

Revision pre-ingestive selection efficiency definition for suspension feeding bivalves: facilitating the material fluxes modelling

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Received 6 March 2002; received in revised form 27 January 2003; accepted 3 March 2003

Abstract

The importance of the particle selective feeding of bivalves becomes more evident and it is necessary to incorporate this phenomenon into ecological models in order to reflect correctly the material fluxes inside the organism and ecosystem as well. The problems related to the modelling of organic matter selection are considered in this paper and a new definition of pre-ingestive selection efficiency is proposed. It differs from the classical one in using the organic material fraction in ingested food instead of pseudofaeces. The newly defined selection efficiency exhibits an advantage in simplified shape of experimental relationship to the organic matter fraction in seston and easier derivation of formulas related to mathematical food processing formulation.

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Keywords: Pre-ingestive selection efficiency; Suspension feeding bivalves; Modelling of material fluxes

1. Introduction

Suspension feeding bivalves play important role in many coastal ecosystems. Their feeding activity may result in multiple changes of organic matter transformation and accumulation processes. An overview of interactions between bivalve grazing and ecosystem functional processes was presented in Prins et al. (1998). These interactions consist of a number of positive and negative feedbacks. Bivalve grazing may result in local food depletion reducing the growth of mussels. On a larger scale, top-down control of phytoplankton biomass, and structural shifts in plankton community might also be expected. Processing of large amounts of particulate matter may alter nutrient cycling, and result in changes of pelagic nutrient pool

at the ecosystem scale. Through regeneration of nutrients from algal biomass, nutrient limitation of the phytoplankton might be diminished and algal growth rates stimulated.

Efforts to synthesise knowledge on suspension feeders functioning has resulted in development of various ecological models. Two main categories of bivalve models are distinguished according to hierarchy level considered. Eco-physiological or organism level models (Bayne and Worall, 1980; Ross and Nisbet, 1990; Brylinsky and Sephton, 1991; Haren van and Kooijman, 1993; Willows, 1992; 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 the ecosystem modelling effort (for example, creation of individual-based models).

According to the goals, the ecosystem level models might be divided again into two categories.

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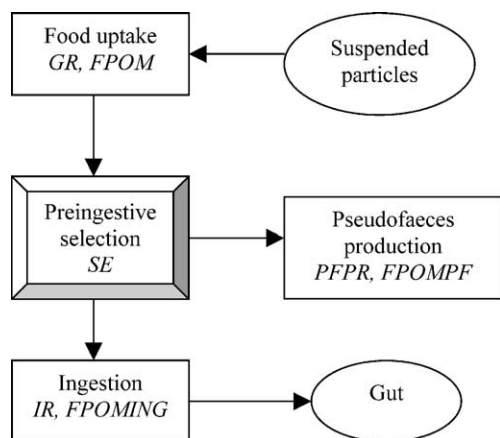


Fig. 1. The food processing diagram with selection activity and accompanying processes.

The first category models consider the ability of suspension-feeders to stabilise coastal ecosystems by controlling primary production by filtration, biodeposition, nutrient release, and other processes (Officer et al., 1982; Dame and Patten, 1981; Finn and Leschine, 1980; Herman and Scholten, 1990; Ulanowich and Tuttle, 1992; Herman, 1993; Klepper et al., 1994; Scholten and Van der Tol, 1994; Van der Tol and Scholten, 1998). 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 general model structure, both types of ecosystem level models differ in relative importance of involved processes and variables. For example, organism growth and size are of crucial importance in carrying capacity models while they might be considered unimportant as the model assesses bivalves' role in the ecosystem.

In this paper, the modelling of one of feeding activity processes—pre-ingestive food selection—is considered. The suspension feeding bivalves reject part of filtered food as pseudofaeces at certain level of seston concentration. An important process accompanying pseudofaeces production is the selection of particles causing an increase of organic material fraction in ingested food (Fig. 1). Although this process was rejected by some authors (Jørgensen, 1996), a number in vitro and in situ investigations (Kiørboe and Møhlenberg, 1981; Hawkins et al., 1996, 1998;

Defosse and Hawkins, 1997; Ward et al., 1998; Schneider et al., 1998; Baker et al., 2000) confirmed the selective feeding of mussels. The selection efficiency of organic matter may reach 60% (Hawkins et al., 1998) and hence considerably change the organic and inorganic material ratio of ingested food and biodeposits.

