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HELEN ORAV-KOTTA

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HELEN ORAV-KOTTA

TARTU UNIVERSITY
PRESS

Institute of Zoology and Hydrobiology, Faculty of Biology and Geography, University of Tartu, Estonia.

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LIST OF ORIGINAL PUBLICATIONS

I. Orav-Kotta H., Kotta J. & Kaljurand K. Factors controlling seasonal changes in biodeposition and estimates of grazing pressure of *Mytilus edulis* in Kakumäe Bay, Northern Baltic Sea (submitted manuscript).

II. Orav-Kotta, H. & Kotta, J. 2004. Food and habitat choice of the isopod *Idotea baltica* in the northeastern Baltic Sea. *Hydrobiologia*, **514**, 79–85.

III. Kotta, J. & Orav, H. 2001. Role of benthic macroalgae in regulating macrozoobenthic assemblages in the Väinameri (north-eastern Baltic Sea). *Ann. Zool. Fenn.*, **38**, 163–171.

IV. Orav-Kotta, H. & Kotta, J. 2003. Seasonal variations in the grazing of *Gammarus oceanicus*, *Idotea baltica* and *Palaemon adspersus* on benthic macroalgae. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **52**, 141–148.

V. Paalme, T., Kukk, H., Kotta, J. & Orav, H. 2002. "In vitro" and "in situ" decomposition of nuisance macroalgae *Cladophora glomerata* and *Pilayella littoralis*. *Hydrobiologia*, **475/476**, 469–476.

VI. Kotta, J., Orav, H. & Sandberg-Kilpi, E. 2001. Ecological consequence of the introduction of the polychaete *Marenzelleria viridis* into a shallow water biotope of the northern Baltic Sea. *J. Sea Res.*, **46**, 273–280.

The author's involvement in studies I, II and IV was substantial including the generation of hypotheses, fieldwork and writing process. As for publications III, V and VI the responsibility was shared with other coauthors and my main activities were participation in the experimental design, fieldwork, laboratory analysis and writing the chapters related to the specific field of this dissertation.

ABSTRACT

The aim of the dissertation is to describe how the changes in eutrophication affect the habitat choice and feeding activity of the prevailing benthic suspension feeders and mesograzers in the northern Baltic Sea. Functional relationships between ambient temperature, salinity, bottom currents, concentration of nutrients in water, chlorophyll *a*, biomass of phytoplankton species and biodeposition rates of the bivalves *Dreissena polymorpha* and *Mytilus edulis* were estimated. Except for the central Gulf of Finland the biodeposition rates of the bivalves increased with ambient temperature. In more eutrophicated regions the biodeposition rate increased curvilinearly with ambient concentration of chlorophyll *a* and levelled off at high food concentration. In less eutrophicated conditions a linear model gave the best fit suggesting that the saturation level was not obtained. The biomass of benthic diatoms described better the biodeposition of *M. edulis* than chlorophyll *a* concentration alone. This result suggests that the bivalves are highly selective between phytoplankton species and a significant part of their diet consists of benthic microalgae. The population of benthic suspension feeders cleared daily on average from 3 to 2426% of overlaying water in the littoral area constituting an important sink for primary production. The impact of the benthic suspension feeders on pelagic communities was smaller in eutrophicated systems relative to cleaner environments.

The habitat selectivity and feeding activity of the benthic mesograzer *Idotea baltica* were studied in different algal communities representing the gradient of eutrophication. In the least eutrophicated system, where *Fucus vesiculosus* was dominating, the brown alga provided both food and shelter to *I. baltica*. In moderately eutrophicated communities, dominated by the filamentous *Pilayella littoralis*, *F. vesiculosus* served as a shelter and *P. littoralis* contributed practically 100% of the diet of the isopod.

Seasonal variability in the grazing of *I. baltica*, *Gammarus oceanicus* and *Palaemon adspersus* on benthic macroalgae was studied in a moderately eutrophicated site. *P. littoralis* was the prime diet of the studied invertebrates. When its biomass declined in the field invertebrate grazing on *F. vesiculosus* increased. The highest grazing rates were shown by *I. baltica* followed by *G. oceanicus* and *P. adspersus*. In general invertebrate grazing was high in summer, moderate in autumn and low in spring.

The effect of water temperature, salinity, influx of nutrients, species composition, structure and physiological state of macrophytes on the grazing intensity of mesoherbivores was tested. The grazing of *P. littoralis* and *F. vesiculosus* by *I. baltica* and *G. oceanicus* was primarily a function of the photosynthetic activity of the algae. When the algae were photosynthetically active their consumption was almost negligible. The grazing increased exponen-

tially prior to the decomposition of *P. littoralis*. When two algal species were incubated together, the presence of *P. littoralis* modified the grazing of *F. vesiculosus* whereas the presence of *F. vesiculosus* did not modify the grazing on *P. littoralis*.

At very high eutrophication levels the drift algal mats replaced the attached algal communities. Benthic mesograzers significantly consumed the drift algae. 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. oceanicus* had a stronger effect on *P. littoralis* whereas *I. baltica* contributed mostly to the decomposition of *Cladophora glomerata*. Benthic suspension feeders indirectly affected the algal decomposition. When algae were photosynthetically active *M. edulis*, through the fertilising effect of biodeposition, promoted the growth of the algae and, hence, retarded the algal decomposition.

To conclude, the mobile mesoherbivores, by facilitating the breakdown of the ephemeral algae, contribute to the stability of macrophythe and invertebrate communities. The suspension feeders constitute an important sink for primary production and, hence, increase the relative importance of the benthic system over the pelagic system. By prolonging the persistence of the drift algae, they may indirectly increase the instability of benthic assemblages.

INTRODUCTION

Since the early 1990s, particular attention has been paid to coupling and energy transfer between benthos and plankton (Bonsdorff & Blomqvist, 1993; Kautsky, 1995; Dame, 1996; Herman *et al.*, 1999; Peterson & Heck, 2001). In this transport suspension feeders, especially bivalves, are very important as they capture large quantities of phytoplankton and, hence, directly regulate primary production and indirectly regulate secondary production (Cloern, 1982, 1991; Loo & Rosenberg, 1989; Møhlenberg, 1995; Gili & Coma, 1998). Therefore, it is essential to know which factors regulate the feeding activity of suspension feeders.

Phytoplankton is considered to be the prime food for bivalves (*e.g.* Gili & Coma, 1998). The capture rates are usually derived from artificial diets or laboratory estimates (*e.g.* Riisgård, 2001), which limits their usefulness in analysing natural communities (Cranford, 2001; Widdows, 2001). The *in situ* studies quantifying the effect of the suspension feeders are few (Kautsky & Evans, 1987; Cranford *et al.*, 1998; Cranford & Hill, 1999; Kotta & Møhlenberg, 2002). These studies suggest that suspension feeders in nature exploit their full clearance capacity for short periods and often feed at a much reduced rate (*e.g.* Cranford, 2001).

Besides water temperature (Bayne *et al.*, 1977), salinity (Widdows, 1985) and pollution (Widdows *et al.*, 1995) the quality and concentration of seston coupled with flow regime have a significant impact on the mussels' activity (Kiørboe *et al.*, 1980; Fréchette *et al.*, 1989; Asmus & Asmus, 1993) and may account for the major variability of their *in situ* feeding behaviour. Therefore, there is a need for field measurements of the feeding behaviour of suspension feeders combined with the measurement of hydrobiological conditions in the nearbottom layer. The functional relationships between these variables have to be estimated for different areas and different times of the year to assess the importance of the suspension feeders grazing on the coastal ecosystem.

Benthic mesoherbivores constitute another important trophic component in the coastal ecosystems. Grazing by invertebrate mesoherbivores can regulate the structure and productivity of macroalgal communities (Orth & Van Montfrans, 1984). However, the share of "bottom-up control" and "top-down" effects is thought to be highly variable between sites and seasons (Menge, 1992; Worm, 2000). 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).

In recent decades, anthropogenic pollution has caused changes in plant biomasses and species composition in the whole coastal area of the Baltic Sea. The most drastic changes were the excessive growth of the filamentous macroalgae *Pilayella littoralis* (L.) Kjellm. and *Cladophora glomerata* (L.)

Kütz. and the decline of perennial and slow growing *Fucus vesiculosus* L. (Kangas *et al.*, 1982; Kautsky *et al.*, 1986; Vogt & Schramm, 1991; Kotta *et al.*, 2000). This raised the question about the role of benthic grazers: do they buffer or amplify the effect of eutrophication? The grazers are potentially able to consume a significant proportion of the macroalgal production and, hence, control the blooms of filamentous algae. On the other hand, the grazers may selectively consume perennial algae, which in turn favours the development of fast growing species and destabilises the communities.

