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Research Article

**MODELLING THE MATERIAL UPTAKE AND DEPOSITION OF THE  
*MYTILUS EDULIS* IN THE BALTIC COASTAL ECOSYSTEM**

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**Abstract**

A model was developed to describe the material uptake and biodeposition of bivalve *Mytilus edulis*. The existing blue mussel organism level models are based on contradictory assumptions and no agreement has still been found regarding the processes and environmental factors to be included into the model. A reconciliation of contradictory approaches was successfully done in the present model. Using seston concentration, seston organic content and mussel size as input data, the model is able to predict the uptake of suspended material, selection of organic particles and material allocation as pseudofaeces, ingested, assimilated fractions and faeces. The results of the model application to mussels in the south-eastern Baltic conditions are discussed.

**INTRODUCTION**

Blue mussels are common in shallow benthic communities of the Baltic Sea. Mussel beds are found on different substrata: soft bottom habitats in the southern Baltic; stony bottoms in the southeastern part and rocks in the northern and western areas. The species is able to colonise the depths down to 89 m, though most preferable depth range in the Baltic Sea is between 0 and 30 m.

(*e.g.* Järvekülg 1979, Kautsky 1982, Olenin 1997). In shallow bottom habitats in an excess of primary pelagic production blue mussels often make up more than 80% of the total benthic macrofauna biomass (Järvekülg 1979, Kautsky 1982, Wiktor 1990, Warzocha and Gostkowska 1996, Olenin 1997).

Blue mussels obtain food by filtering large volumes of water through the gills. This activity may alter the organic matter transformation and accumulation processes in the ecosystem (*e.g.* Kautsky 1982). An overview of interactions between bivalve grazing and ecosystem functional processes was presented in Prins *et al.* (1998). These interactions cover a number of positive and negative feedbacks. Bivalve grazing may result in local food depletion, which may reduce the growth of mussels. On a larger scale, top-down control of phytoplankton biomass, and structural shifts in plankton community might be also expected. Processing of large amounts of particulate matter may change nutrient cycling, and result in changes of pelagic nutrient pool on the ecosystem scale. Through the regeneration of nutrients from algal biomass, nutrient limitation of phytoplankton might be diminished and algal growth rates stimulated.

Efforts to synthesise knowledge on the suspension feeder bivalves functioning has resulted in the development of various ecological models. Two main categories of bivalve models are distinguished according to the hierarchy level considered: eco-physiological or organism level models and ecosystem level models.

Eco-physiological or organism level models (Bayne and Worrall 1980, Ross and Nisbet 1990, Brylinsky and Sephton 1991, Haren and Kooijman 1993, Willows 1992, Smaal 1997, Scholten and Smaal 1999) are unaware of ecosystem level processes including feedback mechanisms. Even though these models are not directly applicable at the ecosystem level, they could serve as a part of an ecosystem modelling effort.

According to the goals the ecosystem level models might be divided again into two categories. The first category models consider the ability of suspension-feeders to stabilise coastal ecosystems by controlling the production of primary producers by filtration, biodeposition, nutrient release, and other processes (Officer *et al.* 1982, Dame and Patten 1981, Finn and Leschine 1980, Ulanowich and Tuttle 1992, Herman 1993, Herman and Scholten 1990, Klepper *et al.* 1994, Scholten and Van der Tol 1994, Van der Tol and Scholten 1998). The other group of models addresses the questions of environment carrying capacity for bivalve culture (Héral 1993, Railard and Menesguen 1994, Bacher *et al.* 1998, Grant *et al.* 1993, Newell *et al.* 1998). While often sharing the general model structure, both types of ecosystem level models differ in the relative importance of involved processes and variables. For example, the

organism growth and size are of crucial importance in carrying capacity models while they might be considered as unimportant when assessing the role of bivalves in the ecosystem.

In the Baltic coastal areas the role of blue mussels was studied by descriptive (Wiktor 1990, Warzocha and Gostkowska 1996, Kube 1996) and experimental studies (Kautsky 1982, Kautsky and Evans 1987, Kotta 2000) only. The estimated effects of bivalves to the material flow in the ecosystem are considerable. For example, *Mytilus edulis* (in the northern Baltic proper) increases carbon and phosphorus annual deposition by 10% and recycles 12 and 22% of the annual nitrogen and phosphorus demand for pelagic primary production respectively (Kautsky and Evans 1987).

In the present study we focus on the material uptake and deposition modelling as the most important for benthic-pelagic exchange processes. The model is limited to the organism scale treating environmental factors as forcing functions. Much attention is paid to overcoming uncertainties and contradictions existing in the recent knowledge. Model predictions of the mussels' material uptake and biodeposition in the south-eastern Baltic conditions are discussed. Since most of the used parameters and variables were taken from the studies on *M. edulis* (some being performed even before the discussion of the systematic position of both *M. edulis* and *M. trossulus*, (e.g. Gosling 1992, Seed 1992)), in the model description we refer to the same name.

On the other hand, there is an evident lack of data to compare the rates of various physiological processes for *Mytilus* complex species, and therefore we do not assume there are significant differences at this stage of our knowledge.

## PROCESSES AND VARIABLES

The model is aimed at describing the relationship between material uptake, biodeposition rates and the factors influencing them. The variables describing material uptake and biodeposition rates are considered in the model to be output variables, while variables describing factors influencing them as input variables. Full lists of model parameters and variables are presented in Tables 1, 2.

The main quantitative characteristic determining food uptake is termed the clearance or filtration rate which defines the amount of water that is fully cleared during a time period by an animal (absolute clearance rate) or by a unit of biomass (specific clearance rate). Some authors use the filtration rate for the amount of material filtered per time unit (Hawkins *et al.* 1998). In this paper the uptake rate is used for this purpose. Other terms such as the pumping or ventilation rate are also used to characterise the amount of water that passes the animal filtering apparatus per time unit.

Table 1

Parameters used in the material uptake and deposition model.

