Adaptive Monitoring Strategies in dredging;

Case Study Mussels – Modeling the effect of dredging on filter-feeding bivalves

EcoShape – Building with Nature

Project: Adaptive monitoring strategies 1

Report title: Case Study Mussels – Modeling the effect of dredging on filter-feeding bivalves

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Summary

One of the effects of dredging activities is the (temporal) increase of inorganic silt particles in the water column. These increased silt concentrations can affect the quality of the water by increasing the turbidity and changing the relative composition of organic and inorganic particulate matter in the water column, e.g. by increasing the silt:algae ratio. Bivalves are filter feeders that are capable of continuously filtering food and other particles out large volumes of water. Indigestible or excess material is egested as pseudofaeces. Increase in suspended sediment concentration will reduce the efficiency of the filtration process.

In this study an overview is given on the literature data on the effect of increased silt concentrations on the filtration processes (clearance rate, filtration rate, pseudofaeces production and assimilation efficiency). Overall, the available data imply a decrease in clearance rates with increasing particle concentrations. Pseudofaeces production increases with increased silt content of the water.

The literature observations are compared with a simple functional response that describes the energy uptake rate of a filter feeding bivalve as a function of food and silt concentration. The patterns of the functional response is quite comparable with the literature observations. The functional response is included in a Dynamic Energy Budget (DEB) model for a mussel in order to calculate the effect on growth and development of a mussel. This model is extended with a formulation to simulate the effect on clearance rates and pseudofaeces production.

The DEB model can be used to simulate the impact of increased suspended sediment concentration due to dredging activities on mussel growth and development. From this study it is concluded that low concentrations of particulate inorganic matter already have an effect on the food-uptake rate. This is because the filterfeeding shellfish need to invest time and energy in the processing of the inorganic matter. The North Sea coast is a turbid environment due to wave action and currents and organisms living in this environment are adapted to the turbid conditions. Dredging and nourishment activities will increase the suspended matter concentration. Short-term increases of particulate inorganic matter has less impact on the growth performance of the shellfish compared to a continuous increase. The timing of dredging activities is also important. In winter period, when the activity of the shellfish are low, the impact of increased suspended sediment concentration is much lower than during summer period.

Contents

1 Introduction

1.1 Background

Every year, large amounts of sand are extracted from the North Sea to meet the demands for construction and nourishment activities (Baptist et al. 2009). Potential ecological effects of these sand mining activities have to be examined and reported in Environmental Impact Assessments (EIAs).

These EIA's concluded that the primary environmental effect of sand mining is an increase in silt concentrations, which can be both a local, short term strong increase of silt concentrations as well as a far field, long term, low increase. Increased silt concentrations can affect the quality of the water by increasing turbidity, and changing the relative composition of organic and inorganic particulate matter in the water column, e.g. by increasing the silt:algae ratio, and reducing primary production by increased light limitation.

Many bivalves are filter feeders that are capable of continuously filtering food and other particles out large volumes of water. Indigestible or excess material is egested as pseudofaeces. As bivalve filterfeeders are an important food source for higher trophic levels, it is for management purposes important to know how the increase of suspended particles due to dredging and nourishment activities effects the filter feeders. If an impact assessment is to be made of the possible effects that an increase in silt concentrations could have on bivalve populations, extensive knowledge of how silt concentrations influence life history parameters of the bivalves is essential.

1.2 Objective

The objective of this project is to study the effect of suspended silt concentrations on the activity of filter feeding bivalves (e.g. clearance, ingestion, pseudofaeces production and growth). Deterministic models will be presented that describe the effect of various silt concentrations on the model species for this study, the blue mussel (*Mytilus edulis*). These models can be used to investigate the impact of dredging on filterfeeding bivalve populations. The results of this study can be used to decide how much increase in suspended solids is acceptable and what is the best period of dredging and nourishment activities.

1.3 Approach

An extensive literature search was performed as to identify potential effects of sand mining activities on bivalve populations. We focused on one species in this study, the bivalve *Mytilus edulis* or blue mussel. The blue mussel is a well-studied species that has a wide distribution and commercial importance, as such, it can be regarded as an indicator species for the filter feeding bivalves, and applicable for our evaluation of impacts of sand extraction on bivalves. It must be stated however that although the processes of filterfeeding and particle selection are comparable for other suspension-feeding lamellibranchiate bivalve species, the parameterization and rates will differ (Cranford et al. 2011).

Two deterministic models are presented and their behavior is compared with the literature data. This comparison is only to get an impression of the order of magnitude of the rates and the patterns of the relationships The literature data were not used to calibrate the model parameters.

2 Effects of dredging on blue mussels

2.1 Increased suspended solid concentrations

Sand extraction activities lead to a release of fine sand and silt particles into the water column. During the dredging process a sand-water mixture is pumped up from the seabed into the hold of the dredging vessel. Although most of the sandy part of this mixture settles in the hold, the excess transport water containing fine particles of up to 150 μm flows back into the sea. Whilst sand particles (>63 μm) settle relatively quickly on the seabed, the silt particles (<63 μm) remain suspended in the water column. These suspended silt particles cause a 'dredging plume' near the dredging vessel. As a result of tidal currents and wave action, this dredging plume will be spread out over a larger area. After settling on the seabed, the silt particles can be stirred up again during stormy periods by wave motions.

Sand extractions dominantly occur in the coastal zone at ~20 m depth and 20 km out at sea. Sand extractions can increase silt concentrations to ~300 mg l^{-1} (Rozemeijer, pers. Comm), and may locally reach concentrations as high as ~1000 mg l^{-1} (de Kock, pers. Comm). A direct effect of increased silt particles in the water column are higher turbidity levels that may affect phytoplankton productivity and consequently food supply to higher trophic levels. The actual impact may be local and restricted in time, although when dredging taking place at the seaward end of, e.g. an estuary, a larger water mass could be affected (Essink 1999). Potential ecological implications consist of significant decreases in biomass and productivity of phytoplankton, zooplankton and filter-feeding benthos such as *Mytilus edulis*. For instance, deposition of sediment layers of 1-2cm thickness can result in increased mortality (Bijkerk 1988). Another important effect of sand extraction is the increased silt concentrations that can clog the filter apparatus of shellfish and impede growth. Although filter-feeders, such as *M. edulis*, grow naturally within turbid nearshore waters where the total particulate matter (TPM) of fine resuspended silt can reach temporary maxima of up to about 300 mg l^{-1} (Hawkins et al. 1998), anthropogenic environmental disruptions such as sand extraction, may have a substantial impact of *M. edulis*.

Apart from the TPM that is released during the dredging process, seawater always contains a certain background concentration of TPM. This background concentration is not constant, but fluctuates due to wave action, current velocities, tide and river discharges. In addition to the TPM-concentration, phytoplankton concentrations also influence the transparency of seawater. The concentration of phytoplankton can be limited by the availability of nutrients or by the light intensity in the water column. The light intensity in the water column depends on the light intensity at the water surface and on the water transparency. If light intensity is the limiting factor for primary production, an increase of the TPM-concentration (leading to less transparency) can also lead to a decrease of phytoplankton concentrations.

To what extent the cumulative effect of increased suspension of silt, deposition of sediment, potential changes in substrate composition and food availability (i.e. primary productivity) will affect filter feeders as *M. edulis* depends on their capacity to selectively sort edible particles from non-edible particles. Clarifying how various processes are intrinsically related and affect *M. edulis* ecology and ecophysiology allows for modeling of potential consequences of sand mining for bivalve species.

2.2   Ecology of blue mussels (*Mytilus edulis*)

Blue mussels (*Mytilus edulis*) are widely distributed in European waters, extending from the White Sea, Russia as far as south as the Atlantic coast of Southern France (for global distribution see Figure 1). Its wide distributional pattern is the result of its ability to withstand wide fluctuations in salinity, desiccation, temperature, and oxygen tension, in combination with high fecundity, extensive larval and post-larval dispersal capability, fast growth and their ability to attach by byssus threads to non-specific substrates and to one another (Gosling 1992). As a result, *M. edulis* can occupy a broad variety of microhabitats, expanding its zonation range from the high intertidal to subtidal regions and its salinity range from estuarine areas to fully oceanic seawaters. Its climatic regime varies from mild, subtropical locations to frequently frozen habitats. These characteristics make that *M. edulis* often is a very significant and abundant element of the ecology of many inter-tidal and sub-tidal habitats (Gosling 1992).

The typical distribution of *M. edulis* in intertidal habitats appears to be mostly controlled by biological factors (predation, food competition). When predators are lacking, subtidal aggregations of *M. edulis* can reach high local densities and individuals attain large sizes in a relatively short period of time. In the wild, *M. edulis* settles in patches of open spaces, quickly building a dense population referred to as 'mussel beds'.

*Figure 1:   Global distribution of the blue mussel (Mytilus edulis) (from
                http://www.fao.org/fishery/species/2688/en)*

2.3   Feeding and food selection by filter feeders

Filterfeeders pump the water over their gills by the activity of the lateral cilia of their gills which creates the water flow. The pumping rate is actively controlled by the activtity of the lateral cilia and the various musculature that affects the shell gape, the exhaling siphon area and the interfilamentary distance of the gill (Cranford et al. 2011).

Mytilus edulis are non-selective filter-feeders, meaning they do not discriminate between individual food particles. They feed by actively filtering particles from the water (for reviews, see Cranford et al. 2011; Jørgensen 1996), which passes into and out of the mantle cavity through the frilled siphons (or sipho, Figure 2a and b). The gills retain all particles greater than 2 – 5 µm with 100% efficiency (Bayne et al. 1977; Vahl 1972) and the filtered material is then transferred to the food grooves (ciliary tracts) on the gills and on to the labial palps (Figure 2a). The function of the labial palps is the continuous removal of

materials from the lamellar food tracts, whether to be ingested as food or to be rejected as pseudofaeces (Foster-Smith 1974). Respiration simultaneously occurs as this stream of water passes over the mussels' gills. Phytoplankton cells both living and dead, constitute the main source of food, but other sources of carbon such as decomposed macrophytes or resuspended detritus may also supplement their diet. Pseudofaeces can comprise inorganic matter, such as silt, or excess phytoplankton cells, egested under high cell concentrations (e.g. $\sim>8.5x\ 10^3$ cells ml^{-1} (*Rhodomonas* sp.) or under increased silt concentrations (Clausen and Riisgård 1996).

(a)
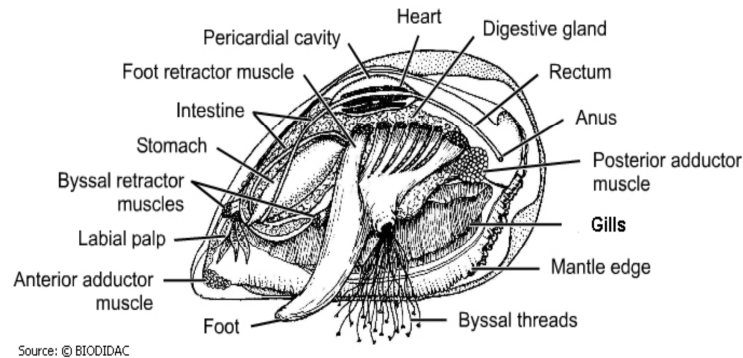
(b)
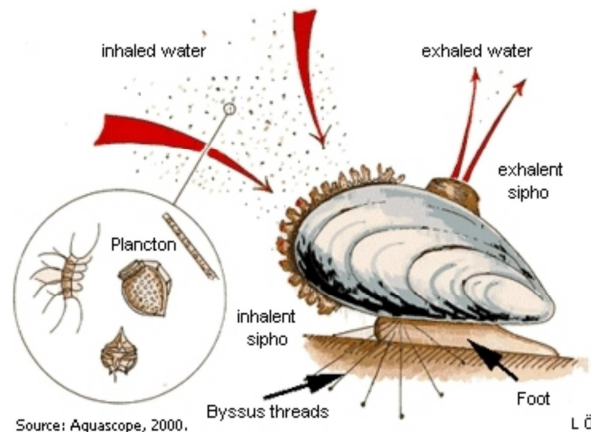
Figure 2:   a) Major internal anatomical and (b) filtration process of a mussel (from http://www.glf.dfo-mpo.gc.ca/pe/profil/mussel-moule/mussel-moule-e.php)

Mussels have been shown to be able to adapt their palp size to variable TPM-concentrations (Essink 1999). Furthermore, *M. edulis* can adapt its filtration and ingestion rate to the particle concentration (Clausen and Riisgård 1996) and particle size (Strohmeier et al. 2012) in the water. At very low particle concentrations (< 0.25 mg l^{-1} (Thompson and Bayne 1974; Widdows 1978), all suspended material (> 2 µm diameter) is filtered by the gill, ingested through the mouth and transported to the digestive gland for digestion. As the seston concentration increases, the digestive gland cannot digest and assimilate all the material entering the stomach. Such excess material, after bypassing the digestive gland, is transported through the gut undigested and rejected as intestinal faeces (Bayne et al. 1993; Vanweel 1961). The ratio of intestinal to glandular faeces, therefore, increases with increasing ingestion rate (mg h^{-1}), which is reflected in a decline in assimilation efficiency (Thompson and Bayne 1974; Widdows 1978).

Ingestion rate increases with increasing particle concentration and organic matter content (Bayne et al. 1993) until a threshold (value is dependent on body size and ~4 mg l^{-1}) is reached, above which further material filtered by the gills is carried away from the mouth by rejection tracts on the labial palps and deposited as pseudofaeces (Thompson and Bayne 1974). Amount of pseudofaeces produced can range from zero rejection at 3 mg l^{-1} to about 40% rejection at seston concentrations of ~6-10 mg l^{-1} for low organic content (~0.75 mg l^{-1}) (Bayne et al. 1993). It has been shown that for an average mussel of 3 centimeters of length, the maximum filtration occurs at TPM-concentrations of ~125 mg l^{-1}, at ~225 mg l^{-1}, the filtering capacity decreases to ~30% and ceased at a TPM concentration of ~250 mg l^{-1} (Widdows et al. 1979). More recent studies did not test the effect of such high TPM concentrations on mussels, however, Bayne et al. (1993) showed that TPM concentration above the critical value of 4 mg l^{-1} resulted in an increased rejection (pseudofaeces production) with time (Table 1).

Table 1: *Pseudofaeces production (expressed as % rejection) for mussels (4-5 cm) in 3 experiments (CI, CII and CIII (Bayne et al. 1993).*

experiment	Seston concentration (mg l^{-1})	% rejection at 2d	% rejection at 12d
CI	4.57	19.3	49.6
CII	4.14	25.2	48.9
CIII	4.93	31.7	38.9

The selection efficiency, i.e. the efficiency with which filtered material is sorted in organic and inorganic fractions prior to ingestion, is shown to decrease under increasing organic content of the seston. The absorption efficiency, the efficiency by which the organic fraction of ingested material is absorbed by the animal, increases with the increase in concentration of POM (Bayne et al. 1993).

2.4 Effects of increased concentration of suspended solids

2.4.1 Food quality

Food quality is defined in this report as the silt: algae ratio. The higher the silt: algae ratio, the lower the food quality, thus an increase in silt decreases the food quality.

It is important to note, however, that the optimal food conditions for bivalves is not necessarily when food quality is at its highest. It has been suggested that bivalves can filter algae more efficiently when some silt (~5 mg l^{-1}) is present (Kiørboe et al. 1981), although a more recent study suggests such benefits from suspended silt do not occur (Clausen and Riisgård 1996). More specifically, *M. edulis* appears to be able to adjust its clearance rate and sustain a relatively stable particle uptake under different algae and silt concentrations (Table 2), albeit that concentrations need to remain below/ above a certain threshold. As summarised by (Riisgård et al. 2011): At a very low seston concentration, mussels exhibit low feeding (Newell et al. 1998). As particle concentration increases (1 to 4 mg l^{-1}), mussels exhibit increased feeding rates, and demonstrate maximum clearance rates at seston concentrations of 3 to 10 mg l^{-1} (e.g. Kiørboe et al. 1980; Newell et al. 2001; Widdows et al. 1979). At higher seston concentrations, however, clearance rates rapidly decline according to some authors (Kiørboe et al. 1980; Newell and Shumway 1993; Richoux and Thompson 2001), while other authors show a stable clearance rate over large ranges of TPM concentrations (Hawkins et al. 1996; Smaal et al. 1997).

Table 2:   Mean (±SD) filtration rates in short (5h) and long-time (9 to 14 d) experiments with groups of 25 mussels exposed to different concentrations of pure algae or algae + silt. Number of measurements are given in parentheses and production of pseudofaeces shown by asterisks (Clausen and Riisgård 1996).