The evidence about the effect of invertebrate grazing on macroalgae is highly variable and controversial. The prevalent benthic herbivores inhabiting the northern Baltic Sea are omnivorous (Nicotry, 1980; Franke & Janke, 1998) but they may be quite selective within food categories (Salemaa, 1978; Schaffelke *et al.*, 1995). Besides, the effect of grazers has strong temporal and spatial variation (Kotta *et al.*, 2000; Worm, 2000).

One section of the dissertation focuses on the grazing impact of the suspension feeders on the pelagic algal community in the northern Baltic Sea. The blue mussel *Mytilus edulis* L. and the zebra mussel *Dreissena polymorpha* (Pallas) were selected as the experimental species due to their ubiquity and, hence their significant potential contribution to phytoplankton removal. When writing this section I had in mind two major aims:

- to establish the functional relationships between ambient temperature, salinity, current velocity, phytoplankton biomass and the *in situ* biodeposition of the bivalves along the eutrophication gradient during different times of the year, and
- to estimate the algal grazing by the mussel population from these functional relationships taking into account the measured environmental variables, abundance and size distribution of the mussel population.

Another part of the dissertation focuses on the grazing impact of the mesoherbivores on the benthic macroalgal community. The test animals were the isopod *Idotea baltica* (Pallas), the amphipod *Gammarus oceanicus* Segerstråle and the shrimp *Palaemon adspersus* (Rathke). The specific aims were

- to study the habitat selectivity and feeding activity of *I. baltica* at different stages of algal succession representing the gradient of eutrophication,
- to measure seasonality in the grazing of all studied test animals,
- to describe the effect of water temperature, salinity, influx of nutrients, species composition, structure and physiological state of macrophytes on the grazing intensity of the mesoherbivores and
- to estimate the role of the mesoherbivores *I. baltica* and *G. oceanicus* and the suspension feeder *M. edulis* on the decomposition of the drift algae.

MATERIAL AND METHODS

Suspension feeding bivalves

M. edulis and *D. polymorpha* are the most conspicuous suspension feeders in the northern Baltic Sea. The species are most prevalent on hard bottoms above the halocline where, owing to low predation and high input of nutrients, they often form extensive multilayered mats (Segerstråle, 1957; Kautsky, 1981; Kautsky, 1995; Öst & Kilpi, 1997; Kotta *et al.*, 1998). *D. polymorpha* dominates at salinities less than 5 psu and *M. edulis* in the more saline environments (Kotta, 2000).

The biodeposition of the bivalves was estimated at three transects in the littoral zone of the Gulf of Riga (GOR) and two transects in the Gulf of Finland (GOF) from March to October during 1996–2002 (Fig. 1; **I**). The northern GOR sites were characterised by a wide coastal zone with a diverse bottom topography and extensive reaches of boulders. Depending on the salinity values a scattered population of *M. edulis* or *D. polymorpha* occurred on the boulders. The southern GOR transect had a narrow coastal zone. Coarse sandy substrate prevailed down to a depth of 4 m being replaced by boulders at greater depths. The boulders housed a dense population of *D. polymorpha*. Hard substrate prevailed at the northern GOF site. The coverage of *M. edulis* was almost 100% along this transect. The southern GOF was characterised by a mixture of sand, pebbles and boulders above 3 m depth. Deeper down only sandy substrate was found and, hence, the area was practically devoid of suspension feeding bivalves.

In each season the abundance, biomass and size-frequency distribution of the suspension feeders were estimated along the five above-mentioned transects and an additional transect in a more exposed part of GOF. Samples were collected from the seashore down to 12 m depth at a step of 1 m. Metal frames of 20×20 cm surface area were placed randomly on the bottom by a diver. All suspension feeders within the frame were collected. Three replicates were taken at each location. The length of the suspension feeders was measured to the nearest 0.1 mm using vernier callipers.

The *in situ* grazing rates of *M. edulis* and *D. polymorpha* were estimated by quantifying the defecation of chlorophyll *a* (Chl *a*) by the mussels. Bivalves were collected by a diver in the vicinity of deployment. Three individuals were placed on the net of the funnel allowing biodeposits to sediment to the collecting vial below. The incubation lasted 4–12 hours. In each season at least five incubations replicated three times were performed. The control treatment did not consist of mussels. During deployment the temperature and salinity were monitored. In Kakumäe Bay plaster balls were used to estimate the water currents in the nearbottom layer. The method is recognised as a simple and

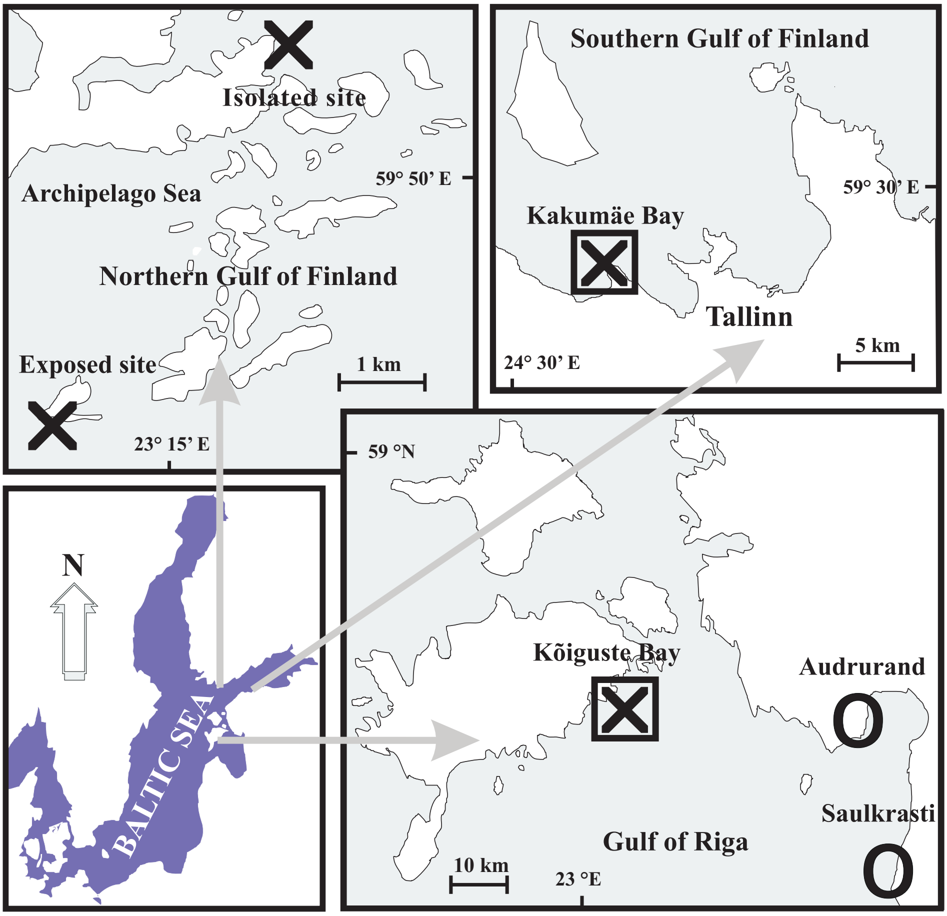


Figure 1. Study area. Crosses show the transects of *M. edulis*, open circles the transects of *D. polymorpha*, and squares the transects of mesograzers.

inexpensive tool for measuring integrated water motion over a wide range of flow rates. The dissolution rates of plaster balls are mainly a function of water velocity and less influenced by salinity and temperature within a range of our study (Muus, 1968; Thompson & Glenn, 1994).

After deployment the shell lengths were recorded, the sedimented material in the vials was sorted under a dissecting microscope and faeces was collected with a pipette and filtered on Whatman CF/F filters within 4 h of retrieval. Filters were extracted in dark in 96% ethanol overnight. Chl *a* was quantified fluorometrically correcting for phaeopigments (Pha) (Strickland & Parsons, 1972). The values of Chl *a* equivalent or total Chl *a* (Chl *a* eq) were calculated as Chl *a* eq = Chl *a* + 1.52 × Pha. Control treatments demonstrated no significant settling of particles (Chl *a* eq < 0.01 µg Chl *a* eq vial^{-1} h^{-1}).

Water samples for Chl *a* were taken at a distance of 25 cm from the cages in connection with retrieving biodeposits (*i.e.* in every 4–12 h). Hence, the average concentration of Chl *a* sampled at the start and end of an incubation was used as a measure of food concentration during incubation. Filtration and extraction of these samples were carried out within 1 h after sampling. The water samples were filtered onto Whatman GF/F filters. Chl *a* and Pha were measured as noted above.

