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Growth characteristics of the copepods *Eurytemora affinis* and *E. herdmani* in laboratory cultures

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ABSTRACT: **Wachstum von *Eurytemora affinis* und *E. herdmani* in Laboratoriumskulturen.** Die calanoiden Copepoden *Eurytemora affinis* (POPPE) und *E. herdmani* THOMPSON & SCOTT wurden über zahlreiche Generationen im Laboratorium gezüchtet. Mit einem Überschuß an Algennahrung vermehrt sich *E. affinis* in Salzgehalten zwischen 5 und 33 ‰ und bei Temperaturen zwischen 2° und 23,5° C. *E. herdmani* pflanzt sich in Salzgehalten unter 15 ‰ und bei 21,5° C und höheren Temperaturen nicht fort. Diese Ergebnisse stimmen überein mit Untersuchungen im natürlichen Lebensraum und zeigen, daß *E. herdmani* an kälteres und salzhaltigeres Wasser gebunden ist als die weiter verbreitete *E. affinis*. An den Jungtieren, die von einzelnen Weibchen erhalten worden waren, wurden die Entwicklungszeitspannen vom Ei bis zum ersten Nauplius, ersten Copepoditen, Adultus und eiertragenden Weibchen ermittelt. In 20 ‰ Salzgehalt variiert die Generationszeit bei *E. affinis* von etwa 105 Tagen bei 2° C bis 9 Tagen bei 23,5° C. Die entsprechenden Generationszeiten für *E. herdmani* betragen 73 Tage bei 2° C und 19 Tage bei 15° C. Die Körperlänge beider Arten nimmt bei niedrigeren Temperaturen zu. Die Errechnung des Zahlenverhältnisses der Geschlechter der Jungtiere einzelner Weibchen legt die Vermutung nahe, daß die Temperatur das Geschlechtsverhältnis beeinflußt. Überlebenszeiten wurden ermittelt für Weibchen, welche unter verschiedenen Temperatur- und Salzgehaltsbedingungen gehalten worden waren. Die Lebensspannen von Weibchen beider Arten übertreffen 100 Tage bei 2° C und nehmen bei höheren Temperaturen ab. Weibchen beider Arten vermögen noch lange nach der Kopulation fertile Eier zu produzieren. Diese Beobachtungen sprechen dafür, daß kleine Lokalpopulationen möglicherweise im Herbst kopulieren, dann überwintern und daß die Weibchen im Frühjahr ohne erneute Kopulation Junge produzieren.

INTRODUCTION

Relatively few planktonic calanoid copepod species have been bred successfully in the laboratory. Summaries of work in this area may be found in HEINLE (1969b) and MULLIN & BROOKS (1967). Laboratory cultures providing a dependable supply of healthy copepods are of exceptional importance to investigations of the biology of these plankton animals since their normally "patchy", seasonal distribution may limit experimentation.

According to GURNEY (1931) the genus *Eurytemora* includes about 15 species, all of northern distribution and characteristically found in coastal and brackish regions, but also in fresh water lakes and rivers. The genus may have originated from

the marine genus *Temora* in the Arctic sea of glacial times. Several additional species have been described by HERON (1964) and WILSON & TASH (1966).

Eurytemora affinis (POPPE) is very widely distributed, inhabiting the Baltic Sea, North Sea, Caspian Sea, fresh water lakes in Central Asia, eastern North America and rivers and estuaries of the Gulf of Mexico (TOLLINGER 1911, WILSON 1932). *Eurytemora herdmani* THOMPSON & SCOTT is found in certain coastal and estuarine waters along the northeastern and northwestern coasts of North America and also the northeastern coast of Asia from the Japan Sea (HERON 1964, JOHNSON 1966).

Although *Eurytemora affinis* may be found in water of all salinities from nearly fresh to pure ocean water, it apparently prefers water of 5–15 ‰ S (JEFFRIES 1962). It is often important in estuaries, sometimes comprising over 90 % by numbers of the holoplanktonic copepods, reaching population densities of up to 100,000 adults and copepodites per m^3 and becoming an important food for many fishes (JEFFRIES 1962, HAERTEL & OSTERBERG 1967). HARDY (1924) found *E. affinis* to be the most important item in the food of young herring *Clupea harengus* in the Thames estuary. *E. herdmani* is probably of more local importance as a food source for other animals, as it is usually not as numerous as *E. affinis*.

