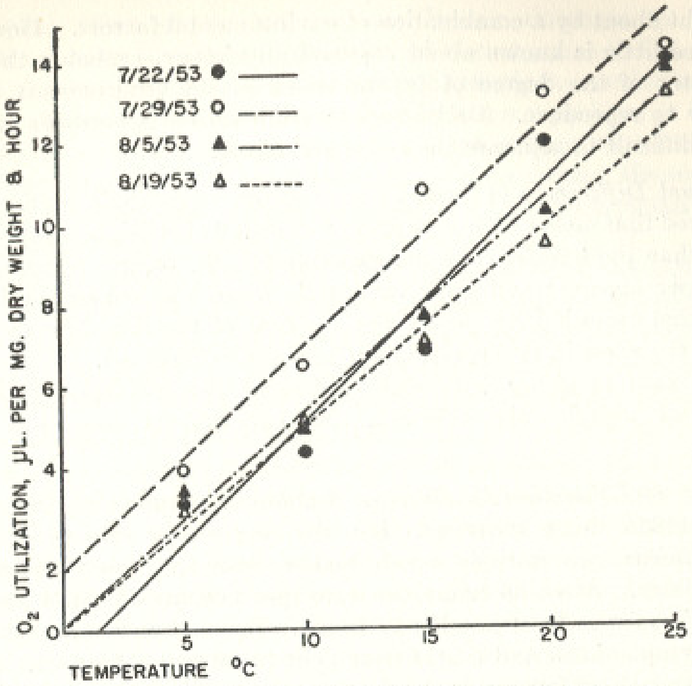

Figure 20. Regression lines for oxygen consumption of *tonsa* with temperature on four different dates during summer 1953.

Since the first experiment on July 22 was run during the period of most rapid growth of the *tonsa* population, the plankton tows during this period were examined to determine the relationship, if any, between breeding activity and respiration. An index was obtained by dividing the number of nauplii per cubic meter by the number of adult females which could have produced them. When this was done for the particular station from which the experimental animals were taken, the following index values were recorded: July 22 (slope = 0.59), index 48.0; July 29 (slope = 0.55), index 5.8; August 5 (slope = 0.53), index 3.8; August 11 (no respiration experiment), index 2.0; and August 19 (slope = 0.50), index 1.0.

It may be argued with good reason that the variation in oxygen uptake recorded for *clausi* and *tonsa* had nothing to do with reproduction but simply reflected a depression or acceleration of metabolism brought about by a combination of environmental factors. However, since so little is known about copepod physiology, probably the best indicator of the degree of favorableness of the environment is the ability to reproduce. Under such circumstances, it becomes exceedingly difficult to separate the cause and effect.

Sexual Differences in Oxygen Consumption. Marshall, *et al.* (1935) observed that male *Calanus finmarchicus* usually had higher respiratory rates than the females. In our experiments, the oxygen consumption in μl per copepod and hour for female *tonsa* was somewhat higher than that recorded for males, but because of the size difference between the sexes in this species, this was not unexpected. Conversion of the data to μl/mg dry weight indicated that the rates probably were not significantly different. No experiments were run with *clausi*.

Effect of Laboratory Conditions. Laboratory studies by Marshall, *et al.* (1935) have indicated that the respiratory rate of *Calanus finmarchicus* was initially much higher than that observed a few hours later. After 36 hours the rate had become constant and remained so for at least another 36 hours. Some of their animals were fed phytoplankton and others were kept in filtered sea water. Since there was no difference in respiratory metabolism between fed and nonfed specimens, these authors concluded that starvation was not the cause of the initial decline.

Two explanations have been put forward to account for this behavior. Keys (1930) found that several hours were required before the metabolism of certain fish became "normal" once they had been placed in the respiratory chamber. He believed that this length of time was necessary for recovery from the disturbance of setting up the experiment. In some of our own experiments (see Fig. 17), the initial respiratory rates were relatively higher than those obtained over a longer period. Certainly the process of capture and dilution must be disturbing to the organisms, but neither Key's fish nor our copepods required 36 hours for complete "recovery." Furthermore, if this initially high respiration was the result of capture and handling, it should be possible to "re-excite" the animals after they have been "conditioned"; however, this cannot be done. On the other hand, it seems possible that confining an actively swimming animal such as *Calanus* to small experimental vessels in the laboratory may have a depressing effect on its metabolism. In our attempts to culture *Acartia* species, we found that most of the organisms died within a week's time, leaving a few hardier individuals to survive up to a month or more. Bacterial growth also becomes a problem in limited containers. At any rate, if "normal" respiratory rates attained after "conditioning" in the laboratory were really normal, the copepods should behave as they do in nature, that is, breed and maintain themselves in persistent culture.

On several occasions, the same collections of *tonsa* and *clausi* had to be used for more than one day's experimentation. Even though the animals were fed, their behavior on the second day was erratic and was frequently different from that observed the day before. Consequently, it seemed desirable to determine more about their behavior under laboratory conditions.

Samples taken from the Sound were diluted and placed in replicate containers (two quart mason jars) previously seasoned in sea water. The specimens in some of the mason jars received an aliquot of *Skeletonema costatum* sufficient to provide a cell concentration of about 16 million cells/l while those in the remaining jars were unfed. *S. costatum* is the dominant plankton diatom in the Sound during a large portion of the year, and examination of gut contents revealed that it is an important food source for both species of *Acartia* for at least part of the year. Raymont and Gross (1941) found it suitable as a culture food for *Calanus finmarchicus*. The high concentration of *S. costatum* was deemed necessary since the copepods were considerably more concentrated in these jars than they would have been in nature.

After an overnight recuperation period, the respiratory rates at 15° C of both fed and unfed copepods were measured every 24 hours for six days (Fig. 21). During the first two days of the experiment, *clausi* outnumbered *tonsa* in the vessels to such an extent that it was not practical to run comparative experiments, but by the third day, sufficient *clausi* had been removed so that *tonsa* could be isolated. The *clausi* curve shows clearly that a sharp drop in oxygen utilization occurred between the first and second days in both fed and nonfed samples. By the third day, unlike the results of Marshall, *et al.*, a significant difference between the fed and starved animals was evident. Following the initial decrease (which probably occurred for *tonsa* as well as *clausi*), the copepods fed *S. costatum* maintained an essentially uniform respiratory rate, while those that went hungry showed a progressively declining rate. The last observation for starved *tonsa* was not completely consistent with the other observations; by this time so few animals remained that only one replication was possible. Daily examination of the gut contents showed that, throughout the six days of the experiment, the guts of the fed animals were clearly packed with green cell remains while those of the starved copepods were quite colorless.