Parameter	Value	Units	Explanation	Reference	Equation number
<i>aae</i>	1.15	-	Assimilation efficiency intercept coefficient	Hawkins <i>et al.</i> (1998)	(22)
<i>bae</i>	0.149	-	Assimilation efficiency 1/ <i>FPOM</i> slope coefficient	Hawkins <i>et al.</i> (1998)	(22)
<i>acr</i>	0.158	m <sup>3</sup> g <sup>-1</sup> day <sup>-1</sup>	Clearance rate linear coefficient	Hawkins <i>et al.</i> (1998)	(3)
<i>bcr</i>	0.67	-	Clearance rate biomass power coefficient	Hawkins <i>et al.</i> (1998), Riisgård (2001)	(3)
<i>ase</i>	0.77	-	Selection efficiency intercept coefficient	Hawkins <i>et al.</i> (1998)	(13)
<i>bse</i>	0.097	-	Selection efficiency 1/ <i>FPOM</i> slope coefficient	Hawkins <i>et al.</i> (1998)	(13)
<i>cse</i>	0.067	g day <sup>-1</sup>	Selection efficiency <i>TPM</i> slope coefficient	Hawkins <i>et al.</i> (1998)	(13)
<i>agc</i>	10.45	mm <sup>3</sup> g <sup>-1</sup>	Gut contents linear coefficient	Calibrated	(5)
<i>bgc</i>	0.67	-	Gut contents power coefficient	Hawkins <i>et al.</i> (1998)	(5)
<i>gptmin</i>	1.45	h	Minimal gut passage time	Scholten and Smaal (1999)	(6)
<i>gptmax</i>	10.9	h	Maximal gut passage time	Scholten and Smaal (1999)	(6)
<i>spfm</i>	0.001	g mm <sup>-3</sup>	Specific seston weight	Scholten and Smaal (1999)	(4)
$\alpha$	0.91	-	Clearance rate <i>TPM</i> power coefficient	Hawkins <i>et al.</i> (1998)	(3)
$\beta$	2.26	-	Clearance rate <i>FPOM</i> power coefficient	Hawkins <i>et al.</i> (1998)	(3)

**Table 2**

Variables used in the material uptake and deposition model.

Variable	Units	Explanation	Equation number
<b>Input variables:</b>			
<i>FPOM</i>	-	Fraction of organic material in seston	-
<i>TPM</i>	g m <sup>-3</sup>	Total particulate material	-
<i>W</i>	g	Mussel shell-free dry weight	-
<b>Output variables:</b>			
<i>FPOMBIODEP</i>	-	Fraction of organic material in biodeposits	(28)
<i>FPOMF</i>	-	Fraction of organic material in faeces	(25)
<i>FPOMPF</i>	-	Fraction of organic material in pseudofaeces	(20)
<i>FPR</i>	g day <sup>-1</sup>	Faeces production rate	(23)
<i>GR</i>	g day <sup>-1</sup>	Seston uptake rate by mussel	(1a)
<i>PFPR</i>	g day <sup>-1</sup>	Pseudofaeces production rate	(19)
<i>TBIODEP</i>	g day <sup>-1</sup>	Total biodeposition rate	(27)
<b>Auxiliary variables:</b>			
<i>A1</i>	g day <sup>-1</sup>	Maximal ingestion rate at no organic material in seston ( <i>FPOM=0</i> )	(7)
<i>A2</i>	g day <sup>-1</sup>	Maximal ingestion rate at pure organic seston ( <i>FPOM=1</i> )	(7)
<i>AE</i>	-	Assimilation efficiency	(22)
<i>CR</i>	m <sup>3</sup> day <sup>-1</sup>	Clearance rate	(3), (3a)
<i>FPOMING</i>	-	Fraction of organic material in ingested food	(21)
<i>GC</i>	mm <sup>3</sup>	Gut content	(5)
<i>GPT</i>	hour	Gut passage time	(6)
<i>IR</i>	g day <sup>-1</sup>	Ingestion rate	(26)
<i>IRMAX</i>	g day <sup>-1</sup>	Maximal ingestion rate	(7) or (4)
<i>SEC</i>	-	Selection efficiency for all conditions	(18)
<i>SEMAX</i>	-	Upper limit for selection efficiency	(14)
<i>SES</i>	-	Selection efficiency for saturation condition ( <i>FPOMING=1</i> )	(18b)
<i>SEU</i>	-	Selection efficiency when saturation condition is still not reached	(18a)

In most cases one does not make a difference between the clearance and pumping rates assuming all particles retained from the filtered water. Then the uptake rate equals the product of clearance or the pumping rate and seston concentration. The overall retention efficiency varies for particles of different size (Vahl 1972, Mølenberg and Riisgard 1978, Stuart and Klumpp 1984, Kautsky and Evans 1987) but this effect is considered to be unimportant for natural seston in bivalve models.

The clearance rate of *Mytilus edulis* has been extensively studied at the organism level. There is a well-known allometric relationship

$$CR = a \cdot W^b \quad (1)$$

between the maximal clearance rate of an organism and its body weight (e.g. Riisgård *et al.* 1980, Riisgård 2001, Alimov 1981, Klepper *et al.* 1994, Smaal *et al.* 1997), where  $CR$  is the clearance rate of an organism (e.g.  $\text{m}^3 \text{day}^{-1}$ );  $W$  is the shell-free dry weight of an organism (SFDW);  $a$ ,  $b$  ( $a > 0$ ,  $0 < b < 1$ ) are constants. In real feeding conditions the clearance rate should be corrected depending on environmental factors (temperature, abundance of food, current velocity, *etc.*). However no agreement exists as to which factors are the most important (see discussion in the next chapter).

The biodeposition process is described by faeces and the pseudofaeces production rates. The fate of filtered material is based on the following balance equations:

- filtered material = pseudofaeces (biodeposits) + ingested material
- ingested material = assimilated material + faeces (biodeposits)

We omit processes related to the fate of assimilated material (respiration, growth, excretion, *etc.*) as unimportant for processes considered in this model.

When the concentration of the total particulate material ( $TPM$ ) exceeds the ingestion capacity of the retained material, its part is rejected as pseudofaeces (Dame 1996). This is modelled by the condition that the uptake rate

$$GR = CR \cdot TPM \quad (1a)$$

exceeds the maximal ingestion rate. Pseudofaeces play a crucial role in phytoplankton control by reducing the uptake saturation at high food concentrations (Herman and Scholten 1990).

An important process accompanying pseudofaeces production is the selection of particles resulting in an increased fraction of organic material in the ingested food. The selection effect could be evaluated by selection efficiency ( $SE$ ) usually defined as:

$$SE = (1 - FPOMPF / FPOM) \quad (\text{Hawkins } et al. 1996) \quad (2)$$

where *FPOMPF* is the organic material fraction in pseudofaeces; *FPOM* is the organic material fraction in seston, also called food quality. An alternative way for the evaluation of selection efficiency has been proposed recently (Zemlys *et al.*, in print), but we still use equation (2) for this purpose in our model for a more convenient use of the existing experimental relationships. Though the selection activity was dismissed by some authors (Jørgensen 1996), a number of *in vitro* and *in situ* investigations (Kiørboe and Møhlenberg 1981, Defosse and Hawkins 1997, Ward *et al.* 1998, Hawkins *et al.* 1998) confirmed the selective feeding character of mussels. According to Hawkins *et al.* (1998) selection efficiency may reach 60% and hence considerably change the organic and inorganic material ratio in biodeposits.

#### **FOOD ABUNDANCE AND FOOD QUALITY EFFECTS TO FOOD UPTAKE**

Estimates of the clearance rate reported by different authors vary considerably. Some authors suggest that this variability is attributed to erroneous measurements of the clearance rate (Jørgensen 1996, Riisgård 2001). Another explanation is that the wide range of clearance rate measurements reported in literature clearly conflicts with the view that bivalve feeding is a highly automated and unregulated process (Cranford and Hill 1999, Cranford 2001). A number of authors have shown that the large variance in experimental and observed responses might be explained by direct physiological control (Heip *et al.* 1995, Hawkins *et al.* 1996, Bayne 1998, Cranford and Hill 1999, Cranford 2001).