Although the pre-ingestive selectivity becomes generally recognised, the factors influencing preferential ingestion remain uncertain. Various proposed criteria include particle size, shape, motility, density, and chemical cues such as algal ectotrichs (for review see Defosse and Hawkins, 1997). The organic material selection activity defined as selection efficiency, however, can be quantitatively described by experimental relationships that are already proposed for some species of marine bivalves (Hawkins et al., 1996, 1998). This gives a reason to include description of this process into bivalve models. Different empirical, biological and ecological observations were already explained in terms of comprehensive thermodynamic hypothesis (maximum principle) (Jørgensen, 2002; Jørgensen et al., 2002; Odum, 2002). Application of this approach seems promising for explanation of selection efficiency relationships as well. Therefore, in order to facilitate investigation in this direction it is important to have the consistent selection efficiency definition.

There are still few bivalve models considering the organic selection activity, therefore the problems related to incorporation of this phenomenon are analysed minimally. This is equally true for the technique of its inclusion into the model and for the selection of appropriate measure for selection activity itself. The goal of this study is to give a comprehensive analysis of these problems and to offer solutions facilitating the creation of mathematical models for bivalves.

2. Definitions of selective efficiency

The organic selection activity is defined as selection efficiency. The classical selection efficiency (SE) is defined as (Bayne et al., 1993):

$$SE = 1 - \frac{FPOMPF}{FPOM} \quad (1)$$

Table 1
List of notations

Notation	Explanation
A_1	Maximal ingestion rate when FPOMING = 0
A_2	Maximal ingestion rate when FPOMING = 1
agc	Parameter in gut content Eq. (9)
bgc	Parameter in gut content Eq. (9)
bs	Parameter in FPOMING Eq. (15)
FPOM	Organic content of seston (fraction)
FPOMING	Organic content of ingested material
FPOMPF	Organic content of pseudofaeces
GC	Gut content
GPT	Gut passage time
gptmax	Maximal gut passage time
gptmin	Minimal gut passage time
GR	Seston uptake rate
IR	Ingestion rate
IRMAX	Maximal ingestion rate
OGR	Uptake rate of organic material
OINR	Organic to inorganic material ratio in seston
PFIR	Pseudofaeces to ingestion rate ratio
SE	Classical selection efficiency
SE1	Alternative selection efficiency
SEMAX	Maximal possible selection efficiency
VAR	List of variables that IRMAX depends on

where FPOM is organic content (fraction) of seston, i.e. food quality; FPOMPF is organic content of pseudofaeces (for complete list of variables used see Table 1). We propose an alternative definition of selection efficiency based on organic content of ingested food using the equation

$$SE1 = \frac{FPOMING - FPOM}{1 - FPOM} \quad (2)$$

where SE1 is alternative selection efficiency; FPOMING is organic content of ingested food. SE1 is similar to selection index used in Hawkins et al. (1998) but it is normalised by maximal value of difference FPOMING–FPOM instead of FPOMING. The advantages of this definition will be presented below. We confine ourselves in this chapter to the short analysis of interpretation for both definitions.

The classical selection efficiency (1) might be interpreted as index characterising the decrease of organic content in pseudofaeces in comparison to organic content in seston, while the alternative one (2) as index characterising the increase of organic content in ingested material. The value 0 of both classical and alternative selection efficiency means the absence of selection activity ($FPOM = FPOMING =$

FPOMPF), however, the interpretation of value 1 differs. For the classical selection efficiency it means pure inorganic material in pseudofaeces, while for the new definition it means pure organic material in ingested food. SE1 does not require any measurement of additional characteristics in comparison to SE and can be easily obtained during complex food processing measurements by using the organic and total ingestion rate (for review see Hawkins et al., 1998).

