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# Grazing impact of *Mytilus edulis* L. and *Dreissena polymorpha* (Pallas) in the Gulf of Riga, Baltic Sea estimated from biodeposition rates of algal pigments

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Grazing rates of *Mytilus edulis* and *Dreissena polymorpha* were estimated in the Gulf of Riga in May and July 1996. The faecal material was quantified using chlorophyll *a* (Chl *a*) as tracer for planktonic algae. Faeces production rate of *M. edulis* (shell length: 20 mm) ranged from 0.02 to 0.40 $\mu$g Chl *a* equivalent ind.$^{-1}$ h$^{-1}$ and that of *D. polymorpha* from 0.01 to 0.85 $\mu$g Chl *a* equivalent ind.$^{-1}$ h$^{-1}$, respectively. Filtration rates of the mussels were lower at lower temperatures in May. The defaecation rate increased curvlinearly with ambient concentration of Chl *a* and levelled off at high food concentration. After correcting for loss of fluorescent material during gut passage the population grazing impact of *M. edulis* was estimated at 8% d$^{-1}$ of the Chl *a* stock in the littoral zone in May and 67% d$^{-1}$ in July. The values for *D. polymorpha* were 5% d$^{-1}$ and 29% d$^{-1}$, respectively. A high grazing impact by *M. edulis* in the coastal zone during summer was supported by strong horizontal and vertical gradients in Chl *a*. Hence, the populations of benthic suspension feeders in the littoral zone of the Gulf of Riga constitute an important sink for primary production, especially in summer.

## Introduction

Suspension feeders such as mussels, clams and tunicates often dominate the macrofaunal communities in shallow coastal waters. Because of their large filtration capacity such populations are theoretically able to filter major parts of the water column each day (Riisgård & Møhlenberg 1979), and thereby via grazing directly control the standing stock of pelagic primary producers. Traditionally, the impact of benthic suspension feeders on plankton has been calculated combining laboratory derived filtration rates with field estimates of population densities (e.g. Cloern 1982, Nichols 1984, Loo & Rosenberg 1989, Petersen & Riisgård 1992). However, also field studies have shown that dense populations of suspension-feeding bivalves can deplete the overlaying water of algae (Wright *et al*. 1982, Fréchette *et al*. 1989, Asmus & Asmus 1991, Peterson & Black 1991, Muschenheim & Newell 1992). In dense bottom cultures, for example, depletion of algae can occur within meters of the leading edge of a mussel bed (Newell *et al*. 1989). *In situ* studies quantifying broad-scale effects of evenly dispersed and less dense bivalve populations are scarce, however, and usually they are based on indirect evidence and modelling approaches (e.g. Cloern 1982, Møhlenberg 1995).

Phytoplankton is considered to be the prime food for benthic filter feeders. Therefore, the content of phytoplankton pigments in benthic filter feeders has previously been used to assess food availability *in situ* (Jensen & Sakshaug 1970a, 1970b, Ansell 1974a, 1974b, Mann 1977, Christensen & Kanneworff 1985, Kamermans 1993, Josefson *et al*. 1995). However, the gut residence time of 1–2 hours in mussels (Kiørboe *et al*. 1980) makes studies with weekly–monthly sampling intervals unsuitable for assessing the temporal variation in the feeding of suspension feeding benthos. This problem was overcome by Kautsky and Evans (1987) and later by Cranford and Hargrave (1994) by applying an *in situ* trap technique to quantify the rate of biodeposition in *Mytilus edulis* L. and *Placopecten magellanius* (Gmelin), respectively.

In this study, we adopted a similar approach to estimate the grazing rates of the dominant suspension-feeders, *M. edulis* and *Dreissena polymorpha* (Pallas), in the Gulf of Riga, Baltic Sea. However, in contrast to these previous studies, which quantified biodeposition in terms of carbon and nutrients, we chose Chl *a* as a proxy for planktonic algae to calculate the grazing impact of the mussels on the algal community.