It is obvious that no agreement was found among scientists concerning the relationship between food abundance and the clearance rate of *Mytilus edulis*. Riisgård and Randflow (1981) and Riisgård (2001) have found clearance rate reductions at low and high concentrations. They explained the depression of the clearance rate by a valve closure at low food abundance and by overloading the filtration and/or digestive system at high food abundance. The reported constant clearance rates correspond to a concentration range of 1500-30000 phytoplankton cells ml<sup>-1</sup> (Riisgård and Randflow 1981), which according to the conversion coefficients presented by Smaal *et al.* (1997), might be approximated to 0.04-0.8 g m<sup>-3</sup> of particulate material. Assuming that such low concentrations are rarely found in natural conditions, only negative trends were

used for the clearance rate in some models (*e.g.* Herman 1993, Klepper *et al.* 1994).

Even though the valve closure effect is neglected, a variety of relationships can still be found in literature. Smaal and Scholten (1999) used a constant clearance rate for food concentration 0-50 g m<sup>-3</sup>, linearly decreasing for 50-200 g m<sup>-3</sup>, and constant for concentrations higher than 200 g m<sup>-3</sup>. A linear depression at low food concentrations for high values of the organic material fraction (higher than 0.6) was suggested later (Scholten and Smaal 1999). Hawkins *et al.* (1996) have found the clearance rate to be linearly increasing at seston concentrations of 10 to 90 g m<sup>-3</sup>. Thus, even if extreme seston concentrations are neglected, still three different trends should be considered: negative, constant and positive. Using the optimal digestive investment model, Willows (1992) demonstrated a feeding strategy that maximizes the net rate of energy gain from the available food. That points out the possibility to express the clearance rate as a function of seston concentration and food quality (for example, the fraction of organic material in seston). The following experimental relationship for this was proposed by Hawkins *et al.* (1998):

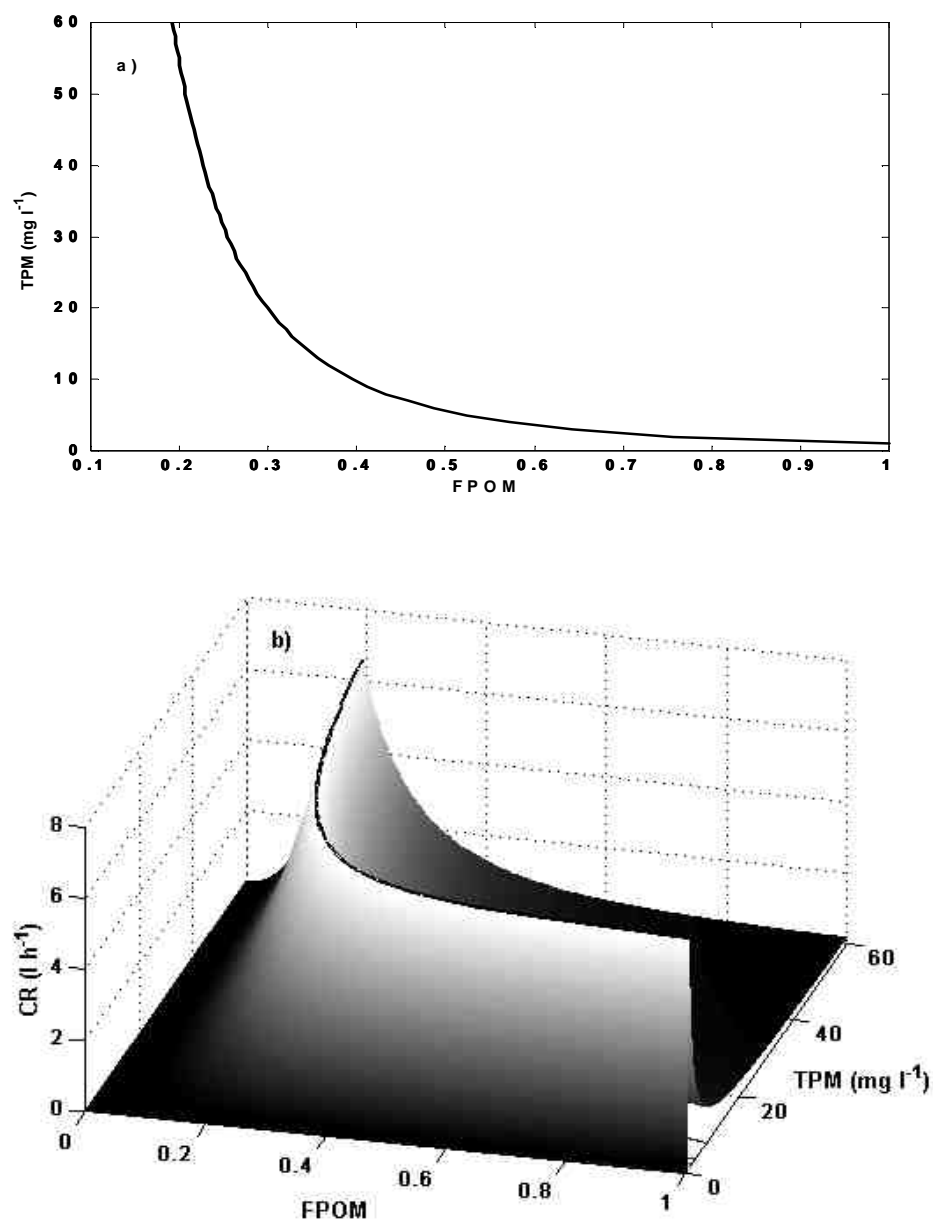
$$CR = acr \cdot W^{bcr} \cdot TPM^{\alpha} \cdot FPOM^{\beta} \quad (3)$$

where  $CR$  is the clearance rate;  $W$  is the biomass of mussel (g SFDW);  $TPM$  is the total particulate material (g m<sup>-3</sup>);  $FPOM$  is the fraction of organic material in seston;  $acr$ ,  $bcr$ ,  $\alpha$ ,  $\beta$  are parameters (see Table 1). It is important that this relationship can describe all trends mentioned above as instances of different relationships between food quality and seston concentration. Introduction of the allometric relationship  $FPOM = \gamma \cdot TPM^{-\delta}$  (Navarro and Iglesias 1993, Hawkins *et al.* 1996, Hawkins *et al.* 1998) into (3) yields

$$CR = acr \cdot \gamma^{\beta} \cdot w^{bcr} \cdot TPM^{\alpha - \beta \cdot \delta}$$

Thus, the clearance rate, which is independent of seston concentration if  $\delta = \alpha / \beta \approx 0.4$ , is a decreasing function for  $\delta > 0.4$ , and is an increasing function if  $\delta < 0.4$ . Clearance as an increasing function for  $\delta = 0.27$  was found by Hawkins *et al.* (1996). For  $acr \cdot \gamma^{\beta} = 1.371 \text{ h}^{-1} \text{ g}^{-1}$ , when  $\gamma = 0.5$ ,  $\delta = 0.4$  from (3) one gets an expression for the clearance rate that is similar to the one used by Smaal (1997).

