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Perspectives on the ecological factors regulating *Pontoporeia* populations in the northern Baltic Sea

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The deposit-feeding *Pontoporeia affinis* (Lindström) and *P. femorata* (Kröyer) (Crustacea, Amphipoda) are the dominant macrobenthic animals in deep soft bottom areas of the northern Baltic Sea. Their abundance, growth and life cycle vary according to local temperature and food conditions. Both species seem to be food-limited. In the Tvärminne area, on the southwest coast of Finland, the seasonal timing of growth differs between species, indicating either competition or differing food sources.

Abiotic and biotic factors regulating *Pontoporeia* populations make up an intertwined network, with numerous one-way effects and two-way interactions. For example, temperature and salinity limit the distribution of *Pontoporeia*, and temperature also directly affects the rates of feeding, respiration and growth; however, because of complicated food-web effects, the overall influence of temperature, as of any single factor, is difficult to evaluate.

The omnivory of *Pontoporeia* on three successive levels (sediment detrital carbon, bacteria and meiofauna) confuses predator-prey and competitive relationships in the detritus-based benthic system. Calculations based on the observed growth and production show that *Pontoporeia* species must obtain most of their energy requirements from detrital carbon. Nonselective feeding by *Pontoporeia* decreases the populations of bacteria and the meiofauna, and thus probably releases *Pontoporeia* from their competition for the detrital carbon source, but at the same time decreases the availability of high quality food.

1. Introduction

The soft bottom community of the northern Baltic proper is in deep areas dominated by *Pontoporeia affinis* (Lindström) and *P. femorata* (Kröyer) (Crustacea, Amphipoda). These species are important consumers in the benthic subsystem, and many fish and carnivorous invertebrates feed upon them (Aneer 1975). Their abundance, growth and life cycle vary according to local temperature and

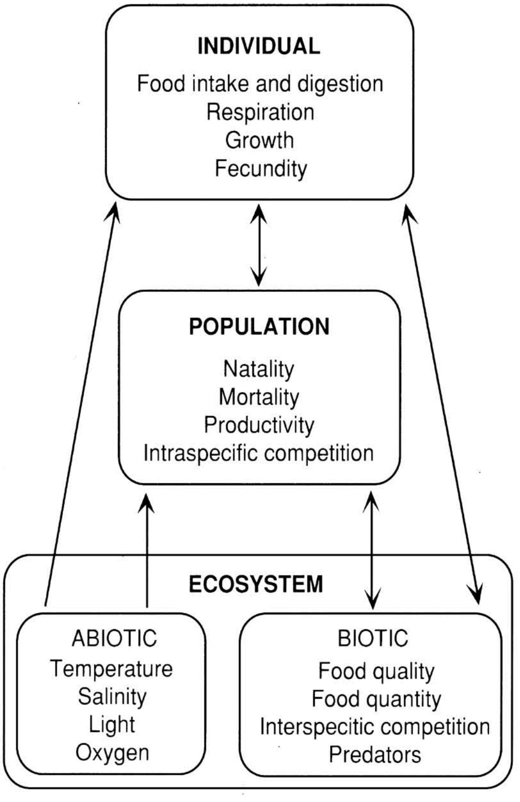

Fig. 1. Interactions between the soft bottom ecosystem and the population and individual levels of *Pontoporeia*. The arrows show the direction of regulation. A line with one arrowhead shows a oneway effect, a line with two arrowheads an interaction between two levels.

food conditions (Segerstråle 1937, Sarvala 1986, Leonardsson et al. 1988). *P. affinis* breeds at an age of 1–4 years. Adults copulate in late autumn, and the female bears the embryos in her brood pouch until the spring when the young are released (Segerstråle 1937). *P. femorata* has a similar life cycle in the shallowest parts of its range (depths of 30–40 m) (Segerstråle 1938). At greater depths both species switch to breeding in summer or continuously (Segerstråle 1967, 1971).

Both *Pontoporeia* species are non-selective sediment feeding omnivores, which can use benthic organic matter with bacteria, microalgae and meiofauna as food (Ankar 1977, Elmgren 1978, Slepukhina & Kurashov 1987). Both species seem to be food-limited in the Baltic Sea (Elmgren 1978), as evidenced by the density-dependent interannual variation of growth in *P. affinis* in the Tvärminne area, on the southwest coast of Finland (Sarvala 1986).