The studied bivalves form the dense populations along the whole coastal range of the Gulf of Riga (Kotta 2000). Despite of their ubiquity and potential stabilizing effect on the coastal ecosystems (Herman & Scholten 1990) the *in situ* studies about the effect of the filter feeders on planktonic communities in the Baltic Sea are practically missing. This study provides the first knowledge of the functional relationships between filter-feeding and environmental settings and estimates the impact of the filter-feeders on pelagic system in a eutrophicated bay of the Baltic Sea.

## Material and methods

### Environmental setting

The study was carried out on two transects in the littoral zone of the Gulf of Riga in May and August 1996 (Fig. 1). One transect was located in Estonian coastal waters (Kõiguste Bay) characterised by a wide coastal zone with a diverse bottom topography and extensive reaches of boulders. In the shallower areas boulders were covered by *Pilayella littoralis* Kjellm. (coverage 100%) and *Fucus vesiculosus* L. (25%) and in the deeper area by *P. littoralis* (100%). A scattered population of *M. edulis* occurred on the boulders. The length of the transect was 3 km.

At the Saulkrasti transect coarse sandy bottom prevailed down to a depth of 4 m. At greater depths sand was replaced by boulders (coverage 75%) and stones (25%). The boulders were practically devoid of vegetation but housed a dense population of *D. polymorpha*. The transect is located close to the mouth of the Daugava river and the site is affected by irregular freshwater load (Stålnacke *et al*. 1999, Tamminen & Seppälä 1999). The length of the transect was 0.7 km.

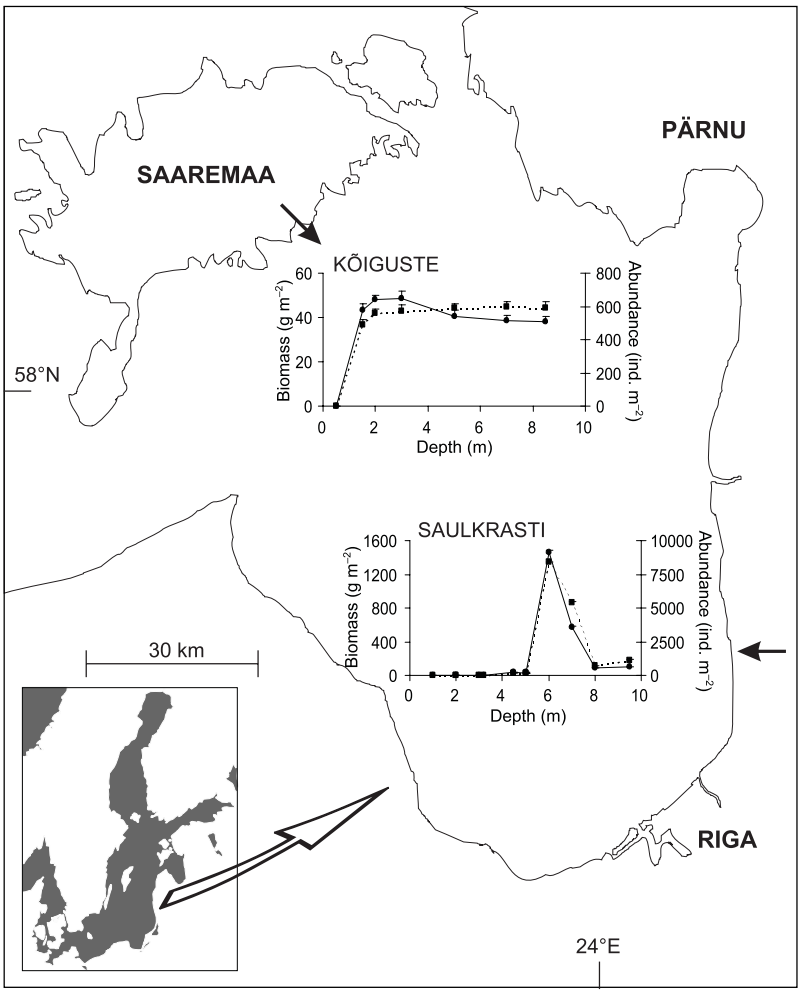


**Fig. 1.** Study area. Arrows indicate the location of transects. Solid line in the graphs show biomass distribution (g dry weight m$^{-2}$) and dotted line abundance distribution (ind. m$^{-2}$) of *M. edulis* (at Kõiguste) and *D. polymorpha* (at Saulkrasti) by depth. Standard errors are shown as bars.

