Oecologia (Berl.) 24, 229 – 245 (1976)

Oecologia

3551 ?

The Life-Cycle of *Cyprideis torosa* (Crustacea, Ostracoda)*

Carlo Heip

Laboratorium voor Morfologie en Systematiek, Ledeganckstraat 35, B-9000 Gent, Belgium

Summary. The life-cycle of the dominant brackish water ostracod *Cyprideis torosa* (Jones, 1850) has been studied during 4 years. The species has only one generation anually. Reproduction is fairly similar throughout the years and appears to be tuned in to temperature. The number of adults has one peak every year and can be described by two exponential functions, one for the increase and one for the decrease. Mortality is very similar every year and approximately constant for months. *Cyprideis torosa* is on top of the food chain: regulation of numbers is probably not external and may be a function of the past of the habitat. A model is described which permits the evaluation of the duration of development from field data only. Predicted values are in good agreement with observed values.

Introduction

Cyprideis torosa (Jones 1850) [= *C. littoralis* (Brady 1868)] is a dominant species of the meiobenthos in brackish water areas throughout Europe; it occurs in North America, Asia, and Africa as well. The distribution of the species has been reviewed by Vesper (1972). *Cyprideis torosa* is a holeuryhaline and strongly eurythermic species, but its main distribution is on soft sediments of shallow brackish water habitats where large amounts of organic detritus are present. Hartmann (cit. Vesper, 1972) has observed that the entire sediment seems to consist of this species at times, while Redeke (1936) has found that the valves constitute a characteristic component of the sediment of the former Zuiderzee (now IJsselmeer) in the Netherlands. Remane (1941) defined the benthic biocoenosis of shallow brackish bays (Stillwasserbuchten) as the *Cyprideis-Manayunkia* community, herewith clearly stressing the importance of the species in these biotopes.

Information on the life-cycle of meiobenthic organisms is still scarce and only slowly accumulating. The life-cycle of ostracods in particular has been studied

---

* This paper was given as a lecture on the Second International Conference on Meiofauna, York, September 1973

only on a few occasions. The important studies concerning brackish water and benthic marine species are those of Elofson (1941), Hagerman (1966, 1968, 1969), Theisen (1966), and Muus (1967). All these authors worked in Scandinavian waters and all have given information on *C. torosa* but their material was insufficient to permit detailed analysis. Because of the importance of this species in large areas and in view of the scarcity of data on meiobenthos we have followed the changes in numbers of a population of *C. torosa* for nearly seven years.

As Watt (1970) observed, ecology is remarkably short of long runs of data. If one wishes to study patterns of fluctuations over long periods of time in order to assess the relative impact of density-dependent and density-independent factors on the population dynamics of a species one needs data of a type which are not frequently collected.

The number of factors which influence the number of individuals in a population is probably very large. As it is impossible to solve systems of n equations with more than n unknowns it appears that a very large number of years is required to discern between the influence of factors following a yearly cycle. The number of relevant factors may be substantially smaller than the total number of influences, but it still appears improbable that one or two years of investigation will suffice to prove anything about regulation of numbers in a population which inhabits an environment where yearly cycling factors prevail.

In the habitat I examined, the number of possible regulating factors will be smaller than in other habitats: it is well known that the number of species is smaller in brackish water habitats than in either fresh water or the sea. Moreover, the habitat in question, a pond in a polder, is very recent, originating from 1872 when the polder was diked, and the number of species is consequently still lower than in comparable habitats. Careful analysis has revealed the presence of only two molluscs, three polychaetes, six higher crustaceans (of which two were only found once), one insect larva and three fishes (of which one very rare). Numbers of meiobenthic species are somewhat higher, with about twenty species of nematodes (Smol, personal communication), eleven species of copepods and four species of ostracods (Heip, 1971). The polyp *Protohydra leuckarti* is also present.

Material and Methods

Samples were collected fortnightly from August 1968 till now (February 1976) with the exception of a 6-month period from August 1969 till November 1969. The series is still being continued, giving values of population density and composition for nearly 8 years. This paper reports the analysis of 4 years (August 1968 till December 1972).

Three samples were taken with a glass tube covering a surface area of 6 cm^2 to a depth of 5 cm. It had been proven that ostracods do not descend into the anaerobic layers of the sediment, which extend below 1 or 2 cm from the surface. The sediment which is sampled covers the bottom of a very shallow brackish water pond, called Dievengat and situated in northern Belgium. The sediment is a fine sand (median grain size 0.223 mm), well sorted and covered with large amounts of detritus, derived from reed beds (*Phragmites communis*) at the border. Depth at the sampling station is approximately 10 cm.

The samples were fixed with alcohol 70% or Formalin 4%, brough to and elutriated in the laboratory, using the method described by Barnett (1968). In this method the sample is put on a horizontal trough, 90 cm lang and 2 cm wide. Tapwater is allowed to run over the sample for about

Table 1. Length of the larval stages and the adults of *C. torosa*. Mean length and standard error from *n* observations

Stage	Mean length	*n*
I	0.132 ± .005 mm	9
II	0.167 ± .002 mm	10
III	0.208 ± .004 mm	9
IV	0.267 ± .002 mm	50
V	0.328 ± .001 mm	90
VI	0.415 ± .001 mm	117
VII	0.555 ± .003 mm	74
VIII	0.741 ± .003 mm	130
♀♀	0.966 ± .005 mm	95
♂♂	1.028 ± .008 mm	15

30 min. The sand is periodically stirred with the aid of a siphon. Although it allows only small samples to be treated, this method is superior to other elutriation methods for ostracods, which pose problems because of their heaviness.

After elutriation and separation from the detritus the animals were counted. Distinction was made between the sexes, females carrying or not carrying eggs and the eight larval stages. Because it proved to be difficult to separate the first three larval stages under the dissecting microscope they were counted together. The distinction between the larvae was made by grouping them according to their size; this is possible because increases in size occur during moults and differences between individuals belonging to the same stage are much smaller than differences between the mean size of the stages (Table 1).