3. Equations derivation for output variables of selection activity

The organic fraction in pseudofaeces and the organic fraction in ingested food can be treated as main output variables of selection activity describing allocation of organic and inorganic material. We assume here that the empirical equation for selection efficiency is already given (for possible shape and independent variables of such equations see next chapter). Both output variables must be expressed through selection efficiency when food processing is modelled. For the classical definition, the equation for FPOMPF can be easily derived from Eq. (1). However, equation for FPOMING may be obtained only after the analysis of material balance. The allocation of total filtered material between pseudofaeces and ingested food can be determined only when maximal ingestion rate (ingestion rate when pseudofaeces production starts, also called ingestion capacity) is known. The maximal ingestion rate depends mainly on the organism biomass (Bayne and Worall, 1980; Brylinsky and Sephton, 1991; Sprung, 1995). The additional variables such as ambient or ingested food quality and seston concentration are also used by some authors (Hawkins et al., 1998; Scholten and Smaal, 1999). Let us denote

$$IRMAX = F(VAR) \quad (3)$$

for the maximal ingestion rate IRMAX, where $F(VAR)$ is a function with a list of independent variables VAR.

In case of $FPOMING \in VAR$, Eq. (3) may not be used for calculation of IRMAX while FPOMING is unknown. The solution of problem is based on following balance equation validity, while seston uptake rate

is greater than IRMAX:

$$\begin{aligned} \text{FPOMPF} \cdot \text{PFPR} + \text{FPOMING} \cdot \text{IRMAX} \\ = \text{FPOM} \cdot \text{GR} \end{aligned} \quad (4)$$

where PFPR is pseudofaeces production rate; GR is the seston uptake rate of bivalve. Employing formula (1) in (4) and substituting PFPR by (IRMAX – GR) this equation is combined as

$$\begin{aligned} (1 - \text{SE}) \cdot \text{FPOM} \cdot (\text{GR} - \text{IRMAX}) \\ + \text{FPOMING} \cdot \text{IRMAX} = \text{FPOM} \cdot \text{GR} \end{aligned} \quad (5)$$

After IRMAX elimination from Eqs. (3) and (5), one obtains the equation

$$\frac{\text{FPOM} \cdot \text{GR} \cdot \text{SE}}{\text{FPOMING} - (1 - \text{SE}) \cdot \text{FPOM}} = F(\text{VAR}) \quad (6)$$

that should be solved in regard to FPOMING. When $\text{FPOMING} \notin \text{VAR}$, the solution of Eq. (4) is

$$\text{FPOMING} = \text{FROM} \cdot \left[1 + \text{SE} \cdot \left(\frac{\text{GR}}{F(\text{VAR})} - 1 \right) \right] \quad (7)$$

However, in case of $\text{FPOMING} \in \text{VAR}$, the possibility to solve Eq. (6) depends on the expression $F(\text{VAR})$. If it has a simple structure, we can directly solve the Eq. (6), otherwise iterative methods should be applied.

We will demonstrate the solution of this problem in case of $\text{FPOMING} \in \text{VAR}$ for the following expression $F(\text{VAR})$ earlier used in *Mytilus edulis* growth model (Scholten and Smaal, 1999):

$$\text{IRMAX} = F(W, \text{FPOMING}) = \frac{\text{GC} \cdot \text{spfm}}{\text{GPT}/24} \quad (8)$$

$$\text{GC} = \text{agc} \cdot W^{\text{bgc}} \quad (9)$$

$$\text{GPT} = \text{gptmax} + (\text{gptmin} - \text{gptmax}) \cdot \text{FPOMING} \quad (10)$$

where GC is gut content (mm^3), GPT is gut passage time (h); FPOMING is organic content of ingested food; spfm is specific food mass (g mm^{-3}), W is soft tissue dry weight (g) of mussel; agc, bgc, gptmin and gptmax ($\text{gptmax} > \text{gptmin}$) are parameters. Using the following notations

$$\begin{aligned} A_1 = \text{IRMAX}(0) &= \frac{\text{spfm} \cdot \text{GC}}{24 \cdot \text{gptmax}}; \quad A_2 = \text{IRMAX}(1) \\ &= \frac{\text{spfm} \cdot \text{GC}}{24 \cdot \text{gptmin}} \end{aligned} \quad (11)$$

expressions (8), (9) and (10) may be rewritten in a more compact form:

$$\text{IRMAX} = \frac{A_1 \cdot A_2}{A_2 + (A_1 - A_2) \cdot \text{FPOMING}} \quad (12)$$