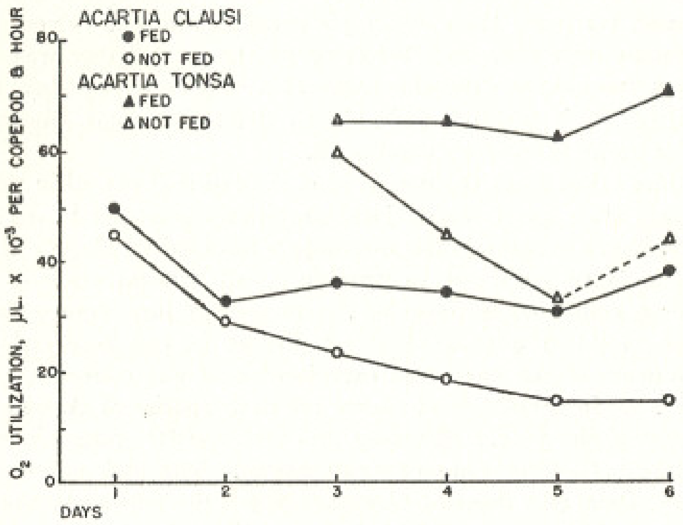

Figure 21. Comparison of respiratory rates of both species at 15° C when starved and when fed *Skeletonema costatum*.

To be sure, this experiment does not prove that all of the respiratory discrepancies noted in the literature result from the inadequacies of the laboratory. However, the evidence does suggest that the further removed an animal is from its natural environment the less likely it will be to exhibit behavior characteristic of that environment.

Relationship between Copepods and Available Food

The biological as well as the physical environment must be important in governing copepod distribution. Qualitative studies by Lebour (1922) have indicated that different species of marine copepods have quite different eating habits. Harvey (1937) showed that *Calanus finmarchicus* selected the larger diatom *Ditylum brightwellii* in preference to the smaller *Lauderia borealis*. According to Fuller (1937), *Calanus finmarchicus* could not capture enough *Nitzschia closterium* to meet its food requirements, but Gauld (1951) obtained quite high grazing rates when a species of *Chlamydomonas* only slightly larger than *Nitzschia* was used as a food source. Aside from the study by Riley, *et al.* (1949), no truly quantitative work has been undertaken to determine the inter-relationships of the zooplankton and its food supply. Therefore a series of experiments was initiated to determine how the biological environment might affect the distribution of *clausi* and *tonsa* and how the physical factors might affect their ability to survive in this environment.

Methods. In the sea, nonmotile phytoplankton such as the diatoms are maintained in the upper waters principally by vertical turbulence, but in the laboratory, phytoplankton quickly settle to the bottom of a vessel unless some type of artificial turbulence is supplied. In previous grazing experiments, conventional stirring or shaking techniques injured the animals or at least inhibited their activity. Figs. 22, 23, and 24 illustrate the structural details of the apparatus used in our experiments. The same constant temperature baths used

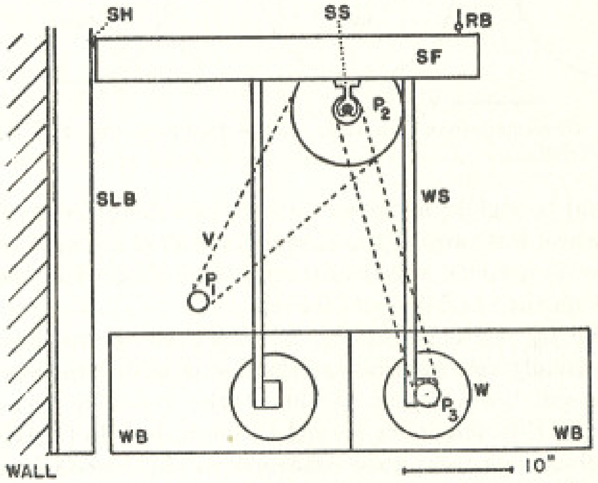

Figure 22. Grazing apparatus, end view. P_1 = 2" pulley. P_2 = 10" pulley. P_3 = 2½" pulley. RB = Ring bolt for attachment to overhead support. SF = Supporting frame. SH = Strap hinge. SLB = Steel L beam. SS = Brass bearing line shaft hanger. V = ½" V belt. W = Wheel. WB = Water bath. WS = Wheel support.

for the respiration experiments were also used for the grazing studies (Figs. 22, 23). Five "wheels" were so suspended from an overhead frame that they could be rotated entirely beneath the surface of each water bath. Power from a friction drive Warburg shaker motor was supplied by a system of pulleys which connected the power source to a main shaft and thence to each wheel (Fig. 22). Pulley diameters were selected so that each wheel made about eight revolutions per minute. Each wheel was constructed so that eight experimental vessels could be rigidly attached near its periphery (Fig. 24). Thus, when the wheel was turning the direction of fall of a suspended particle in response to gravity was continually changing with respect to a fixed point on the outside of the vessel.

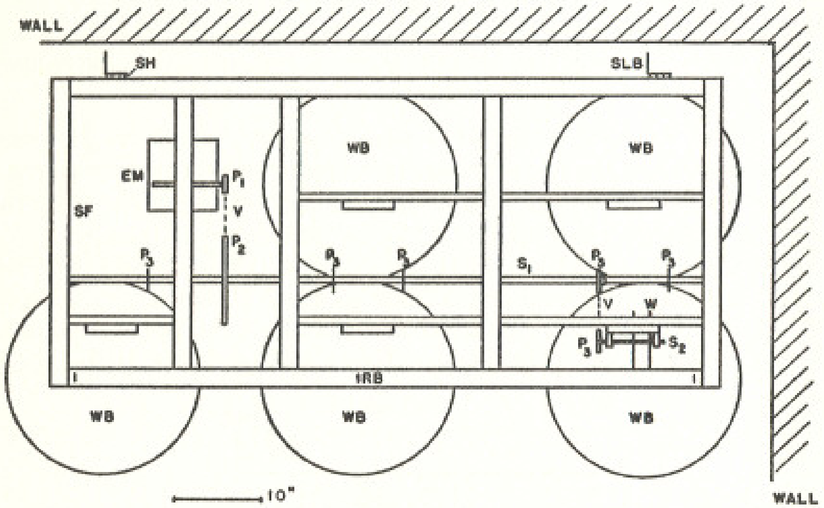

Figure 23. Grazing apparatus, top view. EM = Electric motor. S_1 = ¾″ line shaft. S_2 = ½″ brass shaft.

