The Comparative Roles of Suspension-Feeders in Ecosystems

Edited by

Richard F. Dame and
Sergej Olenin

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PREFACE

Animals are a major link between the water column (pelagic) and the bottom (benthic) habitats in most shallow systems. This coupling is dominated by active processes such as suspension-feeding in which the organism actively uses energy to pump water that is then filtered to remove suspended particles that are consumed while undigested remains are deposited on the bottom. As a result of this feeding on and metabolism of particles, the animals excrete dissolved inorganic and organic waste back into the water column, and thus, become major components in the cycling and feedback of essential elements. With relatively high weight specific filtration rates of 1–10 liters/hour/gram dry tissue and a propensity to form large aggregated populations (beds, reefs, schools and swarms), these organisms can play an important role in regulating water column processes

Although estuarine bivalve molluscs such as oysters and mussels dominate the suspension-feeder literature, other groups including plankton and nekton that are found in estuarine as well as other aquatic systems are also potentially important removers of suspended particles. Thus, a significant part of the NATO Advanced Research Workshop focused on suspension-feeders as controllers of plankton abundance, biomass and diversity, system metabolism, nutrient cycling and scale dependency.

Systems dominated by suspension-feeders are typically impacted by human activities including recreation, aquaculture, human and industrial pollution, and bilge water from shipping. Suspension-feeders are often impacted by fisheries and over-exploitation. These impacts commonly result in changes in ecosystem structure either through the food chain concentration of harmful substances or diseases, the introduction of alien species of suspension-feeders, or the instability of suspension-feeders systems through species displacement or phase shifts in the dominance between different suspension-feeding components such as nekton or zooplankton. These issues were addressed near the close of the workshop along with conclusions and syntheses developed by the working groups.

In the almost 10 years since one of us (RFD) led a NATO ARW in The Netherlands on bivalve filter feeders, interest in suspension-feeders as major influences on aquatic ecosystem processes has grown dramatically. This development is particularly evident in freshwater systems, yet the communications between the freshwater and the estuarine-marine scientific communities are weak (probably because of scientific, societal and funding agency structure and habitat separation). Thus, one of our major goals was to balance process orientated topics with presentations from the three general aquatic environments, freshwater, estuarine and marine. An additional overarching aim was to bridge the geographical distribution of NATO and partner countries. Our workshop proposal is timely and compliments

NATO's new approach involving partner countries because many partner countries have mainly freshwater and brackish systems while most NATO members also have large estuarine-marine components. In addition to chronicling the current status of suspension-feeder research, we believe that this workshop has and will foster greater communications between the various groups and support the cross-fertilisation strategy has been shown to have a strong positive effect on the generation of new scientific approaches, theories and knowledge.

The participants are grateful for the financial and logistics support and guidance provided by the NATO staff. We also thank the Kluwer editorial staff for their timely and constructive support.

MODELLING PARTICLE SELECTION EFFICIENCY OF BIVALVE SUSPENSION FEEDERS

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Abstract: The choice of an appropriate index to adequately describe the efficiency of pre-ingestive organic material selection is important for modelling the material flux within the suspension feeding process. Recently, a new selection efficiency index was suggested by Zemlys et al. (2003) which simplifies the quantification of the selection activity. A simple equation with interpretable parameters calculates the selection efficiency index using literature values of uptake rate and food quality. This analysis suggests the possibility of developing more general and biologically interpretable models.

Keywords: Pre-ingestive selection efficiency; suspension feeding bivalves; modelling food processing

INTRODUCTION

Bivalve suspension feeders reject part of the food they filter as pseudofeces depending on seston concentration. An important process accompanying pseudofeces production is the selection of particles that result in an increase in the organic material fraction of the ingested food (Fig. 1). Although the physiological regulation of feeding and selection of particles in particular is rejected by some authors (Jørgensen 1996), a number of *in vitro* and *in situ* investigations (Kiørboe and Mølenberg, 1981; Hawkins et al. 1996; Defossez and Hawkins 1997; Ward et al. 1998; Hawkins et al. 1998; Schneider et al. 1998; Baker et al. 2000) confirm the selective feeding by bivalves. The selection efficiency of organic matter can be as high as 60% under certain conditions (Hawkins et al. 1998). Therefore, this efficiency may considerably change the organic and inorganic material ratio of ingested food and biodeposits.