The Eq. (6) for FPOMING in this case is

$$\begin{aligned} \frac{\text{FPOM} \cdot \text{GR} \cdot \text{SE}}{\text{FPOMING} - (1 - \text{SE}) \cdot \text{FPOM}} \\ = \frac{A_1 \cdot A_2}{A_2 + (A_1 - A_2) \cdot \text{FPOMING}} \end{aligned} \quad (13)$$

The equation can still be solved analytically and its solution is

$$\begin{aligned} \text{FPOMING} = \text{FPOM} \\ \cdot \left\{ \frac{A_2 \cdot [A_1 \cdot (1 - \text{SE}) + \text{GR} \cdot \text{SE}]}{A_1 \cdot A_2 + (A_2 - A_1) \cdot \text{SE} \cdot \text{FPOM} \cdot \text{GR}} \right\} \end{aligned} \quad (14)$$

The Eq. (13) was solved analytically owing to linearity of GPT expression only, whereas non-linear expression might make Eq. (13) analytically unsolvable.

Scholten and Smaal (1999) used an alternative approach for FPOMING determination that does not require solution of Eq. (6) using the following simple relationship:

$$\text{FPOMING} = \text{FPOM}^{\text{bs}} \quad (15)$$

where bs is a parameter, $0 < \text{bs} < 1$. However, this approach brings a couple of difficulties. Firstly, ingested food quality (Eq. (15)) is not achievable when organic content of seston is small. Then, instead of using Eq. (15) it is necessary to assume ingestion of a whole filtered organic material (i.e. to assume the selection efficiency equal to 100%). Even though this might be easily corrected by modifying the Eq. (15), this approach still leads to contradiction in the results of selection efficiency measurements as will be demonstrated below.

The 100% selection efficiency is reached when grazing rate of organic material (OGR) is less or equal to organic material ingestion rate, i.e. when

$$\text{OGR} \leq \text{FPOMING} \cdot \text{IRMAX}$$

which after employing Eqs. (12) and (15) becomes

$$\text{GR} \leq \frac{A_1 \cdot A_2}{A_2 \cdot \text{FPOM}^{1-\text{bs}} + (A_1 - A_2) \cdot \text{FPOM}} \quad (16)$$

Combining Eq. (16) with condition $\text{GR} > \text{IRMAX}$ (selection starts simultaneously with pseudofaeces

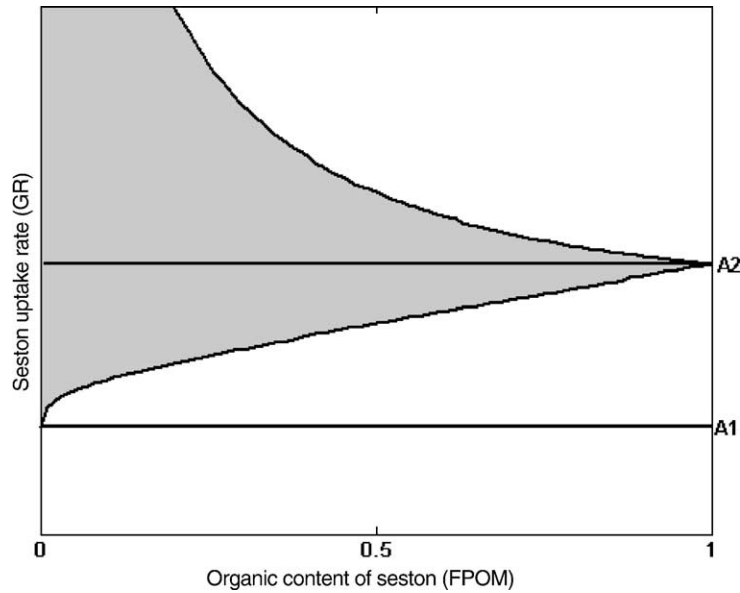


Fig. 2. The shape of area of 100% selection efficiency (shaded area solution of (17)), when selectivity effect is described by relationship (15).

production or later), we obtain the area of 100% selection efficiency being defined by

$$\frac{A_1 \cdot A_2}{A_2 + (A_1 - A_2) \cdot \text{FPOM}^{\text{bs}}} < \text{GR}$$

$$\leq \frac{A_1 \cdot A_2}{A_2 \cdot \text{FPOM}^{1-\text{bs}} + (A_1 - A_2) \cdot \text{FPOM}} \quad (17)$$

Since the right-hand expression approaches to infinity when $\text{FPOM} \rightarrow 0$, this area contains the points with small values of GR and FPOM (Fig. 2). This is contradictory to experimental results (Hawkins et al., 1996, 1998) that show the selection efficiency being closer to 0 rather than 1 for small FPOM and GR. Thus, the approach based on relationship (14) should not be used in food processing modelling.

