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Benthos studies in the Estonian coastal sea during 1998–2001

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Abstract. This paper presents the recent findings related to experimental studies on benthos in the Estonian coastal sea. Pelagic–benthic coupling, interspecific competition for food, and plant–herbivore interactions are the three main topics. In the final section we present some ideas and directions that might serve as a base for further studies.

Key words: Baltic, competition, filter-feeding, macroalgal–herbivore interaction.

INTRODUCTION

The structure of benthic communities in the Baltic Sea is simple, which provides a unique opportunity to study the mechanisms and detect the driving forces of changes in these communities. The popularity of experimental studies, as a tool to describe the processes in different subsystems of the Baltic Sea, increased notably during the previous decade. These studies included for example the development of methods that detect human induced changes relative to natural variability (Kraufvelin, 2000) or the interactions and flows of matter and energy between different components of the system (Kautsky, 1995; Sandberg, 1996; Kotta, 2000).

In the Estonian coastal sea, however, the majority of evidences about various benthic processes are circumstantial. This is due to the fact that the researchers have primarily concentrated on the issues of spatial distribution or temporal trends of the biota whereas experimental studies were almost nonexistent (Järvekülg, 1979; Kotta et al., 1998a). It was not until the mid-1990s that the process studies

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gained more attention. In this review we give the state of the art of the process studies at the Estonian Marine Institute and propose some directions to which we should aim.

OVERVIEW OF BENTHOS EXPERIMENTS

Pelagic–benthic coupling

Recent studies focused on *in situ* grazing rates of the mussels *Dreissena polymorpha* and *Mytilus edulis* and the cirriped *Balanus improvisus* (Kotta et al., 1998b; Kotta, 2000; Kotta & Møhlenberg, 2002). These studies were carried out in the Gulf of Riga and at the Finnish side of the Gulf of Finland. Seasonal and spatial variability in the functional relationships between ambient phytoplankton biomass and the grazing rates of the filter-feeders was estimated. Chlorophyll *a* (Chl *a*) concentration was used as a parameter for estimating the amount of planktonic algae. The changes of Chl *a* in water and biodeposit production in terms of Chl *a* were quantified. The filtration rates (filtered water, L ind^{-1} h^{-1}) of the studied species increased with ambient temperature. In more eutrophicated regions (Gulf of Riga) the filtration rate increased curvilinearly with the ambient concentration of Chl *a* and levelled off at a high food concentration of 70 μg total Chl *a* L^{-1}. In less eutrophicated conditions (Gulf of Finland) a linear model gave the best fit suggesting that the saturation level was not obtained. Filtration rates increased in the order *D. polymorpha* at highly eutrophicated site < *M. edulis* at moderately eutrophicated site < *B. improvisus* at slightly eutrophicated site < *M. edulis* at slightly eutrophicated site. Grazing rates (phytoplankton consumed, μg Chl *a* ind^{-1} h^{-1}) followed the same trend as filtration rates with the greatest values occurring under conditions of maximum temperature (16 °C) and ambient Chl *a*. Grazing rates were significantly lower in more eutrophicated than in less eutrophicated areas. Taking into account the abundance distribution of the filter-feeders in the study area the population grazing rate (% of phytoplankton consumed m^{-2} d^{-1}) was the highest in summer owing to low phytoplankton biomasses and high filtration activity. The population of filter-feeders grazed daily on average from 6 to 3150% of the phytoplankton stock in the littoral area, constituting an important sink for primary production. Differences in filtration rates were primarily related to the spatial variability of the density of filter-feeders. Very high grazing pressure was explained by the narrow mussel belt and intensive water exchange in the area.

Competition for food

Since 1994 the North American polychaete *Marenzelleria viridis* has been found in the Estonian coastal sea. The polychaete is a deep burrowing deposit feeder – a new function, which has not previously been observed in the northern Baltic Sea. We estimated whether the appearance of the new function affected the

native benthic invertebrate communities. Changes in the interspecific competition within benthic communities were examined in relation to the addition of *M. viridis* into the ecosystem of the northern Baltic Sea (Kotta et al., 2001; Kotta & Ólafsson, 2003).

Our experiments gave further information confirming that (1) the introduced polychaete *M. viridis* has a negative influence on the native polychaete species *Nereis diversicolor* and the amphipod *Monoporeia affinis*; (2) this effect is likely to decrease with the increasing density of adult specimens of the bivalve *Macoma balthica*; (3) competitive interactions between *M. viridis* and *M. balthica* appear to be a key factor determining the distribution pattern of *M. viridis* in the Baltic Sea; (4) competitive superiority of *M. balthica* over *M. viridis* is likely due to the more efficient feeding regime of the bivalve. The pilot experiment indicated that *M. balthica* consumes sedimented phytodetritus from a wider surface area and its consumption rates are higher than those of *M. viridis*.