The abiotic and biotic factors regulating *Pontoporeia* populations make up an intertwined network, with numerous one-way effects and two-way interactions. In the present paper, we briefly outline this complicated system of positive and negative feedbacks affecting *Pontoporeia* in the soft bottom ecosystem of the northern Baltic Sea.

2. One-way effects in the ecosystem

The structure and functioning of an ecosystem are affected by abiotic and biotic factors (Fig. 1). The abiotic factors, such as temperature and salinity, show one-way effects. They e.g. set the limits for the distribution of species and influence their success in competition. The community at a certain depth is moulded by these factors. For example, owing to its salinity requirements, *P. femorata* in the Tvärminne area is abundant only in the sea zone, and is only sparsely found in the outer archipelago. The more euryhaline *P. affinis* is abundant both within and outside the archipelago. Due to the salinity-related release from interspecific competition, *P. affinis* may thus be provided with better growth conditions within the archipelago than in the sea zone (Uitto & Sarvala unpubl.).

Temperature regulates the rates of all life processes in the benthic system, including the bacterial and meiofaunal production, and thus influences indirectly the quality and quantity of benthic food for *Pontoporeia*. But temperature also has direct one-way effects on *Pontoporeia* individuals by influencing their feeding, respiration and growth. Although increasing temperatures initially enhance the growth of *Pontoporeia*, high temperatures may lead to impaired growth because of disproportionately increased metabolic losses in respiration (Moore 1979, Semenchenko 1979; see Sarvala 1986). High temperatures, although uncommon, may also increase the mortality during summer. However, because of the complicated food web effects, the overall influence of temperature, as of any single factor, is difficult to evaluate.

3. Two-way effects in the ecosystem

There are many two-way effects or interactions between the individual, population, and biotic ecosystem levels (Fig. 1). Phenomena at the population level, such as natality, mortality and productivity, are to a large extent regulated by interactions within the population level and between the population and ecosystem levels. The population processes also reflect the conditions of the benthic community. Interspecific and intraspecific competition decrease the individual growth rate and population productivity of *Pontoporeia* in communities with a high biomass. Heavy grazing on organic matter, bacteria and meiofauna decreases the quantity and quality of benthic food, thus decreasing the community carrying capacity, and finally affecting the abundance and biomass of *Pontoporeia* (Uitto & Sarvala unpubl.).

Because fecundity in *Pontoporeia* is coupled to body size (Cederwall 1977), slow growth also leads to low fecundity. Moreover, in a dense population the maturation is delayed, because it takes a longer time to reach the minimum size for reproduction. Differences in the growth rate are thus reflected in the number of parallel age groups. In dense, slowly growing *Pontoporeia* populations in the Tvärminne area, there may be as many as four parallel age groups, while in sparser populations there are usually only two parallel groups (Sarvala 1986, Uitto & Sarvala unpubl.).

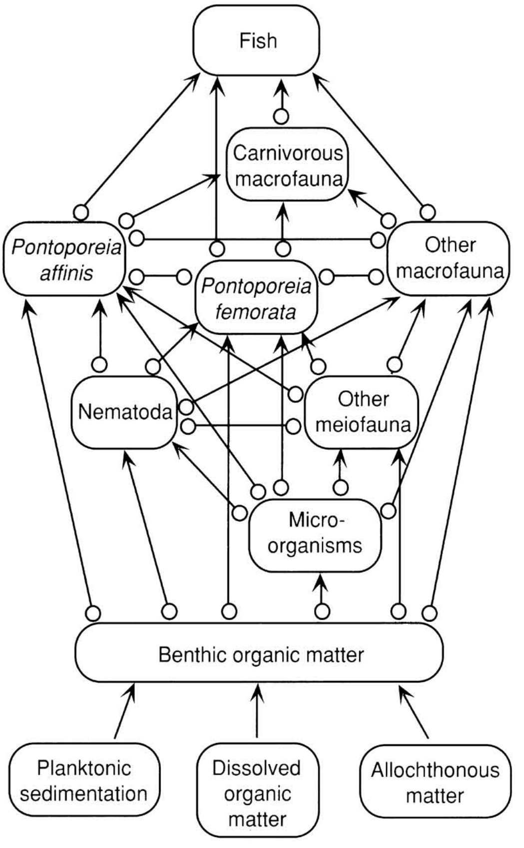

Fig. 2. Soft bottom community interactions. Arrowhead = positive link; circlehead = negative link; line-end without symbol = indifferent link.

4. Community interactions

Fig. 2 shows a more detailed model of network interactions in the benthic community, using the symbols of loop analysis (Lane 1985). In this model, ranging from sedimentation to invertebrate-feeding fish, there are different levels according to the origin of food, and the size and feeding type of each organism. Only the most important species or functional groups are included.