In setting up the experiments, a known concentration of phytoplankton, usually *Skeletonema costatum,* was added to several 35 ml glass stoppered bottles; part of the bottles received from 25 to 50 copepods and the remainder served as controls. Both experimental and control bottles were then attached to the wheels in the water baths. At the end of a run, the entire contents of each bottle were preserved in formalin, allowed to settle and concentrated by decanting. Counts were made with a Sedgewick-Rafter counting chamber and

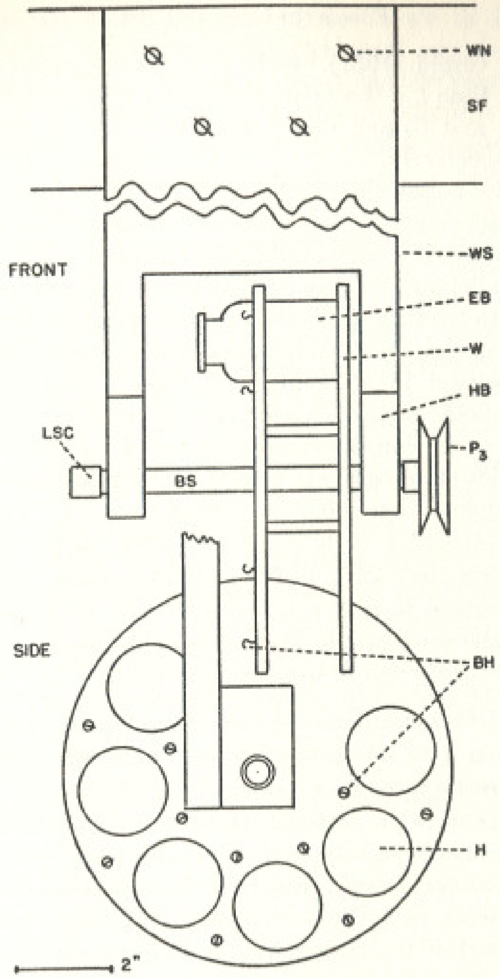

Figure 24. Grazing apparatus, detail of wheel and support. BH = Brass cuphooks. BS = ½″ brass shaft. EB = Experimental bottle. H = Hole; experimental bottle inserted here. HB = Hardwood bearing. LSC = Line shaft collar. W = Wheel, ¼″ marine plywood. WN = Wing nut. WS = Wheel support, ¾″ pine.

a Spencer microscope equipped with a 16 mm apochromatic objective and 15x compensating oculars. The amount of water filtered by the copepods was determined from the difference in cell counts between experimental bottles and controls, using the equation

$$F = v\,(\ln C_o - \ln C_t)/t, \qquad (2)$$

modified from Gauld (1951), where F is the amount of water swept free of food in time t, v the volume of water per animal in the experimental bottle, and C_t and C_o the experimental and control cell concentrations respectively.

The error in Sedgewick-Rafter counts was assessed as follows. As a general working criterion, at least 100 organisms were counted; with this standard, it was found that 30 random fields in linear transects, one parallel to the long dimension of the cell and two others perpendicular to the first, gave the smallest standard error. An effort was made to concentrate the original sample so that at least 100 organisms were observed in 30 fields, but when this was not possible, additional ten-field transects were counted until 100 organisms were found. On one occasion the standard error of log difference was computed for a series of 10 replicate counts, the log difference being 1.1408 with a standard deviation of 0.0966. With these data it was calculated that an error of 8.47% or less occurred 68% of the time and that the error was less than 25% in 99% of the counts. Thus, if experiments were designed to give a log difference of over 1.0, the order of magnitude of the error would be in good agreement with that previously obtained for the respiratory experiments.

Effect of Cell Concentrations on Grazing. Gauld (1951) has shown that the grazing rate of three different copepods was independent of cell concentrations over a range of an order of magnitude. In our study, no extensive analysis of cell concentration and grazing rates was made except to establish criteria for experimental prodecure. When experiments covering a range of cell concentrations of two orders of magnitude were performed on *clausi* and *tonsa*, a lower grazing rate was obtained at the highest phytoplankton concentration. This concentration, about the midrange for Gauld's experiments, was only slightly greater than the spring flowering peak in Long Island Sound. Much of the previous work was done with higher cell concentrations than those normally found in nature; however, the three concentrations employed in our experiments were near the minimum, the average, and the maximum phytoplankton concentrations recorded in the Sound. It is not clear whether the low grazing rate of *clausi* and *tonsa* at spring flowering concentrations was due to satiation or simply to mechanical inability to handle so much food.

Effect of Copepod Waste Products on the Growth of Phytoplankton. Lucas (1947) has pointed out that "external metabolites" in the water can have profound effects on certain marine organisms. Since living copepods presumably excrete waste products continuously as organic compounds and inorganic ions which might be beneficial or inhibitory to the growth of phytoplankton, it seemed advisable to determine whether or not control and experimental vessels represent the same environment in so far as phytoplankton growth requirements were concerned. Replicate bottles were prepared to the same initial concentration of phytoplankton with aged Berkefeld filtered sea water and with water previously inhabited by living copepods. Both sets of bottles were then subjected to normal experimental procedure, and numbers were estimated in the usual way. For temperatures below 15° C, the normal Berkefeld control appeared to be adequate, but at higher temperatures the results were inconclusive. In one experiment no difference was detected between the two sets of bottles at 25°, whereas in another, the copepod water encouraged a higher growth rate at 15° but seemed to suppress growth at 20°. Since there was no pronounced or systematic effect on phytoplankton growth metabolism, the work was not pursued further.

Effect of Culture Age on Grazing Rates. In our preliminary experiments, considerable variation was noted in the amount of water filtered by copepods under supposedly similar conditions. Ryther (1954) found that senescent cultures of *Chlorella vulgaris*, *Scenedesmus quadricauda*, and *Navicula pelliculosa* gave lower grazing rates for *Daphnia magna* than log phase cultures. Ryther's observations suggested that the physiological state of the *Skeletonema costatum* cultures employed by us might explain some of the variation noted in grazing rates.

Food cultures of *S. costatum* were started on December 5, 8, 11, and 13, using the same medium and the same strain of cells as inocula on each date. On December 17, the grazing rate of *tonsa* was measured at three different temperatures, using grazing cultures made up from the different stock cultures. Thus the grazing cultures ranged in age from four to 12 days. The cell concentrations were adjusted so that all experimental and control bottles contained approximately the same initial number of cells per liter. The six day old culture, clearly in log phase (see Fig. 25B), gave a significantly higher grazing rate at all temperatures than the 12 day culture, and it was also

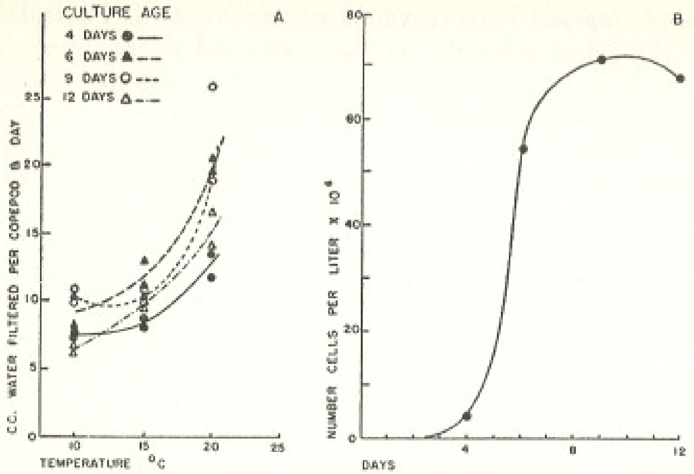

Figure 25. A, Grazing rates of *tonsa* fed *Skeletonema costatum* culture of different ages. B, Hypothetical growth curve for *Skeletonema costatum* based on cell concentrations in cultures of four different ages.

superior in most cases to the four and nine day cultures (Fig. 25A). Thus the experiment suggests that culture age is a primary concern in determining the feeding rates of zooplankton.