## Methods

The abundance and biomass of bivalves were estimated along the transects. Samples were collected by divers using 20 × 20 and 40 × 40 cm frames placed randomly at a location. All bivalves within the frame were collected. Three replicates were taken at each location (a total of 15 samples in Kõiguste and 18 samples in Saulkrasti during both seasons). The length of the bivalves was measured to the nearest 0.1 mm using vernier calipers. Dry weight of the mussels was determined after drying the individuals at 60 °C for 48 hours. At least 60 individuals in a sample were randomly selected and analysed.

The grazing rates of the dominant suspension feeders, *M. edulis* and *D. polymorpha*, were estimated by quantifying the egestion of total Chl *a* by the individuals deployed *in situ* at 2 and 5 m depth at the transects. Bivalves of 13–28 mm shell length were collected by 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 (Fig. 2). Four replicates were used at each location. Biodeposits were retrieved after 12 h incubation (8:00–20:00; 20:00–8:00). At each location 2–6 incubations were carried out. During deployment the temperature was monitored continuously using EBRO loggers that record data every 10 min. Every 12 h salinity was measured at the distance of 25 cm from the experimental cages. After deployment the shell lengths were recorded, the sedimented material

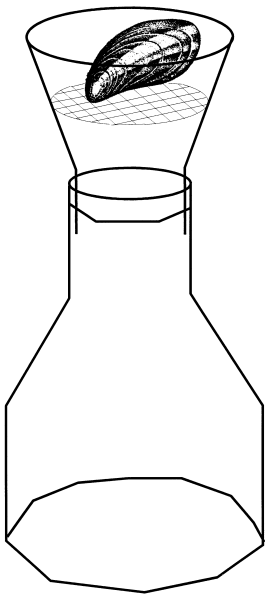

**Fig. 2.** Experimental cage used for the measurement of biodeposition rates of the mussels.

in the vials was sorted under a dissecting microscope, faeces was collected with a pipette and filtered on Whatman CF/C filters within 4 h of retrieval. Filters were extracted in dark in 96% ethanol overnight. Chl *a* was quantified fluorometrically using a Turner Design 10-AU. In order to correct for phaeopigments (Pha) the samples (5 ml) were acidified with 3 drops of 1M HCl after initial fluorescense reading and fluorescense was measured again after 1 min of mixing (Strickland & Parsons 1972). The fluorometer was calibrated against HPLC-purified standards of Chl *a* obtained at the International Agency of 14-C Determination, Denmark. Chl *a* and Pha were calculated as follows: Chl *a* ($\mu$g $l^{-1}$ or $\mu$g unit $faeces^{-1}$) = [1.3433(FB – FA) – 0.0839] × *v* × $V^{-1}$ and Pha = [1.3433(2.2FA – FB) – 0.0839] × *v* × $V^{-1}$, where FB and FA are the fluorencence without acidification and after acidification, *v* = extraction volume and *V* = volume of water filtered or amount of faeces produced. Previous studies have shown a good agreement between standard fluorometric and HPLC determinations of chloropigment concentrations in both filtered algal cultures and mussel faeces (Redden *et al*. 1993). The values of Chl *a* equivalent or total Chl *a* (Chl *a* eq) were calculated as Chl *a* eq = Chl *a* + 1.52Pha. During gut passage in bivalves Chl *a* may degrade to various pigments including chlorophyllide *a*, phaeothytin *a*, phaeophorbide *a* or be absorbed in the alimentary canal (Gelder & Robinson 1980, Hawkins *et al*. 1986, Redden *et al*. 1993). Hawkins et al. (1986) showed that phaeophorbide *a* was the dominating degradation product in *Mytilus*. Assuming that phaeophorbide *a* was the sole degradation product in this study the estimated concentration of Pha was converted to Chl *a* equivalents using the ratio of molar masses between Chl *a* and phaeophorbide *a* (1.52).

