The Influence of Competition and Predation on Production of Meiobenthic Copepods

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ABSTRACT: An assemblage of meiobenthic copepods was monitored twice monthly between 1968 and 1976 in a shallow brackish water habitat. Four species dominated and accounted for nearly all the production. All species have only one or two generations per year and each peak has similar dynamic characteristics. Production is determined primarily by the number of generations, and it is suggested that competition and predation determine the life-history characteristics.

INTRODUCTION

Increasing species diversity over time is a common property of communities where disturbances do not occur frequently enough to cause important spatial or temporal heterogeneity. Theoretical ecologists consider competition and predation to have the most profound effect on the community diversity in temperate latitudes (McArthur, 1972), but there is still much discussion on the relative importance of each in the process. For example, Menge and Sutherland (1976) suggest that competition is more important in higher trophic levels, while predation regulates the number of species at lower trophic levels.

There has also been much discussion on the role of energy and matter flow through ecosystems as a structuring force. Recent developments in thermodynamic theory of open systems has provided firm theoretical basis for these ideas, i.e., when systems are brought far from equilibrium, they can only be maintained by a flow of energy and matter which is itself a source of order. This new order has a stability regime characterized by periodicities and cycles and the cycle is therefore the fundamental unit in systems organization (Nicolis and Prigogine, 1977).

Although a possible link between trophic structure and species interactions has been implicit in much theoretical work, the different approaches converge only slowly, and in an important recent book the approach to community ecology has remained largely empirical (May, 1976).

Much effort in aquatic biology has been devoted to measurement of production of populations and communities, rather than to species interactions. The parameter of interest is usually biomass of the population rather than its density, and interactions are ignored or expressed as a mortality term without further explanation. Although there is, of course, a relationship between biomass and density, they are not equivalent in age-structured populations in which the age structure is not stable.

The purpose of this paper is to illustrate how life-history characteristics can be explained by competitive or predator-prey interactions and how these characteristics influence production of populations. It is a purely empirical study and I will nowhere try to prove causal relationships or to model them. The interest of this study is the fact that the populations have been studied over so many years that some patterns are discerned which can be explained in some ways. I acknowledge that some of the evidence presented is rather speculative. This will partly be remedied in forthcoming papers in which many points made here will be elaborated in more detail.

MATERIALS AND METHODS

The animals from this study are meiobenthic copepods from a brackish water pond in northern Belgium (Heip, 1976). Their density was estimated from fortnightly samples taken from 12 August 1968 to 29 December 1976 with a core covering a surface area of 6 cm^2. According to season one (in winter) or two (in summer) samples were counted. The data were smoothed using the running median of three successive estimates and the trendline was calculated using a weighted running mean of three samples (Velleman, 1977). In so doing, variance introduced by spatial patchiness is considered as noise which is filtered by the low-pass filter applied here. However, as the procedure is unusual in ecology, all calculations were performed on the raw data as well, but there was never a large difference (i.e., more than 10-20%) between them. Rates of increase ($r = 1/t \ln N_t/N_o$) will be consistently too low when calculated from trendlines, but the bias is small: the average overall peak for *Tachidius discipes* was r = 0.042 per day for the raw data as well as for trendline data with and without smoothing; for *Parony-*

chocamptus nanus, with less well-defined peaks, the values are r = 0.042 (raw data), r = 0.038 (trendline values without smoothing) and r = 0.036 (trendline values with smoothing).