Although the pre-ingestive selectivity of particles by bivalves is generally recognised, the factors influencing preferential ingestion remain

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uncertain. Various proposed criteria include particle size, shape, motility, density, and chemical cues such as algal ectotrines (for review see Defossez and Hawkins 1997). The organic material selection activity defined as selection efficiency, however, can be quantitatively described by experimental relationships that already have been determined for some species of marine bivalves (Hawkins et al. 1996, 1998). These findings strongly suggest that particle selectivity should be included in models of bivalve feeding.
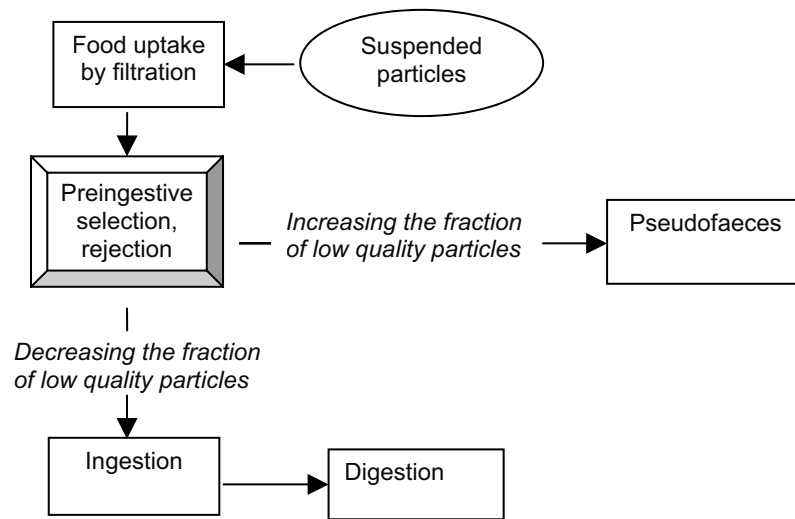
Fig. 1. A conceptual model of food processing by suspension feeders exhibiting active particle selection.

When selection activity is absent the quantitative description of the allocation of seston fractions (organic, inorganic material, etc.) in pseudofeces and ingested food is easily expressed by the difference between food uptake rate and pseudofeces production or ingestion rate. In the case of selection activity there are two options. One option is to model the rejection (ingestion) rates of different seston fractions separately (e.g. Hawkins et al. 2002; Scholten and Smaal 1999). In this case, the selection efficiency index serves an auxiliary role and can be used as output variable characterising the selection activity. Alternatively, the selection efficiency index can be used to determine by mass balance the different seston fractions beforehand and to estimate the allocation of seston fractions in pseudofeces and ingested food (e.g. Bendell-Young and Arifin 2004). Problems with the last approach arise when the seston is fractionated into organic and inorganic material (Zemlys et al. 2003). They found that the choice of an appropriate selection efficiency index is critical. The most widely used selection efficiency index is that defined in Bayne et al. (1993) and based on the comparison of organic content

in pseudofeces and seston. However, Zemlys et al. (2003) demonstrated that using a different selection efficiency index based on comparison of organic content in seston and ingested food could result in series of advantages for food processing modelling. These advantages can be summarised as follows (see Zemlys et al. (2003) for details):

- The traditional selection efficiency estimate is generally applicable to obtain organic content in pseudofeces and ingested food, however in some cases it may lead to analytically unsolvable equations. The introduction of an alternative selection efficiency considerably simplifies the solution and never requires iterative methods;
- The analysis of constraints originating from mass balance determinations revealed an advantage of employing the alternative selection efficiency estimate. These constraints are more straightforward and obvious for alternative selection efficiency, for example the traditional selection efficiency is limited by certain value that is less than one while alternative index is limited by number one only (see formula (4) in the text below for more details);
- Utilising the response surface approach for estimating the alternative selection efficiency as a function from food uptake rate and seston organic content is expected to produce a monotonously increasing function. This function might also have interpretational and analytical advantages in comparison to the traditional bell-shaped response surface.

The aim of the study is to compare the response surfaces of traditional and newly defined selection efficiency index for three bivalve species *Mytilus edulis*, *Cerastoderma edule* and *Crassostrea gigas* and to determine an analytical expression for the alternative selection efficiency index. Data from the experimental studies of Hawkins et al. (1998) are used in this paper.

CALCULATION OF RESPONSE SURFACES

Traditionally, the selection efficiency (*SE*) is defined as (Bayne et al., 1993)

$$SE = (1 - FPOMPF / FPOM) \qquad (1)$$

where *FPOM* is organic content of seston (fraction particulate organic material), i.e. food quality; *FPOMPF* is organic content of pseudofeces (for complete list of variables and parameters used see Table 1). An alternative

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Table 1. List of notations with explanations.

Notation	Explanation
a	Parameter in selection efficiency equation (7)
ase	Parameter in equation (3)
bse	Parameter in selection efficiency equation (3)
cse	Parameter in selection efficiency equation (3)
dse	Parameter in selection efficiency equation (3)
$FPIM$	Inorganic content of seston
$FPOM$	Organic content of seston (fraction)
$FPOM_0$	The value of seston organic content at which the selection activity starts
$FPIMING$	Inorganic content of ingested material
$FPOMING$	Organic content of ingested material
$FPOMPF$	Organic content of pseudofeces
$IRMAX$	Maximal ingestion rate, g day^{-1}
r	Coefficient of proportionality in equation (6)
SE	Traditional selection efficiency
$SE1$	Alternative selection efficiency
$SEMAX$	Maximal possible selection efficiency value
UPR	Seston uptake rate, g day^{-1}

definition of selection efficiency based on organic content of ingested food (Zemlys et al. 2003) was defined as

$$SE1 = (FPOMING - FPOM)/(1 - FPOM) \qquad (2)$$

where $SE1$ is alternative selection efficiency; $FPOMING$ is organic content of ingested food. $SE1$ is similar to selection index reported in Hawkins et al. (1998) but it is normalized by maximal value of difference $FPOMING - FPOM$ instead of $FPOMING$. The equation (2) can be expressed in form similar to (1) but in terms of inorganic content:

$$SE1 = 1 - FPIM / FPIMING$$

where FPIM is inorganic content in seston; FPIMING is inorganic content in ingested material.