Algal concentration ($\times 10^3$ cells ml^{-1})	Silt concentration (mg l^{-1})	Filtration rate (ml min^{-1} ind.$^{-1}$)
Short-time (5 h)		
2.7 ± 0.1		27.8 ± 1.7 (3)
2.3 ± 0.1	6.5 ± 0.1	32.2 ± 1.1 (3)*
8.5 ± 1.6		29.7 ± 2.5 (3)*
8.7 ± 0.6	4.0 ± 1.2	33.3 ± 4.2 (3)*
13.7 ± 3.2		12.1 ± 1.7 (3)*
13.0 ± 1.3	4.9 ± 1.2	26.1 ± 0.9 (3)*
24.0 ± 3.4		11.7 ± 3.6 (3)*
21.3 ± 2.1	4.9 ± 1.0	20.1 ± 1.7 (3)*
Long-time (9 to 14 d)		
4.1 ± 0.8		31.9 ± 5.3 (10)
4.1 ± 1.4	2.9 ± 0.5	31.2 ± 6.2 (9)*
6.0 ± 1.5		27.9 ± 4.3 (9)*
5.6 ± 1.8	2.9 ± 0.8	27.9 ± 3.2 (8)*
13.6 ± 7.0		14.7 ± 3.4 (5)*
12.2 ± 4.3	4.8 ± 1.5	13.1 ± 2.8 (9)*

2.4.2   Clearance rates

Clearance rates are defined as the volume of water cleared of particles per unit time. Mussels can efficiently counteract the food diluting effect of suspended particulate matter by selective sorting of particles, by increasing their clearance and ingestion rates, by utilizing food attached to the silt and/or by achieving a higher utilization of ingested algae (Kiørboe et al. 1980). It is important to note that mussels adapt to the natural conditions of suspended particulate matter (background silt concentrations) through adjusting their palp size (Essink et al. 1989), and therefore the effects of increased silt concentration on clearance rates will be relative to the mussels adaptation to background conditions.

Clearance rates of bivalves show often an allometric relation with body size (Jørgensen and Des 1990).

$$CR = a \times W^b$$

For *Mytilus edulis* the parameters for a range from 0.86 to 3.16 l h^{-1} and for b range from 0.21 to 0.74 (Table 3)

Table 3:   Allometric relation between clearance rate (CR) or pumping rate and dry tissue weight (adapted from Cranford et al. 2011).

Size	T °C	n	Relation	Reference
0.01-2.1g	10-12	24	$P=3.16W^{0.72}$	(Jones et al. 1992)
0.01-2.1g	10-12	24	$P=1.78W^{0.70}$	(Jones et al. 1992)
0.02-3.9g	0.4-19	139	$CR=1.66\pm0.55W^{0.57\pm0.17}$	(Smaal et al. 1997)
45-57 mm	-	-	$CR=aW^{0.45}$	(Hawkins et al. 1990)
0.07-4.2g	0-15	128	$CR=1.73\pm0.19W^{0.41\pm0.06}$	(Thompson 1984)
0.01-1.17g	9-15	20	$CR=1.65\pm0.79W^{0.61\pm0.20}$	(Smaal et al. 1986)
0.01-2.4g	15	50	$CR=2.65W^{0.38}$	(Widdows 1978)
0.15-2.9g	7-21	122	$CR=1.98\pm0.49W^{0.45\pm0.24}$	(Bayne and Widdows 1978)
0.13-2.8g	10-17	105	$CR=1.57\pm0.36W^{0.47\pm0.11}$	(Bayne and Widdows 1978)

Kjørboe et al. (1981) studied the influence of suspended, natural silt (0 to 20 mg l^{-1}) in addition to unicellular algal cells (*Phaeodactylum tricornutum*) (0 to 20,000 cells ml^{-1}) on clearance, growth and energetics in *Mytilus edulis* (Table 4), showing that mussels (*Mytilus edulis*) react differently to variations in silt exposure. Essink et al. (1990) observed reduced growth in mussels at a high suspended silt concentrations. Growth of the soft parts in bottom waters with a mean TPM concentration that was 17% higher, whereas growth under more frequent (2-3 x) occurrences of TPM concentrations of > 250 mg l^{-1} was reduced, although not significantly. In case of a prolonged exposure to such high silt concentrations, a significant decrease in growth as a result of decreased clearance rates (down to zero at 250 mg l^{-1}) (Widdows et al. 1979) may be expected, as indicated by results obtained during laboratory studies (Widdows et al. 1979). For instance, the capacity to optimally use food in mussels starts to decline at a suspended silt concentration of 50 mg l^{-1} and at concentrations higher than 100 mg l^{-1} weight loss occurs (Prins and Smaal 1989). However, under higher TPM concentrations (~90 mg l^{-1}), a faster growth has been observed (Hawkins et al. 1996), which could be attributed to higher organic matter concentrations at higher TPM levels. Under laboratory conditions it was found that algal concentrations at which *M. edulis* ceased or decreased filtration were 0.5 µg chl *a* l^{-1} and ~6 µg chl *a* l^{-1} (Riisgård et al. 2011).

Clearance rates measured from growth experiments at different silt/algae ratios are given in Table 4. In the study by Kiørboe et al. (1981), the clearance rate increases by the addition of silt by 32 to 43% (average: 37%) at the low silt (~5%) concentration, and decreases somewhat again at the high concentration of silt (~20%). Clearances are similar in Al (low algae) and Am (medium algae) experiments, but significantly higher in the Ah (high algae) experiments. This is probably caused by the somewhat higher temperature in these experiments, making it difficult to draw conclusions from the experiment.

Table 4:   *Outline of experiments and experimental conditions from experiments conducted by Kiørboe et al. (1981). Clearance rates are given both as an average of the experiment and calculated for a 30 mg mussel. The experiments are described as follows: A0, Al, Am and Ah refer to zero, low (~5 000 cells ml^{-1}), medium (~10 000 cells ml^{-1}) and high (~20 000 cells ml^{-1}) algae concentrations respectively and S0, Sl, Sh refer to zero, low (5 mg l^{-1}) and high (20 mg l^{-1}) silt concentrations respectively.*

Exp.	Silt [mg/l]	Algae [*10³ cells/ml³]	Temp [°C]	Mussels Nr	Duration [days]	Clearance Average [ml min^{-1}]	Clearance [ml min^{-1}] 30mg mussel	Silt/Algae (=Food quality)
A0S0	0	0		31	30			
A0Sl	8.1±3.7	0	13.4±0.9	55	30			
AlS0	0	6.9±2.9	13.0±1.0	55	19	9.7	9.4	0
AlSl	5.3±2.2	5.3±2.7	13.4±1.0	42	19	14.0	12.7	1
AlSh	25.6±29.2	6.2±2.8	14.3±0.7	45	19	11.2	10.7	4.13
AmS0	0	11.8±4.5	13.4±0.2	60	20	8.7	9.5	0
AmSl	5.7±3.6	9.9±3.6	13.6±0.2	57	20	12.8	12.7	0.58
AmSh	17.1±8.3	7.6±2.0	14.6±0.2	75	20	10.4	10.4	2.25
AhS0	0	20.9±13.6	17.6±1.2	40	13	11.9	11.2	0
AhSl	8.2±6.0	15.3±12.7	16.9±1.1	40	13	18.2	16	0.54

Seston concentration has a strong influence on bivalve clearance rates in general(Cranford et al. 2011). Numerous studies have shown that clearance rates exhibit an initial peak at relatively low concentrations of seston followed by a slow decline. Clearance rates determined by Widdows et al. (1979) for mussels of three different sizes (3, 5 and 7 cm) demonstrated a decrease in in feeding and pumping activity under increasing particle concentration, and showed a minimum at 220, 260 and 330 mg l^{-1}, respectively (Figure 3).
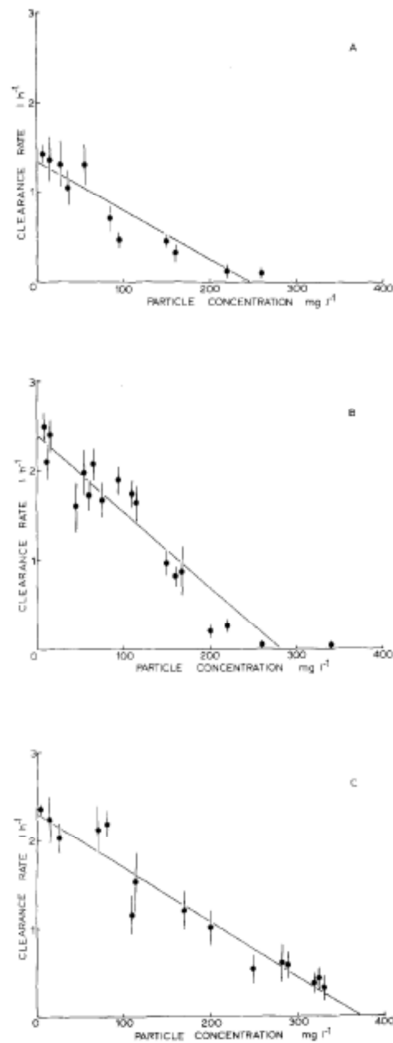
Figure 3: *Effects of particle concentration on clearance rate of (A) 3 cm, (B) 5cm and (C) 7cm mussel. Values are means ± standard errors (from Widdows et al. 1979).*

For Norwegian fjords, low in chlorophyll a concentration, Strohmeier et al. (2009) report an increase in CR with increasing chl *a* concentration (from 2 l hr^{-1}), stabilizing at 4-5 l hr^{-1} at concentrations above 0.2 µg chl *a* l^{-1} for mussels with a shell length of 5.2 – 6.6 cm (Figure 4, Figure 5 and Table 5). Studies on bivalves residing in oligotrophic waters have reported some of the highest feeding rates for the given species measured under natural dietary conditions. This is apparently a necessary adaptation for growth and survival in low seston conditions (Cranford et al. 2011).

Figure 4: *Mean clearance rate (CR) of bivalve cohorts through time (top panel) and repeated measures of individuals CR (bottom panel, circles are individual CR measurements) of M. edulis (ME). Vertical bands indicate 95% confidence limits based on 12 measurements (Strohmeier et al. 2009).*
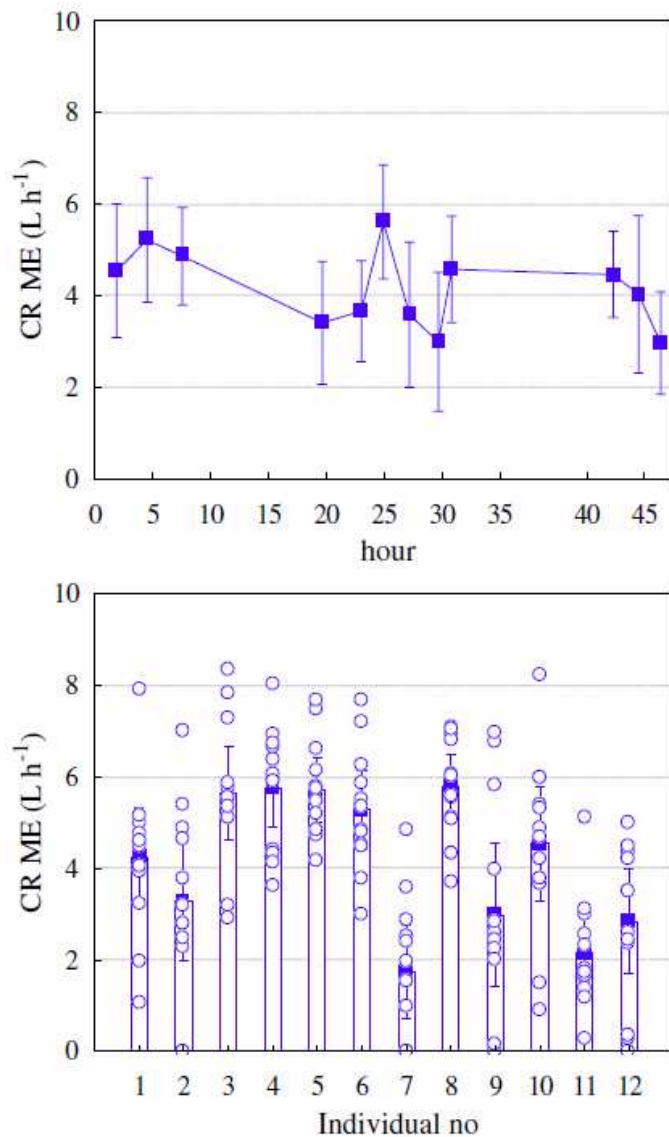
Table 5: *Mean (±SD) clearance rate (CR, l hr^{-1}), weight standardized clearance rate (CR_{ws}, l g dry soft tissue weight $^{-1}$ hr^{-1},) and percent of total animals clearing particles (% CR) for M. edulis from the four seston treatments, varying with amongst others TPM, Chla (Strohmeier et al. 2009) .*

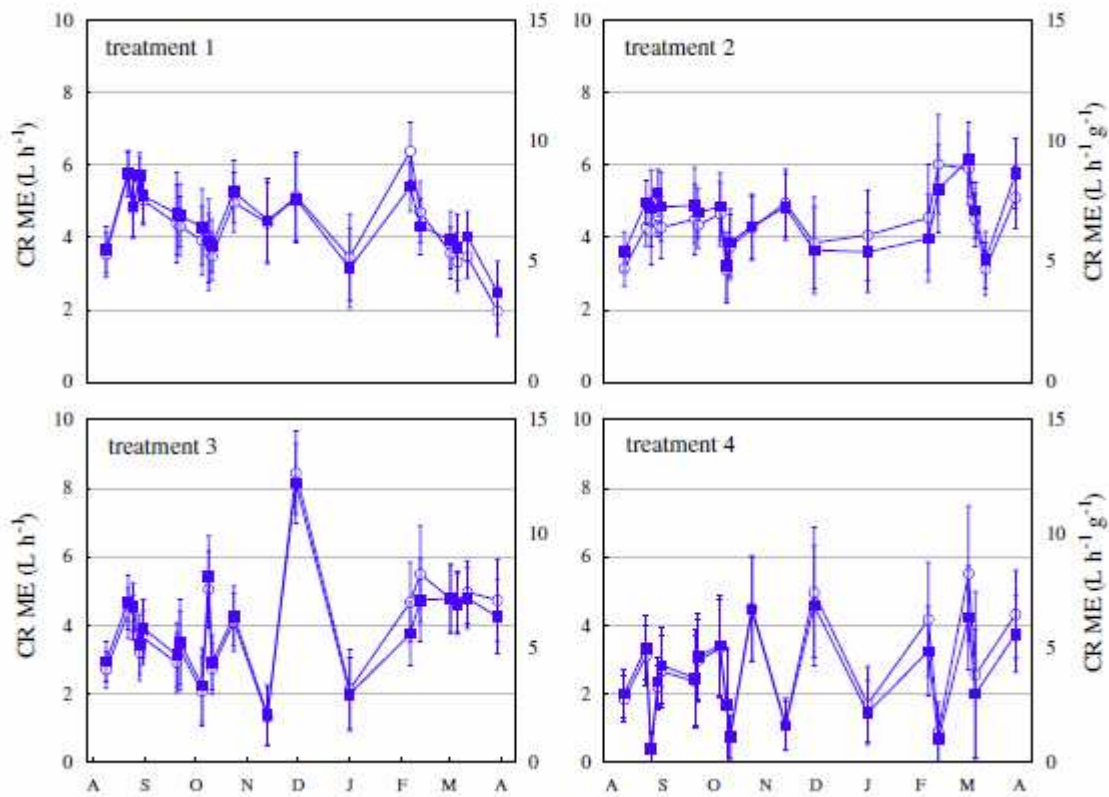| Treatment	TPM mg l^{-1}	Chla µg l^{-1}	CR (l hr^{-1})	CR_{ws} l g^{-1} hr^{-1}	% CR	n
Tr 1	0.43 (0.19)	0.88 (1.18)	4.4 (1.9)	6.4 (2.9)	97	360
Tr 2	0.31 (0.15)	0.54 (0.72)	4.5 (2.0)	6.5 (3.0)	97	359
Tr 3	0.20 (0.11)	0.18 (0.22)	4.0 (2.4)	6.0 (3.7)	93	358
Tr 4	0.15 (0.08)	0.01 (0.01)	2.6 (2.4)	4.0 (4.4)	67	358

Figure 5:   *Time series of mean clearance rate (CR, l hr⁻¹, filled squares, left y-axis) and weight standardized clearance rate (CR, l hr⁻¹ g⁻¹, open circles, right y-axis). Vertical bands indicate 95% confidence limits (n=18 individuals) (Strohmeier et al. 2009).*