As this paper is based on yearly averages, rates and calendar data, which are not influenced by the procedure, the additional precision in the single estimates obtained by counting two or more samples each time was judged to be insufficient to justify the large amount of work needed to sort out and count additional samples. However, estimation of the confidence limits of single estimates is possible. In all the populations that were studied (including ostracods and copepods), the coefficient of variation $s/\bar{x}$ becomes constant and equal to 0.27 when $\bar{x}$ gets large. The relationship between $s/\bar{x}$ and $\bar{x}$ is given by (Heip, 1975b):

$$s/\bar{x} = \frac{3.27 + 0.27\,\bar{x}}{1 + \bar{x}}$$

From this *a priori* knowledge of the standard deviation confidence limits can be easily calculated. When density is extremely low ($\bar{x} \leq 10$), the 95% confidence limits are of the same magnitude as the mean (e.g., 10 ± 10.6 for one sample, 10 ± 7.5 for two samples and 10 ± 6.1 for three samples); for higher densities confidence limits are a fraction of the mean, even for only one sample (e.g., 100 ± 58.7 for one sample, 100 ± 41.5 for two samples and 100 ± 33.9 for three samples). Doubling the effort (counting two samples instead of one) increases precision by 29%; increasing the effort with 50% (counting three samples instead of two) increases precision by only 18%.

Biomass of individual species was determined by weighing a sample of adults with a Mettler ME22 microbalance. Copepodites were assumed to have an eighth of this weight, as there are five copepodite stages each approximately doubling in weight as they moult (Vinc and Heip, in press). All weights are dry weights, i.e., after drying for two hours in an oven at 110°C. Nauplii were neglected as their density was difficult, and their weight impossible, to estimate accurately. Also, they could not be attributed to certain species without great effort. Their production is nearly negligible anyway, because their biomass is, on average, two orders of magnitude lower than that of adults, and they are short-lived; also, much of their production adds up in the production of copepodites and adults.

Production estimates were obtained from P/B-ratios using Banse and Mosher's equation for macrobenthic animals (communicated at the Sixth International Helgoland Symposium, 1976): $\log P/B = -0.16 - 0.35 \log B$ (in which P and B are in kcal). They remarked that copepods fall below this line; when accepting this and taking the slope calculated by Banse and Mosher and the estimate P/B = 3 calculated for *Canuella perplexa* (Heip, Thielemans and Huysseune, in prep.), I obtained the following equation: $\log P/\bar{B} = -1.13 - 0.35 \log (6B.10^{-6})$ or $\log P/\bar{B} = 0.70 - 0.35 \log B$, in which B is in μg.

RESULTS

Four species account for 90-100% of the total copepod density and biomass and their densities (smoothed) are illustrated in Fig. 1. Biomass is very similar but has been omitted. Two species (*Paronychocamptus nanus* and *Canuella perplexa*) are mainly detritivores as adults while the two others (*Tachidius discipes* and *Halicyclops magniceps*) are primarily herbivores. The first species group (*P. nanus; C. perplexa*) shows rather complicated cycles with several peaks during the year, while the second group (*T. discipes; H. magniceps*) shows simple cycles with but one peak in most years. Other species may be rare but regular (*Nitocra typica* and *Mesochra lilljeborgi*) or irregular (*Amphiascoides debilis* and *Schizopera compacta*). These cyclicities were recently discussed (Heip, 1979).

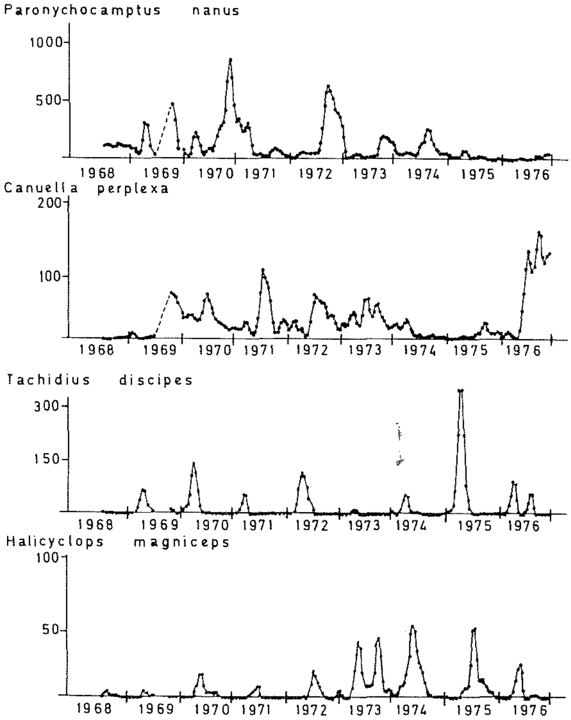

Figure 1. Density of four species of copepods (No./10 cm^2).