The advantages of the alternative index were demonstrated (Zemlys et al. 2003) however equations for evaluation of selection efficiency as a function of food uptake rate and seston organic content exist only for the traditionally defined selection efficiency (Hawkins et al. 1996; Hawkins et al. 1998). The limitations of these empirical equations due to complex response surfaces were also determined by Zemlys et al. (2003). They hypothesized that the response surface shape of newly defined selection efficiency should be considerably simpler.

As the first step the response surfaces for both selection efficiency definitions should be constructed. Traditional selection efficiency depends on food uptake rate (UPR) and organic content of seston ($FPOM$). For three

bivalve species *M. edulis*, *C. edule* and *C. gigas* the following regression equation was proposed by Hawkins et al. (1998):

$$SE = ase - bse / FPOM + cse \cdot UPR + dse \cdot UPR / FPOM \qquad (3)$$

where *ase*, *bse*, *cse* and *dse* are parameters (see Hawkins et al. (1998) for numeric values). Unfortunately this equation is based on the rather narrow range of organic content and does not contain any theoretical information about possible shape of response surface outside this range. The analysis of material balance revealed (Zemlys et al., 2003) that traditionally defined selection efficiency is not increasing with *UPR* and *FPOM* but is limited by certain value (*SEMAX*) defined by formula (Zemlys et al., 2003)

$$SEMAX = [(1 - FPOM) / FPOM] \cdot IRMAX / (UPR - IRMAX) \qquad (4)$$

where *UPR* is seston uptake rate by bivalve; *IRMAX* is maximal ingestion rate. *SEMAX* is the value of *SE* which corresponds to the saturation condition $FPOMING = 1$ (Zemlys et al., 2003). The response surface for SE was constructed assuming $SE = \min\{SEMAX, \ SET\}$, where *SET* are selection efficiency index calculated by equation (3). The empirical equations for the calculation of *UPR* and *IRMAX* that depend on organic content and seston concentration are taken from Hawkins et al. (1998). Does the saturation take place in real conditions or not the question is still open and needs further experimental investigation. However, the shape of *SEMAX* surface gives enough information about possible shape of *SE* surface because *SE* is always less or equal to *SEMAX* (Zemlys et al. 2003). The obtained SE surfaces for all three species are shown in Fig. 2a, 2c, 2e).

The response surface for *SE1* can be easy obtained from *SE* surface using the following relationship between *SE1* and *SE* (Zemlys et al., 2003):

$$SE1 = [FPOM / (1 - FPOM)] \cdot (UPR / IRMAX - 1) \cdot SE \qquad (5)$$

The results of these calculations are presented in Fig. 2b, 2d, 2f.