Retention efficiency (RE) is the efficiency by which particles are filtered out of the water by the gills of shellfish. Small particles (< 2 µm diameter) in natural waters will not be filtered efficiently by most species (Cranford et al. 2011). The retention efficiency can be calculated for the various particles were estimated using the following equation:

$$RE = 100 \times \left(1 - \frac{C2}{C1}\right)$$

where $C1$ is the particle concentration (cells ml⁻¹) in the inflow seawater and $C2$ is the particle concentration (cells ml⁻¹) in the outflow after the water have been filtered by the bivalves. The retention efficiency is depending on particle size but also on the dietary condition. Larger particles are more efficiently filtered by mussels than smaller particles (Figure 6). Mussels seem to be able to increase the retention efficiency at low food conditions (Table 6).
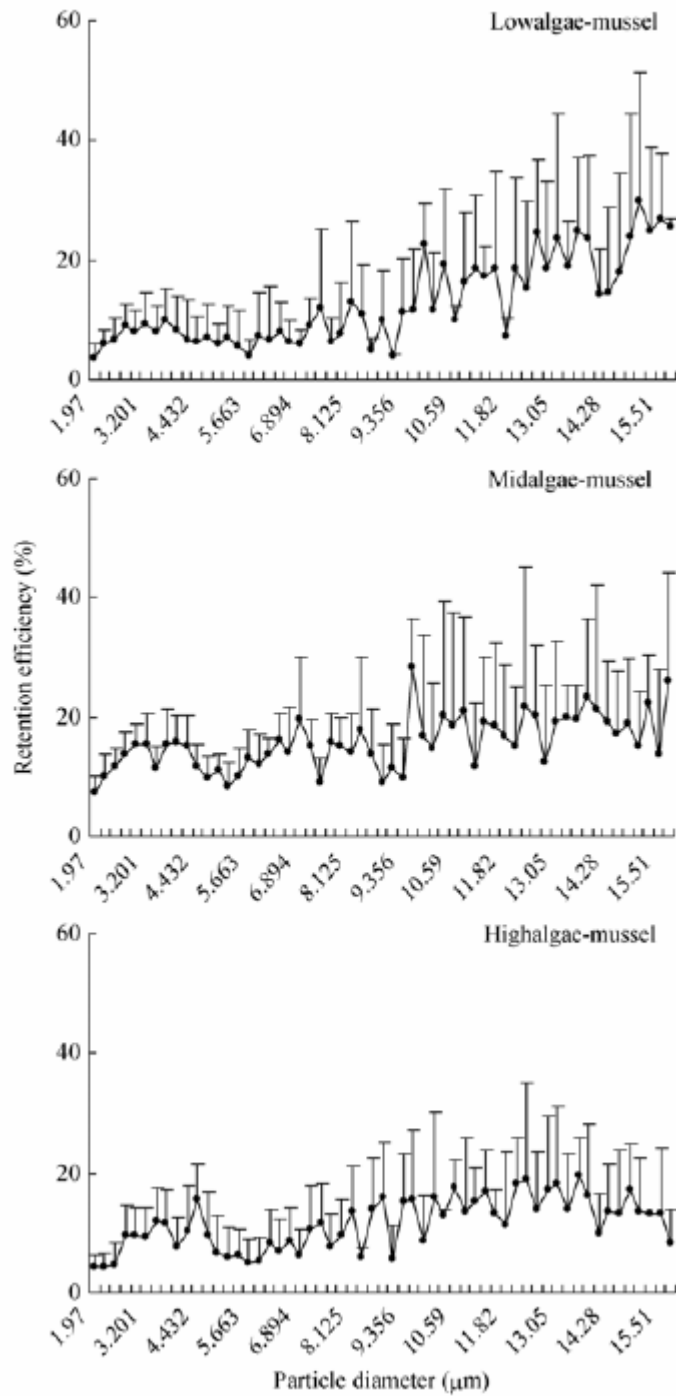
Figure 6:   *Retention efficiency of mussels (Mytilus edulis) for different particle sizes in three experimental diets (Zhang et al. 2010)*

Table 6:   Retention efficiency of mussels (Mytilus edulis) for 2-µm particles under different dietary conditions (Zhang et al. 2010).

Condition	Vol (mm^3 l^{-1})	TPM (mg l^{-1})	POM (mg l^{-1})	Particle nr (cells l^{-1})	Chl (µg l^{-1})	POM (%)	Retention efficiency
NSW	2.9	10	1	8.87	1.5	10	16.85 ±4.81
NSW and Low-Algae	3.1	20.7	3.1	11.04	3.2	14.98	3.81 ±2.00
NSW and Mid-Algae	4.1	6.5	1.8	12.11	21.5	27.69	7.54 ±2.73
NSW and High-Algae	9.5	8.6	4.8	17.11	61.8	55.81	4.29 ±2.05

2.4.3   Ingestion rates

Ingestion rates are calculated using the clearance rates and the concentration of particulate material in suspension, and are therefore directly related (Bayne et al. 1987; Widdows et al. 1979). Bayne et al. (1987) show that ingestion rates of TPM increase with increasing TPM concentrations of the water (Table 7). In the experiments of Hawkins et al. (1996) there was a clear relation between the absorption efficiency and the organic content, and the absorption efficiency and the ingestion rate. This relation was not found in the experiments of Bayne et al. (1987).

Table 7:   Ingestion rates, gut passage times (GPT), absorption efficiency and estimated gut contents for mussels held for 2 weeks on 6 experimental diets. Ingestion rates are standardized to a dry flesh weight of 1 g. The experimental diets were mixed from actively growing Isochrysis galbana and Phaeodactylum tricornutum cultures and ashed silt (Bayne et al. 1989).

Diet	TPM (mg l^{-1})	POM (mg l^{-1})	POM (% of TPM)	Ingestion rate (mg TPM hr^{-1})	Ingestion rate (mg POM hr^{-1})	GPT (hr)	Absorption efficiency	Gut content (mm^3)
1	0.79	0.49	62.1	1.90	1.18	2.67	0.60	6.9
2	1.98	0.43	21.9	4.55	0.99	3.23	0.63	7.9
3	1.25	0.86	70.0	2.27	1.56	2.73	0.53	12.4
4	3.17	0.60	18.8	7.54	1.43	2.49	0.55	13.1
5	2.49	1.79	71.0	2.64	1.90	1.87	0.57	9.7
6	7.43	1.30	17.7	12.78	1.97	1.81	0.50	16.0
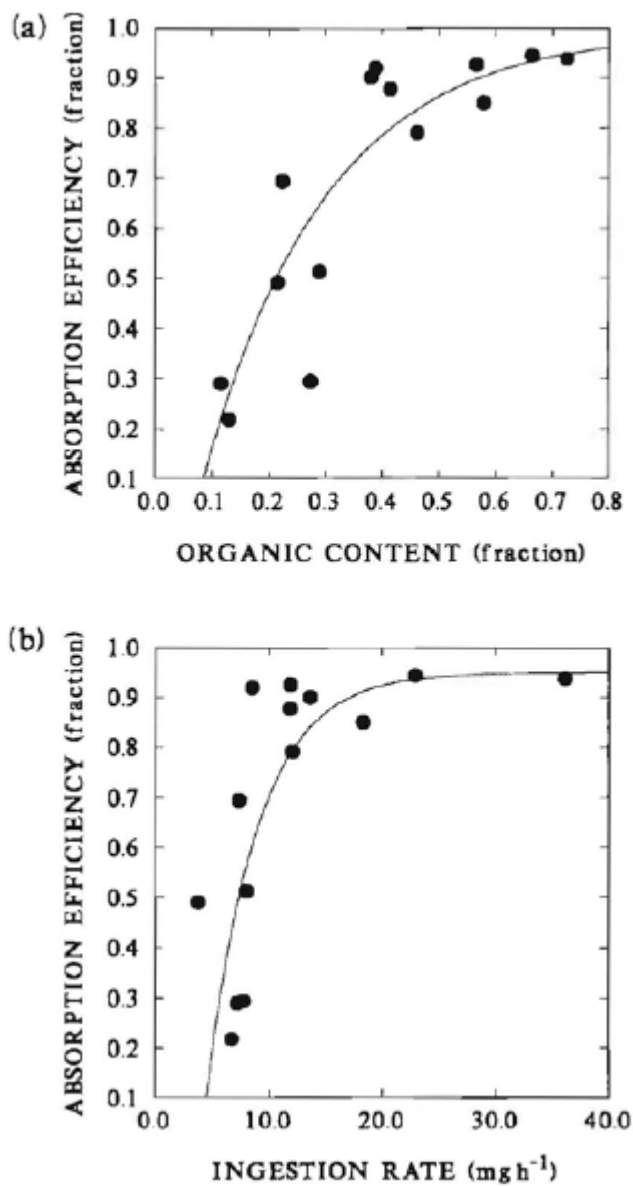
Figure 7:   *Absorption efficiency from ingested organics in relation to both (a) organic content of ingested matter and (b) ingestion rate in mussels standardized to 1 g flesh weight. Data are the mean of separate determinations upon 10 replicate mussels. Lines were fitted by least squares (Hawkins et al. 1996).*

2.4.4   Pseudofaeces production

The rate of production of pseudofaeces (g hr^{-1}) was measured by Widdows et al. (1979) for a 7 cm mussel over a range of seston concentrations (12 – 280 mg seston l^{-1})(Figure 8). The production of pseudofaeces increased with particle concentration, reaching a maximum at ~200 mg seston l^{-1} and then stabilized and possibly declined at higher concentrations.

Figure 8:   *Effects of seston concentration on rate of pseudofaeces production for a 7cm mussel (Widdows et al. 1979)*

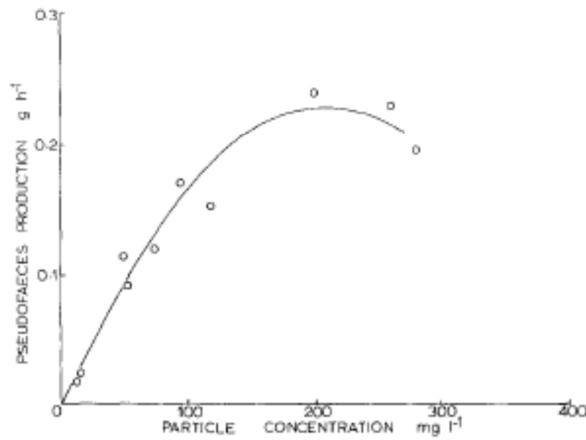Hawkins et al. (1996) measured a similar increase in pseudofaeces production in relation to increasing filtration rate (Figure 9).
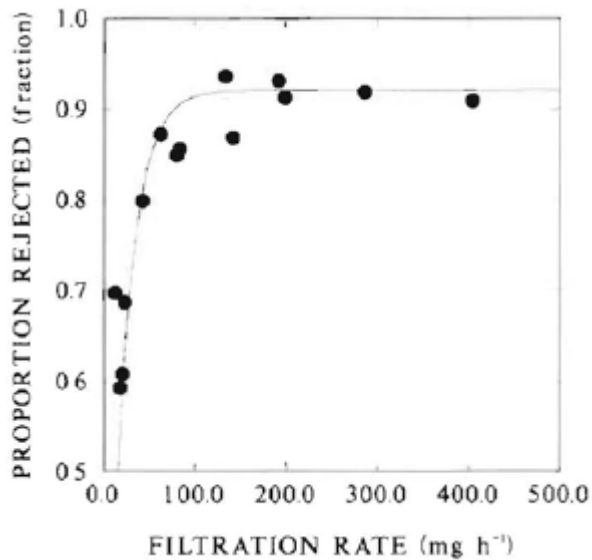
Figure 9:   *Proportion of filtered matter that was rejected as pseudofaeces in relation to filtration rate in mussels standardized to 1 g dry flesh weight. Data are the mean of separate determination upon 10 replicate mussels (Hawkins et al. 1996)*

In their review, Riisgård et al. (2011) presented new data on pseudofaeces production in relation to different cell concentrations of *Rhodonomas salina* (Table 8). It appeared that the production of pseudofaeces started momentarily at algal concentrations above 12,000 cells ml^{-1} (i.e., pseudofaeces trigger concentration). Once the pseudofaeces production was triggered, it continued, although at a reduced rate when the algal concentration gradually, due to grazing by the mussel, came below the trigger threshold concentration.

Table 8: *Pseudofaeces production of Mytilus edulis exposed to different initial algal (Rhodomonas salina) concentrations. Opening degree symbols: 3: fully open, 2: reduced, 1: nearly closed. No observation = no. Filtration rate (F). * New addition of algae (Riisgård et al. 2011).*

Series no.	Shell length (mm)	Time (min)	C (cells mL⁻¹)	Pseudofaeces (no. per 10 min)	Opening degree	F (mL min⁻¹)
1	34.3	0	23,500	22	no	
		52	13,700	46	3	25.5
		112	9,100	22	2	
2	34.3	0	16,700	26	2	
		50	10,200	18	1	23.4
		118	8,900	no	no	
		120*	10,000	34	no	
		170	5,800	19	2	31.5
		235	4,000	9	2	
3	34.3	0	10,000	0	1	
		68	4,900	0	3	15.3
		127	2,600	0	3	
4	36.8	0	19,200	17	1	
		30	9,100	4	3	66.3
		90	2,600	0	3	
5	36.8	0	12,900	8	2	
		8	12,700	26	3	
		42	6,000	1	3	51.6
		90	2,700	0	3	
6	36.8	0	14,600	6	2	
		40	9,400	4	3	50.4
		85	3,500	0	3	
		225*	12,100	0	3	
		300	5,100	0	3	60.3
		342	1,000	0	3	
7	63.7	0	21,500	42	2	
		43	8,500	42	2	67.8
		93	2,600	26	2	
		180*	10,600	41	1	
		227	2,400	14	3	56.7
		285	1,400	5	2	

Experiments by Hawkins et al. (1996) show that the mussels are selectively ingesting the organic-rich particles from the food. Inorganic particles are preferentially rejected by the mussels with pseudofaeces (Figure 10). The organic content of ingested matter was enriched by up to 5 times the organic content of filtered particles. Rates of organic absorption increased with seston filtration rate.
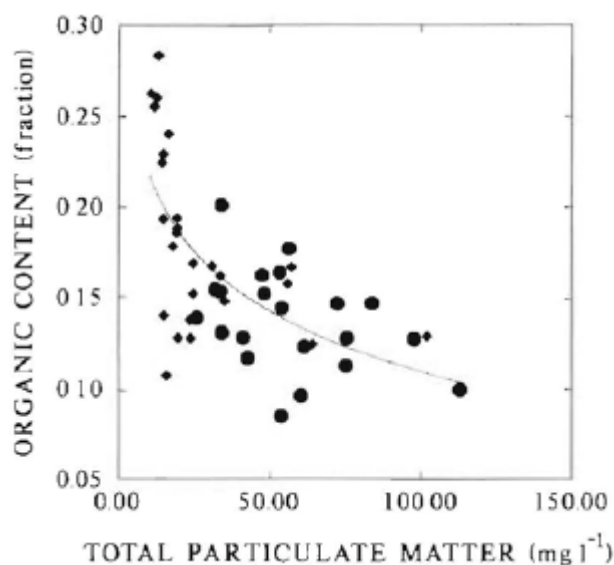

Figure 10: *Organic content of filtered matter (○) and organic content of ingested matter (•) in relation to filtration rate (FR) in mussels standardized to 1 g dry flesh weight. Data are the mean of separate determination upon 10 replicate mussels (Hawkins et al. 1996) .*

2.4.5 Respiration rates

Experiments carried out by Widdows et al. (1979) showed no effects of particle concentration on the rates of oxygen consumption in *M. edulis* (R^2 = 0.16; Table 9). However, changes in clearance rates in response to increased silt concentrations (see above) are reflected in the oxygen extraction efficiency (i.e. the oxygen consumed per hour as a percentage of the oxygen made available to the mussel per hour by the ventilation current). As the ventilation rates decrease with increasing particle concentration, a decrease in the amount of oxygen delivered to the gills per unit time occurs. In order to maintain a constant metabolic rate independent of seston concentrations, the extraction efficiency has to increase exponentially with increasing particle concentration (Figure 11).

Mussels have been shown to maintain a constant metabolic rate up to at least 280 mg seston l^{-1} (Table 9) by increasing the percentage extraction efficiency to 25%. Although Figure 11 predicts that extraction efficiencies will increase rapidly beyond this seston concentration, it is unknown whether or not such high extraction efficiencies can be maintained.