Several physico-chemical parameters were measured at the same time: temperature was recorded continuously with the aid of a Ryan D-30 recorder with a precision of 1° C and measured fortnightly with a thermometer with a precision of 0.1° C. Salinity was calculated from chlorinity determined with Mohr's method by using Knudsen's formula $S = 1.805\,Cl + 0.03$. Oxygen in the water was measured with Winkler's method. Several other parameters which were recorded, e.g. nutrients and chlorophyll, will not be discussed here.

In order to smooth the curves of density changes the value obtained from the middle of three samples succeeding in time was replaced by the running average of the three sample values. This allowed for the processing of only one sample when density was low and but two samples when numbers were changing rapidly. Knowledge of the spatial pattern of this species (Heip, 1976) and the application of an exponential model for the temporal pattern made it possible to prove that the running average gives better estimates of density at a particular date than the sample value at that date (Heip, 1973). This substitution is only valid within a certain range of the value of r, the rate of change of the exponential function $N_t = N_0 e^{rt}$. Values obtained in this study all fall in this range. However, by using the running average the peak density is underestimated when it is a maximum and overestimated when it is a minimum. Therefore, in the case of peaks we used sample values.

To describe the temporal pattern of density we used the simplest model available, i.e. the exponential function $N_t = N_0 e^{rt}$, in which N_t is the number at time t, N_0 the number at the beginning and r the rate of change (positive or negative) observed during the period of time t. r and time must be in the same units, which were days in our study. The exponential function was calculated by regression of numbers against time for each period of continuous increase or decrease. Numerous calculations showed that there was very little difference between the value of r as calculated from the running average or from the sample values, estimates being generally somewhat lower when using the former.

The use of the exponential function calculated by regression of numbers against time permits inference on the date at which density changes reverse direction, i.e. the date of minimum or maximum abundance. When the first change is described by $N_1 e^{r_1 t_1}$ and the second by $N_2 e^{r_2 t_2}$, the intersection, most easily calculated from the logarithms of the numbers, is given by $\ln N_1 + r_1 t_1 = \ln N_2 + r_2 \Delta t$, from which $\ln(N_1/N_2) = r_2 \Delta t - r_1 t_1 = r_2 \Delta t - r_1(t_2 + \Delta t)$ and:

$$\Delta t = \frac{\ln(N_1/N_2) + r_1 t_2}{r_2 - r_1}$$

in which t_1 is the time between N_1 and the intersection, t_2 is the time between N_1 and N_2 and Δt is the time to add to or to substract from t_2 in order to find the time at intersection.

It was thought unnecessary to reproduce the extensive tables used in the calculations. They are available from the author on request.

Results

The Adults

The number of adults (Fig. 1) has one peak every year, with the exception of 1969 when a secondary peak occurred in February. The percentage of adults lies between 10 and 40% throughout the year (Fig. 2) and the majority of them are females at all times (Fig. 1). Numbers vary between a minimum of 20,000 to 40,000 individuals per m^2 and a maximum which differs widely in different years.

By using the exponential function to describe the two density movements each year it is possible to obtain an estimate of the rate of change r and the date of minimum and maximum abundance. Values of these parameters are given in Table 2. As can be seen from this table there is good agreement between the dates of minimum abundance in the different years; the number of adults starts to rise in the beginning of April (earliest date: 5 April 1971, latest date: 15 April 1972). The time at which maximum abundance is attained differs much more widely, being at the end of July in 1970 and at the beginning of August in 1971, but much later, at the end of October, in 1972. In 1969, the peak falls in the missing period. Interpolation between the rising curve from April 1969 onwards and the falling curve from December 1969 onwards gives 7 September 1969 as the date of maximum abundance with an improbably high figure of 744,000 individuals per m^2 as maximum density. It seems more likely that in autumn 1969, as in the spring of the same year, there occurred a second peak in the number of adults.

In Table 2 the rate of increase is compared with the duration of the increase and the mean temperature of the water during the increase. There is a perfect correlation ($r=1$) between the rate of increase and the mean temperature during the increase. The relationship is given by $r=-0.114+0.0080\ T$ or $r=-0.097+0.0064\ T_s$, in which T is the mean temperature as measured by the recorder and T_s is the mean temperature measured fortnightly with a thermometer. $r=0$ for $T=14.2$ °C and $T_s=15.2$ °C. Mean temperature must be higher than these values to permit development. The correlation between duration of increase and temperature is not significant; neither appears there to be a significant correlation between the duration and the rate of increase ($r=-0.786$), but the by far longest duration in 1972 corresponds to the by far smallest rate of increase, whereas the difference in the other two years appears to be insignificant.

The value of r during the exponential decrease of density from the peak to the minimum abundance in April is a measure of adult mortality $r=-d$. These values are given in Table 3, from which it is clear that they are very similar in different years.

I also made a comparison between the sexes which showed little difference. The mean values of four years are given in Table 4. The sex-ratio, defined here