For all three species the response surface of *SE* is asymmetric bell-shaped surface with the maximum along *FPOM* axis which makes it difficult to approximate by simple interpretable analytical expression. In contrast, the *SE1* surface is an increasing function with regard to both arguments monotonically approaching the value 1 and therefore might be approximated by traditional saturation functions, like Michaelis-Menten function or similar. Of course, the numerical analysis of three species only support the hypothesis but does not let to conclude that *SE1* will be increasing function for other bivalve species, however as it is shown by Zemlys et al. (2003) the sufficient
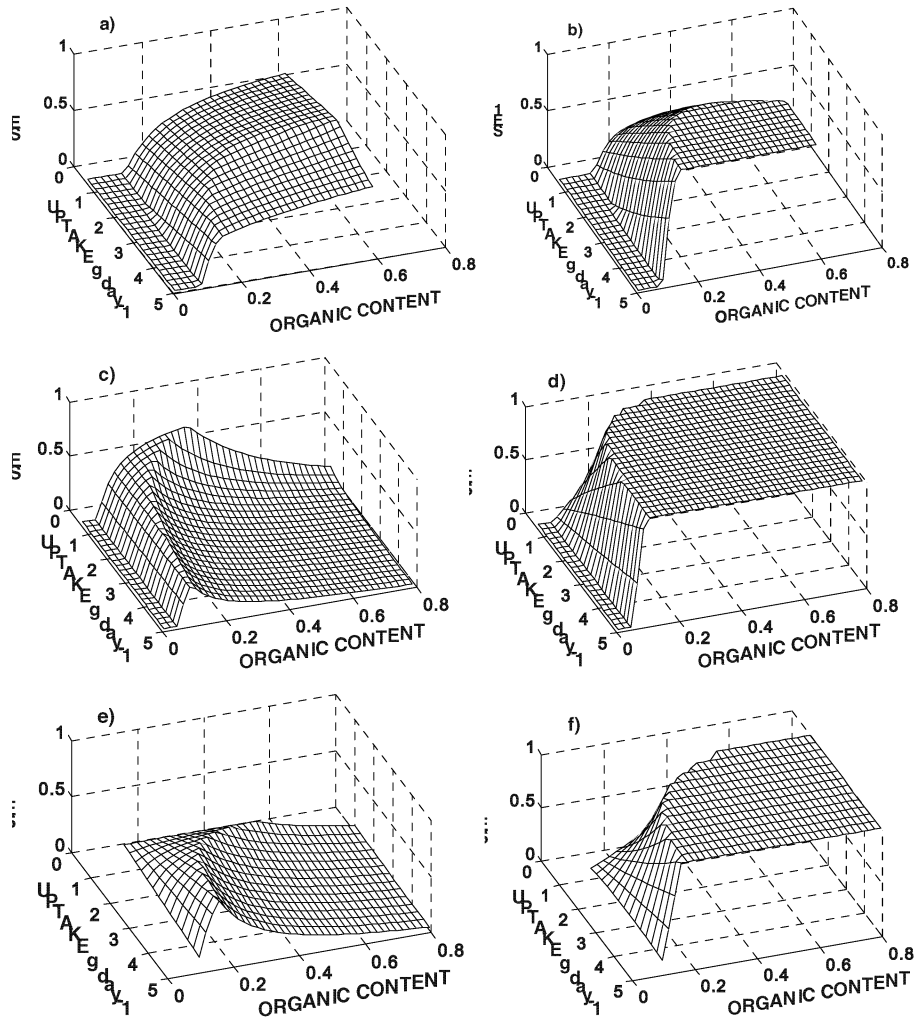
Fig. 2. The *SE* and *SE1* response surfaces for three bivalve species: a), b) – *Mytilus edulis*; c), d) – *Cerastoderma edule* e), f) – *Crassostrea gigas.*

condition to be *SE1* monotonically increasing is the monotonic increasing of relative pseudofeces production. It seems that this condition is realistic for majority of suspension feeding bivalve species at least regard to the uptake rate.

APPROXIMATION FUNCTION

The description of *SE1* directly as a function of UPR and FPOM is very important in order to use the alternative selection efficiency for modeling of food processing. We will demonstrate here that such a function could be

obtained using simple assumptions. The simplest assumption that seems to be acceptable for analyzing *SE1* for all three species is the linearity of the relationship between SE1 changing rate regard to *FPOM* and SE1 that can be formulated by following equation:

$$\frac{\partial SE1}{\partial FPOM} = r(UPR) \cdot (1 - SE1) \qquad (6)$$

where *r(UPR)* is coefficient of proportionality depending on uptake rate. Assuming also linearity for *r(UPR)*, i.e. $r(UPR) = a \cdot UPR$ after integration the following expression is obtained

$$SE1 = \max(0, \ 1 - \exp(a \cdot (FPOM - FPOM_0) \cdot UPR)) \qquad (7)$$

where $SE1(FPOM_0) = 0$, *a* is a parameter and is assumed that *SE1*=0 at $FPOM \leq FPOM_0$. While *SE1* and *SE* equals to zero simultaneously the equation for *FPOM0* can be obtained by assuming $SE = 0$ in (3) and solving it regard to *FPOM*, what results in

$$FPOM0(UPR) = \frac{bse - dse \cdot UPR}{ase + cse \cdot UPR} \qquad (8)$$

The equation (6) has only one unknown parameter *a* which can be interpreted as multiplier determining the rate of *SE1* approach to saturation condition (value 1). Together with (8) the equation (6) was used to approximate the surfaces given in fig. 2a, 2c, and 2g by minimum square method. The estimated values of parameter *a* and mean square error are given in Table 2.

Table 2. The results of approximation SE1 by equation (6)

Bivalve species	*a*	Mean square error
Mytilus edulis	7.89	0.034
Cerastoderma edule	10.08	0.066
Crassostrea gigas	3.59	0.159

The estimated values of parameter *a* allows us to compare the ability of the different species to increase ingested food quality by means of selection

activity when seston food quality and uptake rate are increased. The highest value $a = 10.08$ for *C. edule* (Table 2) shows that this species has the highest capability. Less, but still comparable ($a = 7.89$) capability has *M. edulis* while *C. gigas* is able to exploit less than half of selectivity potential estimated for other two species (Table 2).

DISCUSSION AND CONCLUSIONS

The pre-ingestive food selection by bivalves is an important phenomenon determining the organic content in pseudofeces and ingested food, simultaneously controlling the energy fluxes inside the organism and between the organism and environment. In this paper we parameterize the newly proposed alternative selection efficiency index.

We show that the response surface for the alternative selection efficiency index for three bivalve species has a simpler shape that is more proper for approximation by analytical expressions.

An analytical expression based on simple assumptions for alternative selection efficiency index is proposed and we demonstrate that it can satisfactorily approximate the values of selection efficiency recalculated from traditionally defined selection efficiency for three bivalve species.