MATERIALS AND METHODS

A stock culture of *Eurytemora affinis* (POPPE) was started on July 7, 1967, with 20 ovigerous females taken from a plankton net haul in Oyster Pond, a fresh-brackish pond near Woods Hole Oceanographic Institution (W. H. O. I.), Woods Hole, Massachusetts, U.S.A. The methods for starting and maintaining this type of stock culture are given in KATONA & MOODIE (1969). Briefly, the most successful method has been to isolate a number of animals, wash them several times in sterile sea water, then place them in 1-liter jars to which algal food is added as necessary to keep the water slightly green (about 100,000 cells/ml or more). As the population increases, larger vessels are used. Bacteria-free cultures of *Isochrysis galbana, Cyclotella nana* (W. H. O. I. strain 3 H), *Platymonas* sp. and *Skeletonema costatum* have all been successful foods, especially when several species are added. The first two species have been the easiest to culture and stay in homogeneous suspension better than *Platymonas* sp., which aggregates toward light and coats the sides of culture vessels, or *Skeletonema costatum* which often sinks to the bottom. They may be grown at all salinities from about 5 ‰ to 35 ‰ facilitating work on osmotic tolerance, and at temperatures up to about 25° C allowing work on the physiology of temperature effects on the copepods. Stock cultures of copepods have been maintained at 15° C, 20 ‰ salinity, and in constant light to promote growth of food algae. At the time of writing (August, 1969) the total population of this culture is about 10,000 adults and copepodites distributed in several 5-gallon carboys. Every 2 or 3 weeks the animals are gently strained off, their water changed and new food added. The bottom of the culture vessel must be clean when the females are carrying egg sacs to facilitate hatching of newly laid eggs.

These same methods were used to maintain a stock culture of *Eurytemora affinis*

from the Hamble River during 1967 and 1968 at Southampton, England, and for maintaining stocks of *E. herdmani* isolated from plankton tows near Boston or at Woods Hole. The latter species has proved harder to keep in culture, possibly reflecting its adaptation to inshore waters which are more stable than the upper estuarine conditions to which *E. affinis* appears to be adapted.

Experimental results for *Eurytemora affinis* W. H. O. I. and *E. affinis* HAMBLE refer to animals taken from stock cultures. Experiments on *E. herdmani* were performed on animals freshly isolated from plankton hauls made at Nahant, Massachusetts, where this species is very abundant. Individual ovigerous females were washed in sea water of the desired temperature and salinity, and if necessary acclimatized to the experimental conditions overnight before starting the experiment. *E. affinis* HAMBLE experiments were done in 250 ml beakers, however, since that time loosely corked 25 × 150 mm test tubes holding about 35 ml have proved to be satisfactory and convenient experimental vessels. These vessels are large enough so that nauplii do not become stuck on the surface film as often occurs in smaller vessels (CORKETT 1967). Temperature control is maintained by placing groups of tubes in perforated polythene containers in thermostatically controlled water baths. Experiments are started in sterile sea water. In order to prevent the build-up of detritus on the bottom of the experimental tubes, which would decrease hatching success, food is usually added for the first time after the nauplii have hatched out. At low temperatures some food is added at the start to prevent starvation of the female during the long hatching period. Equal amounts of food algae, grown in medium of the required salinity, is added to all tubes in an experimental series as necessary to keep the water green. If necessary, detritus is carefully removed from the bottom of the tubes with a Pasteur pipette. Tubes are inspected daily. The times until hatching, metamorphosis to first copepodite, and the appearance of adult males, females with egg sacs and second generation nauplii are all easily determined by eye. The first appearance of adult females is slightly harder to observe because of the small difference between Stage V and adult females. After development is completed in a tube either some females with eggs are removed for further investigations or the entire contents are preserved in 3 % formalin-sea water for future analysis.

RESULTS

Generation times

The generation times for *Eurytemora affinis* W. H. O. I., *E. affinis* HAMBLE, and *E. herdmani* are presented in Figure 1. All data included are for experiments run at 20 ‰ salinity. This salinity is slightly higher than that characterizing the main distribution of *E. affinis* (JEFFRIES 1962), however, it is near that commonly inhabited by *E. herdmani*.

Eurytemora herdmani developed faster and more successfully at the lowest temperature used (2° C) than *E. affinis*. Failure of the refrigeration system stopped

the 2° C experiment with *E. affinis* W. H. O. I. after 92 days, however, by that time only 2 adults had matured and development in the experimental tubes was poor when compared with tubes of *E. herdmani* and tubes of *E. affinis* W. H. O. I. at other temperatures. The HAMBLE stock of *E. affinis* developed well at 5° C, however, no experiments were performed at 2° C.