Table 9: Effect of seston concentration on the weight-specific rate of oxygen consumption (VO₂; from (Widdows et al. 1979)

Indi-vidual	Shell length (cm)	Body weight (g)	Seston con-centration (mg l^{-1})	$\bar{V}_{O_2}$ (ml O_2 g^{-1} h^{-1})
1	7	2.066	10	0.716
			200	0.759
			280	0.811
2	7	1.572	10	0.666
			200	0.739
			280	0.675
3	6	1.361	3	0.417
			50	0.494
			100	0.364
4	6	1.290	3	0.637
			50	0.679
			100	0.567
5	4	0.575	5	0.810
			100	0.507
			160	0.677
6	4	0.438	5	0.825
			100	0.752
			160	0.736
7	3	0.211	12	0.717
			180	0.717
8	3	0.307	12	0.770
			100	0.614
9	3	0.297	12	0.711
			100	0.695

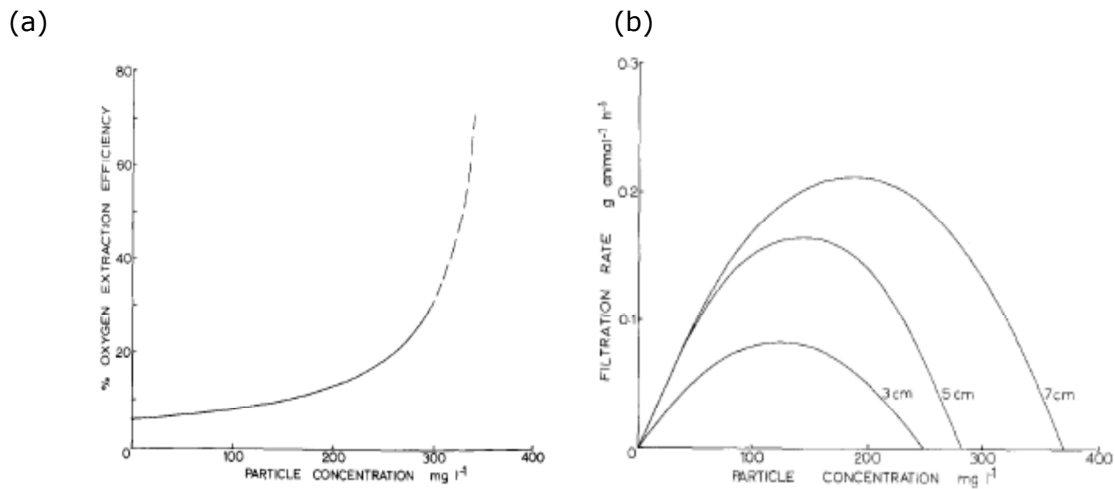(a)   (b)

Figure 11: (a) Relationship between oxygen extraction efficiency and particle concentration for a 7cm mussel at 16 °C and b Effect of particle concentration on filtration rate of three size classes (3, 5 and 7 cm shell length) (Widdows et al. 1979).
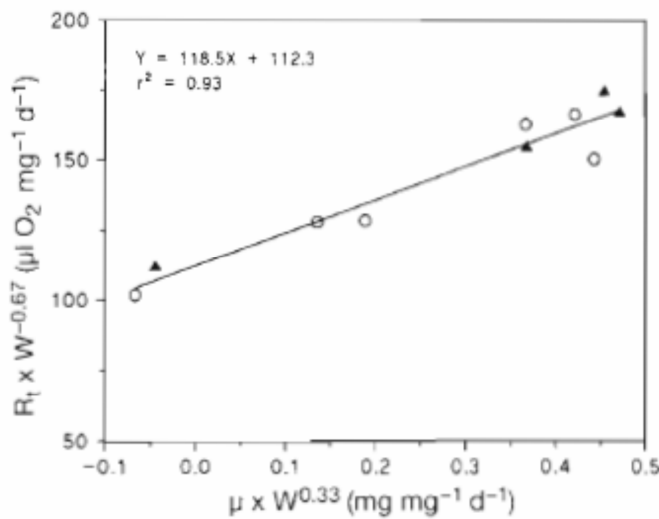

Figure 12: Scaled specific respiration rate ($RW^{-0.67}$) as a function of scaled specific growth rate ($\mu W^{0.33}$). The slope of the line expresses the energy costs of growth (Clausen and Riisgård 1996) (T=15 °C)

Table 10: Rates of oxygen consumption (ml O_2 g^{-1} hr^{-1}) by mussels feeding on 6 diets, and when starved for 2 and 5 days (T = 14 °C). Diets are presented in Table 8 (Bayne et al. 1989).

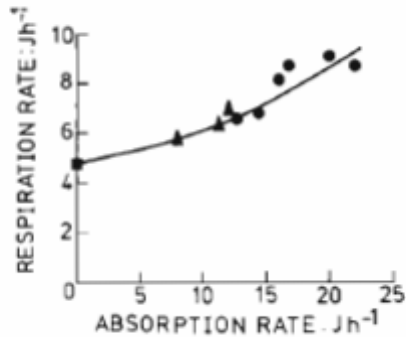| Diet	Fed	Starved 2d	Starved 5d
1	0.337	0.252	0.249
2	0.325	0.252	0.238
3	0.436	0.323	0.272
4	0.405	0.283	0.238
5	0.433	0.337	0.246
6	0.456	0.283	0.249

Figure 13:   Respiration rates Mytilus edulis (J hr^{-1}) as a function to absorbed ration (J hr^{-1}) for mussels of 1 g dry flesh weight (Bayne et al. 1989).

Table 11:   Rates of oxygen consumption (ml O$_2$ hr^{-1}) for mussels at different conditions standardized to a tissue dry mass of 300 mg (T = 15 °C) (Bayne et al. 1989). For rate conditions see Table 12.

Ration condition	Days	Oxygen consumption: (ml O$_2$ h^{-1})
BI	2	0.167±0.027
BII	2	0.182±0.051
BIII	2	0.154±0.030
CI	2	0.186±0.043
CII	2	0.207±0.039
CIII	2	0.215±0.058
BI	12	0.163±0.049
BII	12	0.181±0.051
BIII	12	0.230±0.060
CI	12	0.191±0.042
CII	12	0.178±0.040
CIII	12	0.187±0.032

2.4.6   Assimilation efficiency

Assimilation efficiencies (also indicated as absorption efficiency) are measured as the ratio between fraction of organic matter in the food and in the faeces (Conover-ratio) (Bayne et al. 1987; Conover 1966). There were no consistent differences within the data for absorption efficiency between ration conditions at 2 d. After 12 d, however, there was a significant increase in absorption efficiency for conditions B and C (Table 12 and Table 13). When fed at a high concentration of seston of low organic content, mussels increased their filtration rate, rejected a higher proportion of filtered material as pseudofaeces, and increased the efficiency with which filtered matter of higher organic content was selected for ingestion; this resulted in a constancy of the relationship between ingestion rate and the concentration of particulate organic matter, regardless of differences in seston organic content (Bayne et al. 1993). It is suggested that these responses to changes in the food environment comprise physiological adjustments which result in higher net rates of absorption than would be predicted from considerations only of the organic/inorganic ratio of the suspended particles.

Table 12:   *Ration condition in the experiments. Values are means with 96% confidence limits calculated for at least six determinations made over 2 days (2-d conditions) of 12 days (12-d conditions) (Bayne et al. 1993).*

Ration condition	Days	Total seston: (mg l⁻¹)	POM (mg l⁻¹)	Total seston (mm³ l⁻¹)	Quality (mg POM mm⁻³)
AI	2	1.15±0.11	0.83 ±0.08	1.20 ±0.59	0.69
AII	2	0.99±0.17	0.63 ±0.11	1.19 ±0.32	0.53
AIII	2	1.72±0.42	0.70 ±0.17	1.10 ±0.39	0.64
BI	2	2.71±0.72	1.95 ±0.52	1.90 ±0.69	0.97
BII	2	3.01±0.63	1.91 ±0.40	1.97 ±0.54	0.94
BIII	2	2.89±0.83	1.18 ±0.34	1.72 ±0.92	0.62
CI	2	4.14±0.80	2.98 ±0.58	4.35 ±1.99	0.61
CII	2	4.34±0.91	2.76 ±0.58	4.80 ±2.15	0.56
CIII	2	6.17±1.52	2.59 ±0.64	3.36 ±1.08	0.79
DI	2	8.19±1.65	5.85 ±1.18	9.02 ±1.75	0.65
DII	2	5.99±1.82	3.81 ±1.16	6.92 ±1.12	0.55
DIII	2	10.28±1.20	4.20 ±0.51	6.92 ±1.41	0.61
BI	12	1.45±0.04	1.08 ±0.03	2.00 ±0.64	0.54
BII	12	1.46±0.16	1.15 ±0.13	1.59 ±0.11	0.72
BIII	12	1.47±0.42	0.88 ±0.25	2.06 ±0.25	0.43
CI	12	4.57±0.32	3.41 ±0.24	4.60 ±1.43	0.74
CII	12	4.14±0.40	3.27 ±0.32	4.12 ±1.06	0.79
CIII	12	4.93±0.67	2.95 ±0.40	3.64 ±1.01	0.81

Table 13:   *Absorption efficiencies for each ration condition(see Table 12) Values are means with 95% confidence limits to express the variability between groups of individuals for six determinations of faeces pooled from five individuals. (Bayne et al. 1993).*

Ration condition	Days	Absorption efficiency
AI	2	0.50 ±0.11
AII	2	0.43 ±0.06
AIII	2	0.23 ±0.14
BI	2	0.29 ±0.08
BII	2	0.34 ±0.11
BIII	2	0.35 ±0.07
CI	2	0.40 ±0.19
CII	2	0.60 ±0.13
CIII	2	0.28 ±0.11
DI	2	0.50 ±0.23
DII	2	0.55 ±0.11
DIII	2	0.42 ±0.13
BI	12	0.45 ±0.08
BII	12	0.48 ±0.04
BIII	12	0.58 ±0.08
CI	12	0.46 ±0.14
CII	12	0.48 ±0.16
CIII	12	0.58 ±0.11

2.4.7 Growth

Due to the complex nature of the physiological processes and their interactions with each other, it is worth considering a "black box" approach, whereby food quality is directly linked to growth rates without considering the individual processes. This approach relies on a direct relationship being found between food quality and growth rates, thus providing a link between food quality and growth rates whilst bypassing the unknown relationships between physiological processes.

Kiørboe et al. (1981) studied the influence of suspended, natural silt (0 to 20 mg 1^{-1}) in addition to unicellular algal cells (*Phaeodactylum tricornutum*) (0 to 20,000 cells ml^{-1}) on clearance, growth and energetics in *Mytilus edulis*. The relationship between food quality and clearance rates are provided above and here we consider the direct relationship between food quality and growth.

Growth was measured and expressed in three separate ways: Shell growth, flesh growth and byssus thread growth. Considerable growth of both shell and flesh was recorded in all experiments with algae added (Table 14). Growth rate increased with increasing concentration of algae, both with and without silt in suspension. There was a pronounced effect of silt on growth. At all algal concentrations (except A_o), the daily increase in flesh-weight was significantly higher in the presence of silt at a low concentration (final average flesh weights tested by Student's t-test: S_l-experiments against appropriate S_0-controls; $p < 5\%$ in all instances). At the high silt concentration, growth decreased somewhat (A_lS_l against A_lS_h $p < 5\%$; A_mS_h against A_mS_l $p > 5\%$). The same trends were found for the shell growth, but the differences were statistically significant only in one instance (A_lS_l against A_lS_0). Shell growth formed a significant part of the total organic growth, 21% on average (Kiørboe et al. 1981).

Table 14:   Outline of experimental conditions (Mean values ± SD are given) and average growth of shell, flesh and byssus (adapted from Kiørboe et al. 1981).

| Exp.	Silt [mg/l]	Algae [*103 cells/ml3]	Temp [deg C]	Mussels Nr	Duration [days]	Shell growth [mg dry wt/day]	Flesh growth	Byssus growth	Silt/Algae
A0S0	0	0		31	30	0.74	-0.2	0.06	
A0S1	8.1±3.7	0	13.4±0.9	55	30	0.85	-0.19	0.06	
A1S0	0	6.9±2.9	13.0±1.0	55	19	4.15	0.49	0.09	
A1S1	5.3±2.2	5.3±2.7	13.4±1.0	42	19	5.56	0.9	0.09	
A1Sh	25.6±29.2	6.2±2.8	14.3±0.7	45	19	3.8	0.58	0.09	4.13
AmS0	0	11.8±4.5	13.4±0.2	60	20	2.78	0.68	0.09	0
AmS1	5.7±3.6	9.9±3.6	13.6±0.2	57	20	3.4	1.14	0.09	0.58
AmSh	17.1±8.3	7.6±2.0	14.6±0.2	75	20	3.47	1.04	0.09	2.25
AhS0	0	20.9±13.6	17.6±1.2	40	13	6.1	1.42	0.14	0
AhS1	8.2±6.0	15.3±12.7	16.9±1.1	40	13	7.6	1.95	0.13	0.54
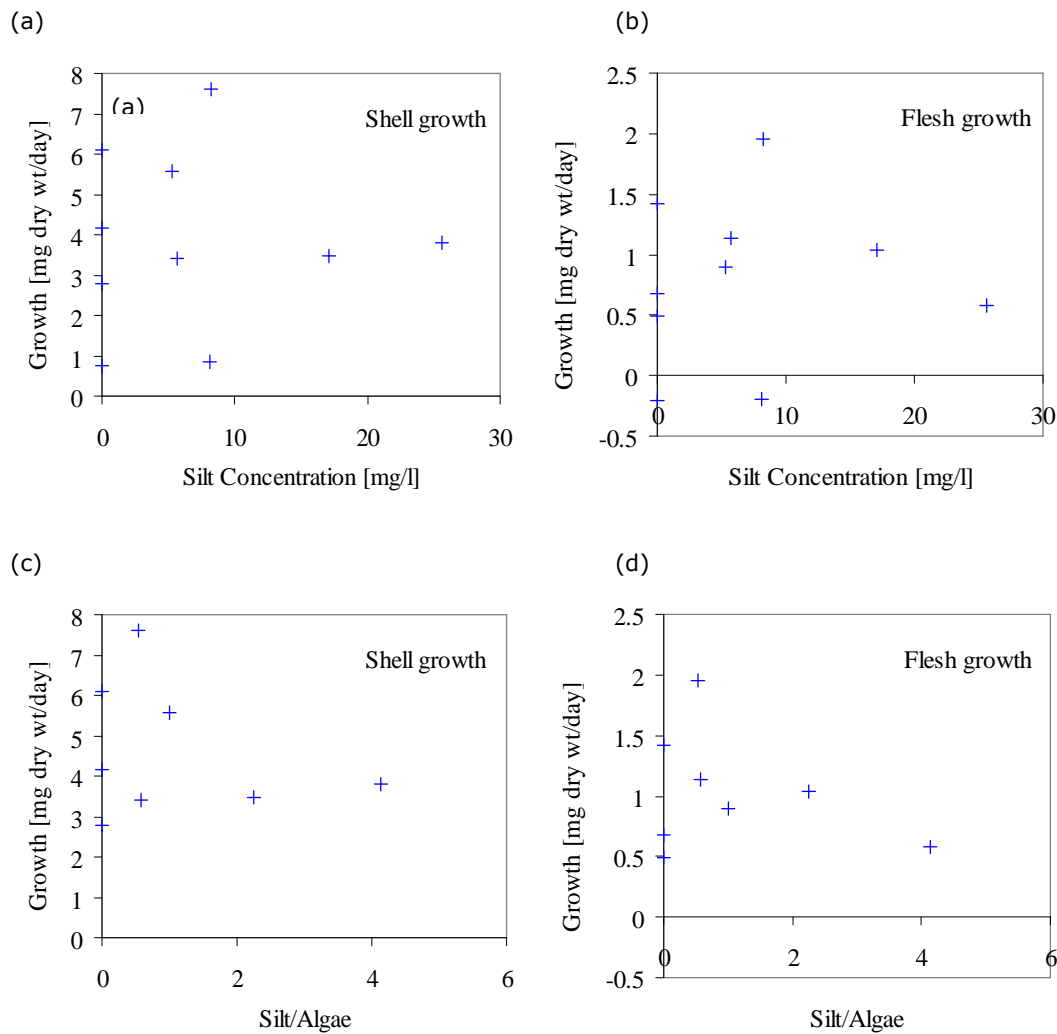
Figure 14:   Growth of Shell (a) and flesh (b) at different silt concentrations and growth of shell (c) and flesh (d) with different food quality (ratio silt:algae) (adapted from Kiørboe et al. 1981).

Although some effects of silt concentrations as well as silt:algae ratios are evident on the growth of mussels, there appears to be no underlying relationship between the two. This may be partly due to varying temperatures during the experiments described in the study, which in turn affect physiological processes. The lack of replicates makes it further difficult to estimate the variability.
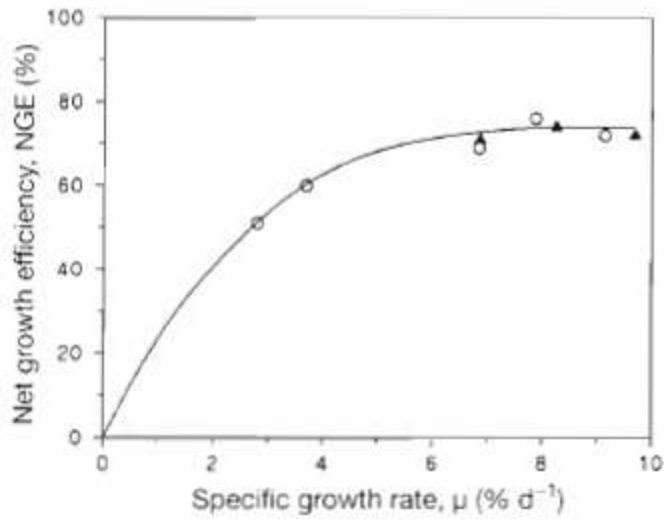
Figure 15: Net growth efficiency (NGE) as a function of specific growth rate (μ) in laboratory experiments (Clausen and Riisgård 1996)
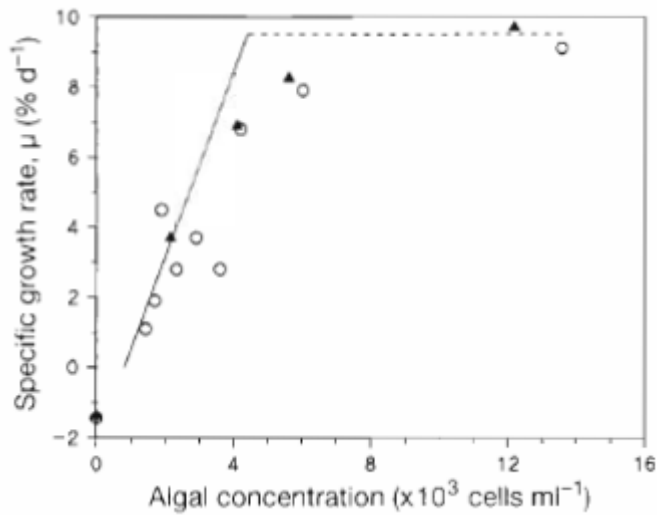

Figure 16: Specific growth rate (μ) as a function of algal concentrations in laboratory experiments (Clausen and Riisgård 1996).