The proposed relationship contains a parameter that enables the comparison of selection activity of different bivalve species, i.e. the capability to exploit the increase of food quality and food uptake to improve the ingested food quality.

Our results lead us to believe that modeling of the allocation of organic and inorganic material in pseudofeces and in ingested food can be based on mass balance and alternative selection efficiency index that can be expressed by simple functions with interpretable parameters. This approach may make food processing models more general than models consisting of purely site and species specific regression equations.

It is important to note that equation (7) could be more simplified. As can be seen from Fig. 2, the selection efficiency index depends much more on seston organic content than uptake rate, thus the dependence on uptake rate can be neglected (at least in some cases). The right side of equation (8) is a constant in this case. The traditional selection efficiency index as a function of seston organic content only was used Bendell-Young and Arifin (2004).

In some cases other fractions of seston than organic and inorganic material are necessary. For example, the organic material was divided to phytoplankton and non-phytoplankton organics (Hawkins et al. 2002). The further development of the approach considered above for this case is an important task for future investigations.

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FIELD MEASUREMENTS ON THE VARIABILITY IN BIODEPOSITION AND ESTIMATES OF GRAZING PRESSURE OF SUSPENSION-FEEDING BIVALVES IN THE NORTHERN BALTIC SEA

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Abstract: Functional relationships between environmental variables, the biodeposition and clearance rates of *Dreissena polymorpha* and *Mytilus edulis* were estimated in the northern Baltic Sea. The biodeposition and clearance of the bivalves increased with ambient temperature. In more eutrophicated regions biodeposition and clearance rates increased curvilinearly with ambient concentrations of chlorophyll *a* and leveled off at high food concentrations. In less eutrophicated conditions a linear model gave the best fit suggesting that saturation level was not obtained. Additional variation in the biodeposition and clearance was explained by the interaction of water temperature, current velocity and chlorophyll *a*. Salinity had a significant effect on the biodeposition and clearance of *D. polymorpha*. The population of suspension-feeders cleared daily on average from 3 to 2426% of overlaying water in the littoral area constituting an important sink for primary production.

Keywords: Baltic Sea, benthic grazing, *Dreissena polymorpha, Mytilus edulis*

INTRODUCTION

Owing to elevated nutrient levels and consequent phytoplankton blooms a dramatic increase of dense populations of benthic suspension feeders has been recorded world-wide (Barnes and Hughes 1988; Kautsky 1995; Dame 1996). At high densities the suspension-feeders are capable to deplete phytoplankton (Cloern, 1982 Fréchette and Bourget 1985) and therefore control the standing stock and production of primary producers and limit via competition the growth of pelagic herbivores and fish (e.g. Officer et al. 1982; Møhlenberg 1995). Consequently, suspension-feeders are considered to play a key role in the stability of coastal ecosystems (Herman and Scholten 1990).

In situ studies quantifying broad-scale effects of suspension-feeder populations are scarce and usually they are based on indirect evidence and modelling approaches (e.g. Cloern 1982; Møhlenberg 1995). It has been demonstrated that laboratory measurements are often difficult to interpret and compare (Riisgård, 2001) and they may overestimate the filtration rate by 1300% (Doering and Oviatt 1986; Cranford and Hill 1999). It suggests that suspension-feeders in nature exploit their full clearance capacity for short periods and more often feed at a much-reduced rate (e.g. Cranford 2001). Water temperature, salinity, the quality and concentration of seston coupled with flow regime have significant impact on the activity of suspension feeders (Bayne et al. 1977; Kiørboe et al. 1980; Widdows 1985; Fréchette at al. 1989; Asmus and Asmus 1993) and may account for the major variability of *in situ* feeding behaviour. Hence, there is a need for field measurements of the feeding behaviour of suspension-feeders combined with the measurement of those environmental variables in the near-bottom layer. These functional relationships have to be estimated for different areas and different times of the year, to assess the importance of suspension feeder grazing to the coastal ecosystem.

Suspension-feeders derive their food by filtering the water column and retaining particulate matter on their gills. Clearance rate refers to an amount of water that is cleared per time unit by animal or biomass. Biodeposition is defined as the production of faeces and pseudofeces. An *in situ* biodeposition approach has been used to evaluate the variations in the feeding behaviour of mussels (Kautsky and Evans 1987; Hawkins et al. 1996; Cranford et al. 1998; Cranford and Hill 1999). By applying an *in situ* trap technique, the biodeposition was quantified in terms of carbon and nutrients. However, as phytoplankton is considered to be the prime food for benthic suspension-feeders, we chose, in contrast to these previous studies, chlorophyll *a* (Chl *a*) as a tracer.

The present study focuses on the grazing impact of suspension-feeders on the pelagic algal community in the northern Baltic Sea. The blue mussel (*Mytilus edulis* Gould) and the zebra mussel (*Dreissena polymorpha* (Pallas)) were selected as experimental species due to their ubiquity and, hence their significant potential contribution to phytoplankton removal. The functional relationships between ambient temperature, salinity, current velocity, phytoplankton biomass and the biodeposition of the suspension-feeders were estimated at five sites differing in their eutrophication level during different times of the year. Based on these functional relationships algal grazing by the mussel populations was estimated in multiple areas taking into account the data on ambient temperature, salinity, Chl *a* concentration, mussel abundance and size distribution.