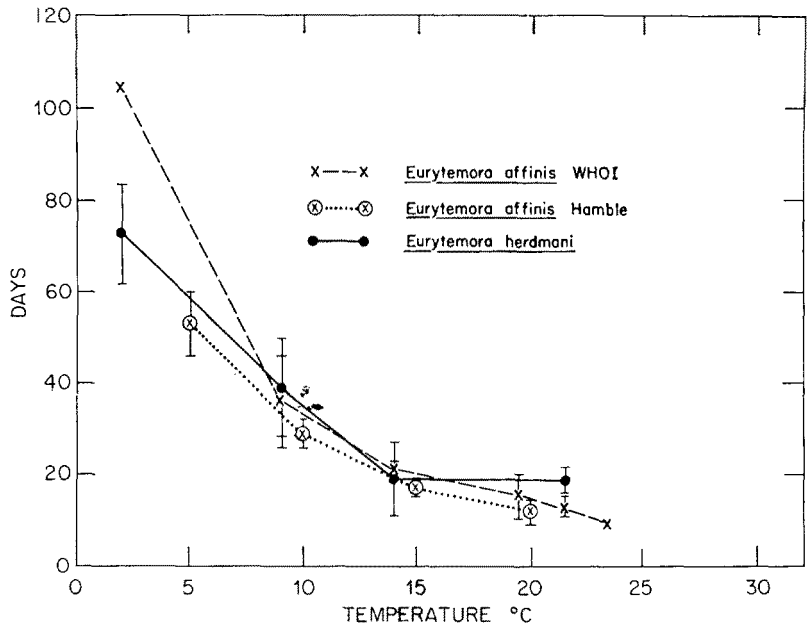

Fig. 1: Generation times (± 2 standard deviations) of *Eurytemora affinis* W. H. O. I., *E. affinis* Hamble and *E. herdmani* in 20 ‰ salinity sea water at different temperatures

Above about 18° C *Eurytemora herdmani* did not reproduce, even though some adults did mature. The generation time at 21.5° C was estimated based on adults that matured. As shown in Fig. 1, this estimated generation time at 21.5° C is about the same as that at 15° C. Both failure of reproduction and inability to decrease generation time with increasing temperature suggest that at 21.5° C. *E. herdmani* is under thermal stress.

Computation of Q_{10} values for development time from similogarithmic graphs of the data presented above yielded values of 3.0 for *Eurytemora affinis* W. H. O. I. and *E. herdmani* and a value of 3.1 for *E. affinis* HAMBLE.

At 21.5° C the generation time of *E. affinis* W. H. O. I. was not significantly different at 33 ‰, 20 ‰, or 5 ‰ S, however, this need not be true at lower temperatures. The rate of development of *E. herdmani* may possibly be more sensitive to salinity than that of *E. affinis*. At 14° C observed generation times of this species were 21 days at 33 ‰ S, 19 days at 20 ‰ S, and 17 days at 15 ‰ S, however, the differences were not statistically significant.

Effects of temperature and salinity on body length

During the two-year period of culture the size of adults in the stock population of *Eurytemora affinis* W. H. O. I. has remained within the normal range of natural populations (1.4–1.6 mm total length, WILSON 1932). The same was true of the *E. affinis* HAMBLE stocks. On the other hand *E. herdmani* raised in the laboratory has always been shorter than field specimens that have matured at comparable temperatures. The phenomenon has also been observed by Dr. G. GRICE of W. H. O. I. (personal communication). This suggests that the culture requirements for *E. herdmani* have not been met as successfully as for *E. affinis.*

Total lengths ± 95 % confidence limits of *Eurytemora affinis* HAMBLE adults, measured under a compound microscope, were significantly greater in individuals raised at 2° C (males 1.498 mm ± 0.044; females 1.778 mm ± 0.064) than in those grown at 20° C (males 1.154 mm ± 0.016; females 1.248 mm ± 0.121). Between 10° and 20° C length was relatively constant. *E. herdmani* males showed the same effect, averaging 1.197 mm ± 0.033 at 2° C and 1.073 mm ± 0.023 at 21.5° C. However, females grown at 2° C (1.105 mm ± 0.057) were nearly equal in size to those raised at 21.5° C (1.097 mm ± 0.037).