Equation (3) is also consistent with laboratory measurements of the clearance rate using phytoplankton diet. For  $TPM$  of 1 mg l<sup>-1</sup>, which is close to



**Fig. 1.** Modelled food quality and quantity effect on the clearance rate (CR) of *Mytilus edulis*: a) maximum clearance rate curve; b) clearance rate versus food quantity (TPM) and quality (FPOM) for standard 1g SFDW mussel.

the upper limit of concentrations that still does not cause reduction of the clearance rate (Riisgård 2001), the clearance rate value for 1g mussel is equal to  $acr=6.6 \text{ l h}^{-1}$ , which is still consistent with the value of  $7.4 \text{ l}^{-1} \text{ h}^{-1}$  reported in Riisgård (2001).

All these considerations support the use of relationship (3) for the clearance rate modelling. Our model does not include any component representing the valve closure effect at low food concentrations, except function (3), which yields a zero clearance rate at zero *TPM* and *FPOM*. This effect, however, does not seem to be important in the eastern coastal area of the Baltic Sea, where moderate seston concentrations prevail (Pustelnikov 1992, Galkus and Joksas 1997).

When high quality food is abundant, the clearance rate being limited by constraints of food digestibility and assimilation rate (Willows 1992) should reach the saturation point. Since value  $CR_{MAX} = \max_{TPM} CR(TPM, FPOM)$  is constant (Willows, 1992) and  $CR_{MAX} = acr \cdot W^{bcr}$  (clearance rate is maximal at  $FPOM=1$ ,  $TPM \approx 1 \text{ mg l}^{-1}$  (Riisgård 2001)), the following relationship derives from (3)

$$TPM = FPOM^{-\left(\frac{\beta}{\alpha}\right)}$$

being valid at the maximum clearance rate (Fig. 1a). We will neglect the narrow plateau (less than  $1 \text{ mg l}^{-1}$  wide at  $FPOM=1$ ) of the clearance rate (Riisgård 2001), assuming that the clearance rate is in accordance with equation (3) until the saturation condition described by the above equation is reached. Since there is no information about the clearance rate pattern in saturation conditions, we assume

$$CR = acr \cdot W^{bcr} \cdot TPM^{-\alpha} \cdot FPOM^{-\beta} \quad (3a)$$

when  $TPM \geq FPOM^{-\left(\frac{\beta}{\alpha}\right)}$  (Fig. 1b).

Certain seeming contradictory results related to the clearance rate saturation threshold might be now explained by equations (3) and (3a). When the seston concentration is increased, keeping a constant organic content, the saturation point is reached earlier for a higher *FPOM* than for a lower one (Fig. 1a). Scholten and Smaal (1999) observed the saturation point at  $FPOM=0.6$  for a seston concentration less than  $5 \text{ mg l}^{-1}$ , which is in a good agreement with the value  $TPM=3.6 \text{ mg l}^{-1}$  obtained from the curve in Fig. 1a for  $FPOM=0.6$ . Hawkins *et al.* (1998) did not observe any saturation increasing seston

concentrations up to 90 mg l<sup>-1</sup>, however the relationship  $FPOM = 0.41 \cdot TPM^{-0.27}$  was valid in their experiments. The saturation seston concentration can be found searching the intersection point between the curve in Fig. 1a and curve  $FPOM = 0.41 \cdot TPM^{-0.27}$ , which yields the saturation threshold at  $TPM=830$  mg l<sup>-1</sup> only. It is clear now why saturation was not reached for seston concentrations lower than 90 mg l<sup>-1</sup>.

### TEMPERATURE EFFECTS AND CONFOUNDING FACTORS

Different approaches have been used to the relationship between the *Mytilus edulis* clearance rate and water temperature. In some studies (Ross and Nisbet 1990, Smaal 1997, Smaal *et al.* 1997) the clearance rate is temperature independent. In contrast, Haren and Kooijman (1993) use a monotonic growing function to reflect clearance changes under variable temperature. As a compromise between these options Brylinsky and Sephton (1991) consider the clearance rate to be affected at low (less than 10°C) and high (more than 20°C) temperatures. Since the clearance rate is dependent on the fraction of organic material in seston (3), the influence of low temperature to some extent is taken into account as periods of low organic material in seston and low temperatures coincide in temperate regions. On the other hand, in eutrophicated water bodies such as the Baltic Sea, abundance peaks of toxic species (particularly of the genus *Microcystis* and *Anabaena*) occur at higher temperatures during summer time. This may result in a reduction of the clearance rate of suspension feeding bivalves (Smaal and Twist 1997), but these effects are too controversial and still poorly quantified to be included into the model.

There have been no attempts made to separate the influence of these two effects and, therefore, no direct temperature effect is included in the model.

### BIODEPOSITION RELATED PROCESSES

The simplest approach used to determine the pseudofaeces threshold was to relate it to the amount of the total suspended material. Kiørboe *et al.* (1980) estimated the threshold value for *Mytilus edulis* approximately at 1 mg l<sup>-1</sup> of suspended material. A more advanced approach was to relate this threshold to the maximal ingestion rate, being an allometric function of the organism body weight (Bayne and Worrall 1980, Brylinsky and Sephton 1991). This function was extended to include the total particulate material and the fraction of organic material as independent variables (Hawkins *et al.* 1998). In this study we use the modified but physiologically interpretable approach developed by Smaal (1997), Scholten and Smaal (1998, 1999). Instead of seston and its organic

content as independent variables, the fraction of organic material in the ingested food, gut content and gut passage time in this approach is considered:

$$IRMAX = (GC \cdot spfm) / (GPT / 24) \quad (4)$$

$$GC = agc \cdot W^{bgc} \quad (5)$$

$$GPT = gptmax + (gptmin - gptmax) \cdot FPOMING \quad (6)$$

where  $IRMAX$  is the maximal ingestion rate ( $\text{g day}^{-1}$ );  $GC$  is gut content, ( $\text{mm}^3$ );  $GPT$  is the gut passage time (h);  $FPOMING$  is the fraction of organic material in the ingested food;  $spfm$  is the specific food mass ( $\text{g mm}^{-3}$ );  $W$  is the soft-tissue, dry weight of mussel (g);  $agc$ ,  $bgc$ ,  $gptmin$  and  $gptmax$  are parameters (Table 1). We use the following more convenient relationships for  $IRMAX$  derived from (4, 5, 6):

$$IRMAX = \frac{A_1 \cdot A_2}{A_2 + (A_1 - A_2) \cdot FPOMING} \quad (7)$$

where

$$A_1 = IRMAX(0) = \frac{spfm \cdot GC}{24 \cdot gptmax}; \quad A_2 = IRMAX(1) = \frac{spfm \cdot GC}{24 \cdot gptmin} \quad (8)$$