MATERIALS AND METHODS

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 and Kilpi 1997). *D. polymorpha* dominates at salinities less than 5 psu and *M. edulis* in more saline environments (Kotta, 2000).

The study was carried out on three transects in the littoral zone of the Gulf of Riga (GOR) and two transects in the Gulf of Finland (GOF) during one year period between 1996 and 2002 (Fig. 1). Sampling was performed during ice-free period in spring (T=2–15ºC), summer (T>15ºC) and autumn (T=2–15ºC). Northern GOR was characterised by a wide and sheltered coastal zone with diverse bottom topography and extensive reaches of boulders. Depending on the salinity, a scattered population of *M. edulis* or *D. polymorpha* occurred on the boulders. The southern transect had a narrow and exposed coastal zone. Coarse sandy substrate prevailed down to a depth of 4 m being replaced by boulders at greater depths. The boulders harboured 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 is found and, hence, the area was practically devoid of suspension-feeding bivalves.

As a result of the differences in exposure to deep waters, the frequency of upwelling was higher in GOF than GOR sites. Due to high riverine load and moderate water exchange the nutrient concentrations were on average twice as high in GOR than in the Baltic Proper. Northern GOR sites were moderately eutrophicated and southern GOR site was highly eutrophicated. The southern GOF site was moderately eutrophicated due to municipal pollution load of Tallinn City. The concentration of nutrients in the northern GOF site was similar to the values of the Baltic Proper and, hence, representing the least disturbed environment in terms of eutrophication (Astok et al. 1999; Hänninen et al. 2000).

In each season the abundance, biomass and size-frequency distribution of the suspension-feeders were estimated along the five above-mentioned and an additional transect in a more exposed part of northern GOF. Samples were collected from the seashore down to 12 m depth at steps 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 bivalves was measured to the nearest 0.1 mm using vernier callipers.

In situ grazing rates of *M. edulis* and *D. polymorpha* were estimated by quantifying the defecation of Chl *a* by the mussels at 1 m in each transect

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during different seasons. Bivalves of 9–31 mm shell length 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 near-bottom temperature and salinity were monitored at the beginning and at the end of the deployment using CTD profiling. Each incubation lasted 4 hours. In each season we performed at least five incubations replicated three times.
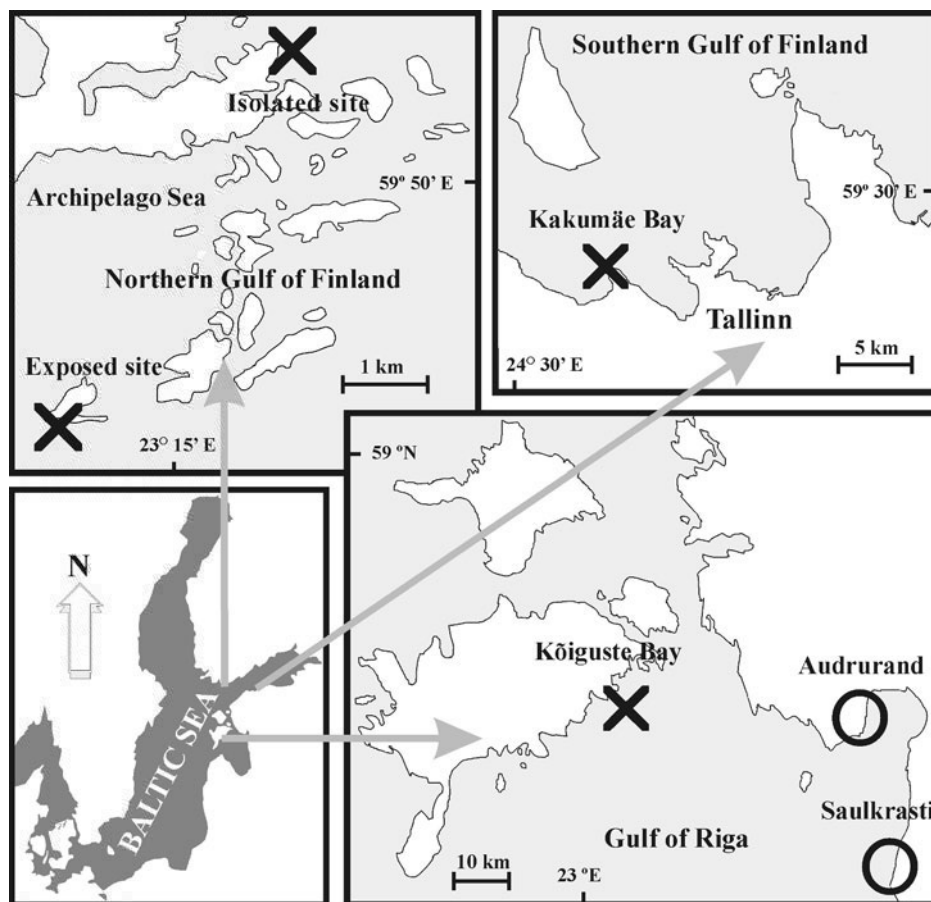

Fig. 1. Study area. The transects of *M. edulis* are indicated by crosses and that of *D. polymorpha* by open circles.