The length of *Eurytemora affinis* HAMBLE at temperatures from 10° to 20° C was not significantly affected by different salinities from 8 ‰ to 35 ‰. At 14° C female *E. herdmani* showed a linear and significant size increase with decreasing salinity from 33 ‰ (0.964 mm ± 0.049) to 20 ‰ (1.127 mm ± 0.022) to 15 ‰ (1.227 mm ± 0.036). The trend was apparent but less pronounced in males.

The above results agree with DEEVEY's (1960) observations that temperature is one of the most important variables governing copepod size. Furthermore, they show that at moderate temperatures the size of *Eurytemora herdmani* may be influenced by environmental salinity. These data suggest that *E. herdmani* is more stenothermal than *E. affinis,* and also that *E. herdmani* may be best adapted to salinities somewhat below full-strength sea water.

Conditions limiting reproduction

The combinations of temperature and salinity allowing successful reproduction of *Eurytemora affinis* and *E. herdmani* are pictured in Figure 2.

Although some *Eurytemora herdmani* adults matured at 21.5° C, no reproduction was observed at either 19.5° or 21.5° C. I have marked in an approximate upper thermal limit for reproduction at about 19° C based on the observation that *E. herdmani* disappears from Vineyard Sound near Woods Hole when the temperature rises much above that point.

Eurytemora affinis breeds successfully at a wider range of temperatures and salinities than does *E. herdmani. E. herdmani* breeds more successfully at low temperature and at high salinity than *E. affinis,* correlating with its more coastal habitat. The reproductive success of *E. affinis* at higher temperatures and low salinities agrees well with its distribution in the upper, fresher regions of estuaries and in brackish coastal ponds.

Eurytemora affinis W. H. O. I. did not develop well in cultures using artificial sea water ("Instant Ocean.", Aquarium Systems, Inc., 1450 East 289 St., Wickliffe, Ohio, U.S.A.) diluted to 20 ‰ salinity at 15° C. HEINLE (1969b) also found that this species developed better in natural than artificial sea water.

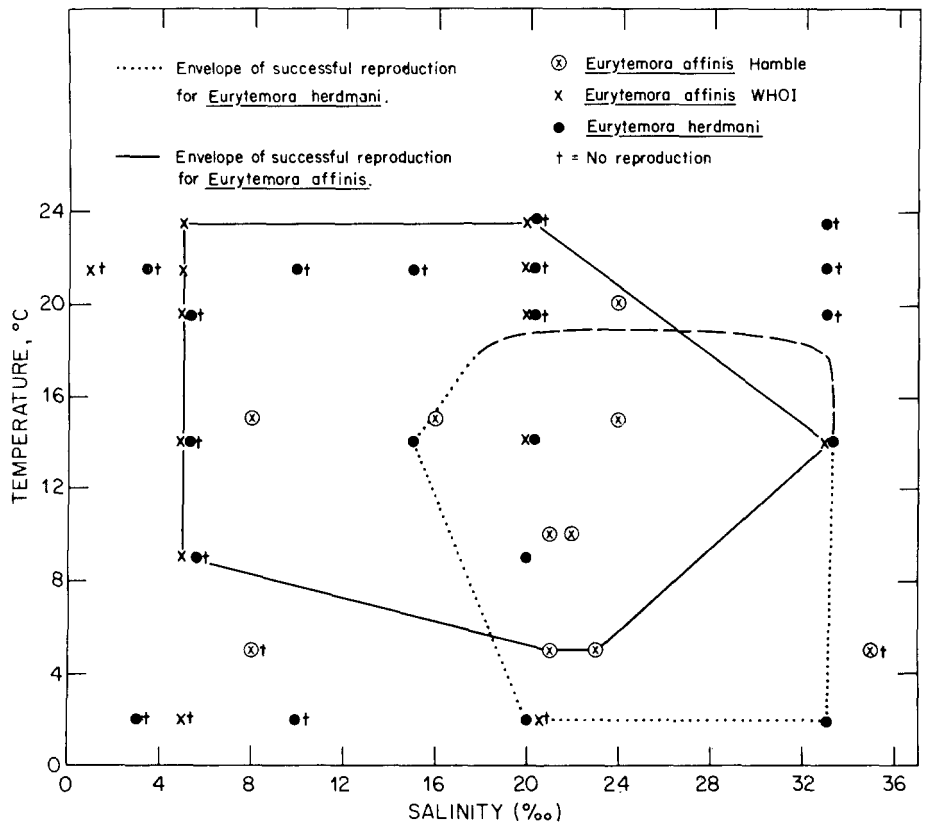

Fig. 2: Temperatures and salinities permitting successful reproduction of *Eurytemora affinis* and *E. herdmani*

More extensive work will undoubtedly modify the envelopes of successful reproduction presented here, however, the main patterns are easily seen from these data.