The dynamics of all species are characterized by peaks in which at a certain moment density starts to increase exponentially and then decreases, again exponentially. When these characteristics are used for the description of the peaks, three important conclusions emerge (Heip, 1978 and in prep.) (for 1968-74):

1) the start of the increase is very similar from year to year for each species (with some interesting exceptions) but differs

widely among species belonging to the same trophic category.

2) the average realized rate of increase does not differ greatly among species; it is between 0.040-0.052 per day as calculated from the raw data, which corresponds to doubling times of 13-17 days. Only the large *Canuella perplexa* has a smaller rate ($r = 0.021$) per day.

3) the average duration of the increase is similar for the different species and varies between 51 days (*Canuella perplexa*) and 77 days (*Amphiascoides debilis*).

As both the rate and the duration of the increase are of the same magnitude in all species, it follows that abundance differences are caused by either different mortality or number of peaks (i.e., probably the number of generations). Both explanations seem true. Mortality in all species is much higher in summer than in winter (when it could be compared). However, within a season it is of the same magnitude in the different species. This indicates that it is the number of generations per year which determines the relative abundance of these species.

The potential number of generations per year is large since generation time is of the order of several weeks for the species which have been investigated (Heip and Smol, 1976a). However, the actual number of generations appears to be much smaller as evidenced by the percentage of females carrying eggs (Fig. 2). For both *Paronychocamptus nanus* and *Canuella perplexa* this is a bimodal curve in most years. For *Tachidius discipes* and *Halicyclops magniceps* it is unimodal, with a tendency to become bimodal in later years for *H. magniceps*. This would indicate only one or two generations annually. Another clue can be found in the percentage of males. Since mortality is larger in males than in females (Heip, 1978 and in preparation) overwintering populations of *Paronychocamptus nanus* consist mainly of females when they start reproduction in spring. The bimodal curve of the percentage of females carrying eggs is followed (with a lag) by an equivalent bimodal curve in percentage of males. This lag has been calculated by cross-correlation between the two series which is at a maximum for lags of six weeks and 26 weeks, corresponding to two generations. Thus the number of generations is much less than expected from laboratory cultures.

There is a remarkable constancy in the date at which species start to increase in density: species start to increase in the same month or even week year after year, a phenomenon which has also been detected in the meiobenthic ostracod *Cyprideis torosa* (Heip, 1976). Total numbers start to increase earliest in *Tachidius discipes* (beginning of February); followed by *Paronychocamptus nanus* (end of March onwards), *Halicyclops magniceps* (beginning of May onwards) and *Canuella perplexa* (mid-June onwards). In *Tachidius discipes* and *Halicyclops magniceps* the increase is from zero in most years, whereas in the other species it is from a minimum value. However, in the case of both *T. discipes* and *H. magniceps* this increase in total numbers is followed, but not preceded by, an increase in the percentage of females carrying eggs. In *P. nanus* and *C. perplexa* it is followed and preceded by such an increase. Indeed, the percentage of females carrying eggs starts to increase in mid-February in *P. nanus*, in the beginning of March in *T. discipes*, mid-April in *C. perplexa* and the beginning of July in *H. magniceps*. There is a second increase for *P. nanus* and *C. perplexa* in August.