The acifidification technique may result in overestimates of Pha, if Chl *b* is present (Gieskes 1991). We did not measure concentration of Chl *b* in connection with experiments, however, the abundance of Chl *b* containing algae, i.e. green algae was consistently very low in the study area. Hence, we assume that the interference of Chl *b* was negligible in the estimates of Pha.

Water for Chl *a* was sampled by divers using 0.5 l screw cap flasks. Care was taken not to resuspend particulate material during sampling. Samples were taken at the distance of 25 cm from the cages in connection with retrieving biodeposits (i.e. every 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 order to estimate the loss of Chl *a* during gut passage the separate experiments were carried out. The mussels, collected in the vicinity of deployment, were incubated on trays in 55 l flow-through tanks. Dry biomasses of mussels ranged between 263–295 g $m^{-2}$. The tanks consisting no experimental animals served as a control. The animals were fed natural particles. Seawater was pumped directly from the incubation site to a head tank and then distributed to the experimental tanks by gravity. Flow rates in the tanks were kept at 250 ml $min^{-1}$. The water in the head and experimental tanks was slowly stirred by aeration. Samples taken from trays not containing mussels demonstrated no significant settlement of particles in head and control

tanks (chl *a* eq < 0.2 μg per tray). On each morning all water from the experimental tanks was exchanged to establish field phytoplankton densities and remove possible sedimented material. In each 2 hours the biodeposits were cleaned from the trays by careful pipetting. Additionally water samples were taken. The content of Chl *a* and phaeopigments 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 aquarium.

## Results

Along the Kõiguste transect the abundance and biomass of *M. edulis* varied little within the depth interval of 1.5–5 m, being on average 600 ind. $m^{-2}$ and 40 g dry wt $m^{-2}$, respectively (Fig. 1). At the Saulkrasti transect a very high abundance (≈ 8000 ind. $m^{-2}$) and biomass (> 1000 g dry wt $m^{-2}$ ) of *D. polymorpha* were confined to the depth interval of 5–7 m. The pooled length-frequency distributions of the mussels are presented in Fig. 3. No seasonal differences between the length-frequency distribution were observed in all studied sites ($p > 0.05$).

The measured values of temperature, salinity and ambient concentration of Chl *a* are given in Table 1. In May, at a high ambient Chl *a* concentration and low temperatures the faeces production rates varied from 0.10 to 0.40 μg tot Chl *a* ind.$^{-1}$ h$^{-1}$ at the Kõiguste transect (*M. edulis*) and from 0.10 to 0.85 μg tot Chl *a* ind.$^{-1}$ h$^{-1}$ at the Saulkrasti transect (*D. polymorpha*). In July, at a lower ambient concentration of total Chl *a*, the faeces production rate varied from 0.02 to 0.22 μg tot Chl *a* ind.$^{-1}$ h$^{-1}$ in *M. edulis* at the Kõiguste transect and from 0.01 to 0.55 μg tot Chl *a* ind.$^{-1}$ h$^{-1}$ in *D. polymorpha* at the Saulkrasti transect. During summer the defaecation rate increased with ambient concentration of Chl *a* (Fig. 4). Fitted polynomial functions suggested a saturation of defaecation rate at higher Chl *a* concentrations.

The algal pigment loss during gut passage was insignificant during May (Fig. 5). An average loss of total Chl *a* in July was 64% for *M. edulis* and 51% for *D. polymorpha*.