Survival times of females at different temperatures

Survival times of individual females used in experiments were recorded. Females always had excess food, however, they were usually in the presence of developing copepods. In some instances females were killed when an experiment was terminated or during failure of cooling systems. For these reasons the survival times presented here probably underestimate the potential lifetimes of females in nature.

Females of both *Eurytemora affinis* W. H. O. I. and *E. herdmani* survived longer than 100 days at 2° C, and the length of survival decreased at higher temperatures. Average and maximum observed survival times for both species are presented in Figure 3. No experiments were run above 23.5° C ± 1.5 because death of the algal foods occurred, however, on several occasions, cultures of *E. affinis* survived high ambient temperatures of 27°–28° C for a few days.

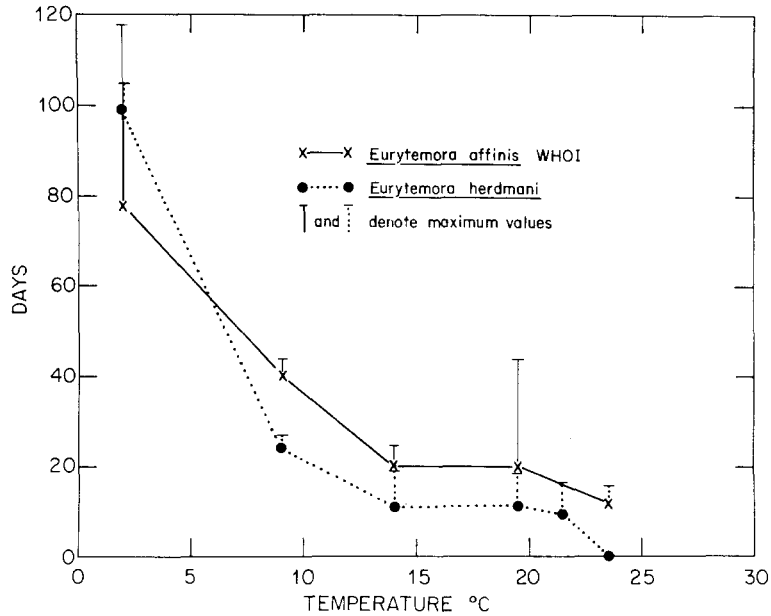

Fig. 3: Average survival times and maximum observed survival times for *Eurytemora affinis* W. H. O. I. and *E. herdmani* females in 20 ‰ salinity sea water at different temperatures

During these observations females often produced several egg sacs. Some females were isolated after laying an initial batch of fertile eggs in order to see whether further batches could hatch. At 2° C one *Eurytemora affinis* W. H. O. I. female produced new nauplii 92 days after isolation. Several *E. affinis* and *E. herdmani* females produced new nauplii after 20 days of isolation. These results show that females of both species can store sperm for long periods after mating, suggesting the possibility that females in nature could mate, survive long unfavorable periods, and then produce new larvae when conditions became more favorable without a further mating. Avoiding the necessity for an additional mating would be especially advantageous during times of low population density when males and females might have trouble finding each other for mating. The degree to which females store sperm in nature is unknown.

Effects of temperature on sex ratio

The sex ratios of progeny developing from single egg sacs of individual females of both species were calculated. From Stage IV copepodite on males and females can be distinguished easily under a compound microscope, especially after staining with a solution of methyl blue in lactic acid. Usually some individuals failed to develop to Stage IV or died before this stage. The effect this might have on the sex ratios obtained is unknown.