Table 15: *Food concentration, carbon specific growth (G) and respiration (R) rate, and net growth efficiency (NGE=G/(G+R)). Experiments performed with pure algae or algae + silt are indicated by A_i, A_iS respectively (Clausen and Riisgård 1996).*

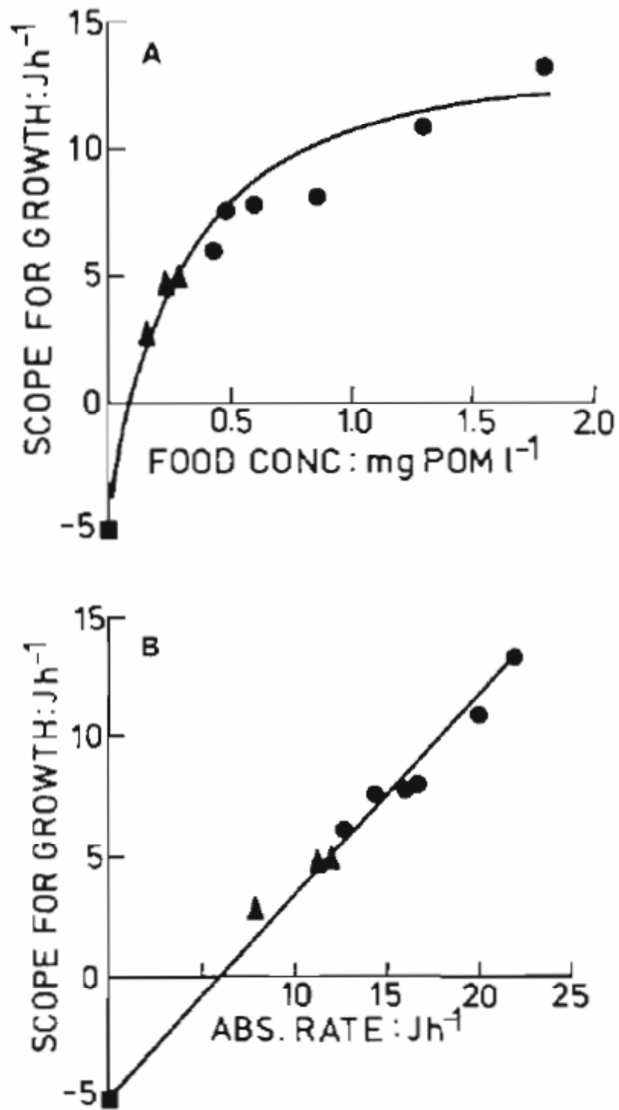| Expt	Algal concentration ($\times 10^3$ cells ml^{-1})	Food concentration (μg C l^{-1})	G (μg C mg^{-1} C d^{-1})	R (μg C mg^{-1} C d^{-1})	NGE (%)
A_0	0 ± 0	0	−14	21	−193
A_1	1.9 ± 0.4	89	45	–	–
A_2	4.1 ± 0.8	196	68	30	69
A_3	6.0 ± 1.5	284	79	25	76
A_4	13.6 ± 7.0	640	91	36	72
A_0S	0 ± 0	0	−14	34	−71
A_1S	2.1 ± 0.5	101	37	–	–
A_2S	4.1 ± 1.4	195	69	29	71
A_3S	5.6 ± 1.8	265	82	29	74
A_4S	12.1 ± 4.3	574	97	37	72
A_5	1.4 ± 0.4	67	–	–	–
A_6	1.7 ± 0.5	80	–	–	–
A_7	2.3 ± 0.8	110	28	27	51
A_8	3.0 ± 0.6	137	37	25	60
A_9	3.6 ± 0.5	170	–	–	–

Figure 17: Growth response. (A) Scope for growth (SFG, J hr^{-1}) as a function of the concentration of particulate organ is matter (POM, mg l^{-1}) (B) Scope for growth (SFG, J hr^{-1}) as a function of the absorbed ration (AR, J hr^{-1}) (Bayne et al. 1989).
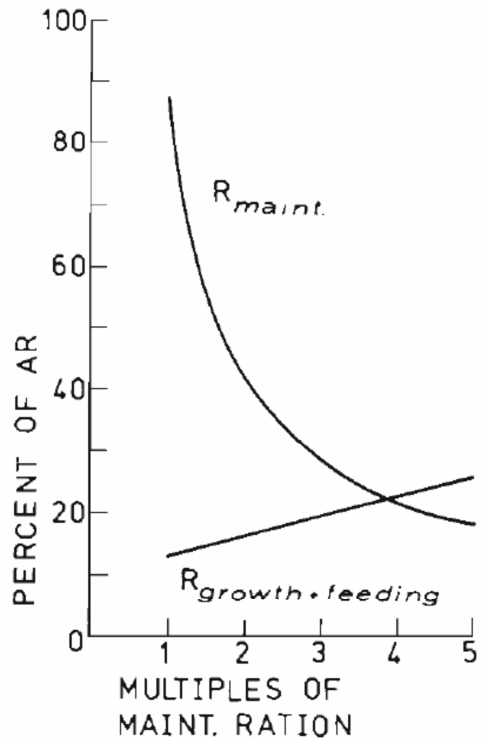
Figure 18:   Proportion of absorbed ration (AR) utilised n maintenance (R_{maint}) and in growth and feeding ($R_{growth + feeding}$) at different multiples of the maintenance ration (Bayne et al. 1989) .

Growth rate
Under laboratory conditions, the growth rate in *M. edulis* increased to a maximum value of 9.5% d^{-1} under increasing food concentrations, irrespective of relatively high silt concentrations (5 mg l^{-1}) ((Clausen and Riisgård 1996).

Net growth efficiency
Net growth efficiency increased with specific growth rate to max. ~75% for μ >6% d^{-1} (Clausen and Riisgård 1996). Field value for specific growth rate: 5%.

3 Dynamic Energy Budget (DEB) model for mussels

3.1 Standard DEB model

Functional responses of filter-feeding bivalves to variations in seston (total amount of particles in the water) have been discussed by numerous authors (e.g. Bayne et al. 1987; Foster-Smith 1975; Navarro and Iglesias 1993; Newell et al. 1989; Riisgård 2001b; Shumway et al. 1985) and implemented into physiological models (Campbell and Newell 1998; Hawkins et al. 2002; Scholten and Smaal 1998). Some of these models are based on the DEB theory (Maar et al. 2009; Rosland et al. 2009; Saraiva et al. 2011; Troost et al. 2010).

The generic dynamic energy budget (DEB) model has been developed by Kooijman 30 years ago (Kooijman 1986; Kooijman 2000; Kooijman 2010). The DEB model describes the energy flow through an organism as a function of its size, its development stage and environmental conditions. An individual organism is described by the state variables structural body volume V (cm^3), Reserves E (Joule) and Reproduction (Joule) (Figure 19). While the processes of the DEB model are generic, the parameters are species specific (Lika et al. 2011).
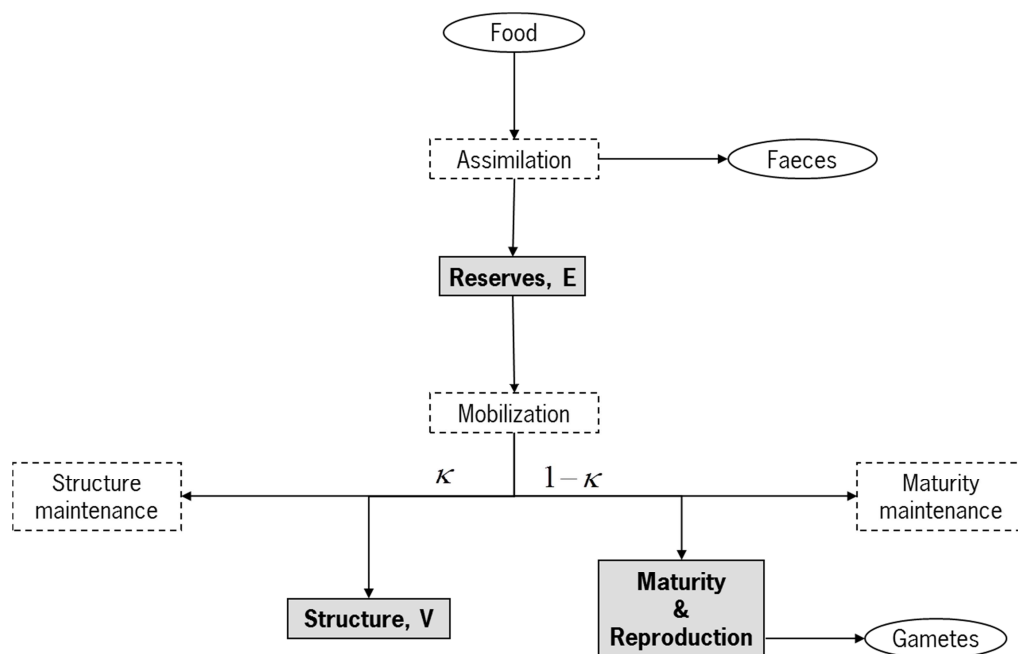

Figure 19:   Schematic representation of the state variables and processes in the DEB model.

The organism acquires energy from food by assimilation. The energy that is not assimilated by the organism is released as faeces. The assimilated energy is first stored into reserves (blood, glycogen). From the reserves, the energy is mobilized into growth, development and maintenance. A fixed fraction (κ) of the energy flow from the reserves is used for growth and somatic maintenance, with priority to maintenance. The rest of the energy flow from the reserves (1-κ) is spent on maturity maintenance and reproduction (gamete production and spawning). For juveniles, energy is spent on maturation.

A key process is the assimilation rate of the food. In DEB, this is generally described by a Holling type II functional response. The scaled functional response (*f*) varies between 0 (no food available) and 1 (infinite amount of food available). At a food concentration $X = X_k$, the functional response equals 0.5.

$$f = \frac{X}{X_k + X}$$

3.2 DEB model for filter feeding bivalves

Suspension feeding bivalves obtain their energy by pumping water with suspended organic particles over their gills. Edible particles are selected using palps and the non-edible fraction of particles is released in the form of pseudo faeces. The energy that is not assimilated by the bivalve is released as faeces.

In DEB models, the effect of inorganic particles can be incorporated in the formulation of a scaled functional response (Kooijman 2006; Wijsman 2011; Wijsman and Smaal 2011).

$$f = \frac{X}{K'(Y) + X}$$

with

$$K'(Y) = X_k \left(1 + \frac{Y}{Y_k}\right)$$

Where X is the food concentration, expressed in (µg chl-a l^{-1}), X_k is the half saturation constant (µg chl-a l^{-1}), Y is the concentration of particulate inorganic matter expressed in mg l^{-1} and Y_k is the saturation constant for the particulate inorganic matter (mg l^{-1}).
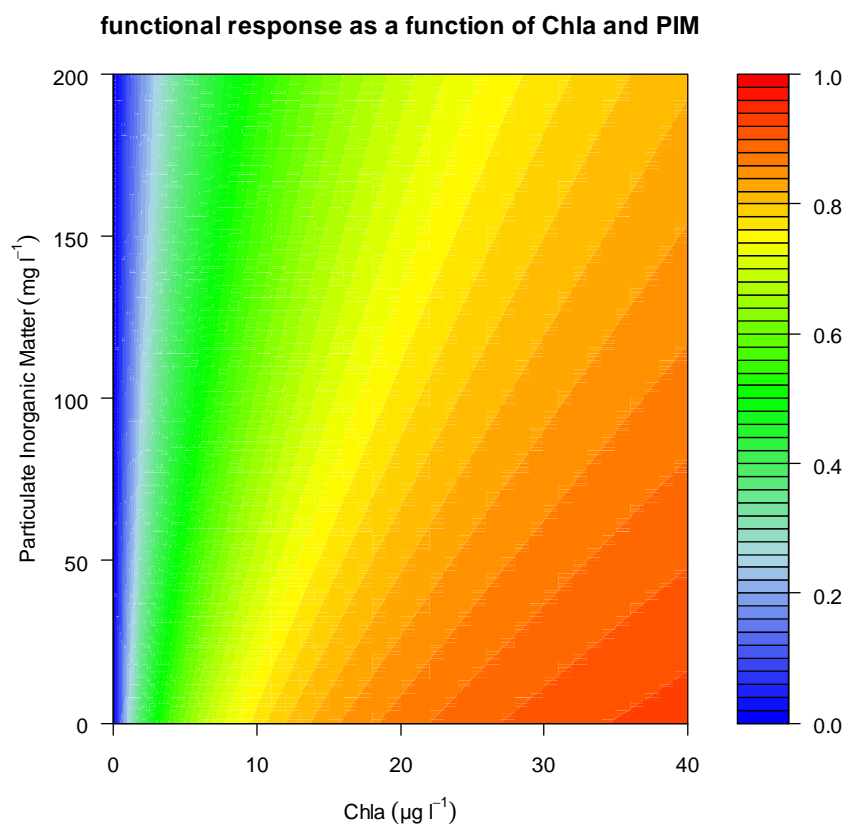

functional response as a function of Chla and PIM

Figure 20: Scaled functional response as a function of Chl-a concentration and Particulate Inorganic Matter (PIM). Parameters used are: Y_k = 100 mg l^{-1} and X_k = 3 µg l^{-1}
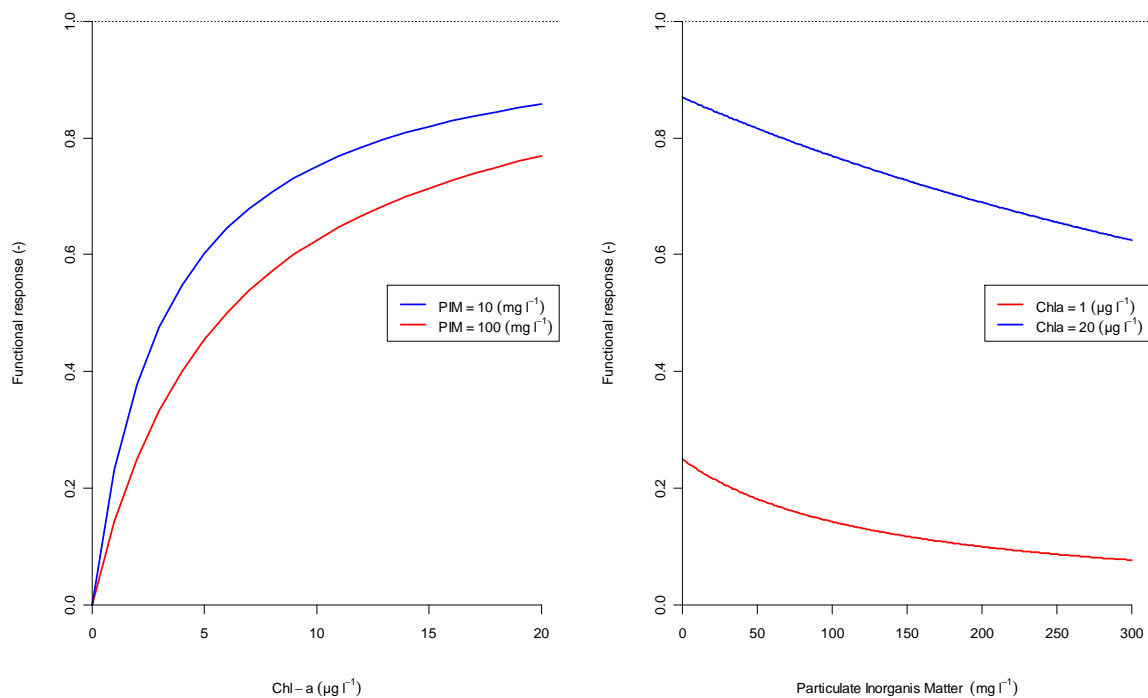
Figure 21: Scaled Functional response as a function of Chl-a concentrations at PIM levels of 10 and 100 mg l^{-1} (left panel) and suspended solid concentrations at Chl-a concentrations of 1 and 20 µg l^{-1} (right panel). Parameters used are: Y_k = 100 mg l^{-1} and X_k = 3 µg l^{-1}.