Sedimented organic matter is the main source of energy for the benthic community, and calculations based on the observed growth and production show that *Pontoporeia* species must likewise obtain most of their energy requirements from detrital carbon (Uitto & Sarvala unpubl.). Although the soft bottom subsystem receives a large proportion of its annual carbon input in the spring from the sedimentation of the vernal phytoplankton maximum (e.g. Kuparinen et al. 1984), the seasonal growth pattern of *Pontoporeia* in Tvärminne is not directly coupled with the sedimentation peak, but more closely follows the seasonality of temperature and total benthic metabolism (Uitto & Sarvala unpubl.). The latter is related to bacterial production (Bergström & Sarvala 1986) and may be regarded as an indirect indicator of the quality and quantity of available benthic food.

The seasonal timing of growth differs between the *Pontoporeia* species, suggesting either competition or differing food sources: in *P. affinis* the growth rates are consistently highest in early to midsummer, while *P. femorata* exhibits no clear maxima and relatively high growth rates in the autumn too. Both species seem to use the same food, viz. organic carbon from the surface layer of the sediment (Lopez & Elmgren 1989), and thus, in spite of a partial vertical segregation (Hill & Elmgren 1987), keen competition between them seems probable. The higher fecundity (Cederwall 1977) and higher rate of feeding (Lopez & Elmgren 1989) of *P. affinis* suggest that it might be competitively superior to *P. femorata*. Indeed, in co-occurring populations the abundance and biomass of *P. affinis* often exceed those of *P. femorata* (Uitto & Sarvala unpubl.). However, we do not know whether there is a difference between the species in the threshold food requirements: when food is limiting, the species with the lower food threshold will, in the long term, win the competition. *P. femorata* has the lower rate of respiration of the two species, and might therefore be a successful competitor in extreme low-food environments. Moreover, *P. femorata* lives on the average slightly deeper in the sediment, and exhibits much lower swimming activity than *P. affinis* (Hill & Elmgren 1987; cf. Lindström & Lindström 1980), and it is therefore probably less susceptible to fish and epibenthic invertebrate predators than *P. affinis*.

In some areas of the northern Baltic Sea, the between-year abundance fluctuations of *P. affinis* follow a fairly regular pattern with a 6–7 year cycle (Andersin et al. 1978, Sarvala 1986). The reasons for these oscillations are not yet clear. *Pontoporeia* populations in the northern Baltic Sea are evidently food limited (Elmgren 1978, Sarvala 1986, Uitto & Sarvala unpubl.), in spite of heavy predation by fish and carnivorous macrofauna. The most important invertebrate predator, *Saduria entomon*, is sparse compared with *Pontoporeia* (Kuparinen et al. 1984), at least off Tvärminne. If the predators do in fact limit *Pontoporeia* populations, there should be a 6–7-year cycle in their numbers as well; there is no evidence of such oscillations.

Omnivory is the dominant feeding mode in meio- and macrofauna. Like many other macrofauna species, *Pontoporeia* are able to use energy from all levels below their own: sediment detrital carbon, bacteria, and meiofauna. Such omnivory confuses predator-prey and competitive relationships in the detritus-based benthic system. Nonselective feeding by *Pontoporeia* reduces the populations of bacteria and meiofauna, and thus probably releases *Pontoporeia* from their competition for the detrital carbon source. At the same time, however, this decrease of sediment microorganisms means a decreased availability of high quality food. Detritus may be the source of energy, but bacteria and meiofauna the source of proteins (cf. Lopez & Levinton 1987). Grazing by a dense *Pontoporeia* population might ultimately decimate some of the essential food sources, resulting in failure of reproduction and a subsequent population decline (Sarvala 1986). The decreased grazing would again allow the recovery of the food source and, with a delay due to the univoltine life cycle, of the *Pontoporeia* population. Omnivory combined with the great abundance of *Pontoporeia* make them key species in the Baltic benthos (Elmgren et al. 1986).

Abiotic and biotic factors affecting events in the benthic ecosystem form a complicated dynamic network. A basic regulating factor, the amount of food, may be controlled indirectly by temperature or directly by the object of the regulation itself (*Pontoporeia*). Although food is the ultimate factor affecting the success of *Pontoporeia*, other factors, such as temperature, or predation, may be important, and their role depends on the dynamic state and interactions between the components of the ecosystem (cf. Levins & Lewontin 1982).

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