Even though pre-ingestive selectivity is generally recognised, the factors influencing preferential ingestion remain uncertain. Various proposed criteria include the particle size, shape, motility, density, and chemical cues such as algal ectotines (for review see Defosse and Hawkins 1997). Therefore, the “black box” approach was used while modelling this phenomenon. The selectivity effect was assumed to be directly linked to the organic material fraction in the ingested food ( $FPOMING$ ), which is a power function of the organic material fraction in seston ( $FPOM$ ) (Smaal 1997, Scholten and Smaal 1998, 1999):

$$FPOMING = FPOM^{bs} \quad (9)$$

where  $bs$  is a parameter,  $0 < bs < 1$ . However, this approach leads to conclusions that contradict the selection efficiency measurements (see discussion in Zemlys *et al.* (in print)). A relationship similar to (8) may be derived deductively. Suppose an empirical function for selection efficiency ( $SE$ ) is already given (expression will be defined below). The balance equation

$$FPOMPF \cdot PFPR + FPOMING \cdot IRMAX = FPOM \cdot GR$$

is valid when pseudofaeces are produced; where  $FPOMPF$  is the organic material fraction in pseudofaeces;  $PFPR$  is the pseudofaeces production rate;  $GR$  is the uptake rate. Employing formula (2) and substituting  $PFPR$  by  $(IRMAX-GR)$  this equation is combined as

$$(1-SE) \cdot FPOM \cdot (GR-IRMAX) + FPOMING \cdot IRMAX = FPOM \cdot GR \quad (10)$$

The solution of (10) with respect to  $IRMAX$  is

$$IRMAX = \frac{FPOM \cdot GR \cdot SE}{FPOMING - (1-SE) \cdot FPOM} \quad (11)$$

A comparison of (7) and (11) yields the equation for  $FPOMING$ :

$$\frac{FPOM \cdot GR \cdot SE}{FPOMING - (1-SE) \cdot FPOM} = \frac{A_1 \cdot A_2}{A_2 + (A_1 - A_2) \cdot FPOMING}$$

Its solution is the function

$$FPOMING = FPOM \cdot \frac{A_2[A_1(1-SE) + GR \cdot SE]}{A_1 \cdot A_2 + (A_2 - A_1) \cdot SE \cdot FPOM \cdot GR} \quad (12)$$

similar to (9).

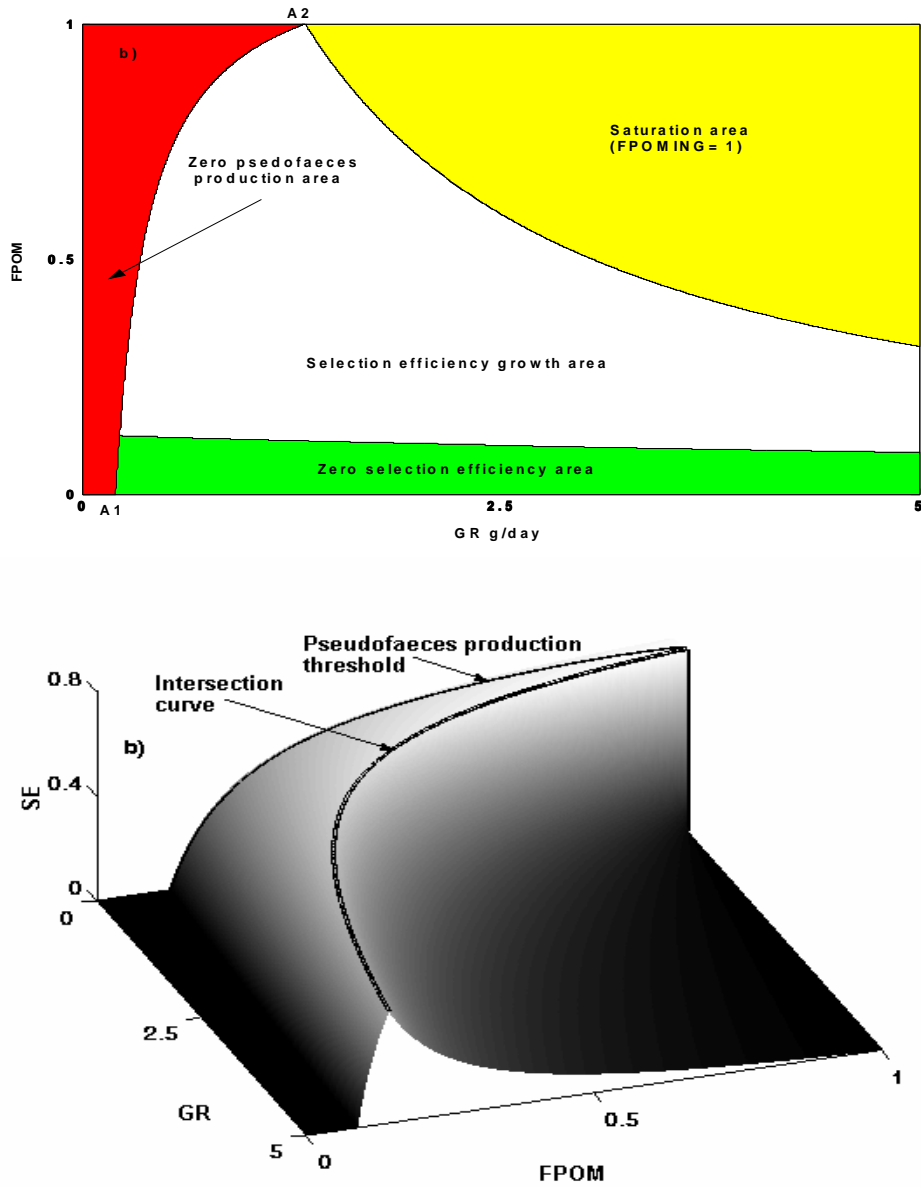
We use the following empirical function from Hawkins *et al.* (1998) for selection efficiency:

$$SE = ase - bse / FPOM + cse \cdot GR \quad (13)$$

where  $ase$ ,  $bse$ ,  $cse$ , are parameters (Table 1). Function (13) cannot be used for all values of independent arguments, since it monotonically increases and for certain quite high values is incompatible with material balance. In fact, if  $SE \geq SEMAX$ , where

$$SEMAX = \frac{1-FPOM}{FPOM} \cdot \frac{A_2}{GR-A_2} \quad (14)$$

$FPOMING \geq 1$  follows from (12). This condition takes place since the amount of organic material in seston is insufficient to ensure the fraction of organic material in pseudofaeces required by  $SE \geq SEMAX$ . Hence, the selection effici-