As can be seen from Figure 20 and Figure 21, the scaled functional response increases with food (expressed as Chl-a concentration) and decreases with inorganic particulate matter solid concentration. The model is in accordance with the Synthesizing Units concept introduced in the DEB theory by Kooijman (1998; 2000; 2010). The model assumes that the handling of inorganic particles costs time for the filtering apparatus and that this handling time is paid by the handling time of food particles (Kooijman 2006). With this approach it is possible to model the effect of inorganic particles on the growth of shellfish. However, it does not describe the process of filtration and the production of pseudo-faeces and faeces explicitly.

3.3   Mechanistic approach

Saraiva et al. (2011) have developed a mechanistic approach to model the filtration of bivalves and the production of faeces and pseudo-faeces based on the Synthesizing Units concept. In this model the filtered material can be divided into various fractions (e.g. silt, algae, zooplankton, detritus). In this example we only use silt (X_0) and algae (X_1).

The feeding process is described by separate processes:
- Filtration: pumping of water and filtration of the particles by the gills.
- Ingestion and pseudo-faeces production: Selection the edible particles and disposal of inedible parts.
- Assimilation and faeces production: influx of food into the reserve pool and production of faeces.

This study focuses on the filtration, ingestion and pseudo-faeces production.

3.3.1 Filtration

Filter feeders create a water flow over the gills by the activity of the cilia. The particles that are transported by the water flow are filtered by the gills. The volume of water filtered (clearance rate) is proportional to the surface area of the gills and hence to the structural Volume to the power 2/3. Mussels are able to retain all particles > 2-5 µm on their gills. There is no active selection of the particles on the gills, which means that silt particles > 5 µm are similarly filtered from the water as algae of the same size.

The clearance rate ($\dot{C}_R$) is described by:

$$\dot{C}_R = \frac{\{\dot{C}_{Rm}\}}{1 + \sum_i^n \frac{X_i\{\dot{C}_{Rm}\}}{\{J_{X_iF_m}\}}} V^{2/3}$$

Where $\dot{C}_R$ is the clearance rate of the water (m^3 d^{-1}), $\{\dot{C}_{Rm}\}$ is the maximum surface area-specific clearance rate (m^3 d^{-1} cm^{-2}), $\{j_{X_iF_m}\}$ is the maximum surface area-specific filtration rate for X_i, with X_0 = silt (mg l^{-1}) and X_1 = algae (µg l^{-1}). The variable V is the structural volume of the organism (cm^{-3}).

The filtration rate (j_{X_iF}) of particles can be calculated by multiplying the clearance rate with the concentration of the particles in the water:

$$j_{X_iF} = \dot{C}_R X_i$$

3.3.2 Ingestion and pseudofaeces production

Filtered particles are transported over the gills to the mouth. The labial palps select edible parts from the inedible parts. The edible parts are ingested in the mouth and the inedible parts are egested in the form of pseudo-faeces. In contrast to filtration, where no selection takes place, ingestion is particle specific. It is assumed that the labial palps have different affinities for each food type (ρ_{X_0I} = binding probability for silt and ρ_{X_1I}= binding probability for algae).

$$j_{X_iI} = \frac{\rho_{X_iI}j_{X_iF}}{1 + \sum_i^n \frac{\rho_{X_iI}j_{X_iF}}{\{j_{X_iIm}\}}}$$

Where j_{X_iI} is the ingestion rate of component X_i, ρ_{X_iI} is the binding probability for X_i, j_{X_iF} is the filtration rate for X_i. j_{X_iIm} is the maximum ingestion rate for X_i. The pseudofaeces production rate can be calculated by:

$$j_{P_iF} = j_{X_iF} - j_{X_iI}$$

Where j_{P_iF} is the pseudofaeces production rate for X_i, j_{X_iF} is the filtration rate and j_{X_iI} is the ingestion rate for X_i.

3.3.3 Model results

The model of Saraiva et al. (2011) was run for a 3 cm shell length mussel (*Mytilus edulis*) at an ambient water temperature of 15°C, with varying silt concentrations (0 – 300 g l^{-1}) and constant algae concentration (1 µg l^{-1}). The model parameters are presented in Table 16.

Table 16:   Overview parameters for filtrations and pseudofaeces production of mussels (Saraiva et al. 2011)

Parameter	Description	Value	Unit	Reference
$\{\dot{C}_{Rm}\}$	Max. surface area specific clearance rate	0.096	$m^3\ d^{-1}\ cm^{-2}$	(Saraiva et al. 2011)
$\{\dot{j}_{X_0F_m}\}$	Max. surface area-specific filtration rate for silt	3.5	$g\ d^{-1}\ cm^{-2}$	(Saraiva et al. 2011)
$\{\dot{j}_{X_1F_m}\}$	Max. surface area-specific filtration rate for algae	4.8×10^{-4}	$molC\ d^{-1}\ cm^{-2}$	(Rosland et al. 2009)
ρ_{X_0I}	Binding probability for silt	0.45	-	(Saraiva et al. 2011)
ρ_{X_1I}	Binding probability for algae	0.99	-	(Saraiva et al. 2011)
$\dot{j}_{X_0Im}$	Max. ingestion rate for silt	0.23	$g\ d^{-1}$	(Saraiva et al. 2011)
$\dot{j}_{X_1Im}$	Max. ingestion rate for algea	0.65×10^{4}	$molC\ d^{-1}$	(Saraiva et al. 2011)

The effect of Particulate Inorganic Matter (PIM) concentration on the feeding processes (Clearance rate, Filtration rate, Ingestion rate and Pseudofaeces production) is presented in Figure 22. The Clearance rate decreases with PIM concentration, which is in correspondence with Widdows et al. (1979). The filtration rate of PIM increases with PIM concentration. Only a fraction of the inorganic particles are ingested while the majority is egested in the form of pseudofaeces. The calculated ingestion rates of PIM are slightly higher than reported by Kiørboe et al. (1980) .
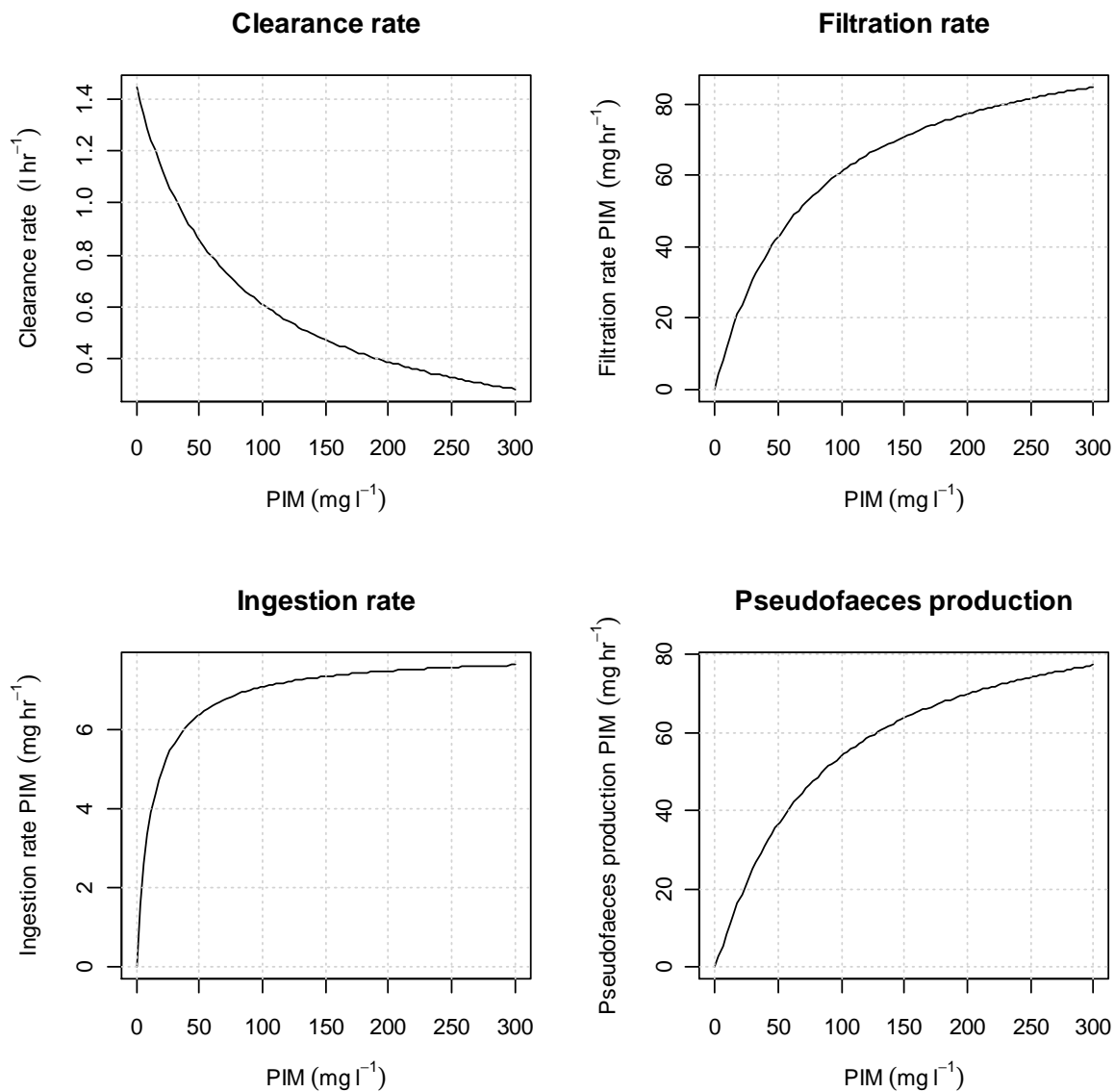
Figure 22:   Clearance rate, Filtration rate, Ingestion rate and Pseudofaeces production for the PIM fraction (mg) for a 3 cm mussel as a function of the PIM concentration in the water.

The effect of PIM on chlorophyll ingestion and egestion is presented in Figure 23. Filtration and Ingestion rate follow the pattern of the clearance rate. Pseudofaeces production however shows an optimum at a TPM concentration of about 30 mg l^{-1}. This is because there is no pseudofaeces production when inorganic particles are absent at these low chlorophyll concentrations (<1 µg l^{-1}).
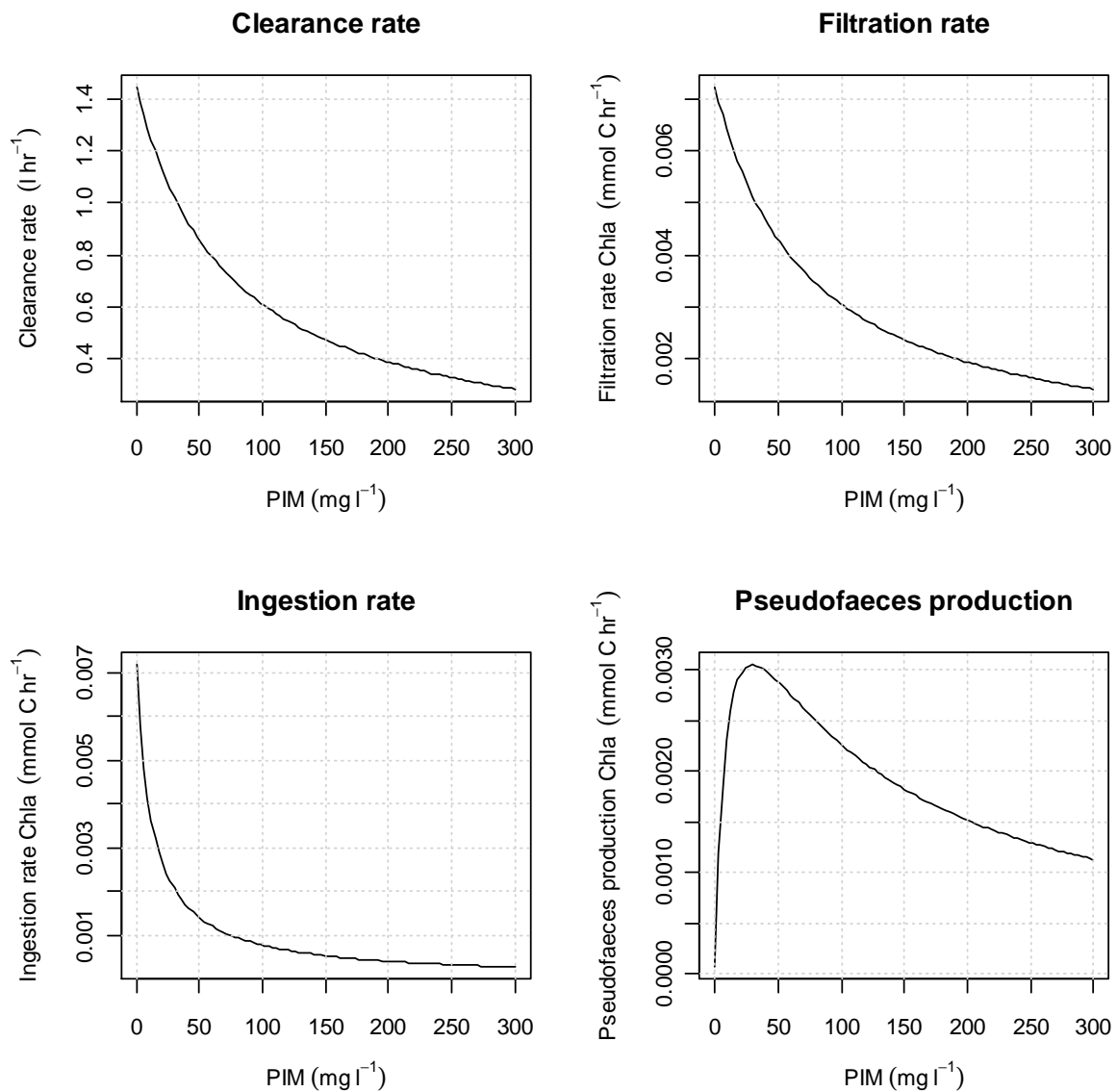
Figure 23:   *Clearance rate, Filtration rate, Ingestion rate and Pseudofaeces production for the Chl-a fraction (expressed as mmolC) for a 3 cm mussel as a function of Particulate Inorganic Matter (PIM).*

In Figure 24, it can be seen that the clearance rate decreases with increasing chlorophyll-a concentration. As a consequence, the filtration and uptake rate of PIM and also the pseudofaeces production decreases with increasing Chla-concentration.
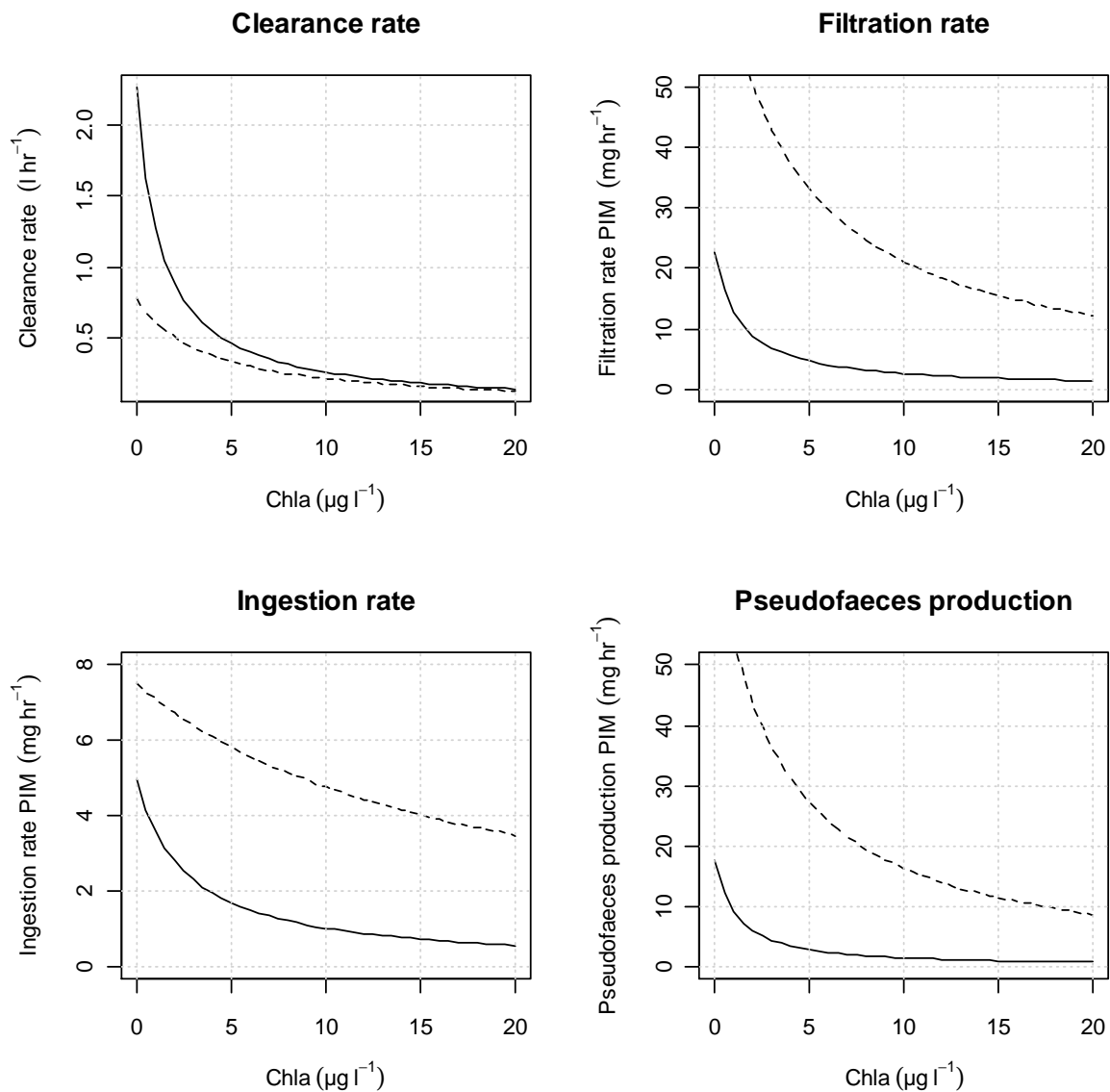
Figure 24:   Clearance rate, Filtration rate, Ingestion rate and Pseudofaeces production for the inorganic fraction (mg) for a 3 cm mussel as a function of chlorophyll-a concentration. Solid lines are for a PIM concentration of 10 mg l^{-1} and broken lines are for a PIM concentration of 100 mg l^{-1}.