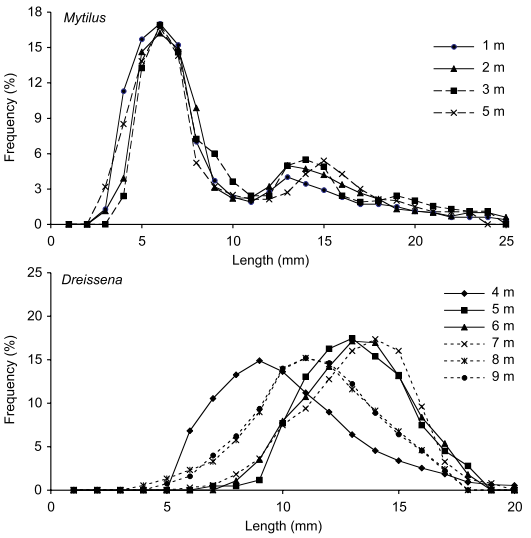


**Fig. 3.** Population length-frequency distribution of *M. edulis* and *D. polymorpha* by depth in the Gulf of Riga during 1996.

Algal grazing by the mussel population was estimated from the functional relations (Fig. 4) after correction for loss of Chl *a* during gut passage and taking into account the data on mussel abundance and size distribution. 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). Besides, the depth integrated samples of Chl *a*, collected daily at 2, 5 and 10 m station (Møhlenberg unpubl.), were used for the calculation of the standing stock values of Chl *a*. The ambient Chl *a* concentration was calculated by linear interpolation between 2–10 m, assuming that concentrations at 1 m and 2 m were identical.

At Kõiguste the population ingestion rate of *M. edulis* showed only a minor variation along the transect in accordance with the horizontal distribution of mussels (Fig. 6). The grazing impact on the standing stock of phytoplankton was low in May, varying between 0% and 15% d$^{-1}$. In July the values were much higher varying between 0% and 90% d$^{-1}$. Along the Saulkrasti transect the grazing of *D. polymorpha* peaked

at 6–7 m (maximum 166% of phytoplankton stock was consumed daily) reflecting the high abundance in this region. However, owing to lower densities in adjacent sea an average grazing impact was only 5.3% in May and 29% in July.

## Discussion

The most important result of this study is the observation that the *in situ* defaecation rate of chloropigments in the bivalves scales to ambient concentration of Chl *a* and levels off at high food concentrations. Such a functional response is in line with numerous studies carried out under controlled conditions in the laboratory (e.g. Winter 1978, Bayne *et al*. 1989, Riisgård 1991) and is caused by either a decrease in the clearance rate, an increase in the rejection rate of food particles (i.e. pseudofaeces production) at high food concentrations or most likely, a combination of both processes (Kiørboe *et al*. 1980). Except for a few studies direct estimates of food uptake in bivalves under natural conditions are rare (Kautsky & Evans 1987, Cranford & Hargrave 1994); however, such estimates are essential to validate the proposed role of filter feeding bivalves in coastal ecosystems (e.g. Cloern 1982). In the natural environment hydrodynamic constraints, sediment load, temporal variation in food concentration and quality vary and act in concert with behavioural variation in filtering activity of the mussels, hence the realized rate of grazing is likely to deviate from laboratory estimates. In contrast to the