In Kakumäe Bay an additional water sample for phytoplankton species composition was taken. The sample was fixed with acetic Lugol's solution to a final concentration of 0.5%. The fixed sample (10 to 50 ml) was settled in a sedimentation chamber for ≥24h and counted using an inverted microscope Olympus IM. Wet weight biomass of phytoplankton was calculated from cell geometry (HELCOM, 1988; Hillebrand *et al.*, 1999) and using cell volume tables (Phyto, Software Kahma Ky) or after original measurements.

In order to estimate the loss of Chl *a* during gut passage separate experiments were carried out. The mussels were incubated in 5 l buckets for 4 h. The bucket that contained no experimental animals served as a control. The animals were fed with natural sea water. At the end of the incubation the biodeposits were cleaned from the buckets by careful pipetting. The water samples for Chl *a* were taken at the beginning and at the end of the incubation. The concentrations of Chl *a* and Pha were estimated in biodeposits and water samples as described above. The loss of Chl *a* during gut passage was estimated as the ratio of the loss of Chl *a* in water to biodeposit production taking into account the algal growth and sedimentation in the control bucket.

The grazing of the mussel population on algae was estimated from the functional relations after correction for loss of Chl *a* during gut passage. In these calculations the data on ambient temperature, salinity, Chl *a* concentration, mussel abundance and their size distribution were taken into account. Grazing by individuals of different size (G_l) was scaled by shell length, *i.e.* $G_l = G_{20} \times l^2/20^2$, where G_{20} is the grazing rate of 20 mm individuals and l the shell length (Kiørboe & Møhlenberg, 1981). For more detailed description of the methods see Kotta & Møhlenberg (2002).

Benthic mesoherbivores

The isopod *Idotea baltica* (Pallas), the amphipod *Gammarus oceanicus* Segerstråle, and the shrimp *Palaemon adspersus* (Rathke) are ranked among the most important necto-benthic herbivores in the northern Baltic Sea (Hällfors *et al.*, 1981). The euryhaline *I. baltica* is originally littoral and sublittoral crustacean of tidal shores with a characteristic pattern of distribution correlated with the tidal level, exposure and salinity variations of the habitat. It has a wide, almost cosmopolitan distribution, and its geographical races have been described (Naylor, 1955; Sywula, 1964). In the Baltic Sea, *I. baltica* is common in the *F. vesiculosus* and *C. glomerata* belts (Jansson, 1974; Haahtela, 1984; Orav *et al.*, 2000), but occurs also on *Zostera marina* L. dominated soft bottoms (Salemaa, 1978; Boström & Bonsdorff, 1997). *G. oceanicus* is a prevailing amphipod on *F. vesiculosus* dominated hard bottoms (**III–IV**; Kautsky *et al.*, 1999; Orav et al., 2000). *P. adspersus* is one of the two decapod species that has adapted to the brackish water of the northern Baltic Sea. The species is found on vegetated hard bottoms; however, the knowledge on the distribution of the species is scarce.

Comparative **experiments on the habitat and food choice** of *I. baltica* at the communities representing low and high eutrophicated systems were performed in Kõiguste Bay in June 2000 (**II**). Adult *I. baltica* were collected from a shallow (1–3 m) hard bottom area within bushes of *F. vesiculosus* by shaking the algae.

Six different macroalgal species were deployed in the experiments: the brown algae *F. vesiculosus, Chorda filum* (L.) Stackh. and *P. littoralis*, the red alga *Ceramium tenuicorne* (Kütz.) Waern and the green algae *C. glomerata* and *Enteromorpha intestinalis* (L.) Nees. *E. intestinalis* and *C. glomerata* are known to cause extensive macroalgal blooms in the shallower areas and *P. littoralis* in the deeper parts of the sea, respectively (Bonsdorff *et al.*, 1997; Bäck *et al.*, 2000; Norkko *et al.*, 2000; Vahteri *et al.*, 2000; Lehvo & Bäck, 2001). Macroalgae were obtained at the same site as the isopods. Besides, four types of artificial plants made of polypropylene were used: *F. vesiculosus*, *Furcellaria*, *Zostera*, fine filamentous alga. These types represent the prevalent morphological forms of algae that idoteids may encounter in the study area.

The habitat choice of idoteids was studied in five series of experiments. In the first experiment live macroalgal species were deployed. Prior to the experiment the epiphytes inhabiting *F. vesiculosus* were removed. Some bushes of *F. vesiculosus* were artificially covered with the epiphyte *P. littoralis*. In the second experiment the attractiveness of the live and artificial *F. vesiculosus* was compared to the artificial *F. vesiculosus* covered with the prevailing epiphytes. If *I. baltica* selected live *F. vesiculosus* then it would indicate its importance in the diet of the isopod. On the other hand, if there was no significant difference in the habitat choice of idoteids between live and artificial *F. vesiculosus* then the algae would serve as a shelter for *I. baltica*. Besides, the experiment tests if the epiphytic *P. littoralis* and *C. glomerata* increase the attractiveness of *F. vesiculosus* as a substrate (*i.e.* artificial *F. vesiculosus*). The third experiment was designed to study the habitat selection of *I. baltica* in less eutrophicated conditions, *i.e.* when *P. littoralis* was removed. Idoteids were provided live and artificial *F. vesiculosus* together with the artificial *F. vesiculosus* covered with the epiphyte *C. glomerata*. In the fourth experiment idoteids were offered the epiphyte-free live *F. vesiculosus*, artificial *Furcellaria* and artificial *Furcellaria* covered with the epiphytic *C. glomerata* and *P. littoralis*. *Furcellaria* is known to be an alternative substrate for *I. baltica* in case of scarcity of *F. vesiculosus*

(Kotta *et al.*, 2000). The experiment tests the attractiveness of live *F. vesiculosus* in relation to another prevailing algal form. Besides, it shows whether the epiphytes affect the habitat selection of *I. baltica*. The fifth experiment included all types of artificial algae and the live *F. vesiculosus*. The aim of the experiment was to demonstrate the role of algal morphology on the habitat selection of *I. baltica*. Besides, it tests whether the live *F. vesiculosus* is favoured over the studied artificial algae, *i.e.* whether the live *F. vesiculosus* has some additional value than being a substrate for *I. baltica*. A feeding preference experiment was performed with those macroalgae that *I. baltica* selected the most often as habitat, *i.e. P. littoralis* and *F. vesiculosus*. For the exact procedure of the experiments see paper **II**.

Seasonality in invertebrate grazing was studied in Kõiguste Bay in April, July and October 2001 (**IV**) and in Kakumäe Bay monthly from April to October 2002. *F. vesiculosus*, *P. littoralis*, *Furcellaria lumbricalis* (Huds.) and *C. glomerata* were deployed in Kõiguste Bay and *F. vesiculosus* and *P. littoralis* in Kakumäe Bay. In Kakumäe Bay *F. vesiculosus* and *P. littoralis* were deployed separately and together. The specimens of *F. vesiculosus* were divided into apical (juvenile) and basal (old) parts and treatments with *F. vesiculosus* overgrown with *P. littoralis* and epiphyte-free *F. vesiculosus* were distinguished. The use of different macroalgal treatments in different seasons depended on the natural occurrence of the algae in the field.

Among mesoherbivores *I. baltica*, *G. oceanicus* and *P. adspersus* were deployed in Kõiguste Bay and the first two species in Kakumäe Bay. *I. baltica* and *G. oceanicus* were collected within the stands of *F. vesiculosus* as described above. *P. adspersus* were caught by dredging the vegetated areas. Only adult specimens were used in the experiment.

Grazing was studied in 5×5×20 cm nylon netbags of 1 mm mesh size. When available in the field, either two specimens of *I. baltica*, two specimens of *G. oceanicus* or one specimen of *P. adspersus* was added each macroalgal treatment. Three replicates of each treatment were used. The wet weight of algae was determined prior to the experiment to the nearest of 0.01 g. Before weighing the algae were gently dried on plotting paper until the paper did not become wet any more. Additional three replicates of each macroalgal treatment served as control to obtain the ratio of wet to dry weight. The algae were dried at 60°C during 48 h.

The netbags were placed at 2 m depth about 0.5 m above the bottom. Each series of the experiment lasted 10 days. In parallel to the grazing experiments, the *in situ* diurnal primary production of the studied macroalgal species was measured using the oxygen method. Small tufts (*c.* 0.05 g dw) with no macroepiphytes and grazers were placed in 600 ml glass bottles, filled with sea water and incubated horizontally on special trays at 0.5 m depth. Bottles that did not include the algae served as controls. There were five replicates per each treatment and five controls (**V**; Kotta *et al.*, 2000). Based on the production estimates, all macroalgal species were photosynthetically active and no decomposition of the macroalgae occurred.

