Long-term dynamics of meiobenthic populations

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INTRODUCTION

The study of long-term ecological time series is a topic of great practical and theoretical interest. In the field of population biology, theoretical models have shown that populations can exhibit very different types of behaviour in time, ranging from extreme stability to apparently random behaviour (May, Oster, 1976). In the field of systems theory, the thermodynamics of non-linear open systems far from equilibrium suggest that ecosystems, that can be considered as typical dissipative structures, should be characterized by periodic behaviour in time and space (Platt, Denman, 1975). From a practical point of view, in the absence of knowledge on the dynamics of a system prediction is only possible when it is based on long enough time series (Poole, 1978).

The link between theoretical ecology and the actual situation in the field is not very clear. What is clear, however, is that cyclicity is an important component of the behaviour of real populations and communities and that ecological variables should be analysed for it. An obvious tool in this study is spectral analysis. This method determines how much of the observed variability of a time series can be explained by cyclical components of varying frequency. Ideally, the important cyclicities thus resolved should be related to hypotheses generated in theoretical models or to observed external oscillators.

In the present study a relatively simple community of meiobenthic copepods was monitored at fortnightly intervals over a seven year period (1970-1976). The study area is a brackish water pond in northern Belgium, called "Dievengat". It is a shallow (10-20 cm depth) habitat with pronounced seasonal fluctuations. Superimposed on these, several physico-chemical parameters such as oxygen concentration, pH and nutrient concentrations show important long-term fluctuations (Herman, Heip, in prep.).
Three copepod populations are discussed here. *Tachidius discipes* Giesbrecht 1882 is a medium size harpacticoid living epibenthically, and feeding on diatoms and other algae. *Canuella perplexa* Scott 1893 is a relatively large animal, the adults measuring well over 1 mm in length. It lives buried in the sediment, which is a mixture of fine sand and detritus, on which this species feeds. *Paronychocamptus nanus* (Sars, 1980) is the smallest species. It is also a detritus feeder.

**MATERIAL AND METHODS**

Samples were taken with a 6.06 cm² glass core to a depth of 5 cm. Elutriation techniques are described by Heip *et al.* (1974). The spectral analysis was performed on detrended In-transformed data with the recently developed “Maximum Entropy Spectral Analysis” (MESA) method (Kirk *et al.*, 1979; Rust, Kirk, 1977 and references therein). This method has the advantage that components with a period about equal to the length of the time series can be resolved. The greater accuracy in the low frequency range is mainly due to the fact that MESA minimizes the assumptions about the unavailable data (i.e. the data of the stationary time series before and after the period that observations were made). Mathematically the method is derived by imposing the condition that the most random spectrum (i.e. with highest entropy in the information theoretical sense) must be found which is consistent with the autocorrelation data of the time series studied.

The time series consist of 184 data points spaced 14 days apart. Fitting of cycles to the data was performed with a multiple linear regression program according to Bulmer (1974).

**RESULTS**

The three time series are shown in Figure 1. In *T. discipes* there is only one peak in spring in each year, except in the very dry summer of 1976 when a second peak is present. The analysis of 3-day interval samples of the 1979 peak showed that it is composed of three overlapping generations, contrary to the opinion of Heip (1980) who thought only one generation present each year.

In contrast, *C. perplexa* is constantly present in the habitat, but it is difficult to reveal a pattern in its abundance. The percentage of ovigerous females in the adult population shows that in most years two reproduction peaks occur. Culture experiments confirmed that this species most probably has two generations annually.

*P. nanus* as well is present throughout the year. Reproduction occurs from early spring till October-November. The analysis of five-day interval samples, combined with laboratory experiments (Smol, Heip, 1974) showed the existence of about eight generations each year, again much more than had been estimated earlier (Heip, 1980).

Figure 2 shows the spectra of the three time series. It is clear that, even in closely related species, a wide variety of time dependent behaviour can be observed. In the spectrum of *T. discipes* (Fig. 2a) there is only one prominent peak corresponding to a period of one year. The minor peaks occurring besides the one year peak are harmonics of this one, showing that although the important cyclicity is yearly the process is not a pure sine wave.

The spectrum of *C. perplexa* (Fig. 2b) is dominated by a peak corresponding to a period of 3.5 years. Next in importance are peaks of 1 year, 1.3 years and 0.5 year. The spectrum of *P. nanus* (Fig. 2c) is dominated by a peak on 1.5-2.0 years. This is followed by peaks on 4.6 years, 1 year, 0.5 year and 0.3 year, the latter two being harmonics of the 1 year period.