Except for northern GOF plaster balls were used to estimate the water currents in near-bottom layer. The method is recognised as a simple and 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 (Thompson and Glenn 1994).

After deployment the shell lengths were recorded, the sedimented material in the vials was sorted under a dissecting microscope; faeces were 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 and 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.

During deployment water for Chl *a* measurement was daily sampled by a diver at near-bottom layer along the whole transect at steps of 1 m. Additional samples 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 order to estimate the loss of Chl *a* during gut passage separate experiments were carried out aboard ship. The mussels were incubated in 5 l buckets for 4 h. Buckets without experimental animals served as controls. The animals were fed natural sea water. At the end of the incubation the biodeposits were cleaned from the buckets by careful pipetting and water samples for Chl *a* were taken. The content 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.

Clearance rate by the mussel population was calculated from the estimates of biodeposition. The functional relations between biodeposition and environmental variables were determined after correction for loss of Chl *a* during gut passage. The data on ambient temperature, salinity, Chl *a* concentration, mussel abundance and size distribution were taken into account when estimating population grazing potential in multiple areas. Annual population grazing potential is defined as the average of the calculated clearance rates of each incubation by transect and depth interval. The minimum and maximum values represent the extremes of the calculated clearance rates. 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 and Møhlenberg, 1981). We assumed no significant spatial variation in current velocity and complete vertical mixing along the transect. At low current velocities water exchange was likely not sufficient to supply the local suspension-feeder communities with phytoplankton. Hence, the grazing potential tends to overestimate the impact of mussels on phytoplankton communities when the water exchange is low.

The biodeposition and clearance of the mussels were analysed by factorial ANOVA including transect and season as the main effects. We employed linear and second-order polynomial linear regression analyses to describe the relationships between the biodeposition and ambient environmental variables. Polynomial regression results are only reported if significantly better fits were achieved using this method compared with the linear model.

Table 1. The mean values ± S.E. of water temperature, salinity, Chl a eq (μg l^{-1}) and current velocity (cm s^{-1}) at the study sites in the Gulf of Riga (GOR) and the Gulf of Finland (GOF) during different seasons.

Site	Year	Season	Temperature	Salinity	Chl a	Current
Seili (GOF-N)	1998	summer	16.4 ± 0.2	5.9 ± 0.1	4.9 ± 1.4	not measured
	1998	autumn	8.2 ± 0.2	5.8 ± 0.1	5.0 ± 1.2	not measured
	1999	spring	2.4 ± 0.2	5.8 ± 0.1	1.2 ± 1.1	not measured
Kakumäe (GOF-S)	2002	spring	12.6 ± 0.4	6.1 ± 0.1	9.4 ± 2.5	0.1±0.0
	2002	summer	20.6 ± 0.2	4.9 ± 0.1	5.7 ± 1.6	29.6±4.3
	2002	autumn	4.4 ± 0.5	5.2 ± 0.2	8.0 ± 3.5	43.0±2.5
Kõiguste (GOR-N)	1996	spring	5.9 ± 0.2	5.5 ± 0.1	19.2 ± 1.0	12.1±0.3
	1996	summer	16.2 ± 0.1	5.7 ± 0.0	4.0 ± 0.7	0.1±0.0
Audrurand (GOR-N)	2002	spring	13.3 ± 0.4	3.2 ± 0.1	1.7 ± 2.5	1.3±0.8
	2002	summer	24.0 ± 0.3	3.1 ± 0.1	6.5 ± 1.9	42.9±7.6
	2002	autumn	2.0 ± 0.5	5.4 ± 0.2	14.9 ± 3.5	61.3±3.0
Saulkrasti (GOR-S)	1996	spring	4.6 ± 0.1	5.0 ± 0.0	65.0 ± 0.9	0.1±0.0
	1996	summer	16.0 ± 0.2	5.1 ± 0.1	14.4 ± 1.0	30.4±5.6

RESULTS

In summer water temperature was higher in southern GOF and northern GOR site *of D. polymorpha*. Salinity values were slightly higher in GOF than in GOR sites. All means were less than 7 psu. The values of maximum water Chl a eq (i.e. a measure of eutrophication level) were higher in GOR than in GOF sites. Highest Chl a eq values were measured in the

southern GOR site during the spring bloom. The summer values in the southern GOR site were in the same magnitude as the spring bloom values in other studied sites. In general, current velocities were lowest in spring, intermediate in summer and highest in autumn. The values varied between sites being lowest in the northern GOR site of *M. edulis*, intermediate in southern GOF and southern GOR site of *D. polymorpha* and highest in the northern GOR site of *D. polymorpha* (Table 1).