At the end of the experiment the test animals were counted and the dry weights of invertebrates and macroalgae were determined. The changes in the dry weight of the algae per dry weight of the invertebrates in the nylon mesocosms served as the estimates of invertebrate grazing in the field. In parallel to the grazing experiments water temperature, salinity and concentration of nutrients were estimated in Kakumäe Bay using standard methods (Grasshoff, 1976; Solorzano & Sharp, 1980; Raimbault & Slawyk, 1991).

Macroalgal decomposition experiments were carried out in Kõiguste Bay during 26.04.–25.05. and 25.07.–24.08.2000 (last checkpoint day 70 in autumn) (**V**). Since 1995 an increased production of the filamentous *P. littoralis* and *C. glomerata* was observed in Kõiguste Bay (Kotta *et al.*, 2000). These opportunistic algal species annually accumulate into unattached mats having maximum occurrence at a depth of 2–4 m from May to September. The size of the algal mats varies from a few square metres to a square kilometre. The thickness of mats usually does not exceed 5 cm. Hence, the decomposition of macroalgae occurs mainly in aerobic conditions and the decomposing material partly consists of live algae. As compared to the adjacent sea, the algal mats are characterised by a notably higher number of mesoherbivores, mainly *Gammarus* spp. and *Idotea* spp. Very dense assemblages of the suspension feeder *Mytilus edulis* are found on boulders.

The brown algae *P. littoralis* and the green algae *C. glomerata* were used in the incubations. The algae were collected from the rocks adjacent to the incubation site. The freshly collected algae with no macroepiphytes were placed into nylon mesh bags as described above. The test organisms were added to three replicate bags per treatment. The herbivore *I. baltica* (5 individuals per bag), the detrivore *G. oceanicus* (5 individuals per bag) and the suspension feeder *M. edulis* (10 individuals per bag) were used. The number of animals in the experimental unit corresponded to the densities recorded in the field. Survival of all species was good in all treatments at the end of experiments (average 92%).

The mesh bags with algal material were incubated at a depth of 2 m (anchored on a rope about 20 cm from the bottom). On average once in a week three mesh bags of each treatment were collected for the determination of the algal decomposition rate in terms of dry weight changes and nutrient content. During sampling the remaining mesh bags were cleaned to avoid clogging. The samples were immediately placed in a freezer (–20ºC). In the laboratory algal material was dried at 60°C for 24 hours. For estimating the physiological state of algal material on different phases of decomposition the net photosynthetic rates were measured using the oxygen method. In parallel to experiments live algae were collected from the rocks adjacent to the experimental site and their photosynthetic activity was measured. This allowed us to compare the productivity of natural and decomposed macroalgae.

RESULTS AND DISCUSSION

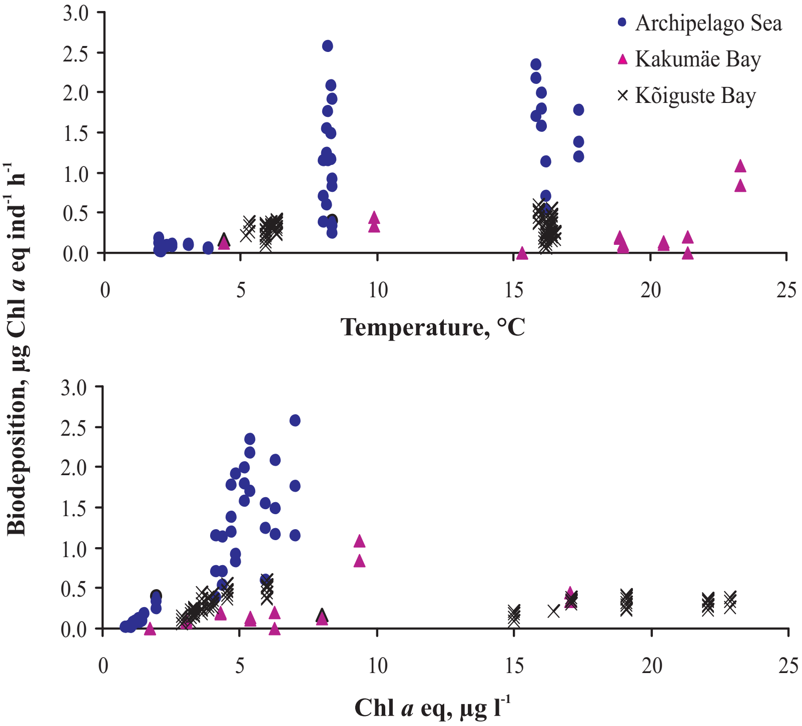
Impact of benthic suspension feeders on phytoplankton communities

Temperature and phytoplankton biomass were the major factors causing temporal and spatial variation in the biodeposition of mussels. However, the relationships varied significantly between species, sites and seasons. The models predicted from 43 to 83% of the variability in the biodeposition rates of the bivalves. Poorest models were described in the areas where food conditions were instable either due to discharges of municipal wastes (Saulkrasti, Audrurand, Kõiguste) (Fig. 2 and 3).

Low temperatures (< 8ºC) reduced the performance of suspension feeders. Low pumping rates at low temperatures can be accounted for by temperature induced change in ciliary beat frequency and the increased viscosity of the water (Jørgensen *et al.*, 1990; Loo, 1992). However, as low temperatures and low food levels coincide in many areas, low temperature can be considered a favourable condition during such periods of food shortage, reducing high costs of suspension feeding when the concentration of food particles is low.

At higher temperatures the relationship between suspension feeding and the water temperature was not constant but depended on the food supply and studied basin. Food availability affects the activity of suspension feeders (Sprung & Rose, 1988; Dolmer, 2000; Hawkins *et al.*, 2001). Suspension feeding increased with increasing ambient concentration of Chl *a* and levelled off at high food concentrations. It is known that high algal concentrations (> 5–10 μg Chl *a* l^{-1}) may lead to reduced valve gape and reduction of the clearance rate (Riisgård & Randløv, 1981; Riisgård, 1991, 2001). Such high Chl *a* values were prevailing in GOR suggesting that fitted polynomial functions between suspension feeding and the food supply reflected the saturation at high Chl *a* concentrations in GOR. In GOF, however, a linear functional response showed that such saturation reduction was never reached.

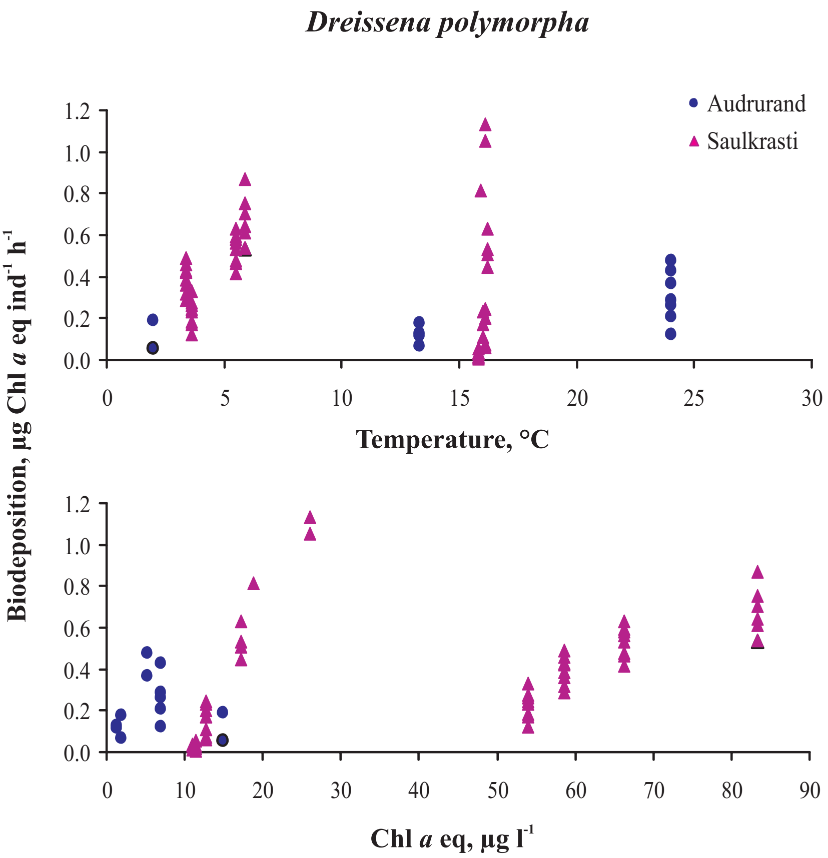
Comparison of the clearance rates of *M. edulis* showed about three times lower suspension feeding activity in GOR than in the northern GOF site despite of similar temperatures and Chl *a* concentrations. Hence, temperature and Chl *a* concentrations *per se* could not explain the behavioural variation in filtering activity. Due to the difference in exposure the current velocities are significantly higher in the northern GOF than in GOR sites. The vertical mixing of the water column increases the amount of available food and promotes the filtration activity of mussels (Dolmer, 2000; Newell *et al.*, 2001). In the southern GOF the inclusion of the current velocity interacting with the water Chl *a* significantly improved the model of clearance rate of *M. edulis* (**I**).