Light and Grazing Rates. Field observations by Wimpenny (1938) suggested that zooplankton feed more at night than during the day. Laboratory studies by Fuller (1937) and Gauld (1951) tended to confirm the presence of a diurnal feeding rhythm. However, when Gauld (1953) re-examined the problem, he found that 80–100% of the *Calanus finmarchicus* taken from the surface waters had been actively feeding regardless of the time of day. Although laboratory studies indicated long periods of low feeding activity, these could not be correlated with amount of light. From these studies he concluded that there is no diurnal rhythm in grazing of copepods distinct from their diurnal rhythm of vertical migration. More food is consumed at night because the copepods tend to congregate in the upper waters where food is more available, but apparently grazing is more or less continuous.

In a preliminary examination of the effect of light, no significant differences in grazing rates were detected in either light or dark. Nor did light have a differential effect on phytoplankton growth rates over the normal experimental period.

Sexual Differences in Grazing Rates. Raymont and Gross (1941) fed male and female *Calanus finmarchicus* different cultures of marine phytoplankton and recorded the number of fecal pellets produced. In almost all of their experiments, more fecal pellets were produced by the females. For instance, with the centric diatom *Ditylum brightwellii*, 25 males produced 540 pellets in 68 hours and consumed an average of 31 cells/cc, while the same number of females produced 4000 pellets during the same period and consumed 476 cells.

In our first experiment, run at 20° C with *tonsa*, males filtered an average of 413 ml water per mg dry weight and day while the females filtered 894 ml, or more than twice as much. When these results are compared with the oxygen consumed, we find that the males actually expended more energy in filtering 413 ml of water than the females did in filtering twice that amount. In another experiment, the average female *tonsa* removed food from 25.1 ml water in a day while the males filtered only 9.12 ml.

Among lower animals the males are often smaller and weaker than the females, and it is possible that male copepods are subservient to the females. Once the spermatophore is attached to the genital segment of the female his function is completed, whereas the female must survive long enough to produce sufficient eggs to insure survival of the species. If the adult male lived only briefly, there would be less competition for food as the progeny developed.

Effect of Temperature on Grazing. During fall and winter of 1953–54 and in early summer 1954, comparative experiments were run to ascertain the effects of temperature on grazing. Fig. 26 represents grazing curves derived from two winter experiments in 1954. The rate for both *clausi* and *tonsa* was essentially linear with respect to temperature on January 6; this linear relation between temperature and grazing was characteristic of results obtained throughout the fall. At lower temperatures the *clausi* grazing rate was significantly higher than that for *tonsa*, with the inverse situation at higher temperatures. However, on February 2, grazing rates for both species increased rapidly with temperature up to 15° C and then declined between 15 and 20°. A grazing curve for *clausi* obtained January 26 was just intermediate in shape between these two; that is, grazing rates rose sharply with temperature up to 15° but merely leveled off at 20° instead of declining as on February 2. There were not enough *tonsa* in the tows to run more than a token experiment on

January 26, so their behavior is mere supposition. Nonetheless, this series of experiments suggests the occurrence of temperature conditioning.

Water temperatures throughout the fall and early winter were several degrees higher in 1953 than in 1952, but about the first of January 1954 a series of cold spells caused a sharp drop in temperature over a period of two weeks, after which temperatures remained around 2° C through the rest of January and February. Thus the animals used on January 6 had a previous temperature history about 4–6° higher than those used on February 2.

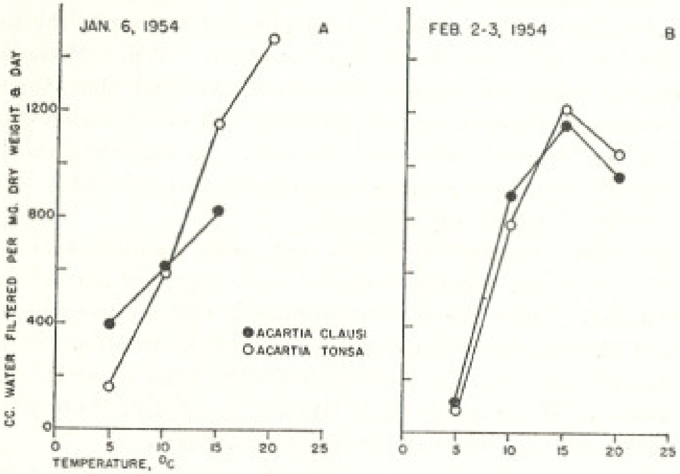

Figure 26. Grazing rates for adults plotted with temperature. A, January 6, 1954; B, February 2–3, 1954.

If the amount of oxygen consumed by an animal in a given period of time is roughly proportional to the amount of organic matter oxidized, it should be possible to compute the theoretical food requirements of each species and compare it with the actual amount of food present in the water. However, before this can be done, certain assumptions are necessary. First, since our understanding of the physiology of copepods is limited, for the sake of simplicity let us assume a carbohydrate metabolism with glucose as the substance oxidized. Second, let us assume that the organic substance of the copepod is 50% carbon. Thus, ml O_2 consumed × 1.4 × 0.375 = mg C oxidized, where 1.4 is the density of oxygen and 0.375 the carbon/oxygen ratio in the glucose equation. The value for carbon obtained may be multiplied by 100/50 to give the results in terms of organic matter oxidized.

If the water temperature in the Sound is known, oxygen consumption rates interpolated from laboratory curves can be used to compute carbon requirements for any given date, and grazing curves can be used to determine the amount of organic matter that is necessary to fulfill this requirement. When the theoretical concentration of plant material (in µg chlorophyll per liter) which is required to maintain the population in a steady state is plotted for both species with the average winter concentration of chlorophyll observed in the Sound, it is clear that *tonsa* was not able to meet its metabolic needs during most of December and January (Fig. 27). To be sure, *clausi* also may

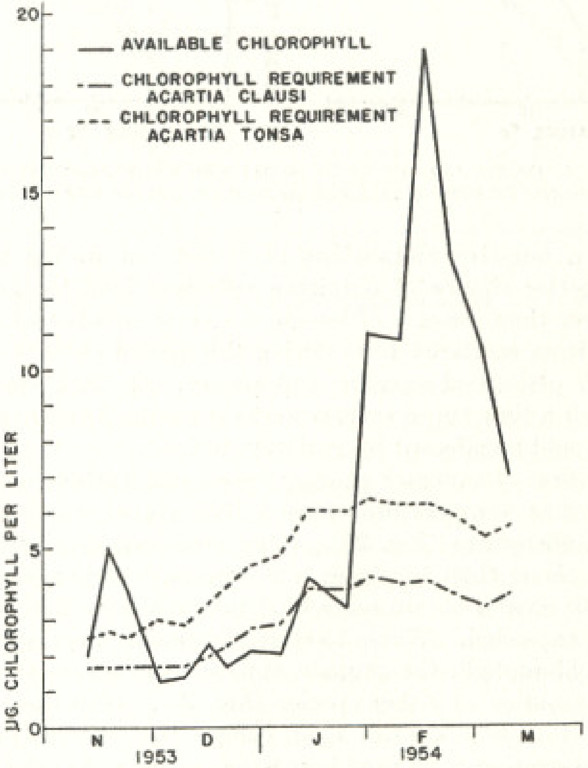

Figure 27. Chlorophyll requirements, in µg per liter, of adults plotted with available chlorophyll; winter, 1953–1954.