Function (14) does not lead to these difficulties since the equalities equivalent to (17) are as follows:

$$\frac{A_1 \cdot A_2}{A_2 + (A_1 - A_2) \cdot \text{FPOMING}} < \text{GR}$$

$$< \frac{A_1 \cdot A_2}{A_2 + (A_1 - A_2) \cdot \text{FPOM}} \quad (18)$$

When $\text{FPOMING} > \text{FPOM}$, the left-hand expression is greater than the right-hand one and 100% selection efficiency cannot be reached.

It might be concluded that classical selection efficiency works quite well in this particular case. However, the alternative definition of the selection efficiency considerably simplifies the determination of FPOMING. It obtains straightforwardly from (2):

$$\text{FPOMING} = \text{SE1} \cdot (1 - \text{FPOM}) + \text{FPOM} \quad (19)$$

The determination of FPOMPF is slightly more complicated but straightforward when a relationship between classical and alternative selection efficiency is established. Combination of Eq. (7) (where $F(\text{VAR})$ is substituted by IRMAX) and Eq. (2) gives the following relationship between SE1 and SE:

$$\text{SE1} = \left(\frac{\text{FPOM}}{(1 - \text{FPOM})} \right) \cdot \left(\frac{\text{GR}}{\text{IRMAX}} - 1 \right) \cdot \text{SE} \quad (20)$$

The first multiplier in Eq. (20) is organic to inorganic material ratio in seston. The meaning of the second multiplier becomes clear when it is written as

$$\frac{\text{GR}}{\text{IRMAX}} - 1 = \frac{\text{GR} - \text{IRMAX}}{\text{IRMAX}}$$

Thus, it might be interpreted as ratio of pseudofaeces production rate to maximal ingestion rate, i.e. relative pseudofaeces production rate and (20) can be

rewritten as follows:

$$SE1 = OINR \cdot PFIR \cdot SE \quad (21)$$

where OINR is seston organic to inorganic material ratio; PFIR is pseudofaeces to ingested material ratio. Formula (21) can also be useful for recalculation of classical selection efficiency to alternative. Now equation for FPOMPF can be easily obtained. From Eq. (1), we have

$$FPOMPF = (1 - SE) \cdot FPOM \quad (22)$$

Employing Eq. (21) in Eq. (22) gives

$$FPOMPF = \left(\frac{1 - SE1}{OINR \cdot PFIR} \right) \cdot FPOM \quad (23)$$

4. The comparison of response surfaces

The site-specific empirical equations of classical selection efficiency for three species of marine bivalves were presented by Hawkins et al. (1998). The selection efficiency was found to be dependent on two variables: organic material fraction in seston and seston uptake rate. The general equation was

$$SE = ase + \frac{bse}{FPOM} + cse \cdot GR + dse \cdot \frac{GR}{FPOM} \quad (24)$$

where ase, bse, cse and dse are parameters. As it is shown in the graphs (see graphs in Hawkins et al., 1998, p. 94), the response surfaces (Eq. (24)) are increasing functions with regard to both arguments, except for *Crassostrea gigas*. The later species exhibits decreasing pattern of selection efficiency with regard to FPOM at low values of GR. We will analyse here the possible shape of this relationship for both definitions. Unfortunately, Eq. (24) was obtained by using quite narrow range of FPOM (0.12–0.22), therefore it is impossible to judge the shape of this relationship in general. However, certain information for high values of FPOM and GR can be obtained from the analysis of constraints originating from material balance. Employing constraint FPOMING \leq 1 in Eq. (7) results in the following inequality:

$$SE \leq SEMAX = \frac{1 - FPOM}{FPOM} \cdot \frac{IRMAX}{GR - IRMAX} \quad (25)$$