Mytilus edulis

$$\mathbf{Biodeposition_{Archipelago} = -0.0054 \times T^2 + 0.0373 \times TChl - 0.0217,}\ p < 0.001,\ r^2 = 0.83$$
$$\mathbf{Biodeposition_{Kakumäe} = 0.000090 \times TChlCurrent - 0.053532,}\ p < 0.001,\ r^2 = 0.71$$
$$\mathbf{Biodeposition_{Kõiguste} = 0.0087 \times TChl - 0.0285 \times Chl - 0.1508,}\ p < 0.001,\ r^2 = 0.61$$

Figure 2. Biodeposition rate of *M. edulis* as a function of ambient temperature and chlorophyll *a* equivalent (Chl *a* eq). Best models of multiple linear regressions describing the biodeposition rates are added. The abbreviations are as follows: T – temperature, Chl – Chl *a* eq, Current – current velocity, multiple terms indicate their interaction.



$$\mathbf{Biodeposition}_{\mathrm{Audrurand}} = 0.0004 \times T^2 + 0.0838,\ p < 0.009,\ r^2 = 0.43$$

$$\mathbf{Biodeposition}_{\mathrm{Saulkrasti}} = 0.002 \times \mathrm{TChl} + 0.036 \times S^2 - 1.094,\ p < 0.001,\ r^2 = 0.64$$

Figure 3. Biodeposition rate of *D. polymorpha* as a function of ambient temperature and chlorophyll *a* equivalent (Chl *a* eq). Best models of multiple linear regressions describing the biodeposition rates are added. The abbreviations are as follows: T – temperature, S – salinity, Chl – Chl *a* eq, multiple terms indicate their interaction.

Kautsky and Evans (1987) measured the highest biodeposition of *M. edulis* during autumn storms in October–December in spite of low temperatures. Moreover, individual and colony sizes but likely also diversity of suspension feeders increase as the current velocity increases (Gili & Ballesteros, 1992; Lesser *et al.*, 1994; Dolmer, 2000).

The quality of the seston affects the filtration activity of mussels (Bayne *et al.*, 1987, 1993; Asmus & Asmus, 1993; Hawkins *et al.*, 2001). In the present study the biomass of benthic diatoms described better the biodeposition rate of *M. edulis* than Chl *a* concentration alone. This indicates that *M. edulis* is highly selective between phytoplankton species. Although the selectivity of different suspension feeders has been documented earlier (Newell & Jordan, 1983; Shumway *et al.*, 1985), the biomass structure of phytoplankton populations is rarely taken into consideration when studying the interactions between suspension feeders and phytoplankton.

Earlier laboratory studies have stressed a significant effect of water temperature on the suspension feeding mussels (Bayne *et al.*, 1977; Newell & Bayne, 1980; Jørgensen *et al.*, 1990). In the laboratory studies food is usually optimal whereas in nature suboptimal conditions prevail. When food is scarce decreased clearance rates of mussels have been observed both in laboratory and field conditions (Famme *et al.*, 1986; Cranford *et al.*, 1998). Therefore, in field the concentration of phytoplankton rather than temperature regulates the feeding behaviour of suspension feeders under suboptimal food conditions. In Kakumäe Bay we did not perform the experiment below 4.4ºC. However, Loo (1992) demonstrated high clearance rate of *M. edulis* using natural seston composition at temperatures between –1 and 4.8ºC, suggesting that the mussel can potentially utilise a significant share of phytoplankton spring-bloom.

Due to the aggregated distribution of mussels the grazing rate of the populations of suspension feeders varied significantly within and between study areas. The grazing rate was orders of magnitude higher in GOF than GOR. However, the northern GOR has extensive shallow areas and moderate water exchange. Hence, the removal of an average 14% of Chl *a* stock in GOR each day is likely to be sufficient for the benthic control of phytoplankton in the area. This was also reflected by the strong horizontal and vertical gradients in Chl *a* measured during the study. In GOF, owing to the small relative share of coastal areas and significant water exchange, it is difficult to estimate the effect of suspension feeders grazing on phytoplankton population at the regional scale. Nevertheless, the accumulation of biodeposits through mussel filtration was an important process at the GOF site. The more exposed was the region the higher were biodeposition values. The utilisation rate of phytoplankton by suspension feeders varies with benthic boundary-layer flow conditions (Fréchette *et al.*, 1989; Dolmer, 2000; Newell *et al.*, 2001). On the population level the biomass of suspension feeders increases with the current intensity and frequency (Gili & Ballesteros, 1992; Lesser *et al.*, 1994). It is likely that in the outer archipelago stronger vertical mixing increased the amount of food available to the suspension feeders and, hence, supported higher biomasses. Lower values of population grazing in the central archipelago might be attributed to the lower wave energy input to the system.

The negative relationship between the water Chl *a* concentration and population grazing of the bivalves indicated that under eutrophicated conditions the impact of suspension feeders on pelagic communities is small relative to cleaner environment (Fig. 4). The studied bivalves exploit their filtration capacity to about 5 µg Chl *a* l^{-1} (Clausen & Riisgård, 1996). Above that level a considerable reduction of clearance rate is observed, presumably caused by overloading of the alimentary canal (Riisgård, 1991). Besides, very high sedimentation and concentration of inorganic particles often observed in eutrophicated areas are detrimental to the suspension feeding bivalves (Kiørboe *et al.*, 1980).

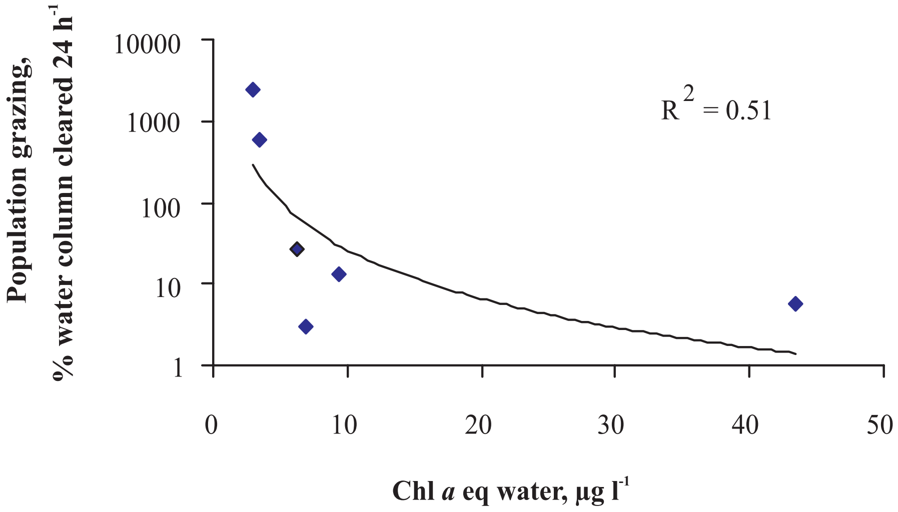


Figure 4. Relationships between water chlorophyll *a* equivalent (Chl *a* eq) and the average population grazing of bivalves in the studied littoral zones (0-12 m).

Food and habitat choice of *Idotea baltica*

Following coastal eutrophication the proportion of filamentous algae increases in macrophyte communities (Bonsdorff *et al.*, 1997; Bäck *et al.*, 2000; Norkko *et al.*, 2000; Vahteri *et al.*, 2000; Lehvo & Bäck, 2001). There exists circumstantial evidence that after the extensive growth of *P. littoralis* and the disappearance of *F. vesiculosus* the density of *I. baltica* has risen hundred of times (Kotta *et al.*, 2000). This suggests other algae than *F. vesiculosus* to be the prime diet for the isopod.

According to the literature *I. baltica* is omnivorous feeding on benthic microalgae, filamentous algae, macroalgae, detritus, small invertebrates and even its conspecifics (Naylor, 1955; Ravanko, 1969; Sywula, 1964; Nicotry, 1980; Robertson & Mann, 1980; Franke & Janke, 1998). Despite its omnivory, *I. baltica* is rather selective within food categories (Salemaa, 1978; Schaffelke *et al.*, 1995). Its dietary choice involves the selection between different algal species (Schaffelke *et al.*, 1995; Schramm *et al.*, 1996) but likely between different parts of the algal thallus (Salemaa, 1987). In the northern Baltic Sea, however, *F. vesiculosus* was considered as the main source of food for *I. baltica* (Salemaa, 1987). The literature does not provide a definite answer if *I. baltica* select *F. vesiculosus* for the shelter or food as the experiments about the microhabitat choice of idoteids usually involved only a single macroalgal species (*e.g.* Salemaa, 1987; Merilaita & Jormalainen, 2000).