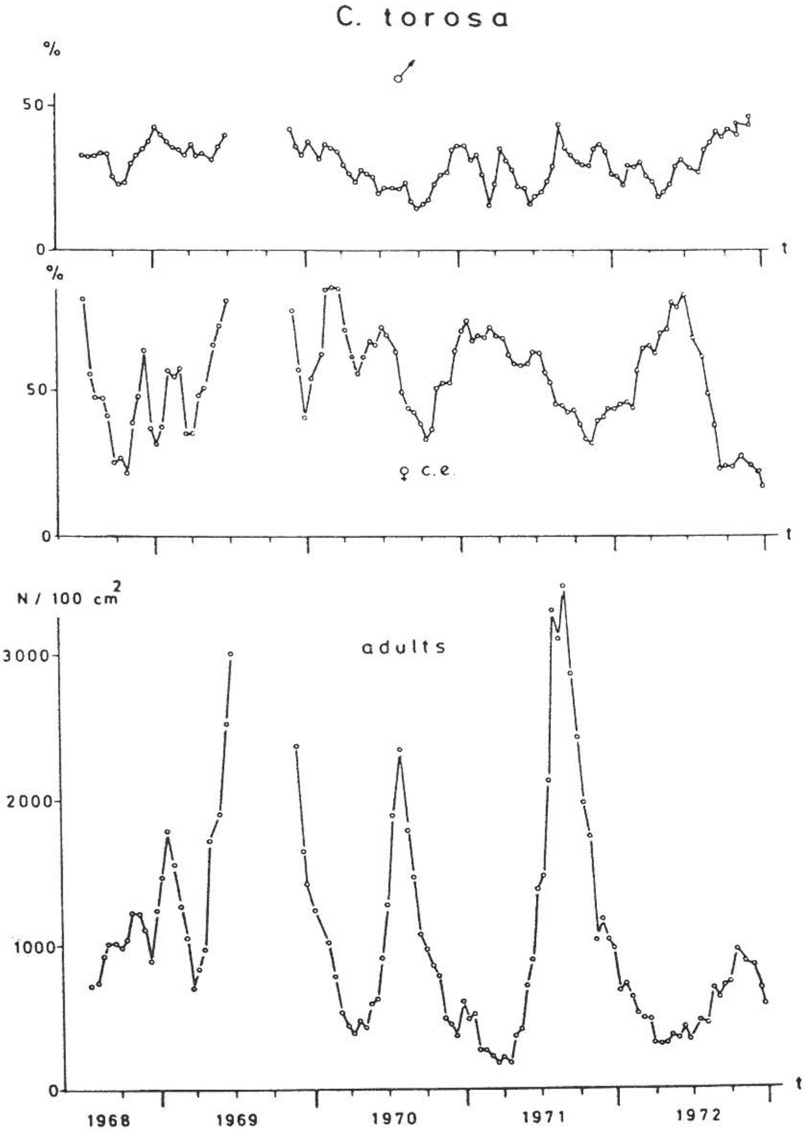

Fig. 1. *Cyprideis torosa*: numbers per 100 cm², percentage of females carrying eggs on the total number of females and percentage of males on the total number of adults

as the percentage of males in the adult population, yields information on periods when moulting from stage VIII to adults occurs (Fig. 1). Migration and patchiness are disregarded in this case. Heip (1976) has shown that there is a significant correlation between the numbers of males and females in samples from different locations, hereby ruling out spatial differences as a consistent source of sex-ratio changes. Differential migration is very improbable since there are no signs that migration occurs in this species at all.

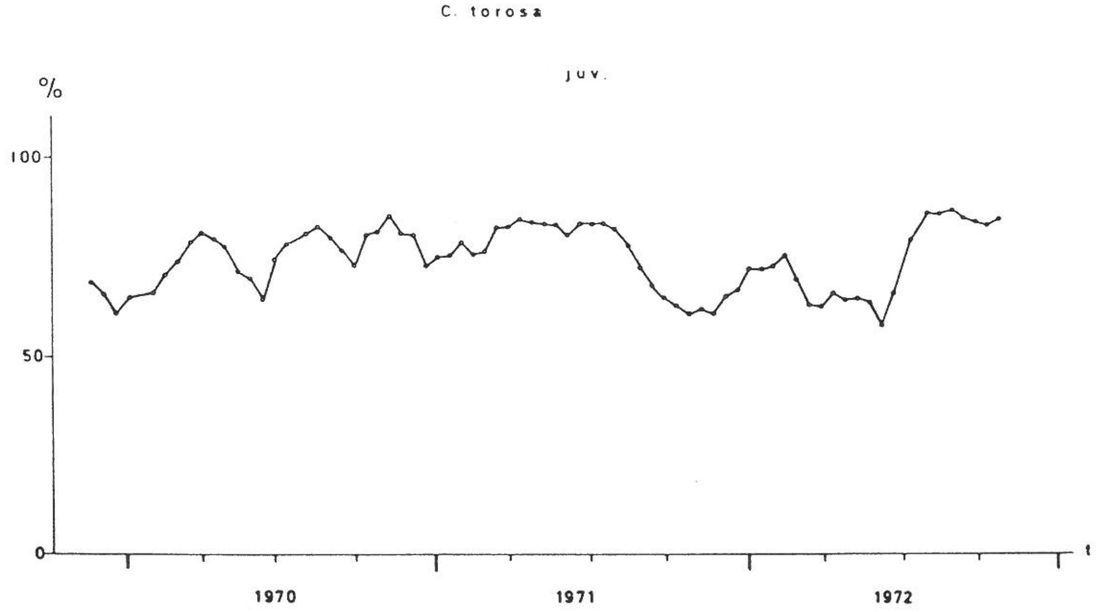

Fig. 2. *Cyprideis torosa*: percentage of juveniles in the population

Table 2. Characterisation of the period during which the number of adult *C. torosa* increased (T=temperature recorded continuously; T_s=temperature recorded for nightly while sampling)

Year	Minimum (date of)	Maximum (date of)	Duration (days)	r (per day)	T	T_s
1969	9 Apr	–	–	.0153	–	16.5
1970	13 Apr	27 Jul	105	.0161	16.2	17.7
1971	5 Apr	7 Aug	124	.0243	17.2	19.0
1972	15 Apr	24 Oct	192	.0058	14.9	16.1

Table 3. *C. torosa*: Rates of change in adult numbers during the annual period of decrease.

Period	$-r$ (per day)
1969–1970	.0138
1970–1971	.0095
1971–1972	.0099
1972–1973	.0098

Table 4. Life-cycle characteristics of females and males of *C. torosa*. Mean values of 4 years

	Rate of increase r (per day)	Rate of decrease $-r$ (per day)	Duration of increase (days)
♀♀	.0158	.0105	135
♂♂	.0163	.0105	142

The percentage of males is clearly at a minimum on 20 Sep 68, 30 Sep 70, 17 Mar 71, 23 Jun 71, 2 Feb 72, 26 Apr 72, and 3 Aug 72. Less clear are minima on 12 Jun 69, 5 May 70, 1 Jul 70, 10 Nov 71, and 28 Sep 72. Although it is not always clear if these minima are real, the general pattern is fairly consistent over the years, changes in sex-ratio occurring three times a year. The first change occurs in Spring during the period of minimum abundance, the second change around July (somewhat later in 1972) during the increase when there are large numbers in the population, the third change in Autumn or in early Winter when numbers are decreasing.