In Figure 25, it can be seen that the ingestion rate of chlorophyll increases with increasing chlorophyll-a concentration. The shape of the curve corresponds to the shape of the scaled functional response (Figure 21) and the effect of inorganic particles on the shape of the curve is the same.
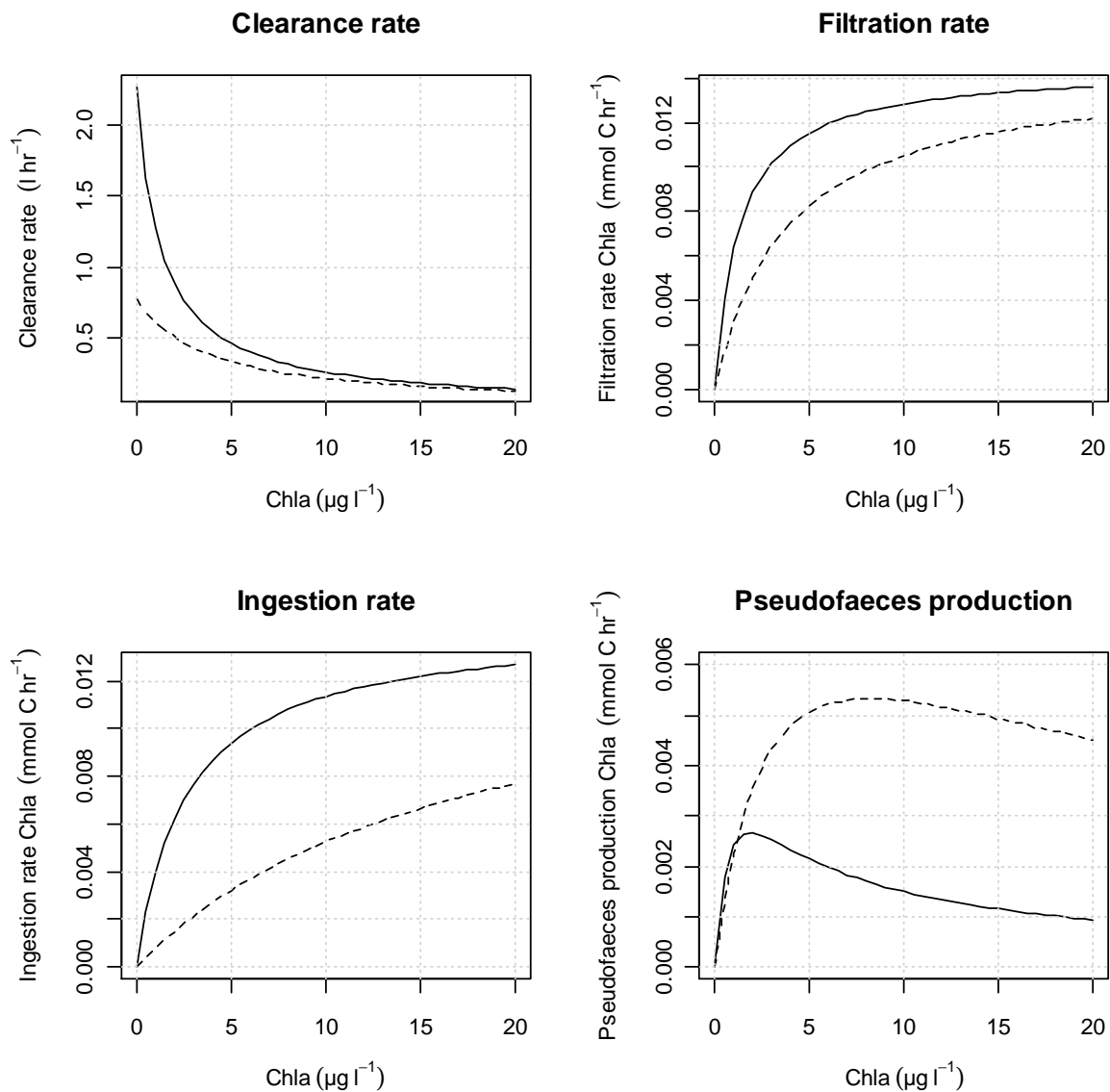
Figure 25:   Clearance rate, Filtration rate, Ingestion rate and Pseudofaeces production for the Chl-a fraction (mmolC) for a 3 cm mussel as a function of chlorophyll-a concentration. Solid lines are for a PIM concentration of 5 mg l^{-1} and broken lines are for a PIM concentration of 50 mg l^{-1}.

3.4   Model results variable environmental conditions

A base line model simulation was run with a standard DEB model for mussels, extended with the formulation of clearance rates and pseudofaeces production as described in the previous paragraph. The model was forced with environmental conditions (Temperature, Chlorophyll-a and Particulate Inorganic Matter) from model calculations for the North Sea (Schellekens 2012) for the location Schouwen 4 near the seabed (Scenario 0, Figure 26). The model was run from May 1st 2007 to 31st December 2011. As can be seen from Figure 26, temperature has a sinusoidal function ranging between about 6 °C during Winter and about 18 °C during Summer. Chl-a concentration has a peak in early Spring and a second peak during the Summer. Particulate Inorganic Matter is highest in Winter due to the wind conditions. In

Summer the concentrations of Particulate Inorganic Matter is lowest. The resulting scaled functional response fluctuates between about 0.1 in the Winter and 0.8 in Spring and Summer.

Table 17:   Overview of primary DEB parameters used in the model

Parameter	Value	Unit	Description
z	4.6897	-	Zoom factor
$\{\dot{F}_m\}$	96	l d^{-1} cm^{-2}	Maximum surface-area-specific filtration rate
κ_X	0.53	-	Digestion efficiency
$\dot{\upsilon}$	0.0721	cm d^{-1}	Energy conductance
κ	0.8085	-	Allocation fraction to soma
κ_R	0.95	-	Reproduction efficiency
$[\dot{p}_M]$	13.74	J d^{-1} cm^{-3}	Volume-specific somatic maintenance
$\{\dot{p}_T\}$	0	J d^{-1} cm^{-2}	Surface-specific somatic maintenance
$\dot{k}_J$	2.873 x10^{-3}	d^{-1}	Maturity maintenance rate coefficient
$[E_G]$	4783	J cm^{-3}	Specific cost for structure
E_H^b	2x10^{-5}	J	Maturity at birth
E_H^j	2x10^{-5}	J	Maturity at metamorphosis
E_H^p	44.8	J	Maturity at puberty
$\ddot{h}_a$	5.13x10^{-9}	d^{-2}	Weibull ageing acceleration
s_G	1x10^{-4}	-	Gompertz stress coefficient

Water temperature

Chlorphyl-a

Particulate Inorganic Matter
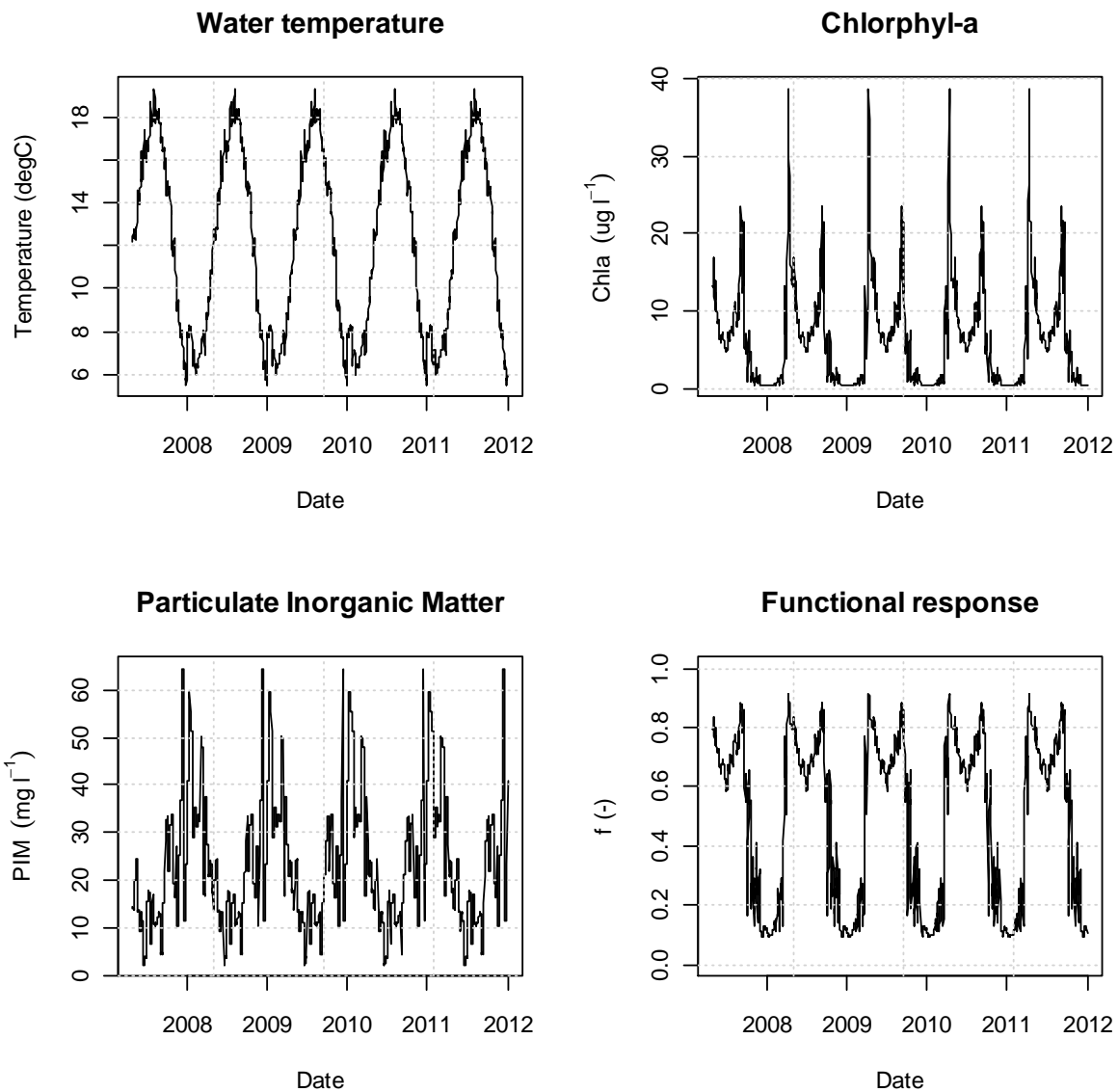

Functional response

Figure 26:   Forcing functions (Temperature, Chl-a and PIM) used for the DEB simulations. The f value (functional response, bottom-right) is calculated by the DEB model based on the Chl-a and PIM concentrations.

From the results of the DEB model, it can be shown that mussel growth is mainly influenced by temperature and Chl-a. Growth is highest during the summer period when the temperatures are highest. During winter time, the mussels do not grow in shell length and weight decreases. This is mainly caused by the poor food conditions. Reserves are built-up during spring and summer and decrease during winter. Spawning occurs in the second year, but is higher in subsequent years. The combined dynamics of length, reserves and gonads are reflected in the weight of the mussels.
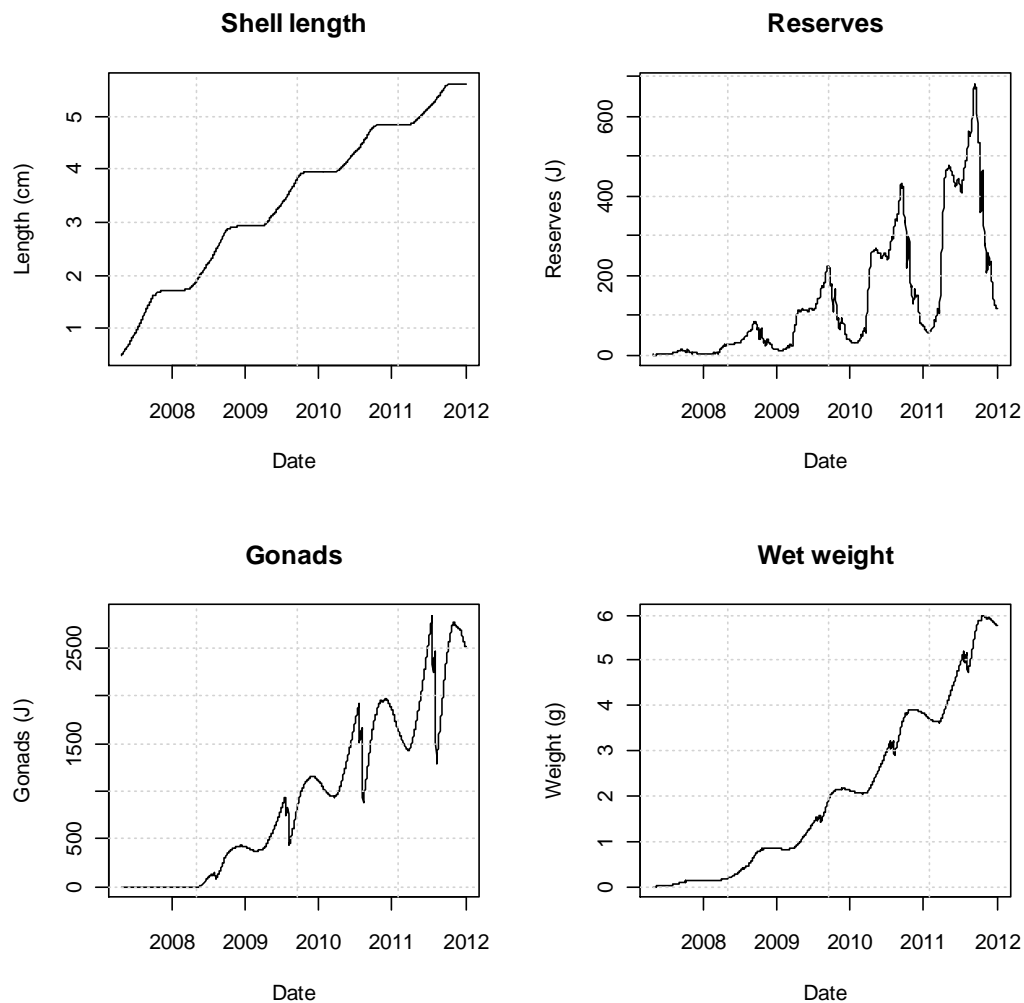
Shell length

Reserves

Gonads

Wet weight

Figure 27:   Growth in shell length (cm) and flesh weight (g) of a mussel as a function of the environmental conditions

The dynamics of clearance rates and production of pseudofaeces are presented in Figure 28. Highest clearance rates (about 3 l hr^{-1}) are achieved by the largest mussels. Clearance rate is highest during the Winter. Although in general the activity of the mussels is low due to the low temperatures, the low concentrations of Chl-a lead to high clearance rates. Since the concentrations of Particulate Inorganic Matter is high, the production of pseudofaeces is also high.