The present study showed that *I. baltica* preferred *P. littoralis* and *F. vesiculosus* over other studied algae. The robust, flat thalli of fucoids provided the isopod mainly shelter but had little food value. The epiphytic macroalga *P. littoralis* significantly added the habitat value of the host alga indicating that *P. littoralis* was a more rewarding site than its host *i.e. F. vesiculosus*. This was also supported by the feeding choice experiment showing that *P. littoralis* constituted an essential part of the diet of the isopod *I. baltica* (**II**).

Earlier studies have suggested that the habitat choice of isopods is mainly a function of algal morphology (*e.g.* Nicotri, 1980; Hacker & Madin, 1991). Despite the relatively low food value *I. baltica* is attracted to large, tough, branched algae to which their dorsoventrally flattened body is well adapted for. However, recent studies have demonstrated the preference of grazers to feed on filamentous algae (Shacklock & Doyle, 1983; D'Antonio, 1985; Worm & Sommer, 2000) and, hence, the epiphytic food resources to be the prime factor that determines the presence of idoteids in macrovegetation (Boström & Mattila, 1999; Pavia *et al.*, 1999). These findings correspond to the field observations of a positive relationships between epiphyte load and grazer density (Kotta *et al.*, 2000; Worm & Sommer, 2000).

It is likely that the increasing epiphyte load in recent decades has triggered a substantial shift in the habitat selection of *I. baltica*. In less eutrophicated conditions with a few epiphytes present, *I. baltica* selected the canopy-forming macroalga (less exposing substrate) in order to increase protection from visual predators (Stoner, 1980; Main, 1987). Nowadays, with increasing epiphyte load, *I. baltica* is attracted to fully overgrown macrovegetation (Kotta *et al.*, 2000; Orav *et al.*, 2000; Worm & Sommer, 2000) but likely to free-floating macroalgal mats consisting of ephemeral algae (Norkko *et al.*, 2000). This selection may be advantageous to the isopods, related to the avoidance of fish in biotopes dominated by ephemeral algae (Salemaa, 1979, 1987). Besides, following the bloom of ephemeral algae the density of *I. baltica* increases notably (Salemaa, 1979; Kangas *et al.*, 1982; Arrontes, 1990; Duffy, 1990; Kotta *et al.*, 2000). Consequently, the isopods might escape from the predation pressure, explaining their occurrence in the more exposed microhabitat.

The results of this study showed that *I. baltica* was highly selective and not all epiphytic macroalgae had an equal food value. As compared to *P. littoralis*, *C. glomerata* significantly reduced the habitat value for the isopods. Live *Cladophora* is known to have thick cell walls and is likely to be highly resistant to herbivory (**V**; Birch *et al.*, 1983; Gabrielson *et al.*, 1983). Besides, it seemed that the adult isopods were not well adapted to crawl along *C. glomerata*. In extreme cases they were trapped into the filaments and died there.

On the other hand, *P. littoralis* was at the earlier stage of its decomposition in the study area during the experiment (**V**). The decomposing alga has less resistant cell walls and high concentration of nitrogen and phosphorus, which makes the alga more attractive to mesoherbivores (Mann, 1988). In the light of high selectivity of *I. baltica*, the poor correlation between epiphyte load and the isopod density (Nicotri, 1980; Pavia *et al.*, 1999) might be explained by the unfavourable species composition of epiphytes. Besides, the seasonal changes in the epiphyte species composition may further mask this relationship.

According to the habitat choice experiment *I. baltica* preferred less robust algae than *F. vesiculosus*. Following the mass bloom of *P. littoralis* and the decline of *F. vesiculosus* in the northern Baltic Sea (Haahtela, 1984; Kangas *et al.*, 1982; Salemaa, 1987), the majority of *I. baltica* switched into an alternative substrate, *i.e. Furcellaria lumbricalis* (Huds.) J. V. Lamour (Kotta *et al.*, 2000). As compared to *F. vesiculosus* the alga is finer and corresponds to the characteristics of "the ideal type". However, under less eutrophicated conditions *F. lumbricalis* has low coverage of epiphytes and, hence, a little food value for the isopod.

The conclusion of this study is that under more eutrophicated conditions the choice of *I. baltica* between various macroalgae is mainly based on their attractiveness as a food. It is likely that under less eutrophicated conditions when the coverage of epiphytes is low, and the active search for food considerably increases the risk to be eaten by predators, the habitat choice of isopods is determined by the structural characteristics of the substrate offering the best protection against the predators.

Owing to the effective removal of epiphytes in eutrophicated conditions the isopod has a positive effect on perennial macroalgae (Brawley & Adey, 1981; Robertson & Lucas, 1983; Brawley & Fei, 1987; Williams & Seed, 1992; Jernakoff & Nielsen, 1996). Hence, the isopods act as stabilisers of the macroalgal communities by compensating for nutrient effects on ephemeral algal growth (Neckles *et al.*, 1993; Williams & Ruckelshaus, 1993; Jernakoff *et al.*, 1996).

Seasonal variations in the grazing of *Gammarus oceanicus*, *Idotea baltica* and *Palaemon adspersus* on benthic macroalgae

Experiments on the seasonal changes in the grazing of the prevalent benthic mesoherbivores indicated that *P. littoralis* was the prime diet of the studied grazers in Kõiguste Bay. The consumption of *F. vesiculosus* was moderate when the biomass of *P. littoralis* was reduced in the field (**IV**).

As mentioned in previous chapter *I. baltica* has a wide food spectrum (Naylor, 1955; Ravanko, 1969; Sywula, 1964; Nicotry, 1980; Robertson &

Mann, 1980; Franke & Janke, 1998) but on the other hand the species is highly selective within food categories (Salemaa, 1978; Schaffelke *et al.,* 1995; Schramm *et al.*, 1996). In the northern Baltic Sea, however, *F. vesiculosus* is considered to be the main source of food for *I. baltica* (Salemaa, 1987). As stressed earlier, the experiments about the microhabitat choice of idoteids usually involved only a single macroalgal species such as *F. vesiculosus* (*e.g.* Salemaa, 1987; Merilaita & Jormalainen, 2000). The present study indicated the prevalence of *P. littoralis* as the main food for *I. baltica*. In the absence of *P. littoralis*, *I. baltica* fed on *F. vesiculosus* and *C. glomerata*.

Gammarids are considered selective omnivores. Their diet consists of decaying organic matter with its microbial community, macroalgae but also other animals such as other invertebrates, fish eggs, wounded fish (*e.g.* Macneil *et al.*, 1997). The utilisation of macrophytes is dependent on plant species, its condition, plant particle size, microbial activity on the plant material and nutritional quality (Hutchinson, 1975; Wetzel, 1983). The growth of limnic gammarids *Gammarus fossarum* Koch and *Gammarus roeseli* Gervais is affected by the type of diet, being high on naturally decaying leaves and fine organic detritus and low on green algae (Pöckl, 1995). Flesh supplements to an algal diet accelerate the growth and maturation of gammarids (Vassallo & Steele, 1980).

My observations demonstrated that besides *P. littoralis*, *G. oceanicus* consumed significant amounts of the green alga *C. glomerata*. A study with the limnic gammarids showed that among a large variety of food, the growth and survival of the amhipods were poorest with *Cladophora* sp. (Pöckl, 1995). The difference between these observations might be attributed to the condition of *Cladophora*. Earlier studies have demonstrated that the attractivity of *Cladophora* to invertebrate grazing is highly dependent on the physiological state of the filamentous algae (**V**).

Palaemon spp. are omnivorous, feeding on algae, moss, debris and small arthropods (Berglund, 1980). Other studies suggest the prevalence of carnivorous habits (Sitts & Knight, 1979; Siegfried, 1982). The dissertation showed that *P. adspersus* consumed relatively high quantities of *P. littoralis* and basal parts of *F. vesiculosus*. However, the consumption rates were manifold lower as compared to *I. baltica* and *Gammarus* spp.

In Kakumäe Bay the invertebrate grazing was mainly a function of the photosynthetic activity of alga both for *P. littoralis* and for *F. vesiculosus*. Grazing increased with decreasing algal photosynthetic activity. When the two algal species were incubated together the presence of *P. littoralis* modified the grazing of *F. vesiculosus*. Invertebrate grazing on *F. vesiculosus* was stronger when the net photosynthetic activity of *P. littoralis* was higher and that of *F. vesiculosus* was lower. The presence of *F. vesiculosus* did not modify the grazing on *P. littoralis*, and the grazing on *P. littoralis* was only affected by its net photosynthetic activity. Water temperature, salinity and nutrient concentration did not correlate with the grazing of the studied mesoherbivores. The results indicated that (1) the physiological state of the algae explains the best the interannual variation in the activity of mesograzers, (2) the grazers are not likely to control the early outbreak of filamentous algae by avoiding young and photosynthetically active algae and (3) the grazers contribute to the stability of the ecosystem by potentially removing large quantities of the ephemeral algae prior to their decomposition.