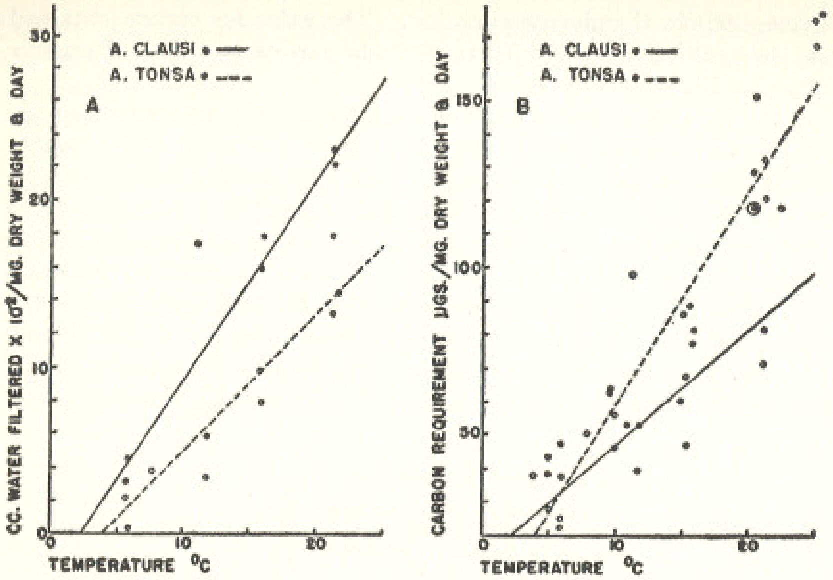

Figure 28. A, Grazing rates for adults plotted with temperature; summer 1954. B, Carbon requirements for adults plotted with temperature; summer 1953 and 1954.

have had a negative metabolism at times, but during the winter it had a better chance of obtaining sufficient food for growth and reproduction than *tonsa*. Although the total number of organisms estimated from scattered tows during this period did not agree perfectly with periods of scarcity and plenty, the data appear to be reasonable if a time lag of several weeks is assumed before population numbers would be affected by variation in food.

Examination of summer grazing rates and carbon requirements plotted against temperature showed that *clausi* was still favored by high temperatures (Fig. 28). Since corrected grazing rates were higher for *clausi* than for *tonsa* and corrected carbon requirements lower, *clausi* should obtain more food than *tonsa* for a given amount of energy expended. When food requirements were plotted with available chlorophyll, the organic matter was sufficient to support a large population of either species (Fig. 29). Nonetheless, if both species ate the same kind of food, competition should favor *clausi*.

All of the grazing rates used here were determined with the diatom *Skeletonema costatum*, primarily a winter and spring form in Long

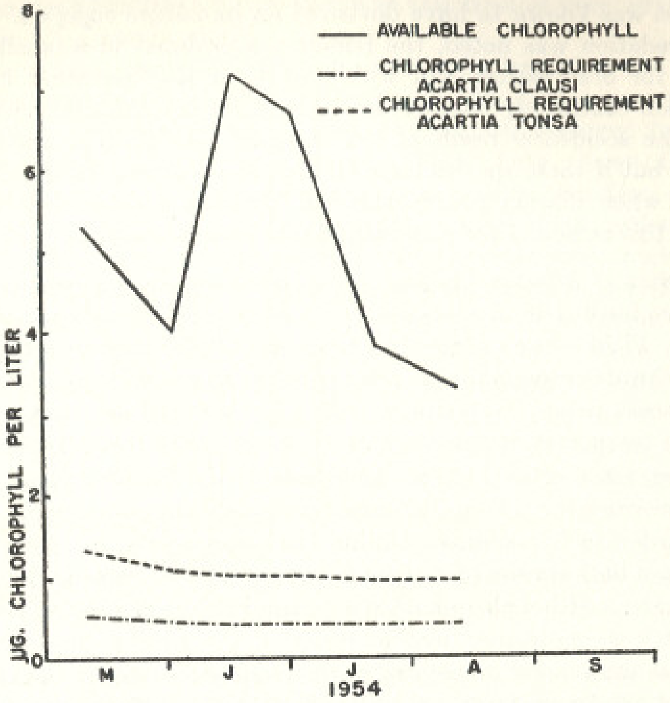

Figure 29. Chlorophyll requirements, in μg per liter, of adults plotted with available chlorophyll; summer 1954.

Island Sound, but during the summer months the diatom population was generally low compared with the flagellate population. Although *tonsa* grazing rates might have been high enough had a summer phytoplankton species been used to account for this discrepancy, it does not seem likely on the basis of available information. In the first place, corrected grazing rates for populations of both species were larger in summer than in winter, except at the lowest temperature, but the amount of increase was greater for *clausi*. Secondly, when the copepods were fed natural summer phytoplankton, *clausi* still had a higher grazing rate than *tonsa*, although neither species fed as well on phytoplankton dominated by flagellates as it did on *S. costatum*.

It is possible that *tonsa* utilized another source of food that was unavailable to *clausi*, for on two occasions a *tonsa* female in laboratory cultures was known to have devoured an immature copepod. When this predation was noted, the female was isolated in a smaller container for observation, and within an hour the immature copepod had been completely consumed. This predatory activity could have been the accidental result of overcrowded conditions in the culture vessel, but if these species have to depend on animal food to a large extent when diatom populations are low, the greater size of *tonsa* during this season of the year should give it an advantage.

Question of Selective Feeding. Previous mention has been made of selective feeding in the laboratory by *Calanus finmarchicus* (Harvey, 1937). Field observations by Lowndes (1935) demonstrated that the freshwater copepod *Diaptomus gracilis* can select its food in nature. In a recent paper, Hutchinson (1951) has pointed out that, particularly in temporary waters, two or more species of copepods of widely differing sizes often coexist; presumably the larger species would not compete with the smaller ones for exactly the same food.

In order to investigate possible food preferences in nature, individuals of both species of *Acartia* were cleared in creosote and mounted in balsam. Although quantitative examination of the type of food present was impossible because many of the smaller phytoplankton elements were badly macerated in the feeding and digestive processes, some of the larger forms could be identified and their numbers were roughly estimated.

During winter, both species appeared to be feeding primarily on two species of *Thalassiosira* and on *Thalassionema nitzschioides*, a colonial pennate diatom. At the height of the spring flowering, the guts of both *clausi* and *tonsa* were packed with *Skeletonema costatum* as well. In addition to identifiable forms, the guts always contained a considerable quantity of greenish material of unknown origin. In summer there was less food in their intestines and a higher percentage of this was unidentifiable. The most common recognizable form at this time of year was the small *Coscinodiscus radiatus*, but fragments of a larger species of *Coscinodiscus* were found occasionally, more frequently in *tonsa*. However, the major difference in gut contents during summer was the frequent occurrence in *tonsa* of a sizable transparent form of indefinite shape; while this object was not positively identified as a plant cell, its size was about the same as that of a naked dinoflagellate of the genus *Prorocentrum* found in considerable abundance in the Sound at this time of year; practically never was it found in *clausi*.