**Fig. 2.** Characteristics of *Mytilus edulis* selection efficiency: a) the areas corresponding to different expressions of the selection efficiency function (18); b) the selection efficiency surface versus FPOM and the grazing rate (equation (18)).

ency may not exceed the value  $SEMAX$ , since pure organic material is ingested (saturation is reached) at  $SE = SEMAX$ . Since  $SEMAX$  is a decreasing function for large-enough argument values, the selection efficiency function should follow the same pattern. Therefore, corrections are needed in function (13) and we assume that selection efficiency is in accordance with (14) when saturation ( $FPOMING=1$ ) is reached; otherwise it is described by (13) (when selection activity occurs). The following characteristic sub-areas of the definition domain for  $SE$  (as the function of  $FPOM$  and  $GR$ ) should be separated in order to exhaustively describe selection efficiency: 1) saturation area ( $FPOMING=1$ ); 2) no pseudofaeces area; 3) no-selection activity at a low food quality area; 4) the area of increasing selection efficiency (Fig. 2a). Selection efficiency is in accordance with (14) in the saturation area. The boundary curve of this area is found as a projection of the intersection curve of surfaces (13) and (14). The equation

$$FPOM = \frac{A_2 + bse \cdot (GR - A_2)}{A_2 + ase \cdot (GR - A_2) + cse \cdot GR \cdot (GR - A_2)} \quad (15)$$

derived as a combination of (13) and (14) is the equation of the boundary curve for the saturation area. Absence of the pseudofaeces area is determined by condition  $GR \leq IRMAX(FPOMING)$ . Since selection activity does not take place here, then  $SE = 0$ . The pseudofaeces threshold curve is obtained from condition  $GR = IRMAX(FPOMING)$ . The employment of (7) produces the equation

$$FPOM = \frac{A_2 \cdot (GR - A_1)}{GR \cdot (A_2 - A_1)} \quad (16)$$

for the pseudofaeces threshold. For small  $FPOM$  no selection occurs (Hawkins *et al.* 1998), therefore the equation for the boundary curve derived from (13), using condition  $SE=0$  is as follows:

$$FPOM = \frac{bse}{ase + cse \cdot GR} \quad (17)$$

The joint expression for selection efficiency ( $SEC$ ) covering all sub-areas (Fig. 2b) is

$$SEC = \begin{cases} \min\{SEU, SES\}, & GR > IRMAX(FPOM) \\ 0, & GR \leq IRMAX(FPOM) \end{cases} \quad (18)$$

where, with regard to (13)

$$SEU = \max\{0, [ase - bse / FPOM + cse \cdot GR]\} \quad (18a)$$

is selection efficiency when saturation is still not reached;

$$SES = \begin{cases} 1, & SEMAX < 0 \\ \min\{1, SEMAX\}, & SEMAX \geq 0 \end{cases} \quad (18b)$$

is saturation selection efficiency.

The declining selection efficiency at high  $FPOM$  observed by Bayne *et al.* (1993) was explained as the saturation effect (Hawkins *et al.* 1998), which is consistent with the surface shape (18).

The pseudofaeces production rate ( $PFPR$ ) is defined by

$$PFPR = \max\{0, GR - IRMAX\} \quad (19)$$

The organic material fraction in pseudofaeces is defined as

$$FPOMPF = (1 - SEC) \cdot FPOM \quad (20)$$

The final organic material fraction in the ingested food according to (12) is

$$FPOMING = FPOM \cdot \frac{A_2 \cdot [A_1 \cdot (1 - SEC) + GR \cdot SEC]}{A_1 \cdot A_2 + (A_2 - A_1) \cdot SEC \cdot FPOM \cdot GR} \quad (21)$$

This formula is valid for any argument values, particularly for  $SEC = 0$ , saturation  $SEC$  values, and for the pair of values  $GR = A_2$ ,  $FPOM = 1$ . The later case yields  $FPOMING = 1$  at  $FPOM = 1$  and  $SEC = (ase - bse) + cse \cdot A_2 \neq 0$  (derived by calculating the  $SEMAX$  limit when  $GR$  approaches  $A_2$  on curve (15)). However, selection activity at  $FPOM = 1$  is unlikely. The reason might be

that function (13) is always increasing with respect to both arguments and used beyond the range argument values that it was fitted for (Hawkins *et al.* 1998). Further experimental investigations are needed to answer whether function (13) decreases at high *FPOM* values, when still  $FPOMING < 1$ . Therefore, care should be taken while applying the model at high *FPOM* values.

Assimilation efficiency should be defined to find the faeces production rate. In some models (Brylinski and Sephton 1991, Herman 1993, Klepper *et al.* 1994) constant assimilation efficiency is assumed. We chose to use the approach based on the dependency of assimilation efficiency (*AE*) on the fraction of organic material in the ingested food (Hawkins *et al.* 1998):

$$AE = aae - bae / FPOMING \quad (22)$$

where *aae*, *bae* are parameters (Table 1). Finally, the following formula for the faeces production rate (*FPR*), fraction of organic material in faeces (*FPOMF*), ingestion rate (*IR*), total biodeposition rate (*TBIODEP*) and fraction of organic material in biodeposits (*FPOMBIODEP*) can be derived from the formulas given above and material balance:

$$FPR = (GR - PFPR) \cdot (1 - AE \cdot FPOMING) \quad (23)$$

$$FPOMF = (1 - AE) \cdot FPOMING \cdot IR \quad (25)$$

$$IR = \min\{GR, IRMAX\} \quad (26)$$

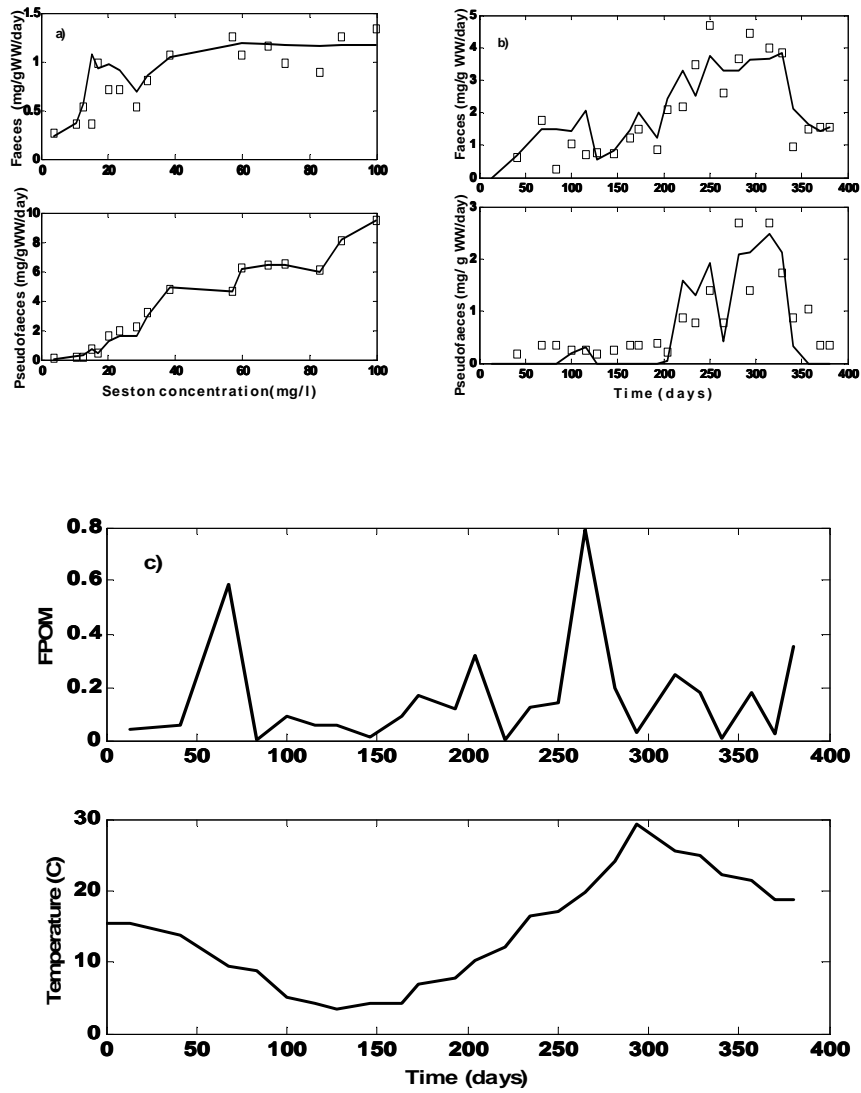
$$TBIODEP = FPR + PFPR \quad (27)$$

$$FPOMBIODEP = \frac{FPOMF \cdot FPR + FPOMPF \cdot PFPR}{TBIODEP} \quad (28)$$

The above model could be used to simulate material uptake and biodeposition at the organism level if seston concentration and the fraction of organic material in seston are given as forcing functions.

## MODEL TESTING

The model presented above was tested on results from short-term and long-term laboratory experiments in Mutsu Bay (Japan) (Tsuchiya 1980). The choice of these experiments was determined by a deficit of experiments with controlled



**Fig. 3.** Correspondence between model predictions (solid line) and experimental results (squares, as derived from Tsuchiya 1980) for: a) short-term (19°C, dark conditions) and b) long-term (small mussels) experiments; and (c) comparison of *FPOM* and water temperature dynamics.

uptake and biodeposition characteristics for the Baltic Sea. Unfortunately food quality was not measured in these experiments and was estimated employing the minimum  $\chi^2$  method for each data point. Of course, such a procedure can be treated only as preliminary testing of the model. The wet weight of mussels used in the experiment was converted to shell-free dry weight according to Rumohr *et al.* (1997). The dynamics of seston in the experimental boxes was simulated using the equation

$$\frac{dTPM}{dt} = \frac{TPM_{in} \cdot Q_{in}}{V} - \frac{TPM \cdot Q_{in}}{V} - \frac{CRT \cdot TPM}{V} \quad (29)$$

where  $TPM$  is seston concentration in the experimental box ( $\text{g m}^{-3}$ );  $V$  is the box volume ( $\text{m}^3$ );  $TPM_{in}$  is the concentration of seston in the incoming water ( $\text{g m}^{-3}$ );  $Q_{in}$  is the water flow rate ( $\text{m}^3 \text{day}^{-1}$ );  $CRT$  is the total clearance rate of mussels in the box ( $\text{m}^3 \text{day}^{-1}$ ) based on (3).  $Q_{in}$ ,  $TPM_{in}$  and  $V$  are reported in the experiment description (Tsuchiya 1980). Parameter values used in simulation are presented in Table 1.

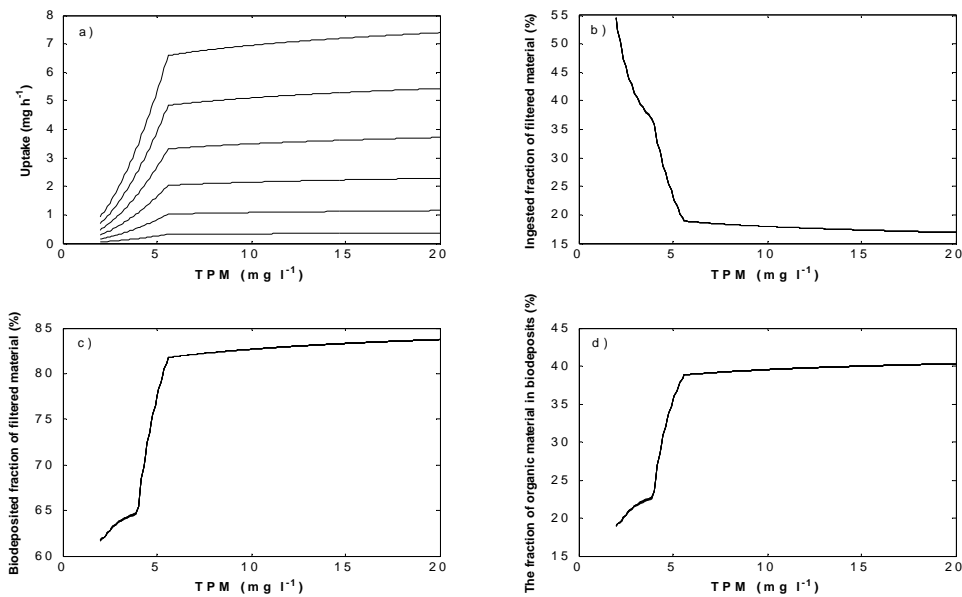
The correspondence between the model prediction and data from short-term experiment is shown in Fig. 3a. Very close correspondence ( $R^2 = 0.99$ ) was obtained for pseudofaeces production. The lower consistency with faeces production ( $R^2 = 0.55$ ) might be attributed to higher variability of the observed faeces production rate in the experiment. Only the linear parameter for gut contents was estimated by calibration since the initial  $agc$  value  $16 \text{ mm}^3 \text{g}^{-1}$  gave a poor fit to the faeces production data. The calibrated  $agc$  value  $10.54(\pm 2.25) \text{ mm}^3 \text{g}^{-1}$  ( $\pm 95\%$  confidence interval) was still close to the lower limit of the range 12-20 found after the calibration of the complex mussel growth model (Smaal and Scholten 1999). However, the obtained  $agc$  value gave a better correspondence to the long-term experiment data as well (Fig. 3b).

The poorer correspondence between the predicted and measured values ( $R^2=0.75$  for faeces and  $R^2=0.62$  for pseudofaeces production) in a long-term experiment might be attributed to the relatively low accuracy of seston concentration values obtained by a linear interpolation of data values measured only twice per month. The low frequency of seston concentration measurements may cause considerable discrepancies between predicted and measured biodeposition values, since daily variation in suspended particulate material may be close to its annual range (Newell *et al.* 1998). Nevertheless, the qualitative correspondence is satisfactory. Calibrated food quality values seem to be also reliable regarding the temperature variation curve as periods of higher

temperature generally coincide with higher food quality during experiment (Fig. 3c).