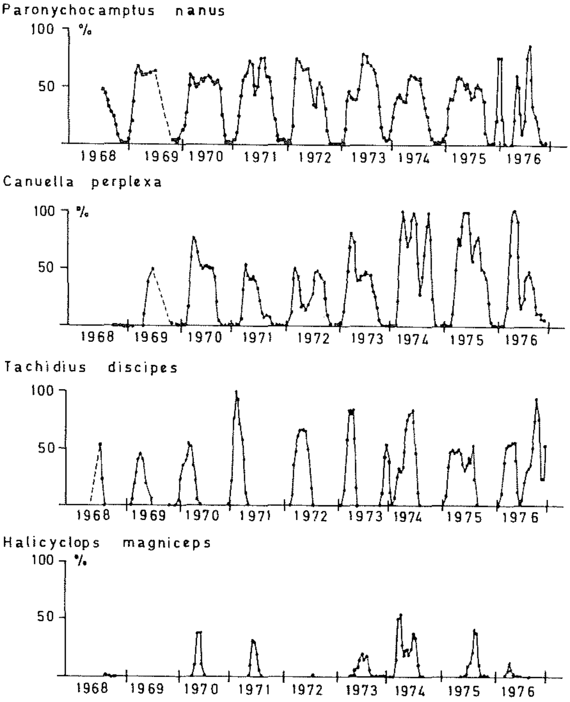

Figure 2. Percentage of females carrying eggs of four species of copepods (of total females).

Although the details differ somewhat from year to year and will be explored fully in forthcoming papers, the scheme is remarkably constant throughout the years. The increase in density of *P. nanus* and *C. perplexa* follows an increase of egg-carrying females six to eight weeks prior and can be explained as the result of this reproductive activity. The increase of *T. discipes* and *H. magniceps* is more difficult to explain. In the case of *H. magniceps* it may be due to reproduction in the previous year, with hibernation of the adults in the burrows of the polychaete *Nereis diversicolor* deep in the sediment (Heip, 1975a). This wintering generation produces new adults about 1½-2 months after it emerges in spring, exactly what happens in both other species, wintering as free-living adult females.

Tachidius discipes is an enigma. Either it winters in extremely low densities (and sometimes single adults were found in winter); or, it produces a wintering stage that is not easily detected, such as resting eggs or small nauplii with delayed development (Coull and Dudley, 1976). Such life-stages were not found, but, if they occur, the strategy of *T. discipes* would then be quite similar to that of *H. magniceps*, i.e., the production of life stages wintering in protected circumstances. This problem requires further investigation.

In most years *Halicyclops magniceps* disappears from the habitat in October, when the environmental conditions become adverse, but this is not true for *Tachidius discipes*. *T. discipes* disappears in June or July, when temperature is still high and when it can reproduce at a high rate (Heip and Smol, 1976a), in fact at a higher rate than either *Paronychocamptus nanus* and *Canuella perplexa* which at that time produce their summer generation. The disappearance of *Tachidius discipes* in early summer cannot be explained by abiotic conditions but can be correlated with predation from the polyp *Protohydra leuckarti* (Heip and Smol, 1976b). Further analysis of this predator-prey relationship (Herman and Heip, in prep.) showed that, contrary to expectation, predation is not a regulatory mechanism, even though the numbers of *Tachidius discipes* and *Protohydra leuckarti* are dependent upon each other.

The polyp appears later in the habitat than its prey, since it does not reproduce below 10°C. Apparently *T. discipes* density has to be high enough before *P. leuckarti* develops; thus evolution towards early and rapid development is expected.

That predation does not regulate density is most clearly seen in 1976, when for some reason *P. leuckarti* is absent but *T. discipes* nevertheless disappears in exactly the same way as in other years. Its later reappearance in that year is due to a different phenomenon, i.e., a catastrophic event in the form of the drying up of the pool in the hottest summer of the century, creating an ecological vacuum.

Summarizing, an important life-history characteristic of *Tachidius discipes* in this environment is the creation of a temporal refuge against predation, probably by producing a stage which is invulnerable; by doing so, maximum population sizes are not attained.

Within both species groups there are clear temporal separations between species which probably prevent competition. This is important, as it is clear that nauplii will have quite different niches than adults and that competitive relationships may differ according to age. Whether this separation is caused by competition in the past, or prevents actual competition but evolved differently, is immaterial. In both species groups the smaller species precedes the larger one in succession.