If *clausi* and *tonsa* are behaving as filter feeders, then the size of the apertures made by the fine hairs on the feeding appendages should determine the minimum size of a particle removed from the water. Lowndes (1935) and Cannon (1928) have shown that, in several species of calanoid copepods, the second maxillae do not participate actively in the food-getting processes but rather serve as a filter or sieve through which a feeding current is maintained by the activities of certain other appendages. Although the second maxillae also serve as the principal filter among members of the genus *Acartia*, they are used actively for "seining" rather than as an immobile net on which food particles are collected. Each second maxilla of the *Acartia* has 12 long curved spines pinnate with short bristles 10–20μ in length. The maxillae are worked in unison; first the spines are spread apart to form an open basket-like structure, and then they are quickly drawn together much as a fisherman might use a drop net. Thus the size of the apertures varies somewhat depending on whether the "seine" is open or closed, but the minimum size still is determined by the distance between adjacent pinnate bristles.

In the case of *tonsa*, this distance, estimated as 7–8 μ, was practically the same in summer and winter. On the other hand, for *clausi* a considerable seasonal variation was noted, the bristles in summer averaging only 4–5μ apart, in winter 9–10μ. Although a sizable percentage of the flagellates would slip through the apertures of either species, *clausi* should be better able to catch the smaller forms present in summer than *tonsa*.

Several grazing experiments which were run to determine if the copepods showed any differences in choice of food in the laboratory gave negative results whether natural populations of phytoplankton or mixed laboratory cultures were used. During the spring flowering, when a natural population dominated by *Skeletonema costatum* and *Thalassiosira nordenskiöldii* was used for grazing experiments, neither species of copepod demonstrated selectivity. However, when laboratory cultures of *S. costatum* were compared with laboratory cultures of *Nitzschia closterium*, both copepods showed a distinct preference for the former. Nevertheless, there was no differential selectivity; that is, the ratio of the filtering rate with *S. costatum* as a food source to that for *N. closterium* was about the same in the case of both *clausi* and *tonsa*. The most interesting feature of this experiment was the result obtained when *clausi* and *tonsa* were fed a mixed culture containing equal numbers of *S. costatum* and *N. closterium*, adjusted to give the same approximate total concentration used with either culture alone. In this case, the grazing rates determined from the consumption of *N. closterium* in the mixed culture were about the same as those determined from *N. closterium* alone, but the grazing rate determined from *S. costatum* in the mixed culture was significantly lower statistically than the rate from *S. costatum* alone. The low numbers of *N. closterium* eaten by *clausi* and *tonsa* cannot be explained entirely on the supposition that it is too small (diameter, 3–4μ) to be captured by the feeding mechanism; rather, it appears to be so unsuitable as food that feeding processes are suppressed.[3]

In another experiment, with summer populations of phytoplankton, the dominant identifiable forms were the dinoflagellates *Ceratium lineatum*, *Dinophysis acuminata*, and *Prorocentrum scutellum* (?). While the individual grazing rates on these dinoflagellates were too low for statistical treatment, the data suggest that *tonsa* might prefer *C. lineatum* to *D. acuminata* and that *clausi* might prefer *D. acuminata* to the larger *C. lineatum*.

GENERAL DISCUSSION

The descriptive data for Long Island Sound have shown that the distribution of each species of *Acartia* is limited seasonally, as was true also in Tisbury Great Pond (Deevey, 1948). Although Deevey's data suggested rigid temperature control, our study seems to indicate that at least the adults of both species can survive the temperature extremes found in the Sound.

In Tisbury Great Pond, a temperature of 22 to 24° C appeared to be lethal to *clausi*. However, in Long Island Sound *clausi* was largely gone from the water before the average temperature reached 20°. Since there is usually a moderate thermocline at this time of year, the temperature of the deeper waters remains below 22° well into August, long after *clausi* has completely disappeared. Moreover, laboratory experiments have shown that summer populations of adult *clausi* are well acclimatized to temperatures around 20°, but by the time Sound temperatures have risen to this level the balance has swung toward *tonsa*. Although the experimental data do not rule out completely the lethal effect of high temperature as a possible limit to *clausi* production, certainly no temperature was recorded which was low enough to cause the abrupt elimination of either species.

It has been shown that the adult *clausi* was definitely the more efficient organism at low temperatures. On the other hand, *tonsa*, the summer form, was still outstripped by *clausi* under laboratory conditions approximating the summer environment. Although both species should be able to meet their energetic needs on the basis of available carbon, *clausi* should dominate in summer as well as in winter unless there is some selection of food favoring *tonsa*. The larger *tonsa* might be more successful with larger food organisms, but evidence suggests that a high percentage of the available organic matter in summer is in the form of small flagellates. The food studies performed on the adult organisms do not adequately explain the absence of *clausi* and dominance of *tonsa* in summer, and yet another explanation must be sought.

Figs. 7 and 8 show that the developmental stages of *clausi* began to disappear somewhat earlier than the adults. Thus the unfavorable trend in the environment must have been operating primarily against the young stages. The nauplii and copepodids may have a lower temperature tolerance than the adults, but the gradual decline in numbers of *clausi* and the steady increase in young *tonsa* suggest a more subtle temperature control. Final resolution of this problem must await the development of a more sensitive experimental procedure and a culture method.

Even if temperature is ruled out as the direct cause of seasonal fluctuations in species composition, its influence must be considerable. In laboratory experiments, temperature change had a profound effect on the organism in several inter-related ways; moreover, the degree of influence was greater on one species than it was on the other, which would imply certain differences in metabolic control. Tem-

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[3] A recent paper by Hendey (1954) has cast considerable doubt on the identity of certain *Nitzschia closterium* cultures. The form used in these experiments and in the majority of other feeding studies was probably the *Nitzschia closterium* (Ehrenberg) Wm. Smith forma *minutissima* which was isolated at Plymouth by Allen and Nelson (1910); this form always contains a few triradiate cells. Hendey believes that this organism is *Phaeodactylum tricornutum* Bohlin rather than *N. closterium*. There is good evidence to suggest that it is not even a diatom.

perature also affected the activity of the animals and thus influenced such important processes as food acquisition. Therefore, it appears that temperature may act to control the distribution of *tonsa* and *clausi* indirectly, first making the environment slightly more favorable for one species and then for the other. From available information on food and vertical distribution, the ecological niches of these two species must at least overlap. In the light of classical theory, these organisms should be in competition.