Other information about periods of reproduction is given by the percentage of females carrying eggs (Fig. 1) in the female population. This percentage follows a clearly defined cycle, except for 1968–1969. The percentage of females carrying eggs is at a minimum in Autumn, the lowest point being on 18 Nov 68, 31 Dec 69, 14 Oct 70, 10 Nov 71, and 13 Sep 72 (in 1972–1973 the percentage starts to rise later than 7 Dec 72). There are much less well defined minima in February and April–May in most years. These minimum percentages are probably the consequence of egg-laying in late Winter, and of moulting in Spring. It is not always easy to distinguish between the possible causes of a decrease in the percentage of females carrying eggs. This may result from either the laying of eggs or from intense moulting resulting in many new adult females not carrying eggs at first. However, the relative increase of females carrying eggs after the deep Autumn minimum is certainly a consequence of the laying eggs, because there is no development at that time.

The Larvae

Comparison between the results obtained before and after the 6-month period between August and November 1969 showed that the number of young larval stages I to IV had been seriously underestimated in the first sample. For this reason the analysis of larval numbers will be restricted to the samples from 9 Dec 69 anwards.

In Figure 3 the density of the eight larval stages is shown. As mentioned before, the difficulty of separating the three youngest stages obliged us to count them as one group. The four younger stages show one peak each year. Stage V is somewhat intermediate, showing one peak in 1971 but probably two in 1970 and 1972. The three older stages have more than one peak every year.

By using the same procedure for the larval stages as for the adults, i.e. calculation of the exponential regression of numbers against time, and calculation of the intersections between the regression curves, it is possible to obtain estimates of the dates of minimum and maximum abundance, the rates of increase and the duration of changes in population density.

The dates of minimum abundance of the larval stages are given in Table 5. The first young larvae appear at the end of March with remarkable constancy every year. Stage IV increases from mid-May onwards, stage V from the beginning of June, stage VI from mid-June, stage VII from near the end of June, and stage VIII from the beginning of July onwards.

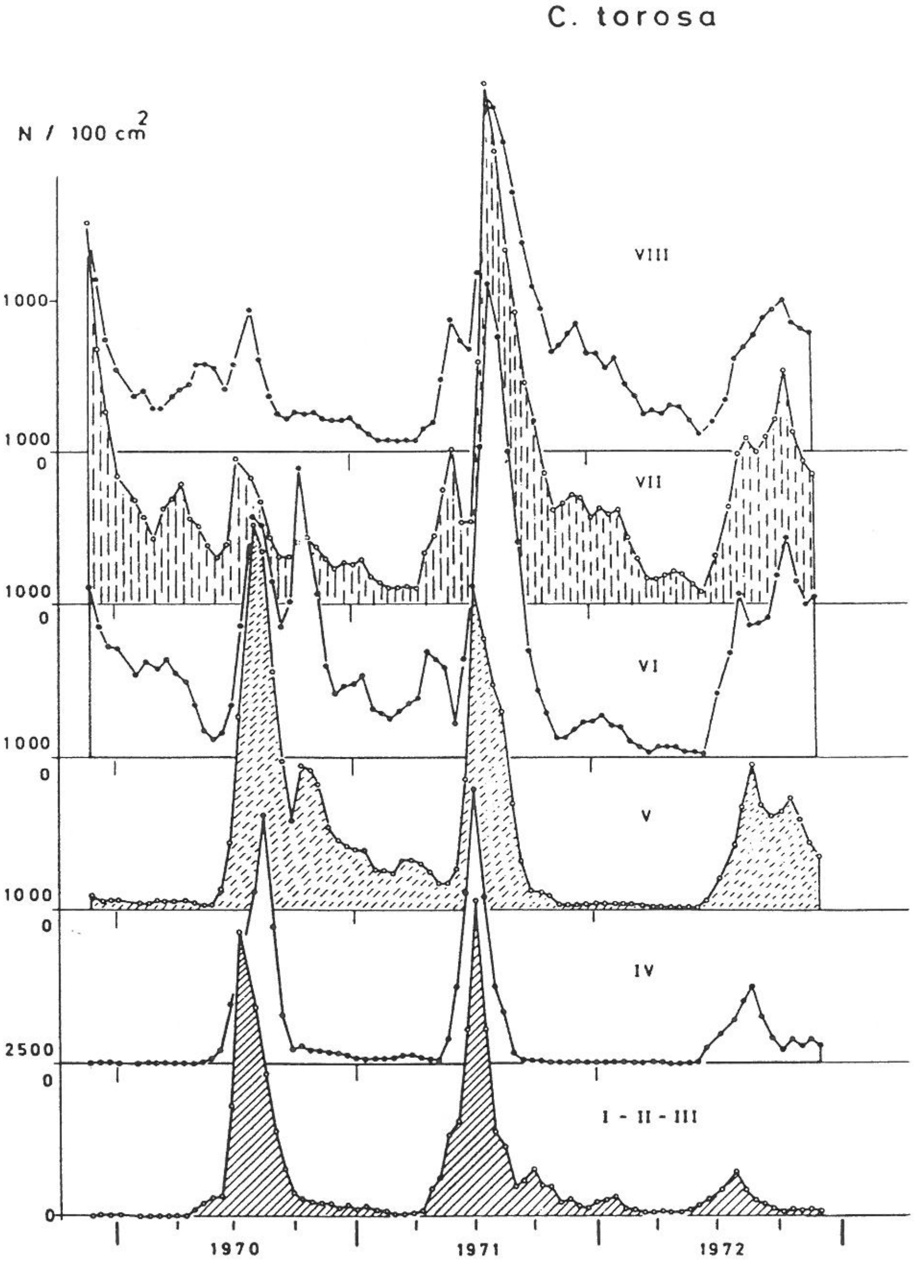

Fig. 3. *Cyprideis torosa*: numbers per 100 cm^2 of the eight larval stages, from 1969 to 1972

Table 5. Dates of minimum abundance of larval and adult stages of *C. torosa*

	1970			1971			1972		
I-II-III		29 Mar			24 Mar			31 Mar	
IV		16 May			8 May			8 May	
V		1 Jun			27 May			6 Jun	
VI		4 Jun	19 Sep	28 Feb	10 Jun	16 Nov		13 Jun	3 Sep
VII	7 Mar	19 Jun	20 Sep	7 Apr	30 Jun	14 Nov	8 Apr	17 Jun	15 Sep
VIII	14 Mar	2 Jul	27 Sep	11 Apr	7 Jul	17 Nov	13 Apr	15 Jun	
Ad.	13 Apr			5 Apr			15 Apr		