### MATERIAL UPTAKE AND BIODEPOSITION PREDICTIONS FOR THE SOUTH-EASTERN BALTIC

The model was applied for an evaluation of possible uptake and biodeposition rates in the south-eastern part of the Baltic Sea near the Curonian lagoon, where bivalves *Mytilus edulis* colonize stony bottom habitats with an average biomass of  $1\,700\text{ g m}^{-2}$  being the highest among the sublittoral bottom macrofauna. With its average density of  $40 \times 10^3$  and  $\text{m}^{-2}$  the species usually contributes to up to 90% of the total macrofauna found on the hard bottom sub-



**Fig. 4.** Model predictions for the Baltic Sea conditions: a) material uptake predictions for different size mussels (5-30mm shell length) at various concentrations of total particulate material (TPM); b) ingested fraction of filtered material predictions for different size mussels (5-30mm shell length) at various concentrations of total particulate material (TPM); c) biodeposited fraction of filtered material predictions for different size mussels (5-30mm shell length) at various concentrations of total particulate material (TPM); d) fraction of organic material in biodeposits predictions for different size mussels (5-30mm shell length) at various concentrations of the total particulate material (TPM).

strates (Olenin 1998). The near bottom waters of the site can be characterised by relatively low maximal ( $20 \text{ mg l}^{-1}$ ) and average ( $2\text{-}8 \text{ mg l}^{-1}$ ) seston concentrations with the fraction of organic material fluctuating near 50% (Galkus and Joksas 1997). The main uptake and biodeposition characteristics were calculated for organisms with a shell-length interval of 5 to 30 mm with an incremental step of 5 mm. Rumohr *et al.* (1997) equation was used for shell-length conversion to shell-free dry weight. A seston concentration interval of 2 to  $20 \text{ mg l}^{-1}$  and fraction of organic material equal to 0.5 were employed in model calculations.

The relationship between the uptake rate and (Fig. 4a) has almost a sigmoidal shape with a slow increase in seston concentrations greater than  $5.6 \text{ mg l}^{-1}$  (saturation threshold for the clearance rate is equal to  $TPM = 0.5 \frac{\beta}{\alpha} \approx 5.6$ ; see Fig. 1a). The uptake slowdown with an increasing seston concentration is caused by a decrease in the clearance rate for  $TPM > 5.6 \text{ mg l}^{-1}$  (see Fig. 1b) and is more advanced for small individuals in comparison to larger ones. The uptake rate increases considerably with the mussel size and differences between different-size individuals' uptake rates also increase with seston concentrations. For instance, the ratio between the uptake rate for individuals of 30 and 5 mm in length at a seston concentration of  $2 \text{ mg l}^{-1}$  is equal to 10, whereas at a seston concentration of  $20 \text{ mg l}^{-1}$  this ratio increases up to 25.

The ingested fraction of filtered material (Fig. 4b) does not almost depend on mussel length and decreases very quickly from 55% up to 17% at a seston concentration of  $5.6 \text{ mg l}^{-1}$  remaining relatively constant for  $TPM > 5.6 \text{ mg l}^{-1}$ . It means that at these concentrations of suspended material in the ambient water approximately 83% of filtered material is deposited on the bottom as pseudofaeces. The curve presented in Fig. 4b has another critical point at  $TPM=4 \text{ mg l}^{-1}$  where the fraction of organic material in the ingested food becomes equal to 1 and the ingestion rate becomes constant. Thus, since the uptake rate still increases at this point, the ingested fraction of filtered material drops more quickly when this concentration is exceeded.

The curves of the biodeposited fraction of filtered material (Fig. 4c) and the fraction of organic material in biodeposits (Fig. 4d) have a similar shape, which could be interpreted as a mirror-image of the curve in Fig. 4b. For seston concentrations higher than  $5.6 \text{ mg l}^{-1}$  about 83% of filtered material goes to biodeposits and a vast part of biodeposits are pseudofaeces. The fraction of organic material in biodeposits reaches 40% at  $TPM=5.6 \text{ mg l}^{-1}$  and is less than the fraction of organic material in seston – only 10%.

## CONCLUSIONS

Though a number of *Mytilus edulis* models have been created, heretofore very contradictory assumptions are used quantifying food processing within the organism and especially the clearance rate. This obviously obscures the application of these models for predictions of mussels' impact on material fluxes in ecosystem. An attempt to reconcile different approaches was made by the material uptake and biodeposition model presented in this paper.

Our analysis shows that many contradictory experimental results and theoretical approaches could be brought together introducing food quality as an additional factor controlling the clearance rate. This approach explains the variety of relationships between the clearance rate and seston concentration as well as various threshold seston concentrations for pseudofaeces production and differences in clearance rates obtained in phytoplankton and natural seston diet experiments.

A lot of existing evidence on pre-ingestive selection of food by mussels was ignored (Jørgensen 1996) or this process was incorrectly described by bivalve models (Smaal and Scholten 1999). In this study we used an empirical relationship (Hawkins *et al.* 1998) to account for this phenomenon. A detailed analysis based on material balance enabled us to avoid difficulties which arose in other models (Smaal and Scholten 1999) when expressing the quality of ingested food directly through the quality of seston. The presented model can be used as a tool for an analysis of the role of selection activity in different conditions. The simulation results for the south-eastern Baltic showed that the importance of selection efficiency varies for different concentrations of seston. At low seston concentrations the fraction of organic material in biodeposits is considerably lower than in the ambient water due to selection activity, however for higher concentrations this difference is only about 10% and little depends on seston concentration (Fig. 4d).

The comparison of model predictions with experimental data was a serious problem for this model. There are few studies quantifying the uptake and biodeposition of food simultaneously. It was impossible to find such data in literature for the Baltic Sea. The data used for comparison does not include the fraction of organic material therefore the comparison can be qualified as qualitative only. Specially designed experiments are needed for a better validation of the presented model and it should be used for an analysis of mechanisms related to material uptake and biodeposition rather than as a prognostic tool.

The current model, being based on the available knowledge strongly depends on the quality of this knowledge. In this study the weak points are also

caused by gaps in experimental research and a lack of quantitative data. The selection efficiency relationship (13) is based on a rather narrow range of the seston organic material fraction. Some uncertainty is caused by contradictory conclusions regarding the temperature influence on the clearance rate; therefore we did not consider this factor in the model, partly taking into account its influence by introducing the clearance rate relationship to the organic material fraction in seston. We expect that the model proposed in this paper and its simulation results will serve as an inspiration for further experimental investigations of the material uptake and biodeposition processes of suspension feeding bivalves, which in turn will enable an improvement of the model itself.

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