**Table 1.** Ambient conditions and the size of mussels during incubations in May and July 1996.

| Transect | Date | Hours | Depth (m) | Temp. (°C) | Salinity (psu) | Chl *a* ($\mu$g l$^{-1}$) start–end | Chl *a* eq ($\mu$g l$^{-1}$) start–end | Shell length range (mm) | Sample *n* |
|---|---|---|---|---|---|---|---|---|---|
| Kõiguste | 9–10 May | 16:00–8:00 | 2 | 6.1 | 5.4 | 16.0–11.3 | 17.1–15.7 | 15–21 | 4 |
| | 9–10 May | 16:00–8:00 | 5 | 6.3 | 5.5 | 14.4–13.4 | 19.1–19.4 | 13–18 | 7 |
| | 10 May | 8:00–21:00 | 2 | 5.9 | 5.5 | 11.3–9.0 | 15.7–14.3 | 16–19 | 4 |
| | 10 May | 8:00–21:00 | 5 | 5.9 | 5.5 | 13.4–8.1 | 19.4–24.7 | 13–16 | 6 |
| | 10–11 May | 21:00–9:00 | 2 | 5.2 | 5.5 | 9.0–11.4 | 14.3–18.6 | 18 | 1 |
| | 10–11 May | 21:00–9:00 | 5 | 5.3 | 5.5 | 8.1–15.3 | 24.7–21.0 | 13–16 | 3 |
| Saulkrasti | 13–14 May | 21:00–9:00 | 2 | 3.6 | 4.8 | 35.2–43.5 | 45.2–62.7 | 13–15 | 7 |
| | 13–14 May | 21:00–9:00 | 5 | 3.4 | 5.2 | 43.5–50.3 | 58.9–58.3 | 16–18 | 8 |
| | 14 May | 9:00–21:00 | 2 | 5.9 | 4.9 | 43.5–71.3 | 62.7–104.0 | 13–16 | 7 |
| | 14 May | 9:00–21:00 | 5 | 5.5 | 5.1 | 50.3–60.8 | 58.3–74.1 | 16–18 | 8 |
| Kõiguste | 23–24 Jul | 20:00–8:30 | 2 | 16.2 | 5.8 | 1.2–1.9 | 3.1–4.1 | 23–28 | 7 |
| | 23–24 Jul | 21:00–9:10 | 5 | 15.9 | 5.7 | 2.5–2.0 | 6.5–5.5 | 21–24 | 8 |
| | 24 Jul | 8:30–20:45 | 2 | 16.4 | 5.8 | 1.9–1.0 | 4.1–2.6 | 24–28 | 4 |
| | 24–25 Jul | 20:45–7:30 | 2 | 16.2 | 5.7 | 1.0–1.4 | 2.6–3.2 | 24–28 | 4 |
| | 25 Jul | 7:30–20:00 | 2 | 16.5 | 5.7 | 1.4–1.4 | 3.2–3.5 | 24–28 | 4 |
| | 25–26 Jul | 20:00–8:20 | 2 | 16.1 | 5.7 | 1.4–1.1 | 3.5–2.9 | 23–26 | 4 |
| | 25–26 Jul | 20:30–8:45 | 5 | 16.2 | 5.7 | 1.4–1.6 | 3.4–4.3 | 23–26 | 4 |
| | 26 Jul | 8:20–20:15 | 2 | 16.3 | 5.7 | 1.1–1.9 | 2.9–5.1 | 23–25 | 4 |
| | 26 Jul | 8:45–20:30 | 5 | 16.4 | 5.7 | 1.6–2.0 | 4.3–4.8 | 23–26 | 5 |
| Saulkrasti | 29–30 Jul | 21:15–8:30 | 5 | 15.9 | 5.1 | 7.6–5.4 | 19.0–10.9 | 15–18 | 4 |
| | 30–31 Jul | 20:30–9:00 | 2 | 15.8 | 5.1 | 4.9–4.2 | 9.0–11.3 | 16–18 | 5 |
| | 30–31 Jul | 20:30–8:45 | 5 | 15.8 | 5.1 | 5.0–3.8 | 10.0–12.4 | 15–18 | 4 |
| | 31 Jul | 9:00–21:00 | 2 | 16.0 | 5.1 | 4.2–5.5 | 11.3–14.6 | 16–18 | 5 |
| | 31 Jul | 8:45–20:30 | 5 | 16.1 | 5.1 | 3.8–6.0 | 12.4–16.0 | 15–18 | 4 |
| | 31 Jul–1 Aug | 21:00–9:30 | 2 | 16.1 | 5.1 | 5.5–10.0 | 14.6–27.3 | 16–18 | 4 |
| | 31 Jul–1 Aug | 20:30–9:15 | 5 | 16.2 | 5.1 | 6.0–7.4 | 16.0–17.4 | 15–18 | 4 |