Table 6. Dates of maximum abundance of larval stages and adults of *C. torosa*

	1970			1971			1972		
I-II-III		20 Jul			4 Jul			28 Jul	
IV		16 Aug			7 Jul			13 Aug	
V		2 Aug	10 Oct		11 Jul			26 Aug	13 Oct
VI		5 Aug	9 Oct	4 May	7 Aug		9 Jan	12 Aug	26 Oct
VII	19 Apr	19 Jul	25 Oct	7 Jun	4 Aug	4 Dec	12 May	23 Aug	25 Oct
VIII	31 May	3 Aug	31 Oct	11 Jun	6 Aug	19 Dec	23 May	9 Oct	
Ad.		27 Jul			7 Aug			24 Oct	

Table 7. Duration of larval development of *C. torosa* and mean temperature during that period

	Duration of development (days)	Mean temperature (°C)
1970	129	15.1
1971	133	15.5
1972	152	15.4

The peak for all stages is attained in July or August, except for the larger ones in 1972 when this occurs much later (Table 6). These larger stages show more than one cycle each year. A second period of increase starts in September (1970, 1972) or November (1971) and gives rise to peaks in October and December which are much smaller than the main one in summer. The third period of increase is in March-April, preceding the increase of the adults in April.

In Table 7 the duration of total development as measured from the dates at which the numbers begin to increase, and the mean temperature during this period, is given. There is a rather large difference in duration of development between 1970 and 1971 on the one hand and 1972 on the other hand although the mean temperature during development is rather similar.

The information from Tables 5 and 6 has been summarized in Figure 4 in which the length of the lines corresponds to the duration of increase.

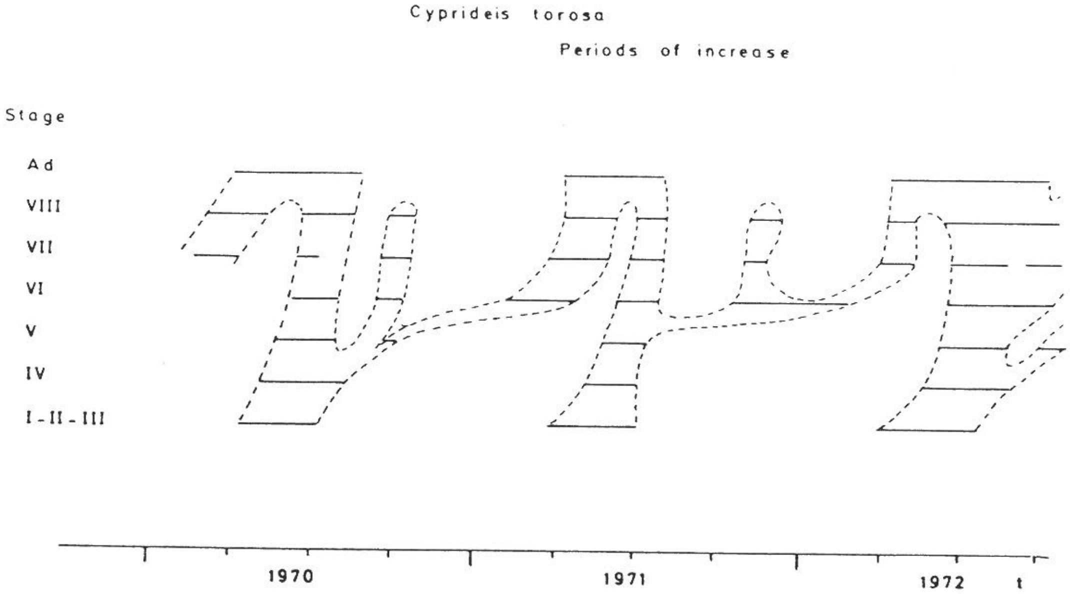

Fig. 4. *Cyprideis torosa*: periods during which the number of the different stages increases

Discussion

Description of the Life-Cycle and Its Causes

From the information summarized in Figures 1 and 4 and Tables 5 and 6 it is possible to describe the life cycle of *Cyprideis torosa*. There is an overwintering population of large larvae and adults belonging to the same generation. These large larvae start moulting from March onwards, giving rise to adults from April onwards. The percentage of males rises and the percentage of females carrying eggs drops. Both overwintering and new adults produce new larvae from the end of March onwards. This new generation reaches a peak in summer (much later in 1972) which, because of the overlap between larvae produced by the overwintering stock and those produced by the spring generation, consists of different larval stages. Some of the earlier larvae reach adulthood during autumn, when a rise in the percentage of males and the percentage of females carrying eggs occurs. Larvae born later do not succeed in attaining adulthood before winter and spend the winter as larger larval stages, moulting to adults in the next spring. There is thus one generation each year but it is split into two because there is no development during winter.

One of the interesting conclusions of this study is that there occurs only one generation per year in this species. This is unexpected for such a small animal (individuals are about 1 mm long when adult), but it appears that a low number of generations is a general characteristic of meiobenthic populations (Gerlach, 1971), although several groups (e.g. the overwhelmingly dominant nematodes)