That competitive interactions occur can also be inferred after *Amphiascoides debilis* successfully entered the system in 1972. This species occurred in low densities in 1969 but disappeared until its first peak in July 1972, followed by a second one in September and a third one in December. All of these peaks in this rapid succession are relatively small. A fourth burst follows in March 1973, and this is highly successful (44,000 ind./m^2 in June). Density remains low through the winter but a new spring peak follows in March 1974 (51,000 ind/m^2 in May), exactly one year after the first one. The appearance of this species is accompanied by a shift to earlier reproduction in *Paronychocamptus nanus*: from 1969-1973 the percentage of females carrying eggs increased in early February but in 1974 the increase started in January. In 1973 and 1974 density of *P. nanus* is much lower than in the preceding years (Table 1) and in 1975, when reproduction is earlier, *P. nanus* and *A. debilis* have extremely low densities and biomass (Table 1). Perhaps their competition early in the year prevents maximum population size. It is in 1975 that *Tachidius discipes* reaches its highest density and biomass of all the years. Since it is an early species as well, some life stage might profit from the extremely low abundance of the two other species.

The two different strategies followed by the two species groups have important consequences for their production. As *Paronychocamptus nanus* and *Canuella perplexa* occur over the whole year and maintain active populations in winter, their production, and, therefore, their part in community metabolism, will be much higher than that of the other species (Table 2). The four species form a series of decreasing biomass in which each term is about twice as large as its follower in the series. Similar patterns in the relative abundance of species are usually explained in terms of competition (May 1976).

Table 1. Mean annual biomass and start of increasing percentage of females carrying eggs in three successive years

	1973	1974	1975
Paronychocamptus nanus	46 mg/m^2 13 Feb	47 mg/m^2 10 Jan	14 mg/m^2 2 Jan
Amphiascoides debilis	7 mg/m^2 1 Feb	16 mg/m^2 24 Jan	4 mg/m^2 16 Jan
Tachidius discipes	4 mg/m^2 11 Apr.	18 mg/m^2 21 Mar	67 mg/m^2 30 Jan

Table 2. Mean biomass and production per year of the four most abundant copepod species during 1970-1976 (n = 185)

	$\bar{B}$ (mg/m^2)	$\bar{P}$ (mg/m^2/yr)	s/$\bar{x}$
Canuella perplexa (4.2 µg)	93	281	0.80
Paronychocamptus nanus (0.6 µg)	47	279	1.23
Tachidius discipes (2.0 µg)	27	105	2.23
Halicyclops magniceps (3.0 µg)	15	52	1.45
Total Copepods	195	769	0.53

DISCUSSION

Species of similar size have similar life histories: they increase at a similar rate and during about the same time. They differ in the number of peaks, which correspond to generations, during a year. *Tachidius discipes* and *Halicyclops magniceps* have only one generation annually because of environmental conditions: avoidance of predation for the former, low temperature for the latter. Production of these species can only be half that of species having two generations, all else being equal. In fact, as *T. discipes* is much more dependent on how quickly it can occupy its habitat, and on how much competition it will encounter in doing so, biomass and production of this species are variable from year to year. The mean annual biomass of *Paronychocamptus nanus* decreases slowly from 79 mg/m^2 in 1969 to 47 mg/m^2 in 1974, and then dramatically to only 14 mg/m^2 in 1975 and 8 mg/m^2 in 1976. This is accompanied by the appearance in 1973 of *Amphiascoides debilis*, a shift towards earlier egg-laying in *P. nanus* in 1974 and poor reproduction of both species in 1975. The vacuum created is filled up by the opportunistic species *T. discipes*, which has an overall average biomass of 105 mg/m^2 but attains 261 mg/m^2 in 1976. As its life cycle, adjusted to predation, permits the development of only one generation, the ecological vacuum reappears after the disappearance of that generation. *T. discipes* is then succeeded by *Halicyclops magniceps*, with much higher biomass from 1973 to 1976 than in previous years.