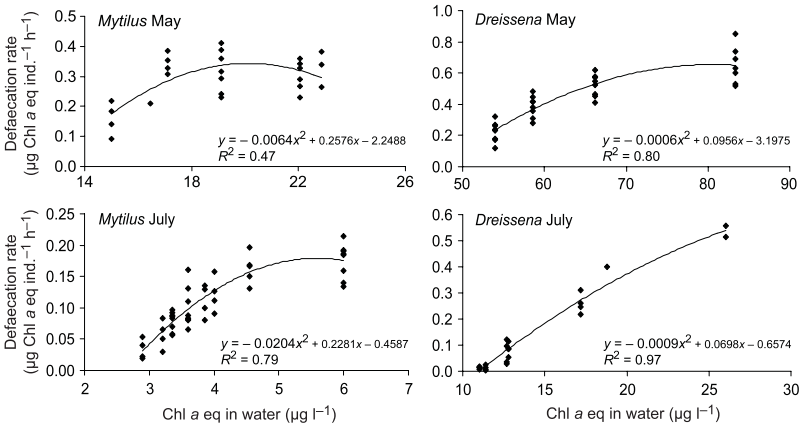


**Fig. 4.** Defaecation rate in *M. edulis* and *D. polymorpha* in May and July as a function of ambient concentration of total Chl *a* (Chl *a* eq). Each value represents the defaecation rate of 3 individuals. Equations of fitted functions are shown.

previous studies our main focus was to quantify the impact of a natural population of bivalves on the phytoplankton stock rather than to quantify their role in the cycling of matter (Kautsky & Evans 1987) or study their feeding response and utilisation efficiency of food (Cranford & Hargrave 1994). To that end we quantified the egestion of the algal Chl *a*. As has been pointed out repeatedly, especially in studies dealing with the grazing in copepods, pigment loss during gut passage is highly variable and should preferably be quantified on each study occasion (e.g. Penry & Frost 1991). The few published studies in bivalves also indicate a significant breakdown of Chl *a* during gut passage even though pigment budgets have not been presented (Hawkins *et al*. 1986, Pastoreaud *et al*. 1996). In addition, intermittent accumulation of phaeopigments in the digestive gland for up till weeks further will complicate the interpretation of results (Redden *et al*. 1993). In this study the Chl *a* loss in the gut passage of mussels was below 2% in spring season. However, these values were estimated at 64% for *M. edulis* and 51% for *D. polymorpha* in summer season. This loss is markedly higher than estimated for *M. edulis* from a Danish estuary using a similar set-up (F. Møhlenberg unpubl.). As evidenced for copepods the previous feeding history and food composition can affect the loss of pigments during gut passage (Penry & Frost 1991). We suggest that individual variation in Chl *a* degradation and temporal storage of pigments are partly responsible for the large variation in the relations of functional

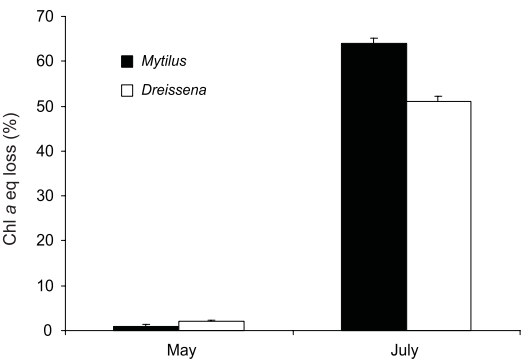


**Fig. 5.** An average loss of total Chl *a* in the guts of mussels in May and July. Standard errors are shown.

response (*see* Fig. 4).