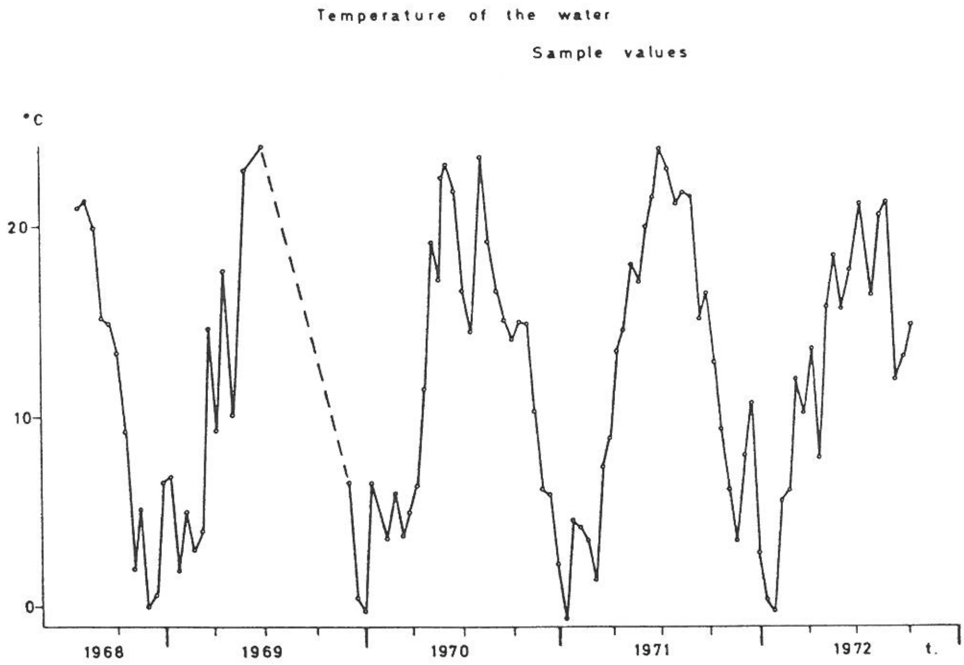

Fig. 5. Temperature of the water when samples were taken

require more study before definite conclusions can be drawn. The phenomenon has been observed in other ostracods studied: Hagerman (1969) described one generation annually for *Hirschmannia viridis* and Elofson (1941) and Theisen (1966) had correctly assumed the existence of one generation annually for *C. torosa*. Theisen (1966) found that one to three generations per year might be the rule for the seven species of ostracods he investigated.

It appears that temperature has the most pronounced influence on the life cycle of this species. Values of temperature as recorded daily were averaged for every fortnight and the regression of temperature against time was calculated using a Fourier analysis. This regression is expressed by $T = 11.2 + 8.3 \sin(t - 117)$ in which T is temperature and t is time, with $t_0 = 31$ December (Heip and Smol, 1976). It allows predicting the mean temperature preceding the sample date or preceding the dates of minimum and maximum abundance as calculated from the exponential regressions.

The daily recordings permitted calculation of the mean temperature of the five days preceding the date of minimum abundance. The means over three years of these 5-day averages are given in Table 8. This mean temperature is lowest for the moulting from larvae VI to larvae VII, which is in agreement with the observation that most larvae belong to stage VII in winter. Stage VI predominated only in winter 1970–1971 and this was also the winter when stage V was numerous. As temperature was much lower in late summer 1970 than in late summer 1971, the reason for this predomination of younger larvae in

Table 8. Mean temperature during 5 days preceding the date when moulting starts in *C. torosa*

From	To	Temperature (°C)
Egg	I-II-III	7.3
I-II-III	IV	15.6
IV	V	16.3
V	VI	10.2
VI	VII	8.4
VII	VIII	8.8
VIII	adult	9.3

1970–1971 is obviously the fact that these larvae did not have enough time to moult, because temperature dropped below some critical value too early.

From Table 8 it might appear that the youngest larvae need a much lower water temperature to develop than larvae IV and V. This is not necessarily so because many of these larvae have developed before winter but are held between the valves of the female; the temperature of 7.3° C in Table 8 is the temperature at which they are released in the environment.

The regression between the rate of change *r* of the number of adults and the mean temperature during development showed that temperature must be above about 15° C before the number of adults increases. The moulting from stage IV to stage V might be the developmental step requiring the highest temperature (Table 8) and therefore determining the minimum temperature needed for complete development.

The existence of a prominent peak in the number of animals seems to indicate predation as a regulating factor. Maximum abundances, with an overall maximum of 1.8 million individuals per m^2 on 4 Aug 71, of which 328,000 were adults, are the highest recorded so far. The total biomass of *Cyprideis torosa* at this data is extraordinary and amounts to 48.9 g dry weight per m^2 (in preparation). After the summer peak the number of adults declines very constantly during eight months, and this remarkably constant mortality is one of the arguments against predation regulating the peak. The other argument is that we have not been able to find numerical or qualitative changes in the community indicating a species or a combination of species responsible for such predation.

Specific predators for ostracods are not known. The only meiobenthic animal whose importance as a predator of meiobenthos has been stressed (Muus, 1967; Heip, 1971) is the polyp *Protohydra leuckarti*. This species is present but I found ostracods in the atrium only once during 4 years of investigation. The polychaetes *Polydora ciliata*, *Nereis diversicolor* and *Streblospio shrubsoli* are potential predators but their densities do not fluctuate widely during the year; the intensity of predation by these organisms might be rather constant. *Pomatoschistus microps* is another potential predator, but its maximum abundance was attained in the same year (1971) as that of the ostracods; moreover, we did not find ostracods during an examination of stomach content in seven individuals. Hesthagen (1971), who examined their food in winter, reported also the absence of ostracods.

Cyprideis torosa is a detritus feeder and the amounts of detritus in the habitat are so large that competion, whether intraspecific or interspecific, does not seem responsible for the decline in numbers after the peak. Moreover, the detritus results from the decay of reed of the previous year and the amount available is therefore not a function of water temperatures during the increase of *C. torosa* in the following year; yet, this increase is directly influenced by water temperature. Bacterial activity is higher at higher temperatures; when we accept that the principal food source in the detritus is bacterial biomass then the higher numbers of ostracods in years with a higher temperature of the water could be explained by the higher production of bacterial biomass.

Another argument against competition as a regulating mechanism is the fact that yearly density fluctuations can be described by only two exponential functions. The sudden change of an exponentially increasing density to an exponentially decreasing density is not consistent with competition, which would lead to a logistic relationship between density and time.

This sudden change from an exponentially increasing to an exponentially decreasing function can be explained by the cessation of one of two exponential processes which were superimposed before. This process appears to be reproduction in the case of *C. torosa*. One generation is raised and the rate at which it develops depends on temperature. The date of maximum abundance is a function of temperature because the rate of increase is a function of temperature. The maximum number, assuming constant mortality, is therefore also a function of temperature besides being a function of the initial number which in turn depends on the maximum number a year before and the period of decrease, both again functions of temperature. There was a considerable difference between the duration of increase in 1970 and 1971 on the one hand and 1972 on the other, but the mean temperature during development was very similar. Although 1972 appears to be the worst year for the species, numbers in October are in fact higher in that year than in others. The net result of reproduction was therefore best in 1972, because more individuals will survive till the next spring. Production on the other hand was lowest in 1972 but this had no direct consequences for the population and is only important on the community level.

