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The negative correlation between the abundances of the amphipod Pontoporeia and the bivalve Macoma in Baltic waters, and the factors involved

SVEN G. SEGERSTRÅLE

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In the northern Baltic a negative correlation has repeatedly been observed between the abundances of *Pontoporeia* (*P. affinis* and *P. femorata*) and *Macoma baltica*. The various views on the factors involved are discussed and predation on young *Macoma* by *Pontoporeia*, doubted in a recent paper by ANKAR, is considered to offer the most likely explanation.

Sven G. Segerstråle, Biological Laboratory of the Institute of Marine Research, Box 136, SF-00121, Helsinki 12, Finland.

In a paper on the bottom fauna of the northern Baltic, HESSLE (1924) reported a negative correlation between the abundances of two amphipods (*Pontoporeia affinis* and *P. femorata*, the latter confined to comparatively deep and saline water) and the bivalve *Macoma baltica*. In the Stockholm archipelago and the whole area north of it to the head of the Gulf of Bothnia, *Macoma* was caught down to depths of 40—50 m, but around Gotland and Öland it was frequent at greater depths; in the former area it was captured as far down as 140 m. HESSLE suspected that *Pontoporeia* was responsible, because the crustacean was found in striking abundance farther north, where *Macoma* was absent. Furthermore, individual samples showed that in deep localities with *Macoma* the population of *Pontoporeia* was generally scanty. Hessle suggested two alternative explanations: (a) *Pontoporeia* may be more successful in competition for food, both animals being detritus feeders, (b) the crustacean may eat the newly settled larvae of *Macoma*. However, these suggestions were not elaborated by HESSLE.

This negative correlation between the abundances of *Pontoporeia* and *Macoma* is typical of Baltic waters (SEGERSTRÅLE 1933, 1960, 1962, 1965, 1973, LUOTAMO 1971, 1976, 1977, CEDERWALL 1972, BERGH 1973, ANKAR & ELMGREN 1976, ANDERSIN *et al.* 1977, ANKAR 1977). In deep water with abundant *Pontoporeia*, *Macoma* has proved to be either totally absent or scarce, owing to periodical failure of recruitment.

HESSLE's suggestion that *Pontoporeia* exerts an adverse influence on *Macoma* was supported by recent field studies carried out in the Koverhar area near the Tvärminne Zoological Station (SW Finland). This area comprises both unpolluted localities and localities polluted by effluents from the Koverhar Iron and Steel Works; the bottom fauna includes both *Pontoporeia affinis* and *Macoma*. *Pontoporeia* is markedly sensitive to pollution, whereas *Macoma* endures considerable contamination (cf., for instance, LEPPÄKOSKI 1975). In two recent papers LUOTAMO & LUOTAMO (1976, 1977) showed that in 1971 *Pontoporeia* was clearly less abundant in polluted situations than in otherwise similar but unpolluted localities. By contrast, strikingly heavy recruitment of *Macoma* was found in those localities where *Pontoporeia* had declined. In 1974, when the polluted area had increased, corresponding changes were observed in the abundances of *Pontoporeia* and *Macoma*. The same trend can be seen from the unpublished results of sampling in 1977 kindly placed at my disposal. Thus these studies convincingly demonstrate that *Macoma* is suppressed by *Pontoporeia*.

Observations made in connection with my extensive sampling of the bottom fauna in the Tvärminne area seem to exclude competition for food: recruitment of *Macoma* was successful even when the species was abundant and consumption of detritus was thus heavy (in these localities *Pontoporeia* was absent or scarce).

To study the role of predation by *Pontoporeia*, I made some experiments at the Tvärminne Zoological Station. Aquaria, whose bottoms were covered with mud, were stocked with *Pontoporeia* and newly settled *Mytilus edulis* — somewhat larger than the first bottom stage of *Macoma*, which was not available. After some weeks the bivalves had completely disappeared (for details, see SEGERSTRÅLE 1962), presumably either because they had been eaten by *Pontoporeia*, or suffocated in connection with the burrowing activity of the crustacean. Predation seemed to me to be the more likely alternative, and this explanation has been referred to by a number of authors without adverse comment (TULKKI 1964, LAAKSO 1965, LUOTAMO 1971, LUOTAMO & LUOTAMO 1976, BERGH 1973, LEPPÄKOSKI 1975, WILDISH 1977).

However, ANKAR (1977) doubts whether predation by *Pontoporeia* on newly settled *Macoma* can be responsible for the negative correlation between the abundances of the two animals. In his opinion competition for food or different habitat selection should be considered.

For the reasons mentioned above, competition for food does not seem to be a likely explanation. The idea of different habitat selection is not supported by the observations in the Koverhar area, and it also disagrees with the data from the Tvärminne waters, where periods of strikingly high abundance of *Pontoporeia* and *Macoma* may alternate in the same locality. Furthermore, HESSLE (1924) points out that both *Pontoporeia* and *Macoma* showed maximum density in localities with practically the same type of bottom substrate (clayey mud with sand).

ANKAR (1977) doubts that *Pontoporeia* is able to swallow young *Macoma*. He found that the gut contents of *Pontoporeia affinis* and *P. femorata* contained mineral particles up to 60 μm in size, and admits that it "is most likely that they can masticate organic aggregates larger than this". Yet he doubts "whether the species can crush and eat newly settled *Macoma* (size about 300 μm)", because the gut of 8 mm long *Pontoporeia* has a diameter of only 250 to 300 μm.

ANKAR's negative attitude towards the suggestion that *Pontoporeia* preys on newly settled *Macoma* is somewhat surprising, because the extremely thin shells of the minute bivalves may be easily crushed by the strong mandibles of *Pontoporeia* and subsequently ingested. Indeed. direct predation by *Pontoporeia* on minute *Macoma* definitely seems to be the most plausible explanation for the negative correlation between the abundances of the two animals.

Further experimental studies will be needed to solve this problem definitely.

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