The best known mathematical description of population growth is probably the logistic of Pearl and Reed (1920), which may be written

$$dN/dt = bN(K - N)/K, \tag{3}$$

where K is the population size at saturation density, N the population size at any given time t, and b a growth coefficient. This equation was rewritten by Gause (1934) to express the inter-relationship between two species inhabiting the same environment,

$$dN_1/dt = b_1N_1(K_1 - N_1 - \alpha N_2)/K_1, \tag{4}$$

$$dN_2/dt = b_2N_2(K_2 - N_2 - \beta N_1)/K_2, \tag{5}$$

where the subscripts $_1$ and $_2$ distinguish the two species and where the terms αN_2 and βN_1 describe the degree of influence each organism has on the other.[4]

From these equations it is possible to predict that one of three things may happen in a competitive system involving two species (Gause and Witt, 1935). First, if $\alpha > K_1/K_2$ and $\beta > K_2/K_1$, then the species which is initially dominant would survive while the subdominant would be eliminated. Such a case might involve some equally strong mutual depressant, such as an antibiotic, but there is no evidence in our investigation for such a direct biotic effect of one species on the other. Second, if the ecological niches coincide precisely and if the uniform environment favors one species (*i.e.*, $\alpha < K_1/K_2$ and $\beta > K_2/K_1$), then the degree of influence of the better adapted species on the other would be sufficient to bring about the elimination of the competitor. Finally, if the ecological niches do not coincide precisely, some interaction may occur, but each species can retreat outside the zone of influence of the other so that coexistence is possible; in this interpretation $\alpha < K_1/K_2$ and $\beta < K_2/K_1$.

In setting up these equations, conditions were considered to be constant, α and β as well, but obviously no such situation exists in nature. Consider what would happen if some external variable, such as temperature, brings about a differential change in the values of α and β; the curves of the struggle for existence would change, and at some critical level the change could be qualitative, resulting essentially in a redefinition of the niche of each species. Furthermore, if the variable were seasonally controlled so that a rhythmic pattern was established, the competitive system would show rhythmic variation as well. First one species would be favored and then the other, as was the case in Long Island Sound.

In recapitulation, during late spring and early summer, when the most pronounced temperature gradient existed, the ecological niches of the two species showed the least amount of overlap. As the water warmed in summer, the environment became essentially homogeneous, leading to competition within a single niche. From the available information it was inferred that competition was strongest between the developmental stages of the two species. As the water cooled in the fall, the niches appeared to separate again. Whatever interaction occurred, it must have taken place between the younger stages, as in summer. The later stages of *tonsa* became relatively dormant, and since winter *tonsa* contained considerable amounts of stored fatty reserve, they scarcely needed to enter into competition with the favored *clausi*. During the spring flowering period, *clausi* multiplied rapidly; this fact, together with the phytoplankton dearth just after the flowering, should result in strong competition for food. By this time, the water had warmed enough to suspend dormancy during a period when the food reserves of *tonsa* were at a low point.

[4] Recently Andrewartha and Birch (1953) have criticized this classical approach to population problems, but a fallacy in their argument should be mentioned. They state that K is conceived ". . . as the maximum or saturation density for a particular place and the particular circumstances in which the population is living." According to G. E. Hutchinson (personal communication), K is conceived only as a saturation density, but there is no reason why K may not be exceeded under artificial or unusual conditions; therefore, K cannot be a maximum as well as a saturation density. If the biologist prefers, he may start with a laboratory population with N higher than K, in which case it is assumed that the population will decline to the level K. The fact that the original mathematical treatment of Gause provides for such an assumption is certainly a point in its favor. Furthermore, no mathematical interpretation of biological phenomena is without some criticism, but until a better description of the problem is put forward, a theory with such wide application (see Riley, 1952) should not be discarded on a technicality.

Once again the niches coincided and *clausi* was successful. Only once during the year were there simultaneous increases of both species. This exception, during and just after the spring flowering, may actually lend support to the theory, for it is probable that competition for food was minimal at this time.

Seasonal Distribution of the *Acartia* in Other Areas

The information accumulated in this study should be of use in the interpretation of previous observations even in areas quite far removed geographically from Long Island Sound.

The coastal waters off southern California, where both *clausi* and *tonsa* occur in fair abundance, were examined by Esterly (1928) by means of surface tows made twice daily for over two years from Scripps Pier at La Jolla. In both years, *clausi* attained maximum numbers in March, decreased through the spring months, and was essentially absent from these waters from the end of June until September. Throughout the fall and winter, a more or less steady increase occurred until the spring maximum was attained once more in March. *A. tonsa*, on the other hand, attained peak numbers in July or August and then declined gradually after the first of September to a winter minimum in February. In March the population underwent some resurgence, only to decline again to a June minimum in 1917 and to an early July minimum in 1918. The seasonal picture, therefore, is not unlike that observed in the Sound, except that *tonsa* was never completely absent from the California waters.

The seasonal temperature variation for these waters was about 8.5° C. Unfortunately Esterly averaged the temperatures for the two years, so that precise comparison of our data with his is not possible; however, maximum temperatures of about 21.5° occurred in late August and minimum temperatures around 13° occurred in late January and early February. The salinity was somewhat higher than that in the Sound, the spring minimum being about 33.30‰ and the fall maximum 33.90. The phytoplankton abundance was not determined by Esterly, but studies by Allen (1927a, 1927b) of the waters off La Jolla during other years indicated diatom peaks in March and April, perhaps another in July, and a fall maximum in November.

Interpretation of the *clausi* cycle off California is relatively simple because of its similarity to that in local waters. The preference for cool waters was unmistakable and the maximum numbers observed in March corresponded reasonably well with the postulated spring diatom flowering. During most of the year the greater number of *clausi* were taken in night tows, but in June and July there was little difference between night and day catches. Thus the evidence is not contradictory to the supposition that a thermocline may restrict the normal diurnal migration of *clausi* after surface waters have warmed to some critical temperature. In the fall, *clausi* numbers increased quite rapidly, with a subsidiary December peak recorded in the second year of the survey. This might be correlated with a fall diatom bloom in November.

Likewise, the *tonsa* cycle was similar to that observed in the Sound when it is considered that conditions of existence were less extreme in California waters. The summer maximum in both places was certainly produced under similar conditions. No information is available concerning the distribution of young stages in winter, but comparison of night and day tows strongly suggests a degree of dormancy. The water temperatures at La Jolla in winter were not nearly so low as those recorded in the Sound, but, since seasonal acclimatization appears to be present in Sound *Acartia* populations, a different level of climatic adjustment to a different set of conditions might well be postulated for copepods in waters with a smaller seasonal temperature variation. Hence the winter metabolism at 13° in one locality might be similar to that found elsewhere at lower temperatures; such regional differences are known for other poikilotherms (Spärck, 1936; Thorson, 1936; Fox and Wingfield, 1937; Scholander, *et al.*, 1953). A spring increase of *tonsa* occurred in Long Island Sound and at La Jolla; this could result only from a temporary superabundance of food during the spring flowering. The major difference in distribution in the two bodies of water occurred after the spring diatom maximum, when zooplankton were abundant and phytoplankton relatively scarce. In Allen's study the diatom numbers in La Jolla waters did not fall away so precipitously after the flowering as they did in the Sound. Nonetheless, the lowest quantity of *tonsa* in the California environment was found in both years during the late spring and early summer when the amount of phytoplankton was low.