The autocorrelation functions of these time series show that in *T. discipes* there is only a short serial correlation (1 to 2 months) whereas in *C. perplexa* and *P. nanus* consecutive densities remain positively correlated over a period of about half a year.

**DISCUSSION**

The appearance of *Tachidius discipes* in the community in early spring is most probably determined by the availability of food algae and thus ultimately by light.
Its disappearance in July is caused by an increasing predation, mainly from the polyp *Protohydra leuckarti* (Heip, Smol, 1975). Culture experiments showed that its intrinsic rate of increase remains high at the temperatures experienced by the population at that time (Smol, Heip, 1974). Furthermore, the animals are well fed and have high reproduction until they disappear. This population is thus regulated by external factors which are seasonal. In the very dry summer of 1976 part of the sediment in the pond dried, and the density of *T. discipes* rapidly increased again in the recovering community. It was followed by a peak in *Protohydra* density, as is normally observed in spring.

In view of this, the short serial correlation and the dominance of the yearly period in the spectrum can be understood as the result of a short generation time and seasonal regulating factors. The important long-term fluctuations in physico-chemical parameters of the environment are not tracked by this species. Its strategy of fast reproduction until it is barred by predation apparently makes it relatively insensitive to the overall state of the environment. Although considerable variation in the height of the peaks exists from year to year, these differences are non-cyclical and probably depend on the density of the population reached before serious predation starts.

For *Canuella perplexa* we first note that its generation time is about half a year. This implies by itself a longer serial correlation, since the population has a longer memory of previous states. The dominance of longer periodicities in the spectrum can be related to density-dependent regulation. There are indications that this indeed exists. The percentage of ovigerous females in the adult population decreases with increasing population density. Figure 3 shows the plot of the logarithmic rate of increase against the log of density. This plot was calculated from the density curve after application of 0.5 year moving average (0.5 year being the estimated generation time of this species). The log rate of increase is given by $R = \log (N_{t+0.5}/N_t)$. The lines in this plot are the time trajectory of the system.

In models of logistic single species systems the slope of the regression line between $R$ and $N$ can be related to the intensity of density dependent regulation mechanisms, whereas the intercept with the y-axis ($y = 0$) relates to the carrying capacity (Royama, 1977; Hassell et al., 1976). It can be seen from Figure 3 that whereas the intercepts differ, the slopes of the $R$-$N$ lines are rather constant. Using values of the parameters estimated from this figure, one can calculate that after perturbation the population of *Canuella perplexa* will return to equilibrium in a series of slowly damped oscillations. Such a population is likely to track cyclical environmental fluctuations and to start oscillating in resonance to them (Nisbet, Gurney, 1982).

A remarkable correlation in this respect exists between the long-term behaviour of the *Canuella perplexa* population and the concentration of ammonium in the habitat. The spectrum of this parameter is also dominated by a 3.5 year periodicity. When fitted to the data, the 3.5 year cycles of *C. perplexa* and ammonium are almost exactly in phase. As the concentration of ammonium can be an indicator of the decomposition rate it may be an indicator of the carrying capacity of the environment for *C. perplexa*.
A more complex problem is posed by the spectrum of Paromyochamptus nana. The long serial correlation in this time series cannot be explained by a long generation time, and neither could we demonstrate density dependence in this population. It has been shown in model systems that long serial correlations can be produced by coupling of several species in competitive interactions (Royama, 1977). There is evidence that such interactions do indeed exist. The time series of the total number of species has a spectrum that is, most remarkably, dominated by peaks of 3.5 and 4.6 years. Not only do these periods correspond to those found in C. perplexa and P. nana but the phases fit as well (Fig. 4). This means that when conditions are bad for C. perplexa and P. nana they are even worse for other species and may cause their disappearance from the habitat. We think that C. perplexa can nevertheless be treated as a single species problem because of its greater size, which makes it a superior competitor (a key-species).

For Paromyochamptus nana both the long serial correlation and the 1.5 and 2.0 years oscillations can be interpreted as resulting from competitive coupling. However, we do not believe this to be true for the 4.6 years periodicity, which may be the result of tracking of a varying parameter in the system which we have not been able to identify.

The results of this study show that long-term cycles or quasi-cycles are important in these short-living species and that spectral analysis may be a useful tool in unraveling temporal patterns. Explanation of these patterns remains difficult: both the characteristic dynamics and interaction patterns of each species determine its apparently variable degree of direct dependence on the physical environment.

![Graphs showing time series analysis](image)

REFERENCES