The ratio of defaecation rate to ambient Chl *a* eq (i.e. the efficiency of mussels feeding) was lower in spring than in July (Fig. 4 and 6). The correlations between ambient Chl *a* concentration and defaecation rate were also poorer in spring. Filtration rate and consequently ingestion rate in mussels increase with temperature (e.g. Jørgensen *et al*. 1990). Hence, in May at a high food concentration (8–70 $\mu$g Chl *a* $l^{-1}$) the ingestion rate was probably limited by temperature rather than by food concentration. In July at 10 times lower food concentration but at much higher temperature (16 °C) the defaecation rate increased gradually with food concentration (Fig. 4).

*D. polymorpha* attained a very high abundance at the Saulkrasti transect in the southern

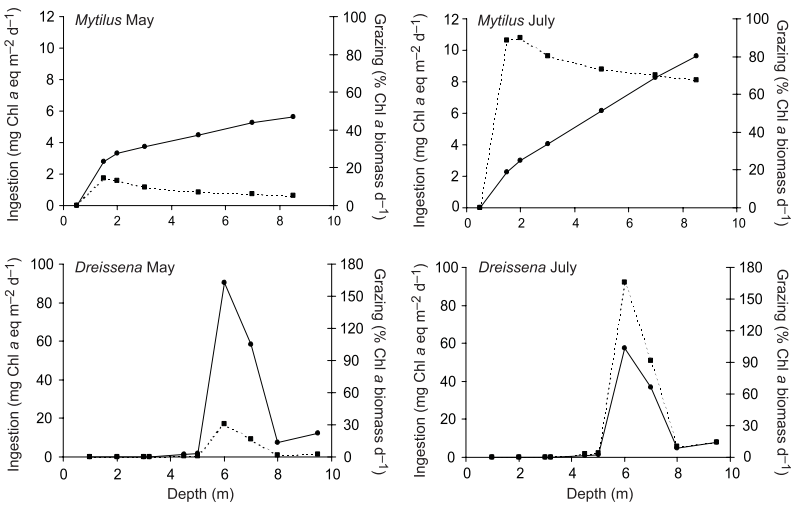


**Fig. 6.** The ingestion rate (solid line) and grazing impact (dotted line) of the populations of *Mytilus* and *Dreissena* on the standing stock of Chl *a* in May and July. Standing stocks of Chl *a* were obtained from depth integrated samples taken daily at 2, 5 and 10 m stations (F. Møhlenberg unpubl.).

Gulf of Riga. The salinity regime here (i.e. 4–5 psu) is close to the upper tolerance limit of the species (Järvekülg 1979). Still, the egestion rate was comparable to that of *M. edulis* at the northern transect. Accounting for the low temperature the measured egestion rate in *D. polymorpha* was comparable to rates measured in their freshwater habitat (Horgan & Mills 1997).

Based on the individual grazing rates and bivalve abundance the benthic grazing impact in the littoral zone at the Kõiguste transect was estimated maximum at 90% of the standing stock of phytoplankton per day in July. In May the grazing impact was insignificant at 0 to 15% of the phytoplankton stock per day due to high algal biomass and low temperature limiting the filtration rate. During our study in July autotrophic and heterotrophic processes in the water column were in close balance (F. Møhlenberg unpubl.), hence the significant benthic grazing pressure was the major sink for algae in the littoral zone. This was clearly reflected in the strong horizontal and vertical gradients in Chl *a* measured during the study. Kõiguste Bay has extensive shallow areas and moderate water exchange — features that favour benthic control over phytoplankton (e.g. Officer *et al.* 1982). Biotopes resembling those of Kõiguste Bay prevail in the northeastern Baltic Sea (Järvekülg 1979, Kotta & Kotta 1995, Kotta & Kotta 1997, Kotta *et al.* 1999). Therefore, it is very likely that benthic control of phytoplankton in the littoral zone is more commonplace in the Baltic Sea than previously thought. Hence, we may assume that phytoplankton dynamics is strongly coupled with benthic processes in these areas.

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