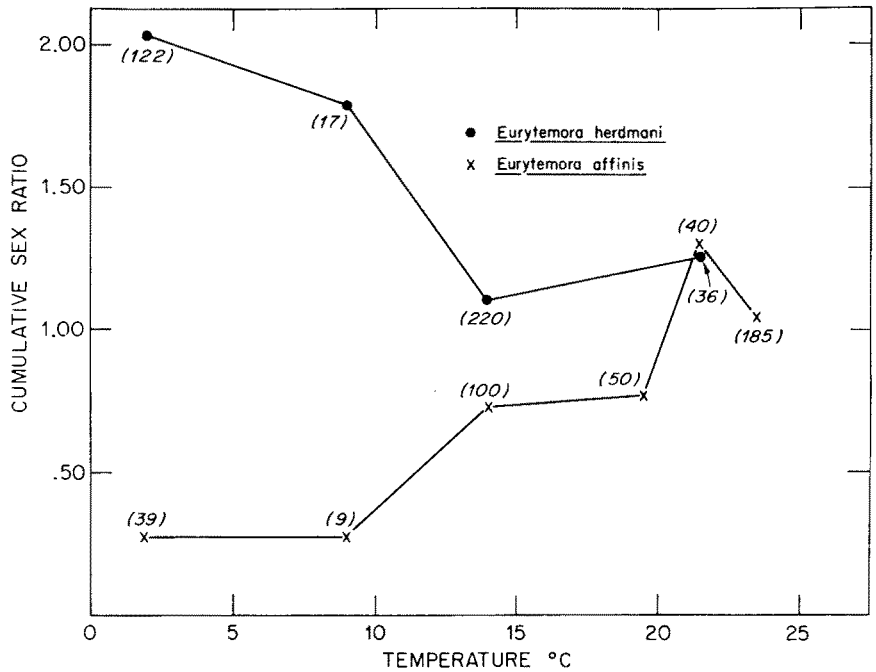

Fig. 4: Cumulative sex ratios of *Eurytemora affinis* W. H. O. I. and *E. herdmani* raised at 20 ‰ salinity and different temperatures. Numbers above or below points indicate total number of animals obtained

The ratios of the total number of males to the total number of females produced at any one temperature ("cumulative sex ratio") are presented in Figure 4. This index minimizes the effects of extreme sex ratios, which were often observed. All experiments included were done in sea water of 20 ‰ salinity.

Figure 4 suggests that developmental temperature may have at least partially determined the sex of developing *Eurytemora* individuals in these tests. The mechanism of this effect is unknown. No correlation was found between sex ratio and number of progeny developing in a tube.

Interpretation of these data is made difficult by the fact that the optimal sex ratio for these animals under natural conditions is unknown. The optimum ratio must depend on several factors including mating behavior, microdistribution of the popu-

lation in the water, potential fecundity of females, and the necessity for partitioning available resources among males and females. Since at least two of these factors vary during the year, and since some of this variation is related to temperature changes, one might expect sex ratio also to vary in this way. Furthermore different optimum sex ratios might be expected for different species.

The reason why temperature seems to affect the sex ratio in a different manner for the two species is also unclear, however, several possibilities can be mentioned. At 20 ‰ salinity *Eurytemora affinis* is apparently under some thermal stress at low temperature, while *E. herdmani* is under stress at high temperatures. Both species produced relatively more females under these conditions, although this trend was more pronounced in *E. affinis* than in *E. herdmani.* Possibly this is an advantageous strategy for tiding the population over unfavorable periods. *E. affinis* females produced by this mechanism could overwinter, as shown by the data on survival times. However, the short survival times at higher temperature would tend to minimize any survival advantage for *E. herdmani* unless some other effect were also operating, such as avoidance of the warm surface layers.

Another possible explanation is that both species tend to produce more males during favorable temperature conditions to insure fertilization of every female. The fact that *Eurytemora herdmani* produced relatively more males at all conditions than did *E. affinis* could possibly reflect adaptation of that species to sparser population concentrations requiring more males to search for and fertilize females.

Very little published work exists with which these data can be compared. CONOVER (1965) noted that the existence of genetic sex determination in calanoid copepods is not proven, and suggested that males may be produced only when needed. MEDNIKOV (1961) postulated that low food availability rather than low temperature was responsible for the numerical dominance of females in deep water calanoid copepod species. HEINLE (1969a) found that sex ratios of *Eurytemora affinis* and *Acartia tonsa* in laboratory cultures varied with the rate of harvesting of the cultures. Increased harvesting increased the proportion of male *E. affinis* but decreased the proportion of male *A. tonsa.* Furthermore the proportion of male *A. tonsa* in the Patuxtent River estuary was directly related to increasing population density.

In my experiments food was always present in excess amounts, salinity was constant, and no relation was found between sex ratio and the number of progeny developing in a tube. The variations in sex ratio observed are therefore probably temperature related.