Plant–herbivore interactions

Habitat choice of animals is determined by several factors, e.g. food, shelter, and access to mates. Vegetation is crucial for herbivores both as a food source and as protection from predation (Puttman, 1986). We estimated whether food and habitat preference of the dominant herbivore species is dependent on macroalgal species and their condition.

In general, habitat and grazing preferences were affected by the availability of macroalgal species. The isopod *Idotea baltica* is common in the *Fucus vesiculosus* and *Cladophora glomerata* belts in the Baltic Sea (Jansson, 1974; Haahtela, 1984). In the northern Baltic Sea *F. vesiculosus* is considered to be the main source of food for *I. baltica* (Salemaa, 1987). Since the notable decline of the biomass of *F. vesiculosus* in the Gulf of Riga in the late 1990s *I. baltica* switched to *Furcellaria lumbricalis* as a habitat and *Pilayella littoralis* as a food (Kotta et al., 2000). The highest densities of *I. baltica* were observed in shallow areas, where the proportion of the filamentous epiphyte *P. littoralis* on *F. lumbricalis* was the highest. By removing fast growing epiphytes, isopods protect slow growing *F. lumbricalis* against a nuisance alga *P. littoralis* (Kotta et al., 2000).

The grazing rates of selected invertebrates on various macroalgae are presented in this volume (see the paper by Orav-Kotta & Kotta, 2003). In another short term study the isopod *I. baltica* was kept in aquaria with different algal species and with and without the predator *Palaemon adspersus*. The main conclusions were: (1) Among the studied algae *P. littoralis* was the best food for *I. baltica*. (2) *F. vesiculosus* offered the idoteids the best protection against the predator *P. adspersus*. As compared to other studied macroalgae, the mortality of *I. baltica* was the lowest in the treatments where *F. vesiculosus* was added as shelter. Besides, *P. adspersus* had no effect on the time the isopod stayed in *F. vesiculosus*. (3) The predator induced mortality of the idoteids was the

highest in *Ceratophyllum demersum* and *Zostera marina*. (4) *In situ* mortality of *I. baltica* was higher in *F. vesiculosus* dominated communities than in *P. littoralis*. It is likely that *I. baltica* actively searched *P. littoralis* (i.e. the most preferred food) in these treatments and hence became more visible to predators, increasing the risk of being consumed.

The proliferation of annual filamentous macroalgae results in the accumulation of drifting algal mats in the whole Estonian coastal range (Trei, 1983, 1991). We tested the importance of the benthic herbivore *I. baltica*, the detrivore *Gammarus salinus*, and the filter-feeder *Mytilus edulis* for the decomposition of the prevalent drift algae *P. littoralis* and *Cladophora glomerata*. The results showed that the benthic invertebrates significantly affect the algal decomposition. However, the character of the effect depended on the algal species, their physiological state, and invertebrate species. When algae were photosynthetically active *M. edulis*, through the fertilizing effect of biodeposition, promoted the growth of the algae and hence retarded the algal decomposition. On the other hand, in the presence of herbivores the complete breakdown of the drift algae was reached already within 30–40 days as compared to the control value of 70 days. *G. salinus* had a stronger effect on *P. littoralis* whereas *I. baltica* contributed mostly to the decomposition of *C. glomerata*. It was concluded that herbivores act as stabilizers of benthic communities whereas filter-feeders are likely to increase the stress caused by the drift algae (Paalme et al., 2002).

PERSPECTIVES

Our previous studies take into account intraspecific interactions or interactions between two species. Experimental tests of processes at ecosystem level require the measurement of the ecosystem response to treatments involving different numbers of species. The ecosystem response of *n* species should be measured separately and compared to the response of a mixture of those species. This would enable us to detect complementary resource use and relative contribution/ significance of separate species (e.g. Emmerson & Raffaelli, 2000).

Two major questions asked in contemporary ecology are (1) how does biodiversity affect the magnitude of ecosystem processes and (2) how does biodiversity contribute to the stability and maintenance of ecosystem processes in the face of perturbations (e.g. Loreau, 2000)? Therefore, we should perform experiments to establish relationships between benthic diversity and the stability of biota at various conditions and scales.

The studies of processes often require a proper definition of functional groups. The usage of functional group approach enables a significant reduction of the number of treatments when planning the experiments. However, the groupings should be based on a specific function (e.g. photosynthetic activity, herbivore resistance) rather than gross morphology (e.g. filamentous algae) (Padilla & Allen, 2000).

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Bentose eksperimentaaluuringud Eesti rannikumeres aastail 1998–2001

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Artikkel võtab kokku teadustööd Eesti rannikumere põhjakoosluste eksperimentaaluuringutest. Kolm põhilist uurimissuunda on interaktsioonid bentose ja pelagose vahel, liikidevaheline toidukonkurents ning taimede ja herbivooride vahelised seosed. Lõpetuseks on tutvustatud uudseid ideid ja uurimissuundi, mille alusel planeerida teadustööd.