The constancy of mean temperature during development might point to the requirement of a constant amount of energy per day development. When development lasts longer, the total amount of energy expended will be larger. As noticed earlier, temperature must be above 15° C before complete development can take place. Taking the mean date of 28 March as the date when development starts (the appearance of young larvae in the environment), the mean temperature of 15° C is attained after 128 days, according to the temperature regression equation. This is nearly exactly the duration of increase as calculated from the dates at which the increase of the different larval stages starts in 1970 and 1971. The temperature regression thus predicts an increase till 3 August on the average.

Cyprideis torosa appears to be another example of a meiobenthic species on top of the food chain. The life-cycle of this species can be more or less predicted from the cycle of temperature in the habitat and a knowledge of mortality.

Although it is not possible to say if it is temperature itself or a factor linked with temperature which is the regulating agent, this is of no importance in describing the influence of temperature on the number of individuals of this species. I would like to speculate somewhat on the nature of these regulating factors. When mortality is constant, as in this species, it is predictable. In stable populations natality and mortality have to balance in the long run. This implies that reproductive patterns are linked with mortality. With a constant amount of energy available there is an inverse relationship between the number of offspring and their individual fitness. In predictable environments selection will act by increasing the fitness of the individual offspring (McArthur and Wilson, 1967) and the total number of offspring will be reduced. This is indeed what can be observed in *C. torosa*. Although seasonal, the environment is relatively predictable. The total number of eggs produced by a female of this species is very low, with a mean of 11. Individual fitness of the offspring is increased by holding the larvae between the values until temperature is high enough for development.

Reducing the number of offspring is a bad strategy when catastrophic and inpredictable mortality is a regular phenomenon. Catastrophic mortality might occur when the bottom freezes, which is tolerated only for a little while (Theisen, 1966). I never observed freezing of the bottom but there seems to be an adaptation against this possibility. Laying of the eggs starts in autumn, several months before temperature is at a minimum. Copulation thus occurs when density is still rather high and this may decrease the risk of not finding a partner. Because the eggs can develop between the valves of a dead female and can stand freezing, this behaviour might be an adaptation to the possibility of freezing.

The absence of catastrophic mortality increases the predictability of the environment and the stability of the link between reproductive processes and environmental parameters. If there is a regulation of this link by selective processes it appears reasonable to postulate mortality as the factor on which the process works: mortality in the past is the touchstone on which fertility in the present is based. When fecundity would have been both too high or too low in the past, the population would have gone extinct. It is easy to see how selection can change parameters of fecundity such as the sex-ratio or the number of offspring per female. The age-structure of the population depends on the reproductive cycle and is therefore directly dependent on the environment. Fecundity could therefore be determined by the history of the population in the particular environment in which it lives. In populations which disperse slowly and where there is little gene flow between populations inhabiting different habitats it is possible that important differences in fecundity could exist.

Because the pond which has been studied here is a relatively stable environment, our conclusions may not hold for some of the habitats where *Cyprideis torosa* is normally found (Gerlach, personal communication). It seems clear that the environment will be less stable when we go farther north or in less sheltered habitats because freezing of the bottom or the destruction of the habitat by storms will be a much more common event there. This might have the consequence that the dynamics of populations living farther north or in less sheltered habitats will not be equilibrated to the extent found in this study. Among other things we may predict a larger number of eggs produced by these less stable populations.

Appendix

A Model for the Reproduction of C. torosa

The change of numbers of a certain stage X during dt may be given by:

$$\frac{dN_x}{dt} = a_{x-1} N_{x-1} - a_x N_x - m_x N_x \tag{1}$$

in which a_{x-1} is the fraction of the previous stage $X-1$ moulting to X during dt, a_x is the fraction of stage X moulting to $X+1$ and m_x is the mortality of stage X during dt.

$$\int_{N_0}^{N_t} \frac{dN_x}{N_x} = \int_{t_0}^{t} \left(a_{x-1} \frac{N_{x-1}}{N_x} - a_x - m_x\right) dt \tag{2}$$

The best estimate of $\int_{t_0}^{t} \frac{N_{x-1}}{N_x} dt$ is obtained by $\frac{\overline{N_{x-1}}}{N_x}(t-t_0)$, in which the ratio of the sum of the numbers of both stages during $t-t_0$ is taken. The solution of (2) is then:

$$N_{x(t)} = N_{x(0)} \exp\left(a_{x-1} \frac{\overline{N_{x-1}}}{N_x} - a_x - m_x\right)(t-t_0)$$

Mortality m_x can be calculated from periods when there is no moulting. To test the model a constant mortality $m=0.012$ per day was accepted for all stages. The value for a_x is calculated beginning with the adults, for which $a_{ad}=0$, of course. Because the rate of increase is known, we may write:

$$r_x = a_{x-1} \frac{\overline{N_{x-1}}}{N_x} - a_x - m_x$$

$$a_{x-1} = (r_x + m_x + a_x) \frac{\overline{N_x}}{N_{x-1}}$$

And for the adults:

$$a_{\mathrm{VIII}} = (r_{ad} + m_{ad}) \frac{\overline{N_{ad}}}{N_{\mathrm{VIII}}}$$

The period during which r_x is calculated is the same for all larval stages and corresponds with the period of increase of the adults.

In Table 9 the values of r_x, m_x, $\sum N_x$ and a_x as calculated in the way described are shown for the three years. Because a_x is the fraction of stage X moulting per unit time, $1/a_x$ is the time required for all individuals to moult. $\sum_{\mathrm{I}}^{ad} 1/a_x$ is therefore the development time of the species. In Table 10 these development times are given for the 3 years. The difference between the years is extremely small, being less than one day in 1970 and 1971 and showing a larger value, as was expected, in 1972. This is a success in view of the simplicity of the model. This model is robust against changes in mortality. When taking the values obtained from periods without reproduction ($m_{\mathrm{I-II-III}}=0.011$; $m_{\mathrm{IV}}=0.010$; $m_{\mathrm{V}}=0.011$; $m_{\mathrm{VI}}=0.014$; $m_{\mathrm{VII}}=0.016$; $m_{\mathrm{VIII}}=0.017$ and $m_{ad}=0.010$), I found for the whole duration of development 59.8 days in 1970, 58.6 days in 1971, and 70.2 days in 1972. The difference between these figures and those of Table 10 is less than 2 days.