Effect of benthic mesoherbivores on the decomposition of the drift algae

In highly eutrophicated systems mass development of filamentous algal species is commonplace in the coastal areas worldwide (Ryther & Dunstan, 1971; Fletcher, 1996; Morand & Briand, 1996; Schramm & Nienhuis, 1996; Valiela *et al.*, 1997; Paerl, 1997). When detached the algae form drifting mats and cover the sea bottom in extensive areas. Drift algae have been increasingly observed also in the Baltic Sea where they have become an ecological and economic problem (Trei, 1983, 1991; Bonsdorff *et al.*, 1997; Bäck *et al.*, 2000; Norkko *et al.*, 2000; Vahteri *et al.*, 2000; Lehvo & Bäck, 2001; Martin *et al.*, 2003). The algal mats modify the nutrient dynamics (Lavery & McComb, 1991; Peckol & Rivers, 1996) and significantly disturb benthic vegetation and invertebrates (Norkko & Bonsdorff, 1996a,b,c; Kotta *et al.*, 2000; Norkko *et al.*, 2000). The decomposition of the algae often results in widespread anoxic conditions, which destroy living organisms in the underlying sediments and destabilise the whole shallow-water ecosystem (Norkko & Bonsdorff, 1996a,b,c; Hansen & Kristensen, 1997; Thiel *et al.*, 1998; Norkko *et al.*, 2000).

There exists circumstantial evidence that algal mats may facilitate the establishment of nonindigenous species. The distribution area of the North-American polychaete *Marenzelleria viridis* (Verrill) coincides with the distribution area of *F. lumbricalis* in the Väinameri sea area (**III**). The species was for the first time observed in the Baltic Sea in 1985 (Bick & Burkhardt, 1989), and since then it has spread quickly around the basin (Zettler *et al.*, 2002). Higher biomass of the polychaete under the mat of *F. lumbricalis* agrees with the hypothesis that low predation and uniformity of assemblage facilitate the establishment of the introduced species (Carlton, 1996). Besides, intermediate disturbance (Connel, 1978) due to temporary hypoxia may be beneficial for the establishment of opportunistic species like *M. viridis*. The polychaete induced additional stress to the infaunal communities by reducing the survival of the native species (**VI**).

Due to the ecological importance of the macroalgal mats it becomes essential to know which variables control the decomposition of the drift algae. According to the literature the decomposition rate of the drift algae is highly variable and species specific. The algal mats may already disappear within a month but likewise persist for more than two years (Buchsbaum *et al*., 1991). The drift algae are often colonised by a dense assemblage of opportunistic macrofaunal species (*e.g.* Norkko *et al*., 2000). Being primarily herbivores or detrivores they likely modify the algal decomposition.

Experiments on the grazing of drift algae showed that the decomposition of macroalgae was related to water temperature and their net photosynthetic rates. The effect of invertebrates was variable ranging from the doubling of the decomposition rate to the promotion of the algal growth. The nature of the invertebrate effects depends on the season, algal species and algal condition as well as on invertebrate species (**V**).

The significance of temperature in regulating the decomposition of macroalgae in field has been demonstrated earlier (*e.g.* Carpenter & Adams, 1979; Birch *et al*., 1983). Besides temperature, the photosynthetic processes were likely as important in our experiment as we used initially live algal material. As shown by the results of the present experiment, the net photosynthetic rate of *C. glomerata* was high enough to compensate the decomposition of the alga. Hence, the value of algal decomposition was mainly a function of its productivity. On the other hand, the net photosynthetic rate of *P. littoralis* was very low already at the beginning of the experiment (*i.e.* alga was at the final stage of growth) and the algal decomposition was primarily controlled by temperature.

The field studies involving manipulation of invertebrates in loose-lying algal mats are scarce (Salovius & Bonsdorff, 2004), and usually concerned with the effects of the alga on the invertebrates (*e.g.* mortality, density) and not *vice versa* (Byren & Davies, 1986; Rieper-Kirchner, 1990; Norkko *et al*., 2000). The present experiment demonstrated that the role of benthic invertebrates on algal decomposition varied between algal and invertebrate species and among seasons. In general, herbivores had no effect on the algae in the first two weeks of deployment. The low impact of herbivory suggests the unpalatability/ resistance of the algae at the beginning of the decomposition. Within some weeks of deployment when the cell walls of the algae are likely to be less resistant to herbivory (Birch *et al*., 1983) and the concentration of nutrients increases in the decomposing material as a result of increased microbial activity (Boyd, 1970; Byren & Davies, 1986; Buchsbaum *et al*., 1991), the algae become more attractive for benthic invertebrates (Mann, 1988).

In the spring season, *I. baltica* significantly increased the production of *C. glomerata* and retarded the decomposition of *P. littoralis*. It is likely that *I. baltica* fed selectively on more degraded parts of the alga and, hence, the condition of the remaining filaments was improved (*i.e.* less shade, more nutrients). Besides, in the light of low grazing pressure, the selective removal of microalgae by *I. baltica* on the studied macroalgae is not unlikely. The positive effect of *I. baltica* on the studied algae was not observed in summer, probably due to the lower photosynthetic activity of the algae.

In summer the filter feeder *M. edulis* significantly reduced the decomposition of *P. littoralis* during the first two weeks of the deployment. It is important to stress that we used initially live algal thalli, and that the growth took place together with the decomposition process. Owing to their high filtration activity and considerable biodeposition (Kotta & Møhlenberg, 2002), *M. edulis* significantly increased the nutrient availability in the benthic system (Kautsky, 1995) and, hence, promoted the growth of opportunistic *P. littoralis*. Similar advantageous effect of *M. edulis* has been previously documented on the eelgrass *Zostera marina* (Reusch *et al.*, 1994). However, *M. edulis* did not affect the decomposition rate of *P. littoralis* at the end of the experiment. This may be attributed to the absence of photosynthetic activity of the algae at the later stages of decomposition. The lack of similar effect in spring suggests a lower filtration (*i.e.* biodeposition) rate of the mussels at low temperatures (Newell & Bayne, 1980; Jørgensen *et al.*, 1990; Loo, 1992; Kotta & Møhlenberg, 2002).

The occurrence of drifting algae is an annually repeated phenomenon in the Baltic Sea (Ólafsson, 1988; Bonsdorff, 1992; Norkko, 1997; Norkko *et al.*, 2000) and as shown in this study, the final breakdown of the algae occurs in the same year. The algal species used in the experiment differ in their seasonality. After a mild winter, the filamentous algal zone is first dominated by *P. littoralis*, which degenerates and detaches before summer (Kiirikki, 1996). However, in our study area the mass development of *P. littoralis* is observed till early August (Martin *et al.*, 2003). *C. glomerata* appear in early summer and the mass development of the species occurs in summer (Kiirikki, 1996). Depending on the population dynamics of *P. littoralis* and *C. glomerata*, the algal mat appears in June-July in the study area. Hence, the decomposition rate measured in summer-autumn is a realistic estimate of the process in the field. The decomposition of algae is probably related to the exposure of the site (Norkko *et al.*, 2000). Drift algae are more stable in the sheltered sites whereas intensive fragmentation of the mat takes place when exposed to wind-wave disturbance. Besides, anoxic conditions develop more frequently in the sheltered areas, which, in turn, notably retard the decomposition of the drift algae. As estimated from a moderately exposed, though typical coastal site of the northern Baltic Sea, our experiment gives “an average” estimate of this process in the area.

The macroalgal mats have been acknowledged as a factor inducing widespread mortality of benthic invertebrates caused by temporal development of anoxic conditions during the decomposition process (Nicholls *et al.*, 1981; Soulsby *et al.*, 1982; Everett, 1994; Norkko & Bonsdorff, 1996a,b,c; Norkko *et al.*, 2000). The drift algae may favour epibenthic detrivores and omnivores (Gore *et al.*, 1981; Kirkman & Kendrik, 1997) but also herbivores normally associated with seagrass beds (Virnstein & Howard, 1987; Holmquist, 1997; Norkko *et al.*, 2000). In that sense, the mobile invertebrates, by facilitating the breakdown of the algae, indirectly contribute to the stability of macrofauna living in the sediment. In other words, the faster decomposition of the drift algae would reduce the frequency and duration of anoxic conditions in sediment under the algal mat. Besides, affecting the rates of detrital decay and nutrient mineralisation of the drift algae, herbivores and/or detrivores control the cycles of primary productivity of phytoplankton (Thayer, 1974). On the other hand, the suspension feeder *M. edulis*, by prolonging the persistence of the drift algae, may indirectly increase the mortality of infaunal suspension feeders (*e.g. Mya arenaria*) and, hence, reduce the stress of the food competition but also the flux of nutrients to the benthic system. In field these processes are not spatially separated and the sum of the abiotic and biotic interactions will determine the characteristics of algal decomposition. To resolve the prevalence of each process in field a number of manipulative experiments at community level are necessary.