Competition cannot be proven in these cases, but is a reasonable hypothesis. Other explanations are possible; however, it is clear that production of these populations is determined mostly by characteristics of the life cycles of the species, far more than by details of development or by abiotic environmental parameters such as temperature, and these life cycles can be interpreted as resulting from species interactions. Whether life cycles are evolutionary-adaptive is, of course, one of the central problems in contemporary ecology. It is clear that restriction of reproduction to only one generation annually when the potential number of generations is at least 10-20 implies that production is only a by-product of reproductive processes. Copepods then are not the typical r-strategists they have been presumed to be (Heip, 1974), a view that has been stressed recently by several authors (Coull and Dudley, 1976; Hoppenheit, 1978; Warwick, 1980).

Although species interactions are important in determining the production of the populations involved, they influence community production far less. Mean biomass and production of the total copepod taxocene are very stable, with only slight differences in mean values over the years and small coefficients of variation (Heip, in prep.). This stability can be related to trophic relationships within the system and the amount of energy and matter flowing through the system rather than to species. When biomass is stabilized, a trend towards larger species in succession will result in lower production of the taxocene, as production is weight-dependent. There is some indication that this is indeed the case, as the biomass of an average copepod increases throughout the years (Heip, in prep.).

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REFERENCES

Coull, B. C. and B. Dudley. 1976. Delayed naupliar development of meiobenthic copepods. Biol. Bull. 150: 38-46.

Heip, C. 1974. A note on the life span of r-strategists. Biol. Jb. Dodonaea. 42: 117-120.

Heip, C. 1975a. Hibernation in the copepod *Halicyclops magniceps* (Lilljeborg, 1853). Crustaceana. 28: 311-313.

Heip, C. 1975b. On the significance of aggregation in some benthic marine invertebrates. Proc. 9th. Europ. mar. biol. Symp. H. Barnes (ed.). 527-538.

Heip, C. 1976. The life cycle of *Cyrpideis torosa* (Crustacea, Ostracoda). Oecologia (Berl.). 24: 229-245.

Heip, C. 1978. Diversiteit, stabiliteit en de niche van Copepoda van een brakwaterhabitat. Aggregaatsthesis State University of Gent. 471 pp. (In Dutch, unpublished).

Heip, C. 1979. Density and diversity of meiobenthic copepods: the oscillatory behavior of population and community parameters. *In* E. Naylor and R. Hartnoll (eds.): Proc. 13th. E.M.B.S. Symposium (in press).

Heip, C. and N. Smol. 1976a. Influence of temperature on the reproductive potential of two brackish water harpacticoids. Mar. Biol. 35: 327-334.

Heip, C. and N. Smol. 1976b. On the importance of *Protohydra leuckarti* as a predator of meiobenthic populations. In G. Persoone and E. Jaspers (eds): Proc. 10th E.M.B.S. Symposium Vol. 2: 285-296.

Hoppenheit, M. 1978. On the dynamics of exploited populations of *Tisbe holothuriae* (Copepoda, Harpacticoida). Helgoländer wiss. Meeresunters. 31: 285-297.

McArthur, R. M. 1972. Geographical Ecology. Harper and Row, New York.

May, R. M. 1976. Theoretical Ecology. Principles and Applications. Blackwell Scientific Publications, Oxford.

Menge, B. A. and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and spatial heterogeneity. Amer. Natur. 110: 351-369.

Nicolis, G. and I. Prigogine. 1977. Self-organization in nonequilibrium systems. From dissipative structures to order through fluctuations. Wiley and Sons, New York.

Velleman, P. F. 1977. Robust nonlinear data smoothers: definitions and recommendations. Proc. Natl. Acad. Sci. U.S. 74: 434-436.

Vincx, M. and C. Heip. Larval development and biology of *Canuella perplexa* T. and A. Scott, 1893 (Copepoda, Harpacticoida). Cah. Biol. Mar. (in press).

Warwick, R. M. 1980. Population dynamics and secondary production of benthos. pp. to *In* K. R. Tenore and B. C. Coull (eds.). Marine Benthic Dynamics. Univ. of South Carolina Press, Columbia.