The duration of development as calculated with the model is in good agreement with observed values. Theisen (1966) found a development time of 63 days at a somewhat higher temperature of 18–24° C, which agrees very well with our calculated value of 63.1 days for the 3 years averaged. On the other hand, the development of a generation takes about 130 days in 1970 and 1971 and about 150 days in 1972. It thus appears again that development is considerably slower at temperatures below 15° C. This is also obvious from Figure 4 when we compare the times at which the increase starts between subsequent stages. The interval between these times becomes shorter when the stages are older, this is later in the season, when temperatures are higher.

Table 9. Observed rate of increase (r_x), mortality (m_x), sum of numbers (N_x) and calculated rate of moulting (a_x) during the period in which the number of adult *C. torosa* increased.

	r_x	m_x	N_x	a_x
	1970 (5 May–5 Aug)			
Adults	.019	.012	8,066	0
VIII	.005	.012	3,996	.062
VII	.006	.012	3,936	.081
VI	.021	.012	3,587	.108
V	.055	.012	4,450	.114
IV	.069	.012	2,198	.366
I-II-III	.043	.012	10,936	.085
	1971 (15 Apr–4 Aug)			
Adults	.024	.012	10,856	0
VIII	.028	.012	6,654	.059
VII	.023	.012	8,719	.075
VI	.015	.012	9,412	.102
V	.023	.012	7,390	.165
IV	.038	.012	5,361	.275
I-II-III	.026	.012	16,760	.104
	1972 (21 Jun–16 Aug)			
Adults	.011	.012	1953	0
VIII	.029	.012	1260	.036
VII	.044	.012	2019	.048
VI	.061	.012	2188	.096
V	.044	.012	1335	.277
IV	.023	.012	1001	.444
I-II-III	.012	.012	1858	.263

Table 10. Duration of development of *C. torosa* as calculated from $1/a_x$

	1970	1971	1972	Mean
I-II-III	11.8	9.6	3.8	8.4
IV	2.7	3.6	2.3	2.9
V	8.8	6.1	3.6	6.2
VI	9.3	9.8	10.4	9.8
VII	12.4	13.3	20.8	15.5
VIII	16.1	17.0	27.8	20.3
Total	61.1	59.4	68.7	63.1

Acknowledgements. I wish to thank W. Hautekiet and W. Decraemer for important technical assistance. Dr. R. Karlson of Duke Marine Laboratory at Beaufort, North Carolina, wrote the program enabling the calculation of the temperature regression.

References

Barnett, P. R. O.: Distribution and ecology of harpacticoid copepods of an intertidal mudflat. Int. Rev. ges. Hydrobiol. Hydrogr. **53**, 177–209 (1968)

Elofson, O.: Zur Kenntnis der marinen Ostracoden Schwedens mit besonderer Berücksichtigung des Skagerraks. Zool. Bidrag. Uppsala **19**, 215–534 (1941)

Gerlach, S. A.: On the importance of marine meiofauna for benthos communities. Oecologia (Berl.) **6**, 176–190 (1971)

Hagerman, L.: The macro- and microfauna associated with *Fucus serratus* L. with some ecological remarks. Ophelia 3, 1–43 (1966)

Hagerman, L.: The ostracod fauna of *Corallina officinalis* L. in western Norway. Sarsia **36**, 49–54 (1968)

Hagerman, L.: Environmental factors affecting *Hirschmannia viridis* (O. F. Müller) (Ostracoda) in shallow brackish water. Ophelia **7**, 79–99 (1969)

Heip, C.: The succession of benthic micrometazoans in a brackish water habitat. Biol. Jaarb. **39**, 191–196 (1971)

Heip, C.: Een populatie-dynamische studie over de benthale Ostracoda en Copepoda van een brakwaterhabitat [in Dutch]. Ph. D. Thesis, State University of Ghent, 429 pp. (1973)

Heip, C.: The spatial pattern of *Cyprideis torosa* (Jones, 1850) (Crustacea, Ostracoda). J. mar. biol. Ass. U.K. **56**, 179–189 (1976)

Heip, C., Smol, N.: The influence of temperature on the reproductive potential of some brackish water Harpacticoida (Crustacea, Copepoda). Mar. Biol. **35**, 327–334 (1976)

Hesthagen, I. H.: The winter food of the gobies from one of the deeper channels of the Belt Sea, with particular reference to the Sand Goby (*Pomatoschistus minutus* (Pallas)). Kiel. Meeresforsch. **27**, 28–35 (1971)

McArthur, R. H., Wilson, E. O.: The theory of island biogeography, 203 pp. Princeton, N.J.: Princeton University Press 1967

Muus, B. J.: The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. Medd. Danm. Fisk. og Havunders. **5**, 1–316 (1967)

Redeke, H. C.: Ostracoda. In: Flora en fauna der Zuiderzee, Supplement (1936)

Remane, A.: Einführung in die zoologische Ökologie der Nord- und Ostsee. Tierwelt der Nord- und Ostsee **1a**, 238 p. (1941)

Theisen, B. F.: The life history of seven species of stracods from a Danish brackish water locality. Medd. Danm. Fisk. og Havunders. **4**, 215–270 (1966)

Vesper, B.: Zur Morphologie und Ökologie von *Cyprideis torosa* (Jones, 1850) (Crustacea, Ostracoda, Cytheridae) unter besonderer Berücksichtigung seiner Biometrie. Mitt. Hamburg Zool. Mus. Inst. **68**, 21–77 (1972)

Watt, K. E. F.: Dynamics of populations: a synthesis. Proc. Adv. Study Inst. No. Pop. (Oosterbeek, 1970), pp. 568–580 (1970)

Received March 28, 1976