Table 2. The models of multiple linear regressions describing the biodeposition and clearance rates of *Mytilus edulis* and *Dreissena polymorpha*. The abbreviations are as follows: T – temperature, S – salinity, Chl – Chlorophyll *a* eq, Curr – current velocity, multiple terms indicate their interaction. *P* values of the regressions are lower than 0.001.

| Site	Species	Model	Model terms	R^2
Seili (GOF-N)	*Mytilus*	Biodeposition	T, T^2, Chl^2T^2	0.85
		Clearance	$TChl$	0.72
Kakumäe (GOF-S)	*Mytilus*	Biodeposition	$TChl$, $TCurr$, Chl^2T^2	0.92
		Clearance	$TChlCurr$	0.92
Kõiguste (GOR-N)	*Mytilus*	Biodeposition	T, T^2Chl	0.85
		Clearance	T^2Chl	0.73
Audrurand (GOR-N)	*Dreissena*	Biodeposition	$TCurr$	0.91
		Clearance	Chl, $ChlCurr$	0.92
Saulkrasti (GOR-S)	*Dreissena*	Biodeposition	$SChl$, T^2Chl, T^2Chl^2	0.91
		Clearance	T, $TChl^2$, T^2Chl, ST^2Chl^2	0.91
All sites	*Mytilus*	Biodeposition	T, T^2, Chl, Chl^2, $TChl$, Chl^2T	0.57
		Clearance	T, T^2, Chl, Chl^2, T^2Chl, Chl^2T^2	0.57
All sites	*Dreissena*	Biodeposition	$TChl$	0.89

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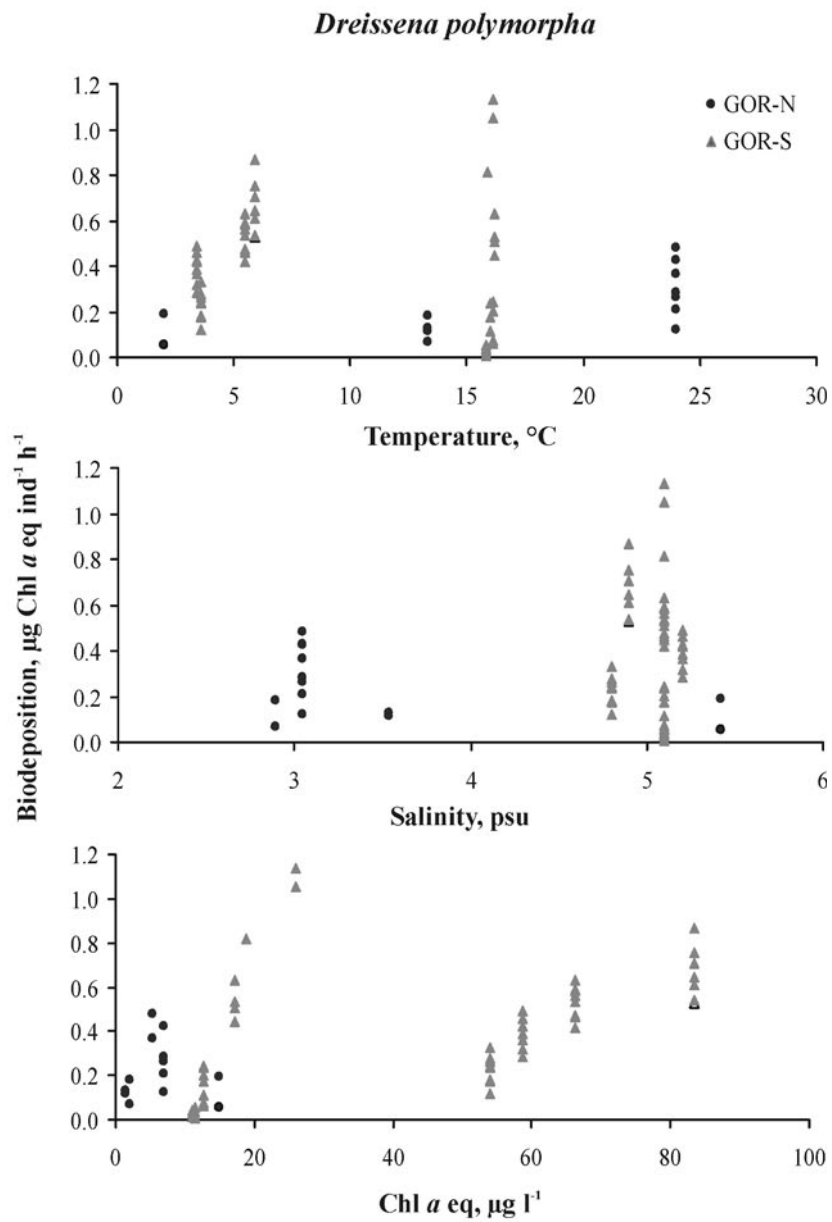
Fig. 2a. Biodeposition rate (μg ind^{-1} h^{-1}) of *D. polymorpha* as a function of ambient temperature, salinity and Chl *a* eq.