Scholten and Smaal (1998) also calculate clearance rates for mussels as a function of seston concentrations in the Oosterschelde, Marennes-Oléron and Upper South Cove using the Emmy model. This model is based on detailed information of food uptake and food processing by mussels. In this study, clearance rates in the Oosterschelde seems to be highest in autumn, when the activity of the mussels is high and Chla/sestion ratios are low.
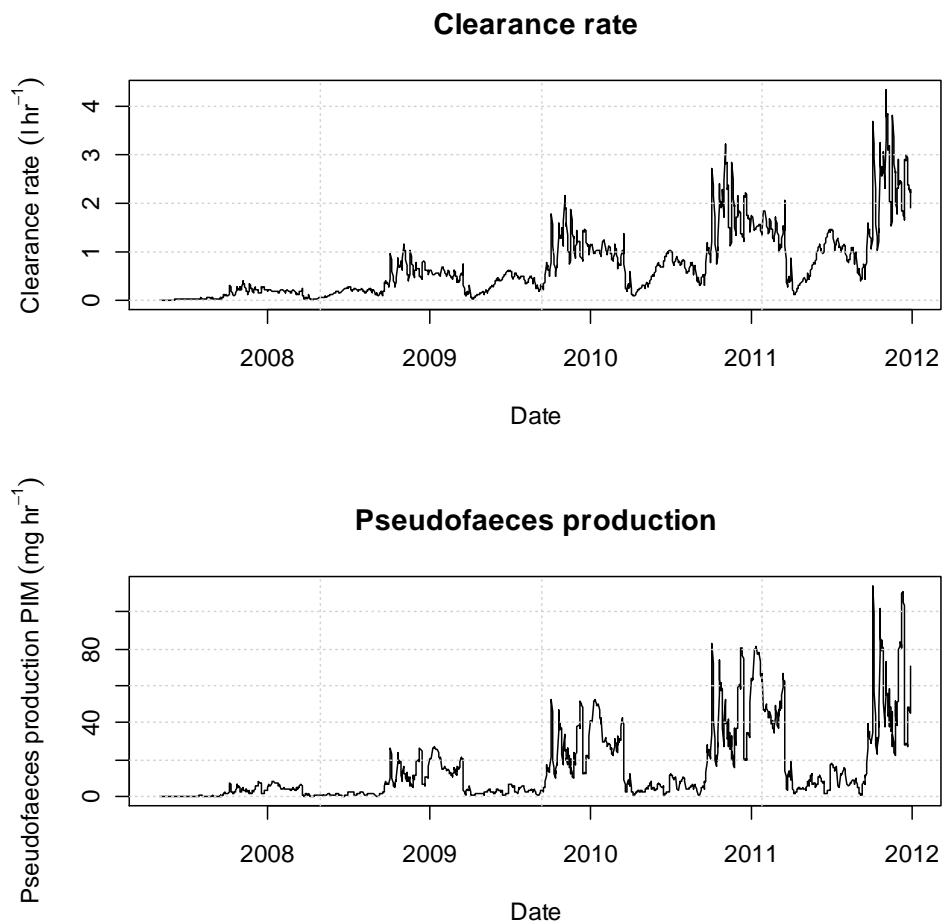
Clearance rate

Pseudofaeces production

Figure 28:   Clearance rate (l h^{-1}) and Pseudofaeces production of PIM by a mussel calculated by the DEB model

3.5   Model results effect increased suspended sediment

In order to study the effect of increased Particulate Inorganic Matter on the growth and development of the mussels, three alternative model scenarios are run and compared to the baseline scenario. In all scenario's the same amount of suspended matter is released, but the scenarios differ in the timing.

- Continuous release increase of Particulate Inorganic Matter with 16.67 g l^{-1} (= 200/12).
- Pulse increase with 200 g l^{-1} in June of each year
- Pulse increase with 200 g l^{-1} in January of each year

The resulting forcing functions of Particulate Inorganic Matter for the scenarios are presented in Figure 29 together with the concentrations from the baseline scenario. The other forcing functions, temperature and chl-a were kept the same as in the baseline scenario.

The resulting clearance rates and pseudofaeces production are presented in Figure 30, which shows that the pulse inputs cause an increase in Particulate inorganic matter, and a decrease the clearance rates. The decrease is more pronounced when the pulse input takes place in January (blue lines). The pulse inputs have a positive effect on pseudofaeces production.
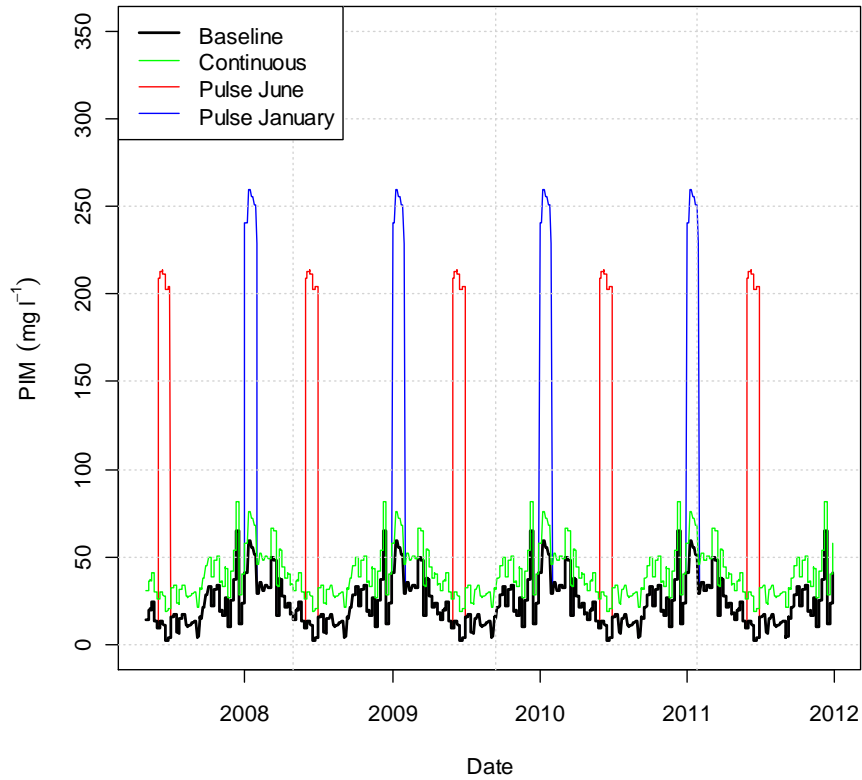
Particulate Inorganic Matter

Figure 29:   Forcing functions of PIM for the different model scenarios. The other forcing functions (Chl-a and Temperature were the same for each scenario.
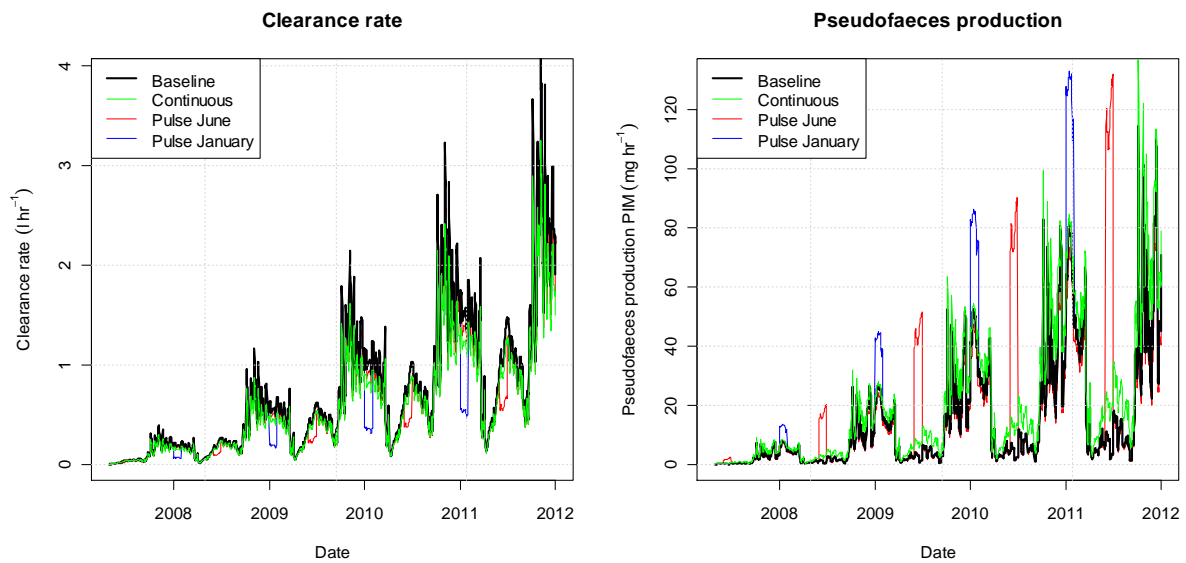

Figure 30:   Clearance rate (l h⁻¹) and Pseudofaeces production of PIM by a mussel calculated by the DEB model for the different model scenarios

The continuous release of Particulate Inorganic Matter and the Pulse release in June have comparable effects on mussel growth, where the effect on weight is more pronounced than on length. The pulse release in January has almost no effect on mussel growth.
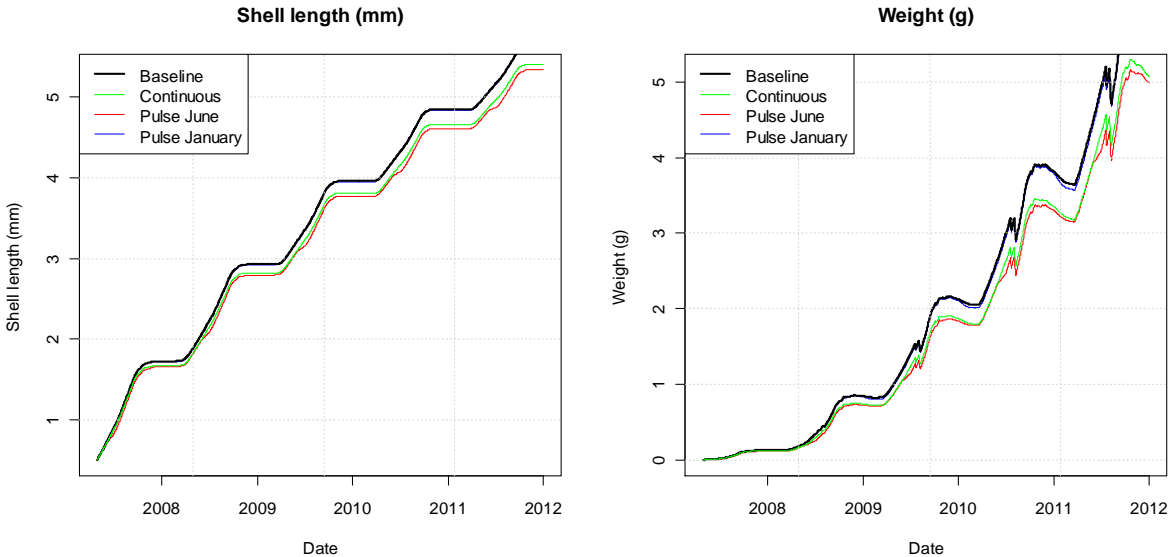

Figure 31:   Growth in shell length (cm) and flesh weight (g) for the different model scenarios.

4   Discussion and recommendations

4.1   Impact of suspended sediment on filterfeeding

The impact of dredging activities on filterfeeding bivalves is studied by a combination of literature research and modeling. The increased suspended sediment concentration in the water decreases the efficiency of the filtration process, since part of the filtered material is rejected and excreted in the form of faeces and pseudofaeces. Laboratory studies show that the clearance rate by filterfeeding bivalves decreases with increasing particle concentration. Laboratory studies also show that the production of pseudofaeces increases with increased silt content. As a result of the decreased feeding efficiency, the growth and development of filterfeeding bivalves will be reduced and this might have a knock-on effect on fish and birds that depend on the bivalves as a food source.

It can be concluded from this study that low concentrations of particulate inorganic matter already have an effect on the food-uptake rate. This is because the filterfeeding shellfish need to invest time and energy in the processing of the inorganic matter. Short-term increases of particulate inorganic matter has less impact on the growth performance of the shellfish compared to a continuous increase. The timing of dredging activities is also important. In the winter period, when the activity of the shellfish are low, the impact of increased suspended sediment concentration is much lower than during summertime.

Under natural conditions, many factors may influence the filtration rate of bivalves and feeding under laboratory conditions may not always accurately reflect *in situ* filtration where a wide spectrum of changing environmental factors and species interactions may influence the feeding behavior. Field measurements with benthic chambers and benthic tunnels have been used to overcome this problem and validate the lab measurements. In laboratory conditions, filterfeeding bivalves are easily disturbed, which is reflected in the clearance rates. Therefore, it is important to have a good set-up of the laboratory experiments.

The present study is believed to reflect important basic features of mussels' feeding behavior in nature where phytoplankton is the main source of nutrition. Among the many parameters that may affect the in situ feeding behavior, phytoplankton biomass (expressed as chl-a concentration) seems to be the most important although, for example, high concentrations of silt/seston leading to pre-ingestive rejection/pseudofaeces production may also affect the feeding of mussels in many estuaries and exposed coastal waters.

Although there is still no general agreement regarding physiological control of water pumping in response to (very) high concentrations of particles in the ambient water, present consensus tends to be that the filtration rate is high and constant, that is, basically autonomous, between a lower critical level and an upper seston concentration threshold. However, it remains to be clarified if reduced filtration rate at high seston concentrations is caused by physiological regulation (supporting maximum assimilation and growth) or overloading (adversely affecting food uptake and growth) (Riisgård 2001a).

A substantial amount of knowledge is available on the feeding behavior of filterfeeding bivalves. Physiological models (e.g. Hawkins et al. 2002; Rueda et al. 2005) integrate this knowledge into more complex formulations. Alternatively, in DEB models a relatively simple description using a scaled functional response is applied. The scaled functional response describes the energy uptake rate as a function of food concentration. The effect of suspended sediment concentration can be incorporated in the functional response. The functional response does not include any knowledge on the feeding behavior of the organism. The results of the formulation, however, are quite comparable with laboratory observations.

Processes as clearance rates and pseudofaeces production are no standard output of DEB models. The formulation of Saraiva et al. (2011) provides an interesting method to model these processes using the DEB formulation. This approach can be used efficiently to quantify the impact of increased suspended sediment concentrations due to dredging activities on the growth and activity of filterfeeding bivalves.

Chapter 3 describes how the impact of changes in silt and/or phytoplankton concentrations on the growth of an individual blue mussel (*Mytilus edulis*) can be modeled in a deterministic way, using the DEB-model. However, in cases where worst-case or conservative assumptions are made to model ecological impacts deterministically, the use of a probabilistic instead of a deterministic approach can have several advantages(Van Kruchten 2008). For example: in a probabilistic approach worst-case assumptions can largely be prevented by incorporating the uncertainty itself in the cause-effect chain modeling. In such case, deterministic modeling may lead to an overestimation of the ecological effect, whereas the probabilistic modeling results give information on the probability of occurrence of possible effects. Although in the DEB-model uncertain parameters or variables can be identified, these are realistic instead of conservative assumptions that are made in deterministic models to deal with these uncertainties. In order to quantify the uncertainty, Monte Carlo simulations with varying parameter values can be made.

Because of this, the results of the model presented in chapter 3 can be considered a realistic estimate of the impact of the (fictitious) dredging project on blue mussels. The added value of applying a probabilistic analysis to this case is limited and will not make a difference between a highly conservative and a realistic estimate of the impact on mussels. A probabilistic analysis might be used to quantify the uncertainty margin of the final prediction. However, as a probabilistic analysis is quite elaborative, a sensitivity analysis instead of a probabilistic analysis is recommended to give insight into the uncertainty margin of the result.

4.2 Recommendation

Because mussels are able to adapt to different conditions of silt concentrations in the water column, it is important that studies of impact effects take into account the natural variability of silt concentrations the area, as well as the length of time these conditions may remain modified. Short term increases in suspended sediment concentration will have less impact on the food intake of shellfish than a continuous release.

This study is primarily focused on blue mussels as a model species for suspension-feeding lamellibranchiate bivalves. It is assumed that the processes will be comparable for other suspension-feeding lamellibranchiate bivalves and that only the values of the parameters will differ. However, it is good to check this assumption using literature data from other species.

The models that were used in this study were not directly calibrated with field observations and literature information on filtration rates and pseudofaeces production. It would be an improvement to perform an additional calibration with the appropriate data.

5 Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 57846-2009-AQ-NLD-RvA). This certificate is valid until 15 December 2012. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

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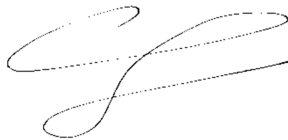
Justification

Rapport C123/12
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The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department of IMARES.

Approved: Prof. Dr. A.C. Smaal
                   Senior researcher

Signature:

Date: 26 oktober 2012

Approved: Dr. B.D. Dauwe
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