High temperature or chemicals which accelerated development increased the number of males produced in cultures of the harpacticoid copepod *Tigriopus japonicus,* whereas low temperature or agents which suppressed metabolism increased the number of females (TAKEDA 1950, EGAMI 1951). The Stage VI nauplius appeared to be the critical period for sex determination. Increased environmental temperature may also increase the proportion of males of the harpacticoid copepod *Porcellidium fimbriatum* CLAUS in the lagoon at Venice (BATTAGLIA 1959).

More laboratory work and also more field studies to provide data on seasonal and geographical changes in sex ratio and on the fine scale distribution of copepod species will be required in order to understand these phenomena.

DISCUSSION

The generation times for *Eurytemora affinis* at different temperatures are nearly identical to those obtained by HEINLE (1969a). Those for *E. herdmani* are somewhat longer, especially at low temperature, than generation times observed by Dr. G. GRICE of W. H. O. I. (personal communication). In GRICE's experiments 5 species of food algae were used, salinity was 33 ‰, however, the lowest temperature used was 4° C. Possibly culture conditions for *E. herdmani* were more favorable than in my experiments even though the animals obtained were smaller than wild specimens. In any case these works strengthen the conclusion that *E. herdmani* tolerates low temperature better than *E. affinis*.

The data presented above correlate well with the field observations for these two species compiled by WILSON (1932), HERON (1964) and NORTHCOTE et al. (1964). The ability of *Eurytemora herdmani* to reproduce better and develop faster at 2° C than *E. affinis* agrees with the fact that it penetrates as far north as the coast of Alaska, whereas *E. affinis* in North America is found only as far north as the Gulf of St. Lawrence and British Columbia. In Europe *E. affinis* is found along the Norwegian coast (SARS 1903). On the other hand, the ability of *E. affinis* to reproduce at temperatures approaching 25° C correlates with its distribution as far south as the Gulf of Mexico, whereas the southern limit of *E. herdmani* is Narragansett Bay.

The wider range of temperatures and salinities tolerated by *Eurytemora affinis* as compared to *E. herdmani* helps explain its great ability to colonize the upper reaches of estuaries (JEFFRIES 1962, HEINLE 1969a) and even freshwater lakes (ENGEL 1962, see also NORTHCOTE et al. 1964). *E. herdmani* is not found in these environments.

The results and discussions presented above demonstrate how laboratory culture methods can contribute to a better understanding of the zoogeography of copepods and can facilitate investigations of the physiology of these animals.

SUMMARY

1. The calanoid copepods *Eurytemora affinis* (POPPE) and *E. herdmani* THOMPSON & SCOTT were cultured for numerous generations in the laboratory.
2. With excess algal food, *Eurytemora affinis* reproduced at salinities between 5 ‰ and 33 ‰ and at temperatures between 2° and 23.5° C. Reproduction of *E. herdmani* failed at salinities below 15 ‰ and at temperatures of 19.5° C and higher.
3. Using the progeny from individual females, generation times were calculated as the time required for development from eggs to ovigerous females. At 20 ‰ salinity, generation times for *Eurytemora affinis* ranged from about 105 days at 2° C to 9 days at 23.5° C. Corresponding generation times for *E. herdmani* ranged from 73 days at 2° C to 19 days at 15° C.
4. The body length of cultured *Eurytemora affinis* was within the normal range for wild specimens. Cultured *E. herdmani* individuals were always smaller than wild specimens, suggesting that the culture conditions for this species were not optimal. Body lengths of both species were greater at 2° C than at 21.5° C with the exception of *E. herdmani* females.

5. Low developmental temperatures increased the proportion of female *Eurytemora affinis* and increased the proportion of male *E. herdmani* in cultures. Possible adaptive advantages of these variations are discussed.
6. Females of both species lived longer than 100 days at 2° C, and survival time decreased at higher temperatures. Females of both species could produce fertile eggs long after mating. These results suggest the possibility that females could mate in autumn, then overwinter and produce larvae in spring without a further mating.
7. Better reproduction and faster development of *Eurytemora herdmani* at low temperature helps explain its more northerly distribution. The ability of *E. affinis* to reproduce at temperatures approaching 25° C correlates with distribution as far south as the Gulf of Mexico. The tolerance of *E. affinis* to a wide range of temperatures and salinities helps explain its great ability to colonize upper estuarine regions and even fresh water lakes.

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