Thus the distribution in both areas was probably controlled by the same environmental factors, but the more moderate conditions at La Jolla seem to favor only limited competition during most of the year. When more severe competition did occur, it was approximately at the same season as in the Sound.

In northern European waters, *Acartia clausi* has a different seasonal cycle. Maxima are usually obtained in middle or late summer and minima occur in winter (Marshall, 1949; Digby, 1950; Wiborg, 1954). Wiborg has presented rather extensive hydrographic data for comparison with zooplankton distribution, and the data for three of his stations include reasonably complete seasonal cycles for *clausi:* Sognesjøen, at the mouth of Sognesfjord, 61° 04′ N, 04° 50′ W, depth 300 m; Ona, off Møre, 62° 54′ N, 06° 30′ E, depth 200 m; and Eggum, on the ocean side of the Lofoten Islands, 68° 23′ N, 13° 39′ E, depth 200 m.

At Sognesjøen, on the basis of incomplete data, maxima of *clausi* are indicated for June and September 1950; at Ona, in the same year, there was a major peak in August and a secondary one in November; at Eggum, the primary maximum occurred in September 1950, with a smaller peak in November. The two peaks recorded for each station suggest that two generations were produced. At Sognesjøen, surface temperatures warmed quickly from 10° at the beginning of June to 16° by the end of August, but in the fall, cooling was more gradual, with deepening of isotherms. At Ona, temperatures above 13° were recorded down to 50 m from August well into September and above 10° until mid-November. At Eggum maximum temperatures occurred in September, but temperatures remained fairly high until about the first of December. Thus, with the exception of Sognesjøen, where data were limited, the zooplankton and temperature maxima corresponded in 1950. Few if any *clausi* were produced until water temperatures reached 10° C, and breeding ceased in the fall when temperatures fell below this figure. In 1949, on the basis of such zooplankton data as were available, the seasonal picture for all stations was somewhat different. At each station the *clausi* maxima were about one month later, and only one successful generation was produced. The temperature distribution suggests that this was a much cooler summer, with maximum temperatures later and somewhat lower than those in 1950. Nonetheless, the abundance of *clausi* and the temperature distribution were closely correlated.

In Long Island Sound, respiratory and grazing observations indicate that *clausi* has an excellent chance of success in meeting food requirements at temperatures between 8–16° C, but contrary to the situation in Norwegian waters, it also existed at much lower temperatures in local waters. Although *clausi* has a world-wide distribution and a wide range of temperature and salinity tolerances, in northern temperate waters, at least, it becomes a zooplankton dominant only under estuarine conditions.

It was mentioned earlier that the *Acartia* are not filter feeders in the strict sense (Lowndes, 1935); they do not make continuous vibratory movements of the head appendages, nor do they glide slowly while feeding in the manner of *Calanus finmarchicus*, creating a feeding current by their movements (Cannon, 1928). Instead, the *Acartia* obtain food by a series of grasping or raking movements, principally by the second maxillae. These movements are not nearly as rapid as those of *C. finmarchicus*, and they are made for only a short period, not more than a few seconds on the average.

Since the feeding mechanism of the *Acartia* appears to be less efficient than that of other copepods, they may not be successful in competition with "true" filtering forms; hence, the *Acartia* may attain an important position in the zooplankton community only when salinity restricts the distribution of other copepods.

Wiborg's data lend two important items of confirmatory evidence to this theory. First, the "true" filtering copepods, such as *Calanus*, had spring maxima in these northern waters, and second, the salinity minimum occurred in late summer and early fall at all of his stations. Thus salinity rather than temperature may be the most important limiting factor for the *Acartia* in competition with copepods of other genera. However, in the case of intrageneric competition such as has been described for Long Island Sound, temperature is probably the most significant physical factor.

Daily Zooplankton Production in the Sound

From the respiratory and grazing data accumulated in this study, the daily rate of zooplankton production can be estimated. The average displacement volume of total No. 10 net zooplankton from the Sound over a two year period was about 1 cc/m^3, and the average water depth is about 20 m (see Riley's INTRODUCTION in this volume). Therefore, the total zooplankton mass per square meter of sea surface would be 20 g, assuming a specific gravity of about 1 for the plankton. At a mean temperature of 10.6° C, it can be estimated from Fig. 28A (average of the two curves) that the grazing rate would be around 760 ml water/mg dry weight and day. The average weight loss on desiccation of mixed zooplankton samples was 90% which can be used to estimate that the water filtered per mg wet weight is about 85 ml/day. Hence, 20 × 1000 × 85 or roughly 1700 liters of water were filtered by the zooplankton in 24 hours in a water column having an area of one square meter. The average chlorophyll content of Sound waters, exclusive of bloom periods, was about 5 μg chlorophyll/l and the chlorophyll varied seasonally in percent of organic matter from 0.60 to 1.40; an estimated mean of 0.75% seems reasonable. Assuming that approximately half of the organic content was carbon, the daily intake of the zooplankton would be $1700 \times (5 \times 10^{-6}) \times 0.50/0.0075 = 0.57$ g carbon. Since the organic matter of zooplankton was of the order of 10% of the wet weight and since half of this was carbon, it can be shown that the total zooplankton carbon in the water column was approximately 1 g. Thus the zooplankton would appear to consume over 50% of their carbon weight in 24 hours. From respiratory data for *Acartia* (converted to oxygen consumed per mg wet weight), a mean oxygen consumption of 0.028 ml O_2/day can be calculated. Since there were 20 g of zooplankton in the water column, 0.56 ml represents total oxygen consumption per square meter, which may be converted to the daily carbon requirement in the manner previously described. Thus, 290 mg organic carbon are lost each day through respiration. The difference between carbon accrued in feeding and that lost in respiration is obviously the carbon production per day, or 570 − 290 = 280 mg, assuming that 100% of the carbon ingested was assimilated. The rate of production, then, would be (280/1000) × 100, or 28%.

Recent experiments by Marshall and Orr (1955) have shown that digestive efficiencies for *Calanus finmarchicus* are surprisingly high when fed several different phytoplankton species labeled with P_{32}. Experiments which we performed with *Acartia clausi* from British waters confirmed these high assimilation rates, using *Skeletonema costatum* and *Chaetoceros decipiens* as food organisms. Although only a few experiments were run with *clausi*, 80% assimilation would seem to be a reasonable estimate. Using this figure, our previous estimate of carbon intake becomes 456 mg, from which a revised daily production rate of 166 mg or 16.6% can be derived.

Respiration and grazing figures used for our estimate assumed that *clausi* and *tonsa* were representative of the total zooplankton community and that grazing rates obtained with *Skeletonema costatum* were an index to the amount of water filtered by all species under all food conditions. Since the data presented in earlier sections of this paper indicate that feeding rates may vary with different food sources, the second assumption is probably unjustified. Moreover, since *clausi* and *tonsa* are dominant in the Sound, they might be better adapted than other members of the community. Although subject to these inadequacies, the Long Island Sound estimate compares favorably with Deevey's (1952b) figure of 16.7% for Block Island Sound (based on an assumption of 100% assimilation) and is slightly higher than Harvey's (1950) estimate of 10% for the English Channel.

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