The inequality (25) gives the upper selection efficiency boundary. In case if the relative pseudofaeces production rate is an increasing function (it always takes place

when IRMAX depends only on organism biomass), the behaviour of SEMAX is simple. The right-hand expression is a decreasing function with respect to both arguments; hence, function SE(FPOM, GR) may be increasing only in the area where SEMAX \geq 1, i.e. FPOM and GR are small, and should approach 0 when FPOM \rightarrow 1, GR \rightarrow ∞ as SEMAX \rightarrow 0. For example, for IRMAX given by Eq. (12), using condition FPOMING \leq 1 for Eq. (14) results in

$$SEMAX = \frac{1 - FPOM}{FPOM} \cdot \frac{A_2}{GR - A_2}$$

SEMAX is a decreasing function with respect to both arguments. It is important to note that if condition FPOMING = 1 (pure organic is ingested) is true, then SE might be found directly from equality SE = SEMAX. The declining selection efficiency at high FPOM was already observed (Bayne et al., 1993; Iglesias et al., 1996). Thus, the classical selection efficiency is most likely bell-shaped with respect to FPOM and GR.

In contrast to classical selection efficiency SE, SE1 is free of constraints originated from material balance, since in Eq. (19) FPOMING \leq 1 for $0 \leq SE1 \leq 1$. The only possible constraint might be the condition FPOMPF \leq 1, however Eq. (1) gives

$$FPOMPF = (1 - SE) \cdot FPOM \quad (26)$$

Employing Eq. (21) in Eq. (26) gives that condition FPOMPF \leq 1 will be violated when

$$\left(1 - \frac{SE1}{OINR \cdot PFIR} \right) \cdot FPOM > 1$$

which is equivalent to

$$SE1 < -PFIR$$

However, negative SE1 values are possible when FPOMING < FPOM only. Thus, other constraints, except for the natural one, $0 \leq SE1 \leq 1$, do not exist for SE1. It is also important that SE1 = 1 when SE = SEMAX, which follows directly from Eqs. (20) and (24). From Eq. (20), SE1 is monotonically increasing if SE is growing under condition that relative pseudofaeces production rate is an increasing function. Hence, the analysis above lets us expect that relationship SE1(FPOM, GR) might be approximated by more simple monotonously increasing function

with asymptotic value 1 in contrast to bell-shaped function required by classical selection efficiency.

5. Conclusions

The pre-ingestive food selection by bivalves is important phenomenon determining the organic content in pseudofaeces and ingested food simultaneously controlling the energy fluxes inside the organism and between the organism and environment. The selection efficiency based on comparison of organic content in pseudofaeces and seston as a measure of selection activity was used up to now (Bayne et al., 1993; Hawkins et al., 1996, 1998; Scholten and Smaal, 1999). In this paper, an alternative definition of the selection efficiency is proposed. It is based on comparison of organic content in ingested food and seston and can be obtained by using the same set of food processing characteristics usually measured in experiments. Since experimental data and empirical relationships for classical selection efficiency already exist, the obtained relationship between classical and alternative selection efficiency can be used for recalculation.

Both definitions were compared by solving problems arising by modelling of bivalve food processing. The classical selection efficiency generally is applicable to obtain organic content in pseudofaeces and ingested food, however sometimes it may lead to solution of equations that require iterative methods. The introduction of alternative selection efficiency considerably simplifies the solution and never requires iterative methods.

The analysis of constraints originating from material balance also revealed an advantage of alternative selection efficiency employment. These constraints are more straightforward and obvious for alternative selection efficiency. It was also revealed that response surface for alternative selection efficiency can be expected to being a monotonously increasing function that might also be advantageous in comparison to the bell-shaped classical one. Moreover, the existing empirical relationships for classical selection efficiency (Hawkins et al., 1996, 1998) are incapable to reproduce the shape of response surface comprehensively and their application is limited.

An abstract model of selection activity considered in this paper could serve as a framework for creation

of concrete models and enables to avoid the incorrect use and interpretations of selection activity occurring in some models (e.g. Scholten and Smaal, 1999).

Acknowledgements

This work was founded by the European Union under the MAST contract MAS3-CT96-0058 (DG12-DTEE) and by Lithuanian State Science and Studies Foundation.

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