CONCLUSIONS

In this dissertation I have observed the feeding behaviour of suspension feeding bivalves under a wide range of environmental conditions. The main conclusions are as follows:

- There were significant interactions between temperature, phytoplankton biomass and current velocities when affecting the biodeposition and clearance rates of the bivalves.
- A significant share of the phytoplankton stock is grazed by benthic suspension feeders in the northern Baltic Sea.
- The suspension feeders constitute an important sink for primary production and, hence, increase the relative importance of the benthic system over the pelagic system. By prolonging the persistence of the drift algae, they may indirectly increase the instability of benthic assemblages.
- The results not only contribute to the knowledge of the functional relationships between suspension feeders and environment but show the necessity of further *in situ* measurements on undisturbed systems in order to explain and model large natural spatial variation of suspension feeding.

The experiments on the habitat and feeding activity of mesograzers showed the following:

- When the density of filamentous algae is low, *i.e.* in slightly eutrophicated conditions, *F. vesiculosus* provides benthic mesoherbivores both food and shelter.
- Under eutrophicated conditions the filamentous algae are the prime food for grazers and they significantly modify their habitat choice.
- Seasonal variability in the biomass of ephemeral algae affects the grazing of mesoherbivores on the studied macroalgal species.
- The physiological state of the algae is the best explanation for the seasonal variation in the activity of mesograzers. Thus, the grazers are not likely to control the early outbreak of filamentous algae as they avoid young and photosynthetically active algae.
- Owing to the effective removal of epiphytes in eutrophicated conditions the grazers have a positive effect on perennial macroalgae. Hence, they act as a stabilisers of the macroalgal communities by compensating for nutrient effects on ephemeral algal growth.

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SUMMARY IN ESTONIA

BENTILISTE FILTREERIJATE JA MESOHERBIVOORIDE ELUPAIGAVALIK JA TOITUMISAKTIIVSUS LÄÄNEMERE PÕHJAOSAS

Doktoritöö eesmärgiks oli selgitada, kuidas veekogu eutrofeerumine avaldab mõju Läänemere põhjaosa bentiliste filtreerijate ja mesoherbivooride elupaigavalikule ja toitumisaktiivsusele. Uuriti temperatuuri, soolsuse, hoovuste, vee toitainete sisalduste, klorofüll *a*, fütoplanktoni liikide biomassi ja limuste *Mytilus edulis* ja *Dreissena polymorpha* toitumisaktiivsuse vahelisi funktsionaalseid seoseid. Limuste toitumisele avaldasid olulist mõju vee temperatuur, fütoplanktoni biomass ja hoovuste kiirus. Eutrofeerunud merealadel täheldati toitumisküllastumist kõrgete klorofüllikontsentratsioonide juures. Filtreerijate populatsioonid on potentsiaalselt võimelised päevas filtreerima 3–2426% nende kohal olevast veemassist, olles seega olulised primaarproduktsiooni tarbijad rannikumeres. Bentiliste filtreerijate roll väheneb veekogu eutrofeerumisega.

Uuriti mesoherbivoori *Idotea baltica* elupaigavalikut ja toitumisaktiivsust erinevates vetikakooslustes. Puhastes merepiirkondades, kus domineeris pruunvetikas *Fucus vesiculosus*, oli liik oluline nii varje- kui ka toiduobjektina. Mõõdukalt eutrofeerunud merealadel domineeris niitjas vetikas *Pilayella littoralis*. Sellistes süsteemides kasutati *F. vesiculosus*'t varjepaigana ning *P. Littoralis*'t toiduobjektina. Sesoonsed toitumisuuringud näitasid, et domineerivad mesoherbivoorid *I. baltica*, *Gammarus oceanicus* ja *Palaemon adspersus* tarbisid peamiselt *P. littoralis*'t. Niitja vetika vähenemisel suurenes taas *F. vesiculosus*'e osakaal toidus. *I. baltica* toitumisaktiivsus oli suurim. Temale järgnesid *G. oceanicus* ja *P. adspersus*. Selgrootute toitumine oli intensiivsem suvel ja madalaim kevadel.

Toitumisaktiivsust mõjutas enim vetika fotosünteetiline aktiivsus. Vetika fotosünteetilise aktiivsuse suurenemisel tema toiteväärtus (atraktiivsus) vähenes. *P. littoralis*'e fotosünteetiline aktiivsus mõjutas *F. vesiculosus*'e tarbimist. *F. vesiculosus*'e fotosünteetilise aktiivsuse mõju *P. littoralis*'e tarbimisele ei täheldatud.

Väga eutrofeerunud rannikumeres täheldati kinnitumata vetikamattide moodustumist ja kinnitunud vetikakoosluste hävingut. Mesoherbivoorid aitasid oluliselt kaasa vetikamattide lagunemisele. Filtreerijate elutegevus pidurdas vetikamattide lagunemist.

Mesoherbivoorid tarbivad olulise osa efemeersetest makrovetikatest ning sellega aitavad kaudselt kaasa rannikumere koosluste stabiilsuse säilitamisele. Filtreerijad suunavad suure osa pelaagilisest primaarproduktsioonist setetesse ning seega suurendavad bentilise süsteemi osatähtsust pelaagilise süsteemi ees. Pikendades kinnitumata vetikamattide eluiga võivad filtreerijad suurendada rannikumere koosluste ebastabiilsust.

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of the polychaete *Marenzelleria viridis*
into a shallow water biotope of the northern Baltic Sea.
J. Sea Res., **46**, 273–280.

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CURRICULUM VITAE

HELEN ORAV-KOTTA

17.08.1975, Tallinn
Estonia
Married
Mäealuse 10a, 12618 Tallinn, tel: +3726718902, fax: +3726718900,
e-mail: helen.orav@sea.ee
Estonian Marine Institute, University of Tartu

Education

Master's degree in biology, Tallinn Pedagogical University, 2000
Bachelor's degree in geoecology, Tallinn Pedagogical University, 1998

Professional employment

2001 to date Estonian Marine Institute, University of Tartu, research scientist
2001, 2002 EuroUniversity, lecturer
2000, 2001 University of Helsinki, invasion ecology
1995–2000 Estonian Marine Institute, technician
1999 West-Estonian Archipelago Biosphere Reserve, specialist in nature education
1998–1999 Tallinn Lilleküla Secondary School, teacher of biology

Scientific work

The main fields of study are the interspecific interactions between benthic organisms and processes in the coastal sea. Emphasis is on the effect of macrophytes on the habitat and food selectivity of prevailing benthic invertebrates. The role of key species in the development and persistence of communities is investigated. An important topic is the influence of benthic nonindigenous species on the native assemblages. Relationships between hydrological conditions, dynamics of plankton communities and suspension feeding of bivalves are studied.

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ELULOOKIRJELDUS

HELEN ORAV-KOTTA

17.08.1975, Tallinn
Eesti
abielus
Mäealuse 10a, 12618 Tallinn, tel: +3726718902, faks: +3726718900,
e-post: helen.orav@sea.ee
TÜ Eesti Mereinstituut

Haridus

Magistrikraad bioloogias, Tallinna Pedagoogikaülikool, 2000
Bakalaureusekraad geoökoloogias, Tallinna Pedagoogikaülikool, 1998

Teenistuskäik

2001 kuni käesoleva ajani TÜ Eesti Mereinstituut, teadur
2001, 2002 Euroülikool, lektor
2000, 2001 Helsingi Ülikool, invasiooniökoloogia uuringud
1995–2000 Eesti Mereinstituut, laborant
1999 Lääne-Eesti Saarestiku Biosfääri Kaitseala, loodushariduse spetsialist
1998–1999 Tallinna Lilleküla Gümnaasium, bioloogia õpetaja

Teaduslik tegevus

Peamisteks uurimisvaldkondadeks on põhjaelustiku vahelised seosed ja rannikumeres toimuvad protsessid. Põhjaloomastiku ja makrovetikate uuringutes keskendutakse eelkõige enam levinud selgrootute toidu- ja elupaigavalikule. Vaadeldakse võtmeliikide osa koosluste kujunemisel ja püsimisel. Olulise tähelepanu all on sellest tulenevalt ka bentiliste võõrliikide mõju põhjakooslustele. Filtreerijate uuringud käsitlevad domineerivate limuste toitumisbioloogia sõltuvust vee hüdroloogiast ja planktonikooslustest.

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